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Proceedings of the Missouri Ozark Forest Ecosystem Project Symposium:

An Experimental Approach to Landscape Research

Brian L. Brookshire and Stephen R. Shifley, Editors

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Describes the Missouri Ozark Forest Ecosystem Project (MOFEP) that was initiated in 1991 in southeastern Missouri. Describes in detail the coordinated research studies examining vegetation dynamics, down wood, fungi, birds, small mammals, herpetofauna, invertebrates, and genetics. Soil, geolandforms, ecological landtypes, and climate at the sites are described. Provides extensive baseline data on forest plant and animal communities.

Key Words: Ecosystem management, vegetation dynamics, coarse woody debris, neotropical migrant birds, herpetofauna, Armillaria, small mammals, forest soils, geolandforms, insects, synthesis, ecology.

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Forward

The Missouri Ozark Forest Ecosystem Project, or MOFEP, is one of the most comprehensive ecological investigations of forest response ever undertaken in upland oak ecosystems. Great attention has been given to the design of the MOFEP experiment and to coordination of the numerous associated research studies. Initial efforts have been devoted to documentation and analysis of baseline conditions prior to implementation of harvest treatments.

This proceedings was prepared in conjunction with the Missouri Ozark Forest Ecosystem Project Symposium held June 3-5, 1997, in St. Louis Missouri. The 23 papers in this proceedings summarize the results of years of research by dozens of scientists and technicians. After 5 years of pre-treatment monitoring, the first MOFEP harvest treatments were implemented in 1996. Conditions at the MOFEP sites presented and analyzed in the proceedings are the foundation that will be used to analyze and interpret the results of the treatments. In addition, the results of the pre-treatment monitoring provides the most comprehensive ecological examination ever conducted on an Ozark forest landscape. Already the results are providing new insights into relationships among flora, fauna, and the physical environment. The rate of our learning will increase as the post-treatment results are observed and analyzed.

This proceedings is a testimony to the dedication of scientists working together toward a common goal. We are grateful to the scientists and technicians who prepared the proceedings papers or collected the basic data on which the papers are based. We thank the dedicated Department of Conservation Resource Professionals, particularly on the Eminence and Clearwater Districts, for their day to day support of the MOFEP study. We are also grateful to those in the Missouri Department of Conservation who had the foresight to support this long-term research and to the people of Missouri for their continued support of Conservation Department activities. Finally, we thank Marvin Brown, Missouri's State Forester, for his dedication and support of the MOFEP study since its inception.

Each manuscript included in the proceedings was independently reviewed by one or more subject matter specialists. Each manuscript also received a statistical review from Carl Mize (Iowa State University), Steven Sheriff (Missouri Department of Conservation) and Zhuoqiong He (Missouri Department of Conservation). Steve Westin (Missouri Department of Conservation) prepared all the color maps within this document. We thank them all for their time and effort. We also sincerely thank Victoria Sork, David Klostermann and Betty Jarvis at the University of Missouri-St. Louis and Kay Morton at the Missouri Department of Conservation for their help in preparing for this symposium and ensuring that the program went smoothly.

Finally, our special thanks to Mary Peterson and Lucy Burde from the North Central Forest Experiment Station, St. Paul, Minnesota. They spent long hours casting a keen editorial eye on every manuscript and handling the infinite details associated with literature citations, grammar, mechanics, layout, and printing. This document would not have been possible without their exceptional efforts.

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The Missouri Ozark Forest Ecosystem Project: Past, Present, and Future

Brian L. Brookshire[1], Randy Jensen[2], and Daniel C. Dey[1]

Abstract.—In 1989, the Missouri Department of Conservation initiated a research project to examine the impacts of forest management practices on multiple ecosystem components. The Missouri Ozark Forest Ecosystem Project (MOFEP) is a landscape experiment comparing the impacts of even-aged management, uneven-aged management, and no harvesting on a wide array of ecosystem attributes. These three harvest treatments were replicated in three complete blocks on a total of nine sites in the southeast Missouri Ozarks. Each study site is approximately 1,000 acres (400 ha) in extent. More than 50 scientists are participating in this coordinated ecosystem research project.

Public attitudes toward natural resource management have changed considerably over the past 50 years, and in particular, the last decade. Since the late 19th century, we have exploited the forest for commodities, often with a short-term mentality. Now, the public enthusiastically supports a stronger conservation and stewardship ethic in forest management decisions (Missouri Department of Conservation 1996, Palmer 1996). In particular, the public has increasingly voiced concerns about tree harvest impacts on non-timber forest resources. Natural resource managers share these concerns and have embraced new concepts, such as adaptive and ecosystem management (Baskerville 1985, Baskerville and Moore 1988, Gordon 1993, Walters 1986). However, past forest management and research have concentrated heavily on the production of commodities, such as timber and game species. The Missouri Ozark Forest Ecosystem Project (MOFEP) was initiated in 1989 to investigate forest management impacts on multiple biotic and abiotic ecosystem attributes. In this paper, we present background information about the origin, design, status, and future direction of MOFEP.

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CONCEPT AND OBJECTIVES

During the mid-1980's, impacts of forest management on neotropical migrant songbirds became the subject of great debate following reports of their apparent population declines (Annand and Thompson 1997, Robbins *et al.* 1989, Robinson *et al.* 1995, Thompson *et al.* 1993). Population declines were attributed to forest fragmentation, brown-headed cowbird *(Molothrus ater)* parasitism of nests, predation of nests, and tropical deforestation (Rothstein *et al.* 1986, Thompson *et al.* 1993). In response to these concerns, scientists from the Missouri Department of Conservation (MDC) and the University of Missouri-Columbia proposed a project to determine the impacts of forest management on neotropical migrant songbirds (Clawson *et al.* 1997). The internal and external reviewers of this proposal suggested expanding the scope of the project to include the evaluation of forest management impacts on multiple ecosystem components, rather than just songbirds. Consequently, the objectives were broadened to evaluate forest management impacts on multiple ecosystem attributes for large sites (600+ ac (240 ha)). Additional objectives were derived to ultimately accomplish the goal of providing sound scientific information for the refinement of forest management practices in Missouri. Through numerous iterations, an experimental approach for determining forest management impacts on multiple ecosystem components was designed and was subse-

quently named the Missouri Ozark Forest Ecosystem Project (Kurzejeski *et al.* 1993). Sheriff and He (1997) explain the experimental design and evaluation procedures for MOFEP and associated studies. Each individual MOFEP study has associated objectives that are discussed in this volume.

SITE SELECTION

Selecting experimental sites for MOFEP was challenging. Suitable sites had to be: (1) at least 600 ac (240 ha) in size; (2) contiguous tracts with minimal edge; (3) largely free from manipulation for at least 40 years and preferably longer (less than 5 percent of area disturbed); (4) owned by MDC; (5) located in the southeast Missouri Ozarks; and (6) in close proximity to each other. Project leaders searched MDC records, talked with site managers, and made numerous aerial and field evaluations before finally selecting the nine sites that were used to develop the overall experimental design (fig. 1) (Sheriff and He 1997). A detailed description of the study area is provided by Brookshire and Hauser (1993) and Meinert *et al.* (1997).

Each MOFEP experimental site was divided into areas of common slope and aspect. These were further divided into stands that averaged approximately 12 ac (5 ha) in size (figs. 2 and 3). Stands were used to stratify the placement of 648 permanent vegetation plots (Sheriff and He 1997). Additionally, stand boundaries were used to implement the experimental treatments that will be discussed later in this paper.

TREATMENTS

Forest management treatments selected for MOFEP were even-aged management (EAM), uneven-aged management (UAM), and no-harvest management (NHM). The three treatments were each randomly assigned within three blocks, each containing three of the nine MOFEP sites (Sheriff and He 1997) (fig. 3). The treatments are briefly described below; additional detail is available in Brookshire and Hauser (1993).

Even-aged Management

Even-aged management was implemented according to MDC Forest Land Management Guidelines (1986), with a cutting rotation of 80 to 100 years per site resulting in a regulated harvest of 10 to 12 percent of the trees per entry on a 10-year re-entry period. This is Management Level II in the 1986 Guidelines and approximates the treatments applied to most MDC-administered forest land before these guidelines were developed. At this management level, 10 percent of each site is left as "old growth," and the desirable tree size class distribution on the remaining area is 10 percent seedlings, 20 percent small trees 2.5 to 5.5 in. (6 to 14 cm) d.b.h., 30 percent poles 5.6 to 11.5 in. (14 to 29 cm) d.b.h., and 40 percent sawtimber >11.5 in. (29 cm) d.b.h. Harvest prescriptions follow Roach and Gingrich (1968). In general, total area designated with a silvicultural prescription of regeneration by clearcutting was restricted to approximately 10 to 12 percent of the site, with those stands in greatest need of regeneration selected first (fig. 3). Remaining stands needing regeneration were deferred to the next entry. Immature stands with site index 55 (base age 50 years) and greater were treated with intermediate cutting according to Roach and Gingrich (1986) (fig. 3). Glades, food plots, ponds, and other amenities were managed according to the 1986 Guidelines.

Uneven-aged Management

Uneven-aged management was also implemented using MDC Forest Land Management Guidelines (1986) with stand treatments following Law and Lorimer (1989). Approximately 10 percent of each site was designated to be managed as "old growth," and the remaining 90 percent was available for UAM silvicultural treatment (fig. 3). Treatments on UAM sites will be timed to coincide with treatments for EAM sites over the next 80 to 100 years. Each UAM site was divided into management units of 20 to 80 ac (8 to 32 ha), and objectives were set for largest diameter tree (LDT), residual basal area (RBA), and q-value. The LDT objective was equal to the desired sawtimber size objective for an identical site under EAM. An overall RBA equivalent to B-level stocking was chosen, with adjustments made to anticipate for logging damage (Roach and Gingrich 1968). Q-value objectives ranged from 1.3 to 1.7 (Law and Lorimer 1989). The target tree size class distribution for UAM was identical to the composite size class distribution across the EAM sites. For example, for a mean poletimber diameter of

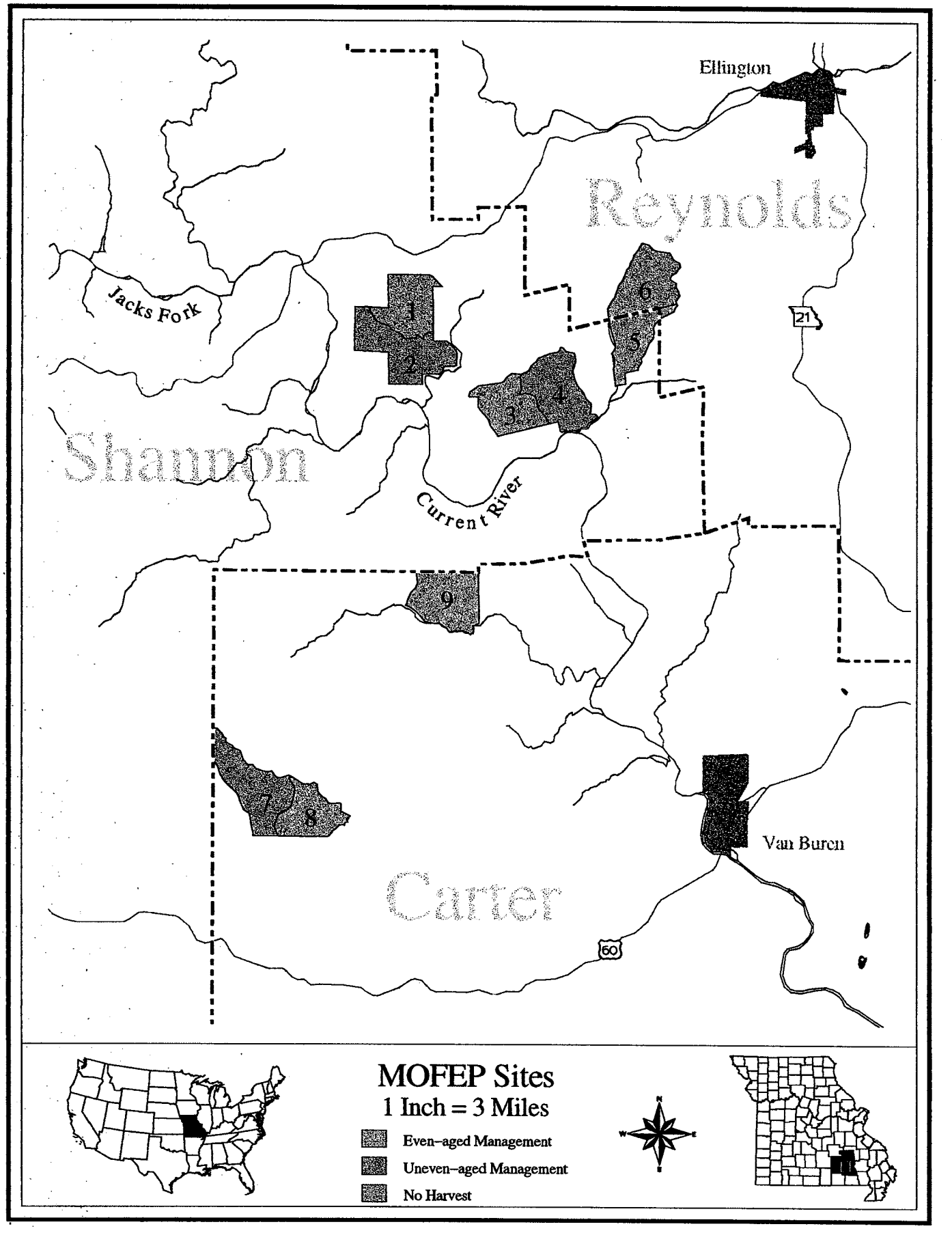
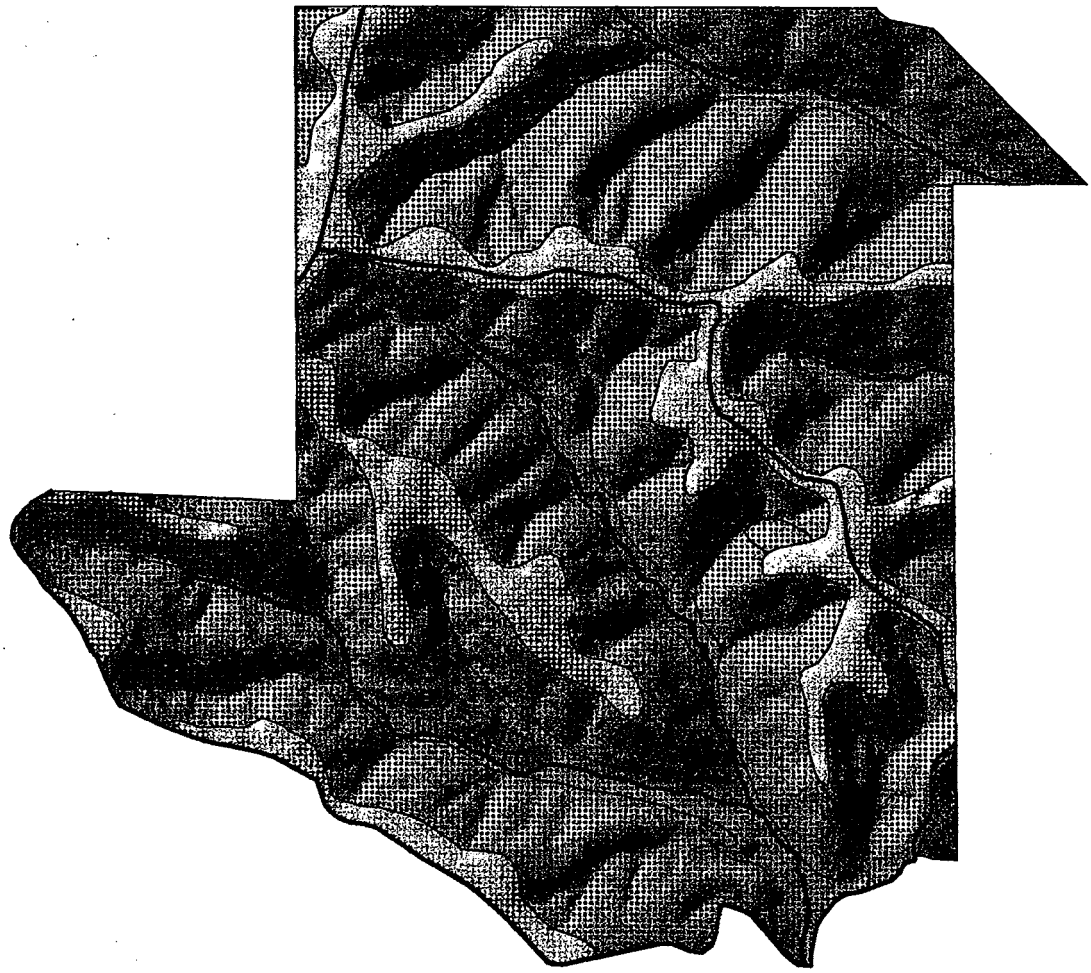


Figure 1.—*Location of the nine MOFEP experimental sites. Colors indicate assigned treatment.*

Site 1 Ecological Landtypes
Non–manipulative Management



Upland Waterway – Dry Bottomland Forest
Ridge
Side Slope – South and West Aspects
Side Slope – North and East Aspects
Hydrology
Roads

1 mile

Map Scale 1:18480
1 inch = 2/7 mile

Figure 2A.—*Ecological landtypes, hydrology, and roads on MOFEP site 1.*

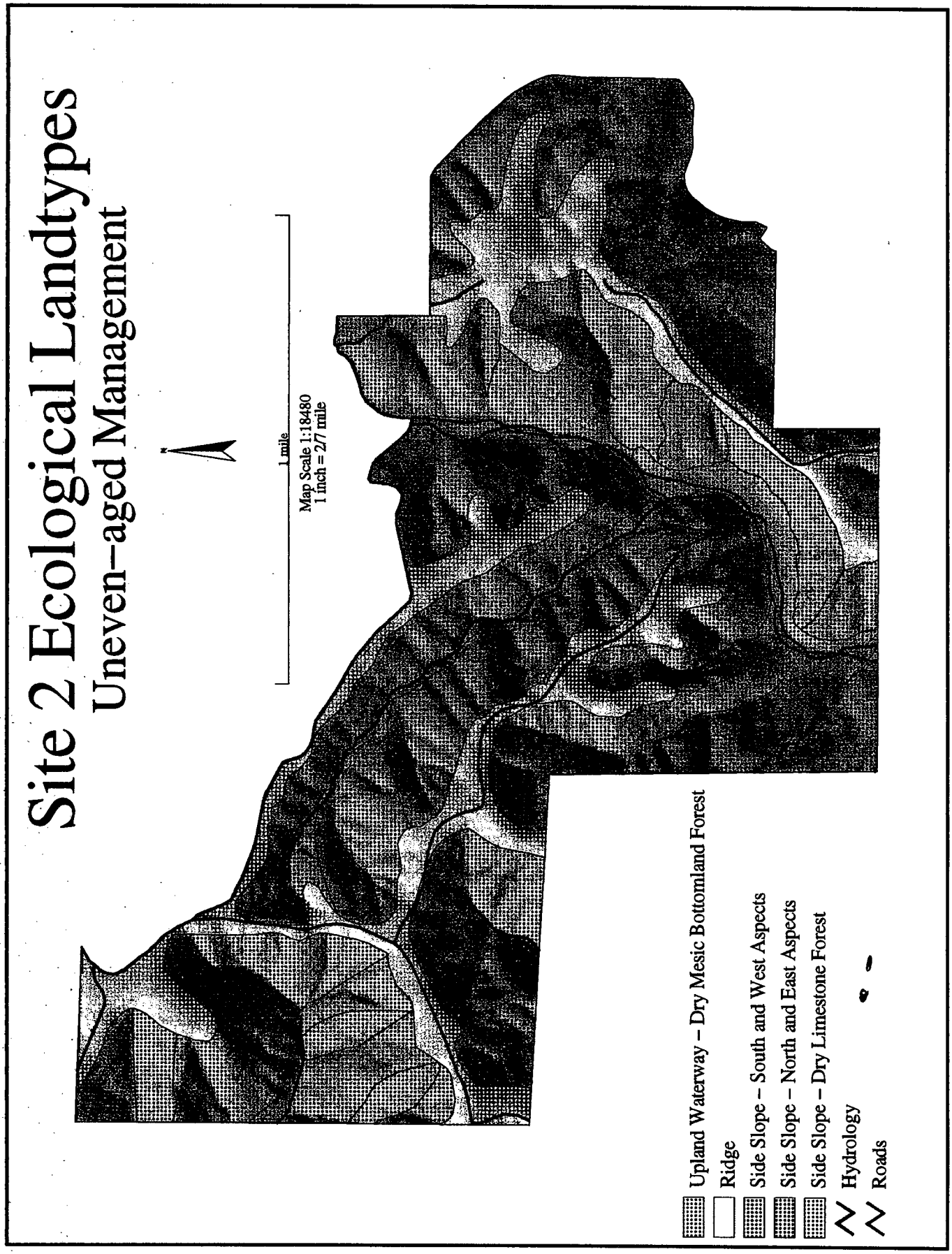
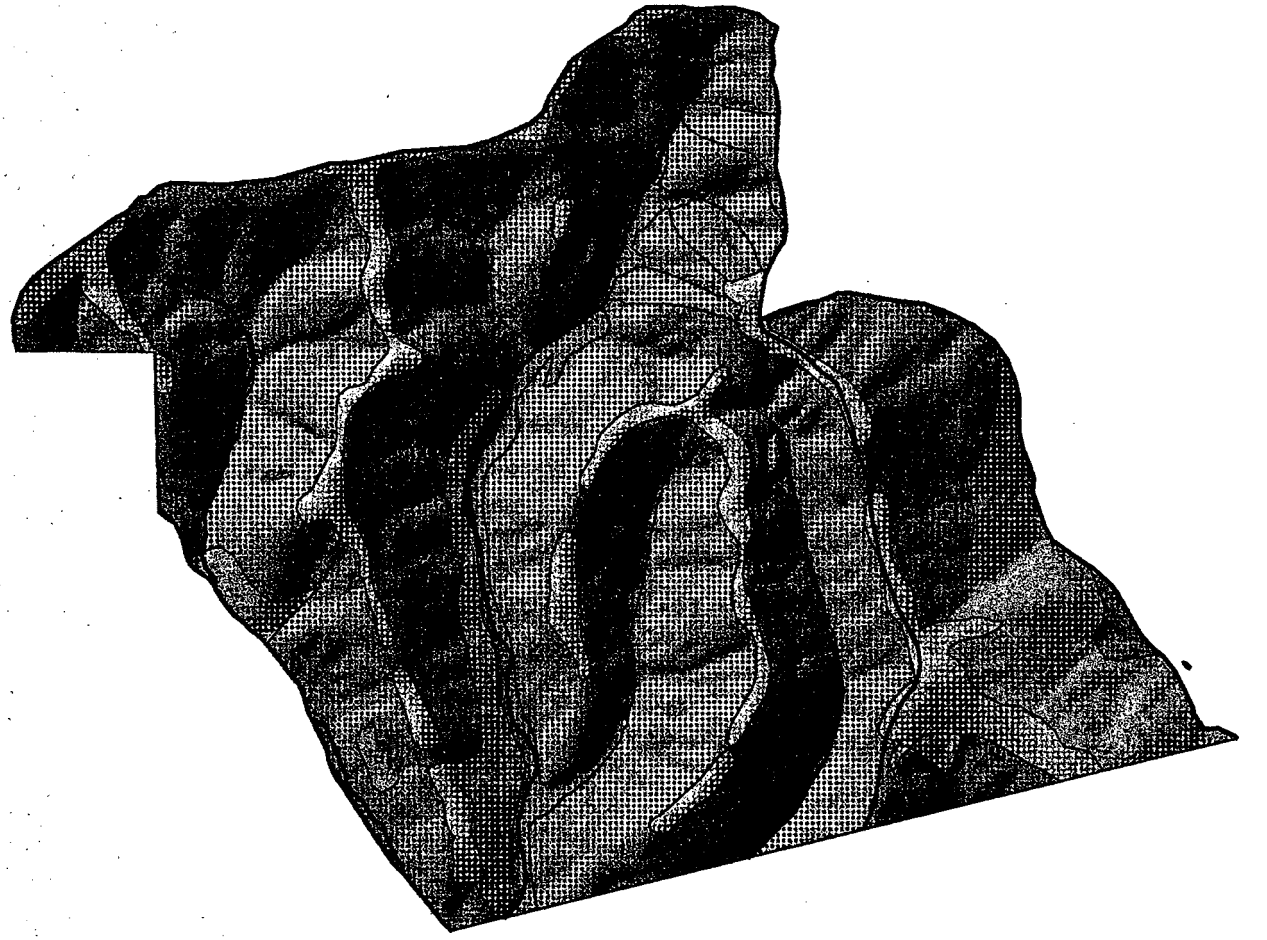


Figure 2B.—*Ecological landtypes, hydrology, and roads on MOFEP site 2.*

Site 3 Ecological Landtypes
Even–aged Management



Upland Waterway – Dry Bottomland Forest
Ridge
Side Slope – South and West Aspects
Side Slope – North and East Aspects
Side Slope – S and W Aspects – Glade Savanna
Side Slope – N and E Aspects – Dry Mesic Limestone Forest
Hydrology
Roads

N

1 mile

Map Scale 1:18480
1 inch = 2/7 mile

Figure 2C.—*Ecological landtypes, hydrology, and roads on MOFEP site 3.*

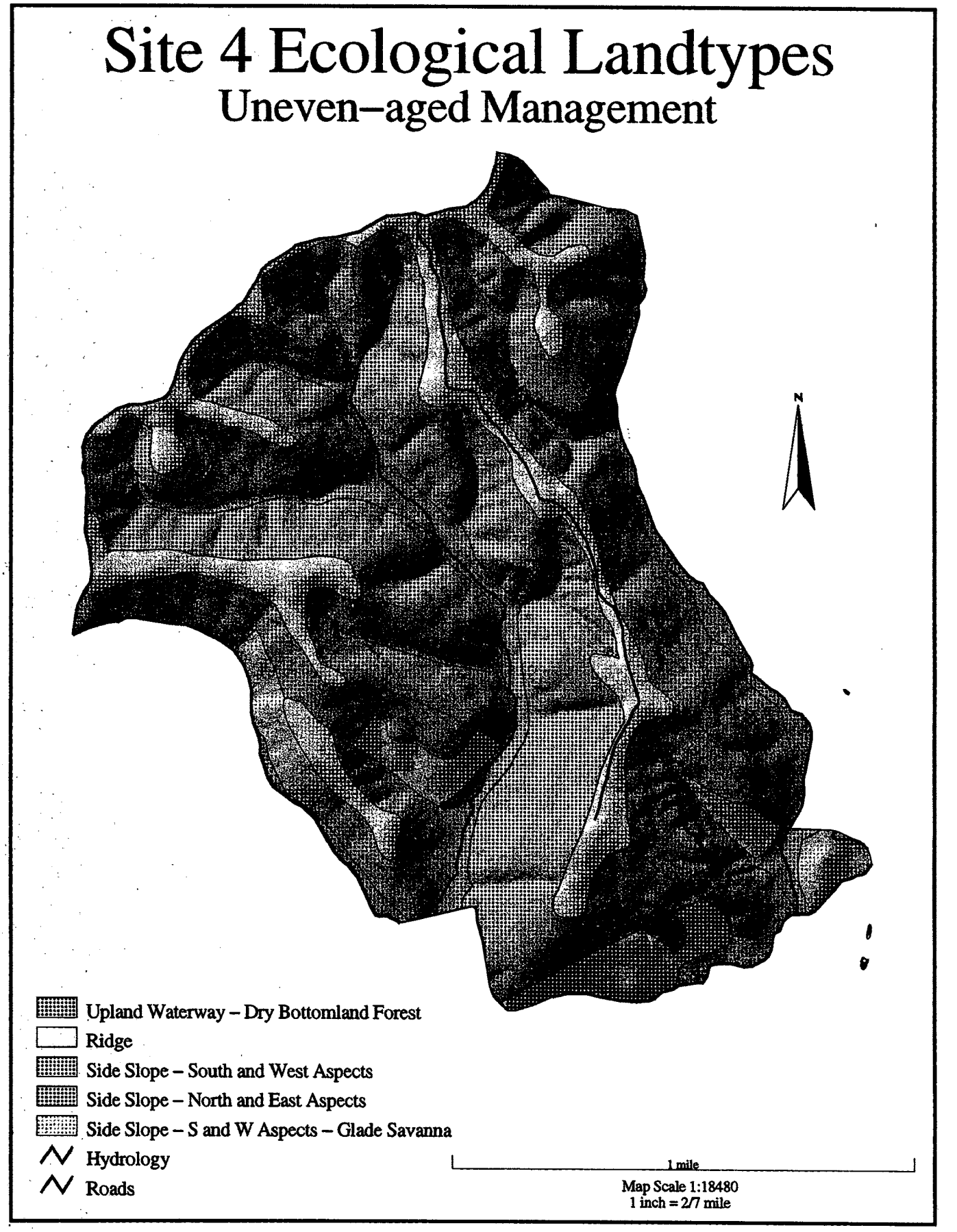


Figure 2D.—*Ecological landtypes, hydrology, and roads on MOFEP site 4.*

Site 5 Ecological Landtypes
Even–aged Management

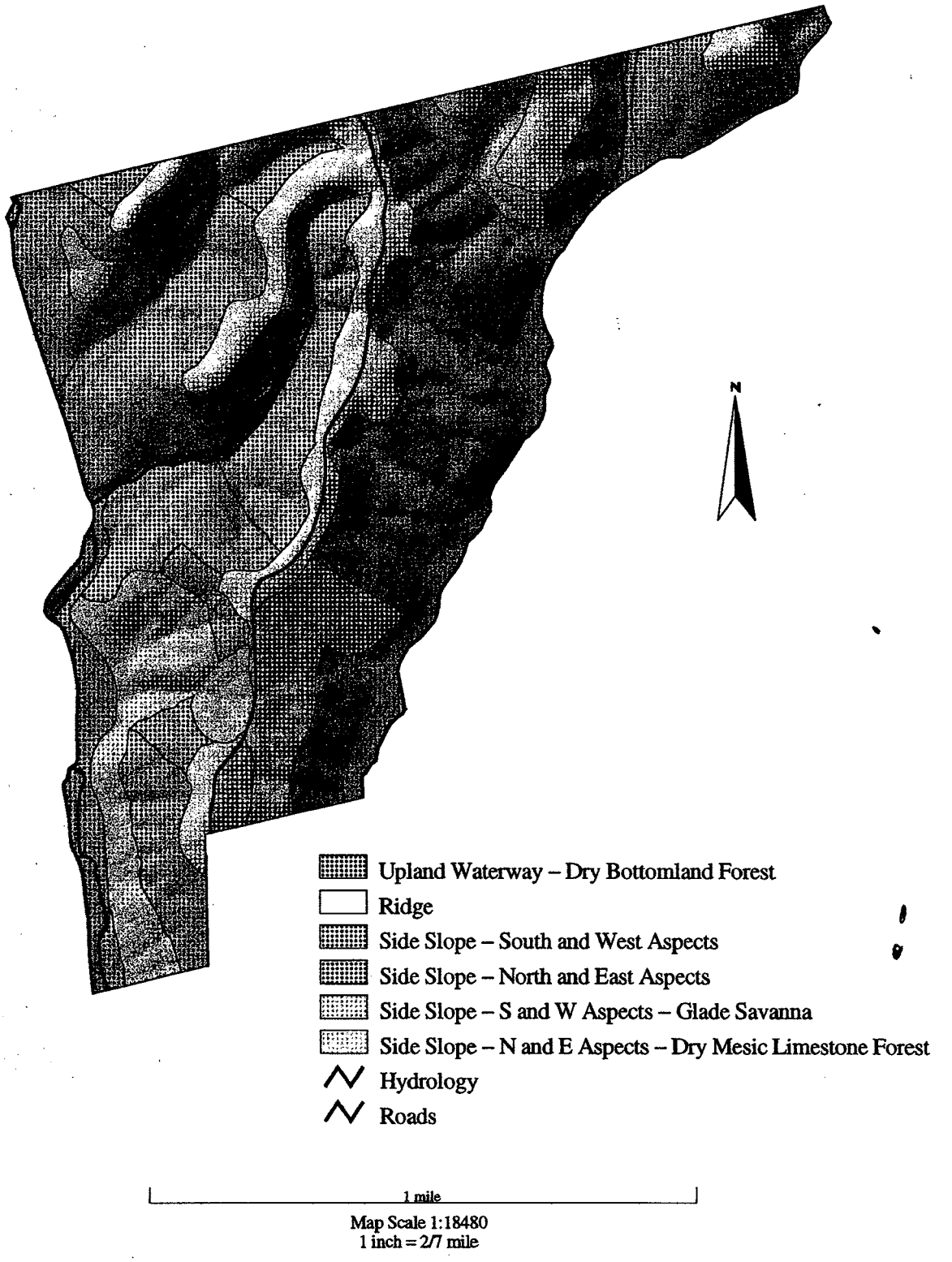


Figure 2E.—*Ecological landtypes, hydrology, and roads on MOFEP site 5.*

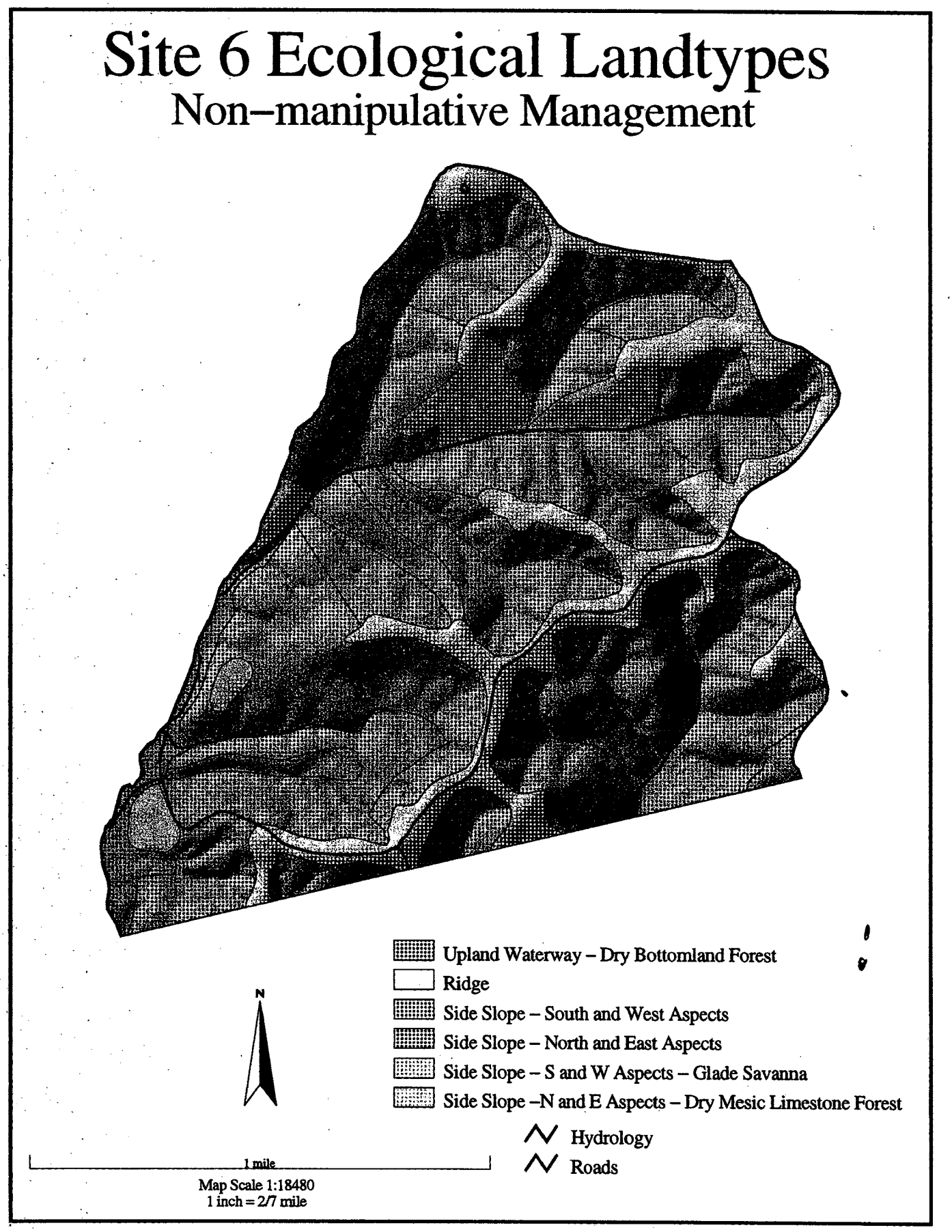


Figure 2F.—*Ecological landtypes, hydrology, and roads on MOFEP site 6.*

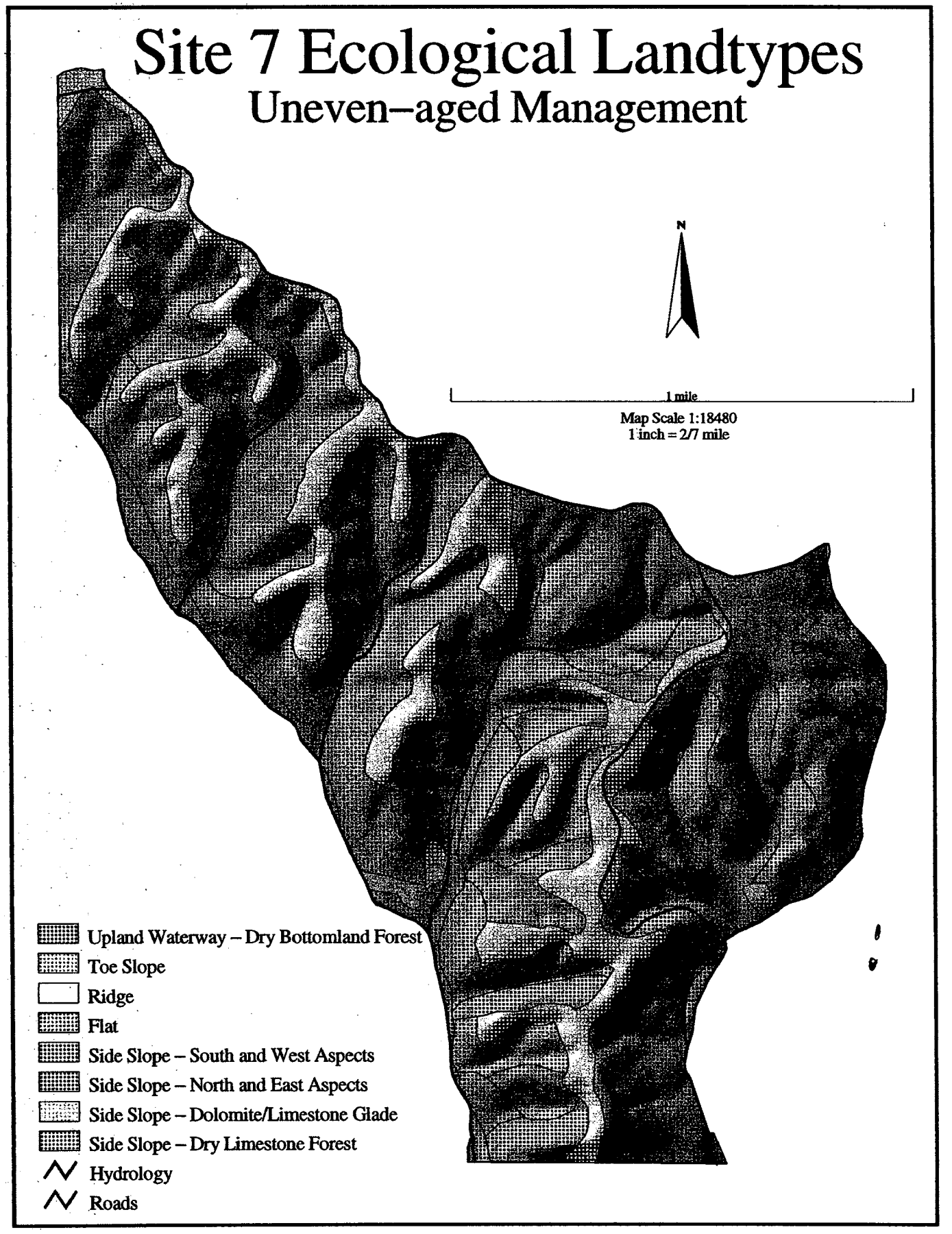
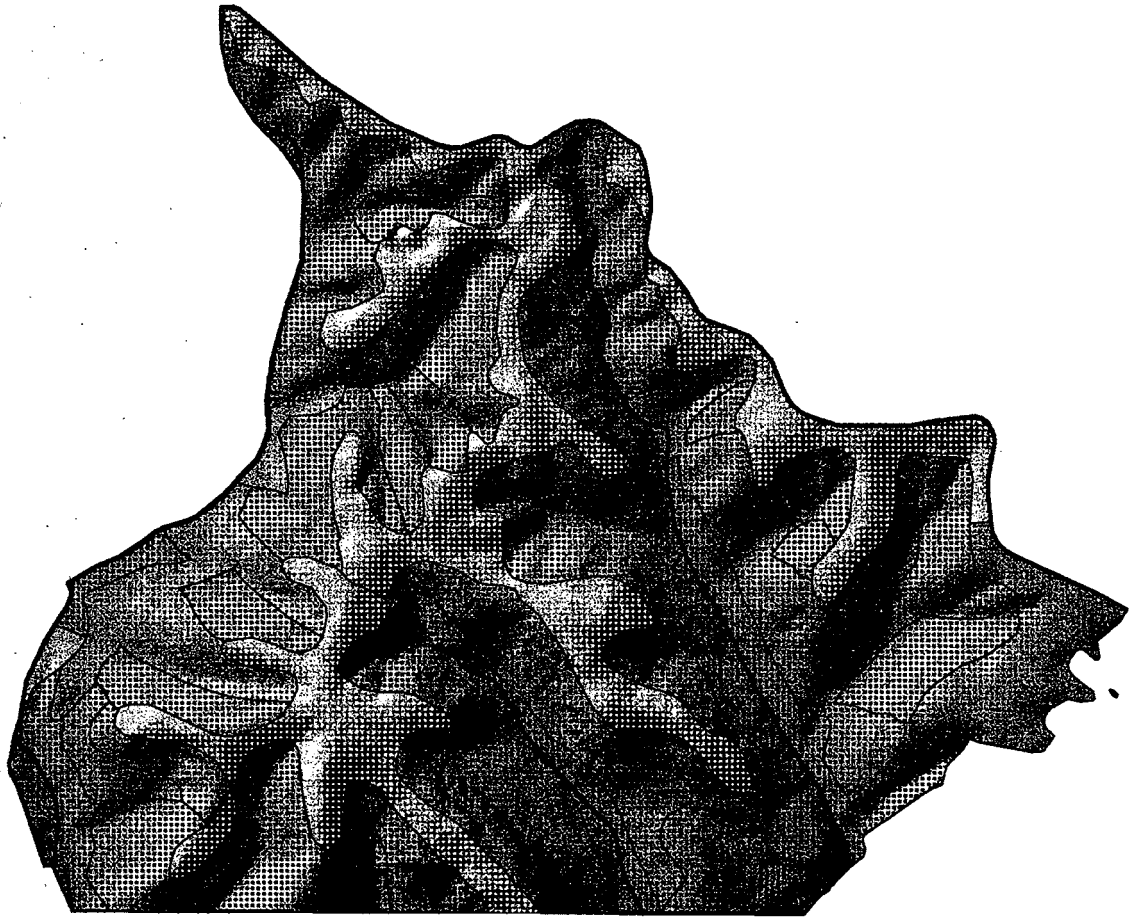


Figure 2G.—*Ecological landtypes, hydrology, and roads on MOFEP site 7.*

Site 8 Ecological Landtypes
Non–manipulative Management



High Flood Plain
Upland Waterway – Dry Bottomland Forest
Toe Slope
Ridge
Flat
Side Slope – South and West Aspects
Side Slope – North and East Aspects
Side Slope – Xeric Limestone Forest
Side Slope – Dry Limestone Forest
Hydrology
Roads

N

1 mile

Map Scale 1:18480
1 inch = 2/7 mile

Figure 2H.—*Ecological landtypes, hydrology, and roads on MOFEP site 8.*

Site 9 Ecological Landtypes
Even–aged Management

Upland Waterway – Dry Bottomland Forest
Toe Slope
Ridge
Side Slope – South and West Aspects
Side Slope – North and East Aspects
Side Slope – Dry Limestone Forest
Hydrology
Roads

N

1 mile

Map Scale 1:18480
1 inch = 2/7 mile

Figure 2I.—*Ecological landtypes, hydrology, and roads on MOFEP site 9.*

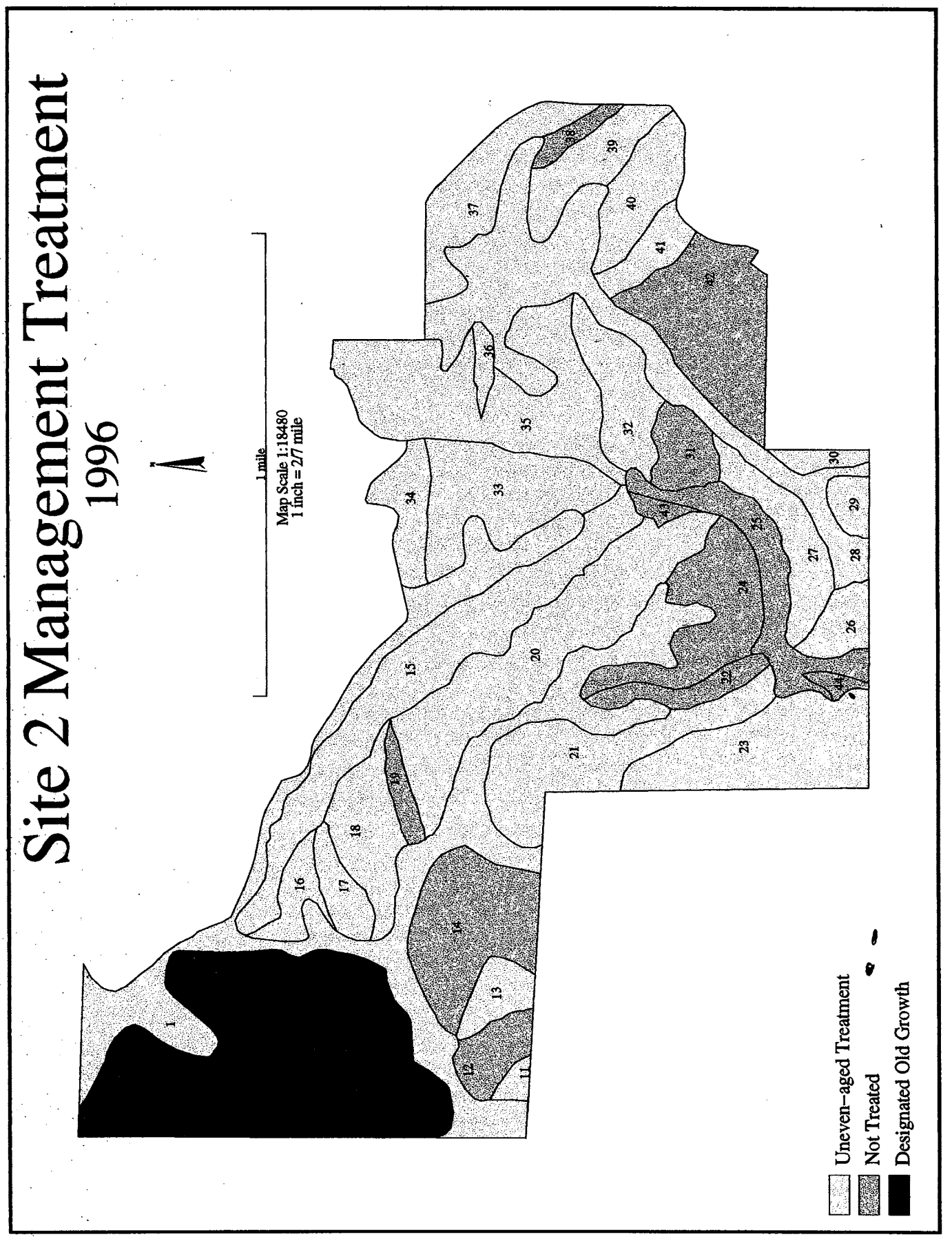


Figure 3A.—*Stand boundaries and assigned treatments, MOFEP site 2.*

Site 3 Management Treatment
1996

Figure 3B.—*Stand boundaries and assigned treatments, MOFEP site 3.*

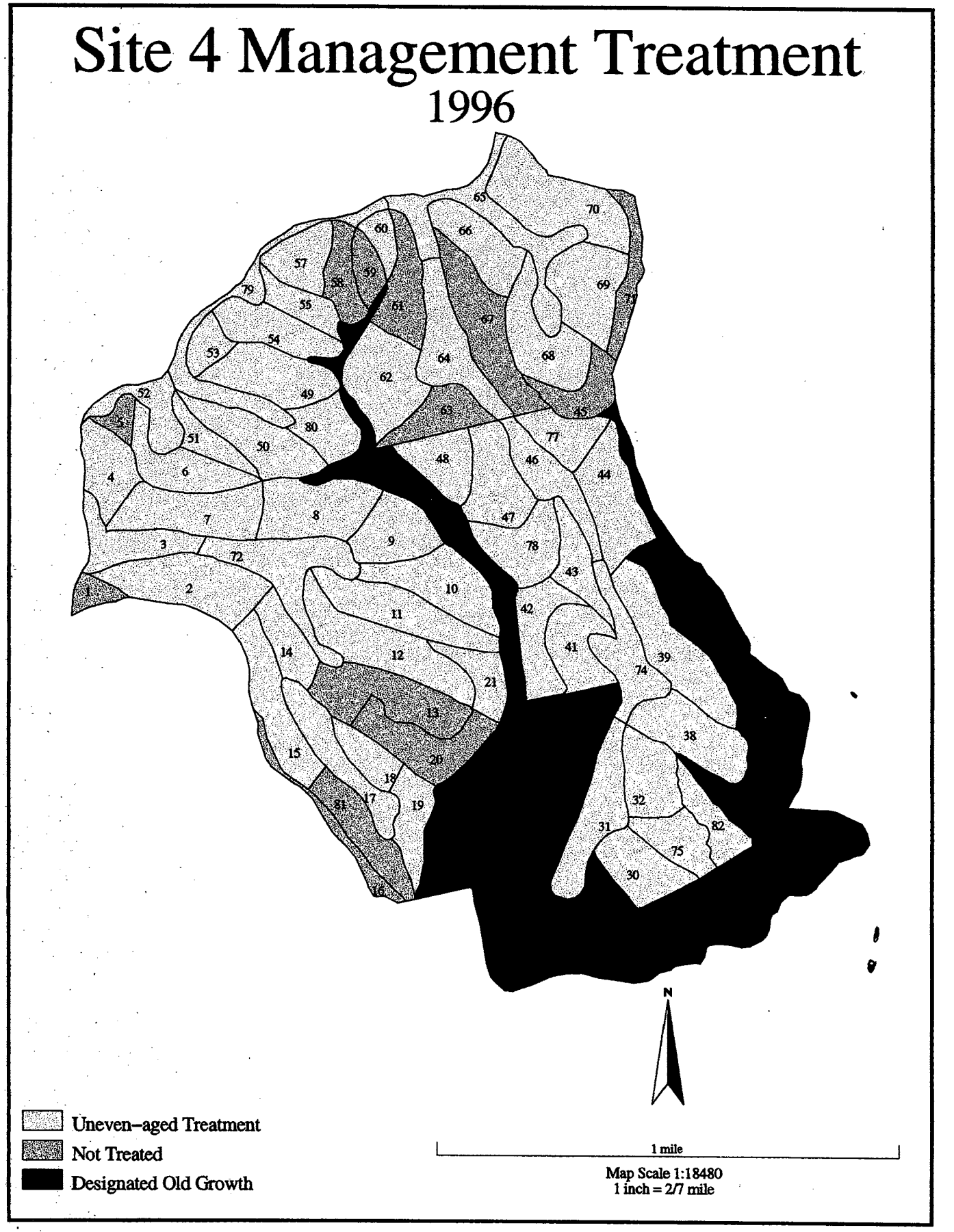


Figure 3C.—*Stand boundaries and assigned treatments, MOFEP site 4.*

Site 5 Management Treatment
1996

Figure 3D.—*Stand boundaries and assigned treatments, MOFEP site 5.*

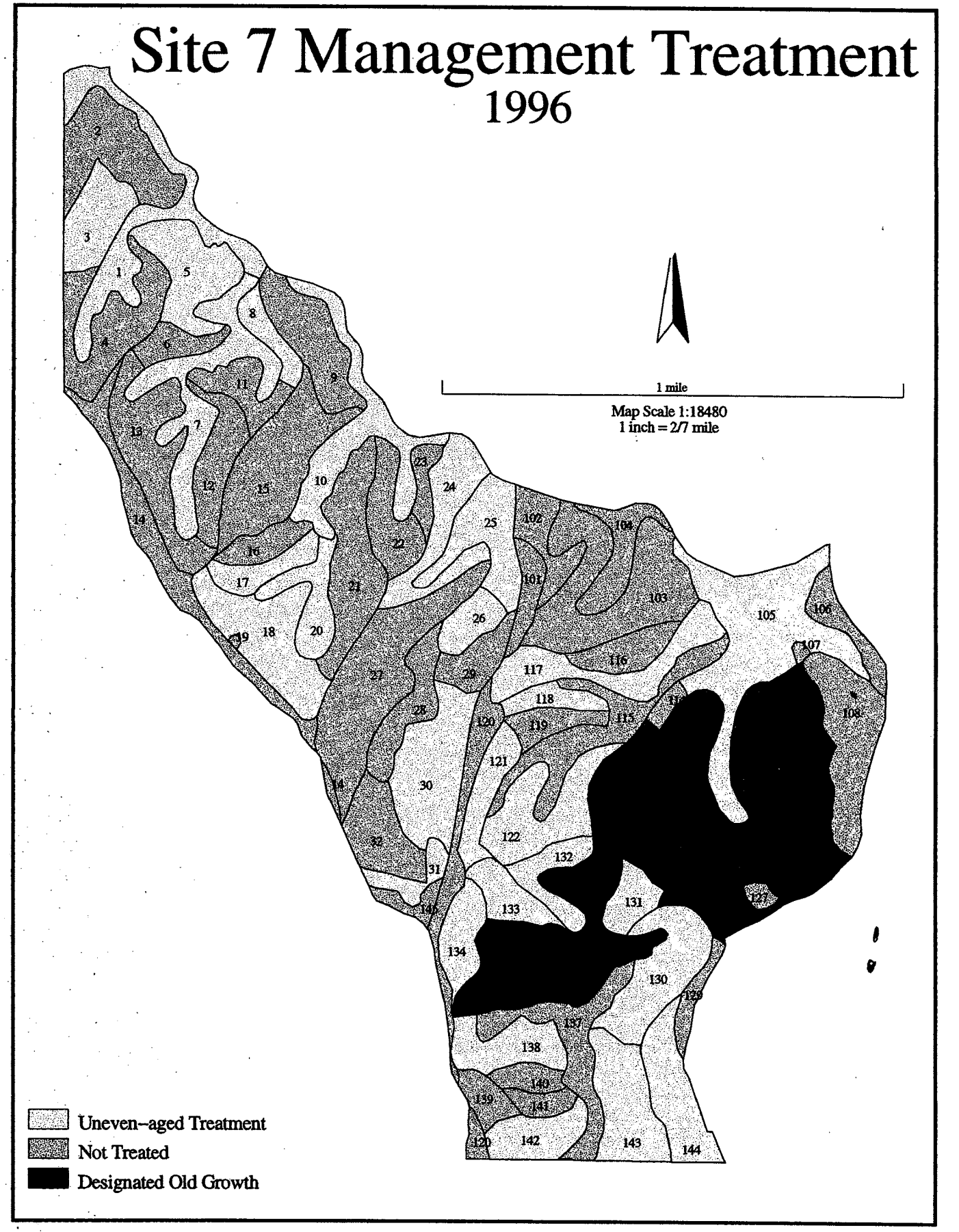


Figure 3E.—*Stand boundaries and assigned treatments, MOFEP site 7.*

Site 9 Management Treatment
1996

Regeneration Cut
Intermediate Cut
Timber Stand Improvement
Not Treated
Designated Old Growth

N

1 mile

Map Scale 1:18480
1 inch = 2/7 mile

Figure 3F.—*Stand boundaries and assigned treatments, MOFEP site 9.*

8.5 in. (22 cm) and sawtimber diameter of 15.5 in. (39 cm) (midpoints of ranges, assuming 20 in. (51 cm) maximum), with both size classes at B-level stocking, a typical EAM site of 1,000 ac (400 ha) would have 19,200 ft^2 (1,728 m^2) of poletimber basal area and 29,600 ft^2 (2,664 m^2) of sawtimber basal area. According to Law and Lorimer (1989), this is equivalent to a q-value of 1.5.

No Harvest Management

Sites under no-harvest management received no anthropogenic manipulation. Natural catastrophic events, including tornadoes, fires, insects, or disease, will be treated as if on any other State-owned forest land, except that salvage harvests will not occur. Wildfires will be suppressed and areas will receive control measures applied to surrounding areas in the event of a large-scale damaging insect outbreak. This treatment will somewhat resemble "old growth" management and will serve as an experimental control treatment in this project (Sheriff and He 1997).

Implementation

Treatments were implemented operationally by MDC foresters located on the Clearwater and Eminence Forest Districts. Each treatment site was divided into sale units with each sale comprised of a comparable amount of timber volume in both the even-aged and uneven-aged treatment sites (table 1). This ensured that each site received an equal influence from a particular logging operator. A total of seven timber sale contracts were prepared and advertised for sale to harvest contractors throughout Missouri and adjoining States.

Table 1.—*Acres harvested and tree volume taken from MOFEP management sites.*

MOFEP Site	Acres harvested [1]	Volume
		Thousand bd ft
2 (UAM)	860	1,146
3 (EAM)	272	754
4 (UAM)	697	952
5 (EAM)	244	927
7 (UAM)	502	1,344
9 (EAM)	192	773

[1]ha = ac/2.47

Meetings were held with prospective logging companies to explain how this project would differ from their usual operation. The experimental nature of MOFEP required companies to frequently move crews and machinery from one location to the other. Additionally, uneven-aged silviculture was explained because most companies were not familiar with that cutting practice. The meetings were an effort to inform prospective bidders of these requirements to help ensure an appropriate bid.

Commercial timber harvest began in early May 1996 and concluded by that November. Table 1 provides a summary of the acreage impacted and the volume harvested from each site. Removal of non-merchantable stems marked for removal during implementation of silvicultural prescriptions began in early November 1996, and continued through April 1997.

We are currently concentrating on documenting treatment impact on all permanent forest vegetation plots that were affected by harvest in 1996. Each plot is being mapped to indicate presence of primary and secondary skid trails, rut depths, log landings, and residual tree damage. This effort will be completed by June 1997.

Scientists resumed data collection on their respective studies in May 1997. No data collection occurred during the summer of 1996, as a result of harvest treatment implementation. We intend to collect data yearly for at least the next 5 years to properly document the response of specified ecosystem components to the treatments. Then we will evaluate the need for yearly collections and adjust sampling periods accordingly.

ONGOING RESEARCH PROJECTS

All MOFEP studies are administered by the Missouri Department of Conservation with research conducted by MDC, university, and Forest Service employees. Two studies, (1) Forest Vegetation and (2) Ecological Classification Refinement, provide baseline data used by all other investigators. These studies are discussed in the following sections.

Forest Vegetation

A system of 648 permanent cluster plots was distributed across the nine MOFEP sites to

document forest vegetation response to treatment (fig. 4). Plots were allocated among stands based on stand size with the constraint that each stand receive at least one plot. Location of plots within stands was random.

Data collected for each tree ≥ 4.5 in. (11 cm) d.b.h. included species, d.b.h., status (live or dead), crown class, size of cavities, and location of cavities. Height, canopy volume, form class, and merchantable volume were measured for up to 15 trees per plot (5 trees each in the white oak group, the red oak group, and shortleaf pine, where available). Species and d.b.h. were recorded for all trees at least 1.5 in. (4 cm) d.b.h. but less than 4.5 in. (11 cm) d.b.h. Trees less than 1.5 in. (4 cm) d.b.h. and at least 3.3 ft (1 m) tall were tallied by species and d.b.h. class.

Herbaceous vegetation was inventoried in 16 quadrats systematically distributed within each vegetation plot (fig. 4). Sampling protocols for herbaceous vegetation are described in Grabner *et al.* (1997).

Table 2 summarizes structural characteristics of trees on each of the nine MOFEP sites. A total of 49 woody species were observed (table 3).

Forest vegetation information will be used by all cooperating MOFEP scientists to help understand the response of various ecosystem components to forest management. Therefore, tremendous financial and personnel resources have been dedicated to the installation and subsequent data collection on the permanent vegetation plots. Initial data collection from permanent plots began in October 1990 and concluded 22 months later. A complete set of data was collected again on all MOFEP plots beginning in June 1994 and concluding 17 months later.

Ecological Classification Refinement

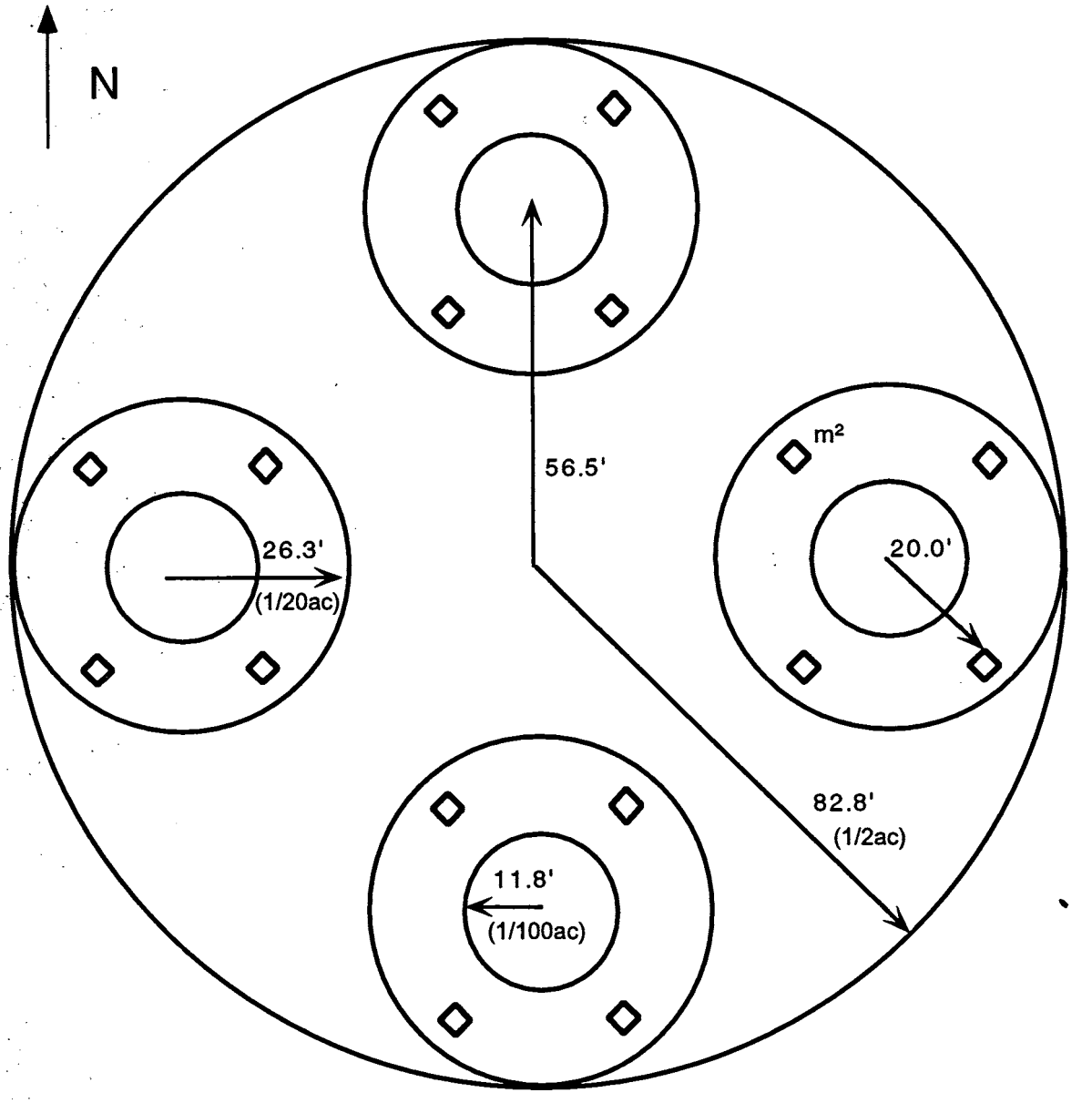
To develop a better understanding of forest vegetation and its relation to the physical environment, we classified the study region into Ecological Landtypes (ELT) following Miller (1981). Ecological landtypes were originally defined on MOFEP sites primarily by slope and aspect. ELT boundaries were drawn on 1:24,000 topographic maps and subsequently field checked. Detailed geology, soils, and vegetation information was not available when ELT designations were made in 1990.

Through field checking of ELT boundaries, we determined that additional geology, soils, and

Table 2.—*Pre-treatment characteristics of woody vegetation ≥ 1.5 in. d.b.h. for all MOFEP sites*[1].

	Trees ≥1.5 in. d.b.h.				Trees ≥ 4.5 in. d.b.h.					
Site	Plots	Trees	Basal area	Stocking	Trees	Basal area	Stocking	Volume[2]	Volume[3]	Down wood[4]
	Number	*n/ac*	*ft²/ac*	*Percent*	*n/ac*	*ft²/ac*	*Percent*	*ft³/ac*	*bd.ft/ac*	*ft³/ac*
1	76	515	95	90	184	82	70	1,180	5,340	194
2	73	557	96	91	176	80	69	1,160	5,300	155
3	72	500	99	90	169	85	71	1,270	6,060	302
4	74	499	96	88	167	82	69	1,220	5,770	107
5	70	498	96	88	160	32	68	1,210	5,770	153
6	71	429	100	87	160	89	72	1,370	6,730	429
7	71	389	91	81	140	81	67	1,280	6,700	225
8	70	279	92	81	133	83	68	1,280	6,730	250
9	71	546	88	83	126	73	60	1,130	5,740	355

[1]Metric equivalents: 1.5 in. = 4 cm; 4.5 in. = 11 cm; number/ha = 2.47 (number/ac); m²/ha = (ft²/ac)/4.356; m³/ha = (ft³/ac)/14.29.
[3]Trees ≥ 5.0 in. (13 cm) d.b.h.
[4]Trees ≥ 8.0 in. (20 cm) d.b.h.
[5]Material ≥ 2 in. (5 cm) in diameter and ≥ 2 ft (0.6 m) in length.



Size Limits for plots and sublots

1/2 acre includes trees ≥ 4.5" DBH
1/20 acre includes trees ≥ 1.5" and < 4.5" DBH
1/100 acre includes trees ≥ 1 m tall and < 1.5" DBH
1 m² for herbaceous vegetation

Down, dead wood transects

56.5' transects (4 per plot) used to measure down dead wood ≥ 2" diameter and ≥ 2' in length

Figure 4.—*MOFEP vegetation plot design.*

Table 3.—*MOFEP Importance Values*[1] *by site and species.*

Species	Scientific name	Importance value (percent)									
		Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8	Site 9	All sites
Black oak	*Quercus velutina*	27.28	27.30	25.14	18.92	20.92	17.12	23.99	26.06	27.00	23.668
Scarlet oak	*Quercus coccinea*	24.70	19.83	20.12	21.28	14.51	16.61	31.45	22.39	21.37	21.330
White oak	*Quercus alba*	21.38	20.42	25.00	22.06	24.48	26.24	11.97	16.12	21.10	21.168
Shortleaf pine	*Pinus echinata*	10.30	5.61	8.35	9.66	9.10	13.52	12.11	7.40	4.38	9.019
Post oak	*Quercus stellata*	3.41	2.63	4.18	4.41	7.83	4.99	11.81	12.46	7.53	6.325
Black hickory	*Carya texana*	5.20	4.87	3.82	1.89	6.12	5.27	3.18	5.03	3.50	4.324
Pignut hickory	*Carya glabra*	2.62	6.36	3.16	6.43	5.36	4.62	0.60	2.63	3.28	3.972
Mockernut hickory	*Carya tomentosa*	2.54	4.47	4.03	6.73	4.71	3.82	2.35	0.64	6.33	3.968
Blackgum	*Nyssa sylvatica*	1.31	1.99	2.24	2.23	1.80	2.62	0.69	1.45	1.01	1.720
Chinkapin oak	*Quercus meuhlenbergii*	--	1.12	0.69	1.75	0.97	0.66	0.14	0.90	0.42	0.749
Flowering dogwood	*Cornus florida*	0.59	0.81	0.60	0.48	0.82	1.12	0.73	0.67	0.59	0.710
Blackjack oak	*Quercus marilandica*	0.25	0.63	0.30	0.26	0.27	0.03	0.64	2.54	1.40	0.655
Black walnut	*Juglans nigra*	0.07	1.12	0.16	0.63	0.79	0.39	--	--	0.63	0.424
Slippery elm	*Ulmus rubra*	0.01	0.36	0.34	0.71	0.46	0.36	0.02	0.03	0.34	0.297
White ash	*Fraxinus americana*	0.01	0.47	0.39	0.87	0.17	0.14	--	0.19	0.04	0.264
Winged elm	*Ulmus alata*	--	0.19	0.19	0.43	0.40	0.42	0.04	0.15	0.01	0.211
Red maple	*Acer rubrum*	0.25	0.09	0.29	0.06	0.15	0.57	0.04	0.11	0.18	0.197
Bitternut hickory	*Carya cordiformis*	--	0.19	--	0.37	0.14	0.24	0.03	0.01	0.32	0.144
Sassafras	*Sassafras albidum*	0.04	0.23	0.16	0.04	0.19	0.30	0.02	0.07	0.23	0.142
Eastern redcedar	*Juniperus virginiana*	--	0.31	0.05	0.09	0.02	0.39	0.06	0.31	0.03	0.139
Sugar maple	*Acer saccharum*	--	0.31	0.19	0.31	0.23	0.02	--	--	0.03	0 128
Red mulberry	*Morus rubra*	--	0.11	0.06	0.14	0.04	0.04	0.05	--	--	0.052
American sycamore	*Platanus occidentalis*	--	--	0.13	0.06	0.14	0.09	--	--	0.04	0.052
Black cherry	*Prunus serotina*	0.01	0.11	0.03	0.04	0.11	0.05	0.01	--	0.07	0.048
American elm	*Ulmus americana*	--	0.04	0.01	0.04	0.05	0.07	0.01	0.10	0.04	0.041
Redbud	*Cercis canadensis*	--	0.05	--	0.01	0.06	0.05	--	0.15	0.01	0.036
Shagbark hickory	*Carya ovata*	--	0.22	0.02	--	0.01	--	--	0.04	--	0.035
Persimmon	*Diospyros virginiana*	--	0.05	0.03	0.01	0.03	0.04	0.01	0.07	0.01	0.029
Shellbark hickory	*Carya laciniosa*	--	--	0.16	--	--	0.04	--	--	--	0.023
Shumard oak	*Quercus shumardii*	--	--	--	--	0.04	--	0.01	0.15	--	0.021
Gum bumelia	*Bumelia lanuginosa*	--	--	0.04	0.04	0.01	0.01	--	0.05	0.01	0.018
Serviceberry	*Amelanchier arborea*	0.02	0.01	0.02	--	0.04	0.01	--	--	0.05	0.015
Northern red oak	*Quercus rubra*	--	--	--	0.01	--	0.10	--	0.02	--	0.015
Green ash	*Fraxinus pennsylvanica*	--	--	--	--	--	--	--	0.11	--	0.011
Honeylocust	*Gleditsia triacanthos*	--	--	0.03	0.03	--	--	0.01	--	0.01	0.009
Hackberry	*Celtis occidentalis*	--	--	--	--	--	0.02	0.01	0.05	--	0.009
Hack/Sugarberry	*Celtis laevigata*	--	0.05	--	--	--	0.01	--	--	--	0.007
Carolina buckthorn	*Rhamnus caroliniana*	--	--	0.01	--	0.02	0.01	--	--	--	0.005
Smooth sumac	*Rhus glabra*	--	--	--	--	--	--	--	0.04	--	0.004
Overcup oak	*Quercus lyrata*	--	--	0.03	--	--	--	--	--	--	0.003
Pin oak	*Quercus. palustris*	--	0.01	--	--	--	--	--	0.02	--	0.003
Southern catalpa	*Catalpa bignonioides*	--	--	--	--	--	--	--	0.02	--	0.002
Mulberry spp.	*Morus* spp..	--	--	--	0.01	--	--	--	--	--	0.001
Water oak	*Quercus nigra*	--	0.01	--	--	--	--	--	--	--	0.001
Hawthorn	*Crataegus* spp.	--	--	0.01	--	--	--	--	--	--	0.001
Kentucky Coffeetree	*Gymnocladus dioicus*	--	--	0.01	--	--	--	--	--	--	0.001
Plum	*Prunus* spp.	--	--	--	--	--	--	0.01	--	--	0.001
American hornbeam	*Carpinus caroliniana*	--	--	--	--	--	0.01	--	--	--	0.001
Ironwood	*Ostrya* spp	--	--	--	--	--	--	--	0.01	--	0.001
	TOTAL	100	100	100	100	100	100	100	100	100	100

[1]Importance Value = (Relative basal area + Relative density)/2

vegetation information was needed to adequately designate ELT's on the MOFEP sites. In 1994 we initiated an intensive 1:12,000 geology and soil survey to provide this information (Meinert *et al.* 1997). Moreover, in 1995 we began supplementing existing herbaceous inventory information to further support ELT delineations. Revised ELT designations for the MOFEP sites will be available in early 1998.

The original ELT's represented the best available classification at the time of study initiation, and in this volume some MOFEP scientists report their results based on these ELT's.

Table 4. *Studies associated with the Missouri Ozark Forest Ecosystem Project.*

Principal investigator(s)	Study title
1. J. Bruhn, J. Wetteroff, Jr., J. Mihail	Determination of the Ecological and Geographic Distributions of *Armillaria* Species in Missouri Ozark Forest Ecosystems
2. J. Bruhn, J. Mihail, D. Stokke, S. Burks	Mechanical Damage to Residual Stem Root Systems Associated with Forest Operations in Ozark Forest Ecosystems
3. R. Cecich	White Oak Acorn Production Along a Slope Transect
4. J. Chen, M. Xu, K. Brosofske	Microclimatic Characteristics in Southeastern Missouri's Ozarks
5. R. Clawson, J. Faaborg, E. Seon	The Effects of Selected Timber Management Practices on Forest Interior Birds in Missouri Oak-Hickory Forests
6. D. Dey, D. Larsen, R. Jensen	Stump Sprout Response to MOFEP Harvest Treatments
7. J. Dwyer	Economic Comparisons of Harvest Practices on MOFEP Study Sites
8. J. Dwyer	Tree Grading on the MOFEP Study Sites
9. J. Dwyer, R. Jensen	Documenting Harvest Damage to MOFEP Study Sites
10. D. Fantz, D. Hamilton	Abundance and Production of Berry Producing Plants on MOFEP study Sites: The Soft Mast Study (Pre-Harvest Conditions)
11. D. Fantz, R. Renken	Small Mammal Communities on MOFEP Sites and Their Response to Treatment
12. J. Grabner, D. Larsen, J. Kabrick	Composition, Structure and Dynamics of MOFEP Ground Flora
13. W. Gram, V. Sork, R. Marquis	Synthesis and Integration of Pretreatment Results from the Missouri Ozark Forest Ecosystem Project
14. R. Guyette, D. Dey	Historic Shortleaf Pine (*Pinus echinata* Mill.) Abundance and Fire Frequency in a Mixed Oak-Pine Forest (MOFEP, compartment 8).
15. L. Herbeck, D. Larsen	Ecological Interactions of Vegetation and Plethodontial Salamanders in Missouri Ozark Forests
16. R. Jensen, E Wiggers	Tree Cavity Abundance, Size and Use on MOFEP Study Sites
17. J. Kabrick, D. Larsen, S. Shifley	Analysis of MOFEP Woody Vegetation and Environmental Data
18. D. Ladd	Profiling MOFEP Lichen Vegetation
19. D. Larsen	Simulated Long-Term Effects of the MOFEP Cutting Treatments
20. R. Marquis, J. Le Corff	The Oak Herbivore Fauna of the Missouri Ozark Forest Ecosystem Project
21. S. Pallardy	Vegetation Analysis, Environmental Relationships, and Potential Successional Trends in the Missouri Ozark Forest Ecosystem Project
22. R. Renken	The Herpetofaunal Communities on Missouri Ozark Forest Ecosystem Project (MOFEP) Study Sites
23. S. Sheriff, Z. He	The Experimental Design of the Missouri Ozarks Forest Ecosystem Project
24. S. Shifley, B. Brookshire, D. Larsen, L. Herbeck, R. Jensen	Snags and Down Wood on Upland Oak Sites in the Missouri Ozark Forest Ecosystem Project
25. V. Sork, A. Koop, M. de la Fuente, P. Foster, J. Raveill	Patterns of Genetic Variation in Woody Plant Species in the Missouri Ozark Forest Ecosystem Project
26. H. Spratt, Jr.	Aspects of Carbon and Sulfur Transformations in MOFEP Surface Soils
27. L. Vangilder	Acorn Production on the MOFEP Study Sites: Pretreatment Data
28. J. Weaver, S. Heyman	The Distribution and Abundance of Leaf Litter Arthropods

Stratification by ELT was done to reduce variation. Under the current ELT designations, three predominant ELT's exist: ridges (ELT #11), south- and west-facing side slopes (ELT #17), and north- and east-facing side slopes (ELT #18) (Miller 1981). Additional ELT's and their designated numbers are defined by Miller (1981).

Additional Projects

To date, 28 research projects have been initiated on the MOFEP sites, and 22 of these are currently active (table 4). Research plots are spread across 9,200 ac (3,680 ha) included in the MOFEP study. Research plots for current projects are identified in figure 5 (map pocket, back cover). Throughout this volume, authors will refer back to figure 5. Authors will provide specific details about their respective sampling sites.

THE FUTURE OF MOFEP

The future emphasis of MOFEP will be to support collaborative, integrated research. To date, we have concentrated on collecting information on various components of an Ozark ecosystem. In the future, we will support efforts to investigate how the ecosystem components fit together and how they are ultimately affected by forest management practices. Management recommendations will be developed that address the mandate of MDC and the concerns of Missourians regarding the use and condition of their forests.

Since the inception of MOFEP in 1989, the project has grown exponentially. We have concentrated on supporting research to better understand forest ecosystem components that have received little or no support in the past. This volume is designed to present information compiled from the pre-treatment phase of MOFEP. It provides an excellent opportunity for MOFEP scientists to thoroughly document their methodology and pre-treatment findings and to archive that information for decades to come. MOFEP is designed to be a century-long project, and the initial documentation of pre-treatment findings will help ensure its future success.

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The Experimental Design of the Missouri Ozark Forest Ecosystem Project

Steven L. Sheriff and Zhuoqiong He[1]

Abstract.—The Missouri Ozark Forest Ecosystem Project (MOFEP) is an experiment that examines the effects of three forest management practices on the forest community. MOFEP is designed as a randomized complete block design using nine sites divided into three blocks. Treatments of uneven-aged, even-aged, and no-harvest management were randomly assigned to sites within each block. Pre-treatment data have been collected to ensure that results can be adjusted in terms of pre-existing conditions. Interdisciplinary studies are conducted within this design to provide information about relationships of different forest components. MOFEP's design was selected to allow the most flexibility to forest managers during the implementation phase while accounting for among block variation in examining treatment effects.

Many studies of forest and wildlife resources have been conducted in the Missouri Ozarks. The objectives of these studies have covered the breadth of forest and wildlife management. Several have even examined forest-wildlife habitat relationships (e.g., Robinson *et al.* 1995, Thompson *et al.* 1992). Despite the number of studies conducted, controversy surrounding the impacts of forest management upon wildlife populations remains (Kurzejeski *et al.* 1993). The controversy is due to different factions basing their arguments on studies that were observational in nature and done under different conditions and at different times. Most wildlife studies are not designed to answer questions concerning management effects, but are designed to develop hypotheses about these possible effects (Romesburg 1981). To overcome these problems and issues, a study was planned that would examine how forest management affects the forest-wildlife community in the Missouri Ozark Plateau. In other words, a project was needed to test hypotheses that these other studies had established and to provide a reliable knowledge base for decision processes in forest management.

The Missouri Ozark Forest Ecosystem Project (MOFEP) is designed to collect data to estimate effects and test hypotheses. The design allows the examination of cause-and-effect relationships within the forest ecosystem. MOFEP differs from earlier studies in many ways. First, MOFEP is a large-scale experiment conducted at the landscape scale used in forest planning and management in Missouri. Second, it examines management concerns that are not only pertinent today but will be of concern to future forest managers in Missouri's Ozark forests. Third, MOFEP is the first attempt to coordinate a multidiscipline approach for examining the effects of forest management practices on the forest ecosystem through an experimental approach.

In this paper, we describe (1) reasons for choosing an experimental approach for MOFEP, (2) components of the experiment, (3) experimental design selected, (4) overlap of complementary interdisciplinary studies, (5) limitations of the selected experimental design, and (6) MOFEP as an adaptive management approach.

WHY AN EXPERIMENT?

Forestry and wildlife studies can basically be divided into three conceptual designs: descriptive, correlational, and manipulative (White and Garrott 1990:14-16). These three conceptual designs are analogous to the respective three approaches that can be used in the scientific method—induction, retroduction, and hypothetico-deductive (Romesburg 1981).

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Studies that are designed using the descriptive approach observe and describe natural processes. These types of studies are useful in describing the natural history of a species or the structure of a forest. However, these studies do not test hypotheses. As the term indicates, the useful information derived from a descriptive study is a description of things measured. Often from these descriptive studies, hypotheses are formulated that can be tested under one of the other two approaches.

A more elucidating approach than the descriptive study is to formulate at least one hypothesis and design a correlational or retroductive study (Romesburg 1981). Using this approach, the researcher collects data on the subject over a broad range of environmental factors. For example, Thompson *et al.* (1992) conducted a correlational study of breeding birds. In their study, bird densities were examined on areas that had been either clearcut or on areas where no timber harvest had occurred in recent time. Because areas had been previously treated (clearcut or no harvest) with no randomization of treatments among areas, the analysis could indicate only if there were observed differences in the bird densities between the two types of areas. From this type of design, the forest management treatment cannot be inferred as the cause of differences in bird densities. The forest management treatments and the location of the treatments are mixed or confounded. The location of treatments may be tied, inadvertently or intentionally, to a process that would have shown treatment effects where none might have existed if a different assignment of treatments had been made to the locations. In other words, factors other than treatment may have been responsible for the observed responses due to the choices of areas studied.

Correlational or retroductive studies are very useful (Romesburg 1981). They can provide insights into hypotheses that should be further explored to determine cause-and-effect relationships. In other words, studies, like those reported by Thompson *et al.* (1992) and Robinson *et al.* (1995), should be used to formulate experimental approaches for determining treatment effects upon some set of response variables.

To infer cause-and-effect relationships, one must conduct a manipulative or hypothetico-deductive study (Eberhardt and Thomas 1991, Green 1979, James and McCulloch 1985, Romesburg 1981, White and Garrott 1990). Under this approach, the system must be manipulated in a planned manner to determine if hypothesized cause-and-effect relationships exist. An experimental approach with properly defined treatments, randomization, and replication is used to determine cause and effect. Treatments may entail more than one type of manipulation that may be compared with each other or with a control treatment that remains untouched. Within the experiment, the results from areas treated the same are compared to results of areas treated differently. If proper experimental procedures are applied and data differ among treatments, cause and effect can be inferred. However, if all treatments show similar results, then one would conclude that the treatments had little effect upon the parameters being measured.

Given the public's desire to support a stronger conservation and stewardship ethic for forest management (Brookshire *et al.* 1997), MOFEP was designed as a manipulative or experimental approach. The goal was to determine the effect of forest management upon the forest and wildlife community of the Missouri Ozarks. When we use this scientific approach for determining cause and effect, any impacts or benefits that might be measured during this project may be attributed to forest management practices.

COMPONENTS OF AN EXPERIMENT

According to Hurlbert (1984), an experiment is composed of five components: (1) the hypothesis, (2) the experimental design, (3) the experiment execution, (4) the statistical analysis, and (5) the interpretation of results. Without the first component, the hypothesis, an experiment would be a failure. This would be true even if the other four components were carried out with great attention to detail and protocol. The hypothesis of any experiment is the key to the successful outcome of that experiment. For MOFEP, the hypothesis is that no differences among the selected forest management practices will be found when applied to the experimental units. This hypothesis is stated in terms of equivalence. Statistical procedures normally used in studies like MOFEP examine data under a null hypothesis that allows biologists to determine if equivalence can be supported by the experimental data. In other words, are treatment effects equal or do they exhibit differences? These questions must be

answered within the context of the scope and power of the experiment.

Experimental Design

An experimental design must provide observations that will support tests of hypotheses and estimation of parameters of interest. The description of an experimental design, according to Hurlbert (1984) and McAllister and Peterman (1992), includes (1) the nature of the experimental unit; (2) the number and kinds of treatments, including controls, to be tested in the experiment; (3) replication in time and space, which controls for stochastic factors among replicates that are inherent in the experimental units; (4) interspersion of differently treated units in space to control for properties of the experimental units; (5) randomization in allocating different treatments to experimental units so that biases and stochastic factors associated with the experimental unit do not become influential; and (6) statistically independent experimental units.

The experimental unit chosen for MOFEP was a site (Brookshire *et al.* 1997). Nine sites of 266 to 527 ha were found on Missouri Department of Conservation lands located in Shannon, Reynolds, and Carter Counties in Missouri. Brookshire and Hauser (1993) and Meinert *et al.* (1997) provide extensive descriptions of these nine sites. Three treatments—even-aged management, uneven-aged management, and no harvest management (the control)—are being applied to these sites (Brookshire *et al.* 1997). Visual observations were used to assign each site to one of three blocks based on their subjectively determined similarity. This blocking allows for replication of the three treatments in space, so that no treatment is assigned twice to the same block. These blocks are considered independent of one another. Due to the similarity of sites within each block, we expect that results will be more similar within blocks than among blocks if all sites were treated alike. Sites within each block also are assumed to be independent. We are assuming that the responses in one experimental unit are not related to responses in other units, except that they might share the same treatment.

The three treatments were randomly assigned to sites within a block. Sites from each block were ordered using a random numbers table. Each site within the random ordered list for a block was assigned a treatment number in its turn, again, using a random numbers table. Then, an individual was asked to assign a treatment to each treatment number, without having any prior knowledge of the previous randomization results. Thus, a treatment was randomly assigned to a site within a block. The result of this randomization process is shown in figure 1 of Brookshire *et al.* (1997). Block 1 includes sites 1-3, block 2 includes sites 4-6, and block 3 includes sites 7-9. This design is commonly known as a randomized complete block design (Steel and Torrie 1980:196-197) or randomized blocks (Cochran and Cox 1957:106-107).

The 5 years before treatments were applied (i.e., before timber was harvested) were critical to the experimental design. During this period, data were collected about the characteristics of interest. This pre-treatment information will be critical in understanding if the impacts of treatment were due to treatment or were a continuation of the system as it existed before treatment. To illustrate the importance of the pre-treatment data, an example is shown in figure 1. Figure 1A shows a difference between two treatments, whereas figure 1B shows that there was no impact through time. Without pre-treatment information, we might conclude in both cases that a difference between treatments occurred. Pre-treatment data can be included in the statistical analysis model to increase precision for determining the treatment effects.

Experiment Execution

The execution of the experiment is the next crucial component in the experimental approach. Because MOFEP is a long-term study, it should extend through two or more full rotations of timber harvest, or about 200 years or longer. This length of time may be important in understanding the full and long-term impacts of each management strategy. However, results from shorter periods can be used by resource managers in the forests of Shannon, Reynolds, and Carter Counties. Information derived from MOFEP also can be used by managers in adjusting their approach to each of the harvest treatments. Also, variables measured do not have to be measured every year, but a systematic scheme, which ensures continuity of data collected on all nine sites through time, can be built to periodically remeasure certain variables during this project. The information from MOFEP will become more valuable as each year passes and subsequent

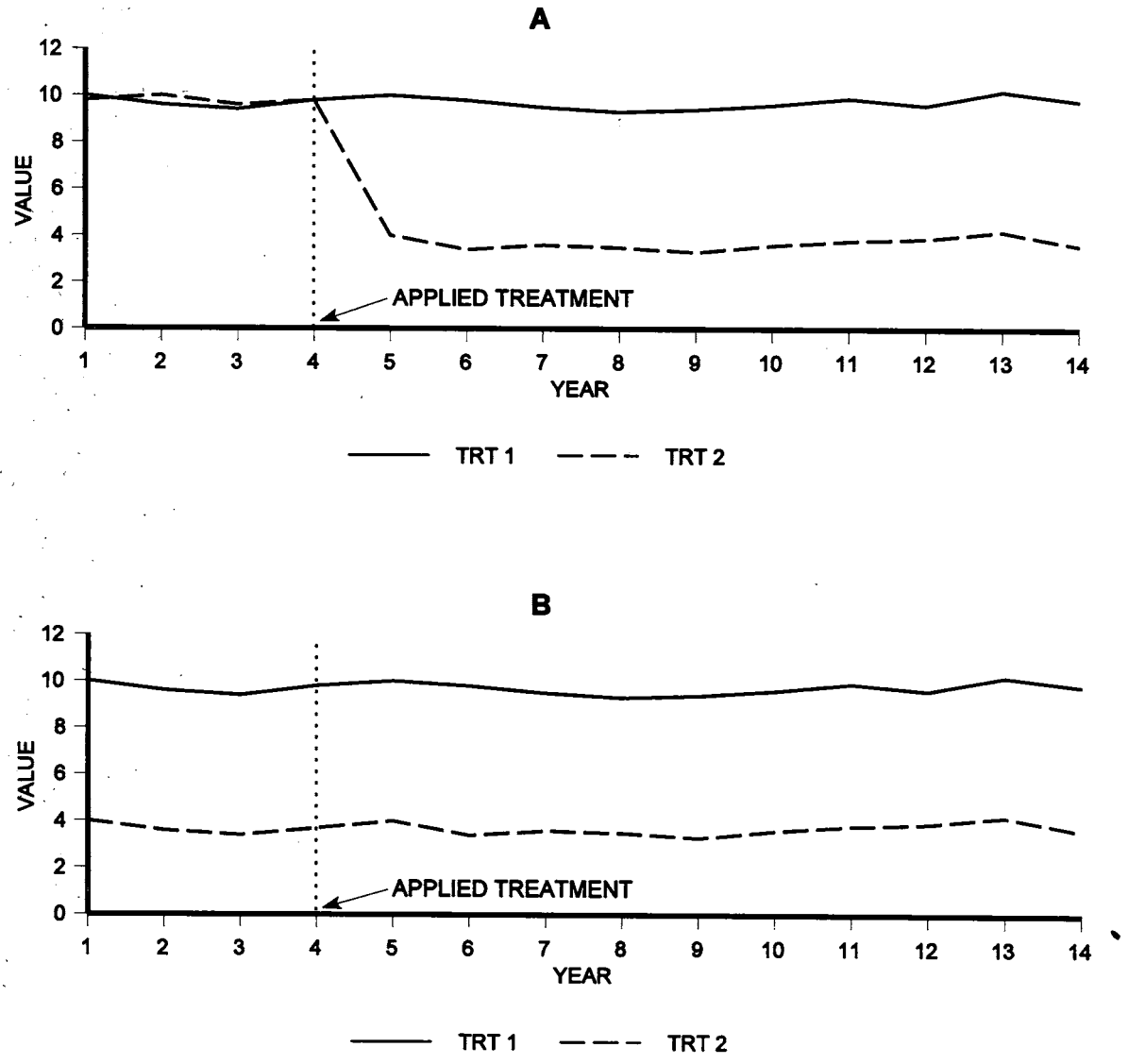

Figure 1.—*Illustration of two experimental studies showing importance of pre-treatment data. Illustration A shows a treatment effect, whereas illustration B has no treatment effect.*

data are added. Coordination of the data collection schedule in the long term will be critical for increasing ecological understanding.

One of the critical factors in executing MOFEP is the application of the two timber harvest treatments. The design requires that all six sites where timber is to be harvested receive their prescribed treatment within the same year. For example, the initial timber harvest had to be done within the 1996-97 cutting season (Brookshire *et al.* 1997). In subsequent re-entry periods, harvest should also be done within a cutting year unless the treatment prescriptions for uneven- and even-aged managed areas are redefined due to some modification of standard forest management practices. If this does not occur, the experiment will not have adequate temporal replication because the applications of treatments will become staggered. If, at any point, timber harvesting is not completed on schedule, the entire experiment should be re-evaluated to determine the potential impacts on replication of the prescribed treatment.

Statistical Analysis

Many statistical models are available for analyzing data from MOFEP studies. The decision of which model to use must be based on the

nature of the response variables (continuous or discrete); assumptions (normality, independence, additive or multiplicative, structure of variance-covariance matrices, etc.); and the inference space, the extent that inferences can be applied in terms of landscape and temporal range restrictions. Also, the size of the MOFEP study (only nine sites are being used) must be taken into account. Because of the large number of possible statistical models to choose from, we will only discuss three basic models expressed in terms of analysis of variance to illustrate potential statistical approaches.

In our illustrations, we assume that the data adhere to the assumptions for the analysis of variance (Steel and Torrie 1980:167-170). The response variable for our illustration will be the differences between the pre-treatment and post-treatment means. In other words, we find the mean of the post-treatment data that were taken over a number of years and subtract it from the mean of the pre-treatment data taken over a similar number of years. This adjustment will take into account the problem illustrated earlier in figure 1.

The first and the simplest model (MODEL 1) can be used only to examine block and treatment effects (table 1). The error term used to test the hypothesis of no treatment effect is the interaction of the block and treatment effects. This understanding of the proper error term is important to remember when data used in the analysis are from a number of measurement plots that were randomly placed within each site. These measurement plots are a subsample of the site and are used to estimate the response variable at the site level (Bergerud 1996). The among-measurement plot variation is not used in testing treatment effects. It is the variation at the site level that is important in this test. MODEL 1 can also be used to compare response variables measured at only one point in time (not repeatedly measured.)

Physiographic or some other characteristics of the sites can be influential in the ecosystem response to treatments. If sites are divided into physiographic characteristics, such as ecological land types (ELT), and studied separately to test the response of the variables to these characteristics, then a different statistical model is needed. The statistical model for this type of data is known as a split-plot analysis of variance (Steel and Torrie 1980:377-382). Table 2 illustrates this analysis of variance table for this design (MODEL 2). Within this model, two error terms exist. The first is the block-by-treatment interaction that is used to test the hypothesis of no treatment effects. This test is the same as in MODEL 1. The other error term, in this case, is used to test the hypothesis of ELT effects. As illustrated, this error term is the block-by-treatment-by-ELT interaction effect. This error term is used to test for ELT effect and ELT-by-treatment interaction effect. This error term can be pooled with the block-by-ELT interaction for testing purposes, but this must be done with caution (Hines 1996).

MODEL 1 and MODEL 2 do not use effectively

Table 1.—*Example of randomized complete block analysis of variance table with block and treatment effects (MODEL 1). This analysis would use site level data representing one point in time or a single measure from the sites.*

Source of variation	DF[1]	MS[2]	F[3]	P-value[4]
Block	2			
Treatment	2			
Error[5]	4			

[1]Degrees of freedom.
[2]Mean square.
[3]Calculated F-statistic.
[4]Probability level of F-statistic.
[5]Error term for treatment effects. This error term is the interaction of block by treatment (Block*Treatment).

Table 2.—*Example of split-plot design analysis of variance table with block and treatment main effects and each site split by Ecological Land Type (ELT) (MODEL 2). This analysis would use ELT information within each site representing one measure.*

Source of variation	DF[1]	MS[2]	F[3]	P-value[4]
Block	2			
Treatment	2			
Error a[5]	4			
ELT[6]	L-1			
Block*ELT	2*(L-1)			
Treatment*ELT	2*(L-1)			
Error b[7]	2*2*(L-1)			

[1]Degrees of freedom.
[2]Mean square.
[3]Calculated F-statistic.
[4]Probability level of F-statistic.
[5]Error term for treatment effects. This error term is the interaction of block by treatment (Block*Treatment).
[6]Ecological Land Type. L categories of ELT are used in this example.
[7]Error term for ELT effects and interaction of ELT by treatment. This error term is the three-way interaction of ELT, block, and treatment effects.

the repeated measures that occur through a sequence of years. In most of the studies that are conducted under MOFEP, the same plots are measured repeatedly through a sequence of years. MODEL 1 and MODEL 2 can only use data from one year at a time or by pooling data over the years, such as through a mean. Our final model for illustrative purposes uses repeated measures from plots across a sequence of years more efficiently than MODEL 1 or MODEL 2. Table 3 shows the split-plot design with repeated measures (MODEL 3). This profile analysis uses a multivariate analysis of variance approach (Littell *et al.* 1996, von Ende 1993). Data used in this approach will no longer be differences between pre-treatment and post-treatment means. The response variable for this analysis can take many forms. For example, the response variables can be the separate repeated measures through the pre-treatment and post-treatment periods. Polynomial growth curves are fit through time for each site. The polynomial coefficients are tested for differences among treatment and, in this case, ELT effects and their interactions. Another form the response variable might take is through differences between post-treatment measures for each year and an index of the pre-treatment measures. The index might be the mean of the pre-treatment measures or even the measure that was taken during the last year of the pre-treatment period. This method will produce as many repeated measures as the number of post-treatment repeated measures used.

These models can also be used to analyze specific sets of data that do not overlap the time boundary between pre-treatment and post-treatment phases of MOFEP. For example, in this proceedings, most of the papers examine only pre-treatment information. During the pre-treatment phase, interest was focused on the block, year, and "pseudo-treatment" effects. We emphasize "pseudo-treatment," because during this period harvesting of trees had not occurred on the sites assigned specific harvest treatments. For MODEL 1 and MODEL 2, data for these analyses would either be from a single year or a pooled measure across the study period (for example, the mean of a variable that was measured each year during the pre-treatment phase). For MODEL 3, data would be in the form of repeated measures (Littell *et al.* 1996) and would not have to be indexed.

Table 3.—*Example of split-plot design analysis of variance table with repeated measures (MODEL 3). Block and treatment are the main effects, each site is split by into ecological land type (ELT) effects, and year effects are a repeated measure of ELT within each site. Measurements would be made in each ELT category within each site over a number of years.*

Between site effects

Source of variation	DF[1]	MS[2]	F[3]	P-value[4]
Block	2			
Treatment	2			
Error a[5]	4			
ELT[6]	T-1			
Block*ELT	2*(T-1)			
Treatment*ELT	2*(T-1)			
Error b[7]	2*2*(T-1)			

Within site effects

Source of variation	Pillai's Trace[8]	F[9]	NumDF[10]	DenDF[11]	P-value
Year					
Year*Block[12]					
Year*Treatment[12]					
Year*ELT					
Year*Block*ELT					
Year*Treatment*ELT					

[1]Degrees of freedom.
[2]Mean square.
[3]Calculated F-statistic.
[4]Probability level of F-statistic.
[5]Error term for treatment effects. This error term is the interaction of block by treatment (Block*Treatment).
[6]Ecological Land Type. T categories of ELT are used in this example.
[7]Error term for ELT effects and interaction of ELT by treatment. This error term is the three-way interaction of ELT, block, and treatment effects.
[8]Pillai's Trace Statistic (Seber 1984:39-40).
[9]F-statistic derived from Pillai's Trace Statistic (Seber 1984:564).
[10]Calculated numerator degrees of freedom for the F-statistic.
[11]Calculated denominator degrees of freedom for the F-statistic.
[12]Error matrix for testing these effects would be from the three-way interaction of year by block by treatment.

Interpretation of Results

The results of any experiment must be correctly interpreted within the constraints of the hypothesis, the experimental design, the execution of the experiment, and the statistical analysis to provide meaningful information about the impacts of treatments. Inferences made beyond the scope of these elements can be misleading and may cause harm to resources. Therefore, interpretation of results is a very important aspect of any experiment and is the ultimate purpose of the experiment. The responsibility of interpretation abides with both the researcher and the user of the information.

As much as the inference space relies upon the other components of the experiment, so do the experimental design, execution, and statistical analysis depend upon the desired inferences that researchers and managers wish from the project. MOFEP has been designed to allow some flexibility in the breadth of inferences that can be drawn from resulting data. This flexibility is granted through the assumptions that researchers and managers might wish to make when analyzing and interpreting results from different MOFEP studies.

For example, if a researcher is reporting to forest managers results that might be used in adapting a treatment during subsequent re-entry harvest periods, then the researcher might wish to assume that the blocks are fixed and represent themselves. In this manner, the blocks can be tested under an analysis of variance using blocks and treatments as fixed effects. However, if the researcher wishes to make statements about the impact of treatments on sites outside of the nine used in MOFEP, then the researcher would need to assume that the blocks represent random effects. In other words, the researcher wants to make statements about the potential treatment effects on a larger population of sites from which the nine sites used in MOFEP were randomly selected. Under the regime where blocks are assumed to be fixed effects, a fixed model analysis would be used in the analysis of variance, because both treatment and blocks are a "fixed" set of effects. Under the latter regime, where inferences would be drawn for sites beyond those used in MOFEP, a mixed model (Littell *et al.* 1996) would be appropriate. Blocks would represent the random effect and treatments would be fixed effects in this case.

Inferences may not be representative of the entire site due to availability of resources. Some researchers have had to confine their views to portions of each site. For example, the reptile and amphibian study examines only those reptile and amphibian populations within two major ELT classes (Renken 1997). Therefore, data from this study are not representative of the entire site, but are limited to the two ELT classes chosen. The experimental design will accommodate this restriction in study scope; however, the interpretation that might be made from these data must also be restricted.

WHY THE RANDOMIZED COMPLETE BLOCK DESIGN

The selection of a manipulative or experimental approach for MOFEP appears to be a logical choice, given the goal of showing cause-and-effect relationships among forest management practices. These impacts are believed to have an influence on biotic and abiotic components within the forest ecosystem. However, many other approaches could have been used in the design of MOFEP. A design could have been selected that would have used regression procedures as the basis for statistical analysis (Draper and Smith 1966). Or, we could have chosen a different experimental layout, such as completely randomized or an incomplete block design (Cochran and Cox 1957).

The regression procedure would have allowed for a wide variety of forest opening sizes to be tested at the site level. Under this design a site would have been randomly assigned a specified size of "clearcut" to be used for the duration of the study. These clearcut sizes could have ranged from zero acres for sites assigned as controls up to one-tenth of the size of a site given a 100-year rotation. The independent variable in the regression analysis would have been the sizes of the assigned "clearcuts" on which the dependent variables would have been regressed. This design would have restricted the options for forest managers in implementing the treatments and would not have allowed forest managers to use information in adapting forest management practices on the project.

Other experimental designs that use the pre- and post-treatment were considered. For example, an incomplete block design with four treatments replicated in three blocks each having three experimental units was considered. However, this design was discounted due

to the decreased power of the statistical analysis and inadequate replication of treatments.

A completely randomized design was also considered. Under this design each site would have been assigned a treatment at random so that each treatment would have appeared three times. This differs from the chosen design in that blocking of sites would not have occurred. This design forces the variation among sites in a completely randomized design into the experimental error and provides less accuracy than a design using blocking of the sites (Cochran and Cox 1957). On-site reconnaissance indicated that all the sites were not alike and that the three sites on Peck Ranch Conservation Area (PRCA) and their underlying soils were different from the other six sites.

Several other considerations that eliminated the use of the completely randomized design were discussed during the design phase of MOFEP. Discussions on the potential of adding other sites to MOFEP were an important factor in eliminating this design. Under a completely randomized design, adding other sites would not be possible without a re-randomization of treatments among sites. Also, the possibilities of site destruction due to some natural cause, such as tornado or fire, were discussed. If these problems impacted a block, then these impacts might also be studied and accounted for within a block design, but not under a completely randomized design. Under a completely random design, these problems could cause irreparable damage to MOFEP. To avoid these problems and to add flexibility, a completely randomized design was not chosen.

The reconnaissance of the MOFEP sites suggested that the nine sites could be divided into three blocks that were nearly homogeneous. That is to say, we would expect results from sites within each block to be more alike than results compared among blocks. Blocking would prevent the chance assignment of only one treatment type occurring on the three sites on PRCA. Therefore, the randomized complete block design was chosen. The randomized complete block design allows us to eliminate the variation due to differences among blocks (block effects) during data analysis. If variation among blocks is included as part of the experimental error, greater differences among treatments would be necessary before the impact of a treatment might be found. This design also allows for flexibility in adding extra blocks at a later date and in different locations. Adding extra blocks makes the analysis more difficult and will require additional assumptions, such as impacts of temporal and spatial confounding.

We believe that the randomized complete block design is the best choice given the number of sites available. This design is simple and allows flexibility so that forest managers can adapt their practices to the state of the art at each reentry period.

ECOSYSTEM PROJECTS WITHIN THE DESIGN

The beauty of MOFEP is the concept of allowing many different ecosystem components to be studied during the life of this project. The treatments will be replicated within the nine sites, and the response to the treatments will be documented through time. Because these sites will be consistently treated under a designed experiment, we have the opportunity to take measurements on a variety of environmental variables. MOFEP will be a valuable source of information for wildlife and forest researchers and managers.

As one might expect, not all types of variables are suitable for measurement within MOFEP. The restrictions on these variables are defined by statistical and practical considerations. During the process of including individual studies under the MOFEP umbrella, these restrictions were taken into account. In the future, as other individual studies are considered, we believe that these restrictions also will be applicable.

The first restriction concerns relationships among variables. Variables that are measured should not be the same ecologically. It does not make sense to measure essentially the same thing in several different ways. However, the selected variables may be related through their influence on each other in the ecological web of the forest ecosystem. MOFEP offers a design under which correlational responses of these interactions of ecological variables can be studied. Statistical modeling offers the opportunity of using data from several individual studies to explore and develop hypotheses about ecological connectivity among ecosystem components.

Methods for measuring each variable should not have an impact on other variables and community components. For example, if all the trees within each site needed to be cut to determine their weight, then tree mass probably should not be considered as a viable candidate to be measured. Therefore, methods and techniques for measuring the forest ecosystem need to be non-destructive in studies like MOFEP. If the process of measuring one variable causes an impact upon other components of the ecosystem, false inferences about treatment impacts could be the result. These false inferences could cause forest managers to make decisions that could damage the forest.

The size, shape, and juxtaposition of the sites needed to be considered in selecting proper variables to study. For example, it would be unwise to measure wild turkey densities on a site-size area. Because turkeys have such a large home range, the numbers of turkeys would vary greatly within any set of given days. This variability would most likely cause the measurement error of density within the sites to be greater than the amount of variability among treatments. The most logical conclusion from this highly variable measure of turkey density would be that treatment could not be shown to have an effect upon turkey density. Therefore, the area of influence that affects variables had to be taken into account, and some important forest ecosystem variables cannot be studied under the MOFEP design due to scale problems.

A restriction that occurs in every research project also affects MOFEP. This restriction is caused by a limited amount of resources—financial, space, and time. It must be cost-effective to collect the data. For example, ground litter invertebrates were found to be highly variable within a site (Weaver and Heyman 1997). To obtain a reliable and precise estimate of these invertebrates for a site would have required a large army of entomologists to collect and classify the samples. The expenditure would have been prohibitive for a ground litter invertebrate study that met the objective of determining the impact of forest management on these invertebrates. Therefore, the objective was changed for ground litter invertebrates to make it cost-effective and accomplishable within a reasonable time (Weaver and Heyman 1997).

Once a variable had been selected for study, proper statistical sampling procedures needed to be identified to ensure that data were representative of the site or some smaller subdivision of the site (Cochran 1977, Thompson 1992). The sampling procedures had to include adequate sample size to obtain a reasonably precise estimate. If the estimates were not reasonably precise due to inadequate sample size or biased due to lack of randomization, then the data could lead to false inferences. Overlaying of individual studies on MOFEP's experimental design required that variables be ecologically dissimilar, the act of measuring them did not impact other ecological components, the precision of each variable was adequate so that the measurement error within sites did not exceed the variation among sites, and data could be collected in a timely and cost-effective manner. The selected variables had to be measured following proper sampling procedures to ensure that data would be representative of the population of interest.

LIMITATIONS OF THE MOFEP DESIGN

MOFEP has a solid experimental design. The randomized complete block design offers many opportunities to examine the impact of forest management on a broad array of ecosystem components; however, MOFEP does have limitations. MOFEP's biggest limitation is that statistical power may be low in most cases (Hurlbert 1984, McAllister and Peterman 1992, Peterman 1990, Steidl *et al.* 1997, Toft and Shea 1983). The statistical power will be low in detecting differences among treatments when the treatment effect is small relative to the experimental error. MOFEP has only three replicates for each treatment. The ability to detect a significant difference among treatments under a null hypothesis of equivalence is usually poor when so few replicates (i.e., small degrees of freedom) are used. The differences among treatments will have to be large in comparison to the experimental-wise error for a statistically significant difference to be detected. In all likelihood, researchers in the field probably will suspect biological differences before they are able to detect them through statistical analyses. We need to be cognizant that even though we might not reject a null hypothesis with the data, this does not mean that forest management practices are not impacting the system in some positive or negative manner.

The problem of not rejecting a null hypothesis when in fact a treatment effect exists (called Type II error) is a major issue concerning

MOFEP. The importance of knowing the probability of detecting a difference if it exists cannot be cast aside as irrelevant (Forbes 1990, Peterman 1990, Simberloff 1990, Steidl *et al.* 1997, Toft 1990, Toft and Shea 1983). So, the question is what can be done in light of low statistical power. A larger probability (the α-level) can be used for determining if the null hypothesis should be rejected. For example, instead of using the usual α-level of 0.05 for a statistical test to show a significant difference, a probability level of 0.10, or even 0.15, might be used. The α-level is inversely related to the probability of making a Type II error (Forbes 1990). Therefore, as the selected α-level becomes larger, the likelihood decreases that a false null hypothesis is accepted. It is important that the α-level be established before data collection and during the design phase of the experiment. Instead of setting large α levels, a better alternative might be the use of confidence intervals on the estimated differences between treatment means (Steidl *et al.* 1997, Gary White, personal communication). This method provides information about the range where differences between treatments are masked by the error.

Another limitation with the MOFEP design is the limited population of sites represented by the nine sites used in this project. In an attempt to find suitable sites that could be included in this long-term study, only the nine sites used in MOFEP met the criteria of age and homogeneity (Brookshire *et al.* 1997). These sites are relatively close in proximity (fig. 1 in Brookshire *et al.* 1997), and are all located on Missouri Department of Conservation lands. Because of their close proximity and land ownership, the "population" of sites represented by these nine sites, probably in strict terms and definitions, is these nine sites. Therefore, researchers and forest and wildlife managers will need to be very careful in making their inferences and extrapolating results beyond MOFEP project sites.

The small number of sites available also made it impossible to replicate the treatments temporally. Weather and possibly other abiotic and biotic components that vary annually impact results. The initial treatment (cutting of trees) was applied to all sites in the same year under one set of temporal impacts. A different set of results might be possible due to conditions in another year when treatments could have been applied. Not enough sites exist to apply timber harvest to sets of sites over several years under this replicated design. For example, four additional sites per block would have been needed to replicate the two timber harvest practices over a 3-year period. This would have allowed us to determine if temporal effects were present during the 3 years when trees were cut, but we would have been unable to detect longer temporal trends. Simply put, the results from MOFEP will represent the "population" of sites that will be cut the same year as we applied the initial timber harvest in MOFEP.

A catastrophic event, such as wildfire or tornado, within one or more sites would cause a major problem for MOFEP because of the low statistical power of the design. If a single site were affected by a catastrophic event, then the design would be unbalanced (Littell *et al.* 1996). At worst, only the statistical power would be affected under this type of circumstance. If an entire block of sites were affected by the event, the design could accommodate this problem. If catastrophic events destroy more than one site in different blocks, judgments about merits of continuing MOFEP will have to be made. The design may be too heavily impacted by this problem to provide meaningful results for all treatments.

MOFEP AS ADAPTIVE MANAGEMENT

Walters and Hilborn (1976) presented the concept of using adaptive control processes in managing natural resources. From this basic concept, adaptive resource management has grown into a management concept of learning while managing (Walters 1986). MOFEP follows this concept of allowing forest managers to learn from the results and to adapt their practices to reach their management goals (Walters 1993).

The principal forest vegetation management practices used by the Missouri Department of Conservation are even-aged, uneven-aged, and no harvest. These practices are competing models of forest managament. Each management practice has a different path in achieving the goal of maximum forest diversity over an infinite time horizon (Larsen 1997), but the impacts on specific forest ecosystem components are not known under each management model.

The experimental design of MOFEP allows forest managers to adapt their management style

within the "flexible" protocol established for each model. The most restrictive model is no-harvest management. This model does not generally allow the forest manager to manipulate any forest stands within these assigned sites. Under the two timber harvest models, forest managers actively manipulate and manage the forest for economic and biological gains (Brookshire *et al.* 1997).

This approach for MOFEP is very passive adaptive management, but it differs significantly from a pure experimental approach. Under a pure experimental approach, researchers would wait until the end of the experiment to analyze their data. Forest managers would be given a set of very restrictive prescriptions for each model, and they would not be allowed to deviate from these prescriptions throughout the life of the experiment. In other words, we could not learn from the results until after the experiment was completed (several hundred years from the start of MOFEP). Adaptive resources management, however, gives us the opportunity to learn while managing through a less restrictive experimental approach (Walters 1993). As Carl Walters says (personal communication), adaptive experiments are necessary to make learning ever happen in situations such as MOFEP.

As foresters adopt dynamic numeric models in their forest management planning, MOFEP will progress from very passive adaptive management to a more active adaptive management approach. Forest managers and researchers will be able to use the data that will be collected and analyzed to develop, evaluate, and change these dynamic models. Numeric procedures, such as stochastic dynamic programming (Lubow 1995, Lubow 1996, Puterman 1994), can be used to optimize timber harvest practices through adaptive resources management (Conroy and Crocker 1996). As data are collected on each site within MOFEP, forest managers can use this information to develop management plans that will establish a more rapid path for achieving optimal resource objectives (Walters 1986).

A cautionary note is important here, because no guarantee can be made that any of the three management practices under study in MOFEP is the "best" for achieving the goal of maximum diversity (Carl Walters, personal communication). Some other practice may actually be the "best." MOFEP can be used only to judge the regime that is the "winner" among these three practices as forest managers adapt their management based on information that is obtained through this experimental approach.

SUMMARY

The experimental approach used in MOFEP will provide results demonstrating cause-and-effect relationships among forest management practices in the associated Ozark forest communities of Shannon, Carter, and Reynolds Counties. These results must be interpreted with the realization of the locational, scalar, and temporal limitations of MOFEP. What makes MOFEP such a unique project is the replication and randomization of treatments. Using these experimental procedures reduces the risk of biased or misleading results. Reliable knowledge about forest management and its impact on forest ecosystems can, and will be, gained under this experimental approach. However, because of the low statistical power of the MOFEP design, results that are not significant in a statistical sense will have to be scrutinized, through the use of confidence intervals of the differences, to determine if one of the treatments might have an impact in a biological sense (Steidl *et al.* 1977). Conversely, if results show statistical significance, we will be assured that differences were large among treatments.

Due to the limitations of the MOFEP design, no simple analytical model is the "best" procedure for determining treatment effects. We foresee that further research of better statistical analysis techniques will have to occur. To derive all the valuable insights possible, data collected under MOFEP will require sophisticated statistical methods that do not exist at present. Research into areas of variance-covariance structure modeling (Littell *et al.* 1996) is needed. As more data are collected, greater insights will be gained about the nature and structure of the information that MOFEP can supply.

The long-term nature of MOFEP is mind-boggling. Realizing that anyone born on the day that MOFEP started will not be alive to see the successful conclusion of this project, one becomes aware of the significance and magnitude of this research project. But throughout the life of MOFEP, managers will be able to use results obtained from individual studies within the project to establish better management practices. Researchers at the same time will be

able to develop new hypotheses to be tested and use new analytical tools to obtain more information from the data. Information from MOFEP will be invaluable to wildlife and forest managers for generations yet to come.

ACKNOWLEDGMENTS

The design and implementation of MOFEP cannot be credited to us or to any single person. MOFEP is the result of a large group of people who have cooperated in tackling a major question of concern to forest and wildlife managers. Cooperation has been the key to MOFEP and its success thus far. The spirit of cooperation emerged during a Wildlife Research Section staff meeting where Rick Clawson and John Faaborg presented their idea of studying birds in a forest that was being fragmented. This cooperative spirit has continued through the design phase and to the point we find ourselves now, at the end of the pre-treatment data collection period. For MOFEP to succeed, cooperation will have to be the standard until the last report is written in several hundred years.

MOFEP would not be possible without the invaluable commitment of the Missouri Department of Conservation. The Department offers cooperating scientists from the academic and natural resource management environments an opportunity to study and address issues in forest management through MOFEP. For the Department's commitment, we and all of the cooperating scientists are very thankful.

As for designing the experiment, many people helped in this regard, and all of these people deserve a great deal of credit for their foresight and insight. We wish personally to thank Larry Vangilder and Steve Westin for helping with the design and an earlier presentation and paper from which we have adopted this manuscript. Their professionalism and opinions have added greatly to MOFEP. We also wish to thank Gary Krause and Mark Ellersieck, University of Missouri, for their help in discussions about the merits of different statistical designs. Carl Mize, Iowa State University, has also provided many insightful comments on the limitations and statistical analysis approaches of MOFEP. We thank Gary White, Gary Krause, Carl Mize, Carl Walters, and an anonymous reviewer of our manuscript for their many suggestions and comments on our paper. Their comments definitely strengthened our message.

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Analysis of Landscape Structure in the Southeastern Missouri Ozarks

Ming Xu, Sari C. Saunders, and Jiquan Chen[1]

Abstract.—We characterized the landscape structure within and surrounding the MOFEP study sites using Landsat TM data and GIS databases. Up to 31 percent of the landscape was within riparian zones. Road density was 1.4 km/km^2 within the landscape but reached 2.0 km/km^2 within 40-m stream buffers. More than 99 percent of the region had a slope <40 percent; about 92 percent of the area had an elevation <300 m. Land was evenly distributed among aspect categories. Upland forest dominated the landscape. Patch types were differentially distributed by elevation and slope but evenly distributed by aspect. An average of >80 percent of patches existed as edge habitat.

Recent research has emphasized the influence of dynamics in spatial pattern on ecological processes as diverse as hydrological activity (Swanson *et al.* 1988), vegetation distribution (Zobel *et al.* 1976), species dispersal (Gustafson and Gardner 1996, Schumaker 1996) microclimatic gradients (Chen *et al.* 1995), and gene flow (Futuyma 1986). The development of landscape ecology has provided new, interdisciplinary avenues to explore the role of spatial heterogeneity in controlling ecological processes at various scales (Wiens *et al.* 1993). Traditional, within-patch explanations for ecological phenomena have been found to be inadequate. Both the heterogeneity across an entire landscape and the structure of boundaries within the landscape influence ecological processes (Pickett and Cadenasso 1995). Advances in the implementation of ecosystem management require an understanding of landscape structure and principles of landscape ecology (Franklin 1997).

Landscape pattern reflects interacting influences of human-induced and natural disturbances over multiple scales of space and time. To study the effects of these patterns on ecosystem functions and processes, scientists must be able to quantify those aspects of structure that are central to the ecological phenomena under consideration. Quantitative characterization of landscape pattern can allow managers to monitor broad-scale ecological change (Hunsaker *et al.* 1994) and assess accurately the impacts of differing management regimes (Baskent and Jordan 1995). Traditionally, landscape structure has been defined by composition (i.e., the types and amounts of vegetation patches found in the landscape) and relative distribution of patches (i.e., patch-corridor-matrix model; Forman 1995). More generally, structure can be defined by the sizes, shapes, numbers, types, and configurations of any landscape components (Turner 1989). Natural features such as streams, riparian zones (Gregory *et al.* 1991, Naiman *et al.* 1993) or geomorphic landforms (Swanson *et al.* 1988) and human-induced features such as roads (Reed *et al.* 1996) may be critical structures influencing ecological processes in managed landscapes. The relative roles of natural versus human-induced attributes in defining landscape structure and affecting landscape functions must be considered (Larsen *et al.* 1997).

The Missouri Ozark Forest Ecosystem Project (MOFEP), initiated by the Missouri Department of Conservation in 1990, was designed as a long-term project to incorporate ecosystem management theories into forest management practices at the landscape level (Brookshire *et al.* 1997, Brookshire and Hauser 1993). Nine experimental compartments averaging 400 ha in size were selected for alternative silvicultural treatments for the MOFEP study. To evaluate the impacts of different management practices

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when applied at the landscape level, it is vital to determine landscape structure both within the study sites and across the Ozark landscape.

We assessed landscape structure within the region of the nine MOFEP study sites to: (a) provide information on structure, such as the distributions of roads and streams, and on composition, such as patch types, across this area and (b) compare the distribution of landscape features within the study sites to the distribution of these same features in the region as a whole. Specifically, we were interested in assessing the importance of streams, roads, and landforms in creating landscape structure.

METHODS

Study Site

The MOFEP is made up of nine compartments, ranging in size from 260 to 527 ha (fig. 1), which are located in Carter, Reynolds, and Shannon Counties in the southeastern Missouri Ozarks (91°01' to 91°13' W and 37°00' to 37°12'N) (Brookshire *et al.* 1997). These counties are 84 percent forested with large contiguous blocks separated only by roads and streams (Brookshire and Hauser 1993, Spencer *et al.* 1992). Agricultural activities are limited to bottomland corridors along primary streams. The study area consists of mature upland oak-hickory and oak-pine forest communities. Dominant tree species include white oak (*Quercus alba* L.), black oak (*Q. velutina* L.), post oak (*Q. stellata* Wang.), scarlet oak (*Q. coccinea* Muenchh.), blackjack oak (*Q. marilandica* Muenchh.), chinkapin oak (*Q. muehlenbergii* Engelm.), shortleaf pine (*Pinus echinata* Mill.), and hickory (*Carya* spp.). Understory species include dogwood (*Cornus* spp.) and blackgum (*Nyssa sylvatica* Marsh). Geologically, this region is underlain mainly by Ordovician age dolomite with areas of Cambrian age dolomite. Precambrian igneous rocks are also present (Meinert *et al.* 1997, Missouri Geological Survey 1979). Weathering of the Ordovician and Cambrian age dolomites has resulted in a deep mantle of leached, very cherty residuum on the MOFEP study sites (Gott 1975, Meinert *et al.* 1997). Soils on this area were formed mostly in residuum. The common series are Viburnum, Midco, Gepp, Bardley, Viraton, Poynor, and Clarksville (Brookshire and Hauser 1993). Mean annual temperature and annual precipitation are 13.3 °C and 1,120 mm, respectively. The MOFEP study sites cover 13 different Ecological Land Types (ELT's); ELT 17 (south- and west-facing slopes), ELT 18 (north- and east-facing slopes), and ELT 11 (ridge top) make up 90 percent of the total area.

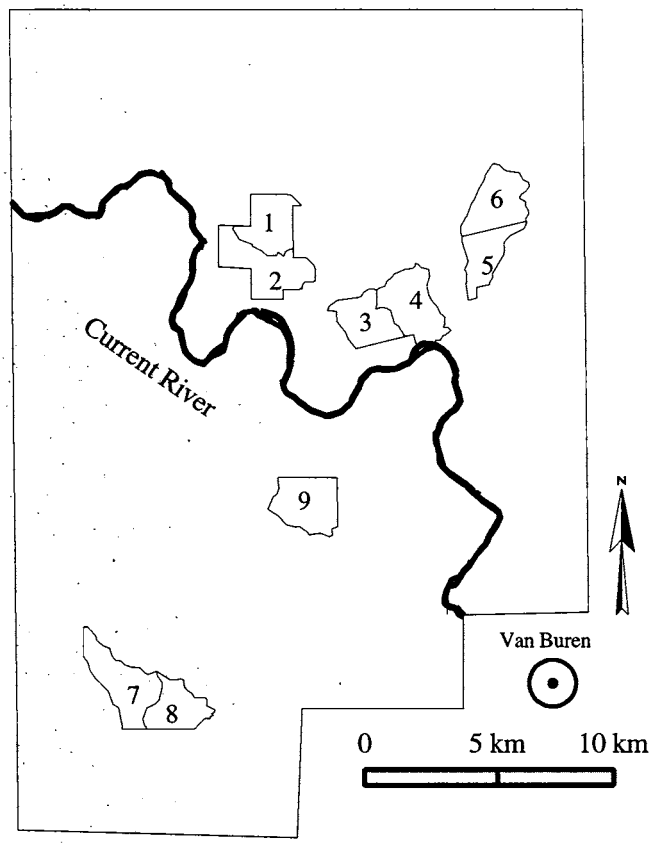

Figure 1.—*Location of the Missouri Ozark Forest Ecosystem Project (MOFEP) sites within the study region, southeastern Missouri.*

Data Analysis

We investigated the distribution of two linear features (roads and streams) and four patch features (vegetation type, slope, aspect, and elevation) relative to each other. For streams and roads, geographic information system (GIS) databases were available from the Missouri Department of Conservation (MDC). These data were based on five USGS 1:24,000 topographical maps: Powder Mill Ferry, Exchange, Van Buren North, Stegall Mountain, and Fremont. We limited our analysis to the area covered from 37°15'N, 91°15'W at the northwest corner to 37°15'N, 91°00'W in the northeast, 36°15'N, 91°14'W in the southwest and 36°15'N, 91°7'W in the southeast. We excluded the area of Van Buren from 37°2'N, 91°3'W to 37°2'N, 91°0'W and south to 37°0'N (fig. 1) to minimize bias in estimates of road density and patch metrics.

We used Landsat TM data (band 1,2,3,4,5, and 7; July 10, 1996) to classify major patch types in the study area using the supervised classification technique in ERDAS/Imagine (version 8.2). Silvicultural treatments on MOFEP site 7 were completed before the July 10, 1996 date of image capture. Atmospheric correction, sun illumination correction, and principal components analysis (PCA) were applied before classification. We eliminated small polygons (area < 1 ha) using the Arc/Info GIS. Initially, eight patch types were identified. We merged dry river beds, bare ground, and urban areas into one category, urban and non-vegetated (U/NV), for this study due to the limited area in each of these categories. We used the resulting seven patch types (table 1, fig. 2) for all subsequent analyses. To determine the classification accuracy, a total of 161 points were chosen within the study area through a combination of stratified random sampling and systematic sampling techniques (Hussin *et al.* 1991, Lillesand and Kiefer 1994). We located each point using a global positioning system (GPS) and recorded patch type and topographic information. Sample size in each category was determined by the relative amount of area in the patch type and the importance of the category for our objectives. Even a completely random assignment of pixels among patch types would produce a certain percentage of correct values in the error matrix. Therefore, the KHAT statistic was used to measure the difference between the actual agreement and the chance agreement between the ground truthed data and a random classifier (Lillesand and Kieffer 1994).

Slope, aspect, and elevation data were generated in Arc/Info using the MDC's digital elevation model (DEM), which corresponded to the USGS contour maps at a 1:24,000 scale. Contour interval was 20 ft for the map sheets of Powder Mill Ferry, Exchange, and Van Buren North. Contour interval was 20 m for the Stegall Mountain and Fremont maps. All contour data were converted to meters using lattice coverages with a resolution of 30x30 m in Arc/Info GIS. Slope was coded into eight categories (table 2), aspect was coded into 10 categories (table 3), and elevation was coded into six categories (table 4).

We buffered all streams and roads with seven buffer widths: 10, 20, 40, 50, 60, 80, and 100 m, and calculated the amount of area in each of these buffer zones using Arc/Info GIS. We determined road density within each buffer, and stream and road densities in the landscape as a

Table 2.—*Slope categories and codes used for intersection with patch types in Arc/Info GIS.*

Slope range	Category
Percent	
≥0 - ≤10	1
>10 - ≤25	2
>25 - ≤40	3
>40 - ≤55	4
>55 - ≤70	5
>70 - ≤85	6
>85 - ≤100	7
>100	8

Table 1.—*Error matrix for accuracy of classification of cover types. Cover types were classified from Landsat TM imagery using supervised classification in ERDAS/Imagine (see figure 2).*

Category	Classification	Ground truth (reference)								
		U/NV	S/EF	F/G	W	UF	LF	SF	Row total	User's accuracy
										Percent
1	Urban and Non-Vegetated (U/NV)[1]	6							6	100.0
2	Shrub and Early Successional Forest (S/EF)		10				1	1	12	83.3
3	Farmland and Grasslands (F/G)	2		4					6	66.7
4	Water (W)				4		1		5	80.0
5	Upland Forest (UF)		1			91	3	3	98	92.9
6	Lowland Forest and Wetlands (LF)						12	4	16	75.0
7	Sparse Forest and Partial Cuts (SF)		1	1		2	1	13	18	72.2
	Column total	8	12	5	4	93	18	21	161	
	Producer's accuracy (percent)	75	83.3	80.0	100	97.8	66.7	61.9		87.0

[1] Includes dry river beds.

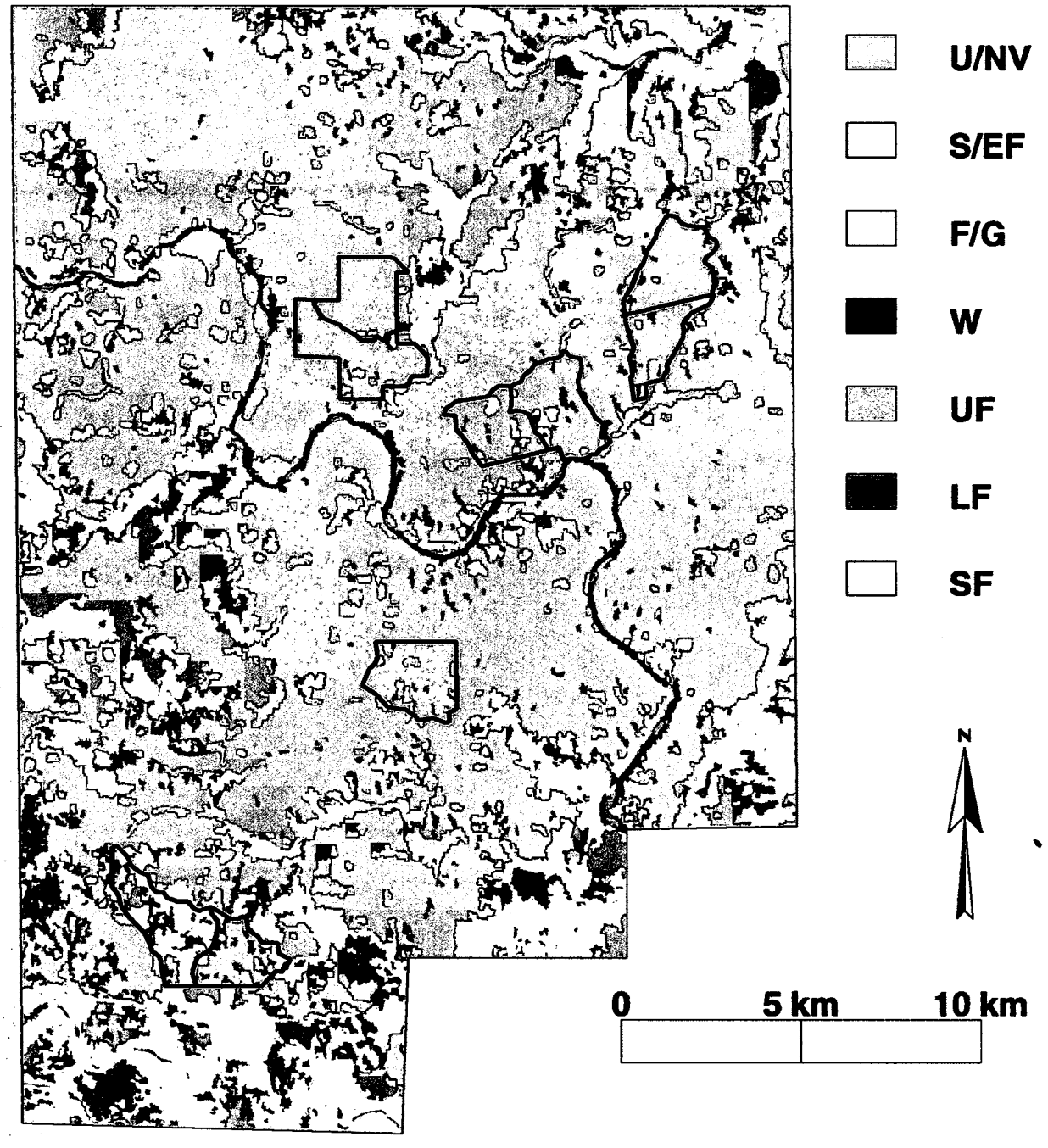

Figure 2.—*Patch types within the MOFEP study region: Urban and Non-vegetated (U/NV), Shrub and Early Successional Forest (S/EF), Farmland and Grasslands (F/G), Water (W), Upland Forest (UF), Lowland Forest and Wetlands (LF), Sparse Forest and Partial Cuts (SF).*

Table 3.—*Aspect categories and codes used for intersection with patch types in Arc/Info GIS.*

Aspect range	Category
Degrees	
flat[1]	flat
0.0 - ≤22.5	N
>22.5 - ≤67.5	NE
>67.5 - ≤112.5	E
>112.5 - ≤157.5	SE
> 157.5 - ≤202.5	S
> 202.5 - ≤247.5	SW
> 247.5 - ≤292.5	W
> 292.5 - ≤337.5	NW
> 337.5 - ≤360.0	N

[1]slope <1 percent

whole. We calculated the area of each patch type within all stream buffers, road buffers, the nine MOFEP study sites, and within the entire landscape. We also examined the distribution of patch types by classes of aspect, slope, and elevation. For each patch type, we determined mean patch area, maximum patch area, mean fractal dimension, mean core area index (using a buffer of 40 m), total edge length, and edge density. Patch metrics and distributions were compared between the MOFEP study sites and the regional landscape. All manipulations of final coverages and statistical summaries were done in Arc/Info GIS Unix version 7.0.4 and SAS Unix version. All patch metrics were calculated using FRAGSTATS version 2.0 (McGarigal and Marks 1995).

RESULTS

Total land area within the boundary designated for this study was 60,727 ha (607.3 km²). Total stream length within this region was 1,036.9 km and road length totaled 861.3 km, giving overall stream and road densities of 1.7 km/km² and 1.4 km/km², respectively. Land area within stream and road buffers increased linearly with increasing buffer width (fig. 3), though at a slower rate for road buffers than stream buffers. Area in road and stream buffers was 1,711 ha (2.8 percent of landscape) and 2,061 ha (3.4 percent of landscape), respectively, for a buffer width of 10 m, and 15,884 ha (26.1 percent of landscape) and 19,115 ha (31.4 percent of landscape), respectively, for a buffer width of 100 m.

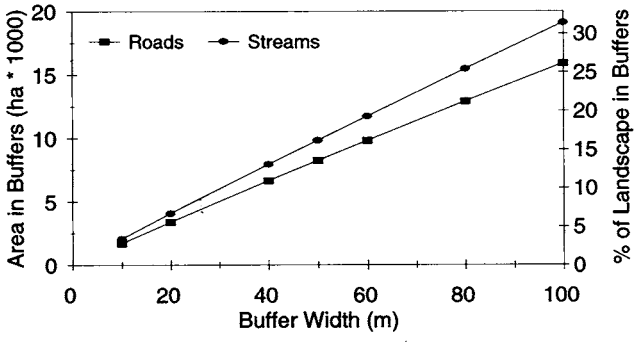

Figure 3.—*Change in buffer area around roads and streams with increasing buffer width.*

Total road length in stream buffer zones was 21.8 km in 10-m buffers and 36.0 km in 100-m buffers (fig. 4A) corresponding to densities of 1.1 km/km² and 1.9 km/km², respectively (fig. 4B). Road density reached a maximum of 2.0 km/km² in 40-m buffers, as compared to 1.4 km/km² in the study region as a whole.

The overall classification accuracy for the landscape was 87 percent (table 1). The KHAT statistic was 79 percent, indicating that the classification was 79 percent better than a random assignment of pixels to patch types. The majority of the landscape was covered with upland forest (UF; 73 percent). Sparse or partially cut forest (SF) and shrub or early successional forest (S/EF) covered about 10 percent of the landscape each. Lowland forest and wetlands (LF) covered 5 percent and farmland or grassland (F/G) covered 2 percent. All other patch types each represented ≤2 percent of the land area (fig. 5). MOFEP study sites, except for site 7, were also dominated by upland forest. Shrub and early successional forest was underrepresented in the MOFEP sites (average = 3 percent) relative to the landscape (9 percent). Farmland, urban/non-vegetated areas, and water were not detected in any MOFEP study

Table 4.—*Elevation categories and codes used for intersection with cover types in Arc/Info GIS.*

Elevation range	Category
Meters	
≥0 - ≤150	1
>150 - ≤200	2
>200 - ≤250	3
>250 - ≤300	4
>300 - ≤350	5
>350	6

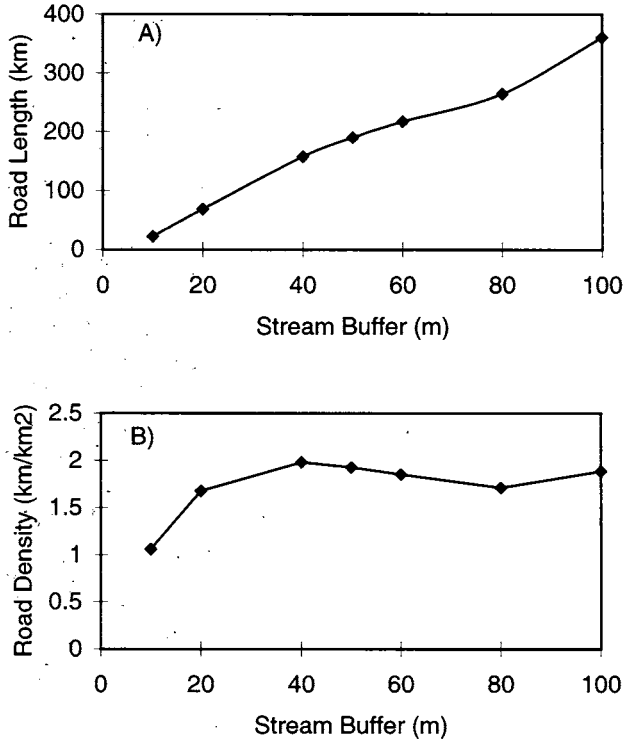

Figure 4.—*Total length (A) and density (B) of roads within stream buffers of different widths within the study landscape, southeastern Missouri.*

sites at this scale of analysis. In general, the study sites were less diverse than the landscape as a whole.

Most of the land area (99.1 percent) had a slope <40 percent; about 50 percent was between 10 and 25 percent slope, and 37 percent of the area was <10 percent slope (table 5). Only about 1 percent of the landscape was on slopes >40 percent. Upland forest dominated all slope categories and was the only patch type in slopes >100 percent (table 5, fig. 6A). About 48 percent of lowland forest and sparse forest was found on slopes <10 percent. The majority of farmland (83 percent) and urban areas (86 percent) were also located on slopes <10 percent. Patch types were more evenly distributed on flat ground where shrub and farmland became more common.

Land area was relatively evenly distributed among aspect categories, with a slightly larger amount (16 percent) of flat land (no aspect) than other categories (table 6). Upland forest dominated in all aspect categories (table 6, fig. 6B). Lowland forest was relatively more common in flat areas and on west-facing slopes. The area of sparse forest and partially cut patches was evenly distributed among aspect categories. Shrub area was more common than other patch types on slopes with an easterly aspect, though the majority of shrub area occurred on flat ground and west-facing slopes. Farmland and urban areas were relatively more common on flat ground and north to northeasterly slopes.

The majority of the landscape was <300 m in elevation (92 percent), with 40 percent of the area between 250 and 300m (table 7). Upland forest dominated all elevation categories except areas <150 m where water and urban land became relatively more common (fig. 6C). Eighty-six percent of urban areas were at elevations <250 m, with about 60 percent between 200 and 250 m. Ninety-nine percent of farmland was located at elevations <300 m and 96 percent of water was found at elevation <200 m. Larger proportions of sparse forest and shrub or early successional forest were found on land >350 m than within other elevation categories (fig. 6C).

Patch types had a similar prevalence within stream buffers and the landscape as a whole, except urban areas (and water), which were slightly more common in the stream buffers (compare fig. 7A to fig. 5). Upland forest was slightly less common in stream buffers than in the landscape. Roads were more closely associated with sparse forest and partially cut areas and farmland than would be expected based on a random road distribution (compare fig. 7B to fig. 5). Shrub and early successional forest was less common in road buffers than in the landscape. Shrub areas were relatively more prevalent in stream buffers than road buffers where farmland was more common. Sparse forest and partially cut areas appeared more common in road buffers than in stream buffers. Patch types were similarly distributed within road buffers between 20 and 100 m wide. However, sparse forest and farmland were more common in 10-m buffers than in wider buffers along roads. The distribution of patch types was similar among stream buffers of different widths, except for water, which was relatively more common in narrower stream buffers.

Only four patch types were detected at this scale in the MOFEP sites. All four had similar

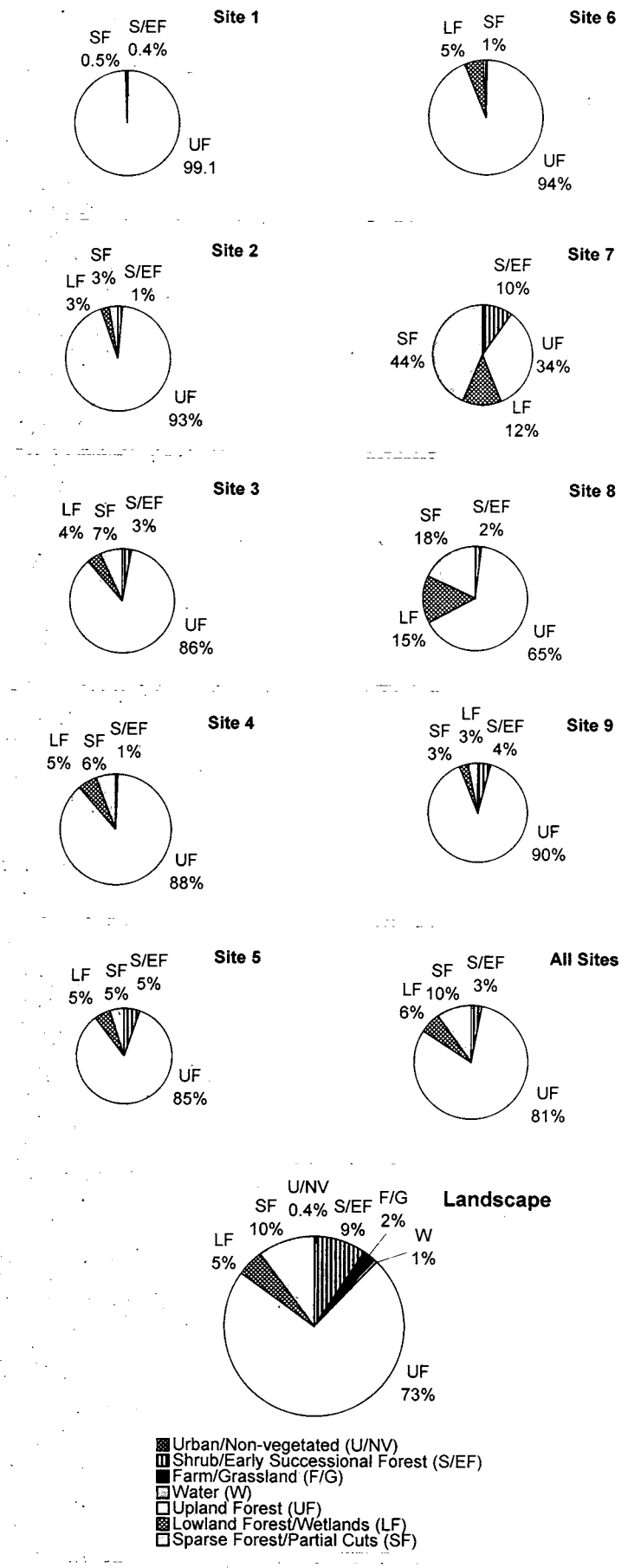

Figure 5.—*Distribution of patch types within the landscape and MOFEP study sites. See table 1 for patch types.*

Table 5.—*Area of each patch type within slope categories for the study landscape, southeastern Missouri.*

Patch type	Slope (percent)									
	>0 - ≤10	>10 - ≤25	>25 - ≤40	>40 - ≤55	>55 - ≤70	>70 - ≤85	>85 - ≤100	>100	Total	Percent
	Hectares									
Urban and non-vegetated	185	28	3	<1	0	0	0	0	215	0.4
Shrub and early successional forest	3,348	1,885	295	34	4	2	<1	0	5,566	9.2
Farmland and grasslands	1,037	207	8	3	0	0	0	0	1,254	2.1
Water	320	85	42	16	2	<1	0	0	465	0.8
Upland forest	13,393	24,340	5,995	300	24	6	1	2	44,061	72.6
Lowland forest and wetlands	1,437	1,266	248	40	10	1	0	0	3,000	4.9
Sparse forest and partial cuts	2,946	2,753	425	39	4	0	0	0	6,167	10.2
Total	22,665	30,562	7,014	432	43	9	2	2	60,728	
Percent	37.3	50.3	11.5	0.7	0.1	<0.1	<0.1	<0.1	100	

Table 6.—*Area of each patch type within aspect categories for the study landscape, southeastern Missouri.*

Patch type	Aspect (degrees)										
	Flat	N	NE	E	SE	S	SW	W	NW	Total	Percent
	Hectares										
Urban and non-vegetated	130	14	12	8	8	7	11	8	17	215	0.4
Shrub and early successional forest	1,555	416	628	745	748	467	333	294	380	5,566	9.2
Farmland and grasslands	544	87	129	116	106	79	49	59	86	1,254	2.1
Water	170	22	62	48	44	26	24	28	42	465	0.8
Upland forest	4,745	4,821	5,183	5,211	5,529	4,858	4,504	4,127	5,084	44,062	72.6
Lowland forest and wetlands	813	121	95	106	163	267	525	595	314	2,999	4.9
Sparse forest and partial cuts	1,501	443	434	470	644	752	804	585	533	6,166	10.2
Total	9,458	5,924	6,544	6,702	7,242	6,456	6,248	5,696	6,457	60,726	
Percent	15.6	9.8	10.8	11.0	11.9	10.6	10.3	9.4	10.6	100	

Table 7.—*Area of each patch type within elevation categories for the study landscape, southeastern Missouri.*

Patch type	Elevation (meters)							
	>0 - ≤150	>150 - ≤200	>200 - ≤250	>250 - ≤300	>300 - ≤350	>350	Total	Percent
	Hectares							
Urban and non-vegetated	17	39	128	22	8	0	215	0.4
Shrub and early successional forest	30	1343	2,454	1,366	278	89	5,561	9.2
Farmland and grasslands	7	293	776	145	7	0	1,228	2.0
Water	55	394	11	6	0	0	465	0.8
Upland forest	107	4,977	16,125	19,358	3,287	207	44,062	72.6
Lowland forest and wetlands	15	409	744	1,536	271	26	3,001	4.9
Sparse forest and partial cuts	37	1,417	2,252	2,017	337	106	6,167	10.2
Total	268	8,872	22,491	24,450	4,189	428	60,698	
Percent	0.4	14.6	37.0	40.3	6.9	0.7	100	

Table 8.—*Landscape metrics by cover type for MOFEP sites and the entire landscape, southeastern Missouri.*

	Patch type[1]	N	Mean fractal dimension	Mean patch size	Max patch size	Mean core area index	Total edge length	Edge density
				Ha	*Ha*	*Percent*	*Km*	*Km/km²*
MOFEP Study sites	S/EF	31	1.37	3.7	23.8	9.0	36.4	31.9
	UF	38	1.33	80.8	479.1	30.7	196.9	6.4
	LF	86	1.36	2.5	12.4	5.8	83.0	38.2
	SF	58	1.35	6.6	48.4	14.6	91.7	24.1
Landscape	U/NV	60	1.37	3.6	21.2	5.5	74.6	34.7
	S/EF	849	1.36	6.6	214.9	12.0	1,409.7	25.3
	F/G	159	1.35	7.9	81.7	17.2	283.9	22.6
	W	838	1.38	12.2	63.2	8.1	130.7	28.1
	UF	332	1.35	132.8	20,876.2	17.7	2,435.8	5.5
	LF	870	1.37	3.5	136.4	6.2	1,011.8	33.7
	SF	1068	1.36	5.8	178.5	11.5	1,614.1	26.1

[1] U/NV—urban and non-vegetated; S/EF—shrub and early successional forest; F/G—farmland and grasslands; W—water; UF—upland forest; LF—lowland forest and wetlands; SF—sparse forest and partial cuts.

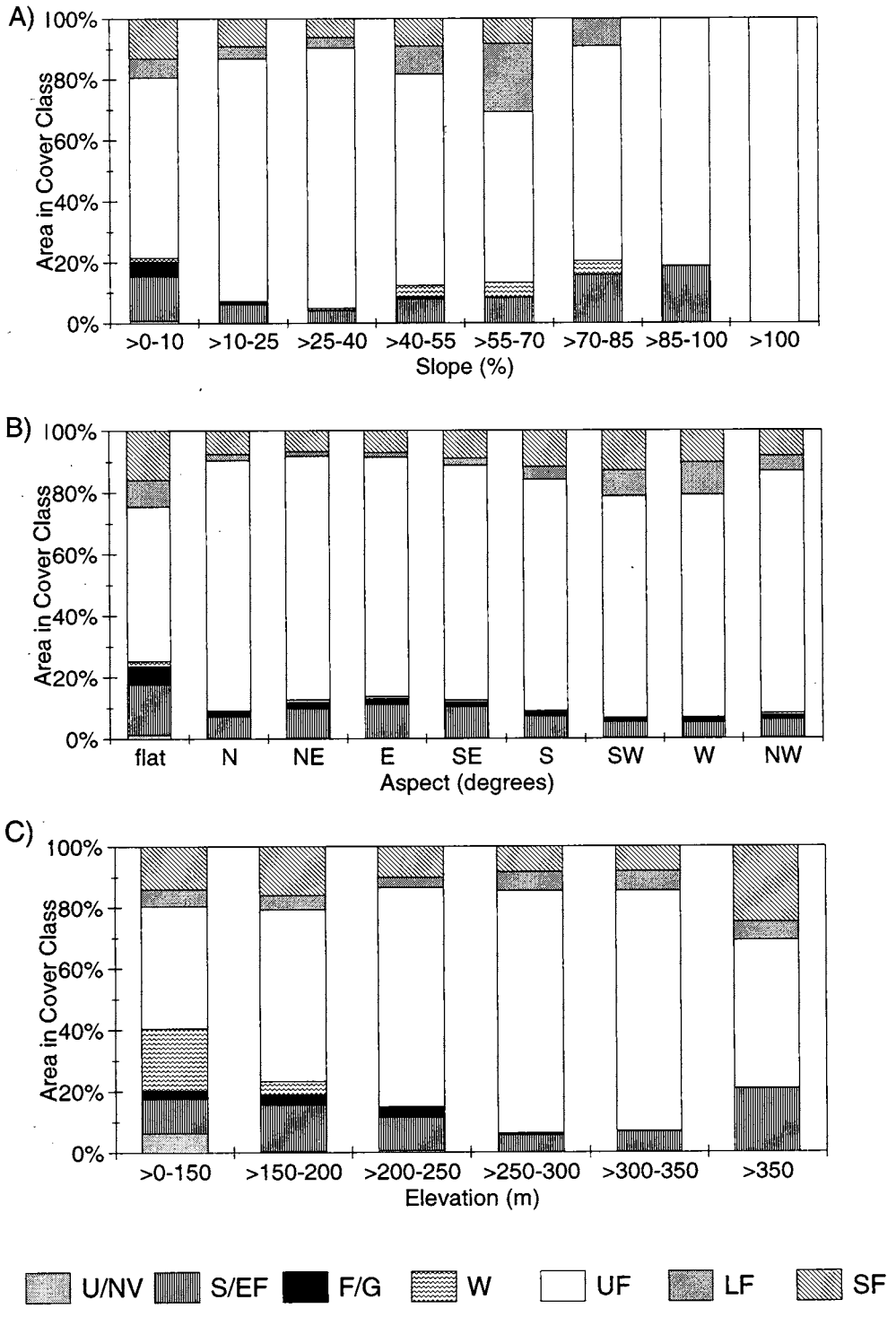

Figure 6.—*Distribution of patch types among: (A) slope categories, (B) aspect categories, and (C) elevation categories for the study landscape, southeastern Missouri. See table 1 for patch types.*

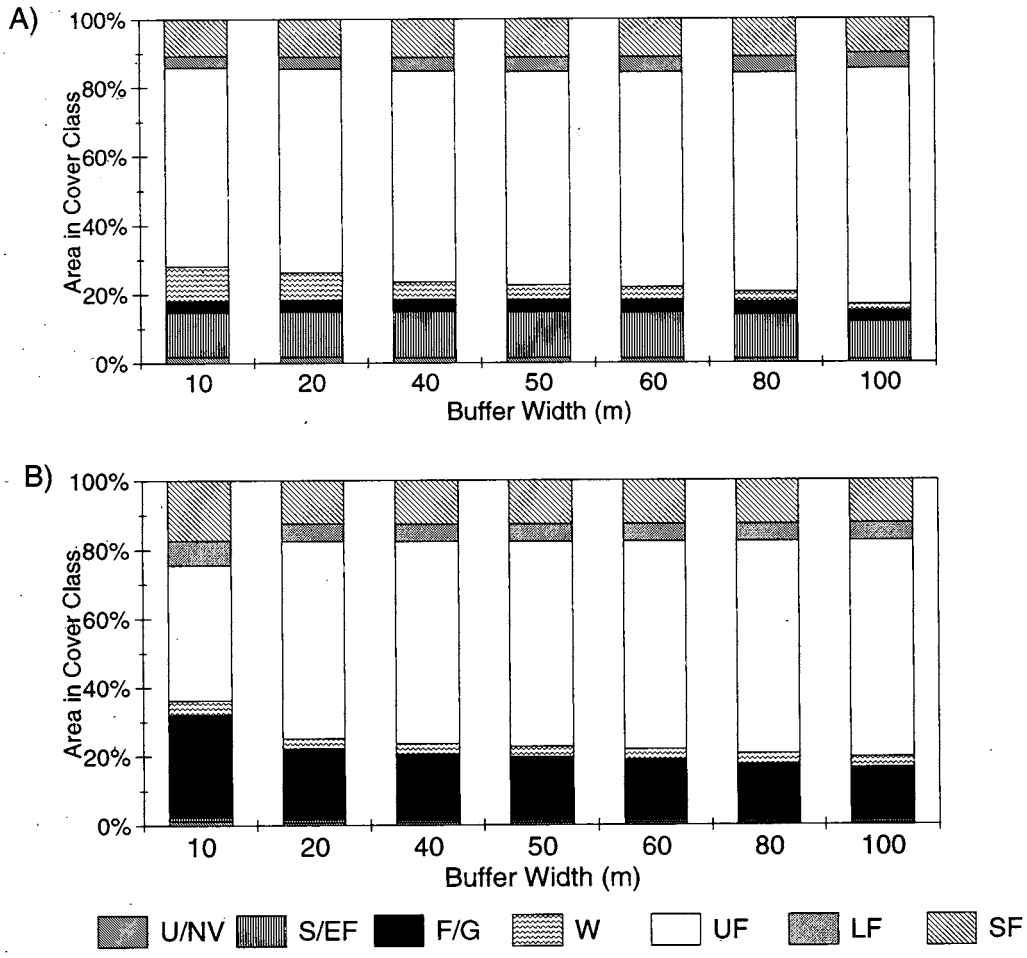

Figure 7.—*Distribution of patch types within stream buffers (A) and road buffers (B) across the study landscape, southeastern Missouri. See table 1 for patch types.*

shapes; mean fractal index ranged from 1.33 to 1.37 (table 8). The largest mean and maximum patch sizes were within upland forest, and the smallest mean and maximum patch sizes were found in lowland forest. Using an edge width of 40 m, we found that shrub, lowland forest, and sparse forest had an average of <15 percent of their patch areas in interior conditions (core area index (CAI), table 8). Upland forest had an average CAI of 31 percent. Edge density was highest for lowland forest (38.2 km/km^2) and lowest for upland forest (6.4 km/km^2), although total edge length was at least twice as great for upland forest than for other patch categories. Fractal dimension was similar among patch types across the landscape as a whole, and similar to values for the same patch types within MOFEP sites. For the landscape, mean patch sizes were highest in upland forest (133 ha) and lowest in lowland forest (3.5 ha). Mean patch sizes for upland forest, lowland forest, and shrub were about 1.6 times as large in the landscape than in the study sites, whereas mean patch size was smaller for sparse forest in the landscape than in MOFEP sites. Maximum patch sizes were greater within the landscape than within the MOFEP sites for all patch types. Farmland and upland forest had similar CAI's within the landscape (17.2 and 17.7 percent, respectively). Lowland forest had the lowest CAI (6.2 percent) and highest edge density (33.7 km/km^2) of any vegetated patch type on the landscape. Edge density in the upland forest (5.5 km/km^2) was much lower than in all other patch types. Values of core area index in the landscape were similar to those in the MOFEP sites, except for upland forest, which had a higher mean CAI in the study sites (31 percent) versus the landscape (18 percent). Edge densities were lower in the landscape as a whole than in the MOFEP study sites, except for sparse forest (table 8).

DISCUSSION AND CONCLUSIONS

The relatively widespread distribution of riparian areas indicates that a large portion of landscape may be contained within these ecotones and have distinct and diverse vegetation communities (Gregory *et al.* 1991, Naiman *et al.* 1993) and microclimate (Brosofske *et al.*, in press). Allowing for an edge effect of 100 m, up to 31 percent of the landscape could be considered riparian zone. These regions also support diverse wildlife communities (Stauffer and Best 1980). Avian species use riparian buffers as habitat for territories and as movement corridors. Individuals may rely more heavily on these residual habitats after harvesting. Machtans *et al.* (1996) found that buffers of 100 m within boreal, mixed-wood forest were able to support movement rates that had been recorded for undisturbed areas.

The importance of roads in creating additional structure within this landscape should be further evaluated. Roads in this landscape are often associated with patch types that are already dominated by humans, such as partially cut stands and farmland. However, given the small percentage of the region in farmland and cut areas, it is likely that road networks play a relatively greater role in fragmentation of the forests than do cutting or other human activities. Previous studies have shown that road density is a critical variable impacting wildlife populations, especially of large animals (Bennett 1991, Lyon 1983). These linear features may provide dispersal corridors for some species (Bennett 1991) but can contribute significantly to fragmentation of habitat and elimination of forest interior (Reed *et al.* 1996). More than one-quarter of this landscape could be considered road-influenced, given an edge effect of 100 m, suggesting widespread influence of this network on habitat availability, vegetation growth, microclimatic environment, and dispersal activity. In the Adirondack Mountain region of New York, black bear (Ursus americanus) density decreased rapidly with increase in road density, due to increased access to remote areas by hunters (Brocke *et al.* 1990). In forests of the Rocky Mountains, road densities of 1.6 km/km^2 reduced the amount of suitable habitat for large ungulates by one-half (Rost and Bailey 1979). We detected similar densities of 1.4 km/km^2 within the Ozark region, suggesting habitat loss for large vertebrates could be a concern here. This road network also represents a significant dispersal barrier for herpetofauna (e.g., van Gelder 1973). We observed that numerous animals (e.g., turtles and snakes) were killed by vehicles in our study areas during the summer, and the extreme microclimatic environment of roads (e.g., high surface temperature) also poses a threat. Road densities reached 1.9 km/km^2 within stream buffers where amphibians and reptiles are most likely to be affected.

Forested areas are represented to a greater degree in MOFEP study sites than in the landscape as a whole. If MOFEP researchers want to expand the applicability of their studies to larger landscapes, the higher diversity and pattern of patch types in the areas surrounding the MOFEP sites must also be considered (Larsen *et al.* 1997). Effects of silvicultural treatments within the study sites must also be considered at the landscape scale. Spatial and temporal distributions of harvested areas may have long-term consequences for landscape-level structure (Wallin *et al.* 1994). Managers should further consider the impact of the variation in landscape cover among the MOFEP study sites when comparing results of study treatments.

Slope, aspect, and elevation influence plant diversity and regional vegetation distributions through their effects on insulation, temperature, moisture, and nutrient gradients (Swanson *et al.* 1988, Zobel *et al.* 1976). Our results suggest that, although the relative coverage of patch types is similar across aspect categories, slope and elevation play important roles in determining distributions of patch types. Note that our elevation data were derived from sources with different contour intervals. This may introduce additional error into the assessment of topographical influences on patch distribution. However, managers should consider the spatial distribution of harvest with respect to these variables, because management practices may differentially influence regeneration of community types and the long-term dynamics of landscape structure.

Characterization of the heterogeneity of structure within landscapes should elucidate the interrelationships between landscape structure and function. On average, using an edge width of 40 m, we found that less than 20 percent of a patch's area was in core habitat for any patch type within MOFEP study sites (except for upland forest) or the regional landscape. The low amount of core area within patches of bare

ground should minimize influences of extreme microclimate that can occur in these areas on the environment in the surrounding landscape. However, with this classification, about four-fifths of the area of all patches within this region were affected by neighboring patches to some degree. For the largest forested patches within the study sites, this would result in a core area of 383.3 ha of upland and 9.9 ha of lowland forest. This is a generous estimate of core area based on an edge width of only 40 m. Many abiotic variables do not exhibit interior values until >100m from a forest edge (Chen *et al.* 1995). Some species that are dependent on interior habitat may be limited by low or fluctuating area of interior habitat (e.g., Glenn and Nudds 1989, Whitcomb *et al.* 1981) although edge species may benefit from the high proportion of ecotones. Note however that lowland, upland, and sparsely forested areas are often adjacent (fig. 2) and the boundaries between these patch types are softer than between other patch types on the landscape. Therefore, if we classified the landscape as forest versus non-forest, average core area of forested patches would increase and the total boundary length would decrease. Evaluation of available edge or interior environments should be conducted with specific ecological questions or species in mind.

The classification of patch types and analysis of landscape structure in this study were based on information from a single point in time. However, we recognize that, at some scales, ecological processes and landscape structure are changing continuously. Although this limits conclusions that can currently be drawn about pattern dynamics, our results provide a reference with which to compare measurements of landscape structure in the future and better evaluate results of other MOFEP studies.

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Landforms, Geology, and Soils of the MOFEP Study Area

Dennis Meinert[1], Tim Nigh[2], and John Kabrick[3]

Abstract.—We summarize important landform, geological, and soil characteristics that affect the distribution of plants and animals at the MOFEP sites and that can potentially affect the observed response to MOFEP experimental treatments. The Missouri Ozark Forest Ecosystem Project (MOFEP) is located within the Current River Hills Subsection of the Ozark Highlands Section. The Ozark Highlands is an assemblage of nearly level to deeply dissected plateaus comprised primarily of Ordovician dolomites or sandstones. Soils are formed primarily in loess, hillslope sediments, and/or residuum. Natural vegetation consists of oak-hickory and oak-pine forests and woodlands, oak savanna, bluestem prairie, and glades. The Current River Hills Subsection encompasses moderately rolling to steeply dissected hills; oak-hickory and oak-pine forests are common. MOFEP occurs in the Current-Black River Breaks (Breaks) and Current-Eleven Point Hills (Hills) Landtype Associations (LTA's). The Breaks LTA has greater relief, more geological strata, greater variety of soils, and more mesic vegetation and glade-savanna complexes than the Hills LTA. Detailed landform, geology, and soil information for each LTA provides a means for (1) interpreting vegetation differences, (2) identifying potential treatment response differences among MOFEP sites, and (3) refining ecological landtype definitions applied during MOFEP initiation.

Landforms, geological parent materials, and soils largely control the distribution of water, nutrients, and sunlight in the landscape. This ultimately influences plant and animal distributions and their responses to land management. A thorough understanding of landforms, geology, and soils is critical for interpreting and integrating results of many studies of the Missouri Ozark Forest Ecosystem Project (MOFEP).

In this paper, we summarize important landform, geological, and soil characteristics potentially affecting plant and animal distributions and responses to cultural treatments implemented in the MOFEP study area. We do this using the USDA Forest Service - Ecological Classification System (ECS) framework (USDA Forest Service 1993). Under this framework, attributes of climate, landform, geology, vegetation, and soil are used at various scales to divide the Earth's surface into progressively finer ecological units. The influence of each of these attributes varies, depending upon the scale of application.

The hierarchical nature of the ECS framework is illustrated in table 1. Broad-scale ecoregions and subregions provide a general ecological context for MOFEP based on regional patterns in climate, geomorphology, soil, and vegetation. Landforms, geology, and associated soils play especially important roles in defining the lower, "working levels" in the classification: landtype associations, ecological landtypes, and ecological landtype phases. These finer scale classification levels are key to understanding patterns in environmental characteristics within and between MOFEP study sites.

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Table 1.—*National hierarchical framework for ecological classification (USDA-FS 1993) and application to MOEFEP.*

Scale	Ecological units	Map scales	Major differentiating criteria	MOFEP types
ECOREGION	Domain Division Province	1:30 Million to 1:100 Million	Continental and regional climate zones Broad soil and vegetation lifeform patterns	Humid temperature domain (2) Hot continental division (22) Moderately humid broadleaf forest province (222)
SUBREGION	Section Subsection	1:1 Million to 1:125,000	Regional and subregional ppt. and temp. Geomorphology Major soil great groups Potential vegetation formations	Ozark Highlands Section (222A) Current River Hills Subsection (222 Af)
LANDSCAPE	Landtype Association (LTA)	1:100,000	Local climate Landform/topography Geologic parent materials Soil associations Potential vegetation alliances	Current-Black River Breaks LTA Current-Eleven Point Hills LTA
LAND UNIT	Landtype (ELT) Landtype Phase (ELT-P)	1:24,000	Landform/topographic position Geologic parent material Soil series Potential vegetation association	To be developed

We begin by providing a broad ecological context for the MOFEP study sites using Forest Service ecological sections and subsections (Bailey 1980, Keys *et al.* 1995, McNab and Avers 1994). Next, we describe the landscapes (landtype associations) that encompass MOFEP (Nigh 1997). We then summarize important landform, geology, and soil characteristics that distinguish MOFEP sites and land units within sites based upon an intensive soil investigation conducted on MOFEP sites (Meinert 1997). Finally, we provide insights of how this and future work may lead to further development of finer scale ecological units (ELT's).

SECTION, SUBSECTION, AND LANDTYPE ASSOCIATIONS OF THE MOFEP STUDY AREA

Ozark Highlands Section

The MOFEP study area is located in the Ozark Highlands Section (fig. 1) (McNab *et al.* 1995). The Ozark Highlands is an assemblage of maturely dissected, high plateaus, where millennia of erosion have created a region of variable topography and relief. High, flat to gently rolling plateau remnants are dissected by dendritic and radial drainages. Crystal clear, spring-fed streams have cut deeply into the plateaus, forming a region of steep to moderately rolling hills with local relief mainly 200 to 500 ft (60 to 150 m), but occasionally up to 1,000 ft (300 m). Karst features, including caves, springs, and sinkholes, are common.

Bedrock stratigraphy is dominated by Ordovician dolomites and sandstones. Silurian, Devonian, Mississippian, and Pennsylvanian bedrock (limestone, chert, sandstone, shale) are less frequent and concentrated around the section's margins. Precambrian rhyolite, andesite, granite, and gabbro occur in the eastern part of the section, forming the highest hills.

Quaternary loess deposits are common on the uplands with thin layers on stable landforms overlying hillslope sediments and/or residuum. On steep or unstable landforms, loess has been eroded or incorporated locally into hillslope sediments. Valley bottoms contain Quaternary gravel, sand, silt, and clay alluvium.

Soils are formed primarily in loess, hillslope sediments, residuum, or gravelly alluvial parent materials. Most soils in the section are highly weathered Ultisols and Alfisols with mesic temperature and humid moisture regimes (USDA 1975). Soils range from shallow unconsolidated materials over bedrock to very deep,

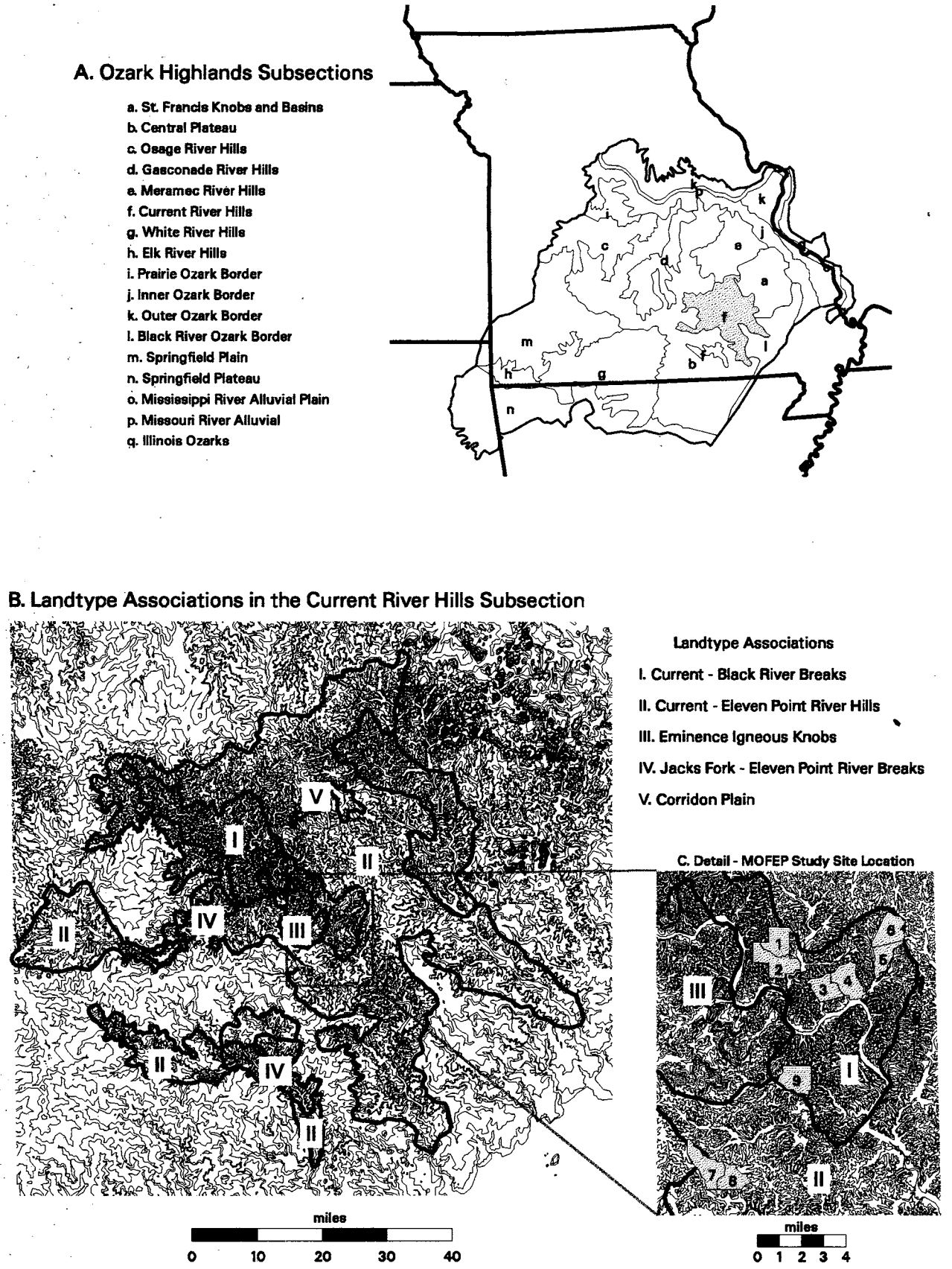


Figure 1.—*MOFEP study sites and ecological units.*

highly weathered soils in hillslope sediments and residuum. Bedrock outcrops and fragipans are common in many soils of the section.

The natural vegetation of the Ozark Highlands consists mainly of oak-hickory and oak-shortleaf pine forests and woodlands, oak savanna, bluestem prairie, and glades. Bottomland and mixed upland hardwood forests occur in large valleys and adjacent sideslopes. Forest and woodlands were originally common where topography was steeper, while savannas and prairies were common on higher, more gently sloping lands.

Current River Hills Subsection

The Ozarks Highlands Section has been divided into 17 ecological subsections (Keys *et al.* 1995), based mainly on variations in relief, geologic parent materials, soils, and vegetation pattern (fig. 1). The MOFEP study area is located in the center of the Current River Hills Subsection. This subsection encompasses the moderately rolling to steeply dissected hills associated with the Current, Eleven Point, and Black Rivers in the eastern Missouri Ozarks. Here, broad to narrow ridges give way to moderate and steeply sloping sideslopes and narrow, sinuous valley bottoms. Local relief ranges from 150 to over 400 ft (50 to 130 m). High, sheer, rock cliffs are common along the rivers.

Bedrock stratigraphy is dominated by Ordovician cherty sandstone and dolomites from the Roubidoux and Gasconade formations. Areas of Cambrian dolomite from the Eminence and Potosi formations occur nearer the Current and Black Rivers. A relatively small area of Precambrian igneous knobs occurs in the center of the Current River Valley.

Thin layers of Quaternary loess deposits are common on flatter, more stable landforms in this subsection. Most of the landscape is mantled in deeply weathered residual materials and hillslope sediments. Valley bottoms have Quaternary alluvium.

Soils in the region have not been extensively inventoried or studied. They appear to be typical of the hilly subsections of the Ozarks, with deeply weathered Ultisols and Alfisols, interspersed with soils that are shallow to bedrock, contain fragipans, or have formed in alluvium.

The Current River Hills Subsection is located in the center of the largest, contiguous block of forest in the Ozark Highlands, and one of the largest in the Midwestern United States. Oak-hickory and oak-shortleaf pine forests dominate the landscape. Local areas of oak and oak-pine woodlands and savannas occur on shallower soils and exposed slopes. Occasional glades occur on sideslopes, especially near the rivers. Bottomland and upland mixed hardwood forests occur along the streams and adjacent slopes. Cleared pastureland is only a minor component of the subsection and is associated with richer bottomland soils.

Landtype Associations in the Current River Hills Subsection

The Current River Hills Subsection has been divided into five landtype associations (LTA's) based on variations in landform, relief, geologic parent materials, soils, and vegetation patterns (fig. 1) (Nigh 1996).

Two of the LTA's are relatively small, but distinctive. The Corridon Plain is a high, flat to gently rolling divide between the Current and Black River Valleys. This flat plain, covered in a thin layer of loess, underlain by Roubidoux sandstone, historically supported shortleaf pine forest and woodland. Today, it is covered in pasture and second-growth pine-oak forest. The Eminence Igneous Knobs LTA contains an isolated series of Precambrian igneous knobs characterized by unique igneous glades, woodlands, and forests.

The remainder of the subsection is divided into three LTA's: Current-Black River Breaks, Jacks Fork-Eleven Point River Breaks, and Current-Eleven Point River Hills. The two Breaks LTA's are characterized by narrow ridges and steep sideslopes with 300 to 450 ft (90 to 140 m) local relief, narrow sinuous valleys, and common cliffs, caves, and springs; all are associated with the steepest, most dissected lands near the rivers. The two Breaks LTA's are distinguished based on geologic parent materials and corresponding soil and vegetation patterns. The Current-Black River Breaks LTA cuts into Eminence and Potosi dolomites, which add distinctive landforms, soil, and vegetation patterns not found on the Jacks Fork-Eleven Point Breaks. The Current-Eleven Point River Hills LTA makes up the rest of the matrix of this subsection. It consists of broad to narrow ridges and moderately steep sideslopes with

local relief less than 300 ft (90 m). Valleys are generally broader and less sinuous than in the Breaks. The Roubidoux and Gasconade formations make up most of the geologic parent materials. The Hills LTA is covered mainly by forests of shortleaf pine and oak, with occasional glade and woodland openings. Approximately 15 percent of the Current-Eleven Point River Hills is open pasture, associated with richer bottomland soils.

The MOFEP study sites occur in two of these LTA's - the Current-Black River Breaks and the Current-Eleven Point River Hills. Detailed mapping of the landforms, geology and soil patterns of the MOFEP sites provides the basis for more detailed characterization of the physical features at the MOFEP sites and a better understanding of the potential impacts of physical characteristics on MOFEP treatment response.

CHARACTERIZING LANDFORMS, GEOLOGY, AND SOILS OF THE MOFEP STUDY AREA

Integrated Soil Mapping—Geo-landform Approach

A detailed soil investigation and mapping project was initiated at the MOFEP sites in July 1994. Soil investigation and mapping techniques used differed from those of the National Cooperative Soil Survey. First, the hierarchical framework of the ECS was used to explicitly and systematically stratify the landscape by geology and landform before the detailed soil mapping was conducted. Second, mapping was done at a larger scale (1:12,000) than the National Cooperative Soil Survey scales (1:>15,840). Third, *Soil Taxonomy* (USDA 1975), the national soil classification system, was not used to set soil property boundaries for map units. A detailed report with soil maps, map unit descriptions, and MOFEP study site descriptions resulted from this effort (Meinert, In prep.). This section is a synthesis of the soil and geo-landform relationships identified in the more detailed report.

The soil mapping process consisted of two phases. The first "phase" identified key geological strata, landforms, and slope classes within landforms (collectively referred to as "geo-landform") potentially affecting soil distributions. The second phase identified the range and distribution of important soil properties within each geo-landform to delineate map units with meaningful implications for use and management.

Soil descriptions were made at each of the 648 MOFEP vegetation plots (Brookshire *et al.* 1997). Additional soil borings were made where necessary for identifying map units. Important soil properties that distinguished map units were: depth to bedrock, water holding capacity, drainage class, texture and mineralogical character of horizons, and depth to residual clays. Map unit delineations were made on 1:12,000 scale aerial photographs in the field. This photographic base allowed finer resolution than standard 1:15,840 scale aerial photographs used for the National Cooperative Soil Survey; map units as small as 0.1 acre were delineated.

Laboratory soil information was determined for most soil map units. One to four backhoe excavations were made in each major soil map unit. Soils were described, sampled by horizon, and samples were sent to the University of Missouri Soil Characterization Laboratory. Laboratory analyses included: particle size distribution, extractable acidity, extractable aluminum, extractable bases, cation exchange capacity, base saturation, organic carbon content, and pH.

Landforms, Geology, and Soils of the MOFEP Study Area

The 12 landforms used in the MOFEP soils investigation are defined in table 2. Definitions generally follow Ruhe (1960, 1975), but they have been refined for the MOFEP study area.

Landforms are important because they locally affect water flow, soil parent material movement, and consequently, soil development. Landform positions relatively high in elevation (e.g., summits, shoulders, shoulder ridges, upper backslopes) are sources of subsurface water, nutrients, and eroded sediment that collects in lower landform positions (e.g., lower backslopes, footslopes). In addition, the shape of a landform (linear, convex, or concave) influences the degree and type of water and sediment movement. Convex landforms normally lose surface water and sediment, concave landforms gain surface water/sediment, and linear landforms are neutral. For example, sinkholes occurring on summit landform positions are concave and accumulate eroded silty sediments from slightly higher elevations around them. Shoulders and shoulder ridges are convex areas high in the landscape that tend to lose both surface water and sediments

Table 2.—*Landforms in the MOFEP study region.*

Alluvial Fan — A low, outspread mass of loose materials and/or rock material, commonly with gentle slopes, shaped like an open fan or a segment of a cone, deposited by a stream at the junction of a narrow drain with a higher order drain.

Backslope — The landscape position that forms the steepest inclined surface and principal element of many hillslopes. Slope (>20 percent) contains sideslope, noseslope, and headslope components.

Flood Plain — The nearly level plain that borders a stream and is subject to inundation under floodstage conditions. Slopes 0-4 percent.

Footslope — The landscape position that forms the inner, inclined surface at the base of a hillslope. It is a transition zone, commonly concave in profile. Slopes 0-20 percent.

Shoulder — The landscape position that forms the uppermost inclined surface near the top of a hillslope. It is commonly convex in shape and comprises the transition from summit to backslope. Slopes 8-20 percent.

Shoulder Ridge — A long, narrow elevation of the land surface, usually sharp crested and convex with steep sides, and forming an extended upland between valleys. Slopes 8-20 percent.

Sinkhole — A closed depression formed either by solution of the surficial bedrock or by collapse of underlying caves.

Strath Terrace — Erosional surfaces cut into bedrock and thinly mantled with stream deposits.

Structural Bench — A platform-like, nearly level to gently inclined erosional surface developed on resistant strata in areas surrounded by otherwise sloping land surfaces.

Summit — The topographically highest hillslope position of a hillslope profile and exhibiting a nearly level surface. Slopes 0-8 percent.

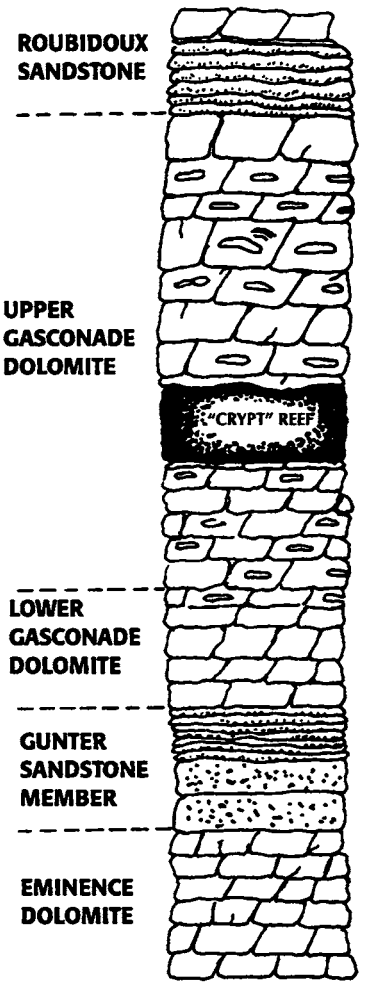
Terrace — One of a series of platforms in a stream valley, flanking and more or less parallel to the stream channel, originally formed near the level of the stream, and representing the dissected remnants of an abandoned flood plain, stream bed, or valley floor produced during a former state of erosion or deposition.

Upland Drainages — Narrow, sloping (>8 percent) concave-shaped waterways, which carry intermittent flows of water during rain events.

to backslopes below. Upland drainages, terraces, and floodplains are relatively low in the landscape and are domains of sediment accumulation and transport, primarily by water.

Roubidoux, Upper and Lower Gasconade, and Eminence are the dominant geologic formations within the MOFEP study area (fig. 2). The compositon of these strata influences the character of the soil parent materials across the site. Strata within these formations strongly affect hillslope sediment textures. Sandier hillslope sediment textures are associated with sandstone in the Roubidoux formation and with the Gunter member of the Lower Gasconade formation. While most strata yield very cherty residual materials, the degree of stoniness varies somewhat between strata. The Lower Gasconade and Eminence formations, for example, are relatively chert-free compared to

Figure 2.—*Bedrock stratigraphy in MOFEP region.*



Description

Interbedded sandstone, silicified sandstone, sandy dolomite, cherty dolomite and silicified stromatolite algal and chert beds.

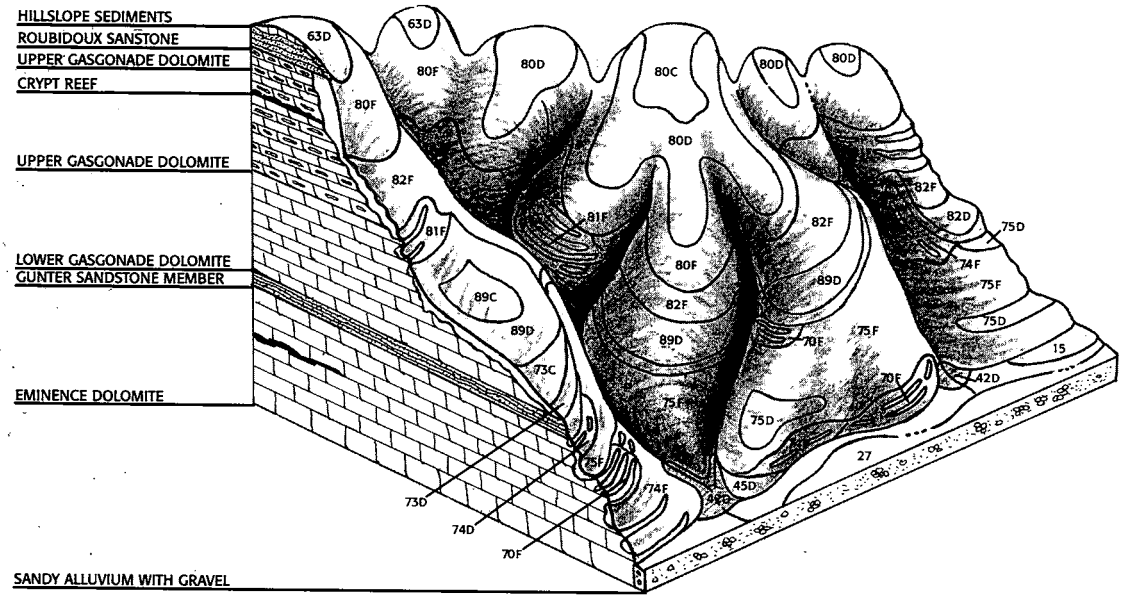
Thick beds of dolomites and cherty dolomites dominate; coarsely crystalline with high percentages of chert; layers of silicified stromatolites are interspersed.

Finely crystalline dolomite with infrequent chert nodules.

5-15' thick beds of sandstone and quartzose.

Medium to thick beds of dolomite with small amounts of chert; medium to coarsely crystaline; beds of chert ranging from 4-6" thick occur in some areas.

Current-Black River Oak-Hickory Forest Breaks LTA

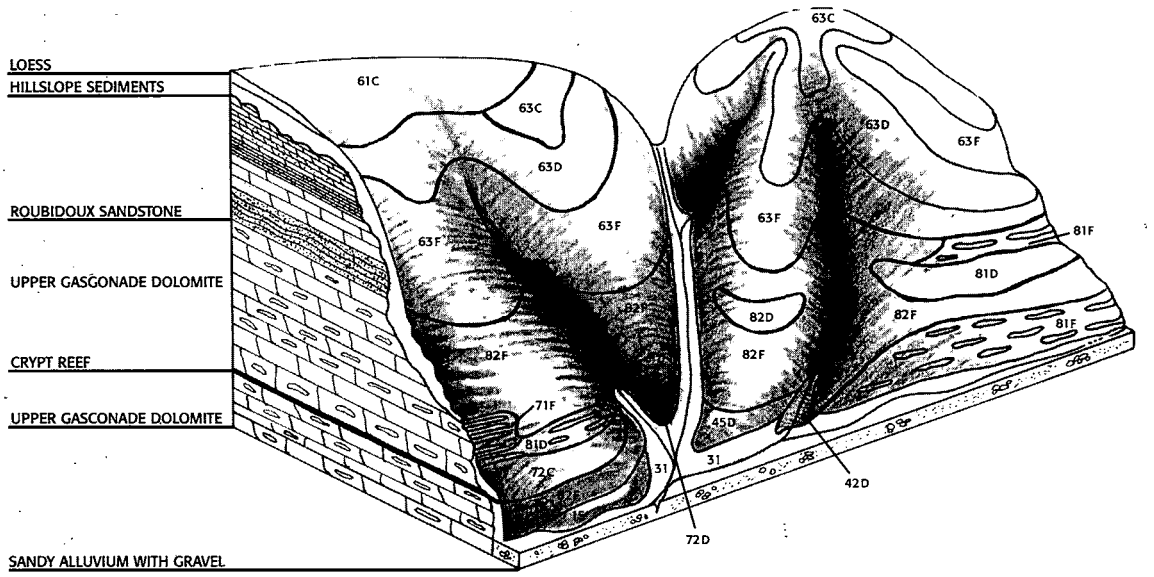


GEOLOGY	LANDFORM	SOIL CHARACTERISTICS	MAP UNIT
Roubidoux	Summits	Very deep soil with fragipan at 20 to 26"; moderately well to well drained; fine-loamy; low base saturation.	61C
	Summits	Moderately to very deep soil with intermittent fragipan; moderately well to well drained; loamy-skeletal/clayey and loamy-skeletal; low base saturation.	63C
	Shoulder/Shoulder Ridges	Moderately to very deep soil with intermittent fragipan; moderately well to well drained; loamy-skeletal/clayey and loamy-skeletal; low base saturation.	63D
	Backslopes	Moderately to very deep soil with intermittent fragipan; moderately well to well drained; loamy-skeletal/clayey and loamy-skeletal; low base saturation.	63F
Upper Gasconade	Summits	Very deep soil with fragipan at 20 to 26"; moderately well drained; fine-loamy; low base saturation.	61C
	Summits	Very deep soil with intermittent fragipans; moderately well to well drained; loamy-skeletal/clayey and loamy-skeletal; low base saturation.	80C
	Shoulder/Shoulder Ridges	Very deep soil with intermittent fragipans; moderately well to well drained; loamy-skeletal/clayey and loamy-skeletal; low base saturation.	80D
	Backslopes	Very deep soil with few intermittent fragipans on lower side slopes; well drained; loamy-skeletal and loamy-skeletal/clayey; low base saturation.	80F
	Benches (Cryp Reef)	Very deep soil with intermittent fragipans at 20 to 40"; moderately well drained; fine-loamy; low to medium base saturation.	72C, 72D
Lower Gasconade (Van Buren)	Shoulder Ridges	Shallow soils, well drained; loamy-skeletal; high base saturation; >50% rock outcrop.	71D
	Shoulder Ridges	Shallow to moderately deep soils; moderately well to well drained; very fine; high base saturation; 10 to 50% rock outcrop.	81D
	Shoulder Ridges	Deep to very deep soils; well drained; loamy-skeletal/clayey and loamy skeletal; low to high base saturation.	82D
	Backslopes	Shallow soils, well drained; loamy-skeletal; high base saturation; >50% rock outcrop.	71F
	Backslopes	Shallow to moderately deep soils; moderately well to well drained; very fine; high base saturation; 10 to 50% rock outcrop.	81F
	Backslopes	Deep to very deep soils; well drained; loamy-skeletal/clayey and loamy skeletal; low to high base saturation.	82F

Figure 3.—*Integrated Soil Map Units on the MOFEP Sites (Meinert 1997).*

Figure 3.—Continued

Current-Eleven Point River Hills LTA



GEOLOGY	LANDFORM	SOIL CHARACTERISTICS	MAP UNIT
Lower Gasconade (Continued)	Benches	Deep to very deep; moderately well drained; loamy-skeletal/clayey and very-fine; low to high base saturation.	89C
	Benches	Deep to very deep; moderately well drained; loamy-skeletal/clayey and very-fine; low to high base saturation.	89D
	Benches	Very deep soils with intermittent fragipans at 20 to 40"; moderately well drained, fine-loamy; low to medium base saturation.	73C
	Benches	Very deep soils with intermittent fragipans at 20 to 40"; moderately well drained; loamy skeletal and loamy-skeletal/clayey; low to medium base saturation.	73D
Eminence/ Gunter	Shoulder Ridges	Shallow soils; well drained; very fine; high bases; >50% rock outcrop.	70D
	Shoulder Ridges	Shallow to deep soils; well drained; very fine; high base saturation; 10 to 50% rock outcrops.	74D
	Shoulder Ridges	Deep to very deep soils; well drained; loamy skeletal/clayey and loamy skeletal; medium to high base saturation.	75D
	Backslopes	Shallow soils; well drained; loamy skeletal; high bases; >50% rock outcrop.	70F
	Backslopes	Shallow soils; well drained; very fine; high base saturation; 10 to 50% rock outcrop.	74F
	Backslopes	Deep to very deep soils; well drained; loamy skeletal/clayey and loamy skeletal; medium to high base saturation.	75F
Hillslope Sediments	Footslopes	Very deep soils; moderately well drained and well drained; fine-loamy; low base saturation.	45D
Alluvium	Upland Drainage	Very deep soils; well drained; loamy-skeletal; medium base saturation.	27
	Strath Terraces	Very deep soils; moderately well drained; fine-loamy; low to medium base saturation.	41D
	Terraces	Very deep soil; well drained; fine-loamy to loamy-skeletal; low to medium base saturation.	15
	Terraces	Very deep soils; somewhat excessively drained; loamy-skeletal; coarse-loamy; low to medium base saturation.	18
	Alluvial Fans	Very deep soils; well drained; loamy-skeletal; low to medium base saturation.	42D
	Floodplains	Very deep soils; excessively well drained; loamy-skeletal and coarse-loamy; low to medium base saturation.	31

the other strata. Residuum from dolomites in these formations is chert-free compared to the other strata. Residuum from dolomites in these formations is clayey, but the depth to clay and clay mineralogy vary with parent material and landform.

Strata within these formations also affect landform shape or occurrence in the MOFEP study region. Midslope structural benches in the Current-Black River Breaks LTA occur primarily on the Gunter sandstone member of the Lower Gasconade formation. Gunter sandstones are more resistant to weathering than the surrounding strata. The Cryptozoan reef chert bed of the Upper Gasconade formation controls the occurrence of structural benches when located in mid slope and low slope positions, and it controls the elevation of summits and ridges when located in high slope positions. Sinkholes are most common in the Roubidoux formation and form as underlying Upper Gasconade dolomites partially dissolve and collapse.

The landforms and geologic strata used to hierarchically and systematically stratify the landscape, as well as important soil characteristics and map units, are summarized in figure 3. Forty-three map units were developed for the MOFEP study area, but only common units are illustrated in figure 3. There was considerable variation in soil depths, fragipan occurrence, drainage class, soil family level classification, base saturation, and degree of rock outcropping within each geo-landform. Several soil map units within each geo-landform were created to accommodate some of this variation (fig. 3). However, considerable soil variation occurs *within* soil map units and is described in the soil mapping report (Meinert 1997).

Despite the degree of variation in soil properties, some meaningful generalizations can be drawn. Soils of Roubidoux and Upper Gasconade summits, shoulders, and backslopes are typically very deep cherty silt loams with few rock outcrops, intermittent fragipans, and low base saturation; many of these soils are classified as Ultisols. In contrast, while soils of Lower Gasconade and Eminence shoulder ridges, backslopes, and benches are mainly deep, they have higher base saturation, more variable in depths, and many rock outcrops. Most soils in these geo-landforms are classified as Alfisols. Flat summit and bench landforms often have deep soils with a silty surface horizon and frequent fragipans. Alluvial soils on upland drainages, terraces, and floodplains are deep, coarse-textured, and have medium base saturation (fig. 3).

Patterns in Landform, Geology, and Soil of Landtype Associations and MOFEP Sites

As pointed out earlier, MOFEP sites occur within two distinct Landtype Associations (LTA's): the Current-Black River Breaks LTA (sites 1-6, and 9) and the Current-Eleven Point River Hills LTA (sites 7 and 8). Soil mapping efforts revealed distinctive patterns in landform, geology, and soils between these LTA's and consequently, between MOFEP sites. These patterns are illustrated in figure 3 and are summarized below.

MOFEP sites 1-6, and 9 are in the Current-Black River Breaks LTA. This LTA is characterized by down cutting into bedrock, largely due to proximity to the Current River. Local relief is 300 to 450 ft (90 to 140 m). The Roubidoux formation is restricted to the highest summits, ridges, and backslopes; the Upper and Lower Gasconade formations make up most of the backslopes; and the Eminence formation materials commonly make up the lower backslope. Quaternary loess deposits are confined mainly to isolated summits or broad benches. Narrow, undulating ridges, steep backslopes, and narrow sinuous valleys are typical of landforms in the Current-Black River Breaks LTA. In addition, structural benches supported by the Gunter sandstone are common in midslope positions. Relatively narrow, alluvial floodplains have Quaternary alluvial deposits, consisting of gravel, sand, and to a lesser degree silts. While water-losing stretches of stream are common in the Roubidoux and Upper Gasconade stream reaches, water-gaining streams are common in the Lower Gasconade and Eminence materials.

Deep, loamy-skeletal soils with low base saturation (fig. 3; map units 63,80) formed in Roubidoux and Upper Gasconade residual materials dominate the ridges and upper backslopes in the Current-Black River Breaks LTA. Higher base saturation soils (Alfisols), with clays nearer the surface (fig. 3; map units 82,89,75) are associated with the Lower Gasconade and Eminence landforms. Variable depth, relatively shallow soils with bedrock outcrops (fig. 3; map units 70,71,74,81) occur frequently within the Current-Black River

Breaks LTA, especially in association with the Lower Gasconade and Eminence formations. The Gunter bench has mainly deep, high base saturation soils just below the backslope (fig. 3; map unit 89) and deep, highly weathered, low base saturation soils formed in loess and residuum on its broader, flatter positions (fig. 3; map unit 73). Footslopes, terraces, and bottoms commonly have very deep, colluvial and alluvial soils with texture, drainage, and base saturation varying with parent material (fig. 3; map units 42,45,15,27,18,31,41).

Sites 7 and 8 occur within the Current-Eleven Point River Hills LTA, which is characterized by more gentle relief (150 to 250 ft [45 to 75 m]) and less geologic complexity than the Breaks. The Roubidoux and Upper Gasconade formations make up all of the Hills landscape. Broad, flat ridges are commonly mantled in Quaternary loess deposits. Narrower ridges and upper backslopes are mainly in very deep, highly weathered Roubidoux materials, while middle and lower backslopes are in Upper Gasconade materials. Slopes are more gentle and valley bottoms are wider and less sinuous than in the Breaks. The Cryptozoan Reef forms less prominent structural benches on the lower slopes or occurs across valley bottoms in this LTA. Most stream reaches are water-losing.

There are fewer soil map units in the Hills than in the Breaks. Deep, skeletal, cherty silt loams confined to the highest parts of the Breaks (map unit 63), make up a majority of the soils in the Hills. Sandier textures, associated with the Roubidoux formation, occur. Broad summits, only rarely found in the Breaks, commonly have a silt cap with deep, loamy, ultic soils and fragipans (fig. 3; map unit 61). Deep, higher base soils (fig. 3; map units 82,89) do occur in the Gasconade portion of the landscape. Soils on the Cryptozoan reef benches are very deep, loamy skeletal with occasional fragipans (fig. 3; map unit 72). Variable depth soils with frequent bedrock outcrops (fig. 3; map units 71,81) are less common in the Hills LTA, but are associated with the Upper Gasconade formation.

Vegetation Patterns for Landtype Associations and MOFEP Sites

Both the Hills and Breaks LTA's are largely forested in oak and oak-pine timber types. The composition and structure vary with landscape position and soil-geo-landform environment. Some of these relationships are described in other papers in this volume (Kabrick *et al.* 1997, Grabner *et al.* 1997). Others are being further investigated by the Ecological Classification System Project (Nigh and Amelon 1995). Current observations indicate that mixed oak-pine forests are most prevalent on the deep, ultic soils in both LTA's. Shortleaf pine occurs in mixtures primarily with scarlet oak (*Quercus coccinea*) and black oak (*Q. velutina*) on these sites. Huckleberry (*Vaccinium stamineum*) is a common associate of these forests. While the current presence of pine is variable, old pine stumps indicate that the species was once associated with these conditions. Because the deep, ultic soils are strongly associated with landforms in the Roubidoux and Upper Gasconade materials, this type of mixed oak-pine forest is widespread across sites in the Current-Eleven Point Hills LTA. These site and forest conditions appear less widespread on sites in the Current-Black River Breaks, where they occur most often on ridges and exposed upper backslopes, and on the Gunter bench. Geo-landforms with deep alfic soils appear to have a lower pine component and more abundant white oak (*Q. alba*). These conditions are more frequent in the Current-Black River Breaks LTA. Soils with variable depth to bedrock support glade and savanna complexes on exposed slopes and mixed oak-hardwood forest on protected slopes. Chinkapin oak (*Q. muehlenbergii*), red oak (*Q. rubra*), sugar maple (*Acer saccharum*), and bitternut hickory (*Carya cordiformis*) are more common here and on the more mesic bottomland sites. Again, these variable depth conditions are more prevalent in the Current-Black River Breaks.

Differences within and between these two LTA's help explain some of the variation in the baseline MOFEP data. Further analysis of relationships between geology, landform, soil, and vegetation will lead to the development of a refined of ecological classification system for the MOFEP sites and surrounding regions.

DEVELOPMENT OF ECOLOGICAL LANDTYPES (ELT'S) AND ELT-PHASES FOR MOFEP

Ecological landtypes (ELT's) and their phases are the "finest scale" categories in the ECS heirarchy (table 1). Initial stratification of the MOFEP sites into ELT's relied on definitions developed for Mark Twain National Forest lands (Miller 1981). Table 3 lists the ELT's delineated

Table 3.—*Initial ELT Definitions on MOFEP.*

ELT	Definition
3	**Landform:** High Flood Plain, Low Terrace; **Aspect:** Neutral; **Percent Slope:** 0-4; **Soil Series:** Ashton, Secesh, Huntington, Gladden, Razort, Elk; **Vegetation Community:** Mesic bottomland forest
5	**Landform:** Upland Waterway; **Aspect:** Neutral; **Percent Slope:** 0-4; **Soil Series:** Midco, Elsah, Cedargap; **Vegetation Community:** Dry bottomland forest
6	**Landform:** Upland Waterway; **Aspect:** Neutral; **Percent Slope:** 0-4; **Soil Series:** Midco, Elsah, Cedargap; **Vegetation Community:** Dry-mesic bottomland forest
7	**Landform:** Toe Slope; **Aspect:** All; **Percent Slope:** 0-14; **Soil Series:** Clairborne, Peridge, Mindale, Viraton, Crider; **Vegetation Community:** Mesic forest
11	**Landform:** Ridge; **Aspect:** Neutral; **Percent Slope:** 0-8; **Soil Series:** Clarksville, Coulstone, Poynor, Doniphan; **Vegetation Community:** Dry chert forest
15	**Landform:** Flat; **Aspect:** Neutral; **Percent Slope:** 0-8; **Soil Series:** Captina, Macedonia, Doniphan, Viraton; **Vegetation Community:** Dry chert forest
17	**Landform:** Side Slope; **Aspect:** South and West; **Percent Slope:** 8-99; **Soil Series:** Clarksville, Coulstone, Poynor, Doniphan, Ocie; **Vegetation Community:** Dry chert forest
18	**Landform:** Side Slope; **Aspect:** North and East; **Percent Slope:** 8-99; **Soil Series:** Clarksville, Coulstone, Poynor, Doniphan, Ocie; **Vegetation Community:** Dry-mesic chert forest, Dry-mesic sand forest
19	**Landform:** Side Slope; **Aspect:** South and West; **Percent Slope:** 8-99; **Soil Series:** Bardley, Opequon, Gatewood; **Vegetation Community:** Glade savanna
20	**Landform:** Side Slope; **Aspect:** North and East; **Percent Slope:** 8-99; **Soil Series:** Bardley, Opequon, Gatewood; **Vegetation Community:** Dry mesic limestone forest
21	**Landform:** Side Slope; **Aspect:** All; **Percent Slope:** 5-99; **Soil Series:** Gasconade, Rockland; **Vegetation Community:** Dolomite glade, Limestone glade
22	**Landform:** Side Slope; **Aspect:** All; **Percent Slope:** 5-99; **Soil Series:** Gasconade, Rockland; **Vegetation Community:** Xeric limestone forest
23	**Landform:** Side Slope; **Aspect:** All; **Percent Slope:** 5-99; **Soil Series:** Gasconade, Rockland; **Vegetation Community:** Dry limestone forest

on the MOFEP sites and their definitions. Note that ELT definitions rely on landforms, aspect, soil, and vegetation factors. Using these definitions, we initially stratified the MOFEP sites into 12 ELT's. Because little information on soils or vegetation of MOFEP sites was available at the time of the initial stratification, ELT delineation was based mainly on landform and aspect. Figure 4 illustrates the resulting stratification. While landform and aspect do describe some of the obvious ecological environments within the MOFEP sites, it is apparent that many important relationships between landform, geology, soil, and vegetation are not described by this initial stratification.

The Missouri Ecological Classification System Project (Nigh and Amelon 1995) is currently cooperating with MOFEP scientists to further refine ELT and phase level relationships and definitions in the Current River Hills Subsection. The project is building upon concepts developed through the MOFEP soil-geo-landform mapping effort. Study areas are being stratified by geo-landform and aspect, and are being used for sampling soils and vegetation and for identifying and testing relationships. The objective of the project is to provide a rigorously tested set of ELT and ELT-Phase definitions for the subsection by October 1998.

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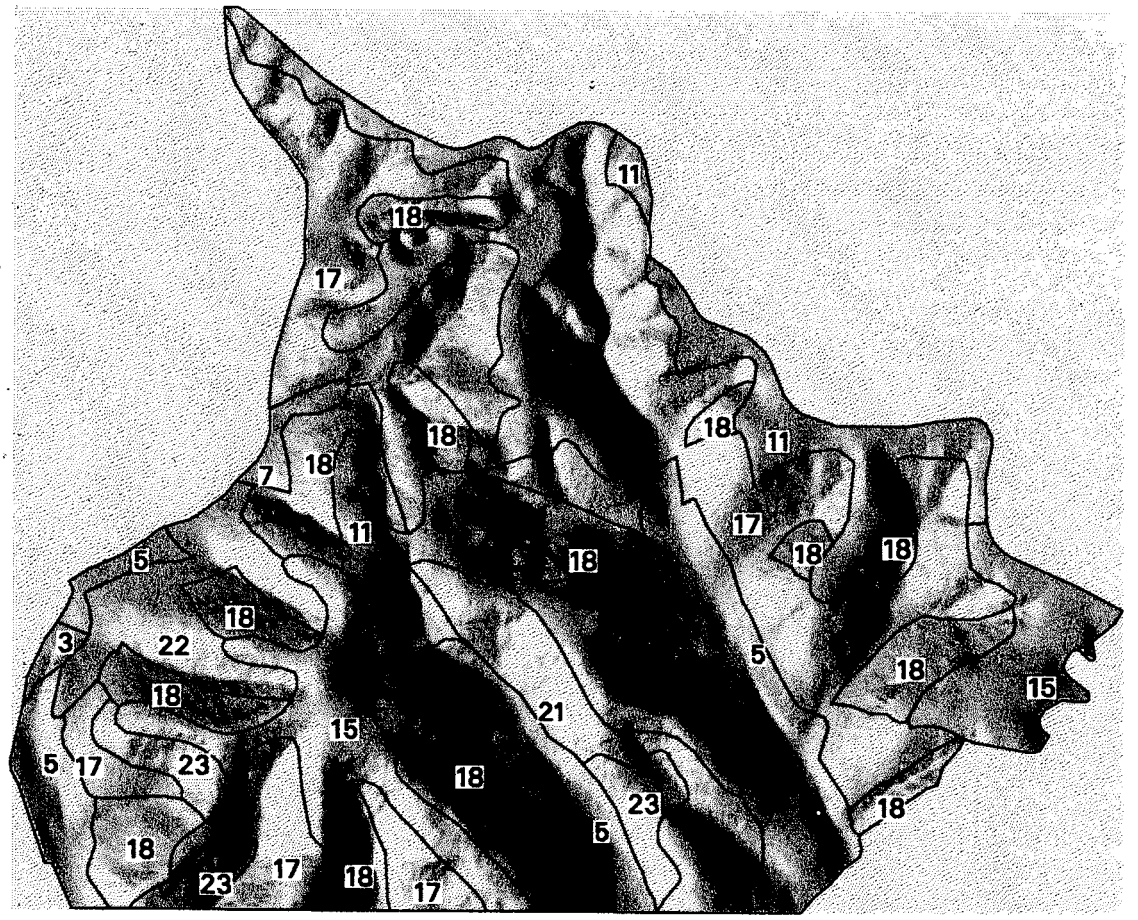

Figure 4.—*Initial ELT Stratification on MOFEP Site 8.*

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Aspects of Carbon and Sulfur Transformations in MOFEP Surface Soils

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Abstract.—Carbon and sulfur transformations were studied in surface soils from plots in MOFEP sites from August 1993 to May 1996 and in plots in watersheds of MOFEP sites 1, 3, and 4 from May 1995 to May 1996. Element pools measured included total carbon, total sulfur, sulfate, and organic sulfur. Transformations quantified included lignocellulose mineralization and organic sulfur production. Most parameters measured were similar compared by plots and sites, with large differences observed when compared by date. This baseline data, compared with post-treatment data, may help determine mechanisms involved in soil carbon and sulfur transformations, and their relation to other soil nutrients, such as potassium and magnesium.

The elements carbon and sulfur are essential to forested ecosystems. As part of the extensive energy transformation system associated with food webs, carbon literally makes up the backbone of the forest. Carbon also interacts with other critical elements in their complex cycles through the ecosystem. Surface soils of forests play a major role in the cycling of both carbon and sulfur, providing decomposing microorganisms responsible for the transformations necessary to keep these elements from becoming sequestered within the soil. Forest primary producers provide the energy that keeps all of these transformations going. The form of carbon primary producers contribute to the forest floor in the greatest concentrations is lignocellulose. Soil microorganisms play critical roles degrading this relatively recalcitrant molecule, and help to recycle the carbon, releasing it to the atmosphere as carbon dioxide (CO_2) (Atlas and Bartha 1993, Stolp 1988). Certain bacterial and fungal species possess cellulases that are capable of splitting the β 1,4 linkages of cellulose (Crawford *et al.* 1977, Stolp 1988). Other bacteria and fungi are capable of producing oxidizing agents that lead to the depolymerization of lignin (Tien and Kirk 1983). Thus, the decomposition of lignocellulose in forest soils is dependent on the presence of bacteria and fungi possessing these degradative abilities.

Sulfur plays important roles in ecosystems both as an essential nutrient and as a reactant. Studies of sulfur cycling in Eastern U.S. forests have indicated that, as a nutrient, sulfur should generally not be limiting (Johnson *et al.* 1982, Likens *et al.* 1977, Shriner and Henderson 1978). However, sulfur interacts with a number of other nutrient elements, including nitrogen (N), phosphorus (P), calcium (Ca), magnesium (Mg), and potassium (K), in some cases influencing their mobility directly (Rechcigl and Sparks 1985, Watwood *et al.* 1993, Wiklander 1978), or indirectly (Homann and Harrison 1992, Mitchell *et al.* 1989). The major pools of sulfur in forest soils include sulfate (soluble or adsorbed) and organic sulfur (C-bonded or ester sulfate; Schindler *et al.* 1986). Studies of forest soils in the U.S., Canada, and Europe indicate that organic sulfur makes up the largest proportion of the soils' total sulfur constituents (Johnson *et al.* 1986, Mitchell and Zhang 1992, Van Loon *et al.* 1987, Zucker and Zech 1985).

Studies of sulfur cycling in forests may involve consideration of the many sources and sinks of sulfur in that habitat (fig. 1). Sulfur is supplied to the forest ecosystem via either weathering or precipitation in the form of sulfate (Mitchell and Lindberg 1992). Concern over the increased input of sulfate to forest soils, as a result of acidic precipitation, has resulted in numerous studies of this problem. These studies have led to a better understanding of the physico-chemical interactions that occur when sulfate is added to a forest soil (Foster 1985, Mitchell and Lindberg 1992, Rechcigl and Sparks 1985,

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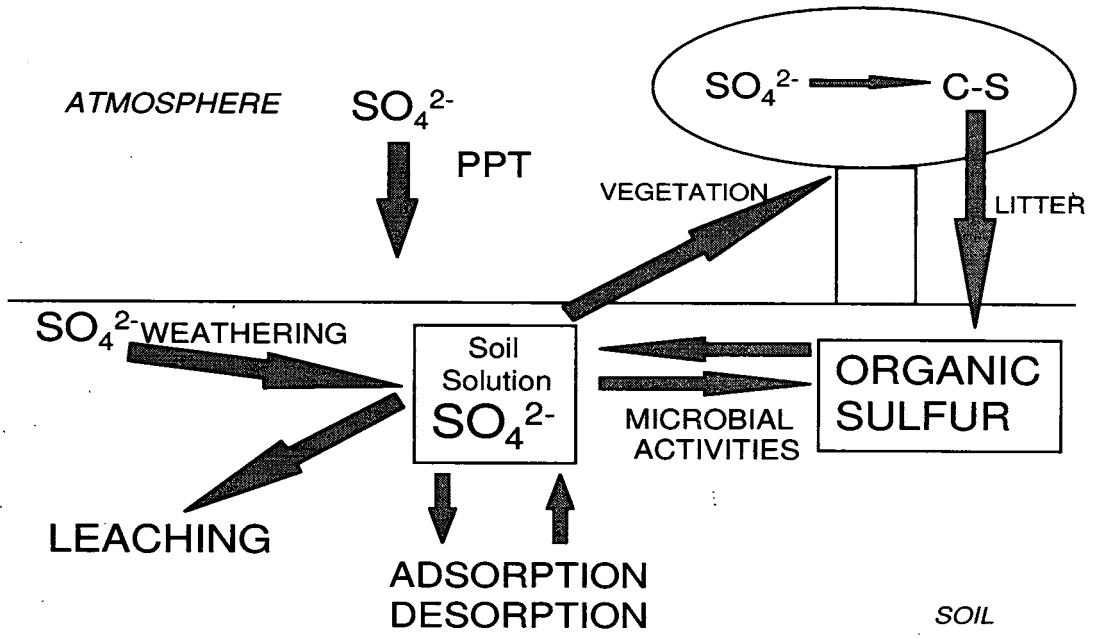
Forest Sulfur Cycling



Modified from Mitchell, David, and Harrison 1992

Figure 1.—*Forest sulfur cycling.*

Ulrich *et al.* 1980, Wiklander 1978). Within forest soils the added sulfate can be adsorbed via abiotic mechanisms to positively charged ion exchange sites, where it may then be taken up by soil microorganisms or plants and converted into a variety of organic sulfur compounds. These organic sulfur compounds of either plant or microbial origin may then be mineralized by soil microorganisms, with the sulfur released back to soil solution as sulfate (Strickland *et al.* 1986). In some mineral soils, however, organic sulfur has been found to be somewhat recalcitrant, resulting in lower potential for microbial mineralization (McLaren *et al.* 1985), and hence may accumulate in the soil. Organic sulfur compounds apparently play a critical role in the retention of nutrient cations within forest soils by possibly serving as cation exchange sites. Watwood *et al.* (1993) demonstrated that mineralization of the organic sulfur fraction in A-horizon forest soils correlates with the loss of nutrient cations (i.e., Ca^{+2}, Mg^{+2}, and K^{+}). Thus, disturbances that may contribute to organic sulfur loss from forest soils may be important to the availability of nutrient cations within the forest ecosystem.

One anthropogenic disturbance of forest ecosystems is the harvesting of timber. Studies of whole-tree harvesting at the Hubbard Brook Experimental Forest in New Hampshire indicated that the greatest short-term (ca. 2 years post-harvest) effect on sulfur cycling in these spodsols was a significant increase in the adsorbed sulfate pool (Mitchell *et al.* 1989). As far as organic sulfur pools were concerned, the only change observed as a result of the harvest was a reduction in the concentration of soil solution organic sulfur as the solution passed from the Oa to the Bs2 horizons, with no significant changes in solution organic sulfur observed for lower mineral horizons. Mitchell *et al.* (1989) made no mention of the potential for cation leaching from the surficial soil horizons as a result of the loss of organic sulfur from this soil.

A preliminary study of the effect that clear-cutting has on sulfur transformations in A-horizon soils of Deer Run State Forest, near Ellington, MO, indicated that significant changes in soil organic sulfur and exchangeable K^{+} and Mg^{2+} were observed for sites that had

been clearcut 2 to 3 or 8 to 10 years previously (Spratt 1997). Studies in other forested sites have indicated that soil bacterial activities are at first stimulated by timber harvest, followed approximately 2 years post harvest by significant reductions in these activities (Lundgren 1982, Pietikäinen and Fritze 1995). The pulse of labile organic materials available to soil microorganisms from decaying debris and root material appears to be instrumental in the pattern of bacterial activity observed following harvest. Once depleted, the concentrations of labile organic materials apparently fall below that necessary to support the populations of microorganisms present in the undisturbed soils. Hence, the marked decline in microbial activities approximately 2 years post harvest.

The results of the preliminary study in Deer Run A-horizon soils led to the development of a large-scale project involving the study of surface soil carbon and sulfur transformations as part of the Missouri Ozark Forest Ecosystem Project (MOFEP) (Brookshire *et al.* 1997). This report summarizes the findings of nearly 3 years of pre-treatment data generated in this component of MOFEP.

OBJECTIVES

The major objectives of this large-scale study are:

1. To determine the short-term and long-term effects of even-aged, uneven-aged, and non-manipulative forest management practices on soil carbon and sulfur constituents in MOFEP soils.
2. To assess any changes in soil microbial lignocellulose or sulfur processing due to even-aged, uneven-aged, and non-manipulative forest management practices in MOFEP soils.
3. To determine relationships that may exist between soil lignocellulose mineralization and organic sulfur production.
4. To determine relationships that may exist between soil microbial sulfur transformations and nutrient cations (e.g., K^+ or Mg^{2+}) as a result of the experimental treatments.

MATERIALS AND METHODS

Sample Sites and Collection

Sample site selection for this study was complicated by the need to keep total sample numbers as low as possible to allow completion of all analytical procedures necessary for that date. At the same time enough samples had to be collected to enable detection of changes in the measured parameters over the noise inherent in the system. It was also desirable to sample all nine MOFEP sites, and, preferably, different locations within the landscape. Sites used in this study were carefully chosen to reflect the above concerns. Beginning in August 1993 and continuing through May 1996, samples were collected from each of the nine MOFEP sites (see figure 1 in Brookshire *et al.* 1997). For each MOFEP site, three plots were randomly placed as described below, with three replicate samples collected from each plot. Soil collection sites were established as a subset of the permanent MOFEP plots selected (see table 1 for details of the locations of these soil collection sites within the sampled plots). All MOFEP plots sampled were located midslope, with south and west aspect (see table 1 for a summary of the plots sampled). Control plots were chosen at random from plots having similar aspect and slope within the site. To ensure that the harvest treatment designated for the site (e.g., even-aged or uneven-aged management) occurred on the experimental plots to be sampled the first year of treatment, the Missouri Department of Conservation (MDC) provided maps of the first timber sales and helped in the selection of sample plots for this study. For sites receiving even-aged harvest, plots were chosen at random from a pool of south and west aspect, midslope plots to be experimentally treated the first year. Because the effects of uneven-aged cutting are much less predictable, the exact location of uneven-aged harvests are unknown in advance of treatment. Plots with the greatest likelihood of being treated were chosen for sample collection (i.e., plots with basal area ≥ the site mean). Soil samples were collected from these MOFEP sites on the following sample dates [field A-horizon soil temperatures indicated in parentheses]: August 17 & 18, 1993 (32°C), December 3 & 4, 1993 (8°C), March 7 & 8, 1994 (7°C), June 1 & 2, 1994 (24°C), September 22 & 23, 1994 (18°C), December 15 & 16, 1994 (9°C), March 9 & 10, 1995 (5°C), and May 23-25, 1995 (20°C), September 21 & 22, 1995 (17°C), March 9 & 10, 1996 (3°C), and May 2 & 3, 1996 (18°C).

Beginning in May 1995, samples were also collected from three paired watersheds located in MOFEP sites 1, 3, and 4. The paired watersheds represented both south and west aspect

Table 1.—*MOFEP plots sampled in the soil carbon and sulfur transformation study.*

Site	Plot sampled [1]	Soil type[2]	ELT[3]
1	21	ultisol	17
1	31	ultisol	17
1	40	alfisol	17*
2	14	alfisol	17*
2	42	alfisol	17*
2	45	alfisol	17*
3	14	alfisol	17*
3	15	ultisol	17
3	37	ultisol	17
4	16	alfisol	17*
4	21	alfisol	17*
4	39	alfisol	17*
5	55	alfisol	17*
5	#1, located in stand 14[4]	alfisol	17*
5	#2, located in stand 14[4]	alfisol	17*
6	18	ultisol	19*
6	34	alfisol	17*
6	58	ultisol	17
7	3	alfisol	17*
7	9	alfisol	17*
7	65	ultisol	17
8	3	ultisol	17
8	16	alfisol	17*
8	70	ultisol	17*
9	26	ultisol	17
9	65	ultisol	17
9	67	alfisol	17*

[1] Soil samples are collected from positions within the plots indicated by small blue flags inserted into the ground. The location of the sampling positions within the plots is determined as follows (all measured from the plot's center post): Sample A - 45°, 70 feet; Sample B - 135°, 70 feet; Sample C - 225°, 70 feet.

[2] As determined by Dennis Meinert in his study of MOFEP soils.

[3] Ecological landtype (ELT), or landscape classification, as estimated by Dennis Meinert after his soil survey of MOFEP plots. Note: * indicates that this ELT classification might change.

[4] Points #1 and #2 are not MOFEP plots. They are located in stand #14 along the side of a ridge on ELT 17. The first of these points is located about three chains, 338° from the center post of site 5, plot 55. The second point is about two chains from the first, also at 338°. The centers of both points are marked with green/black flagging, and the samples A, B, and C are found in the same relationship to the center as at all other plots, and are also marked by blue flags.

and north and east aspect habitat. Two sample collection plots were located in each of the watersheds, with one site located in a convex area high on the slope, and the other site located in a concave area on the slope near the bottom of the watershed. There were 12 plots total in the watershed habitats. Three replicate samples were collected from each of the sample collection sites. These three replicates were not pooled. Soil samples were collected from these watershed sites on the following dates [field A-horizon soil temperatures indicated in parentheses]: May 23 & 24, 1995 (20 °C), September 21, 1995 (17 °C), March 9, 1996 (3 °C), and May 2, 1996 (18 °C).

Also beginning in May 1995, surface water grab samples were collected from streams located near MOFEP plots and from the Current River at Owls Bend. A water sample was collected from a stream located between sites 2 and 3 near Bankers Cave. Three streams in Peck Ranch were sampled; one running between sites 7 and 8, Rodgers Creek (roughly midway between sites 7 and 9), and Mill Creek, at the edge of site 9. These water samples were filtered through 0.45-µm cellulose acetate filters at the site and placed on ice until they could be frozen (within 6 hours). The frozen samples were transported to the University of Tennessee at Chattanooga (UTC) where they were analyzed for SO_4^{2-} and NO_3^- using ion chromatography.

For the locations of MOFEP plots sampled, the watershed plots, and the surface water sample collection sites, please refer to figures 1 through 5 in Brookshire *et al.* (1997).

For the MOFEP plots sampled, A-horizon soil samples were collected by removing the overlying litter layer, and cutting into the A horizon with a sharp spatula. Care was taken to remove only the organic-rich A horizon, and not any of the B horizon (the A-horizon soils are generally much darker than the B-horizon soils). The soil samples were placed in sterile Whirl-pac® bags, and stored in a cooler for the return trip to a laboratory at Southeast Missouri State University (SMSU) in Cape Girardeau (samples taken from August 1993 through June 1994), or to a laboratory at the UTC (samples taken from September 1994 through May 1996).

Sampling in the watershed plots included collection of litter, A-horizon soils, and B-horizon soils. The litter was removed from the forest floor in an area of ca. 100 cm^2 and placed in a sample bag. The A-horizon soil was then carefully cut with a sharp spatula and removed to a sample bag. Finally, B-horizon soils were collected down to a total depth of ca. 15 cm using a small trowel, carefully avoiding contamination of the B-horizon soil with litter or A-horizon soil, and placed in a sample bag.

White oak (*Quercus alba*) distribution on the MOFEP plots sampled in this study was determined using data provided by MOFEP administrators (Brookshire *et al.* 1997). Details of the methodology used to survey the woody vegetation on MOFEP plots may be found in Kabrick *et al.* (1997). All white oak > 4 cm d.b.h. on plots sampled in this study were summed to yield the data presented in table 2.

Table 2.—*Number of white oaks > 1.5 in. d.b.h. on MOFEP plots sampled for the soil carbon and sulfur transformation study.*

Site	Mean white oak	+/- 1SE	Plots	Range white oak
	- - *Number per plot* - -		*Number*	*Number per plot*
1	51.7	12.7	3	31-82
2	46	16.3	3	12-81
3	46	7.6	3	33-64
4	58	11.1	3	31-75
5	42.3	0.3	3	42-43
6	20.3	5.6	3	12-34
7	18	3.1	3	11-24
8	13	7.0	3	3-30
9	30	10.7	3	14-56
All 27 plots	36.1	4.3	27	3-82

Once at the laboratory, the soils and other samples were stored at 5°C and, within 3 days of collection, processed according to the chart in figure 2. From August 1993 until June 1994, each of the 81 individual replicate samples collected from the MOFEP plots and all samples collected from the watershed sample collection sites were processed separately. Beginning in September 1994, samples collected from the MOFEP plots were pooled using equal weight aliquots of the three replicate soil samples from each plot before continuing with sample processing. Unwanted root material, rocks, and any other recognizable litter were removed by passing the soils through a 2-mm polyethylene sieve. The sieved samples were then subdivided into four fractions: one for measurement of extractable sulfate; a second for percent moisture determination, total sulfur measurement, and determination of exchangeable bases (e.g., Mg^+ and K^+); a third to measure ^{35}S-sulfate incorporation; and a fourth to measure ^{14}C-lignocellulose mineralization. The exchangeable sulfate samples were placed in sealed vials and frozen at -20°C until further processing (see below); the samples for percent moisture were weighed and then dried at 60°C until a constant weight was obtained to determine the weight of moisture lost. After the percent moisture was determined, the dried soils were used to determine the soil total sulfur content and extractable base content (see below). Note: all data are presented on a gram dry weight basis to negate changes due to different moisture content throughout the 3 years of sampling.

For the watershed samples, A-horizon soils were treated exactly as the MOFEP plot samples, although replicates were not mixed. Watershed litter and B-horizon soils were dried at 60 °C for ca. 1 week. The litter was then chopped up in a Waring Blender and ground in a mortar and pestle, dried again, and then used for elemental analysis (see below). Dried B-horizon soils were also used for elemental analysis.

Production of ^{14}C-Labeled Lignocellulose

Published techniques to specifically label the lignin or cellulose portion of woody plant tissue were followed (Benner *et al.* 1984, Benner *et al.* 1985, Crawford and Crawford 1976, Crawford *et al.* 1977, Hackett *et al.* 1977). White oak was chosen as the species to be radiolabeled, based on its distribution throughout the MOFEP sites. Cuttings were collected from MOFEP site 8 (well away from any of the plots—the nearest plot

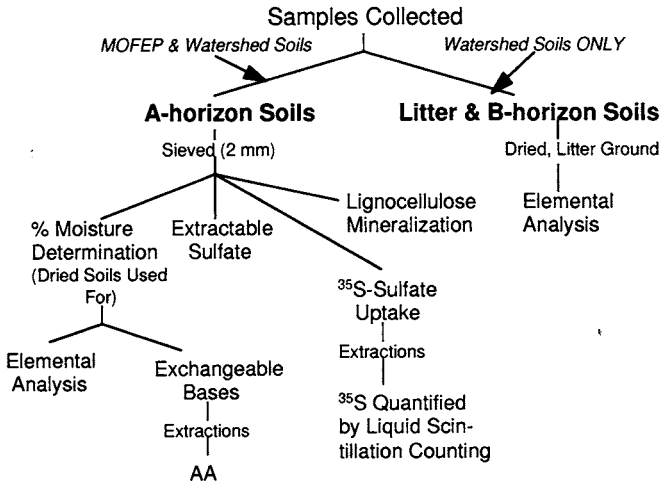


Figure 2.—*Sample processing for carbon and sulfur cycling studies of forest soils.*

was #70) in late July 1993. These cuttings were immediately immersed in water and transported to the Biology Department greenhouse at SMSU, where they were placed on a misting bench. Shortly thereafter, the cuttings were cut into smaller pieces approximately 30 cm in length, ensuring that the leaves were not damaged. The stems of these plants were immersed in water as soon after cutting as possible. About 100 smaller cuttings total were used. Under a hood, the cut ends of the cuttings were carefully cleaned with sterile distilled H_2O, and placed in small beakers containing 10 ml of the ^{14}C-precursor to either lignin or cellulose mixed in distilled H_2O. Uniformly labeled ^{14}C-phenylalanine (New England Nuclear, 50 μCi total for 50 small cuttings) was used as the precursor of lignin (Crawford *et al.* 1977). Uniformly labeled ^{14}C-glucose (ICN, 50 μCi total for the remaining 50 small cuttings) was used as the precursor of cellulose (Crawford *et al.* 1977). The cuttings were kept under constant illumination while the 10 ml of precursor was taken up by the plants, requiring between 2 and 3 hours. At that time, and for the remaining time in the 72-hour incorporation incubation, sterile distilled H_2O was added to the beakers to keep the plants from drying out. The plants were kept under constant illumination throughout the 72-hour period to ensure maximal photosynthetic activity.

After the incorporation process, all of the lignin-labeled and cellulose-labeled plants were pooled into "^{14}C-lignin" and "^{14}C-cellulose" groups and maintained thusly for the remainder of processing. The plants (both leaves and twigs) were cut into pieces no larger than 1 cm in length and

dried at 55 °C for 72 hours. Once dry, the plant material was placed in a Waring blender and ground until it would pass through a #30 sieve (600 μm particles will pass). All work was conducted within a fume hood.

To ensure that no unincorporated ^{14}C-phenylalanine or ^{14}C-glucose remained in the plant materials, a procedure to produce extractive-free lignocellulose was followed (Benner *et al.* 1984, Benner *et al.* 1985). Using a Soxhlet extraction unit, the material was first washed with distilled water for approximately 5 hours. The plant material was then extracted with a 95-percent-ethanol:benzene mixture (1:2 vol:vol) for approximately 24 hours (until the extracted fluid ran clear). Next, the plant material was extracted with 95 percent-ethanol for approximately 24 hours (again until the extracted fluid ran clear). Finally, the plant material was washed with distilled water overnight. The extractive-free plant material was carefully removed from the extraction thimble, placed in a beaker, and dried at 60°C for 48 hours. The total amounts of labeled plant material recovered were: 31.4 g "^{14}C-lignin" and 30.8 g "^{14}C-cellulose." The specific activity (DPM/g dry material) of both the radiolabeled lignin and cellulose material was determined by combusting variable weights of plant material in a Schoniger combustion flask (A.H. Thomas, Swedesboro, NJ), in which 25 ml of a 0.1N NaOH solution was placed. Aliquots of the NaOH were removed and quantified using liquid scintillation counting (see below). The plant material was (and still is) stored desiccated in a -80°C freezer. Over the first 3 years of this project, approximately one-third of the radiolabeled lignocellulosic material was used.

^{14}C-Lignocellulose Mineralization Experiments

Mineralization of white oak ^{14}C-lignin and ^{14}C-cellulose was determined using a modification of previously published techniques (Benner *et al.* 1985, Crawford *et al.* 1977). Microcosms were constructed using 200-ml screw-capped bottles (see figure 3 for a diagram of the microcosm). In place of the screw caps, butyl rubber stoppers were inserted. Suspended below the stoppers was a test tube (3-ml capacity) into which a short length of small diameter tygone tubing was placed. The tygone tubing was connected to a large gage syringe needle, which was inserted through the stopper. On the outside of the stopper, the needle's luer-lock

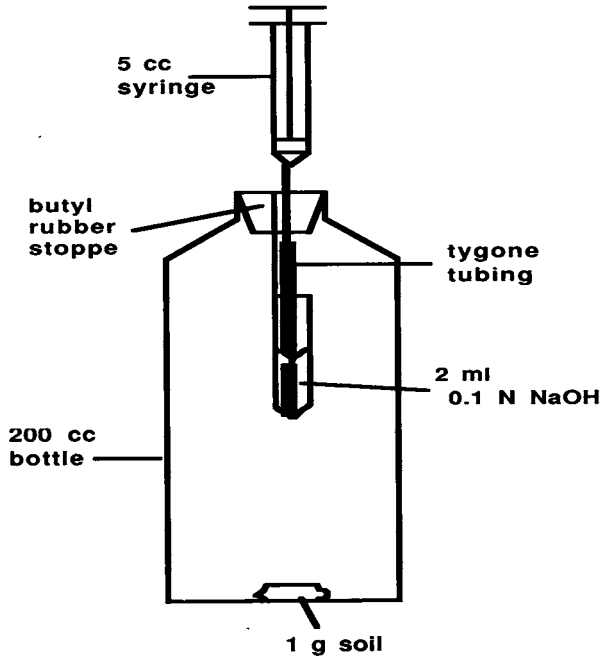


Figure 3.—*Diagram of a microcosm used in the lignocellulose mineralization studies. The volume of the bottle was 200 ml.*

was sealed using a 5-cc plastic syringe. The syringe was used to place exactly 2.0 ml of 0.1N NaOH into the test tube. This NaOH served as the $^{14}CO_2$ trap during the incubation. At each time point during a time-course incubation, the NaOH in the test tube was completely removed by drawing it up into the syringe. Fresh NaOH was immediately added back into the test tube via a second (clean) syringe. This second syringe was left locked in place until the next sampling, effectively sealing the microcosm and minimizing any loss of $^{14}CO_2$. During each incubation, potential loss of $^{14}CO_2$ from the microcosms was monitored via several NaOH traps placed within the incubator. Only on one occasion (August 1993, the first time this procedure was performed) was there any indication of minor leaks.

To initiate the experiments, approximately 1 g of the sieved soil (maintained at field moisture) was placed into a microcosm bottle for the lignin study, and one additional gram was placed into a second microcosm bottle for the cellulose study. Next, approximately 10 mg of the dried extractive-free ^{14}C-labeled lignin or cellulose plant material was added to the microcosms. The soil and plant material were shaken to ensure a homogeneous mixture. "Time zero" in the time course experiments was indicated as the time 0.5-ml distilled H_2O was added to the

soil in each microcosm. This amount of water was found to minimize soil drying, while not saturating the soil. The microcosms were then placed in a dark incubator maintained at field temperature for the duration of the incubations. From this point on, the microcosms remained sealed, except for the time involved to collect samples. This procedure is designed to produce aerobic conditions throughout the experiment (Benner *et al.* 1985). Samplings were made every 3 to 5 days for 3 to 4 weeks. Of the 2 ml of NaOH removed from the microcosm, 1 ml was placed in a scintillation vial for liquid scintillation counting. Maximal rates of lignin or cellulose mineralization were determined by calculating the maximal change in DPM (backgrounds subtracted) recovered for different times in the time course of the incubation. This helped avoid factoring potential lag periods into the rate of lignocellulose mineralization.

^{35}S-Sulfate Incorporation Experiments

Incorporation of ^{35}S-sulfate into different soil sulfur pools was monitored using a modification of the technique of Watwood and Fitzgerald (1988). Two slightly different techniques were used over the sampling period. In the first technique (used in August and December 1993), sieved soil was added to Ace Glass filter sticks (with a fritted glass porosity of 25 to 50 μm), and in the second technique (used for the remainder of sampling dates), sieved soil was added directly into 12-ml conical centrifuge tubes. The reason for the change in techniques was the high rate of breakage of the filter sticks (in December 1993, nearly 15 percent of the samples were lost due to breakage) and the resultant loss of the samples. Approximately 1 g of sieved soil was used in each technique. ^{35}S-sulfate, as $Na_2{}^{35}SO_4$, was added (0.2 ml, ca. 1 μCi containing a total of 8 pmols sulfate) to the top of the soil samples to initiate the incubations. The soils were incubated at field temperature, under aerobic conditions, for 48 hours in the dark. The soils were then placed in a -80°C freezer to arrest any further transformations of the ^{35}S-sulfate, until further processing occurred (within 2 weeks of the completion of the incubation).

^{35}S-Organic Sulfur Mineralization Experiments

For samples collected from the watershed plots in March and May 1996, rates of organic sulfur mineralization were determined using a modification of the technique of Strickland *et al.* (1986). Radiolabeled organic sulfur was prepared using mixed A-horizon soils collected from each of the nine MOFEP sites. Twenty grams total of mixed soil was subdivided into six - 50-cc centrifuge tubes, and a total of 160 μCi of $Na_2{}^{35}SO_4$ was evenly distributed among all of the tubes. The soil was incubated at 20°C for approximately 2 weeks, at which point it was frozen at -20°C. The $^{35}SO_4$ remaining in the soils was removed by washing the soil first with dH_2O, followed by a salt mixture (see below), and again with dH_2O. The soil washes were accomplished by adding the dH_2O or salt mixture to each centrifuge tube (3.0 ml dH_2O, 2.0 ml salt mixture), mixing on a vortex mixer, and centrifuging (2,000 x g, 10 minutes). The washes were repeated four times for the initial dH_2O wash, two times for the salt wash, and then five times for the final dH_2O wash. The soils were then removed from the centrifuge tubes and dried at 60°C for 72 hours. The specific activity of the soils was determined by combusting aliquots of the dried soil in a Schoniger combustion flask, following the technique of Spratt and Morgan (1990). An aliquot of the dH_2O present in the combustion flask was removed after combustion, and the ^{35}S present was quantified by liquid scintillation counting. The specific activity of the soil generated was 1.25 μCi/g. This radiolabeled soil is stored desiccated at -80°C.

Organic sulfur mineralization experiments were set up by adding approximately 1 g of sieved A-horizon soil from each of the watershed plots to conical centrifuge tubes (12 cc), followed by the addition of approximately 10 mg of the dried ^{35}S-organic sulfur-labeled soil. The centrifuge tubes were shaken thoroughly to mix the soils, and 0.3-ml dH_2O was added to initiate the incubation. Separate sets of soils were set up to generate time courses of organic sulfur mineralization. One set of soils, designated t_0, was placed in a freezer at -80°C immediately after addition of the 0.3 ml dH_2O. The remaining sets of soils were incubated at the field temperature of A-horizon soil on the date of collection for various times up to 2 weeks. At the appropriate time in the time course, the incubations were halted by freezing at -80°C. The ^{35}S-sulfate liberated from the mineralized ^{35}S-organic sulfur was recovered using extractions of the soils with dH_2O and a mixture of salts (see below for the details of these extractions). ^{35}S present in the extracts was quantified by liquid scintillation counting.

Recovery of ^{35}S in Soil Sulfur Fractions

The fate of ^{35}S-sulfate added to the soils was determined by sequential extraction of the soils to quantify the radiolabel present in the water soluble and adsorbed sulfate pools, and the organic sulfur fraction (Watwood and Fitzgerald 1988). For August and December 1993 samples, the water soluble fraction was determined by three successive washes through the soils in filter sticks (200 µl of dH_2O each), with centrifugation (2,000 x g, 10 minutes) between each wash. The filtrate recovered in the bottom of the centrifuge tubes was pooled in a scintillation vial. The ^{35}S-sulfate present in this vial represented the radiolabel that remained soluble during the incubation period. The soils collected on all other sample dates were also washed successively (200 µl dH_2O), but, five rinses were used, and the soil/rinse water was thoroughly mixed before centrifugation. After centrifugation, the supernatant was carefully collected using a pipet without removing any of the soil.

Sequential extraction with salts was used to determine the amount of ^{35}S-sulfate adsorbed onto soil surfaces during the incubation. For the August and December 1993 samples, following the water washes, the soil in the filter stick was washed six times with solutions of salt (2-200 µl washes each of 1M Na_2SO_4, 1M NaH_2PO_4, and 1M NH_4Cl). Between each wash, the filter sticks with soil were centrifuged (2,000 x g, 10 minutes), and the filtrate was transferred to a labeled scintillation vial. Soil samples collected on all other sample dates were washed with each of the salts one more time than were the filter stick soils, with mixing before centrifugation, and supernatant collection via pipet (as above with the water rinses).

Determination of the radiolabel incorporated into the organic sulfur fraction of the soil was made using a strong acid/high temperature hydrolysis followed by a strong base extraction. For the acid extraction on samples collected in August and December 1993, 300 µl of 6N HCl was added to each filter stick, and the filter sticks were placed in an autoclave (121°C, 15 PSI) for 20 hours. After cooling, the soils were centrifuged to collect the HCl and then washed (2-300 µl dH_2O washes). These washes were added to a scintillation vial. The strong base extraction involved the addition of 300 µl of 2N NaOH, followed by a 12-hour extraction period at room temperature. After this period, the soils were centrifuged to collect the NaOH and finally washed (2-300 µl dH_2O washes). These washes were also added to a scintillation vial. The ^{35}S present in these fractions were determined using liquid scintillation counting. Soil samples collected on all other sample dates were treated to the same hydrolytic reactions as their filter stick counterparts; the only difference was the rinsing, which used one additional dH_2O rinse, and mixing between centrifugations.

Liquid Scintillation Counting

Quantification of the ^{14}C and ^{35}S used in all of the above experiments was made using a Beckman LS 5000 TA liquid scintillation counter from August 1993 until June 1994. The ^{14}C samples processed from September 1994 until May 1995 were also quantified on the Beckman LS 5000 TA scintillation counter. Beginning in September 1994, the ^{35}S samples were quantified using a Wallac 1409 liquid scintillation counter. Finally, ^{14}C samples were also quantified on the Wallac instrument for the March and May 1996 sample dates. Care was taken to ensure comparability of the samples quantified on different scintillation counters. A biodegradable scintillation cocktail was used (Packard - Ultima Gold XR) for both radionuclides on all dates. Quenching of the samples was accounted for using external quench monitoring techniques (Beckman's "H" number, and Wallac quench correction). For the ^{35}S-extraction samples, specific quench curves were prepared for each scintillation counter using soils with no added ^{35}S, but extracted exactly as the radiolabeled soils. This was necessary because of the dark colors obtained from the soils, due to extracted organic acids, which caused significant color quench.

Determination of Sulfur Pools

Soil total sulfur and the pools of water soluble and adsorbed sulfate were determined for all A-horizon soils sampled. The only analyses performed on litter and B-horizon soils from watershed plots were total sulfur and total carbon (see below). From August 1993 to September 1994, total sulfur was determined by combustion of an aliquot (ca. 30 mg) of soil (initially dried for the percent moisture determination) in a Schoniger flask, followed by quantification of the sulfate adsorbed into dH_2O in the

flask, using a Shimadzu HIC-6A ion chromatograph (Spratt and Morgan 1990). Beginning in January 1995, a Leco CNS 2000 elemental analyzer was available for use on this project. Total carbon and sulfur were quantified in the CNS 2000 by combusting an aliquot (ca. 200 mg) of the dried soils. Sulfamethazine was used to standardize the instrument, and an NIS-traceable soil standard was used for drift correction. To validate the Schoniger flask combustion technique for the analysis of total sulfur, soil samples collected over the period August 1993 to September 1994 were also analyzed on the CNS 2000.

The water soluble sulfate pool in these soils was determined using the soil fraction frozen after sieving. Approximately 0.4 g of soil was transferred to a filter funnel fitted with a 0.45-µm filter, 1 ml of dH_2O was added, and the mixture was shaken for 15 minutes. The filtrate was collected and used to determine the soluble sulfate pool. The soil was rinsed (two 1-ml dH_2O washes), and the final volume extracted from the soil totaled approximately 3 ml. The adsorbed sulfate pool was determined for the soil remaining on the filter in the funnel. One ml of 20 mM Na_2HPO_4 was added to the funnel; the soil was resuspended and then shaken for 1 minute. The phosphate solution was then filtered and collected in a vial. This process was repeated two times, and the total 3 ml of phosphate solution was pooled and used to determine adsorbed sulfate. Both the water soluble and adsorbed sulfate concentrations were quantified using ion chromatography (Watwood and Fitzgerald 1988). Organic sulfur present in the soil was calculated by difference (Organic Sulfur = Total Sulfur - (Water Soluble Sulfate + Adsorbed Sulfate)).

Exchangeable Bases

The exchangeable bases K^+ and Mg^{+2} were determined for all samples using an ammonium acetate extraction procedure (Simard 1993). Five grams of dried soil was placed in a centrifuge tube along with 5 ml of 1N NH_4OAc, pH 7.0. The tube was thoroughly mixed using a vortex mixer, and centrifuged for 10 minutes (2,000 x g). The supernatant was collected and the mixing/centrifugation procedure was repeated twice; 15 ml was the final volume of supernatant collected. This supernatant was analyzed for K^+ and Mg^{+2} using a Perkin-Elmer 1100B atomic adsorption spectrophotometer for August 1993 to June 1994 samples. For samples from September 1994 to May 1996, exchangeable bases were quantified using a Varian Spectr AA10 atomic adsorption spectrophotometer. Atomic adsorption standards were prepared in 1N NH_4OAc, pH 7.0 to reduce the possibility of errors due to matrix effects.

Statistical Methods

Trends in the data were determined by a multivariate repeated-measures analysis of variance (alpha=0.10) using SYSTAT® 5.03 (SPSS, Inc.). Relationships among variables were examined using a Pearson correlation analysis.

RESULTS

MOFEP Plots

For 2 of the 3 years of pre-treatment study on MOFEP plots presented here, seasonal trends were evident for both carbon and sulfur pools in A-horizon soils. The data set for the third year contains only three seasons and was not included in these analyses. The range in A-horizon soil total carbon over all plots and sample dates was from 6 to 32 µmol C/g dry. Overall, the largest differences in total carbon were observed in seasonal comparisons. Samples collected in the late summer/early fall, compared with samples collected in the early spring (fig. 4, $p<0.01$, appendix 1), were noticeably different. Consideration of total carbon in

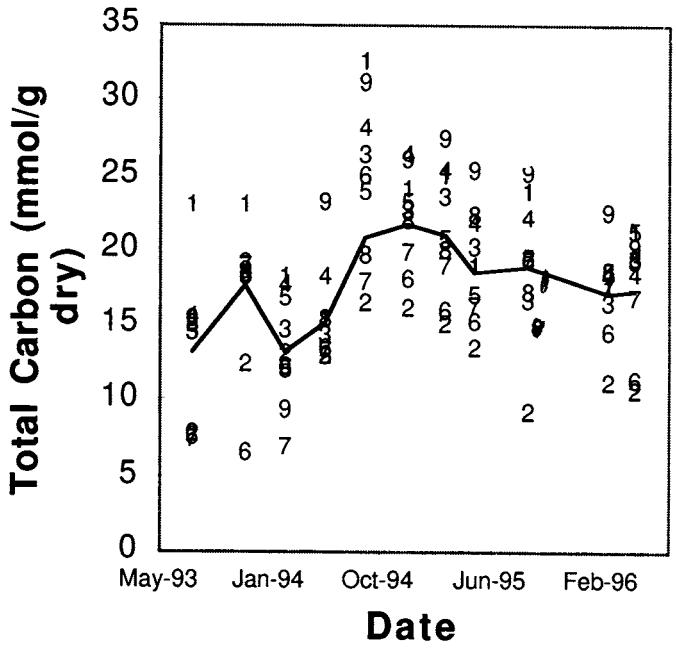


Figure 4.—*MOFEP plots, A-horizon soils - total carbon, August 1993 to May 1996, numbers 1 through 9 represent mean values of 3 plots per site, line represents mean of all 27 plots.*

A-horizon soils by block or treatment indicated no substantial differences.

Total sulfur in MOFEP plot A-horizon soils also exhibited marked yearly trends over the 2 years analyzed ($p<0.01$, appendix 2). Seasonally, the greatest concentrations of total sulfur were observed in late summer/early fall, and the lowest concentrations were observed in late spring (fig. 5). Total sulfur concentrations in A-horizon soils observed for all plots over all sample dates were approximately 10 to 65 μmol/g dry. No substantial differences were observed for A-horizon soil total sulfur when compared by treatment or block.

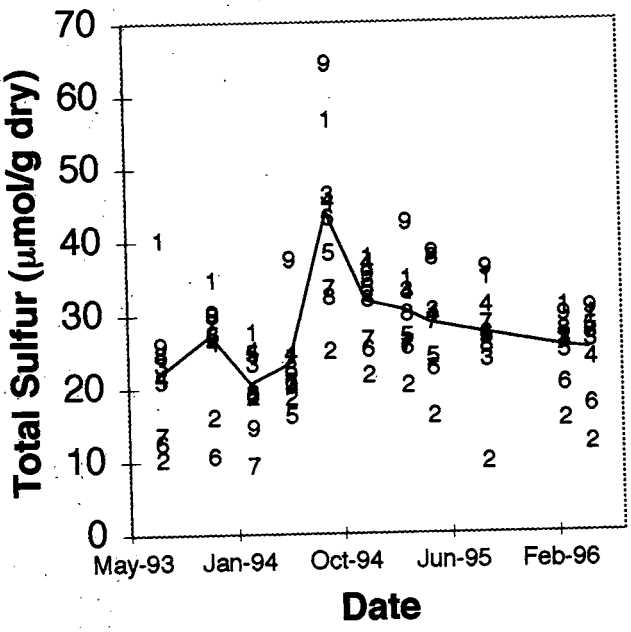


Figure. 5.—*MOFEP plots, A-horizon soils - total sulfur, August 1993 to May 1996; numbers 1 through 9 represent mean values of three plots per site; line represents mean of all 27 plots.*

Organic sulfur in MOFEP plot A-horizon soils was also found to change year to year ($p<0.01$, appendix 3). Seasonally, the highest concentrations of organic sulfur were found in late summer/early fall, and the lowest concentrations were measured in the late spring (fig. 6). Organic sulfur concentrations for all plots over all sample dates ranged from 9 to 64 μmol/g dry. Comparisons of organic sulfur data by treatment or block yielded no noticeable differences. Organic sulfur production rates in A-horizon soils also exhibited large differences from date to date over the pre-treatment period (fig. 7).

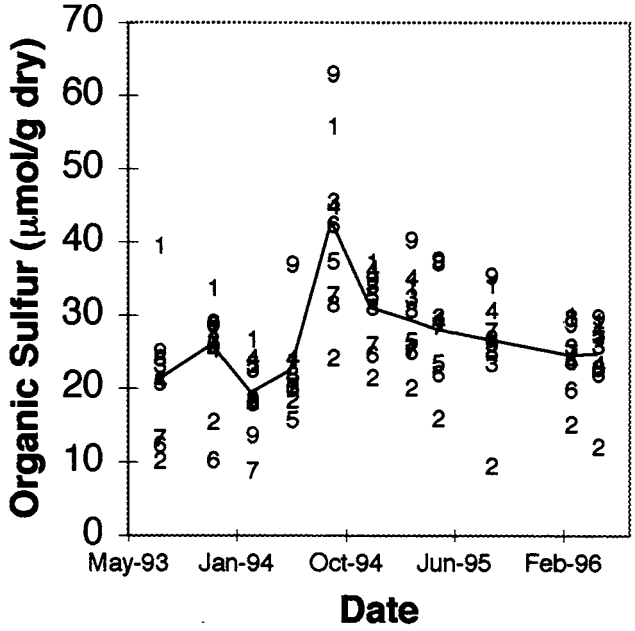


Figure 6.—*MOFEP plots, A-horizon soils - organic sulfur, August 1993 to May 1996; numbers 1 through 9 represent mean values of three plots per site; line represents mean of all 27 plots.*

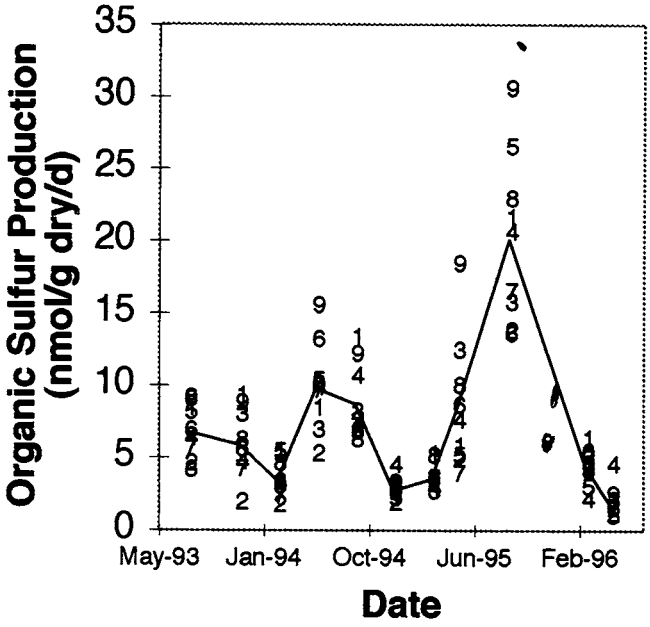


Figure 7.—*MOFEP plots, A-horizon soils - organic sulfur production, August 1993 to May 1996; numbers 1 through 9 represent mean values of three plots per site; line represents mean of all 27 plots.*

Organic sulfur production rates for A-horizon soils over all dates and plots ranged from 1 to 39 nmol/g dry/d. Over the 2 years considered, organic sulfur production exhibited some seasonality (p=0.114, appendix 4), but no other differences in the data were evident.

The presence of white oak on MOFEP plots used for the soil carbon and sulfur transformation study was determined by summing all white oaks > 1.5 in. in diameter (table 2). Some differences (p=0.113, appendix 5) in the numbers of white oak present on the plots sampled were detected when compared by block. No differences were observed in numbers of white oaks on the plots in comparisons by treatment. Plots in blocks 1 and 2 had similar mean numbers of white oak trees present (47.8 and 40.2, respectively), while plots in block 3, on average, had many fewer white oaks (20.3).

Lignocellulose was mineralized in the microcosms used for these analyses following a characteristic time course. Rates of $^{14}CO_2$ released from the soils were not linear, but followed a more logistic-type function (fig. 8-A). For soils cellulose degradation, in August 1993, there was little lag, with rapid exponential mineralization. Emission of $^{14}CO_2$ from the soil then stabilized, with a total of 51 percent of the added labeled plant material mineralized over the 5-week incubation. The lignin moiety of the radiolabeled plant material produced a similar time course of mineralization; however, there was a notable lag period before the onset of exponential $^{14}CO_2$ release (fig. 8-B). Comparison of cellulose and lignin mineralization indicates that the cellulose moiety is much more labile, being mineralized approximately twice as fast as the lignin moiety (1.8 to 2.5 times faster, as calculated for all soils tested from August 1993 to June 1994).

Maximum rates of white oak cellulose mineralization, calculated from the exponential portion of time course experiments, exhibited seasonal differences across the pre-treatment period. The overall range of cellulose mineralization calculated for all plots and dates was from 0.02 to 1.18 mgC/g dry/d (fig. 9-A). Substantial differences (p<0.01, appendix 6) in rates of cellulose mineralization for A-horizon soils were detected in comparisons of the data by season. Rates of cellulose mineralization were lowest in the late fall and winter sampling periods, and highest in the spring and summer sample dates. No block or treatment differences were observed in comparisons of cellulose mineralization rates for all sample dates.

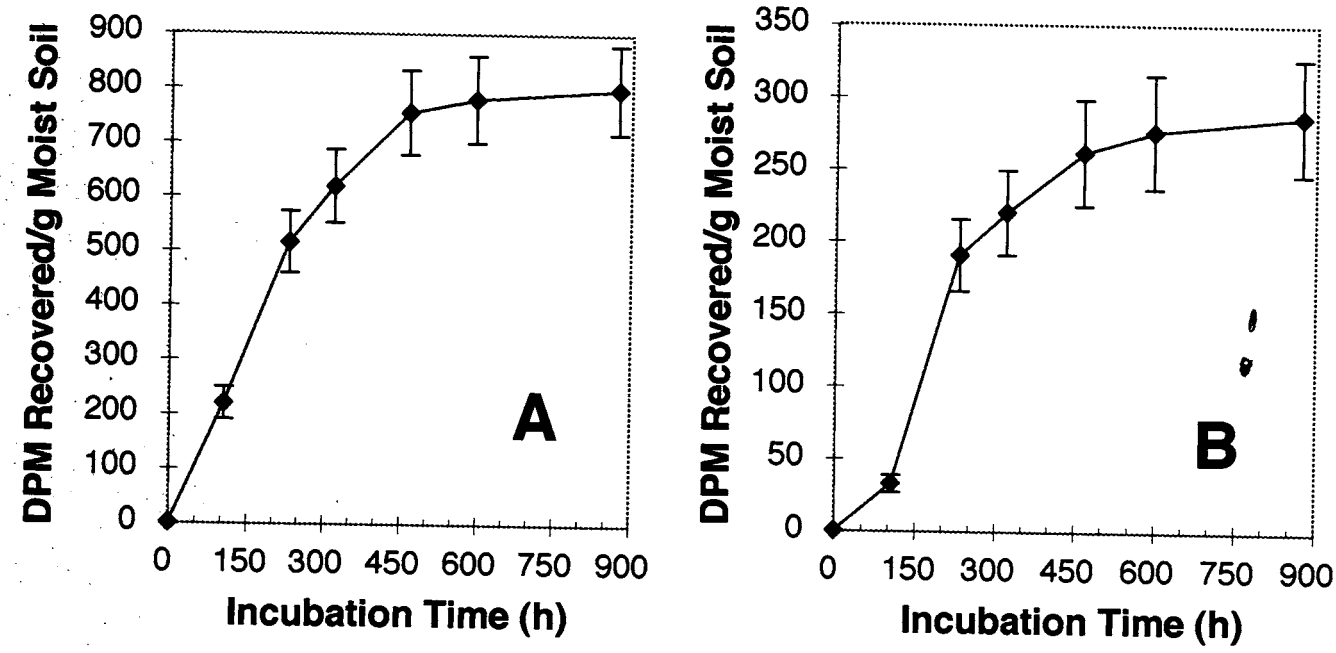


Figure 8.—*MOFEP plots, A-horizon soils - lignocellulose mineralization time course, August 1993, 32°C; mean values for all plots +/- 1 SE, n=9; note differences in vertical scale; A) cellulose mineralization, B) lignin mineralization.*

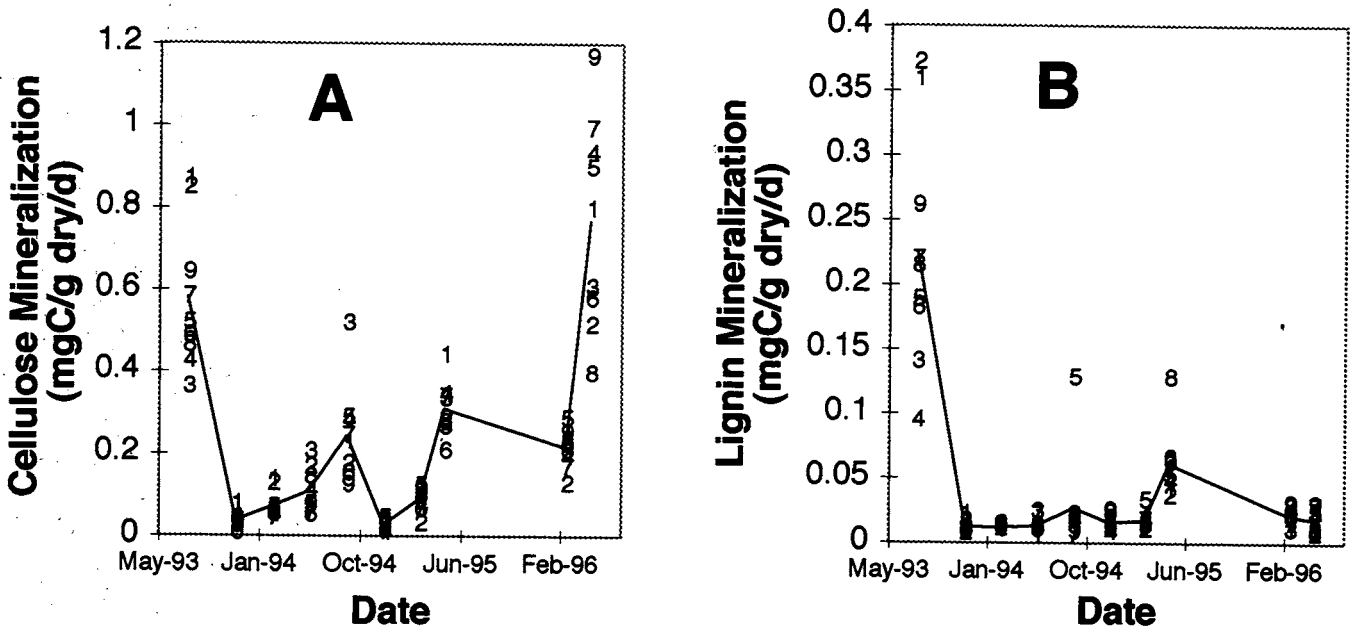


Figure 9.—*MOFEP plots, A-horizon soils - white oak lignocellulose mineralization, August 1993 to May 1996; numbers 1 through 9 represent mean values of three plots per site, line represents mean of all 27 plots; note differences in vertical scale; A) cellulose mineralization, B) lignin mineralization.*

White oak lignin was mineralized at rates that were much lower than the rates of cellulose mineralization for all plots on all dates (compare figs. 9-A and 9-B). Lignin mineralization also exhibited noticeable seasonal differences ($p<0.05$, appendix 7) over the dates sampled. The rates of lignin mineralization for all plots over all dates ranged from 0.01 to 0.37 mgC/g dry/d (fig 9-B). Lowest rates of lignin mineralization for A-horizon soils occurred in late fall or winter. Comparisons of A-horizon soil lignin mineralization by block and future treatment indicated no noticeable differences for the dates sampled.

Comparisons of rates of white oak cellulose or lignin mineralization with the numbers of white oak > 1.5 in. diameter present on the plots studied were made using a Pearson correlation test. No significant correlation between the number of white oak trees present on the plots and the rates of white oak cellulose or lignin mineralization was detected ($r=0.012$ and 0.018, respectively, $n=27$).

Exchangeable K^+ in MOFEP A-horizon soils exhibited noticeable seasonal differences ($p=0.05$, appendix 8) over the period sampled. On an annual basis, the highest concentrations of K^+ were detected in late fall, and the lowest concentrations were measured in late summer (fig. 10-A). For all plots and dates, A-horizon soil K^+ concentrations ranged from 7 to 35 μmol/g dry. There were no differences in the concentration of exchangeable K^+ for A-horizon soils compared by either block or future treatment.

Exchangeable Mg^{+2} in MOFEP A-horizon soils, like exchangeable K^+, also exhibited large seasonal differences ($p<0.01$, appendix 9). A-horizon soils collected in late fall had the greatest concentrations of Mg^{+2}, while late summer samples had lowest concentrations of Mg^{+2} (fig. 10-B). Variation for A-horizon soil Mg^{+2} across all plots and dates ranged from 12 to 76 μmol/g dry. Some differences in A-horizon soil exchangeable Mg^{+2} were detected in comparisons of data from the dates sampled by block ($p=0.062$), while no differences were observed in comparisons by treatment.

A-horizon soil moisture exhibited seasonal variation (table 3). The greatest soil moisture was measured on late fall or winter sample dates; soils were the driest in the late summer.

Stream water SO_4^{2-} for streams in the vicinity of MOFEP plots also exhibited seasonal trends. The lowest concentrations of surface water SO_4^{2-} were measured in September 1995, SO_4^{2-} concentrations varied only little over the other

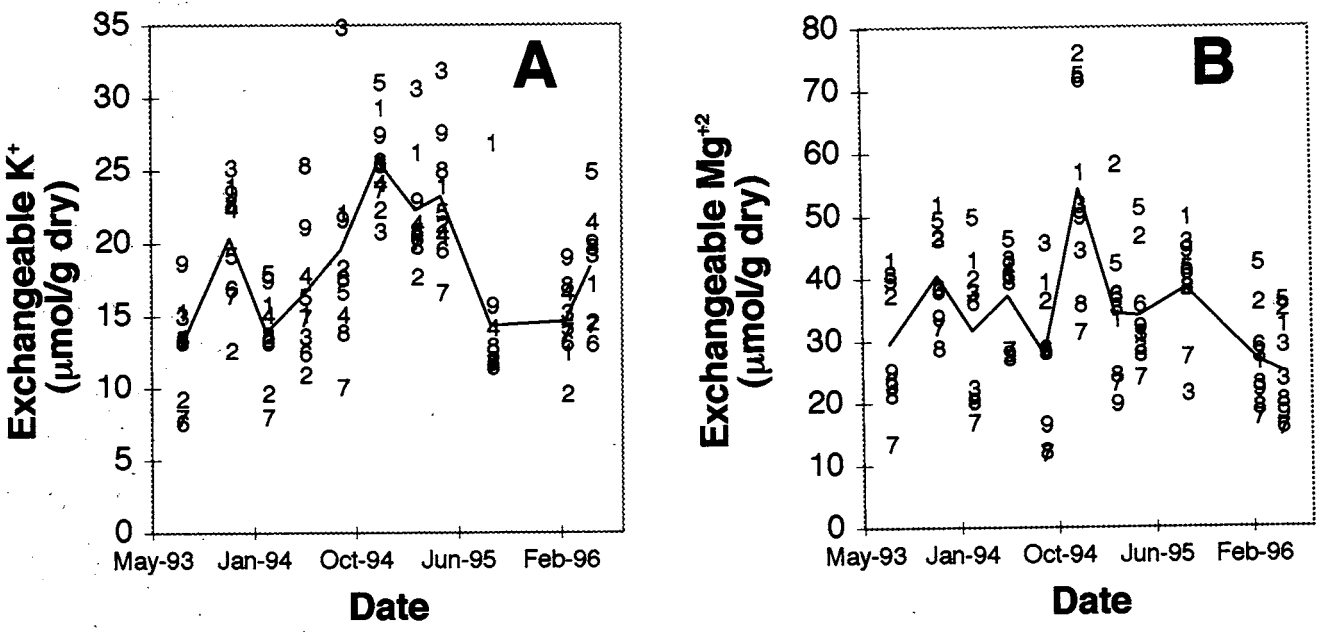


Figure 10.—*MOFEP plots, A-horizon soils - exchangeable potassium and magnesium, August 1993 to May 1996; numbers 1 through 9 represent mean values of three plots per site, line represents mean of all 27 plots; A) potassium, B) magnesium.*

sample dates (fig. 11). Sulfate concentrations from all collection sites over all dates ranged from 12 to 57 µM.

Watershed Plots

The watershed plots, located in MOFEP sites 1, 3, and 4, represent a subsample of the larger carbon and sulfur study of MOFEP, including sample plots with both south and west aspect and north and east aspect, as well as plots positioned both high and low on the slopes. If we consider data from two dates (March and May 1996), total carbon in watershed plots was greatest in forest floor litter on the winter sampling date (mean values across south and west and east and west aspects, and both landscape positions were approximately 40 µmol/g dry), and somewhat lower in the spring (mean values ranging from 37 to 39 µmol/g dry, figs. 12-A and 12-B, $p<0.01$, appendix 10). Total carbon in litter from watershed plots exhibited no noticeable differences when compared by aspect or slope position. In March 1996, A-horizon soil total carbon ranged from 18 to 24 µmol/g dry; the largest difference between the total carbon in litter and A-horizon soil was found for samples from south and west aspect sites, high in the landscape. Total carbon in B-horizon soils exhibited noticeable differences ($p=0.086$, appendix 11) when compared by season. Sample site aspect and slope location resulted in little difference in the B-horizon total carbon. From March to May 1996, the largest change in total carbon for litter, A-, and B-horizon soils was measured for A-horizon soils collected from south and west aspect plots, high in the landscape (figs. 12-A and 12-B). The change in total carbon for these soils from March to May was an increase of nearly 30 percent (from 18 to 23 µmol/g dry).

A closer look at total carbon in A-horizon soils from south and west aspect watershed plots high in the landscape indicated these soils followed the same basic pattern for total carbon observed in A-horizon soils from the MOFEP plots (see fig. 4). The highest concentrations of total carbon in these watershed A-horizon soils (up to 30 µmol/g dry) were measured in the early fall; the lowest concentrations were observed in the winter (as low as 20 µmol/g dry, fig. 13). The only possible difference in A-horizon soil total carbon for watershed plots ($p=0.145$, appendix 12), occurred when the data were compared by season. Comparison of the data by aspect or slope position indicated minimal differences in the A-horizon soil total carbon.

Lignocellulose mineralization in A-horizon soils of watersheds also followed the general trends

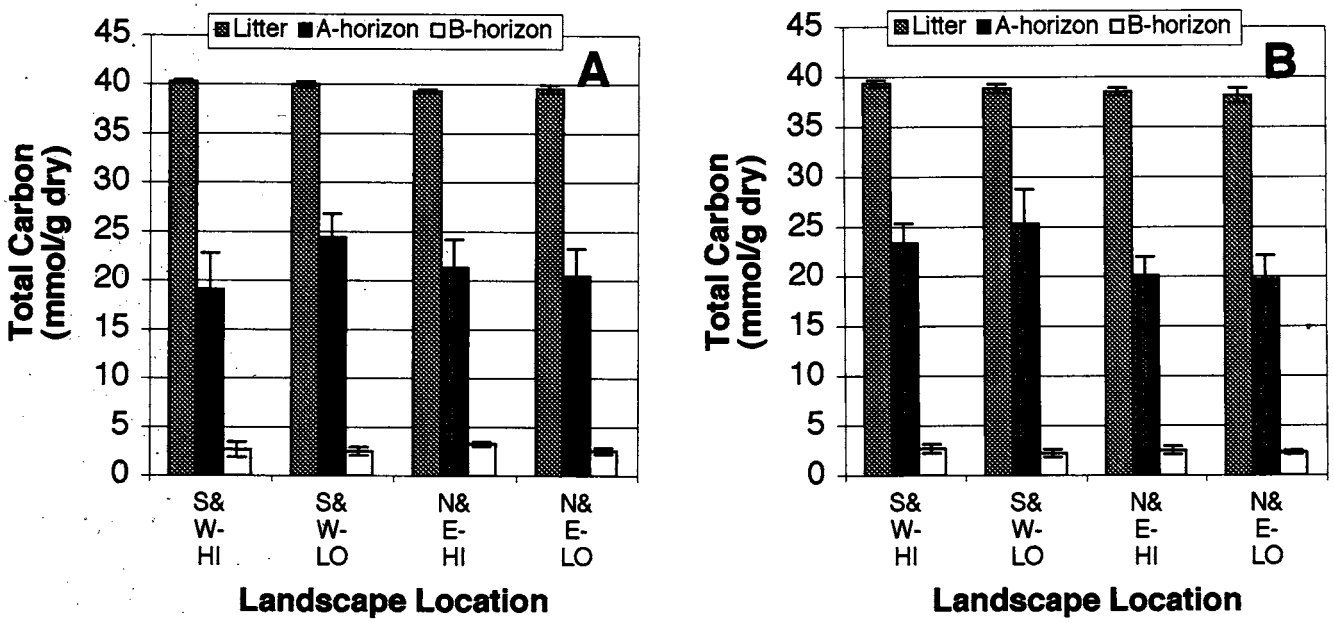


Figure 12.—*Watershed plots, litter, A- and B-horizon soils - total carbon, March and May 1996; S&W=southwest aspect, N&E=northeast aspect, HI=near top of slope, LO=near bottom of slope; mean values +/- 1 SE, n=9; A) March 1996, B) May 1996.*

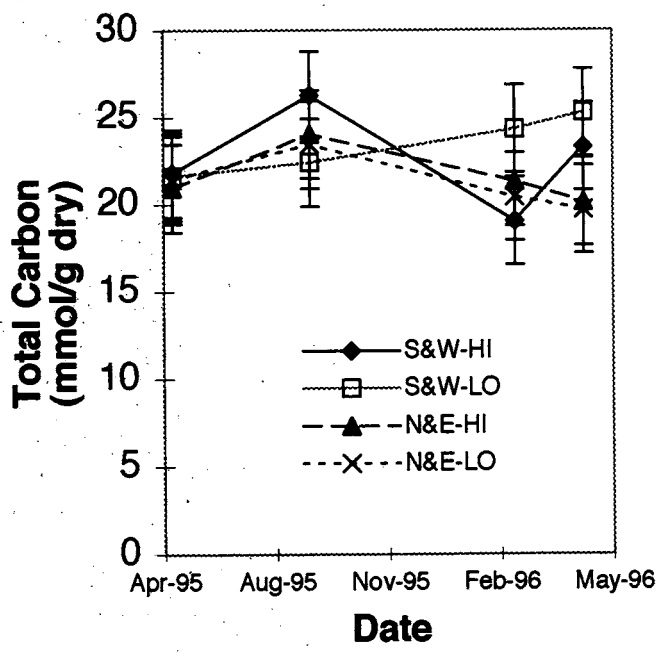


Figure 13.—*Watershed plots, A-horizon soils - total carbon, May 1995 to May 1996; S&W= southwest aspect, N&E=northeast aspect, HI=near top of slope, LO=near bottom of slope; mean values +/- 1 SE, n=9.*

observed for A-horizon soil from MOFEP plots over the period May 1995 to May 1996 (see fig. 9-A). Noticeable differences in cellulose mineralization were observed for A-horizon soils comparing May 1995 and March 1996; May 1996 had the highest rates (fig. 14-A, p=0.024, appendix 13). The rates of cellulose mineralization in May 1995 and March 1996 ranged from 0.2 to 0.3 mgC/g dry/d for A-horizon soils from all watershed plots. No notable differences in rates of cellulose mineralization were detected in comparisons of site aspect or slope location.

White oak lignin mineralization in A-horizon soils from watershed plots, as observed for MOFEP plots (see figs. 9-A and 9-B), was much lower than cellulose mineralization for all dates and sample locations. The differences in rates of lignin and cellulose mineralization for watershed A-horizon soils ranged from 2.5- to 12.5-fold, with lignin mineralization always lower than cellulose mineralization (fig. 14-B). For all dates and plots, rates of lignin mineralization ranged from 0.02 to 0.08 mgC/g dry/d. Rates of lignin mineralization in A-horizon soils were marginally greater in May 95 than March 96 (p=0.159, appendix 14). No differences in lignin mineralization for watershed plots were observed when compared by site aspect or slope location.

Table 3.—*Mean site A-horizon soil percent moisture on sample dates (+/- 1 SE, n=3)*

Date	Site 1	2	3	4	5	6	7	8	9
Aug 1993	41.8 (6.6)	23.7 (1.2)	18.5 (3.1)	23.6 (0.7)	17.5 (2.2)	17.9 (1.5)	21.4 (4.4)	26.7 (1.4)	26.7 (4.6)
Dec 1993	64.3 (2.8)	47.1 (2.8)	61.6 (3.4)	57.5 (1.9)	60.0 (1.7)	52.1 (4.0)	51.2 (1.6)	57.5 (2.5)	54.2 (4.3)
Mar 1994	53.1 (4.8)	45.5 (2.5)	49.4 (3.2)	51.5 (0.7)	58.3 (1.2)	49.2 (3.4)	44.0 (2.5)	52.9 (1.0)	49.3 (2.2)
Jun 1994	38.4 (2.4)	36.0 (3.0)	36.6 (3.3)	40.9 (2.1)	38.5 (2..0)	35.6 (1.3)	30.0 (3.0)	39.7 (4.6)	39.9 (3.6)
Sep 1994	31.0 (3.6)	29.1 (2.2)	45.6 (4.1)	38.0 (1.4)	49.4 (3.2)	39.2 (5.1)	31.6 (4.8)	38.3 (2.5)	43.9 (1.3)
Dec 1994	56.9 (2.2)	43.0 (2.4)	48.2 (2.2)	53.4 (2.1)	50.4 (2.4)	44.2 (2.9)	54.6 (6.8)	59.4 (1.0)	60.6 (1.4)
Mar 1995	63.1 (2.7)	43.2 (1.8)	54.9 (4.1)	51.6 (4.8)	54.7 (5.5)	48.6 (4.5)	50.0 (2.1)	52.6 (2.1)	55.8 (2.2)
May 1995	53.5 (2.1)	45.3 (4.6)	52.5 (2.1)	50.9 (2.5)	44.2 (1.0)	46.8 (3.3)	51.0 (4.7)	58.0 (2.1)	63.1 (0.5)
Sep 1995	53.2 (5.6)	35.9 (2.4)	41.7 (3.4)	46.8 (1.7)	46.9 (1.6)	42.9 (3.1)	41.0 (4.6)	48.1 (1.2)	51.0 (1.2)
Mar 1996	46.2 (5.0)	39.8 (3.0)	48.3 (2.2)	50.0 (1.3)	49.1 (1.1)	45.5 (2.4)	44.5 (5.2)	47.5 (1.0)	54.5 (1.1)
May 1997	57.0 (6.7)	42.5 (2.5)	53.5 (2.7)	57.9 (1.2)	57.3 (2.3)	39.3 (3.7)	49.5 (3.4)	53.3 (3.0)	56.1 (3.1)

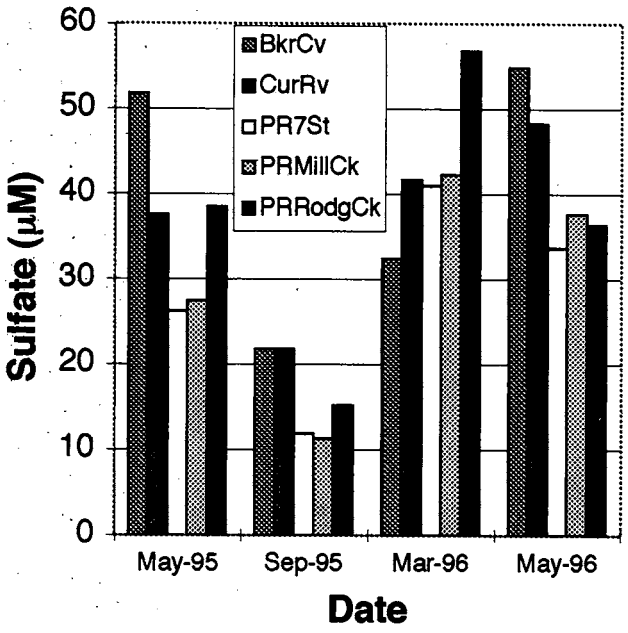


Figure 11.—*MOFEP streams - surface water sulfate, May 1995 to May 1996; BkrCv=Bankers Cave, CurRv=Current River, PR7St=Peck Ranch stream (site 7), PRMillCk=Peck Ranch Mill Creek, PR RodgCk=Peck Ranch Rodgers Creek.*

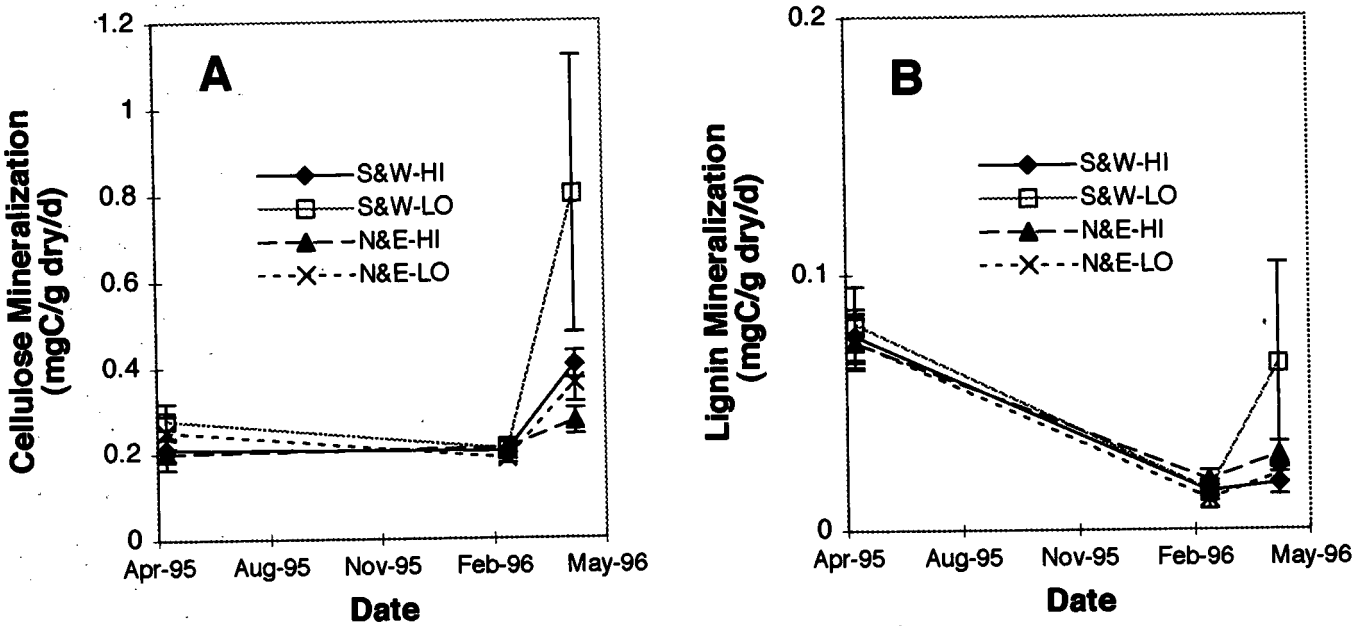


Figure 14.—*Watershed plots, A-horizon soils - white oak lignocellulose mineralization, May 1995 to May 1996; S&W=southwest aspect, N&E=northeast aspect, HI=near top of slope, LO=near bottom of slope; mean values +/- 1 SE, n=9; note differences in vertical scale; A) cellulose mineralization, B) lignin mineralization.*

Total sulfur in the watershed plots was usually greater in the A-horizon soils than in either litter or B-horizon soils, ranging from approximately 31 to 47 μmol/g dry for both aspects studied and landscape positions on both dates analyzed (figs. 15-A and 15-B). In all cases, the total sulfur concentrations in B-horizon soils were much lower than in either litter or A-horizon soil, ranging from 2 to 5 μmol/g dry for all samples on the two dates. Substantial differences ($p<0.01$, appendix 15) were detected in comparisons of B-horizon soil total sulfur on the different dates sampled. Litter had total sulfur concentrations ranging from 27 to 42 μmol/g dry for all samples on both dates. Comparison of litter total sulfur by sample collection date indicated notable differences in this data ($p<0.01$, appendix 16). A-horizon soils from south and west aspect sites had the highest concentration of total sulfur measured for litter, or A- or B-horizon soils, on both sample dates. Soils from both south and west aspect, and north and east aspect sites had essentially the same concentrations of total sulfur in March 1996. In May 1996, north and east aspect A-horizon soils had very slightly increased concentrations of total sulfur compared with March 1996 soils, while south and west aspect A-horizon soils had noticeable increases ($p=0.022$, appendix 17) in total sulfur compared with March 1996 soils (increases of from 21 to 35 percent). B-horizon soils also exhibited substantial changes in total sulfur from March to May 1996 ($p<0.01$, appendix 15), losing approximately 50 percent of the March concentration by May (loss of approximately 2 μmol/g dry).

Extending the study of A-horizon soil total sulfur in watershed plots to 1 year indicated that south and west aspect plots tend to have somewhat higher concentrations of total sulfur than do north and east aspect plots on all sampling dates (fig. 16, $p=0.069$, appendix 17). Comparison of the A-horizon soil total sulfur data for watershed plots with the 3-year database of total sulfur from MOFEP plots (see fig. 5) indicates that the same trend (highest concentrations of total sulfur found in early fall, lowest concentrations in May for MOFEP plots) was not evident for the watershed plots over the year sampled, although the differences measured were significant ($p=0.022$). The year sampled, however, did not include a late fall sample collection.

Organic sulfur concentrations in A-horizon soils of watersheds from south and west aspect plots high in the landscape followed the same basic seasonal pattern observed for A-horizon soils in MOFEP plots of the same aspect (see fig. 6). The organic sulfur concentrations in A-horizon

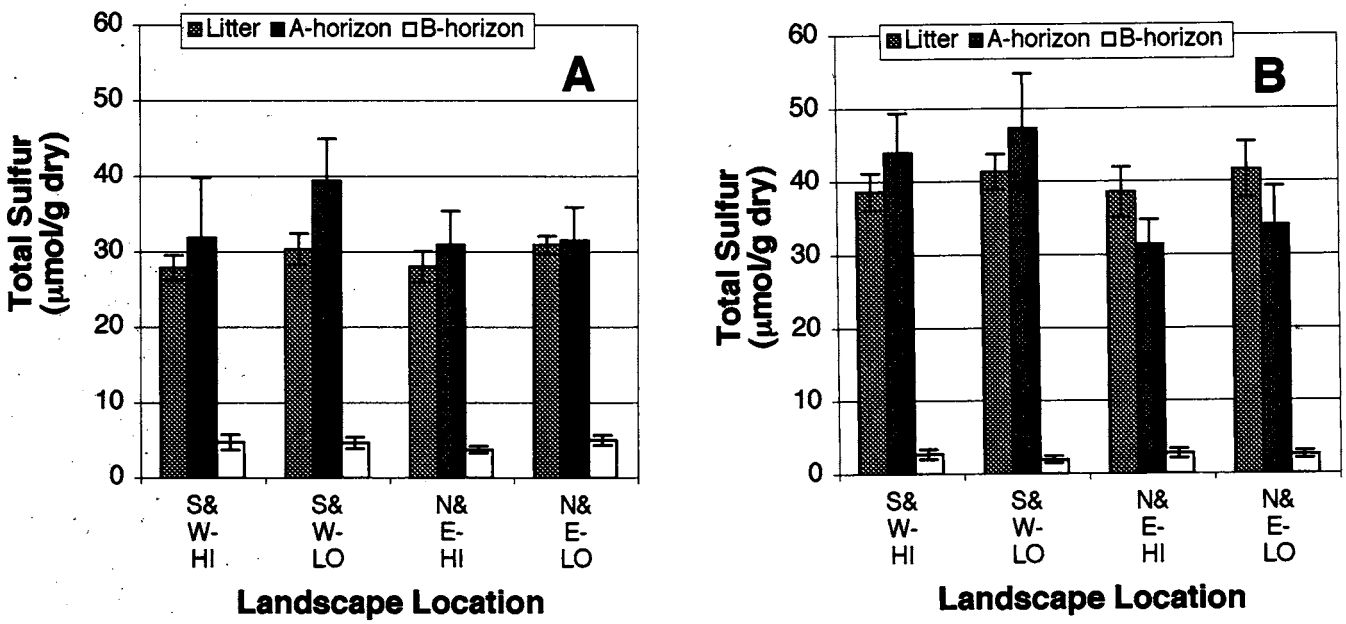


Figure 15.—*Watershed plots, litter, A- and B-horizon soils - total sulfur, March and May 1996; S&W=southwest aspect, N&E=northeast aspect, HI=near top of slope, LO=near bottom of slope; mean values +/- 1 SE, n=9; A) March 1996, B) May 1996.*

soils from south and west aspect watershed plots were greatest in the early fall and declined steadily through the next spring (fig. 17, p=0.019, appendix 18). A-horizon soils from south and west aspect plots located low in the landscape had a slight increase in organic sulfur over the sample period (from 33 up to 38 µmol/g dry). Soils from both slope locations in

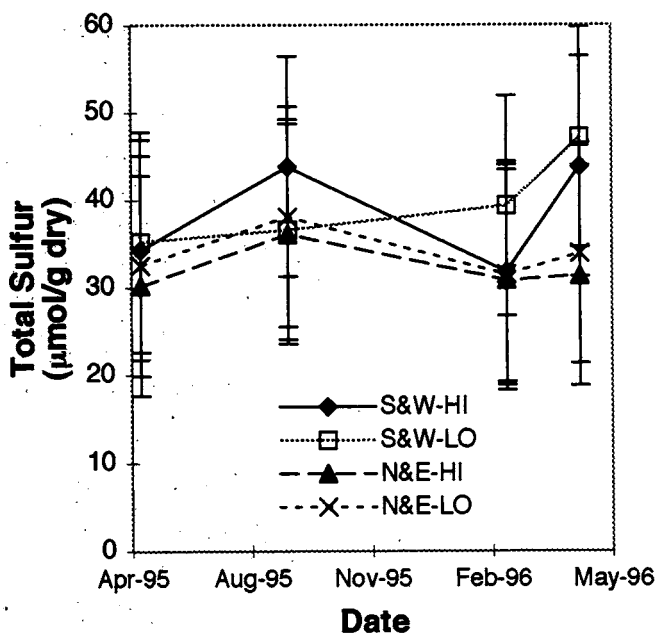


Figure 16.—*Watershed plots, A-horizon soils - total sulfur, May 1995 to May 1996; S&W=southwest aspect, N&E=northeast aspect, HI=near top of slope, LO=near bottom of slope; mean values +/- 1 SE, n=9.*

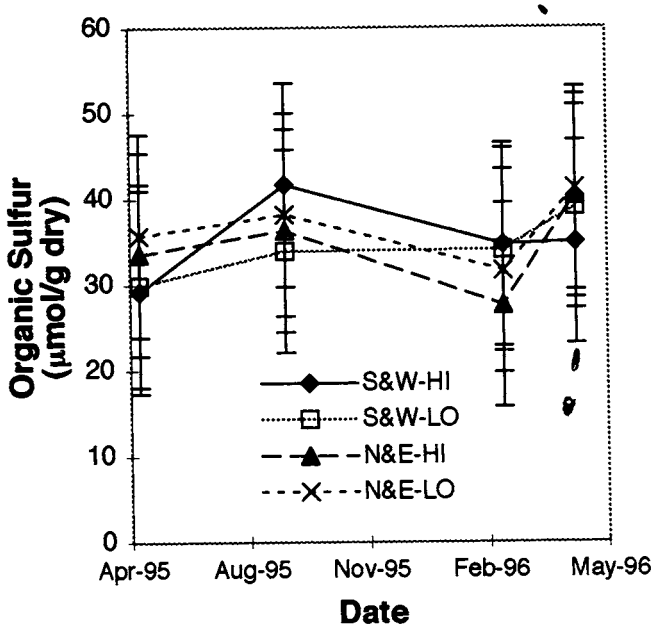


Figure 17.—*Watershed plots, A-horizon soils - organic sulfur, May 1995 to May 1996; S&W= southwest aspect, N&E=northeast aspect, HI=near top of slope, LO=near bottom of slope; mean values +/- 1 SE, n=9.*

north and east aspect sites had declining concentrations of organic sulfur in A-horizon soils from early fall through late winter, but then increased about 34 percent (from 30 to 41 μmol/g dry) in the late spring.

A-horizon soils from watershed plots supported the production of organic sulfur consistently over the sample dates, with notable differences (p=0.020, appendix 19) observed based on comparisons by date (fig. 18). For all watershed plots, organic sulfur production rates ranged from 3 to 55 nmol/g dry/d. The highest rates of organic sulfur production were measured in late fall, with rates declining during the winter, basically supporting the seasonal trend observed for organic sulfur production in MOFEP plots (fig. 7). The rate of organic sulfur production measured for samples collected in May 1996 was much lower than that measured for May 1995 samples.

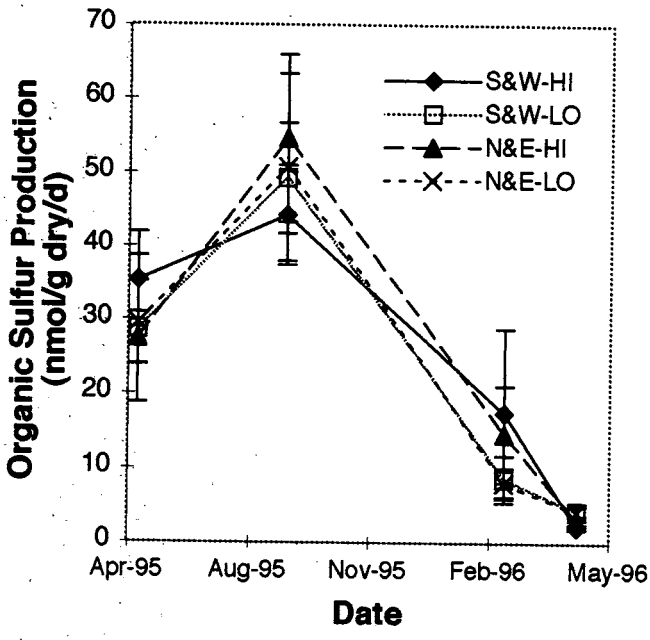


Figure 18.—*Watershed plots, A-horizon soils - organic sulfur production, May 1995 to May 1996; S&W=southwest aspect, N&E=northeast aspect, HI=near top of slope, LO=near bottom of slope; mean values +/- 1 SE, n=9.*

Mineralization of organic sulfur for A-horizon soils from watershed plots was measured in March and May 1996. In March 1996, the rate of organic sulfur mineralization for A-horizon soils from all watershed plots ranged from approximately 150 to 300 nmol/g dry/d (fig. 19). In May 1996, the rate of organic sulfur

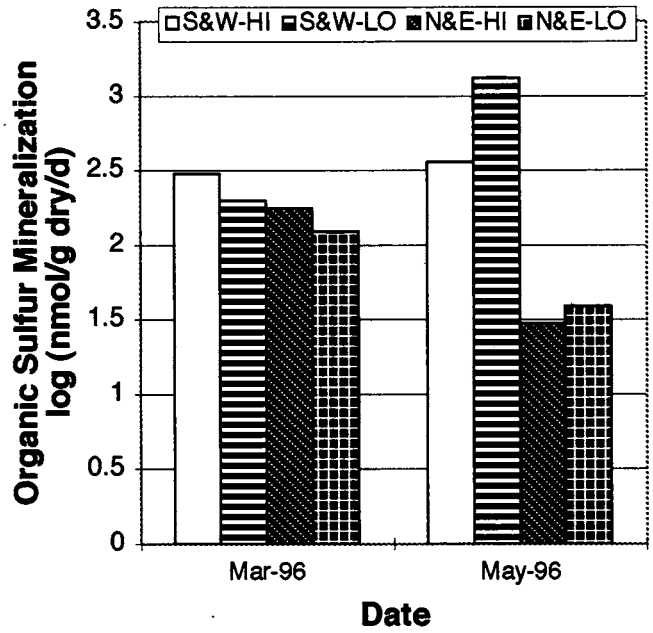


Figure 19.—*Watershed plots, A-horizon soils - organic sulfur mineralization, March and May 1996; S&W=southwest aspect, N&E=northeast aspect, HI=near top of slope, LO=near bottom of slope; mean values +/- 1 SE, n=9.*

mineralization increased for south and west aspect plots low on the landscape, compared with the March 1996 data (increases of greater than fourfold, up to approximately 1,300 nmol/g dry/d, p=0.104, appendix 20).

Exchangeable K^+ in A-horizon soils from watershed plots followed the same seasonal pattern as observed for MOFEP plots (see figs. 10-A and 10-B). Highest concentrations were observed on spring sample dates (fig. 20-A), while concentrations were lowest from late fall through winter. For A-horizon soils from south and west aspect plots the change in K^+ from March to May 1996 was approximately 34 percent, increasing from 22 to 30 μmol/g dry. Potassium in A-horizon soils of north and east aspect plots also increased between March and May 1996, but only by about 13 percent (from 22 to 25 μmol/g dry). Comparison of exchangeable K^+ in A-horizon soils indicated some differences (p=0.137, appendix 21) from date to date.

A-horizon soil exchangeable Mg^{+2} concentrations in watershed plots were not appreciably different when compared by date, aspect, or slope location (fig. 20-B, p>0.2, appendix 22). Exchangeable Mg^{+2} was higher in A-horizon soils from north and east aspect sites than in

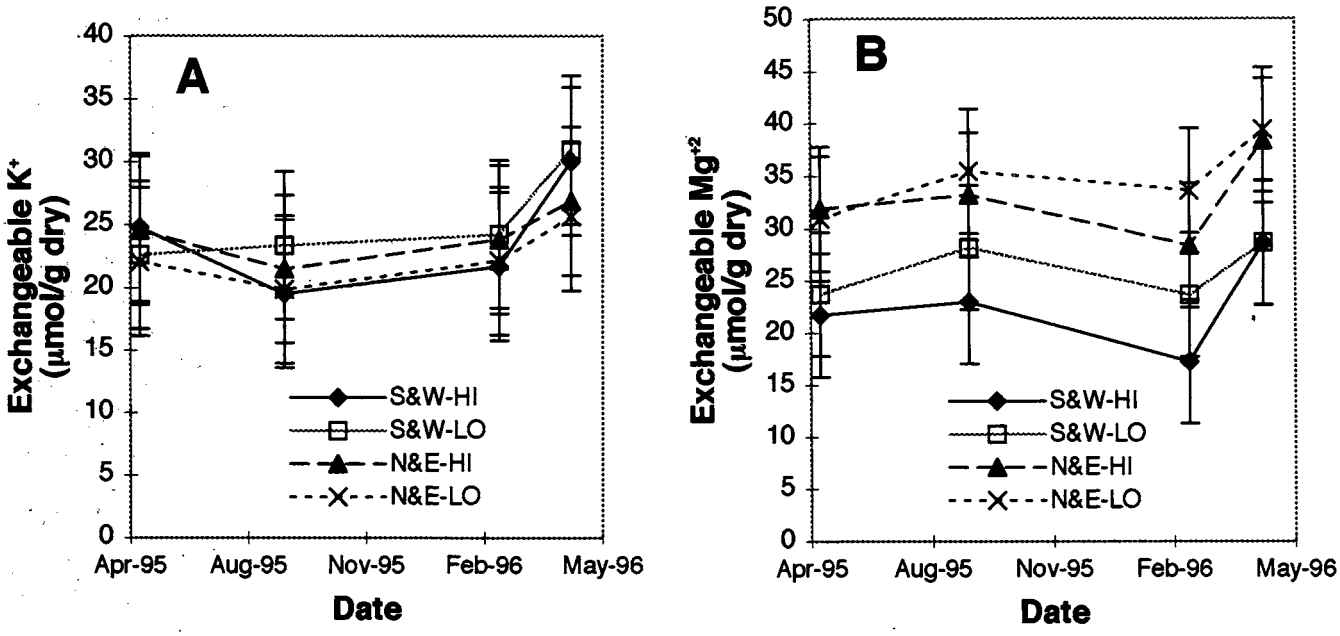


Figure 20.—*Watershed plots, A-horizon soils - exchangeable potassium and magnesium, May 1995 to May 1996; S&W=southwest aspect, N&E=northeast aspect, HI=near top of slope, LO=near bottom of slope; mean values +/- 1 SE, n=9; A) potassium, B) magnesium.*

soils from south and west aspect sites. Comparison of the watershed exchangeable Mg^{+2} data with that from the MOFEP plots (see fig. 10-B) indicates some differences in the two datasets. For example, between March and May 1996, Mg^{+2} A-horizon soils declined somewhat for MOFEP plots, but increased for watershed plots.

DISCUSSION

The pre-treatment portion of this study has served a vital role in helping to establish baseline data that will be used to determine if changes in the parameters measured after treatment might be due to the treatment. Natural variation in forest ecosystems is great; however, if any trends in data sets can be determined prior to an experimental treatment, then a higher level of certainty of the treatment effect should be obtained. In the pre-treatment carbon and sulfur transformation data presented here, the data have been compared by season, replicate grouping of sites (block), site aspect, and slope location (high or low). In many cases very noticeable differences ($p<0.01$) in the pre-treatment data exist when compared by season. This finding reflects the variability that might be expected of biological processes over different seasons. In many cases differences detected in the parameters measured in this report may be due to changes in soil moisture content over the year. Moisture levels can have pronounced effects on the activity of microorganisms (Atlas and Bartha 1993), and if the parameter being tested is the result (either direct or indirect) of some microbial activity, then it should be expected to differ by soil moisture content. Whatever the difference detected in the pre-treatment dataset, having a baseline of the parameter of interest, and knowing something of the natural variation over several seasons occurring in that parameter should help in comparing data collected after the experimental treatment.

In looking at the data sets presented in this report, we found that soil total carbon varied from the litter layer down through the A and B horizons. This would be expected, because the primary source of carbon to the surface soils would be litter fall. As soil microorganisms decompose this litter, labile components of the litter will be released as CO_2, leaving behind more refractile compounds to become part of the soil humus (Atlas and Bartha 1993). For MOFEP soils, the major accumulation of organic carbon appears to be found in the A-horizon soils, at least in a comparison of A-horizon soils with B-horizon soils from no deeper than approximately 15 cm. The A-horizon soil total carbon was also found to differ by sample date.

These variations may be due to differences in rates of microbial activities in these soils, which in turn may be due to physical parameters such as soil moisture and temperature. Finally, activities of decomposers are critical to the larger ecosystem, since they are required to recycle essential nutrients used by primary producers. Therefore, indications of substantial changes in surface soil microbial activities may foreshadow future nutrient limitations to the producers.

The means used here to monitor rates of soil microbial metabolism is the rate of white oak lignocellulose mineralization in A-horizon soils. One of the major sources of carbon to microorganisms found on the forest floor is the lignocellulose of trees present in these Ozark forests. The choice of white oak lignocellulose for studies of A-horizon soil microbial activity was made after consultation with forest ecologists working on MOFEP. White oak was determined to be the dominant tree species of MOFEP south and west aspect plots. Due to equipment availability and experience, the ^{14}C-lignocellulose mineralization assay was chosen to monitor soil microbial activity. Time courses of $^{14}CO_2$ emission from soils amended with ^{14}C-lignocellulose in the microcosms used here were very similar to those obtained for other studies of cellulose and lignin mineralization by microorganisms found in soils (Benner *et al.* 1984, Benner *et al.* 1985, Crawford and Crawford 1976, Crawford *et al.* 1977, Hackett *et al.* 1977), indicating that similar microbial processes occur in different forest soils.

Is white oak lignocellulose mineralization an adequate measure of A-horizon soil microbial metabolic activity? It's possible that differences in the structures of lignin, and possibly cellulose, known to exist from plant species to species (Atlas and Bartha 1993), might predispose the decomposing microorganisms in the soil to lignocellulose from a particular species. Hence, the rates of lignocellulose mineralization determined using radiolabeled white oak lignocellulose might be expected to correlate with the presence or absence of this species in the plots studied if the decomposers preferred one species lignocellulose over another. To address this question, rates of cellulose or lignin mineralization were compared with the number of white oaks >1.5 in. diameter found on the plots studied. No correlations were detected between white oak number and either cellulose or lignin mineralization rates. This finding suggests that A-horizon soil microorganisms, at least on the MOFEP plots sampled, do not discriminate between lignocellulose sources based on the species from which the lignocellulose comes. Therefore, in this study, the rate of lignocellulose mineralization is used to represent microbial metabolic activity.

Lignocellulose from one of the dominant tree species on the MOFEP plots may also be a good indicator of future changes to these plots following experimental treatment. Because leaf litter will be greatly reduced in plots where trees are harvested, provision of the principal carbon source to the soil will be greatly altered. The reduced contribution of organic matter due to lower inputs of leaf litter to A-horizon soils of clearcut sites may also affect the microorganisms in these soils by removing potential carbon and energy sources. Pietikäinen and Fritze (1995) observed an approximate 25 percent decrease in soil total microbial carbon from clearcut forests in Finland 2 years after harvest. Clearcutting has been found to increase soil bacterial biomass for the first 2 years after harvest, followed by a decrease in soil bacterial biomass in subsequent years as labile carbon sources from the decaying woody-debris and roots are depleted (Lundgren 1982). Although not specifically measured in a study of sulfur transformations in Deer Run State Forest (Spratt 1997), there is suggestive evidence that lower inputs of labile carbon from litter or decaying woody-debris or roots may have resulted in reduced microbial growth in these soils, as measured 2 to 3 or 8 to 10 years after harvest. Hence, rates of white oak lignocellulose mineralization presented here may offer a good baseline against which estimation of any changes in soil microbial processes after harvest may be made.

Total sulfur in MOFEP soils was generally higher than that determined for non-leached U.S. soils (Jordan and Reisenauer 1957, Stevenson 1986). The grand mean of A-horizon soil total sulfur, calculated for all MOFEP plots on all dates, was 27.6 μmol/g dry, which is considerably greater than the average for non-leached U.S. soils (16.9 μmol/g dry). At the concentrations observed in the MOFEP plots, sulfur should not be limiting to vegetation in the ecosystem (Shriner and Henderson 1978). In a previous study of sulfur transformations in A-horizon soils of Deer Run State Forest (one of

the State Forests included in MOFEP), on plots not part of MOFEP, clearcutting led to a significant reduction (54 percent, $p<0.01$) in the total sulfur of these soils when compared with control soils. The lack of substantial differences in A-horizon soil total sulfur, when compared by MOFEP block or treatment, should provide a good baseline to observe any changes in soil total sulfur of the magnitude observed in the Deer Run soils.

One potential concern in comparing forest soil total sulfur analyzed in different laboratories has to do with the method used to quantify the sulfur. Dry combustion techniques, similar to those used in this study, require dried soils and have been found to underestimate total sulfur content of some soils (Amaral *et al.* 1989). The greatest loss of sulfur on drying, however, appears to occur for aquic or udic soils. Other researchers have not observed substantial loss of total sulfur when analyzing dried and moist forest soils (David *et al.* 1982, Wieder *et al.* 1985). Since MOFEP soils are mostly xeric, there is the possibility that samples collected during the wetter sampling periods may actually have slightly higher total sulfur values than are reported here.

Sulfur in MOFEP A-horizon soils was dominated by organic sulfur. Organic sulfur made up from 90 to 99 percent of the A-horizon soil total sulfur over all dates and sites sampled. This finding is in keeping with findings from diverse sites around the world (Mitchell and Zhang 1992), indicating that organic sulfur is the predominant form of sulfur in most forest soils. Organic sulfur of plant origin was not directly measured, but it may be inferred that the very large seasonal increases in this compound in the fall must be due to litter drop or some form of root release.

^{35}S-sulfate added to MOFEP A-horizon soils was principally incorporated into the organic sulfur fraction in short-term incubations, similar to other soils amended with this isotope (Fitzgerald *et al.* 1983, McLaren *et al.* 1985, Schindler *et al.* 1986, Strickland and Fitzgerald 1984, Strickland *et al.* 1986). Microbially produced organic sulfur also represents a major portion of the organic sulfur found in MOFEP A-horizon soils. It is possible that the rates of organic sulfur production presented here for MOFEP A-horizon soils may be somewhat underestimated. The methodology used here to quantify organic sulfur utilizes an extraction of soluble and adsorbed sulfate before the organic sulfur fraction is quantified. If appreciable quantities of soluble organic sulfur (e.g., sulfur-containing amino acids) are present in MOFEP soils, then the methodology used here would not detect this soluble organic sulfur. However, soluble organic sulfur compounds have not made up a substantial fraction of other forest soil total organic sulfur (Strickland and Fitzgerald 1984, Strickland *et al.* 1986).

Microbial production of organic sulfur measured for MOFEP soils was found to correlate with rates of lignocellulose mineralization in those soils, suggesting that microorganisms play a role in the formation of this compound in the soil. Abundant evidence is available supporting microbial involvement in the production of organic sulfur in forest soils (David *et al.* 1982, Fitzgerald *et al.* 1983, Schindler *et al.* 1986, Spratt 1997, Strick *et al.* 1982, Swank *et al.* 1984, Watwood *et al.* 1993).

Rates of organic sulfur mineralization in A-horizon soils for two sampling dates were much higher than rates of microbial organic sulfur production over the same period. This suggests that maintenance of organic sulfur in MOFEP A-horizon soils at the levels found in these pretreatment soils over many years requires the annual contribution of organic sulfur that comes from litter fall. The implications that reductions in litter fall, as a result of timber harvest, may negatively affect A-horizon soil organic sulfur are great, at least in the short term (<10 years). In a previous study of sulfur transformations in A-horizon soils from Deer Run State Forest (Spratt 1997), substantial differences ($p<0.01$) in total sulfur (again, mostly organic sulfur) were found for soils clearcut either 2 to 3 or 8 to 10 years prior to sampling. Mitchell *et al.* (1989) came to a different conclusion in their study of whole-tree harvesting, where no significant change in A-horizon total sulfur was found 2 years after whole-tree harvesting in the Hubbard Brook Experimental Forest in New Hampshire. Although no mention was made in the Hubbard Brook study of any changes in litter layers after harvest, the clearcut Missouri sites in Deer Run State Forest had much thinner litter layers than control sites. In addition, A-horizon soils of clearcut sites in Deer Run State Forest were all much thinner than soils of control sites. This finding suggests that erosion of the A-horizon soils down the steep slopes may have been greater for the clearcut sites than the control

sites, leading to loss of the A-horizon soils observed in the Missouri study. This loss, coupled with reduced litter layers, may have resulted in lower concentrations of sulfur, especially organic sulfur, in clearcut A-horizon soils. There is good evidence from other forested ecosystems indicating that A-horizon soils generally contain much higher total and organic sulfur fractions than the lower mineral horizons (Schindler *et al.* 1986). By comparing post-treatment data on soil organic sulfur in MOFEP plots with the baseline data on A-horizon soil organic sulfur presented here, potential mechanisms of organic sulfur loss observed in Deer Run State Forest soils after clearcutting (Spratt 1997) may be elucidated.

Another important aspect of A-horizon soil organic sulfur to nutrient availability in the ecosystem is the role these compounds play in the retention of exchangeable bases. Other researchers have noted the relationship between sulfate adsorption (the result of a physico-chemical process) in the B and lower soil horizons and ecosystem-wide retention of cations (e.g., Johnson *et al.* 1980, 1982). Little emphasis has been placed on A-horizon soils and the role they play in cation retention. A study by Watwood *et al.* (1993) suggested that ecosystem leaching of Ca^{+2}, Mg^{+2}, and K^{+} was positively correlated with the loss of soil organic sulfur from the A horizons of a wide range of soils. Loss of nutrient cations from forest ecosystems might have a negative effect on production in those ecosystems.

Soils sampled in this study were classified as either alfisols or ultisols. Both of these soil types tend to be highly weathered, and have very distinct demarcations between A and B horizons (Hausenbuiller 1978). One characteristic of these soils that helps differentiate them is their level of exchangeable bases. Alfisols have higher exchangeable base concentrations than ultisols. Another characteristic of alfisols and ultisols is their limited K-supplying power. In these soils, K that is available to primary producers comes primarily from exchangeable and soluble forms of the mineral. As a result of the limited K-supplying power of the soils of the MOFEP plots, the predominant source of this base to the forest ecosystem must be atmospheric deposition, a noted source of K to eastern U.S. forests (Ragsdale *et al.* 1992). As the vegetation utilizes base cations, deciduous trees tend to accumulate exchangeable bases in surface soils (Johnson 1992). Because the soils sampled in this study were well drained, any changes that might lead to loss of ion exchange sites in the soils for exchangeable bases in the surface soils might lead to a deficit in these nutrients. A-horizon soil K^{+} and Mg^{+2} were selected for study here because they represent vital nutrients to the forest ecosystem, and they have been shown to correlate with organic sulfur concentrations in A-horizon soils (Spratt 1997, Watwood *et al.* 1993). Spratt (1997) has provided evidence that in A-horizon soils from Deer Run State Forest plots that were clearcut 2 to 3 or 8 to 10 years prior to sampling, both exchangeable K^{+} and Mg^{+2} were substantially reduced compared with controls (K^{+} by 40 percent, and Mg^{+2} by 40 to 70 percent). These reductions in exchangeable bases were correlated with loss of organic sulfur from the A-horizon soils as a result of clearcutting.

Is there a minimal limit to the level of organic matter, including organic sulfur, that will retain adequate levels of K^{+} and Mg^{+2} from precipitation to help keep the Missouri Ozark forest ecosystem adequately supplied with these nutrients? The need for further study of relationships between forest disturbance and soil microbial processes, related to nutrient status of the ecosystem, should be evident. Comparison of post-treatment surface soil organic sulfur and nutrient cation data with the baseline data presented here may help answer this question.

Post-treatment Goals

The pre-treatment goals of this project will continue to be the focus of ongoing research. These goals concentrate on identification of potential long-term changes in soil sulfur transformations and lignocellulose mineralization as a result of the experimental treatments, and any relationship they might have with ecosystem nutrient status. During winter and spring 1997, samples were collected from the watershed plots as soon after harvest as possible. These data will help indicate any short-term (on the order of months) changes in sulfur transformations or lignocellulose mineralization that may occur as a result of the harvest. From studies of sulfur transformations conducted in Deer Run State Forest A-horizon soils, we already know that very large changes in sulfur transformations in A-horizon soils from clearcut sites, compared with control sites, have occurred previously (Spratt 1997).

As a result of the study in Deer Run State Forest, this project will concentrate on several things after harvest in the MOFEP plots. First, the status of microbial organic sulfur production and the pools of organic sulfur in A-horizon soils will be carefully monitored after harvest. The pilot study indicated substantial changes in these aspects of soil sulfur cycling. Future research will attempt to determine the relative importance of microbial vs. plant derived organic sulfur to the soil sulfur pool. Because litter drop from clearcut managed sites should be noticeably less than from control plots, the role microorganisms play in the production of soil organic sulfur may gain importance. Monitoring soil organic sulfur mineralization will also be of great importance after harvest. If the balance between organic sulfur production (both microbial and plant) and mineralization is shifted towards mineralization, then the potential for nutrient loss (e.g., K^+ and Mg^{+2}) similar to that observed in the pilot study may exist.

Lignocellulose mineralization is expected to increase in the short-term following harvest (Lundgren 1982, Pietikäinen and Fritze 1995), but later diminish along with litter fall. As with the sulfur study, short-term changes in lignocellulose mineralization should be evident during the 1997 study of watershed plots. Information from the lignocellulose mineralization study will be helpful as an indicator of microbial activity in these soils, and to some degree will be related to carbon cycling in these soils. Any correlations between lignocellulose mineralization and sulfur transformations in these soils after harvest will be noted.

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APPENDIXES

Appendix 1.—*ANOVA table, total carbon in MOFEP A-horizon soils (August 1993 to May 1996).*

Source	DF	MS	F	P
Between site effects				
Block	2	1.040	0.007	0.993
Treatment	2	60.612	0.400	0.694
Error A (Block*Treatment)	4	151.410		
	F	**Num DF**	**Den DF**	**P**
Within sitet effects				
Year	92.68[1]	1	4	0.001
Year*Treatment	0.446[1]	2	4	0.668
Season	16.361[2]	3	2	0.058
Season*Treatment	0.814[2]	6	6	0.596
Year*Season	6.003[2]	3	2	0.146
Year*Season*Treatment	0.243[2]	6	6	0.945

[1] Systat® outputs analysis for year, with only 1 DF, in the univariate ANOVA table. F-value from univariate tables.
[2] Pillai's Trace F.

Appendix 2.—*ANOVA table, total sulfur in MOFEP A-horizon soils (August 93 to May 96)*

Source	DF	MS	F	P
Between site effects				
Block	2	51.006	0.130	0.882
Treatment	2	291.512	0.741	0.532
Error A (Block*Treatment)	4	393.380		
	F	**Num DF**	**Den DF**	**P**
Within site effects				
Year	61.640[1]	1	4	0.001
Year*Treatment	0.755[1]	2	4	0.527
Season	4.961[2]	3	2	0.172
Season*Treatment	0.826[2]	6	6	0.589
Year*Season	26.518[2]	3	2	0.037
Year*Season*Treatment	0.297[2]	6	6	0.917

[1] Systat® outputs analysis for year, with only 1 DF, in the univariate ANOVA table. F-value from univariate tables.
[2] Pillai's Trace F.

Appendix 3.—*ANOVA table, organic sulfur in MOFEP A-horizon soils (August 1993 to May 1996)*

Source	DF	MS	F	P
Between site effects				
Block	2	46.328	0.120	0.890
Treatment	2	260.543	0.675	0.559
Error A (Block*Treatment)	4	386.223		
	F	**Num DF**	**Den DF**	**P**
Within site effects				
Year	66.632[1]	1	4	0.001
Year*Treatment	0.640[1]	2	4	0.574
Season	3.778[2]	3	2	0.216
Season*Treatment	0.945[2]	6	6	0.527
Year*Season	13.832[2]	3	2	0.068
Year*Season*Treatment	0.338[2]	6	6	0.894

[1] Systat® outputs analysis for year, with only 1 DF, in the univariate ANOVA table. F-value from univariate tables.
[2] Pillai's Trace F.

Appendix 4.—*ANOVA table, organic sulfur production in MOFEP A-horizon soils (August 1993 to May 1996)*

Source	DF	MS	F	P
Between site effects				
Block	2	9.745	0.582	0.600
Treatment	2	28.013	1.672	0.297
Error A (Block*Treatment)	4	16.755		
	F	**Num DF**	**Den DF**	**P**
Within site effects				
Year	2.085[1]	1	4	0.222
Year*Treatment	0.807[1]	2	4	0.508
Season	7.917[2]	3	2	0.114
Season*Treamentt	0.363[2]	6	6	0.879
Year*Season	35.086[2]	3	2	0.020
Year*Season*Treatment	2.235[2]	6	6	0.175

[1] Systat® outputs analysis for year, with only 1 DF, in the univariate ANOVA table. F-value from univariate tables.
[2] Pillai's Trace F.

Appendix 5.—*ANOVA table, white oak enumeration (>1.5 in. diam.), MOFEP plots*

Source	DF	MS	F	P
Block	2	606.827	3.959	0.113
Treatment	2	138.531	0.904	0.474
Error A (Block*Treatment)	4	153.272		

Appendix 6.—*ANOVA table, white oak cellulose mineralization, MOFEP A-horizon soils (August 1993 to May 1996)*

Source	DF	MS	F	P
Between site effects				
Block	2	0.029	6.254	0.059
Treatment	2	0.000	0.041	0.960
Error A (Block*Treatment)	4	0.005		
	F	**Num DF**	**Den DF**	**P**
Within site effects				
Year	1.335[1]	1	4	0.312
Year*Treatment	0.494[1]	2	4	0.646
Season	502.776[2]	3	2	0.002
Season*Treatment	1.187[2]	6	6	0.420
Year*Season	9.219[2]	3	2	0.099
Year*Season*Treatment	0.912[2]	6	6	0.543

[1] Systat® outputs analysis for year, with only 1 DF, in the univariate ANOVA table. F-value from univariate tables.
[2] Pillai's Trace F.

Appendix 7.—*ANOVA table, white oak lignin mineralization, MOFEP A-horizon soils (August 1993 to May 1996)*

Source	DF	MS	F	P
Between site effects				
Block	2	0.001	0.697	0.550
Treatment	2	0.000	0.298	0.757
Error A (Block*Treatment)	4	0.001		
	F	**Num DF**	**Den DF**	**P**
Within site effects				
Year	19.009[1]	1	4	0.012
Year*Treatment	0.734[1]	2	4	0.535
Season	34.300[2]	3	2	0.028
Season*Treatment	0.687[2]	6	6	0.670
Year*Season	46.316[2]	3	2	0.021
Year*Season*Treatment	0.944[2]	6	6	0.527

[1] Systat® outputs analysis for year, with only 1 DF, in the univariate ANOVA table. F-value from univariate tables.
[2] Pillai's Trace F.

Appendix 8.—*ANOVA table, exchangeable potassium, MOFEP A-horizon soils (August 93 to May 96)*

Source	DF	MS	F	P
Between site effects				
Block	2	15.583	0.315	0.747
Treatment	2	187.124	3.777	0.120
Error A (Block*Treatment)	4	49.549		
	F	**Num DF**	**Den DF**	**P**
Within site effects				
Year	60.624[1]	1	4	0.001
Year*Treatment	0.446[1]	2	4	0.668
Season	19.211[2]	3	2	0.050
Season*Treatment	0.716[2]	6	6	0.652
Year*Season	0.732[2]	3	2	0.621
Year*Season*Treatment	0.881[2]	6	6	0.559

[1] Systat® outputs analysis for year, with only 1 DF, in the univariate ANOVA table. F-value from univariate tables.
[2] Pillai's Trace F.

Appendix 9.—*ANOVA table, exchangeable magnesium, MOFEP A-horizon soils (August 1993 to May 1996)*

Source	DF	MS	F	P
Between site effects				
Block	2	2023.293	6.009	0.062
Treatment	2	3.111	0.009	0.991
Error A (Block*Treatment)	4	336.724		
	F	**Num DF**	**Den DF**	**P**
Within site effects				
Year	1.045[1]	1	4	0.365
Year*Treatment	0.275[1]	2	4	0.773
Season	345.518[2]	3	2	0.003
Season*Treamentt	1.019[2]	6	6	0.491
Year*Season	7.065[2]	3	2	0.127
Year*Season*Treatment	2.083[2]	6	6	0.197

[1] Systat® outputs analysis for year, with only 1 DF, in the univariate ANOVA table. F-value from univariate tables.
[2] Pillai's Trace F.

Appendix 10.—*ANOVA table, total carbon in litter of watershed plots (March and May 1996)*

Source	DF	MS	F	P
Between site effects				
Rep	2	0.111	0.667	0.562
ELT	1	3.342	3.094	0.221
Error A (Rep*ELT)	2	1.080	6.476	0.056
Slope	1	0.306	1.837	0.247
ELT*Slope	1	0.139	0.831	0.414
Error B (Rep*Slope+Rep*Slope*ELT))	4	0.167		

	F[1]	Num DF	Den DF	P
Within site effects				
Season	413.279	1	4	0.000
Season*ELT	0.036	1	4	0.858
Season*Slope	15.958	1	4	0.016
Season*ELT*Slope	3.748	1	4	0.125

[1] F-value from univariate tables.

Appendix 11.—*ANOVA table, total carbon in B-horizon soils of watershed plots (March and May 96)*

Source	DF	MS	F	P
Between site effects				
Rep	2	1.695	6.824	0.051
ELT	1	0.119	0.293	0.642
Error A (Rep*ELT)	2	0.405	1.632	0.303
Slope	1	0.857	3.448	0.137
ELT*Slope	1	0.036	0.146	0.721
Error B (Rep*Slope+Rep*Slope*ELT))	4	0.248		

	F[1]	Num DF	Den DF	P
Within site effects				
Season	5.138	1	4	0.086
Season*ELT	1.680	1	4	0.265
Season*Slope	0.116	1	4	0.750
Season*ELT*Slope	1.840	1	4	0.246

[1] F-value from univariate tables.

Appendix 12.—*ANOVA table, total carbon in A-horizon soils of watershed plots (May 1995 to May 1996)*

Source	DF	MS	F	P
Between site effects				
Rep	2	48.538	1.602	0.308
ELT	1	30.608	0.304	0.637
Error A (Rep*ELT)	2	100.595	3.320	0.141
Slope	1	0.473	0.016	0.907
ELT*Slope	1	3.700	0.122	0.744
Error B (Rep*Slope+Rep*Slope*ELT))	4	30.300		

	F[1]	Num DF	Den DF	P
Within site effects				
Season	6.068	3	2	0.145
Season*ELT	3.438	3	2	0.233
Season*Slope	2.633	3	2	0.287
Season*ELT*Slope	2.741	3	2	0.279

[1] F-value from univariate tables.

Appendix 13.—*ANOVA table, white oak cellulose mineralization in A-horizon soils of watershed plots (May 1995 to May 1996)*

Source	DF	MS	F	P
Between site effects				
Rep	2	0.058	1.398	0.346
ELT	1	0.128	3.879	0.188
Error A (Rep*ELT)	2	0.033	0.792	0.513
Slope	1	0.081	1.948	0.235
ELT*Slope	1	0.042	1.015	0.371
Error B (Rep*Slope+Rep*Slope*ELT))	4	0.042		

	F[1]	Num DF	Den DF	P
Within site effects				
Season	12.618	1	4	0.024
Season*ELT	3.726	1	4	0.126
Season*Slope	3.014	1	4	0.158
Season*ELT*Slope	0.937	1	4	0.388

[1] F-value from univariate tables.

Appendix 14.—*ANOVA table, white oak lignin mineralization in A-horizon soils of watershed plots (May 1995 to May 1996)*

Source	DF	MS	F	P
Between site effects				
Rep	2	0.607 e-03	0.794	0.512
ELT	1	0.364 e-03	0.556	0.534
Error A (Rep*ELT)	2	0.654 e-03	0.855	0.491
Slope	1	0.378 e-03	0.494	0.521
ELT*Slope	1	0.001	1.910	0.239
Error B (Rep*Slope+Rep*Slope*ELT))	4	0.765 e-03		

	F[1]	Num DF	Den DF	P
Within site effects				
Season	2.979	1	4	0.159
Season*ELT	0.629	1	4	0.472
Season*Slope	1.238	1	4	0.328
Season*ELT*Slope	1.256	1	4	0.325

[1] F-value from univariate tables.

Appendix 15.—*ANOVA table, total sulfur in B-horizon soils of watershed plots (March and May 1996)*

Source	DF	MS	F	P
Between site effects				
Rep	2	3.541	11.182	0.023
ELT	1	0.004	0.011	0.926
Error A (Rep*ELT)	2	0.350	1.105	0.415
Slope	1	0.022	0.070	0.805
ELT*Slope	1	1.363	4.303	0.107
Error B (Rep*Slope+Rep*Slope*ELT))	4	0.317		

	F[1]	Num DF	Den DF	P
Within site effects				
Season	54.672	1	4	0.002
Season*ELT	1.532	1	4	0.284
Season*Slope	3.272	1	4	0.145
Season*ELT*Slope	0.444	1	4	0.542

[1] F-value from univariate tables.

Appendix 16.—*ANOVA table, total sulfur in litter of watershed plots (March and May 96)*

Source	DF	MS	F	P
Between site effects				
Rep	2	77.449	5.211	0.077
ELT	1	0.304	0.009	0.933
Error A (Rep*ELT)	2	32.575	2.192	0.228
Slope	1	46.124	3.104	0.153
ELT*Slope	1	0.218	0.015	0.909
Error B (Rep*Slope+Rep*Slope*ELT))	4	14.862		

	F[1]	Num DF	Den DF	P
Within site effects				
Season	39.599	1	4	0.003
Season*ELT	0.008	1	4	0.931
Season*Slope	0.004	1	4	0.954
Season*ELT*Slope	0.000	1	4	0.992

[1] F-value from univariate tables.

Appendix 17.—*ANOVA table, total sulfur in A-horizon soils of watershed plots (May 1995 to May 1996)*

Source	DF	MS	F	P
Between site effects				
Rep	2	166.023	1.099	0.416
ELT	1	449.342	0.868	0.450
Error A (Rep*ELT)	2	517.272	3.425	0.136
Slope	1	22.135	0.147	0.721
ELT*Slope	1	3.163	0.021	0.892
Error B (Rep*Slope+Rep*Slope*ELT))	4	151.028		

	F[1]	Num DF	Den DF	P
Within site effects				
Season	44.283	3	2	0.022
Season*ELT	12.281	3	2	0.076
Season*Slope	13.628	3	2	0.069
Season*ELT*Slope	17.424	3	2	0.055

[1] F-value from univariate tables.

Appendix 18.—*ANOVA table, organic sulfur in A-horizon soils of watershed plots (May 1995 to May 1996)*

Source	DF	MS	F	P
Between site effects				
Rep	2	140.957	0.990	0.448
ELT	1	507.906	1.039	0.415
Error A (Rep*ELT)	2	488.813	3.432	0.136
Slope	1	22.469	0.158	0.712
ELT*Slope	1	0.424	0.003	0.959
Error B (Rep*Slope+Rep*Slope*ELT))	4	142.440		

	F[1]	Num DF	Den DF	P
Within site effects				
Season	51.247	3	2	0.019
Season*ELT	9.943	3	2	0.093
Season*Slope	3.189	3	2	0.248
Season*ELT*Slope	14.791	3	2	0.064

[1] F-value from univariate tables.

Appendix 19.—*ANOVA table, organic sulfur production in A-horizon soils of watershed plots (May 1995 to May 1996)*

Source	DF	MS	F	P
Between site effects				
Rep	2	802.524	3.238	0.146
ELT	1	5.197	0.024	0.891
Error A (Rep*ELT)	2	215.256	0.869	0.486
Slope	1	25.568	0.103	0.764
ELT*Slope	1	49.916	0.201	0.677
Error B (Rep*Slope+Rep*Slope*ELT))	4	247.842		

	F[1]	Num DF	Den DF	P
Within site effects				
Season	50.038	3	2	0.020
Season*ELT	18.122	3	2	0.053
Season*Slope	1.132	3	2	0.501
Season*ELT*Slope	1.527	3	2	0.419

[1] F-value from univariate tables.

Appendix 20.—*ANOVA table, organic sulfur mineralization in A-horizon soils of watershed plots (March and May 1996, note: data were log transformed before analysis)*

Source	DF	MS	F	P
Between site effects				
Rep	2	0.019	2.029	0.246
ELT	1	0.091	7.000	0.118
Error A (Rep*ELT)	2	0.013	1.417	0.343
Slope	1	0.008	0.838	0.412
ELT*Slope	1	0.005	0.564	0.494
Error B (Rep*Slope+Rep*Slope*ELT))	4	0.009		

	F[1]	Num DF	Den DF	P
Within site effects				
Season	4.396	1	4	0.104
Season*ELT	1.358	1	4	0.309
Season*Slope	0.116	1	4	0.751
Season*ELT*Slope	1.789	1	4	0.252

[1] F-value from univariate tables.

Appendix 21.—*ANOVA table, exchangeable potassium in A-horizon soils of watershed plots (May 1995 to May 1996)*

Source	DF	MS	F	P
Between site effects				
Rep	2	78.118	1.104	0.415
ELT	1	21.653	0.485	0.558
Error A (Rep*ELT)	2	44.639	0.631	0.578
Slope	1	0.710	0.010	0.925
ELT*Slope	1	27.946	0.395	0.564
Error B (Rep*Slope+Rep*Slope*ELT))	4	70.757		

	F[1]	Num DF	Den DF	P
Within site effects				
Season	6.467	3	2	0.137
Season*ELT	0.418	3	2	0.761
Season*Slope	0.854	3	2	0.579
Season*ELT*Slope	0.435	3	2	0.752

[1] F-value from univariate tables.

Appendix 22.—*ANOVA table, exchangeable magnesium in A-horizon soils of watershed plots (May 1995 to May 1996)*

Source	DF	MS	F	P
Between site effects				
Rep	2	6.722	0.094	0.912
ELT	1	1101.826	3.522	0.201
Error A (Rep*ELT)	2	312.877	4.392	0.098
Slope	1	84.748	1.190	0.337
ELT*Slope	1	6.962	0.098	0.770
Error B (Rep*Slope+Rep*Slope*ELT))	4	71.233		

	F[1]	Num DF	Den DF	P
Within site effects				
Season	3.556	3	2	0.227
Season*ELT	1.740	3	2	0.385
Season*Slope	6.401	3	2	0.138
Season*ELT*Slope	0.715	3	2	0.628

[1] F-value from univariate tables.

Missouri Ozark Forest Soils: Perspectives and Realities

R. David Hammer[1]

Abstract.—Ozark forest soils are dynamic in space and time, and most formed in multiple parent materials. Erosion and mass movement have been variable and extensive. Soil attributes including texture, cation exchange capacity, and mineralogy are related to geologic strata and to geomorphic conditions. Soil organic carbon content is influenced by surface shape, position in landscape, and aspect. Phosphorus is universally low, and most P is occluded. Many soil attributes are distributed in patterns related to topographic, geologic, and geomorphic features, but the patterns often are masked by site-specific variability such as tree throw, micro-relief, and slumps. Generalizations about Ozark soil landscapes must be given cautiously and are most meaningful in the context of attribute ranges rather than means.

The Missouri Ozark Forest Ecosystem Project (MOFEP) has provided an opportunity to investigate Ozark forest soils in a context and with a rigor not previously possible. Soils are as essential for most terrestrial life as water and solar energy. However, soils are complex bodies that are difficult to study. They do not exist as discrete individual entities, such as trees, deer, or fish. Soils have many attributes, most of which vary temporarily and are difficult to measure. All soil attributes change at different spatial rates into other attributes. Soils are not as aesthetically appealing to most natural resources students as the biota, particularly trees, fish, and wildlife. Consequently, soils are not so well understood as other ecosystem components and are infrequently included as components of ecosystem studies. When they are included, soils often are trivialized. Misconceptions and untested assumptions often guide sampling schemes, thus ensuring that the sampling will not test the hypothesis. These circumstances have created an unfortunate, often costly situation. One of the most fundamental ecosystem components is poorly understood and frequently mismanaged.

This paper investigates prevailing concepts of Ozark forest soils and compares them with ideas being developed as a consequence of recent studies and projects. The objective is to illustrate important soil-landscape principles, with particular emphasis on their applicabilities in Ozark forests. Rigorous, systematic data evaluation will not be employed because it is assumed that most readers are not well versed in soil science concepts and terminology. The presentation will be framed within a systematic evaluation of a previously published document whose primary tenents seem to persist among non-soil scientists. The purpose in comparing new ideas with old is not to discredit or embarrass others. Rather, it is to force readers to confront old belief systems with new ones and to make conscious, informed choices. Old paradigms are replaced slowly and reluctantly, even when individuals are confronted with hard evidence (Peters 1991, Rowe 1984, Simonson 1968).

"Landscape" is a currently popular term in biological sciences, but it has not been well defined and often is presented in the context of "scale." In this paper, a landscape is defined as a population of geomorphically related landforms. Geomorphology is the study of processes that shape the Earth's surface features. Geomorphology and pedology (the study of soil-forming processes) are synergistic because the temporal and spatial distributions of water and energy control both (Daniels and Hammer 1992). A landform is an individual Earth

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surface feature that can be described in the context of: (1) its location with respect to other landforms, (2) its surface shape (concave or convex), (3) soil attributes within the landform, and (4) stratigraphic attributes (Hammer 1997a). Stratigraphy is the layering of geologic materials. Thus, landforms are three-dimensional entities that vary spatially and temporally. A landscape is welded by the fluxes of materials and energy through its composing parts (landforms), and the parts segregate materials and energy in space and time.

PREVAILING CONCEPTS OF OZARK FOREST SOILS

Sources of Ideas Espousing System Homogeneity

Sources of Ideas

Primary sources of information about Ozark forest soils are published soil surveys (Gilbert 1971, Gott 1975) and an overview of Ozark soils and vegetation (Krusekopf 1963). The ruggedness of the Ozark landscape limited access to sites, the stoney, clayey soils were difficult to investigate, and the lack of perceived need for more precise information all combined, until recently, to limit detailed, systematic investigations of Ozark soils. Discussions with foresters, ecologists, botanists, and wildlife biologists during the early phases of MOFEP and continuing to the present, suggest that early concepts about Ozark soils remain widely held and persistent. For example, the review of Ozark region soil attributes in a recently completed M.S. thesis investigating oak decline in the Ozarks (Jenkins 1992) cited only Krusekopf (1963).

Illustrating the Problem

Scientists representing several disciplines met recently to discuss a proposed statewide ecological classification system (ECS). A botanist suggested that "historic" vegetation, which he defined as the plant communities indicated by the early 19th century land survey, should be a key ECS component. He said this knowledge would be a target towards which to manage native vegetation in the future. A forester argued that the survey records were a very coarse, simple, single "point-in-time" representation of a botanical system whose temporal and spatial variability are widely acknowledged. A soil scientist said that most Missouri soils have been eroded since the original land surveys, and that establishing "original" vegetation might be impossible because the eroded soils differ in various and important ways from the soils which supported the "historic" vegetation. The botanist countered that the soils could be restored to their previous condition by re-establishing the native vegetation.

Most of pre-settlement Missouri was mantled by a veneer of Wisconsin-aged, silt-size loess. The loess originated as water-born sediments deposited on the Missouri River floodplain, from which it was subsequently removed and distributed across the landscape by wind. The loess is underlain by older soil materials of various origins and ages. Erosion of the loess mantle is irreversible and adds to the complexity of the soil landscape (Ruhe 1956).

Several lessons emerge. Rowe's (1984) observation that skeptics are not easily converted in a competitive world is reinforced. Second, the idea that vegetation can "restore" removed material of specific and unusual geologic origin illustrates fundamental ignorance of basic Earth science.

Apparently few botanists, foresters, ecologists and others who work with natural systems include soils beyond the introductory course as part of their professional training. Pervasive evidence illustrates the synergisms of soils with the biota and of the complexities of the interactions of soils, waters and biota. Why do simple system models continue to prevail? These situations are not unique to Missouri (Hammer 1997a), are widespread, and limit the success of all natural sciences (Peters 1991).

Krusekopf's Perceptions

Krusekopf's (1963) research bulletin remains a frequently cited source of information about Ozark forest soils. Unfortunately, many of Krusekopf's key ideas about Ozark soils are untrue:

> ". . . except for a few small spots on the Salem and Lebanon plateaus, the entire Ozark region was originally forested" (p. 5).

> "In their main physical features, both the forests and the soils of the Ozark region are characterized by their sameness." (p. 6).

"Soils are consistently light in color—either gray or brown, shallow in thickness of surface soil, of medium (silt loam) texture, and of relatively low fertility. Varying amounts of chert stone characterize nearly all the soils except in the Ozark Border region." (p. 7).

"The lower subsoil tends to have a brown or reddish-brown color and is consistently acid—a pH value of less than 5. The percent of base saturation is low." (p. 7).

"There are no sharp contrasts in either forests or soils, and all changes tend to be gradational." (p. 7).

"Variations in the forest cannot be correlated with depth or thickness of the surface soil because the latter is remarkably uniform throughout the region." (p. 10).

"On ridges and on slopes of less than 10 percent, most Ozark soils have a fragipan." (p. 14).

"Fragipans do not occur in very stony soils, on steep slopes, or in soils that have a reddish clay subsoil." (p. 14).

". . . geologic boundaries and soil boundaries rarely conform." (p. 16).

"Soil erosion is not a serious problem in most of the Ozark region." (p. 16).

"Soil boundaries are too rigid to serve as forest type boundaries, especially over large areas." (p. 17).

"In general, moisture appears to be the most important soil factor that can be consistently related to forest type distribution and then only as the extreme of soil moisture condition is reached." (p. 17).

The preceding statements will be addressed individually in the context of current knowledge.

Soil Surveys

Soil surveys traditionally have presented foresters with unique and consistent challenges, many of which have been addressed by Grigal (1984) and Hammer (1997b). The two soil surveys published prior to the 1990's and containing areas of Ozark forest soils were Dent County (Gilbert 1971) and the Mark Twain National Forest Area (Gott 1975). The legends of both surveys have relatively few soil series. The Dent County survey contains 14 series, 4 of which are alluvial (table 1). Five of the 12 series mapped in the Mark Twain National Forest are alluvial (table 2). Thus, the complex upland landscape is portrayed as a small group of relatively uniform soils. Is this phenomenon a consequence of Krusekopf's perspective of "sameness" of soils in the Ozark region?

Conversely, site-specific soils investigations conducted by Meinert (Meinert *et al.*, 1977) on the MOFEP sites, an area much smaller then either Dent County or the Mark Twain National Forest, resulted in 47 soil mapping units. Meinert's soil units were conceived to meet MOFEP needs, and were based upon a combination of soil and geomorphic attributes important for forest composition and growth. One would expect scores of mappable soils to be identified in individual Ozark counties, particularly if mappers attempt to identify soil attributes important to the variety of current and potential land uses.

Many of the upland soils in Dent County and the Mark Twain National Forest are mapped across ridges and sideslopes (backslopes). Slope phases within series separate slope soils from ridgetop soils. This conveys a false perspective of soil homogeneity. Many soils are mapped on multiple aspects. Figure 1, an excerpt from the Mark Twain National Forest Area survey, illustrates this model. In the lower center is a ridge with west- and east-facing slopes. Dashed lines on the backslopes indicate ephemeral drainageways. These drainageway incisions indicate that the backslopes contain a mosaic of convex and concave surfaces. A single soil series, with separate "phases" for slope steepness is mapped over the entire ridge. This is a false perception and false portrayal of the soil.

Pedologic studies indicate that different soils occupy different geomorphic surfaces in complex, steeply sloping terrain, and that aspect creates measurable differences in soil attributes which are important for tree growth (Carmean 1975, Hammer *et al.* 1991). Such relationships now are being observed and quantified in Missouri Ozark forest landscapes.

Table 1.—*Soil series mapped in the Dent County, MO soil survey (Gilbert 1971). Series are presented with taxonomic classifications to the subgroup, with parent materials and landscape settings.*

Soil series	Subgroup classification	Parent material	Landscape setting
Ashton	Mollic Hapludalfs	Alluvium	Stream terraces
Captina	Typic Fragiudults	Loess over residuum	Ridges and upper slopes
Claiborne	Typic Paleudults	Colluvium	Toe and footslopes
Clarksville	Typic Paleudults	Cherty dolomite	Ridges and sideslopes
Coustone	Typic Paleudults	Dolomite and sandstone	Ridges and sideslopes
Doniphan	Typic Paleudults	Cherty dolomite or limestone	Ridges and sideslopes
Macedonia	Typic Paleudults	Loess over cherty dolomite	Ridges and sideslopes
Midco	Dystric Eutrochrepts	Cherty alluvium	Narrow stream bottoms
Newark	Aeric Fluvaquents	Alluvium	Lower stream bottoms
Opequon	Lithic Hapludalfs	Dolomitic limestone	Slopes near major rivers
Poynor	Typic Paleudults	Cherty dolomite or limestone	Ridges and sideslopes
Secesh	Ultic Hapludalfs	Alluvium	Low terraces
Viraton	Typic Fragiudalfs	Colluvium	Toe slopes
Wilderness	Typic Fragiudalfs	Loess and residuum	Ridges and upper slopes

Table 2.—*Soil series mapped in the Mark Twain National Forest Area, MO (Gott 1975). Series are presented with taxonomic classifications to the subgroup, with parent materials and landscape settings.*

Soil series	Subgroup classification	Parent material	Landscape setting
Ashton	Mollic Hapludalfs	Alluvium	Terraces and bottoms
Atkins	Fluventic Haplaquepts	Alluvium	Bottoms
Bado	Typic Fragiaqualfs	Loess over cherty dolomite	Broad ridges
Baxter	Tyipic Paleudults	Colluvium	Lower sideslopes/coves
Clarksville	Typic Haplaquepts	Residuum-cherty dolomite	Narrow ridges and sideslopes
Coulstone	Tyupic Paleudults	Resdiuum from sandstone	Ridges and sideslopes
Elkins	Fluventic Humaquepts	Alluvium	Depressions in bottoms
Elsah	Typic Udifluvents	Alluvium	Narrow stream valleys
Gladden	Fluventic Dystrochrepts	Alluvium	Narrow bottoms and valleys
Hobson	Typic Fragiudalfs	Loess over depression fill	Ancient depressions
Lebanon	Typic Fragiudalfs	Loess over cherty residuum	Broad ridges
Moniteau	Typic Ochraqualfs	Loess over cherty residuum	Ridges

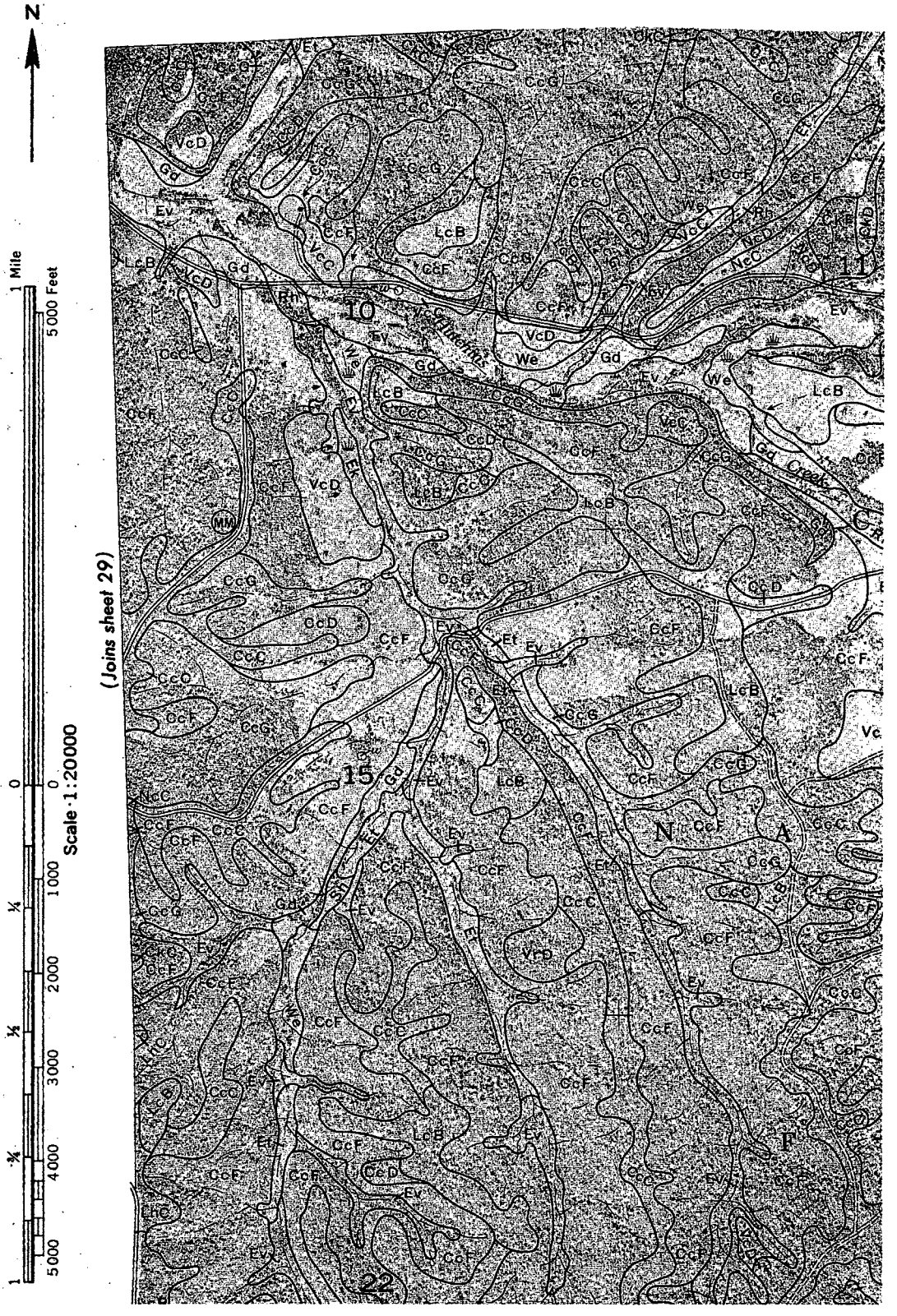

Figure 1.—*A portion of the Mark Twain Area soil survey (Gott 1975) showing a single soil series mapped across all aspects and landforms on a ridge. This figure is from the survey field sheet number 30. Letter and number combinations within delineations are mapping unit symbols. The first two letters of mapping unit symbols represent the soil series and the last letter indicates the slope class.*

Krusekopf's perceptions (1963) seem to have been based upon a two-dimensional concept of soils. He displayed geology as a two-dimensional surface feature (fig. 2), rather than as a three-dimensional feature of a dissected landscape (fig. 3). Krusekopf's geology map conveys to the uninformed user the false perception that only a single stratigraphic layer is locally important. Figure 3 clearly indicates that all exposed stratigraphic components are important in a dissected landscape.

Neither Krusekopf nor the early soil surveys mention geomorphic attributes as determinants of soil conditions and regulators of soil-forming processes. Thus, Ozark region soil surveys which preceded the current mapping effort perpetuated the idea of relatively uniform soils across the spectrum of topographic and geomorphic conditions. Soil series were perceived as widespread, and most soils were thought to have formed primarily in residuum (geologic material which has weathered in place). Most pedologists now would agree that soils formed from a single parent material or single depositional event are rarely found.

THE COMPLEX OZARK SOIL LANDSCAPE

Countering Krusekopf's Perceptions

Original Forest Vegetation

The statement that most of the Ozark region was originally forested is no longer accepted. Much of the Ozark area was a mosaic of forest and savanna (Nelson 1987). Although erosion has removed most original surface horizons, thick buried A-horizons remain in some depressions where hillslope sediments accumulated from higher landscape positions. Hillslope sediment is defined as surficial material which moves slowly downslope under the combined influences of water and gravity (Daniels and

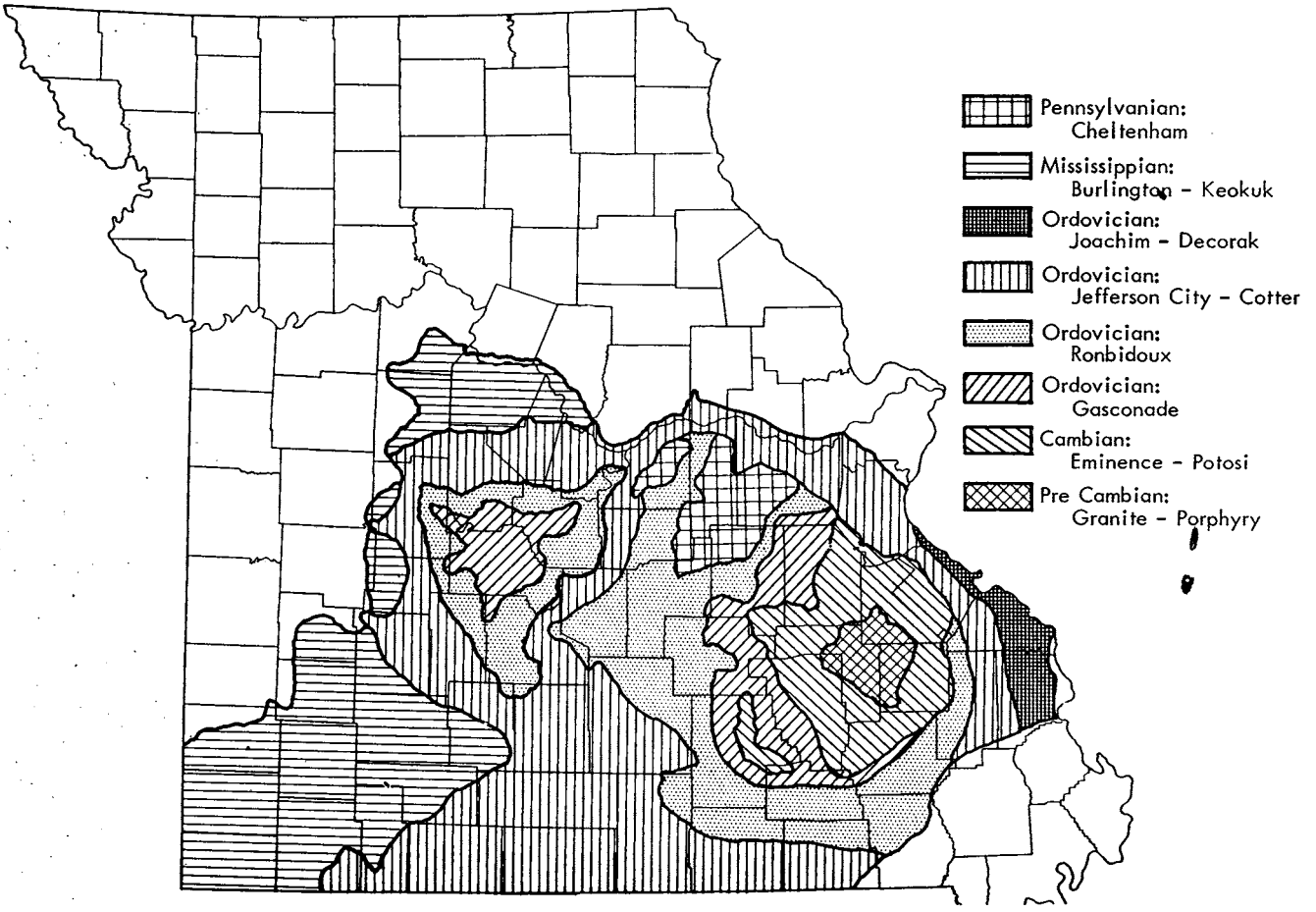

Figure 2.—*A representation of "surficial geology" in the Ozark Highlands by Krusekopf (1963). The lower portion of the figure in the cited text was absent.*

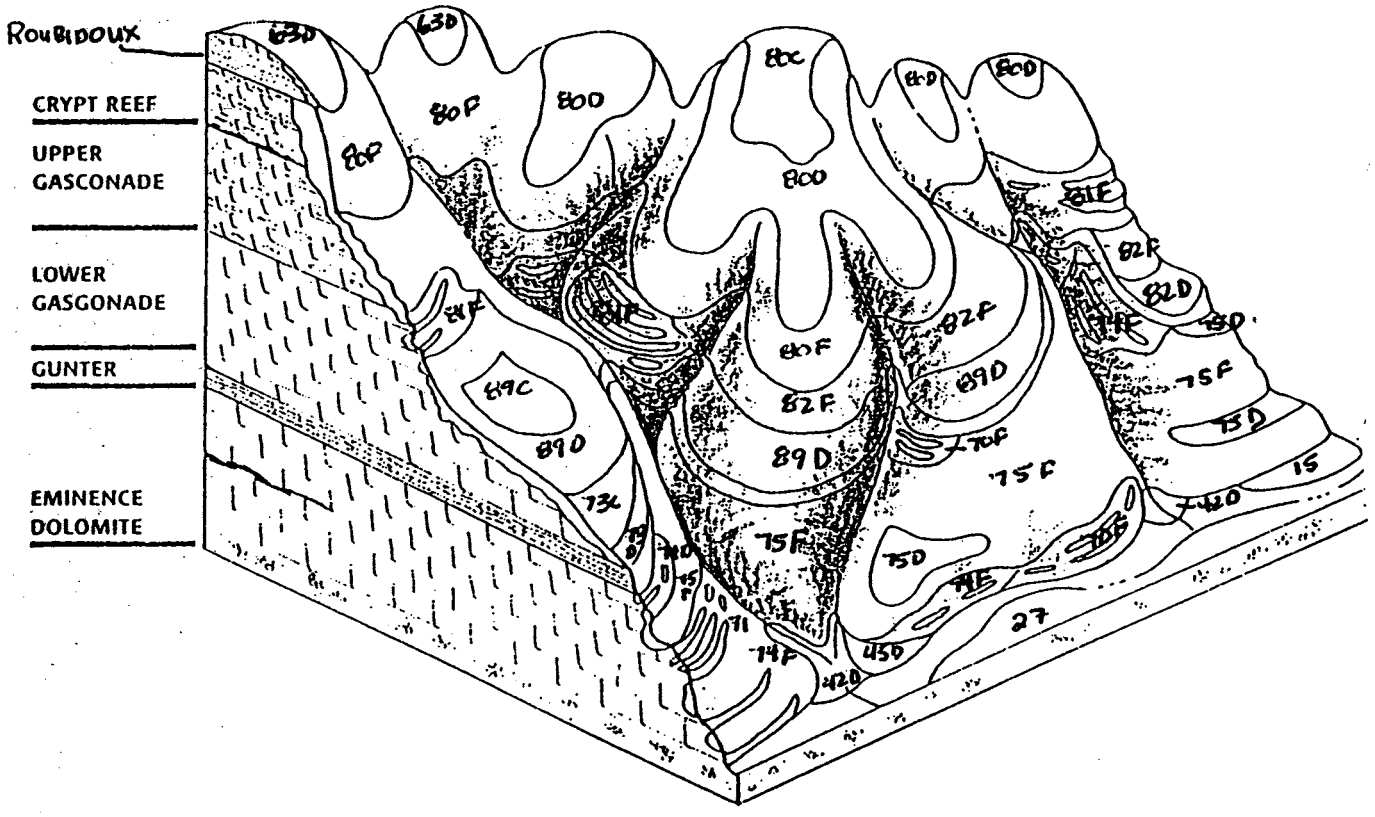

Figure 3.—*A three-dimensional representation of stratrigraphic- and landform-related soils in a dissected portion of the Ozark Highland landscape. Specific soils are delineated by lines and and identified by mapping symbols (63D, 80F, etc.). This figure illustrates the importance of geologic strata on soil distributions in a dissected Ozark landscape. From Meinert* et al. *(1997).*

Hammer 1992). Knowing how to recognize depositional from erosional surfaces is a key to locating buried soils which preserve soil features inherited from past vegetation communities. An excellent buried savanna Mollisol (prairie soil with a thick surface horizon) recently was exhumed at Ha-Ha Tonka State Park just below a ridge summit. A monolith was taken for subsequent display at the park's tourist center. Laboratory analyses are being conducted on samples taken from the profile. A recent visit to upland summits at MOFEP site 8 revealed silty depositional surfaces similar to the one containing a buried Mollisol at Ha-Ha Tonka. Soils at site 8 will be examined carefully to determine if they retain a record of savanna vegetation. Experienced pedologists and geomorphologists would expect to find "relict" soils of past conditions underlying depositional surfaces.

Striking differences in Ozark soil attributes can be found within relatively short distances and often within single soil profiles. The buried Mollisol mentioned in the previous paragraph was underlain by a red paleosol (old soil). Within 100 feet of the Mollisol were an Alfisol (soil with illuvial clay and high base saturation) and an Ultisol (soil with illuvial clay and low base saturation). Thus, three soil orders exist within an area that many people would perceive as a single geomorphic surface, in this case, an upper backslope.

The Sameness of Soils

This idea was partially addressed in the preceding paragraph. Pronounced differences in soil texture, stoniness, structure, base saturation, pH, and color exist over short distances on MOFEP sites. For example, a 5-acre site near a ridgetop on MOFEP site 1 contained distinct differences in base saturation in three soils within 60 m of each other (fig. 4). Base saturation is the percentage of a soil's exchange capacity which is occupied by nutrient cations.

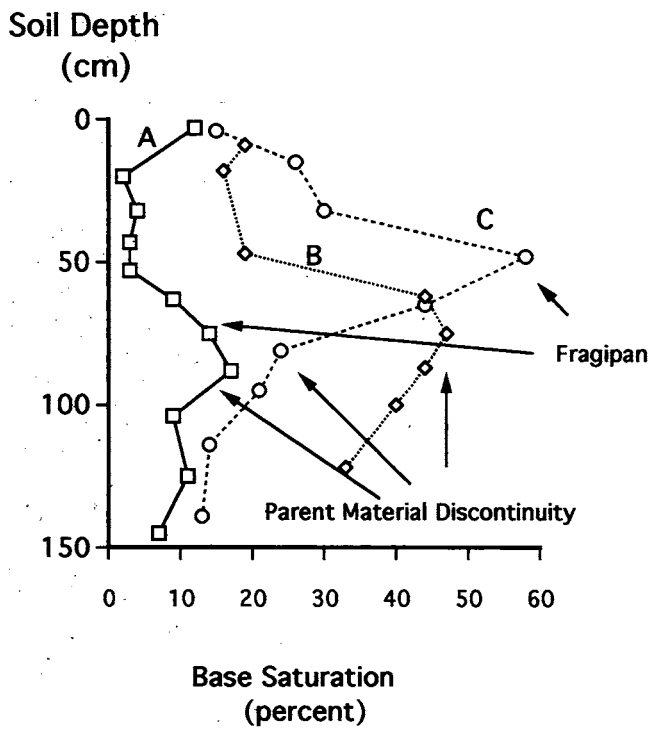

Figure 4.—*Soil depth distributions of base saturation for three soil profiles on MOFEP site 1. All three soil profiles were from the same small watershed and were within 60 m of one another. Fragipan horizons and parent material discontinuities are indicated.*

Aluminum, which is toxic to roots of many plant species, occupies much of the exchange complex in acid soils.

Soil A was on a convex position 60 m below soil C, which was on a shoulder surface with minimal microtopography. Soil B was on a concave position the same distance below soil C and about 10 m from soil B. Soil C had a silt loam surface to a depth of 74 cm, below which the clay content increased abruptly (from 17 to 59 percent). The textural discontinuity was below a fragipan. A fragipan is a layer of high bulk density and massive structure, the combination of which limit both downward percolation of water and infiltration by plant roots. The clay in this profile was primarily kaolinite. Kaolinite has a relatively low cation exchange capacity and is structurally unresponsive through wetting and drying cycles. Soil B appeared to have formed in two deposits of silty material, the upper of which probably was hillslope sediments of relatively recent origin. The sand content increased significantly below the discontinuity, which was at 80 cm. The clay mineralogy was primarily vermiculite, with a trace of montmorillonite. Vermiculite and montmorillonite have higher cation exchange capacities than kaolinite. They also swell when wet and shrink and harden when dry. Montmorilonite expresses these temporal physical attributes more strongly than vermiculite. Soil A contained an exceptionally thick fragipan overlying a leached, stony, red, silty clay loam residuum. The clay in the residuum was kaolinite. The clay mineralogy within a particular soil horizon is partially controlled by pH, which, in turn, is affected by parent material, intensity of leaching, and cation cycling.

Light-Colored Soils, Shallow Surface Horizons, and Low Fertility

Most residual materials in the soils we have observed are red. Laboratory analyses have indicated that the red color is inherited from iron oxides, which concentrate in well-drained soils as more mobile constituents are slowly leached. The reddening of soils requires geologic time periods and a warm, humid environment.

Surface horizons, particularly in concavities in lower slope positions, can be tens of cm thick. Soil B in the preceding section contained a relatively high organic carbon concentration (0.3 percent) to a depth of over 100 cm. This kind of carbon depth distribution can indicate a continuous input of organic material and sediments from higher landscape positions. More than 30 percent of the approximately 130 soil profiles on MOFEP sites for which laboratory data have been collected have base saturations exceeding 40 percent in some portion of the B-horizon. Alfisols and Ultisols co-exist within short distances.

Brown, Acid Lower Subsoil

This statement has been refuted in both preceding sections. About 40 percent of the examined soil profiles had B-horizons in which some portion contained a pH exceeding 5.0. Base saturations tend to increase in lower backslope positions and in soils on depositional surfaces. Clay content in B-horizons is correlated with mineralogy. Soils with 2:1 clay minerals (vermiculite and montmorillonite) have higher base saturations than B-horizons enriched with kaolinitic clay. Generally, but with some exceptions, soils on convex surfaces and soils higher in the landscape tend to be more intensely

leached and to have kaolinitic clay mineralogy. Red subsoils are common, but often underly several layers of hillslope sediment and/or mass movement materials.

No Sharp Contrasts in Soils, Gradational Changes

Sharp color, textural, and structural contrasts exist within and among soil profiles. Abrupt changes are associated with different parent materials within profiles, with different geomorphic surfaces within small and large watersheds, and with different geologic strata on backslopes. Alluvial soils have numerous abrupt changes over short distances, both horizontally and vertically. Abrupt differences in stone content are found on surfaces and within soil profiles. Buried stone lines, which indicate past erosional episodes (Ruhe 1956), are common. Abrupt textural discontinuities often occur across buried stone lines, because the stone lines often overly eroded argillic (enriched by illuvial clay) horizons.

Stone line genesis is illustrated in figure 5. Erosion selectively removes sand, silt, and clay, concentrating coarse fragments on the erosional surface. Subsequent deposits can bury the stone line. New surface (A and E) horizons form in the truncated profile, but have different textural and chemical attributes than surface horizons in nearby, uneroded soils.

Mass movements and hillslope sediments are the most common burial processes. Many existing soil surfaces have high concentrations of stones (sometimes called "armor plating" by soil mappers), which indicate that erosion has occurred relatively recently. High surface stone concentrations impede subsequent surface erosion. These attributes combine to support the idea of geologically recent accelerated soil erosion, probably caused by past land use practices in the Ozarks.

Remarkably Uniform Surface Soil, Lack of Correlation with Forest Variation

As previously mentioned, A-horizon thicknesses vary considerably across the Ozarks. Some of this variation is the natural consequence of soil-forming processes across the mosaic of aspects, slope steepnesses, slope lengths, slope surface

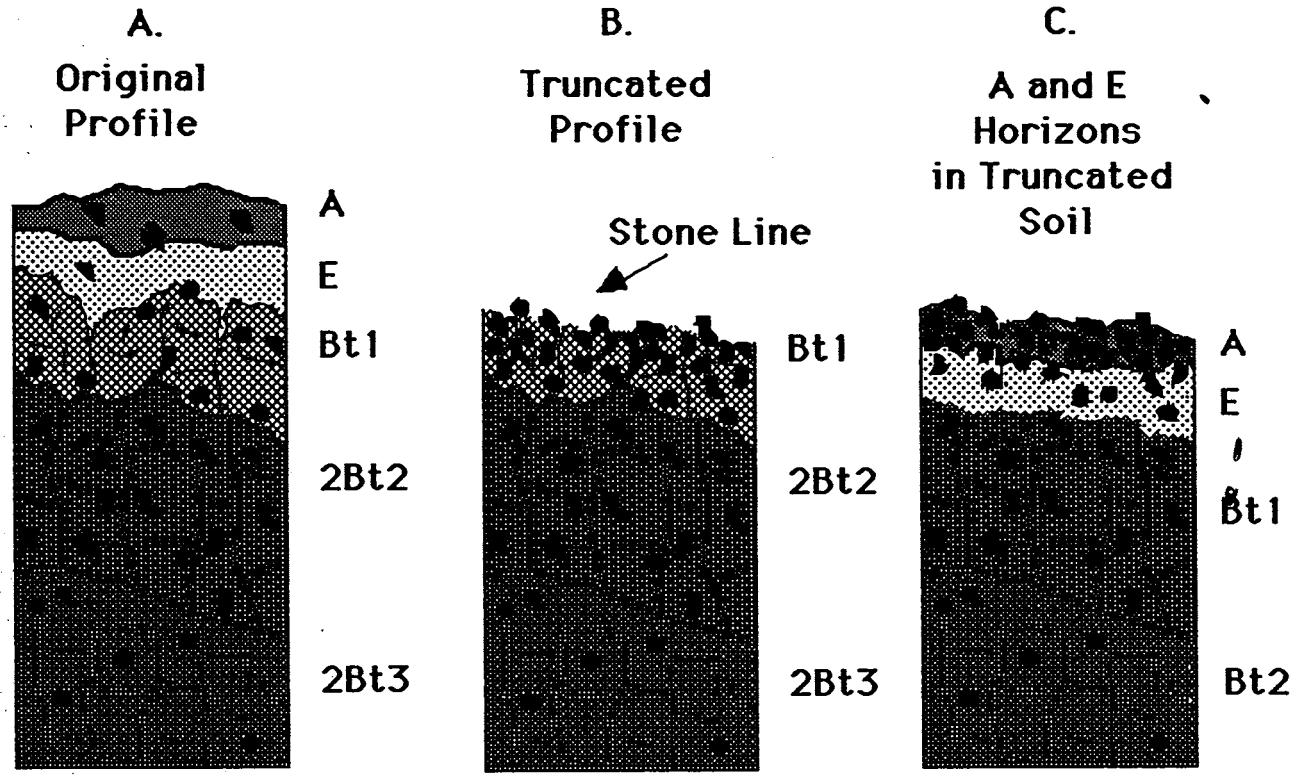

Figure 5.—*Representation of stone line development in an eroded soil. Part A is the uneroded soil. Part B illustrates the concentration of rock fragments on the eroded soil surface after finer particles have been removed. Part C illustrates the new soil surface (A and E) horizons developing after the new surface has stabilized.*

shapes, soil textures, and botanical communities within the Ozark uplands. The natural variation has been exacerbated by differential erosion and deposition resulting from human activities, including timber harvest, farming, home-building, and recreation. Table 3 presents A-horizon and combined A- and E-horizon thicknesses from 48 soil pits on the MOFEP sites. These profiles are from six small watersheds near interfluve ridge summits. They represent a small portion of the total area between interfluve summits and perennial streams. These data clearly illustrate variable horizon thicknesses both within and among watersheds.

Forest site index research has demonstrated the relationships of soil attributes with tree growth. Graney and Ferguson (1972) showed that shortleaf pine (*Pinus echinata* Mill.) site index in the Ozark uplands is correlated with aspect, slope shape, soil organic carbon in the A-horizons and depth to fragipan. McQuilkin (1972) observed increasing black oak (*Quercus velutina* Lam.) site index with increasing A-horizon thickness and with decreasing A-horizon sand content. Carmean's (1975) review of forest site productivity cites numerous instances in which site index has been correlated with surface horizon attributes.

On Ridges and on Slopes of Less Than 10 Percent, Most Ozark Soils Have a Fragipan

Fragipans are volumes of material within a soil profile which have higher bulk density and coarser structure than overlying and underlying materials. Fragipans generally restrict, but do not necessarily prohibit, the infiltration of water and penetration of plant roots (Witty and Knox

Table 3.—*Statistical information for soil surface horizon thickness in six Missouri Ozark Forest Ecosystem Project study plots. The plots represent three forest management treatments, a control, an uneven-aged cut, and an even-aged cut. All forest management treatments were observed on east- and west-facing aspects.*

Plot	Number of samples	Horizon thickness: Minimum	Maximum	Mean	Variance	Standard deviation
				cm		
A-Horizon						
Control east	10	2	7	5.1	3.2	1.8
Control west	6	2	4	2.5	0.7	0.8
Even-aged east	8	2	6	3.5	2.6	1.6
Even-aged west	9	3	8	4.7	3.0	1.7
Uneven-aged east	7	3	7	5.4	2.3	1.5
Uneven-aged west	7	2	7	4.1	3.5	1.9
All sites	48	2	8	4.3	3.3	1.8
A- and E-Horizons						
Control east	10	4	18	9.9	19.0	4.4
Control west	6	5	27	12.5	63.5	8.0
Even-aged east	8	5	10	7.8	3.9	1.9
Even-aged west	9	4	21	10.6	23.0	4.8
Uneven-aged east	7	7	15	10.6	6.3	2.5
Uneven-aged west	7	6	14	9.7	9.6	3.1
All sites	48	4	27	10.6	19.1	4.4

1989). Fragipans occur where relatively unweathered parent material overlies an older soil surface (Franzmeier *et al.* 1989). Fragipans seldom are in alluvial deposits, regardless of slope. Fragipans are not always on summits. They occur most often on broad interfluve divides on which loess was deposited during the Wisconsin glacial epoch. Fragipans may extend off the summit onto upper backslopes.

Fragipans Do Not Occur in Very Stony Soils or in Soils with a Reddish Clay Subsoil

Fragipans in the Ozark Highlands occur in stony soils, in red clay subsoils, and in soils with both stones and clay. Many fragipans in the Missouri Ozarks have physical morphology unlike fragipans in other parts of North America. The Natural Resources Conservation Service, as part of the accelerated soil survey in Missouri, has conducted special characterization investigations to quantify attributes of fragipans in Ozark soils. Less is known about these fragipans than others because, until recently, the Ozark soils had not been studied or mapped in detail.

Geologic Boundaries and Soil Boundaries Rarely Conform

The coincidence of soils with geologic materials is well documented throughout the world. Much work confirming the synergisms of geology, soils, and biota was conducted before Krusekopf's (1963) treatise. Coile's research, summarized in his 1952 treatise, is a noteworthy example. Fletcher and McDermott (1957) established that shortleaf pine growth in Missouri was restricted to four distinct geologic strata, and that the soils developed from those strata were unique. Fletcher and McDermott observed that distinguishing criterea were confusing and unclear for several of the commonly identified Ozark soils, including the Clarksville and Eminence.

Hack and Goodlett's (1960) investigation of soils, geomorphology, and forest ecology in the central Appalachians remains a classic template of how to conduct a systematic evaluation of forest site attributes. Their work revealed the importance of contemporary geomorphic processes as an important determinant of forest hydrology at scales important to forest tree growth within and among watersheds.

Meinert *et al.* (1997) in this symposium have clearly illustrated the importance of geologic strata as structural controls in the landscape and as determinants of soil and landform attributes in the Ozark Highlands. Meinert's work on MOFEP sites has revealed some important general soil-geologic relationships, some of which are portrayed in figure 6.

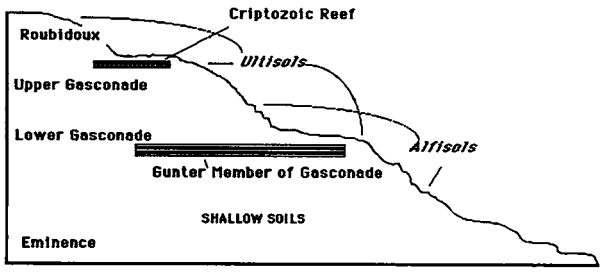

Figure 6.—*A hypothetical cross-section of the lower Ozark Highland landscape indicating soil and geomorphic attributes related to the geologic strata.*

Structural benches are caused by resistant geologic strata such as the Gunter sandstone and the cryptozoic reef. Backslopes in the Roubidoux and Upper Gasconade formations tend to be convex. The Lower Gasconade and Eminence formations produce concave backslopes, often with a "stair-stepping" pattern on backslope surfaces. Soils higher in the landscape tend to be more strongly leached and have lower base saturations with kaolinitic mineralogy. Lower landscape positions, particularly those with soils shallow to dolomite (carbonate rock which contains magnesium in addition to calcium), tend to have higher base saturations and clay mineralogy containing more montmorillonite.

Soil Erosion is not a Serious Problem in Most of the Ozark Region

Soil erosion <u>is</u> a serious problem over much of the Ozark region. Erosion has been widespread and can be locally severe. Disentangling the effects of erosion on species distribution and site productivity will be difficult. The evidence of past erosion is everywhere present in the geomorphic record. The most widespread and obvious is the presence of chert stone lines on much of the contemporary soil surface. Stone

lines were described previously in this manuscript. Other evidence of erosion is accumulation of silty materials in depressions, concavities, and hollows; presence of alluvial fans where upland drainages transition abruptly to nearly level bottoms; and multiple textural and material discontinuities in soil profiles.

Erosion probably has created important plant nutritional and hillslope hydrologic consequences over much of the landscape. In sloping forest landscapes, tree throw mass movement, soil creep and other processes combine to mix the upper portion of the soil profile. The differential effects of these processes are most readily observed in the spatial distributions of surface soil organic matter. Concave surfaces and lower landforms tend to collect forest litter from higher, surrounding areas, and have higher concentrations of organic matter. Wetter locations tend to have higher concentrations of organic matter than drier locations. Thus, one would expect higher concentrations of soil organic matter on north- and east-facing slopes than on drier and cooler south- and west-facing slopes. One also would expect higher soil organic matter concentrations in concave and lower landscape positions. This was confirmed in the Ozarks by 24 soil transects conducted by Udawatta and Hammer (1995). Results are partially summarized in figure 7.

Figure 7 reveals increasing soil organic matter concentrations downslope in concavities, but decreasing concentrations downslope on convexities. This distinction has never previously been reported in the literature. However, no single transect represented the trends indicated by the means of all the data. The system is so heterogeneous that trends are revealed only by means of many transects. Thus the concept of "representative" transects or "representative" soil profiles is suspect in this terrain.

Soil Boundaries are Too Rigid to Serve as Forest Type Boundaries

This is a very puzzling statement by Krusekopf. Considerable research has shown that soil series generally are poor indicators of forest site productivity because the soil series concept and mapping scales create soil inventory units which are too large and too variable to discriminate site productivity attributes (Carmean 1975, Grigal 1984, Hammer *et al.* 1991, Hammer *et al.* 1995, Hammer 1997b). Many land managers and resource scientists not familiar

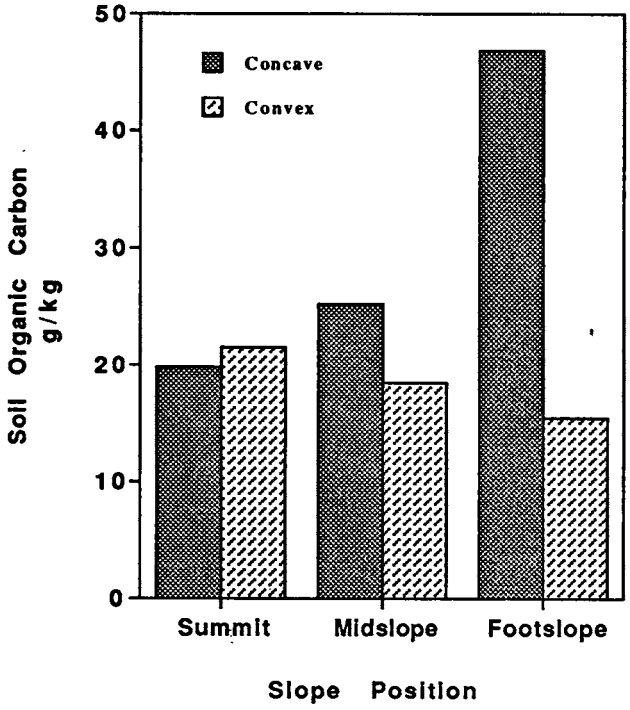

Figure 7.—*A-horizon soil organic carbon distributions along downslope transects on concave and convex surfaces in the Missouri Ozark Forest Ozark Project research area. Transects were primarily on sites 1 and 2.*

with soil survey techniques assume that map units delineate relatively homogeneous soil bodies. All soil mapping units, as astutely observed by an experienced forest biometrician, are hypotheses.

Soil taxonomy has a strong bias towards attributes of agricultural soils and is less suited for mapping forest soils (Grigal 1984, Hammer *et al.* 1995, Hammer 1997b). Mapping scale restricts the sizes of map units which can be delineated. The commonly used soil survey mapping scale of 1:24,000 allows a 5-acre delineation as the smallest mappable unit. Many soil mappers are not familiar with soil-landscape attributes which segregate forest species and contribute to their variable growth patterns.

Further compounding the problem is the multivariate nature of soils. Only a few combinations of soil attributes can be identified and mapped. If managers could afford use-specific maps (a map for roads, a map for species distribution, etc.), many would be surprised to learn that different delineations would be made for different uses of the same area.

The previously discussed synergism of soils and landforms has led many who study forest ecosystems to conclude that a mapping system which more closely identifies related soils and landforms is the most meaningful and useful mapping approach (Rowe 1984, Grigal 1984, Hammer *et al.* 1991, Hammer 1997b). This philosophy has formed the conceptual framework of the MOFEP soil inventory.

In general, moisture appears to be the most important soil factor that can be consistently related to forest type distribution, and then only as the extreme of soil moisture condition is reached.

This statement is generally true, but Krusekopf carried it to extremes. "The extreme of soil moisture condition" could be intrepreted to mean that extremely dry and wet sites are the ends of the continuum he perceived in soils and vegetation, and that only the ends of the continuum were observably different. The forest hydrology, soil, and vegetation mosaic is more subtle and complex, as has previously been discussed.

Nutrient Relationships

General Knowledge

Increasing evidence suggests that nutrient distributions influence forest species distributions, competitive interactions, and growth, yet little is known about Ozark forest nutrient dynamics. Remley's (1992) research in Ozark forest soils revealed tree root response to increased soil pH and to calcium inputs. Remely was unable to determine if the observed responses were to reduced aluminum activity or were positive responses to calcium. Unpublished subsequent work (G.S. Henderson, personal communication) strongly suggests a positive root response to calcium.

Donaldson and Henderson (1990) investigated nitrification dynamics in Ozark forest soils. Their work suggests that low soil pH and the presence of polyphenolic compounds combine to inhibit nitrification. Vegetational repression of nitrification could be a mechanism to conserve a limited biological nitrogen pool. Much remains to be learned about the nitrogen cycle and its effects on other nutrients in Ozark forests.

Phosphorus Dynamics

Phosphorus dynamics may be an important determinant of botanical interactions in the Ozarks. Phosphorus is known to be an important constituent of proteins and amino acids, and is a necessary nutrient for plant metabolism. Primary minerals, primarily apatite, are the sources of soil phosphorus, and the forms of phosphorus in soils are controlled by pH (Walker and Syers 1976). Thus, as soils weather, phosphorus tends to become limiting. As soil acidity increases, phosphorus becomes occluded by iron and aluminum, and the biologically available P pool is reduced. This well-established relationship is illustrated in figure 8.

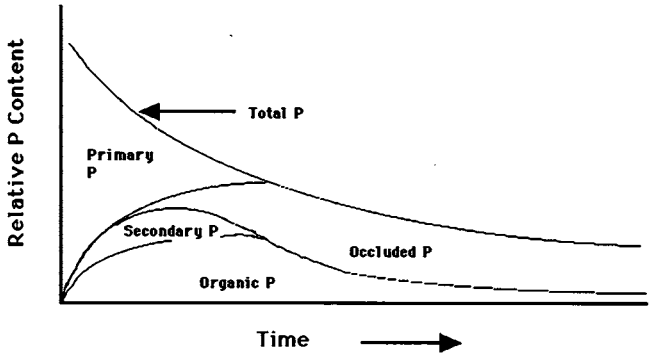

Figure 8.—*Changes in phosphorus form and abundance with weathering and time in a hypothetical soil (from Walker and Syers 1976).*

The primary source of phosphorus in pre-European settlement Ozark soils would have been the veneer of Pleistocene loess, much of which has since eroded. One soil component of the MOFEP soil research is a quantification of phosphorus forms and distributions. Preliminary results indicate that phosphorus concentrations are low in Ozark soils and that most of the total phosphorus is occluded by iron and aluminum. This finding conforms to established knowledge of phosphorus distributions in highly weathered soils.

However, phosphorus distributions are correlated to geologic parent materials as well as to hillslope sediments and silt materials which probably are of loessal origin. Figure 9 shows

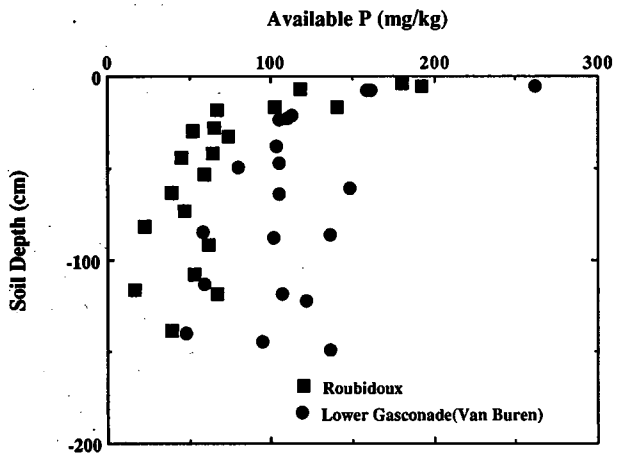

Figure 9.—*Available (organically complexed) soil phosphorus distributions with depth in soil profiles developed in residuum from Gasconade and Roubidous geologic strata on the Missouri Ozark Forest Ecosystem Project research area.*

that available phosphorus concentrations are higher at the surface and with depth in a soil associated with the Lower Gasconade formation than in a soil developed from Roubidoux residuum.

CONCLUSIONS

The Ozark soil landscape is a complex mosaic of parent materials and soil attributes whose relationships with the associated biota are poorly quantified. Early assumptions of ecosystem and soil homogeneity were inaccurate and were based upon supposition rather than systematically acquired data.

Most soils formed in multiple parent materials. Erosion has been widespread and locally severe. Important synergisms exist among soils, geologic materials, and geomorphic landforms. Trends occur in the landscape, but large sample numbers are necessary to identify patterns and relationships. Site-specific variability creates a "noisy" ecosystem in which single transects are unlikely to represent patterns. Data must be interpreted cautiously and in the context of local site attributes.

Much remains to be learned about the role of nutrients in vegetative behavior in the Missouri Ozarks. Preliminary examinations indicate more complex nutrient patterns and processes than are indicated in the literature. The interactions of nitrogen, and phosphorus are unknown, and the potential responses of native vegetation to calcium, nitrogen and phosphorus inputs are unmeasured.

The complex Ozark landscape presents a formidable challenge to scientists wishing to understand ecosystem pattern and process.

ACKNOWLEDGMENTS

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Microclimatic Characteristics in the Southeastern Missouri Ozarks

Jiquan Chen, Ming Xu, and Kimberley D. Brosofske[1]

Abstract.—Weather stations were established to monitor microclimatic variables, including air and soil temperatures, relative humidity, short-wave radiation, wind speed, and precipitation, from September 1994 to June 1996 at the MOFEP sites in southeastern Missouri. Diurnal and seasonal changes were compared between open and closed canopy areas for each of these variables. Data collected between June 1995 and October 1996 show that the southeastern Ozarks received about 45 percent of potential radiation and 1,119 mm rain. More variable wind and radiation were found during the winter. Small differences in microclimatic variables existed among the nine MOFEP experimental sites.

Microclimatic information is becoming a necessary component in integrated ecosystem studies because of its high correlation with many ecosystem properties and the crucial role it plays in affecting ecosystem processes. For example, numerous studies have found that solar radiation can be used as a very reliable (99 percent) predictor of an ecosystem's primary and net productivities (Whiting and Bartlett 1992). Air temperature and related quantities (e.g., degree-days) can serve as effective measurements of plant and animal development. Soil surface temperature functions as a bottleneck variable in determining the movement of small mammals, invertebrates, and amphibians across the landscape (Forman 1995, Kelsey and West 1997). In theoretical ecology, most stand dynamics models (e.g., ZELIG, PROGNOSIS, etc.) require climatic information as the driving force behind seed dispersal, regeneration, growth, mortality, and disturbance (Mladenoff *et al.* 1996, Urban *et al.* 1991, Wykoff *et al.* 1982). Resource managers usually find simple climatic summaries meaningful and helpful in their planning process.

As part of the Missouri Ozark Forest Ecosystem Project (MOFEP) (Brookshire *et al.* 1977), we conducted a study to provide quantitative summaries of microclimate in the forested landscape of the Ozark Highlands of southeastern Missouri. Specifically, our first objective was to quantify the changes in major microclimatic variables in an open area and a closed canopy area from June 1995 to August 1996; these variables included air and soil temperatures, relative humidity, vapor pressure and deficit, short-wave radiation, wind speed, and precipitation. Daily and monthly summaries as well as the diurnal differences between open and closed canopy were characterized. Our second objective was to compare the microclimates and their diurnal changes among the nine silvicultural sites (compartments) of MOFEP prior to harvesting. We intend to provide first-hand microclimatic data on diurnal and seasonal patterns for MOFEP's other ongoing projects.

METHODS

Study Area

MOFEP was initiated in 1990 by the Missouri Department of Conservation as a long-term study of the effects of alternative forest management practices on the ecological processes of those forests (Brookshire and Hauser 1993, Brookshire *et al.* 1997). The study area, ranging from 91° 01' to 91° 13' W and 37° 00' to 37° 12' N, consists of mature upland oak-hickory and oak-pine forest communities. The area lies in the Ozark Highlands Section of the Eastern Broadleaf Forest (Continental) Province (McNab and Avers 1994). Forests are dominated by black oak (*Quercus velutina* Lam.), white oak

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(*Quercus alba* L.), scarlet oak (*Quercus coccinea* Muenchh.), post oak (*Quercus stellata* Wangenh.), hickories (*Carya spp.*), and shortleaf pine (*Pinus echinata* Mill.). Geologically, this region is underlain mainly by Ordovician age dolomite with areas of Cambrian age dolomite and Precambrian igneous rocks also present (MO Geol. Survey 1979, Meinert *et al.* 1997). Weathering of the Ordovician and Cambrian age dolomites has resulted in a deep mantle of leached, very cherty residuum on the MOFEP study sites (Gott 1975). Soils on this area were formed mostly in residuum. The common series are Viburnum, Midco, Gepp, Bardley, Viraton, Poynor, and Clarksville (SCS unpublished data). Mean annual temperature and precipitation are 13.3°C and 1,120 mm, respectively (Barnton 1993). The study area includes 13 Ecological Land Types (ELT's, Miller 1981), of which ELT 17 (south- and west-facing slopes), ELT 18 (north- and east-facing slopes), and ELT 11 (ridge tops) make up 85 percent of the total area.

Data Collection

Long-term climatic changes were monitored by installing two permanent weather stations: one in an open glade in site 5 and one under a closed canopy in site 1. These stations were installed to quantify the local climatic conditions and changes over time, as well as to provide a database that can be used by other MOFEP research projects. Air temperature (T_a, °C) and relative humidity (h, percent) were monitored with Campbell Scientific, Inc. (CSI) 207 probes, solar radiation (R_t, $W.m^{-2}$) with LI-COR200S pyranometers, wind speed (v, $m.s^{-1}$) and wind direction (D) with R. M. Young wind sentry 3-cup anemometers, precipitation (P, mm) with CSI TE525MM tipping bucket rain gauge, soil moisture (M, Bar) with CSI 257 moisture blocks, and soil heat flux (H, $w.m^{-2}$) with CSI HFT1 plates. T_a, h, R_t, v, D, and P were measured at 2 m above the ground. Custom-built thermocouples were used to measure air temperature at 0, 0.5, 1.0, 1.5, and 2.0 m above the ground and soil temperature (T_s, °C) at 0, 5, 10, 15, and 20 cm in the soil. Heat flux plates were buried 2 cm in the soil, and soil moisture blocks were buried between 10 and 20 cm in the soil. The short-wave radiation results collected by LI-COR200S are equivalent to the photosynthetically active radiation (PAR) used by green plants. CSI dataloggers (CR10 and 21X) were programmed to sample every 10 seconds and average every 20 minutes for final storage. Data from June 6, 1995 to August 30, 1996 are included in this study.

A weather station was installed in each of nine sites by selecting a vegetation plot in the center of the site. To avoid trampling of plants during weather station installation and maintenance, stations were installed about 10 m from the west marking rod of the selected vegetation plot. Plot numbers are 43, 34, 36, 37, 38, 28, 30, 25, 34 for sites 1 to 9, respectively (see Brookshire *et al.* 1997 for site and plot locations). These stations were in place from early September 1994 until June 30, 1995, to measure T_a, h, v, R_t, and T_s.

Data Analysis

Monthly statistics were computed for each variable. Soil water potential (bars) was calculated from sensor resistance and soil temperature using the equation developed by Thompson and Armstrong (1987). Effective accumulative temperature (EAT, >5°C) for each month was calculated as the sum of the daily average temperature (T_d) minus 5°C, or

$$EAT = (T_d - 5)$$

EAT, similar to degree-days, has been accepted as an effective means of predicting productivity and other growth measurements of ecosystems (Urban *et al.* 1991). A computer model was developed to compute the monthly average potential solar radiation of the region (91°W and 37°N) for 1995-1996 using the algorithms of NAO (1991) so that atmospheric interception (i.e., percentage of solar radiation reaching the ground from the solar constant, 1367 $W.m^{-2}$) can be quantified. Regression and ANOVA (Neter *et al.* 1990) techniques were used to predict missing data values and to quantify the significance levels for microclimatic comparisons between the forested and open areas.

Vapor pressure deficit (D) is a critical climatic variable affecting many physiological and biological processes (e.g., photosynthesis, evapotranspiration). In this study, we calculated D using simultaneous measurements of air temperature and relative humidity as $D = E_s - E_a$, where E_s is the saturation vapor density ($g.m^{-3}$) for a given T_a, and E_a is the vapor density computed as: $E_a = E_s * h/100$; E_s is calculated as (Campbell 1977):

$$E_s = \frac{P_s}{4.62*10^{-4}*(T_a+273.15)}$$

where P_s is the saturation vapor pressure (kPa) estimated using the empirical parameters provided by Lowe (1977):

$$P_s = (6.1078+T_a(0.44365185+T_a(0.014289458+T_a(2.6506485*10^{-4}+T_a(3.0312404*10^{-6}+T_a(2.0340809*10^{-8}T_a))))))/10$$

where T_a is the air temperature in Celsius, and h is the simultaneous relative humidity in percent.

RESULTS

Monthly mean solar radiation received at the open canopy MOFEP site followed a classic cosine shape over the 24-hour period, which peaked at 237.2 W.m^{-2} in June and reached its minimum of 63.8 W.m^{-2} in December (fig. 1a). These energy counts are about 37 to 59 percent of the potential radiation. The atmospheric transmissivity remained at a relatively stable level of about 45 percent but peaked in October (fig. 1b). The light level inside the forest demonstrated clear responses to the dynamics of canopies—low during the growing season and high after leaf fall. The highest light level was detected in April before leaf shroud (fig. 1a). During the full leaf period (June to October), the light level inside the forest was about 15 percent of full sunlight. This value exponentially increased to 62 percent in April (fig. 1b).

Overall, the study area is predominated by southeasterly and northwesterly winds (fig. 2). This pattern remained the same for both summer (May to October) and winter (November to April) periods, except that winds blew from the south rather than the southeast during the summer. The 20-minute wind speed for the open environment ranged from 0.30 m.s^{-1} in June to 0.91 m.s^{-1} in April, with lower speeds in the summer and higher speeds during the spring (table 1). The maximum wind speed was monitored in January 1996 at 4.55 m.s^{-1}. Average wind speeds inside the forest were lower during the summer but higher in winter when greater turbulence existed in the forest. As indicated by variation in wind direction (degree), it was apparent that wind direction was much more stable inside the forest than in the open area (table 1).

The annual precipitation sampled between June 1995 and October 1996 was 1,119.70 mm, with more than 130 mm of rainfall in each of April, May, and September (39.9 percent) (table 2). February and August had fewer rainy days and lower precipitation during the sampling period. However, the highest 20-minute rainfall events were monitored in the summer (May to September).

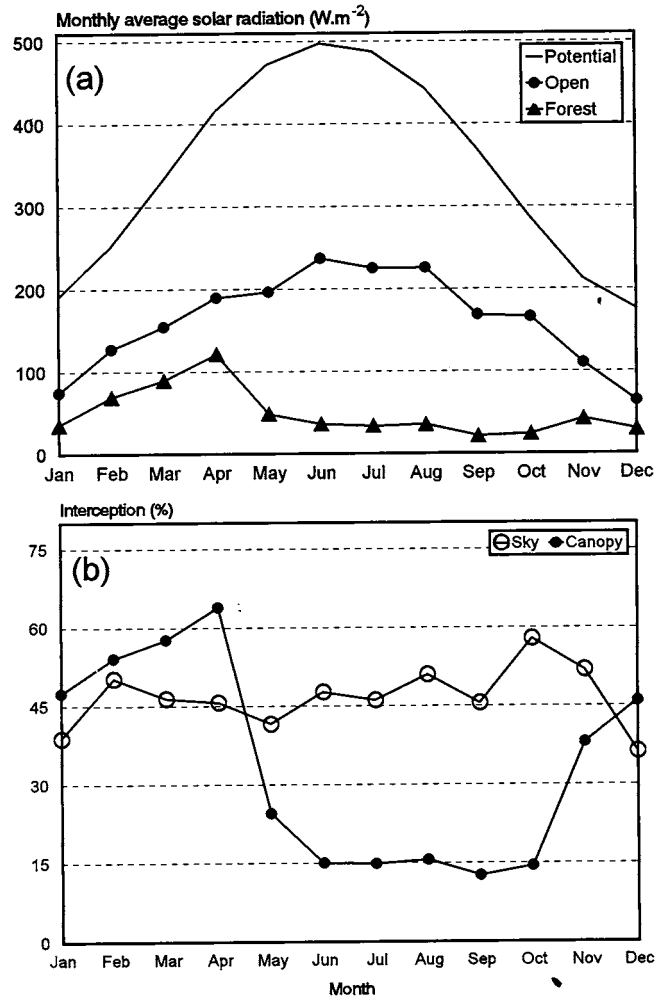

Figure 1.—*Seasonal changes in (a) potential radiation (W.m^{-2}) in the open area and under a closed canopy in the southeastern Missouri Ozarks and (b) interception rate by the atmosphere (i.e., turbidity) and canopies.*

Unique seasonal changes in radiation, wind speed, and precipitation were generally responsible for the seasonal pattern of soil heat flux through energy exchange. Overall, the soil seemed to serve as a heat sink in the summer and a heat source in the winter for both forest and open ecosystems (fig. 3). The soil heat fluxes in both ecosystems were more variable from February through April than any other

Table 1.—*Seasonal changes in wind speed (m s^{-1}) and wind direction (degree) in forest and a forest opening at MOFEP sites, 1995-1996.*

Location	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Year
Forest opening													
Mean V[1]	0.74	0.66	0.73	0.91	0.59	0.30	0.32	0.35	0.36	0.54	0.66	0.46	0.55
Max V	4.55	2.29	3.26	3.56	2.66	2.00	1.84	1.84	2.11	3.09	2.85	2.47	4.55
Swd[2]	40.2	42.7	39.1	45.0	40.8	26.3	28.5	26.1	25.9	31.1	42.9	37.6	35.5
Forest													
Mean V	0.91	0.89	0.91	1.05	0.37	0.22	0.23	0.22	0.23	0.23	0.47	0.84	0.55
Max V	3.16	3.19	3.60	3.13	2.92	1.18	1.19	0.84	1.09	1.43	3.11	2.28	3.16
Swd	21.7	23.2	25.3	24.2	16.7	10.3	12.9	10.8	10.4	14.0	20.7	22.6	17.8

[1] V = wind speed.
[2] Swd = standard deviation of wind direction.

Table 2.—*Seasonal changes in monthly precipitation (mm), rainfall intensity (mm/20min), and rainy days in a forest opening in the southeastern Missouri Ozarks.*

Forest opening	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Year
Precipitation	98.8	21.4	107.2	163.2	151.6	67.7	104.5	40.0	131.6	80.6	55.8	97.4	1,119.7
Max RI[1]	34.8	6.9	41.9	31.2	42.4	46.0	50.0	35.1	47.5	9.4	40.9	28.7	50.0
Rainy days	15	8	11	11	15	10	10	8	11	11	16	13	139

[1] RI = rainfall intensity in mm/20 minutes.

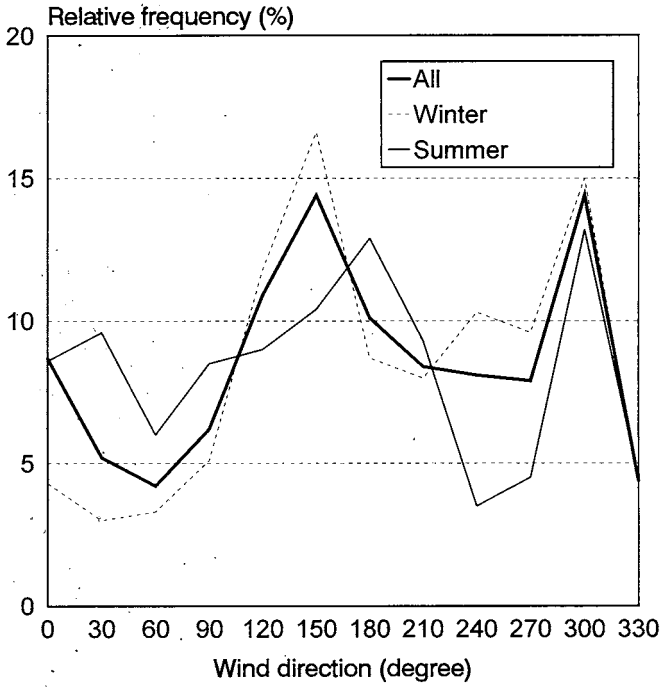

Figure 2.—*Prevailing wind direction (degree) during the summer (Mat - October) and winter (November - April) in the southeastern Missouri Ozarks (1995-1996).*

time of year. It also seemed that soils in the open area warmed up earlier in the spring (February) than the soils inside the forest. A greater fluctuation in heat flux was observed in the open area than inside the forest. The soil in the open area received more energy in the summer, but it also lost more in the winter. The annual budget was 16.08 $W.m^{-2}$ for the open soil and -25.91 $W.m^{-2}$ for the forest soil. This suggests there is horizontal energy transportation from forest openings (source, e.g., glade, gap, road, power line) to forests (sink), viewed over a long time period.

Seasonal changes in mean air temperature were skewed toward a maximum in August at 24.75°C, with the minimum at -0.42°C in January (table 3). A maximum temperature of 38.74°C was monitored in August 1996 and a minimum of -25.19°C in February 1996 at the open station. The differences in air temperature and effective accumulative temperature between the forested and open areas were not significant in monthly average ($P > 0.34$), but were significant for maximum, minimum, and fluctuation ($P < 0.01$).

Relative humidity of the open area demonstrated a clear seasonal pattern and was consistently lower than that in the forest; the highest monthly average was close to 50 percent in August and September (fig. 4). In winter, relative humidity in the open area stabilized at about 26 percent through April, when the forest was the driest. Inside the forest, monthly averages between May and September ranged from 73 to 84 percent.

The seasonal patterns of absolute air moisture (i.e., vapor density) in both the forest and open areas followed a sinusoidal model, with high density between May and September and a peak in August (fig. 5a). Monthly averages of vapor density in the open area were consistently lower than in the forest; the differences ranged from

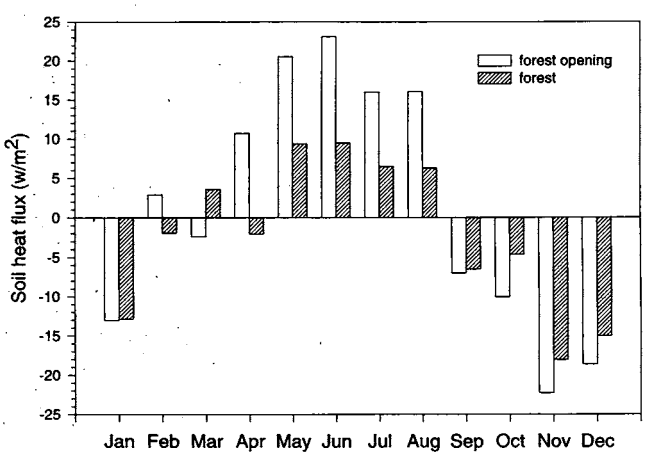

Figure 3.—*Seasonal changes in monthly average soil heat flux ($W.m^{-2}$) in the open and under a closed canopy in the southeastern Missouri Ozarks (1995-1996).*

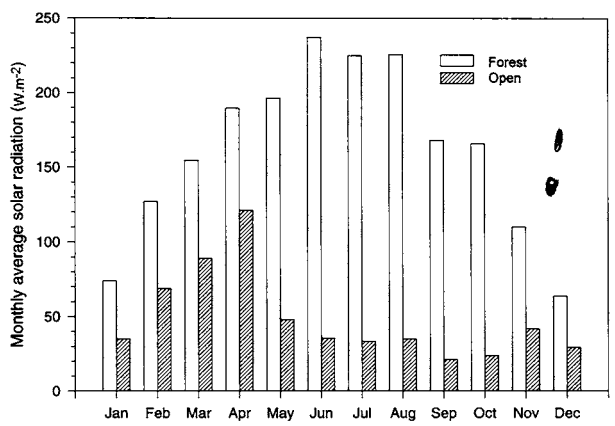

Figure 4.—*Seasonal changes in monthly average relative humidity (percent) in the open and under a closed canopy in the southeastern Missouri Ozarks (1995-1996).*

Table 3.—*Seasonal changes in air temperature (°C) in forest and a forest opening at MOFEP sites.*

Location	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Year
Forest opening													
Mean	-0.4	3.8	4.9	12.5	19.7	22.3	23.8	24.8	17.3	13.6	6.3	2.0	12.5
Max	22.0	29.8	23.3	29.0	33.8	36.2	38.3	38.7	32.4	28.9	21.2	21.3	38.7
Min	-19.8	-25.2	-15.9	-4.8	4.1	8.0	9.9	12.0	-1.3	-2.9	-9.4	-18.6	-25.2
Mean DF[1]	13.0	16.6	15.1	17.0	13.5	14.8	13.9	15.2	13.9	18.7	14.4	10.7	14.7
Max DF	31.9	29.7	23.0	27.8	22.2	19.5	19.7	21.2	22.4	28.5	22.2	18.9	31.9
Min DF	3.4	5.8	4.4	8.4	5.4	3.6	5.0	6.8	5.7	4.3	3.4	2.4	2.4
EAT[2]	20.7	94.3	69.3	225.0	455.5	518.8	582.5	612.3	367.9	266.0	68.7	42.0	3,323.0
Forest													
Mean	-0.5	3.8	4.9	12.7	19.5	22.0	23.6	24.8	17.4	14.4	6.1	1.9	12.6
Max	21.5	27.2	22.6	28.6	31.9	33.0	35.8	36.6	29.7	26.8	20.6	20.5	36.6
Min	-17.3	-22.2	-14.7	-1.8	7.4	11.0	12.4	14.6	14.7	0.6	-7.5	-17.0	-22.2
Mean DF	11.1	13.8	12.8	14.1	9.8	9.9	9.7	11.1	10.0	12.1	12.4	8.2	11.3
Max DF	31.8	24.7	22.0	20.6	17.5	12.9	13.9	16.9	16.8	21.7	19.2	15.7	31.8
Min DF	3.3	5.6	4.3	7.5	3.9	2.9	2.7	4.9	3.3	3.7	2.1	1.9	1.9
EAT	26.4	99.3	73.0	231.7	448.5	510.6	575.4	615.1	373.3	292.0	64.6	65.0	3,374.9

[1] DF = daily difference.
[2] EAT = effective accumulative temperature.

2.57 g.m^{-3} in March to 10.12 g.m^{-3} in July. Regardless of the high vapor density inside the forest, vapor pressure deficits were observed throughout the year (fig. 5b) with extremes in May through August (15-20 g.m^{-3}). Vapor pressure deficit in the open area was even higher, 4.13 g.m^{-3} in January and 19.74 g.m^{-3} in July, compared with vapor pressure deficits of 1.44 g.m^{-3} and 8.22 g.m^{-3} in the forest during the same time periods.

Although soil temperatures in both forested and open areas maintained seasonal patterns similar to but more stable than air temperatures, extremes were detected in soil surface temperature in the open area (table 4) that exceeded > 60°C between May and August. The lowest surface soil temperatures were -7.46°C and -8.07°C for the opening and the forest, respectively. Also, significant differences for soil temperature at 5, 10, 15, and 20 cm between the forest and the open were detected ($P < 0.001$).

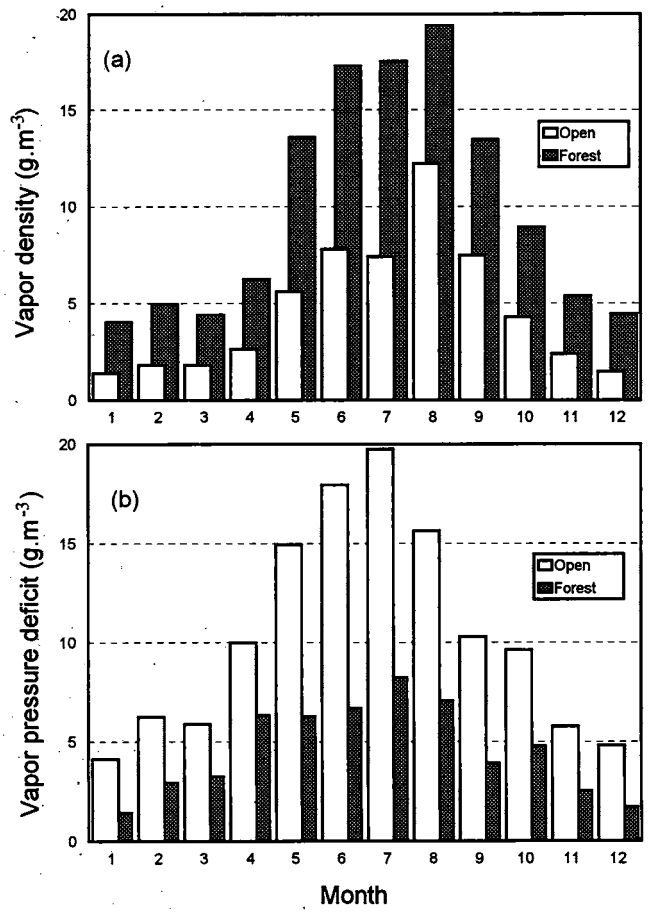

Figure 5.—*Seasonal changes in monthly average (a) vapor density and (b) vapor pressure deficit in the open and under a closed canopy in the southeastern Missouri Ozarks (1995-1996).*

Soil moisture measured by the Watermark soil moisture block has a nonlinear response to its resistance (Thompson and Armstrong 1987), which can be an indirect measurement of soil moisture (fig. 6). It seemed that the drier season began in late May (Julian day 140) and lasted to the end of October (Julian day 300). As indicated by monthly averages, maximum values, and minimum values, soil moisture in the open area was much more variable than that inside the forest, with extremes in mid-July and mid-August, likely caused by limited rainfall in June and August (see table 2).

Diurnal changes of all climatic variables in the open and closed canopies were clearly different for both winter and summer. Inside the forest, a more stable climate appeared to exist. In addition, the open area had higher daytime temperatures (T_a and T_s), lower relative humidity, and higher solar radiation (fig. 7). Soil heat flux was greater during the day at the open station, but lower at night during both summer and winter. The soil inside the forest was wetter in the summer and drier in the winter than that in the open area. Daytime wind speeds inside the forest were higher than those in the open in winter, but generally were lower in summer, when wind speeds inside the forest were relatively stable. At night, wind speeds were similar in both forest and open areas. For all microclimatic variables except wind speed, their diurnal fluctuations appeared smaller in the winter.

The diurnal changes in microclimatic conditions at the nine MOFEP sites were very similar for both winter and summer (fig. 8), except that differences in wind speed and nocturnal relative humidity were clearly greater in winter. Short-term sun flecks also seemed more common in the summer than in winter, as indicated by extremely high 20-minute averages in short-wave radiation inside the forest (fig. 8c). The diurnal differences in soil temperature at 5 and 20 cm were smaller in the summer than in the winter. Although microclimatic patterns for the nine sites were similar seasonally, they did differ diurnally. Differences in relative humidity between sites, for instance, were much greater during the night than during the day.

Table 4.— *Seasonal changes in soil temperature (0 to 20 cm) in forest and a forest opening (°C) at MOFEP sites (1995-96).*

Location	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Year
Forest opening													
Mean Ts0[1]	2.7	7.2	8.8	15.2	23.1	28.6	29.4	29.7	22.1	18.0	9.4	4.9	16.6
Mean Ts5	3.4	6.9	8.5	14.3	21.5	25.9	27.2	27.5	22.0	18.0	10.1	5.6	15.9
Mean Ts10	3.7	7.0	8.6	14.2	21.1	25.3	26.7	27.1	22.1	18.1	10.4	6.0	15.9
Mean Ts15	4.0	7.0	8.7	14.0	20.7	24.8	26.4	26.7	22.1	18.3	10.8	6.4	15.8
Mean Ts20	4.4	7.0	8.7	13.8	20.4	24.5	26.5	26.5	22.2	18.4	11.2	6.8	15.9
Max Ts0	21.5	32.5	41.0	43.1	61.5	66.8	68.0	61.5	46.8	45.0	24.7	25.8	68.0
Min Ts0	-6.7	-7.5	-6.7	-0.8	8.1	12.8	14.9	16.8	5.2	3.6	-1.3	-6.7	-7.5
Forest													
Mean Ts0	2.9	5.1	5.8	13.8	17.5	20.5	22.1	22.6	17.4	13.9	7.9	5.0	12.9
Mean Ts5	3.4	5.2	6.1	11.1	16.8	19.5	21.1	21.7	17.6	14.1	8.4	5.5	12.6
Mean Ts10	3.6	5.2	6.2	11.0	16.5	19.3	20.9	21.5	17.7	14.3	8.7	5.8	12.6
Mean Ts15	4.0	5.3	6.4	10.8	16.2	18.9	20.6	21.2	17.9	14.6	9.2	6.2	12.6
Mean Ts20	4.3	5.4	6.5	10.6	15.9	18.6	20.4	21.0	18.0	14.8	9.6	6.6	12.6
Max Ts0	12.0	20.2	37.3	25.2	28.1	28.9	31.1	32.9	24.7	21.7	15.6	13.7	32.9
Min Ts0	-3.5	-2.2	-8.1	4.6	11.0	13.2	16.6	17.3	7.7	6.6	1.6	0.1	-8.1

[1] Ts0, Ts5, Ts10, Ts15, and Ts20 indicate soil temperature at depths of 0, 5, 10, 15, and 20 cm, respectively.

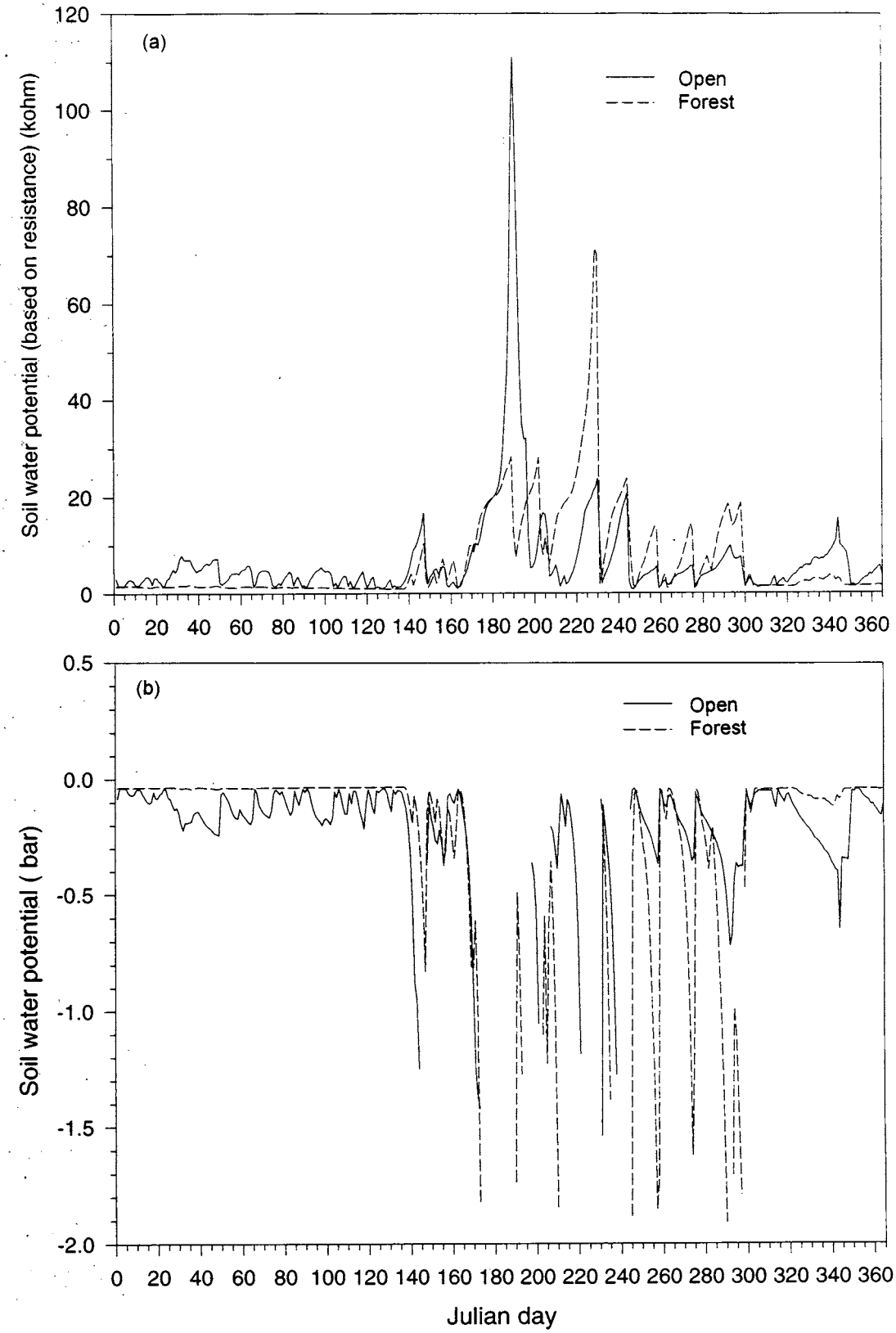

Figure 6.—*Seasonal changes in resistance of (a) Watermark soil moisture block and (b) soil water potential in an open and a closed canopy in the southeastern Missouri Ozarks (1995-1996).*

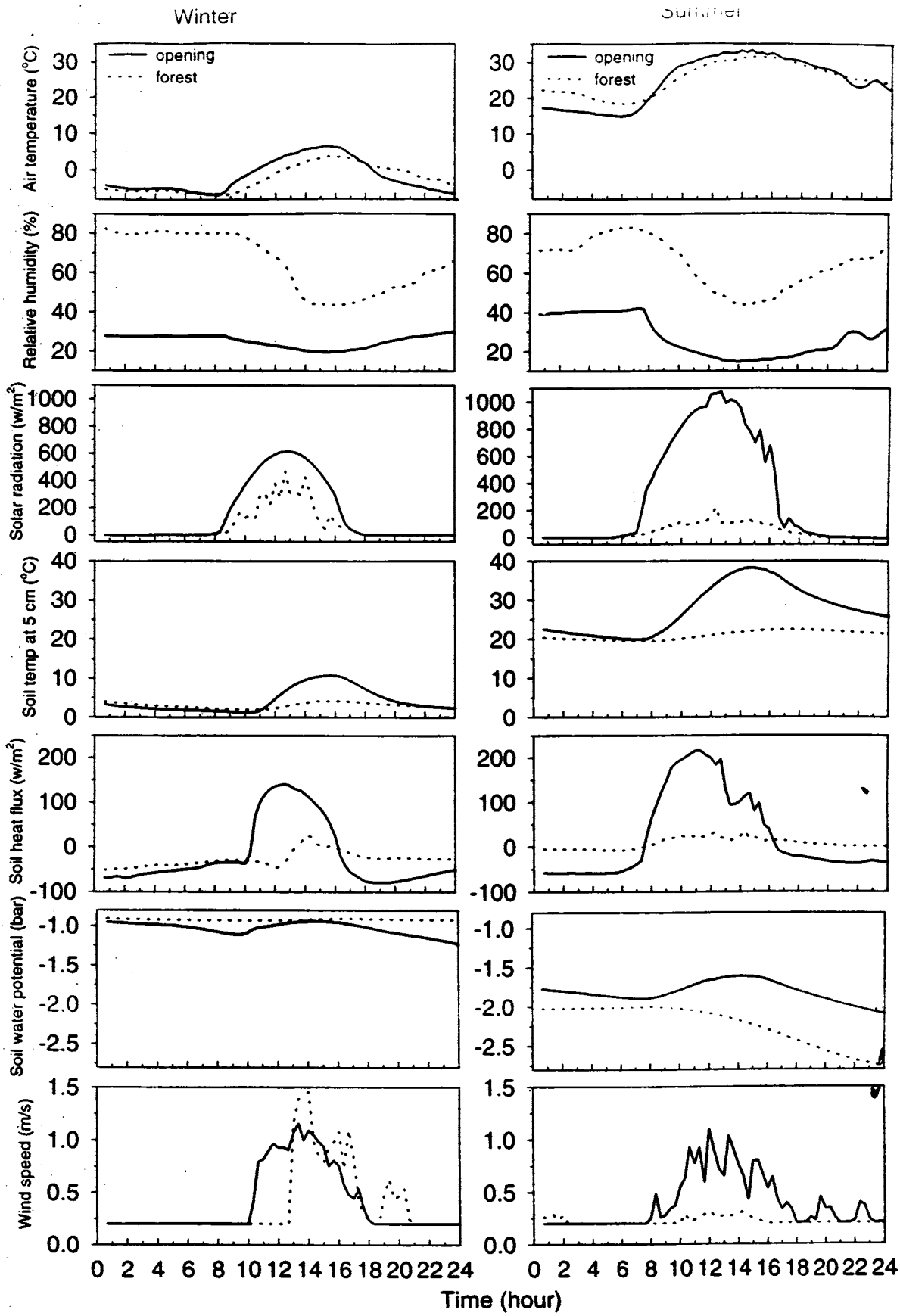

Figure 7.—*Diurnal changes in microclimatic variables in an open area and under a closed canopy for the summer (July 16, 1996) and winter (January 24, 1996) in the southeastern Missouri Ozarks.*

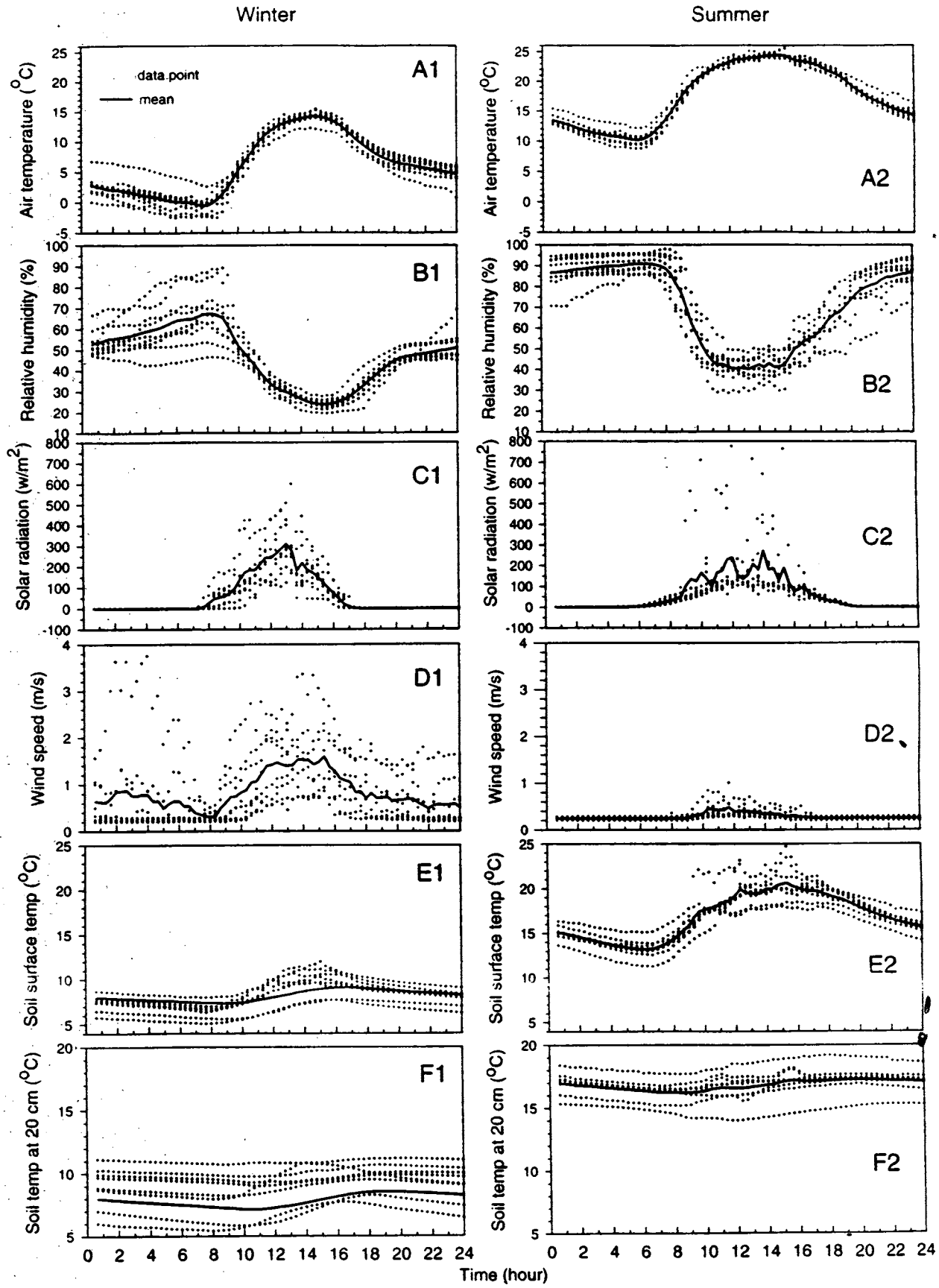

Figure 8.—*Microclimatic variability of diurnal patterns in six microclimatic variables among nine MOFEP sites in the winter (December 1, 1994) and summer (June 13, 1995).*

DISCUSSION

The MOFEP sites are located in the western end of the U.S. continental climate zone, which is characterized by hot, humid summers and warm winters (McNab and Avers 1994, Ward 1925). The amount of solar radiation received on the ground was about 45 percent of the solar constant (fig. 1b), which is slightly lower than an average atmospheric transmissivity of 0.5 (or 0.47-0.53) for most terrestrial ecosystems on the Earth (Campbell 1977). This is probably due to the high rainfall and greater number of rainy days (>30 percent) (table 2). Higher air turbidities were recorded for February, October, and November during the sampling period, during which 50 to 60 percent of potential solar radiation reached the ground. A strong negative correlation (R^2 = 77 percent) exists between monthly precipitation and atmospheric transmissivity.

Soil heat fluxes collected at MOFEP sites suggest that spring is a very dynamic time period for both open and forest environments (fig. 3, tables 3-4). This variable climate for the area may significantly affect ecological and biological processes. For example, Cecich (personal communication) found it very difficult to predict oak flowering times in southeastern Missouri, largely because of this variable climate during the spring. In addition, soils in the open area received a positive annual energy budget, suggesting that forest clearing greatly increases the energy input into the system, or causes a general increase in local temperatures. This conclusion can be further validated based on our long-term monitoring program at MOFEP's harvesting sites. A balanced soil heat budget is expected when various partial harvesting techniques are applied.

The snapshot results included in this study are based on limited climatic data from an open and a closed canopy area and, therefore, cannot represent the microclimatic patterns over longer periods of time and across heterogeneous landscapes. Over temporal scales, the scientific community has been generally convinced that data collected during short time periods will be misleading due to the natural dynamics of the physical environment and gradual changes in global climate (Gates 1993, Greenland and Swift 1988). Across the landscape, microclimates are greatly modified by landform (e.g., slope, aspect, and elevation), vegetation, soil, disturbance (e.g., harvesting), and other landscape components (e.g., roads, streams, edges, etc.) (Chen *et al.* 1993, 1995; Geiger 1965). Scientific investigations of ecological processes must be site- and time-specific in defining landscape patches and mosaics (Chen *et al.* 1996). At smaller scales, microclimatic variability was found to be significant in both the Ozark forest (Xu *et al.* 1997) and elsewhere (Chen and Franklin 1997). In conclusion, we suggest that a long-term monitoring project on microclimate in conjunction with site-specific measurements of climatic responses to land type, forest structure, and soil types are needed for the MOFEP program.

Linkages between our results and other ecological properties (e.g., regeneration, and soil processes such as decomposition, mineralization, microbial activities, etc.) are urgently needed to make the microclimatic study vigorous and meaningful. MOFEP provides a very unique opportunity for such integrations. Questions and hypotheses, such as those concerning effects of microclimate on the development and distribution of fungi, plant phenology, outbreaks of diseases, insects, or fires, regeneration, and movement of wildlife across the landscape, are also scientifically intriguing and necessary for managers. For example, various studies have demonstrated that air and soil temperatures are critical variables affecting the movement and distribution of amphibian and avian species (e.g., Kelsey and West 1997). We expect a high correlation between our data and amphibian abundance and frequency at the MOFEP sites, which has been studied by Renken (1997). As another example, soil temperature and moisture have been documented to be the primary variables responsible for fungi development through their effects on rhizomorph growth (Redfern and Filip 1991). If similar correlations between soil temperature/moisture and armillaria root disease exist, our capability to predict outbreaks will be greatly enhanced through a linkage between this study and MOFEP's armillaria project (e.g., Bruhn *et al.* 1997).

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Historic Shortleaf Pine (*Pinus echinata* Mill.) Abundance and Fire Frequency in a Mixed Oak - Pine Forest (MOFEP, Site 8)

Richard P. Guyette and Daniel C. Dey[1]

Abstract.—Historic and present day shortleaf pine (*Pinus echinata* Mill.) abundance was measured and compared using 84 plots along 16 transects in site 8 of the Missouri Ozark Forest Ecosystem Project. Remnant pine stumps were used to estimate historic pine density and to construct a dendrochronological record of fire frequency. There has been a 66-percent reduction in the relative abundance of pine from historic levels (circa 1900) within the study area. Present day pine abundance is only 21 percent of historic levels on slopes and only 25 percent of historic levels on ridges. Historic and present day pine abundance was not significantly different on toe slopes and in riparian areas. Elevation, slope, and aspect were significantly ($P < 0.05$) correlated with changes in pine abundance. Pine abundance was reduced at 60 percent of the plot locations, increased at 20 percent of the plots, and remained the same at 9 percent of the plots. Mean fire-free intervals were 6.3 years for the period 1701 to 1820 and 3.1 years for the period 1821 to 1900. Patterns in the change in pine abundance were consistent with changes in fire frequency and expected fire behavior at a landscape level. In some areas, such as riparian or road corridors, it was difficult to estimate historic pine abundance because of the disturbance of pine stumps and remnants.

Knowledge of historic shortleaf pine abundance and fire frequency in the oak-pine forests of the Ozarks has important implications for the ecology, regeneration, and perpetuation of this native forest cover. The different chemistry, anatomy, and physiology of gymnosperms adds to the diversity of Ozark forests and may have unknown ecological implications. In a mixed oak-pine forest, the crowns of shortleaf pine emerge above the hardwood canopy layer. Shortleaf pine crowns shade and shelter the surrounding forest in all seasons and provide the only canopy shelter from late fall to spring. The crowns of pines growing above the hardwoods add edge habitat to the surface of the forest canopy, changing its fractal dimensions. Kritz (1989) found that both the Cooper's (*Accipiter cooperi*) and the sharp-shinned hawks (*Accipiter striatus*) nest in conifer stands and trees in Missouri. Shortleaf pine was by far the most common choice by these accipiters for nesting trees. The removal of the shortleaf pine component from mixed oak-pine forest affects the canopy structure of the forest, the pyrodynamics and chemistry of the litter layer, as well as the composition of the herbaceous vegetation.

Surface fires dominate in mixed oak-pine forests. Pine litter is highly flammable because of its volatile high energy compounds, structure, and surface to volume ratio. Pine litter promotes the spread of light surface fires. Periodic surface fires in oak-pine forests result in fuel structures that reduce the likelihood of stand-replacing crown fires. Crown fires in mixed oak-pine forests are less common because hardwoods reduce the volatility of the vertical fuel structure. The discontinuous pine canopy also inhibits the spread of crown fires. Thus, shortleaf pine trees in oak-pine forests are less susceptible to crown injury and death than pine growing in pure stands. Consequently, pines may live longer in mixed oak-pine forests.

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Foresters and others have written about the loss of shortleaf pine (*Pinus echinata* Mill.) and the frequent occurrence of wildland fire in areas of the Ozarks following the nearly complete harvest of the species between the late 1800's and early 1900's (Cunningham and Hauser 1989, Galloway 1961, Krusekopf *et al.* 1921). Liming (1946) surveyed pine range data from "records and informed people ... and the general pine area by car and on foot." He determined the range of pine to be about 2,670,000 ha in the Missouri Ozark Highlands. By 1976, more detailed forest inventories showed that the pine and oak-pine types occurred on only 162,000 ha in the Missouri Ozarks (Essex and Spencer 1976). While qualitative losses of shortleaf pine from mixed oak-pine forests have been documented throughout its natural range in the United States, the degree of loss has not been quantified in relationship to site characteristics. Subjective judgements and selective memories of stands where shortleaf pine did not regenerate may have influenced the perception of how much pine was lost. Frequent wildland fires, extensive logging of shortleaf pine, and overgrazing from about 1880 to 1920 have been given as primary factors causing the loss of shortleaf pine throughout its natural range (Brinkman and Smith 1968, Cunningham and Hauser 1989, Fletcher and McDermott 1957, Law 1984, Liming 1946). Wildfire suppression, which began in the 1930's, favored the development of oak-dominated forests on sites that once had an abundance of pine.

This study compares the numbers of live shortleaf pine with estimated numbers of pine that grew about 100 years ago in site 8 of the Missouri Ozark Forest Ecosystem Project. Old pine stumps and remnants were used to develop a quantitative environmental history of changes in the abundance of shortleaf pine and to document the frequency of wildland fire. The specific objectives of the study were to:

1. Measure changes in shortleaf pine abundance,
2. Determine if there is any pattern to this change,
3. Quantify fire frequency and discuss its potential effects on changes in pine population,
4. Develop methods for comparing the current and historic population of shortleaf pine.

Although shortleaf pine is shade intolerant when mature, young seedlings are able to establish and survive for a time in a shaded understory (Baker 1992, Shelton 1995). Pine seedlings can survive under hardwood canopies for up to 30 years and still respond to release provided they receive sufficient light and moisture to maintain vigor (Brinkman and Rogers 1967, Brinkman and Smith 1968, Fris and Schmollinger 1984). This requires a low to moderately dense overstory (e.g., basal area <14 m^2/ha), a lack of understory hardwoods greater than about 2.5 cm in diameter at the base, and only moderate amounts of herbaceous vegetation (Baker 1992, Shelton and Baker 1992). These conditions characterized pine-oak forests in the 18th and 19th centuries.

Although their early growth is slow, shortleaf pine trees can outgrow most hardwood species in full sunlight if they establish before being overtopped by the hardwoods (Brinkman and Liming 1961). Once shortleaf pine overtops its competitors, it can maintain dominance to maturity (Baker 1992). Pine seedlings growing under dense shade in mature stands, or suppressed by dense oak sprout reproduction grow slowly and do not survive long. In fact, competition for light and moisture is a major cause of regeneration failure (Baker 1992). Initially, some shade benefits shortleaf pine seedlings by moderating environmental extremes and limiting the growth of competitors while the pines establish a root system. However, light levels (e.g., 25 percent of full sunlight) are too low for pine survival under fully stocked pine-oak stands that have a midstory of hardwoods (Shelton and Baker 1992). Although pines grow best in full sunlight, they can develop under moderately dense overstories (e.g., basal area 10 to 14 m^2/ha) where light levels are 55 percent of full sunlight when there is no midstory canopy. This shortleaf pine advance reproduction is competitive when released by overstory removal (Baker 1992, Shelton and Baker 1992).

Periodic light surface fires over long periods create the stand conditions that favor the establishment and development of shortleaf pine so that it can be recruited into the overstory when there is a major reduction in the overstory canopy. Shortleaf pine is well adapted to fire because bud clusters near the root collar produce sprouts when light surface fires kill the shoot. However, the ability to sprout declines with tree age and size, and mature pines or trees over 15 to 20 cm d.b.h. seldom, if ever,

sprout (Brinkman and Rogers 1967, Lawson 1990).

The early logging history of the Missouri Ozarks followed patterns similar to those experienced in other eastern North American pine forests during European settlement. Large timber companies came to the Ozarks and began harvesting in the 1880's (Cunningham and Hauser 1989). Rivers and later railroads provided access throughout the natural range of shortleaf pine in Missouri. Any pine that met minimum specifications of a 12-in. diameter butt (Cunningham and Hauser 1989) was cut without regard for regeneration or the future forest (Record 1910). Many of the oaks and other hardwoods were left, producing a poor environment for pine regeneration. By 1910, 80 percent of the shortleaf pine forests in the Missouri Ozarks had been cut over, and most of the pine had been removed (Record 1910). The annual burning by settlers to improve range conditions and clear land, and the loss of seed-bearing pines resulted in few new pine seedlings becoming established. Similar patterns in settlement, land-use, fire history, and forest succession have been repeated throughout the pine forests of North America including the pine forests of the Ozark and Ouachita National Forests in Arkansas (Shelton and Baker 1992, Smith 1992) and the white and red pine forests in Ontario (Howe and White 1913).

The State of Missouri's once magnificent pine forests, after approximately 30 years of logging and European settlement, were summarized in 1910 by Samuel J. Record, Forest Assistant, Forest Service:

> "The forest resources of the state are being rapidly destroyed with no thought of their continuation. The shortleaf pine forests will soon be entirely cut over, with little opportunity for reproduction. The present methods of lumbering are very destructive and grub trees are rapidly taking the place of valuable timber. Forest fires are of too common occurrence and should be controlled."

Eventually fire control programs would be initiated in Missouri (circa 1930's) by State and Federal agencies, but not until after the shortleaf pine forests had been cut over and repeatedly burned and grazed. With fire control came a succession to hardwoods, primarily the oaks, on sites formerly occupied by shortleaf pine.

METHODS

The site 8 study area is about 335 ha and is located at the headwaters of an unnamed creek in the Pike Creek watershed within the Peck Ranch Wildlife Management Area in the southeast Missouri Ozarks. The study area is now dominated by oak species that are intermixed with some shortleaf pine. Surface fuels are predominantly hardwood leaf litter. The historic fire regime of the region surrounding the study site is one of frequent low-intensity fires resulting from anthropogenic ignitions (Guyette and Cutter 1997).

The presence of pine stumps was used in this study to reconstruct the number of trees per unit area. Shortleaf pine stumps and knots are preserved in the humid-continental climate of the Ozarks by their density and high oleoresin content. Injury by fire, felling, and mechanical stresses, such as wind, stimulates resin formation in the wood, preserving it for many decades. Preservation is, however, usually limited to larger stems because sapwood often decays much more rapidly than the resinous heartwood. Few pine stumps less than 15 cm in diameter were found. Thus, comparison of stumps to live trees is limited to those stems and stumps greater than 15 cm in diameter.

Transect starting points were chosen by a random selection of intervals, spaced at 0.16 km apart, along the access roads. Starting points were selected without replacement, so each point was used only once. At these locations, an azimuth was randomly selected from the set or range of compass points that transected the area from the road to a drainage. A total of 84 circular plots 30 m in diameter were then established every 100 paces along each transect (fig. 1). Sixteen transects were established in site 8. Stumps, and less often, knot traces were used to estimate the number of pines growing at the plots at the time of the first harvest. The remnants of shortleaf pine stumps were very distinctive and could be recognized easily by:

1. The presence of charred wood,
2. The growth of smooth white lichens on the light gray exterior of the wood,
3. A relatively smooth exterior,
4. Mosses at their base,
5. A ring of chert around the stump,
6. The resinous odor of the wood, and
7. The high density of the wood.

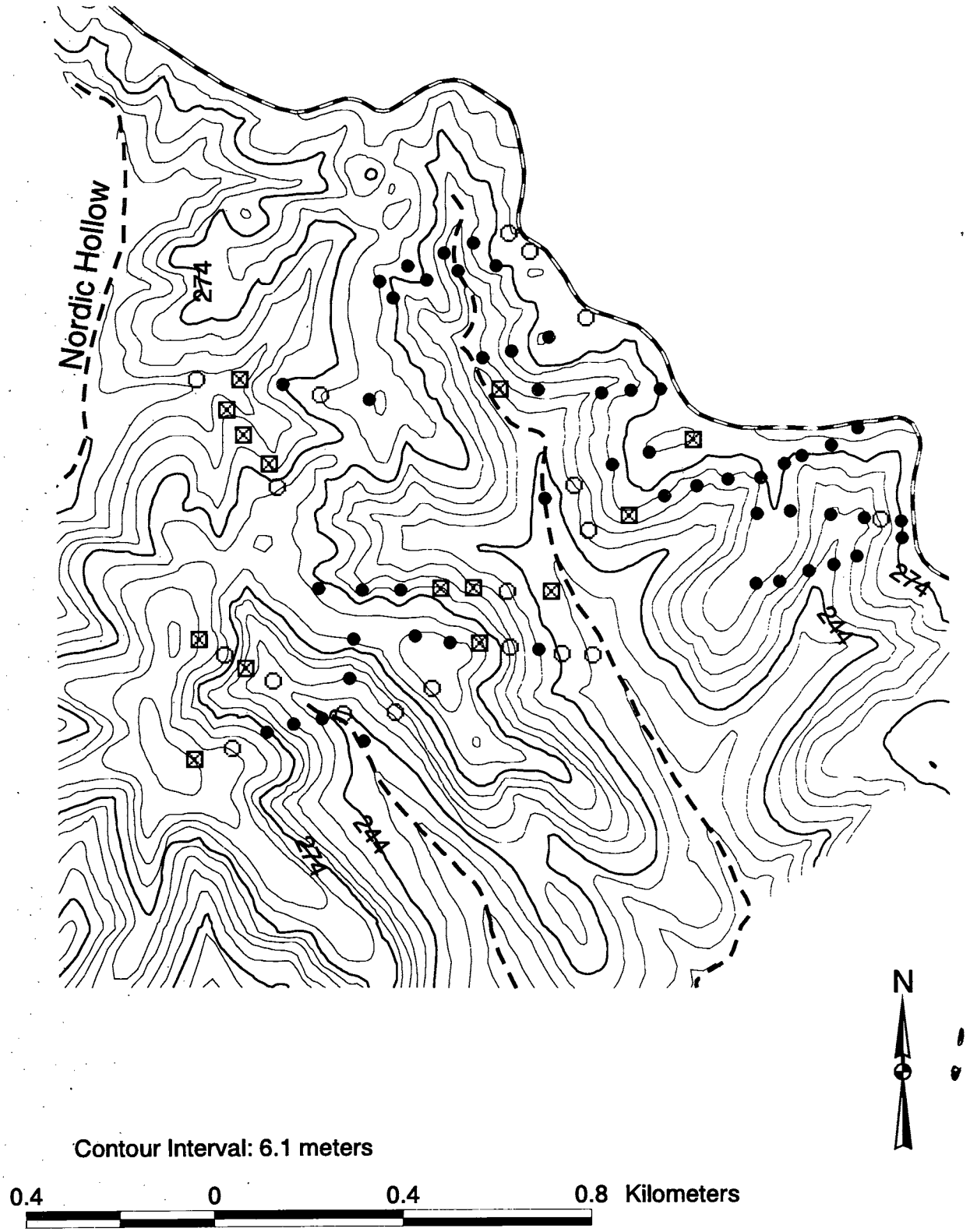


Figure 1.—*Map of study area with 16 transects, 84 sample sites, and changes in pine abundance. Empty circles indicate increased pine abundance, filled circles indicate decreased pine abundance, and circles with a slash indicate no change in pine abundance.*

Slope, aspect, and elevation were taken at each plot, and the number of pine stumps and live trees were counted. Elevation was measured with an altimeter and the aid of topographic maps. Plots were classified into one of four landscape types: (1) ridges, (2) slopes, (3) toe slopes, and (4) riparian areas.

Six fire-scarred cross sections of shortleaf pine remnants were collected in site 8. These cross sections were cut from the only stumps that had fire scars out of all the stumps observed along 5.1 km of transects. Four of the samples were located on south- and west-facing slopes, one on a ridge top, and one along a creek bottom. Compass orientation of the cross section, slope, and aspect were recorded for each sample, as was the location on a topographic map. Fire scars were identified by callus tissue, traumatic resin canals, charcoal, and cambial injury. All samples had charcoal present on the scarred exterior. Scars were dated to the first year of cambial injury.

Cross sections were surfaced with an electric hand planer with a sharp carbide blade. Where rings were very narrow or indistinct, the ring structure and cellular detail were revealed with sandpaper (220 to 600 grit), fine steel wool, or razor cuts. On each cross section, a radius (pith to bark ring series) was selected for measurement that had the (1) least amount of ring-width variability due to reaction wood, injury, or callus tissue, (2) maximum number of rings and (3) most year-to-year ring-width variance. Ring-width series from each sample were measured and plotted. Ring-width plots were used for visual cross-dating of growth patterns. Visual matching of ring-width patterns allows weighing of important *signature years* over years with low common variability between trees, an important environmental-biological process not considered in statistical correlation programs. Ring-width plots also aid greatly in identifying errors resulting from measurement and missing rings associated with injury or drought. The computer program COFECHA (Holmes *et al.* 1986) was used to ensure the accuracy of both relative and absolute dating of the samples by correlation analysis. Absolute dating of the pine remnants was accomplished by cross-dating with a ring-width chronology based on live shortleaf pine growing in Shannon County, Missouri (Guyette 1996a). The dates of the fire scars on the cross sections were identified and combined into a composite fire scar chronology that dated from 1656 to 1899. The computer program FHX2 was used to graph the fire chronology (Grissino-Mayer 1996).

RESULTS AND DISCUSSION

Shortleaf Pine Abundance

Overall change in pine abundance by landscape type in the study area was estimated by multiplying the area (hectares) of the landscape type by the mean density (stems/hectares) of pine stems or remnants (table 1). The number of stems or stumps was then summed for all landscape types. The overall result was (see table 1):

1. Estimated total number historic pine (> 15cm d.b.h.) = 17,143
2. Estimated total number present day pine (> 15cm d.b.h.) = 5,744.

Thus, present day pine abundance is about 34 percent of the historic level. This estimate excludes the four plantations that were sampled. If plantations are included, about 47 percent fewer shortleaf pines are growing now than in the past. Including data from plantations may bias the comparison of historic and present day pine because activities such as site preparation or fuelwood gathering may have removed many of the pine remnants.

The percentage of historic versus present day pine numbers (34 percent, excluding pine plantations) may be very conservative due to differences in the age, size, and stage of stand development of historic pines and pines now present. Shortleaf pine trees in the present day forest are less than 100 years old and rarely exceed 35 cm d.b.h. (Brookshire and Hauser 1993). Shortleaf pines in the historic forest attained ages of 250 to 300 years or more and were more than 70 cm d.b.h. If the existing population of pines were projected through with adjustments for growth and survival until they were similar in size and age to the historic pines, there would be fewer trees than observed in this study at this time. Thus, the 34-percent estimate (present day/historic) may actually underestimate the loss of pine.

The abundance of shortleaf pine declined most on the ridges and side slopes (table 1). Historic and current day pine abundances were similar on toe slopes. Riparian areas showed an insignificant increase ($P > 0.05$) in pine abundance over historic levels, possibly the result of pine

Table 1.—*Area, density, number of sites, and percent change for historic and present shortleaf pine abundances are given by landscape position. The density mean, range and standard deviation are given in stems (> 15 cm d.b.h.) per hectares. Following each landscape type the area is given (hectares). Ratio of current to historic density is: (total # current stems/total # historic stems)x100. Data for sums and totals are density times area. Data for ridges exclude plantations. T-values are given, and ** indicates that the historic and current abundance are significantly different (p < 0.01).*

Landscape position	Historic pine density				Current pine density				Plots	t-value	Current/ historic density
	Density	Range	SD	Total #	Density	Range	SD	Total #			
									n	*t*	*Percent*
Ridges (80)	53.6	0-113	40.4	4,279	11.1	0-28	12.6	886	14	3.75**	21
Slopes (223)	52.9	0-184	39.7	11,821	13.2	0-85	23.0	2,949	46	5.87**	25
Toe slopes (3)	45.7	0-85	28.4	122	45.7	0-99	30.7	122	13	0.00	100
Riparian (29)	32.3	14-57	22.7	921	62.7	14-113	42.0	1,787	7	1.68	194
Sums and % change				17,143				5,744	80		34
Sums and % change with plantations				17,381				9,239	84		53

seeding on abandoned agricultural fields along the streams.

The change in the abundance of shortleaf pine was significantly correlated with elevation, slope, and aspect (table 2). The loss of pine was greatest on slopes with a west or south aspect and least on slopes facing east or north, which may be a result of the greater historic abundance of pine on sites with south and west aspects, where the frequency of fires was greater on these hotter and drier aspects. There are fewer pine trees today than historically at higher elevations in the landscape. This may be due to increased fire intensity from the preheating of stems on upper slopes. Thus, sites with western aspects and moderate slopes (6 to 23 degrees) exhibited a strong correlation (r = -0.60, p < 0.001) among estimates of pine abundance and elevation. Fire was probably a major factor in reducing pine regeneration in relation to landscape type because it was likely to occur more frequently and burn at higher intensities on slopes and upper ridge tops than in riparian areas and along the toe of slopes. At the landscape level, moderate slopes facing south and west have less pine today than in historic times (fig. 1).

About 60 percent of the plots (fig. 2) measured showed a decrease in the number of shortleaf pine stems compared to historic abundance estimates from pine stumps. Of these plots, 41 percent occupied slope positions, 12 percent

Table 2.—*Correlation of plot variables with historic, present, and differences in pine density. Difference is the number of pines > 15cm d.b.h. presently growing on the plots minus the number of pine stumps. Correlations with aspect are for all sites with slopes between 6 and 23 degrees. Correlations (r) are with the natural log (ln) of slope. P-values are given with each correlation coefficient.*

Class	Elevation		Slope (ln)		Aspect	
	r	p-value	r	p-value	r	p-value
Historic	0.08	(0.510)	0.20	(0.080)	0.46	(0.0001)
Present day	-0.35	(0.002)	-0.26	(0.019)	0.17	(0.192)
Difference	-0.28	(0.013)	-0.32	(0.004)	-0.29	(0.021)

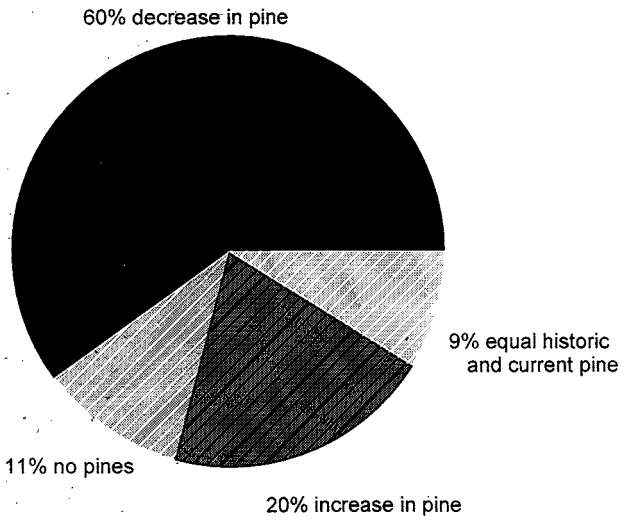


Figure 2.—*Percentage of sample sites showing increases, decreases, and no changes in pine abundance.*

occurred on ridge tops, 6 percent were on toe slopes, and 1 percent were in riparian areas. About 20 percent of the plots measured showed an increase in the number of shortleaf pine stems over estimates of historic abundance. Another 11 percent of the plots measured had no evidence of shortleaf pine growing on the plots during either the present or historic period. About 9 percent of the plots had a present day pine abundance similar to historic densities.

The density of both historic and present day pine on the sites was highly variable. Standard deviations (table 1) were large, about 30 stems per hectare overall. The sample of 84 plots (168 counts of historic and present day pine) was sufficient to detect overall changes in pine density since historic times, especially since the difference between historic and present day pine density was so large, about 40 stems per hectare for ridges and slopes. This number of plots yields overall estimates of mean historic and present day pine density that have better than a 95-percent probability of falling within plus or minus seven stems per hectare ($n=3.92*sd^2/L^2$, or $72=3.92*30^2/7^2$) (Snedecor and Cochran 1989). Comparisons of changes in pine density within and among various ecological land types in site 8 are less precise because of the high variability and relatively low sample size. For instance, on toe slopes, about 35 plots, instead of the measured 13 plots, would be needed for a 95-percent probability of the estimates being within plus or minus 10 stems per hectare ($n=3.92*sd^2/L^2$, or $35=3.92*30^2/10^2$) (Snedecor and Cochran 1989). Thus, there could be undetected differences on toe slopes. Although the standard deviations of density estimates for ecological land types are high, the large differences (about 32 stems per hectare) such as those between toe slopes and slopes for present day pine densities (table 1) allow the detection of differences even with low numbers of plots ($n=3.92*sd^2/L^2$, or $14=3.92*30^2/16^2$) (Snedecor and Cochran 1989).

The use of *ridge to drainage* transects has advantages and disadvantages for comparing present day and historic pine abundances. The *ridge to drainage* transects oversample the toe slopes and riparian areas because headwater locations have much more area in ridge and slopes than in riparian areas. This sample bias is, however, not a problem if accurate information on the area of these ecological land types is available and can be used for estimating the abundance of pine from estimated pine densities for each land type. On the other hand, an advantage to this method is that all land types get sampled with much less effort than is required by a random sampling scheme.

Fire Frequency

Although at least 1,000 pine stumps and remnants were observed along the transects, less than 10 had external and identifiable fire scars. This may be in part due to the relatively large size of the sample trees and their inherent ability to resist scarring. The low incidence of scarring may also be due to less sustained heat from a fine flash fuel matrix, such as might be provided by pine litter and grasses (fig. 4). Also, the moderate slopes of the area (fig. 1) may have decreased the likelihood of scarring by reducing slope-induced fire severity. Only four of the samples were cross-dated and used in constructing a fire chronology.

Fire-free intervals at Nordic Hollow (table 3, fig. 3) were comparable by historic period to fire-free intervals reconstructed for other fire histories in the Current River region. Fire-free intervals at nearby Stegall Mountain (8 km to the north) and Mill Creek (8 km to the northeast) were within one standard deviation of

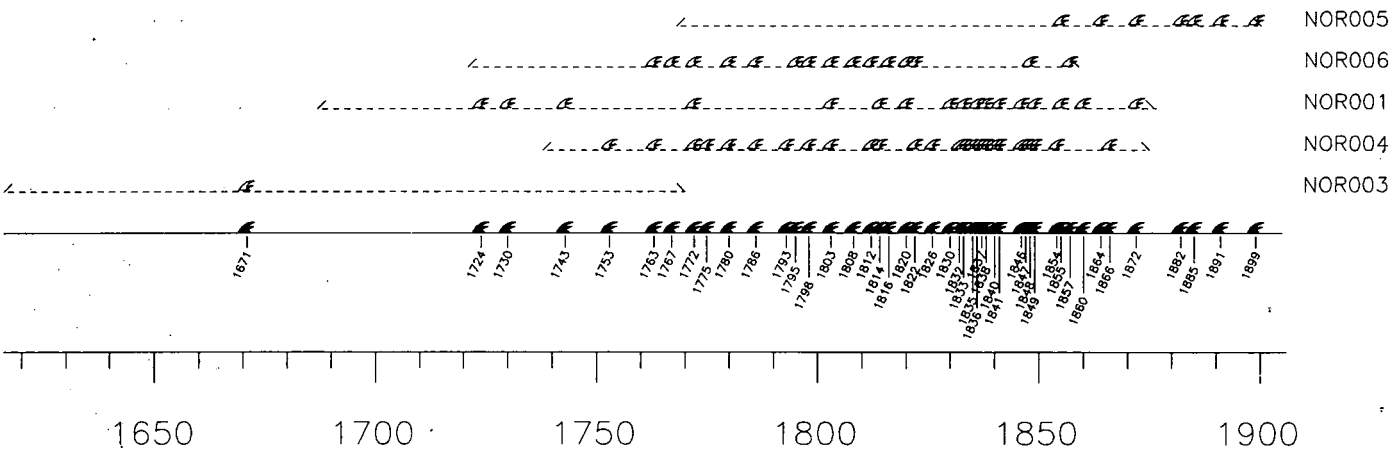


Figure 3.—*Fire scar dates from four stumps and their composite fire scar chronology for the study area. Note that for about 100 years before pine logging (circa 1900's) fires burned so frequently that they inhibited pine regeneration.*

Table 3.— *Means, ranges, and standard deviations for fire-free intervals at Nordic Hollow by historic period. There were insufficient data for the early period as well as for the period after 1900. The mean fire-free intervals for the Native American period (1701-1820) and the Euro-settlement period (1821-1900) are significantly different (t-statistic = 3.41, $p > |t| = 0.002$).*

Period	Mean	Range	Standard deviation
1701-1820	6.3	24 - 2	3.0
1821-1900	3.1	10 - 1	2.4

those at Nordic Hollow (site 8, MOFEP) (Guyette and Cutter 1997).

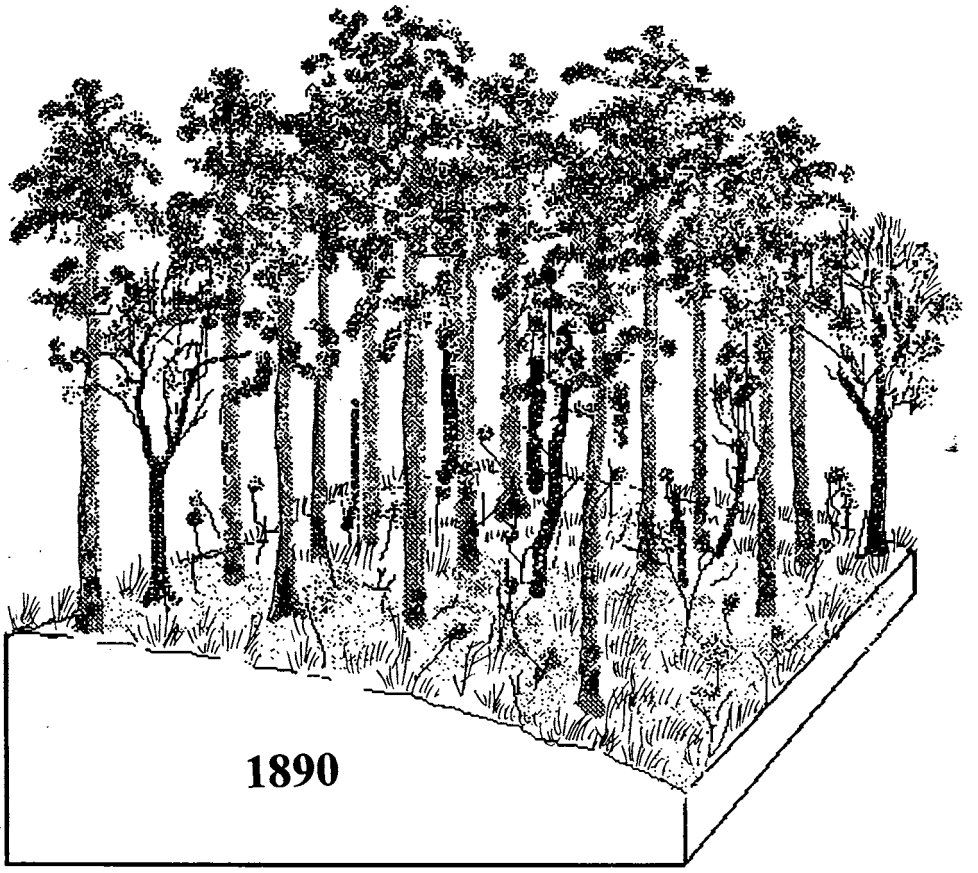
During the 1700's, several extensive fires burned over the Nordic Hollow (table 4). At Nordic Hollow, five of the 13 fire years in the 1700's were among the top 10 fire years in the Current River watershed (Guyette and Cutter 1997). The size and extent of these early fires indicate that they may have been severe (Guyette 1996b). Osage, Quapaw, Shawnee, and Delaware visited the Current River region (Stevens 1991). Between 1780 and 1820, a time of aboriginal immigration into the Current River region, the mean fire-free interval (MFI) was 6.3 years. For example, approximately

Table 4.—*Top 10 fire years during the 1700's in the Current River watershed (Guyette 1996b) ranked by area burned and compared to the percent of trees scarred for the same years in Nordic Hollow.*

Rank	Year	Current River Area (km²)	Nordic Hollow (% trees scarred)
1	1780	1,109	50
2	1728	1,005	0
3	1777	924	0
4	1704	809	0
5	1753	623	25
6	1772	619	75
7	1795	607	50
8	1713	535	0
9	1757	440	0
10	1786	440	50

6,000 Cherokee were living in southeast Missouri and northeast Arkansas at the time (1803) of the Louisiana Purchase (Gilbert 1996). Their settlement in the region increased ignition sources and brought a tradition of burning from the aboriginal peoples of the southeastern United States (Hammett 1992).

Euro-American movement into this area began in the early 1800's. They settled in the Pike Creek watershed (< 5 km from the study site)



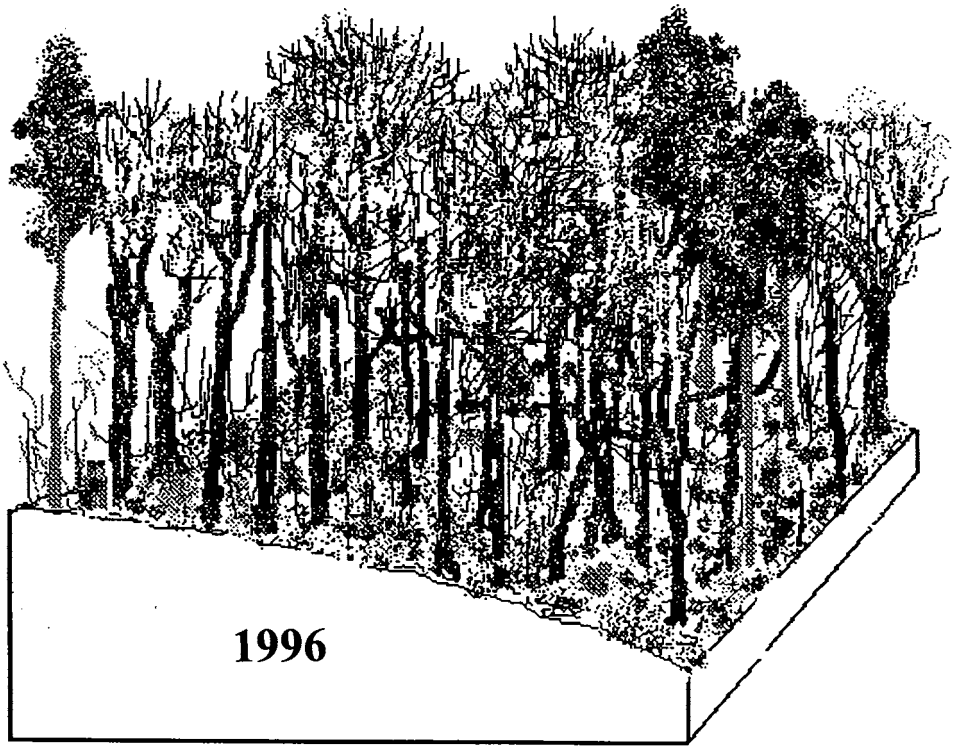


Figure 4.—*Artist concept of changes at site 8 over the last 100 years. Illustrated on a 0.25-ha section are changes of: 1. shortleaf pine to oak dominance, 2. canopy structure and density, 3. the surface fuels from pine litter and grasses to oak leaves, 4. the distribution of pine to lower landscape positions.*

between 1812 and 1860 (Stevens 1991). Settlement by Euro-Americans continued to increase throughout the 19th century, and their land-use practices drastically altered the character of the Ozark forest. Their use of fire to improve grazing conditions in the forests and to clear land for agriculture caused significant increases (P = 0.002) in fire frequency, resulting in an MFI of 3.1 years from 1821 to 1900. The extensive logging of shortleaf pine began in this area of Missouri in the late 1880's and peaked at the turn of the century; by 1920, much of the original pine forest had been harvested (Cunningham and Hauser 1989). No doubt, the frequent fires and heavy amounts of slash left by the loggers led to an increase in fire intensity that affected pine regeneration and thus, the nature of our modern day forests.

Fire and Pine Abundance

Four fire-related factors probably led to the present day density of shortleaf pine in site 8. These factors are consistent with the hypothesis that frequent fire had a negative effect on pine regeneration. They are:

1. Frequent fires during the 100 years (MFI = 3.1 years from 1821-1900) before the pine logging era, which eliminated or reduced advanced pine regeneration.
2. The removal of most, if not all, pines of seed bearing age by logging and intense slash fuel fires.
3. Continued frequent burning after pine logging inhibited pine recruitment.
4. Increased competition for light and nutrients from new sprouts of trees in the red oak group.

Before 1790, fires were frequent enough to promote regeneration of pine seedlings but not so frequent as to prevent recruitment of pine into the overstory. From 1701 to 1790, the MFI was 8.9 years, and it was common for individual fire-free intervals to be from 10 to 20 years. This disturbance regime favored the establishment of shortleaf pine and allowed recruitment of pine into the overstory. Fire improves seed bed conditions for shortleaf pine by reducing the depth of litter or by exposing mineral soil (Baker 1992). Although shortleaf pine does not require mineral soil for germination, seedling establishment decreased as leaf litter depths increased above 6 cm (Shelton and Wittwer 1992, Shelton 1995). Periodic surface fires also favor the development of young pines in the understory by controlling the subcanopy hardwoods, woody perennials, and herbaceous ground cover (Shelton and Baker 1992, Shelton 1995).

Growth of shortleaf pines beyond the seedling stage requires a fire-free period sufficiently long to permit the development of features that increase the resistance of pine to fire. Pines that are 4 to 5 m tall can survive low intensity fires (Baker 1992), and open-grown pines can reach heights of 11 to 12 m by age 25 on site indices between 16.7 and 18.3 m (Brinkman and Rogers 1967). Increasing the distance between the crown and ground reduces the probability that pines will experience crown scorch. Also, bark thickness increases as pines grow, which protects the cambium from heat injury caused by fire. Fires in the study area were frequent enough to maintain low fuel loadings and thus reduce the severity of subsequent fires. Fires were most likely low intensity surface fires in all but the driest years. Only five of the ten fires that occurred between 1701 and 1790 were hot enough to scar 50 percent or more of the pines sampled in this study (fig. 3). At the study site, individual fire-free intervals between 1701 and 1790 were long enough to allow shortleaf pine to grow beyond the seedling stage and develop the characteristics needed to survive fires of low to moderate intensity.

The open, parklike character of shortleaf pine-oak forests of the Ozarks in Missouri and Arkansas at the time of Euro-American settlement has been reported and is attributed to periodic burning (Buckner 1989). Early European settlers continued the aboriginal practice of woods burning but with increased frequency (fig. 3) (Pyne 1982, Sutherland 1997). This maintained and even enhanced the open nature of Ozark pine forests. At the beginning of the 20th century, these forests were severely cut over with low to moderate levels of overstory stocking, little or no undergrowth, and ground flora dominated by grasses (Cunningham and Hauser 1989, Record 1910).

Fire frequency increased as the area around the study site was settled by aboriginal peoples that had been pushed west from eastern regions of the United States and by Euro-American immigrants. Fires became more frequent from 1820 through 1900. The longest fire-free interval during this period was 10 years, which is probably an underestimate because dated fire scars were based on only one sample stump in

the latter part of the record (1872-1899). Fires during this period were probably frequent enough to kill pine seedlings and sprouts, thus eliminating the recruitment of pines for about 100 years before the removal of mature pine from the stand by logging. Record (1910) surveyed the shortleaf pine forest region in Missouri during the early 1900's. In uncut mature pine stands in the Ozarks, he found that the surface fires that burned every year eliminated young pine from the understory and encouraged an undergrowth of *"inferior species"* (i.e., blackjack oak and post oak).

The pattern of change in pine abundance is consistent with a reduction in pine regeneration caused by fire in the various landscape types sampled in this study. Historically, riparian areas had fewer pines than slopes and ridges (table 1). Although pine numbers increased in riparian areas over historic times, the increase was not significant ($P > 0.05$). With lower densities of pines in riparian areas historically, slash fires would have been less intense. Today, pine abundance on toe slopes is similar to historic pine densities. Fire intensity and frequency are reduced on toe slopes by landscape position and surface fuels. Many toe slopes in the study area had a high percentage of rock cover, which would act to reduce fire temperatures, lower herbaceous fuel loading, and protect seedlings. Toe slopes are more mesic, and have greater fuel moisture and slower wind speeds, thus reducing fire intensity. Fire intensities are lower along toe slopes than in upper slope positions because there is no preheating of fuels from fires burning below. On the other hand, at upper slope and ridge sites, where pine abundance has decreased, preheating from the slopes below probably increased fire intensity and pine mortality. Wind speeds are also generally greater on both upper slope and ridge top sites, while fuel moisture tends to be low. Upper slopes and ridges have been found to have more frequent fires than sites at lower elevations in the landscape because fires spread more rapidly uphill (Guyette 1996b).

CONCLUSIONS

About 100 years after the removal of shortleaf pine from site 8, the present day numbers of shortleaf pine are 34 percent of the estimated historic (1890) population. Inclusion of shortleaf pine plantations reduces the overall loss in abundance of shortleaf pine to about 47 percent of historic levels. Data from plantations, however, may be seriously biased by stump removal.

Changes in the relative abundance of pine by slope position and aspect appear to be consistent with the dendrochronological fire history and landscape-level effects on fire behavior. The comparative numbers of pine were most affected along ridges and slopes where fire intensity would be greatest because of exposure to increased wind velocity and preheating of fuels and stems from downslope fire. Frequent burning following the near complete removal of merchantable-size shortleaf pine caused a reduction in pine regeneration on slopes and ridges. Early reports describe advance reproduction as minimal at the time of these early harvests due to the high frequency of burning in the preceding 100 years. Frequent post-harvest fires killed pine seedlings that may have been present or became established following harvest. The intensity of slash fires may have contributed to the reduction in the number of pole-size and other residual pines after harvest.

Current pine abundance on toe slopes and in riparian areas was not significantly ($P > 0.05$) different from historic populations. Although current pine numbers in riparian areas appeared to have increased, high variability, low numbers of sample plots, and possible bias from stump removal leave the change in pine populations in this ecological land type in question. The clearing of forests for agricultural purposes in riparian areas, followed by abandonment of fields and pastures, could have created favorable conditions for pine regeneration and development. The method of using pine remnants for estimating early pine populations is less reliable for areas that experienced high anthropogenic disturbances, such as riparian areas that may also have had low initial pine densities.

Differences in pine abundance were related to slope, elevation, and aspect. The relative abundance of pine was maintained on very steep, rocky slopes, but these sites were rare in the study area. This maintenance of pine numbers relative to earlier populations may be explained by the high percentage of rock cover and the low amount of surface fuel, which likely mitigated the adverse effects of frequent fires on pine regeneration on these sites. The loss of pine was greatest on south- and west-facing slopes at the higher elevations and least on low

east- and north-facing slopes. The strongest correlation of comparative pine abundance with elevation occurred at plots with western aspects and moderate (6 to 23 degrees) slopes.

The use of pine remnants to estimate historic pine abundance provides a quantitative means of measuring changes in pine density with limitations imposed by anthropogenic disturbance of pine remnants. Although this study considered a limited area of the natural range of shortleaf pine and oak-pine forests of the Ozarks, we believe that it presents an approach that can be used to estimate pine abundance on a larger scale. It also provides a means of estimating historic levels of pine where early records cannot be found. Because of the limited scope of this study, it should not be applied to characterize the many changes in shortleaf pine abundance that have taken place across the Ozarks.

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Analysis of Pre-treatment Woody Vegetation and Environmental Data for the Missouri Ozark Forest Ecosystem Project

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Abstract.—We conducted a study to identify pre-treatment trends in woody species density, diameter, and basal area among MOFEP sites, blocks, and treatment areas; relate woody species differences among sites, blocks, and treatment areas to differences in environmental conditions; and identify potential treatment response differences based upon our findings. Sites 2 through 5 had greater numbers of species per unit area. Sites 7 and 8 had fewer trees ≥ 4 cm diameter, less white oak, and more scarlet oak. Block 3 had fewer trees ≥ 11 cm, less overall basal area, and less white oak. Block 2 had less black oak. There were no treatment-level woody vegetation differences. Greater numbers of species per acre, greater abundance of white oak, and lesser abundance of scarlet oak were associated with sites and blocks that have a greater proportion of base-rich geological strata and a greater proportion of soils classified as Alfisols. We hypothesize: (1) no-harvest (NH) and uneven-aged management (UAM) treatment responses will be more variable and more difficult to interpret than even-aged management treatment responses (EAM) because NH and UAM treatments were delegated to more contrasting sites and (2) EAM treatment areas will have greater growth rates because these treatments were delegated to sites having siltier surface soil textures and a greater proportion of base-rich parent materials. The designated blocks were effective in grouping sites with similar vegetational characteristics. However, based on an examination of environmental characteristics, blocks that combined sites 1, 7, and 8; sites 3, 4, and 5; and sites 2, 6, and 9 may improve blocking effectiveness.

The Missouri Ozark Forest Ecosystem Project (MOFEP) is a long-term, large-scale study of responses of a broad range of ecological attributes to silvicultural treatments (Brookshire *et al.* 1997, Brookshire and Hauser 1993). One facet of the study is to compare woody vegetation responses among even-aged management, uneven-aged management, and no-harvest treatments. Identifying differences in woody vegetation pre-treatment conditions and potential differences in treatment response is critical for interpreting treatment responses over the course of the MOFEP study.

Our study had four objectives. The first was to identify pre-treatment trends in woody species density, diameter, and basal area among the nine MOFEP sites, the three blocks, and the three treatment areas. The second objective was to relate woody species differences among sites, blocks, and treatments to differences in environmental conditions (e.g., soil, geology, and landform) and land-use history. Our third objective was to identify potential differences in treatment responses. Our final objective was to evaluate blocking effectiveness based upon the findings of objectives one and two.

METHODS

The MOFEP study is described in detail by Brookshire *et al.* (1997), Brookshire and Hauser

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(1993), and Kurzejeski *et al.* (1993). The study consists of nine sites (or compartments) that range in size from 657 ac (266 ha) to 1,302 ac (527 ha). Sites were grouped into three blocks, each containing three sites. The three treatments—even-aged management (EAM), uneven-aged management (UAM), and no-harvest (NH)—were randomly assigned to the three sites in each block, yielding three replicates of each treatment (Sheriff and He 1997). The site, block, and treatment groupings are summarized in table 1, and their spatial arrangement is illustrated in figure 1 of Brookshire *et al.* (1997).

Data Sources

In 1991-1992, prior to any experimental treatments, a total of 645 half-acre (0.2-ha) sample plots were established across the nine MOFEP sites. Plots were distributed to ensure that at least one plot was located within each identified stand, and plot placement within each stand was random. Live and dead trees ≥ 4.5 in. (11 cm) d.b.h. were sampled in each 0.5-ac (0.2-ha) circular plot. Characteristics recorded for each tree included species, d.b.h., and status (i.e., live or dead). Trees between 1.5 in. (4 cm) and 4.5 in. (11 cm) d.b.h. were measured on four 0.05-ac (0.02-ha) circular subplots within the main plot. Live trees at least 3 ft (1 m) tall and less than 1.5 in. (4 cm) d.b.h. were tallied by species and size class in four 0.01-ac (0.004-ha) subplots. Subplots were combined to obtain a plot average for trees by size class. All values were converted to an acre basis for analysis. Additional details regarding data collection can be found in Brookshire *et al.* (1997).

Soils, geology, and landform information was also collected at each 0.5-ac (0.2-ha) vegetation plot (Meinert *et al.* 1997). Soils were described in small excavations at the center of each plot. Horizon presence and thickness, texture class, stoniness, soil parent materials, location in geologic strata, and soil classification were estimated from samples at each excavation. Elevation, slope, landform, slope shape normal and parallel to slope, and aspect were also estimated. Variation in soil properties and landform characteristics was also noted.

Attributes and Analyses

We evaluated pre-treatment data for the MOFEP sites and tested for block and treatment unit differences in:

1. number of species per plot,
2. trees per acre,
3. basal area per acre, and
4. quadratic mean d.b.h.

Analyses were conducted by size classes corresponding to the sampling thresholds for vegetation plots and subplots: trees ≥ 3 ft (1m) tall, trees ≥ 1.5 in. (4 cm) d.b.h. and trees ≥ 4.5 in. (11 cm) d.b.h. We also tested for differences in items 2 through 4 for the key timber species: white oak (*Quercus alba* L.), black oak (*Quercus velutina* Lam.), scarlet oak (*Quercus coccinea* Muenchh.), and shortleaf pine (*Pinus echinata* Mill). Quadratic mean diameter and basal area were calculated for trees ≥ 1.5 in. (4 cm) d.b.h. using standard methods (Husch *et al.* 1982).

Table 1.—*Assignment of blocks and treatments by site (compartment) for the MOFEP study. Treatments were uneven-aged management (UAM), even-aged management (EAM), and no harvest (NH). Numbers of 0.5-ac (0.2 ha) plots by site, block, and treatment are shown in parentheses.*

Site	Block assignment	Treatment	
1 (73 plots)	1 (218 total plots)	NH	(214 total plots)
2 (73 plots)	1	UAM	(218 total plots)
3 (72 plots)	1	EAM	(213 total plots)
4 (74 plots)	2 (215 total plots)	UAM	
5 (70 plots)	2	EAM	
6 (71 plots)	2	NH	
7 (71 plots)	3 (212 total plots)	UAM	
8 (70 plots)	3	NH	
9 (71 plots)	3	EAM	

Analysis of variance was used to evaluate differences among blocks and treatment units (before treatment implementation) with the fixed effects model:

$$Y_{ij} = \mu + \text{block}_i + \text{treatment}_j + \varepsilon_{ij} \qquad [1]$$

where μ is the overall mean of the attribute, block_i is the effect of each of the three blocks, treatment_j is the effect of each of the three treatment areas in each block, and ε_{ij} is the error effect, $N(0,\sigma^2)$. Blocks and treatments each receive 2 degrees of freedom, leaving 4 degrees of freedom for error.

Several environmental variables were also evaluated to identify site-, block-, and treatment-level differences (table 2). These variables were selected because of their potential to affect energy, water, and nutrient distributions.

Most variables in the MOFEP environmental dataset were categorical and were observed by plot. To analyze these data, we transformed each variable to represent its proportional occurrence by plot within each site. For example, Roubidoux geology occurred in 24 out of 76 plots in site 1. The proportional occurrence relative to other plots within site 1 was:

$$\frac{24}{76} = 0.32.$$

Thus, we inferred that 32 percent of site 1 contained Roubidoux geology. We ranked sites by their proportions of key environmental variables to identify site-level differences. We also used principal components analysis (Gauch 1986, Webster and Oliver 1990) to summarize important site-level differences in environmental variables.

Confidence Interval Interpretations

The MOFEP study design prohibited a rigorous statistical analysis of site-level differences in woody vegetation. Specifically, there was no true replication of each site. To identify differences among sites, we constructed boxplots with confidence intervals. Medians and confidence intervals were generated using plot-level information within each site. This provided a less statistically rigorous but useful visual

Table 2.—*Environmental variables used in analyses.*

Variable	Type	Indicator of:
Slope	continuous	moisture, soil thickness
Aspect	continuous	available moisture
Landform	categorical	strata, moisture gradient
Geology	categorical	strata, materials, texture, base saturation
Profile description, A-horizon		
horizon thickness	continuous	carbon, herbaceous rooting
modifier	categorical	moisture/nutrients, gravel content
texture class	categorical	moisture, nutrient supply
Profile description, E-horizon		
horizon thickness	continuous	herbaceous and seedling rooting
texture modifier	categorical	moisture/nutrients, gravel content
texture class	categorical	moisture, nutrient supply
Profile description, B-horizon		
horizon thickness	continuous	tree rooting
texture modifier	categorical	moisture/nutrients, gravel content
texture class	categorical	moisture, nutrient supply
Depth to clay	categ/continous	major texture discontinuities
Classification	categorical	
subgroup	categorical	key properties: fragic, mollic, lithic
order	categorical	alfic/ultic break
Variable bedrock	categorical	shallow soils
Outcrop, % class	categorical	area percentage of outcrop
Stoniness, % class	categorical	percent of stones, boulders

method for comparing within-site variation and differences among sites. Non-overlapping confidence intervals generated for sample means or medians provide evidence of statistical differences.

RESULTS

Site-Level Differences in Woody Vegetation

Sites 2 through 5 generally had a greater median number of species per plot than site 1 and sites 6 through 9 (fig. 1). Median differences were small in magnitude (e.g., 13 vs. 18 species per plot), but the upper range of data for sites 2 through 5 also exceeded that of the remaining sites. All sites had roughly similar means and ranges for total trees per acre (table 3). Sites 7 and 8 had fewer trees at the 1.5 in. (4 cm) d.b.h. threshold and had relatively large quadratic mean diameters compared to the other sites (figs. 2a, 2b). Basal area was similar in mean and range among sites (table 3). Although the quadratic mean diameter of white oaks ≥ 1.5 in. (4 cm) d.b.h. at sites 7 and 8 was roughly the same as at the other sites (fig. 2d), the number and basal area of white oak at sites 7 and 8 was nearly half the magnitude of that at other sites (figs. 2c, 2g). In contrast, scarlet oak was slightly more abundant and greater in diameter and basal area at sites 7 and 8 (figs. 2e, 2f, 2h). No notable among-site differences in abundance, diameter, and basal area were observed for black oak or shortleaf pine (table 3).

Treatment- and Block-Level Differences in Woody Vegetation

There were no significant treatment-level differences in species numbers, trees per acre, quadratic mean diameter, or basal area for all trees or for important timber species (white oak, black oak, scarlet oak, and shortleaf pine)

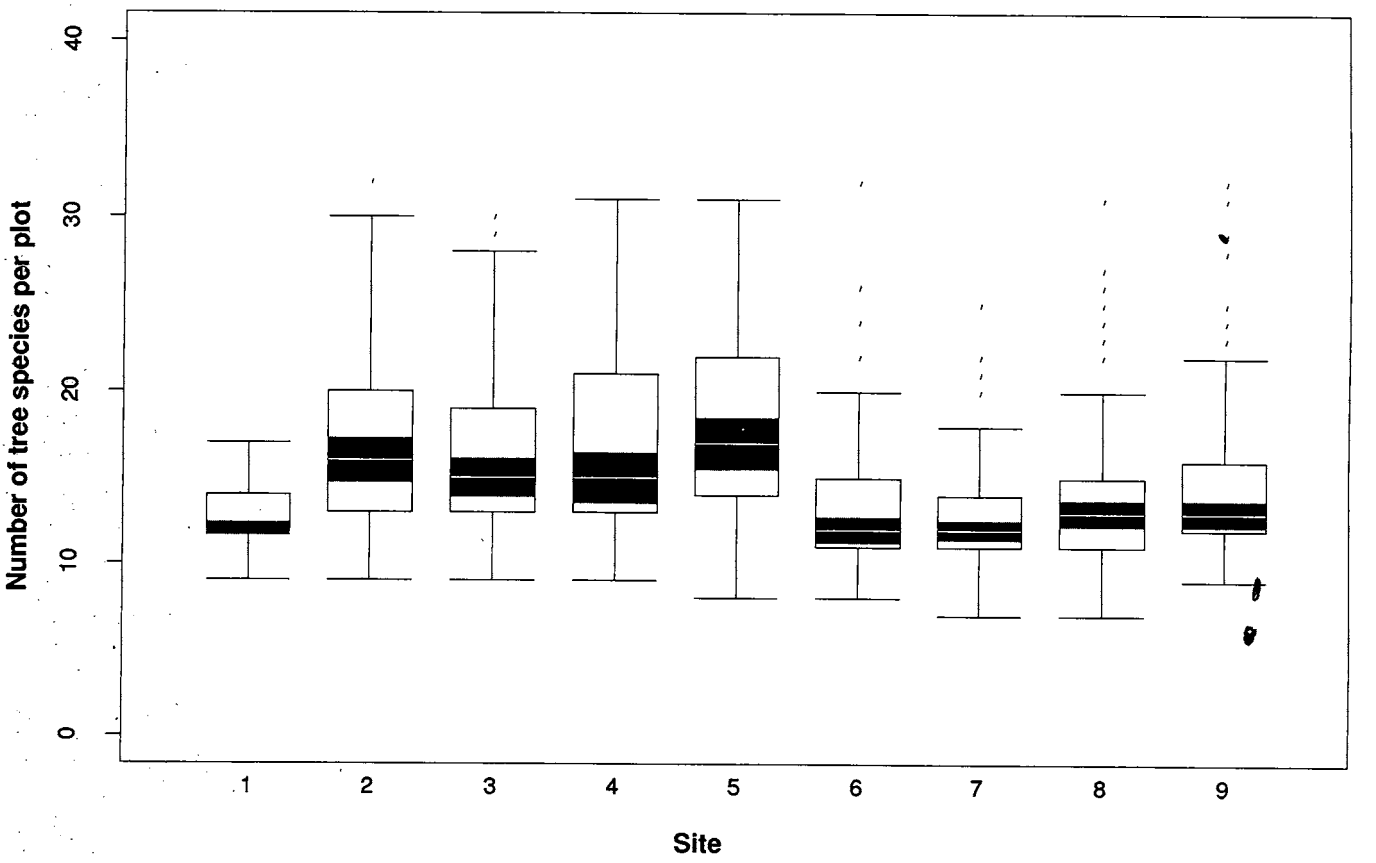

Figure 1.—*Number of tree species per plot summarized by site from plot-level data. The central (white) bar in each box plot represents the median. The black bars around the median show the 95 percent confidence interval for the median. The box indicates the range of 50 percent of the data. Brackets indicate the range of continuous data. Dots at the top or bottom indicate values beyond the range of continuous data.*

Table 3.—*Mean, standard deviation, and minimum and maximum of observations by site for selected attributes. Number of plots per site is shown in table 1.*

Characteristic		Site 1	2	3	4	5	6	7	8	9
All species										
Number of species per plot										
	Mean	13	17	17	17	18	14	13	14	15
	SD	2	5	5	6	5	5	4	5	5
	Min	9	9	9	9	8	8	7	7	9
	Max	17	32	30	36	31	32	25	31	32
No. of trees > 0 in. d.b.h.										
	Mean	1,314	1,749	1,421	1,665	1,715	1,400	1,227	1,528	1,696
	SD	411	897	817	1,082	695	6,011	667	855	682
	Min	710	841	628	573	714	577	264	531	750
	Max	3,003	6,492	5,532	6,472	5,005	3,760	3,324	5,320	4,497
No. of trees ≥ 1.5 in. d.b.h.										
	Mean	515	557	500	499	499	429	390	380	547
	SD	89	102	72	87	88	91	137	118	168
	Min	299	313	344	323	285	229	89	144	217
	Max	814	867	668	836	708	686	905	700	980
No. of trees > 4.5 in. d.b.h.										
	Mean	184	176	169	167	160	160	140	133	126
	SD	36	36	36	356	33	39	42	37	31
	Min	98	86	52	102	64	86	14	78	72
	Max	254	262	262	262	246	292	250	254	204
Qmd[1] ≥ 1.5 in. d.b.h.										
	Mean	6	6	6	6	6	7	7	7	6
	SD	1	1	1	1	1	1	1	1	1
	Min	5	3	3	4	4	5	4	4	4
	Max	7	7	8	8	8	9	11	11	10
Qmd ≥ 4.5 in. d.b.h.										
	Mean	9	9	10	10	10	10	11	11	10
	SD	1	1	1	1	1	1	2	1	2
	Min	7	7	7	7	8	8	7	7	6
	Max	12	13	12	12	13	13	14	14	14
Basal area (ft^2/ac) ≥ 1.5 in. d.b.h.										
	Mean	95	96	99	96	96	100	91	92	88
	SD	11	12	16	16	12	12	15	13	12
	Min	77	55	25	47	40	75	7	38	56
	Max	120	124	127	150	124	136	133	123	113
Basal area (ft^2/ac) ≥ 4.5 in. d.b.h.										
	Mean	82	80	85	82	82	89	81	83	73
	SD	11	14	17	18	12	12	15	14	15
	Min	61	31	13	30	29	60	5	27	36
	Max	108	110	117	139	110	124	125	116	109
White oak										
No. of trees > 0 in. d.b.h.										
	Mean	173	138	157	143	137	108	106	122	195
	SD	82	88	71	99	82	66	116	114	143
	Min	57	0	5	0	0	0	0	0	0
	Max	530	388	322	534	513	308	544	625	790
No. of trees ≥ 1.5 in. d.b.h.										
	Mean	130	102	139	113	100	83	61	76	130
	SD	54	59	63	68	53	52	60	68	114
	Min	45	0	5	0	0	0	0	0	0
	Max	288	289	307	383	220	292	283	379	615

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(table 3 continued)

Characteristic		Site 1	2	3	4	5	6	7	8	9
No. of trees ≥ 4.5 in. d.b.h.										
	Mean	46	41	48	41	42	47	20	24	29
	SD	26	26	24	24	24	30	19	20	22
	Min	8	0	0	0	0	0	0	0	0
	Max	150	128	94	110	118	172	112	84	92
Qmd ≥ 1.5 in. d.b.h.										
	Mean	5	6	5	6	6	7	6	6	5
	SD	1	1	1	2	2	2	2	3	2
	Min	3	0	2	0	0	0	0	0	0
	Max	8	11	9	9	14	17	12	12	11
Qmd ≥ 4.5 in. d.b.h.										
	Mean	8	8	8	9	9	9	8	9	9
	SD	1	2	2	2	2	2	3	3	4
	Min	5	0	0	0	0	0	0	0	0
	Max	12	16	12	18	16	17	15	16	18
Basal area (ft^2/ac) ≥ 1.5 in. d.b.h.										
	Mean	19	17	23	19	22	22	10	14	18
	SD	9	9	11	11	12	13	10	12	14
	Min	5	0	0	0	0	0	0	0	0
	Max	50	45	56	56	52	60	58	53	62
Basal area (ft^2/ac) ≥ 4.5 in. d.b.h.										
	Mean	15	14	18	16	19	20	8	12	14
	SD	8	8	10	10	12	11	10	12	126
	Min	3	0	0	0	0	0	0	0	0
	Max	45	36	51	47	51	53	55	52	58
Black oak										
No. of trees > 0 in. d.b.h.										
	Mean	77	63	52	42	44	37	101	83	95
	SD	62	61	49	37	37	49	130	82	84
	Min	8	0	0	0	0	0	0	2	0
	Max	344	373	226	167	167	301	1,048	374	445
No. of trees ≥ 1.5 in. d.b.h.										
	Mean	50	50	40	34	33	21	48	38	51
	SD	27	37	33	29	23	14	35	29	39
	Min	8	0	0	0	0	0	0	0	0
	Max	145	184	143	139	90	55	236	132	211
No. of trees ≥ 4.5 in. d.b.h.										
	Mean	42	41	36	25	29	19	30	30	29
	SD	25	27	29	20	20	14	22	21	20
	Min	6	0	0	0	0	0	0	0	0
	Max	140	144	138	70	80	54	126	114	104
Qmd ≥ 1.5 in. d.b.h.										
	Mean	10	10	10	10	10	12	9	11	9
	SD	2	3	4	4	4	5	3	3	3
	Min	5	0	0	0	0	0	0	0	0
	Max	15	17	20	16	21	21	16	19	17
Qmd ≥ 4.5 in. d.b.h.										
	Mean	11	10	11	10	11	12	11	12	11
	SD	2	3	4	4	4	4	3	3	3
	Min	7	0	0	0	0	0	0	0	0
	Max	17	17	20	17	21	21	16	19	19
Basal area (ft^2/ac) ≥ 1.5 in. d.b.h.										
	Mean	26	26	25	19	20	20	22	25	24
	SD	15	15	18	15	14	15	17	18	18
	Min	2	0	0	0	0	0	0	0	0
	Max	74	63	70	58	50	64	93	85	97

(table 3 continued on next page)

(table 3 continued)

Characteristic		Site 1	2	3	4	5	6	7	8	9
Basal area (ft²/ac) ≥ 4.5 in. d.b.h.										
	Mean	26	25	25	19	20	20	22	25	23
	SD	15	15	17	15	14	15	17	18	18
	Min	1	0	0	0	0	0	0	0	0
	Max	74	61	70	58	50	64	93	85	97
Scarlet oak										
No. of trees > 0 in. d.b.h.										
	Mean	82	49	54	56	35	27	85	56	93
	SD	73	34	48	45	26	17	75	56	93
	Min	0	0	4	2	2	0	2	0	0
	Max	348	138	292	218	135	71	306	311	655
No. of trees ≥ 1.5 in. d.b.h.										
	Mean	60	40	43	46	29	22	66	31	60
	SD	48	25	32	29	19	14	54	24	48
	Min	0	0	4	2	2	0	0	0	0
	Max	198	108	194	165	96	60	237	108	230
No. of trees ≥ 4.5 in. d.b.h.										
	Mean	45	31	34	32	21	20	41	24	26
	SD	36	19	28	24	15	14	31	17	20
	Min	0	0	2	2	2	0	0	0	0
	Max	170	78	184	160	76	60	158	78	90
Qmd ≥ 1.5 in. d.b.h.										
	Mean	8	9	9	9	9	12	10	12	8
	SD	3	3	3	3	3	4	3	4	3
	Min	0	0	4	4	4	0	0	0	0
	Max	14	17	17	16	22	19	18	17	17
Qmd ≥ 4.5 in. d.b.h.										
	Mean	9	10	10	11	11	12	12	13	10
	SD	2	3	3	2	3	4	3	3	4
	Min	0	0	6	6	6	0	0	0	0
	Max	14	17	19	18	22	19	18	18	17
Basal area (ft²/ac) ≥ 1.5 in. d.b.h.										
	Mean	21	18	18	20	13	18	29	22	18
	SD	14	13	12	13	10	16	17	16	13
	Min	0	0	2	1	1	0	0	0	0
	Max	60	65	60	74	64	66	75	67	61
Basal area (ft²/ac) ≥ 4.5 in. d.b.h.										
	Mean	20	18	17	19	13	18	28	22	16
	SD	15	13	12	13	10	16	17	16	13
	Min	0	0	1	1	0	0	0	0	0
	Max	57	65	59	74	64	66	75	67	61
Shortleaf pine										
No. of trees > 0 in. d.b.h.										
	Mean	26	21	15	17	16	36	20	27	34
	SD	36	45	17	23	24	80	29	61	96
	Min	0	0	0	0	0	0	0	0	0
	Max	182	270	66	96	93	574	135	290	539
No. of trees ≥ 1.5 in. d.b.h.										
	Mean	23	16	15	17	16	30	18	18	18
	SD	30	33	17	23	23	51	261	35	38
	Min	0	0	0	0	0	0	0	0	0
	Max	122	195	66	96	93	289	110	165	239

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(table 3 continued)

Characteristic		Site 1	2	3	4	5	6	7	8	9
No. of trees ≥ 4.5 in. d.b.h.										
	Mean	19	10	13	16	14	25	16	10	5
	SD	25	18	15	21	20	38	23	17	7
	Min	0	0	0	0	0	0	0	0	0
	Max	108	108	66	86	78	214	110	88	36
Qmd ≥ 1.5 in. d.b.h.										
	Mean	7	5	9	7	7	7	9	7	6
	SD	4	5	4	5	5	4	5	5	6
	Min	0	0	4	4	4	0	0	0	0
	Max	14	17	17	16	22	19	18	17	17
Qmd ≥ 4.5 in. d.b.h.										
	Mean	8	5	9	7	7	7	9	7	6
	SD	4	5	4	5	5	4	5	5	6
	Min	0	0	0	0	0	0	0	0	0
	Max	16	17	18	15	17	16	18	17	20
Basal area (ft^2/ac) ≥ 1.5 in. d.b.h.										
	Mean	9	5	8	8	8	11	11	6	4
	SD	11	9	10	10	11	16	16	10	5
	Min	0	0	0	0	0	0	0	0	0
	Max	45	52	55	45	41	87	84	47	21
Basal area (ft^2/ac) ≥ 4.5 in. d.b.h.										
	Mean	8	5	8	8	8	10	11	6	3
	SD	10	8	108	108	108	16	16	10	5
	Min	0	0	0	0	0	0	0	0	0
	Max	44	50	55	44	40	82	84	43	21

[1] Qmd = quadratic mean diameter.

analyzed separately (tables 4-8). The lowest treatment-level P-values at P=0.06 were for differences in white oak basal area, but most P-values were ≥ 0.1.

We found block-level differences in total number of trees per acre ≥ 4.5 in. (11 cm) d.b.h. (P=0.001), quadratic mean diameter of trees ≥ 4.5 in. (11 cm) d.b.h. (P=0.01), and total basal area (P=0.03). When significantly different, variables of one of the three blocks generally had substantially smaller magnitudes than the same variables of the other two blocks (table 4). Although the overall quadratic mean diameter of trees was greatest for block 3, that block contained fewer trees and less total basal area per acre than blocks 1 and 2 (table 4). Much of this difference is attributable to white oaks ≥ 4.5 in. (11 cm) d.b.h., which were least abundant and had the least basal area in block 3 (table 5). Black oak was least abundant and had the least basal area in block 2. The quadratic mean diameter for black oak was the same among blocks (table 6). No significant differences for scarlet oak and shortleaf pine were observed at either the treatment or block levels (tables 7 and 8).

Differences in Environmental Variables

We summarize important site-level differences in key soil, geology, and landform attributes in figures 3 and 4. Sites 7 and 8 have a greater proportion of broad and level summit landform positions, Roubidoux-derived parent materials, and soils with loamy surface textures (figs. 3 and 4). In contrast, sites 3, 4, and 5 have a lower proportion of summit positions, a lower proportion of Roubidoux-derived parent materials, and fewer Ultisols. They also have a greater proportion of Eminence-derived parent materials and soils with silty surfaces (figs. 3 and 4). The remaining sites (1, 2, 6, 9) are intermediate in these characteristics, although sites 2, 6, and 9 are generally similar to sites 3, 4, and 5 while site 1 is similar to sites 7 and 8 (figs. 3 and 4).

Meinert *et al.* (1997) show that MOFEP sites 7 and 8 occur in the Current-Eleven Point Hills Landtype Association (Hills LTA) while the remaining sites occur in the Current-Black River Breaks Landtype Association (Breaks LTA). The Breaks LTA has greater relief, a greater range of geological strata, a greater

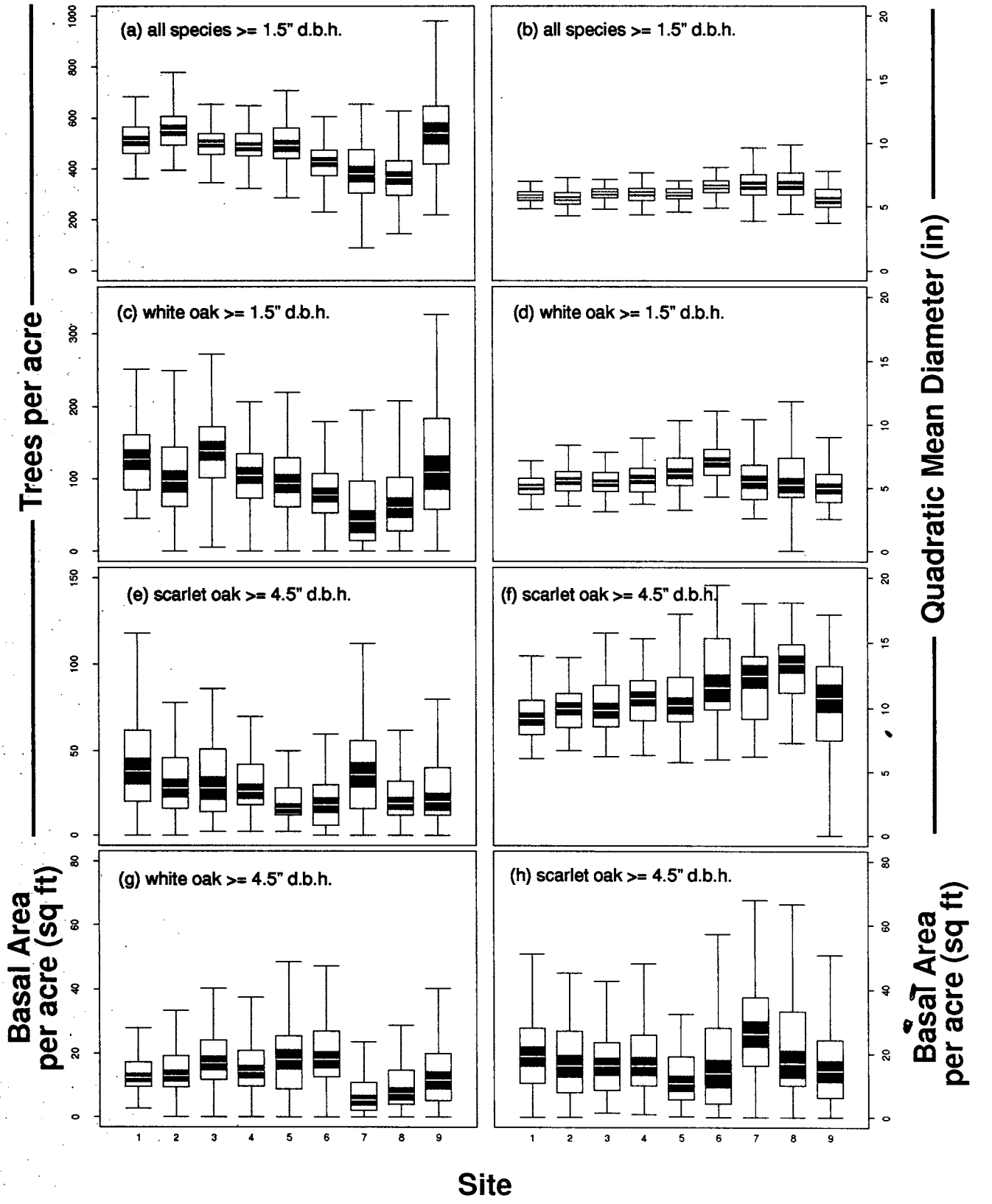

Figure 2.—*Box plots of several attributes summarized by site from plot-level data. The central (white) bar in each box plot represents the median. The black bars around the median show the 95 percent confidence interval for the median. The box indicates the range of 50 percent of the data. Brackets indicate the range of continuous data.*

Table 4.—*Site, block, and treatment means for woody species attributes. Treatment means did not differ significantly (α = 0.05) for any listed attribute, although block effects were significant for some attributes.*

Attribute[1,2] (per acre except as noted)	Site 1	2	3	4	5	6	7	8	9
Number of species per plot	13	17	17	17	18	14	13	14	15
No. of trees > 0 in. d.b.h.	1,314	1,749	4,121	1,665	1,715	1,400	1,227	1,528	1,696
No. of trees ≥ 1.5 in. d.b.h.	514	557	500	466	466	429	390	380	547
No. trees ≥ 4.5 in. d.b.h.	184	176	169	167	160	160	140	133	126
Qmd ≥ 1.5 in. d.b.h.	5.9	5.7	6.0	6.0	6.0	6.6	6.8	6.9	6.0
Qmd ≥ 4.5 in. d.b.h.	9.1	9.2	9.6	9.6	9.8	10.2	10.5	10.9	10.0
Basal area (ft^2/ac) ≥ 1.5 in. d.b.h.	95	96	99	96	96	100	91	92	88
Basal area (ft^2/ac) ≥ 4.5 in. d.b.h.	82	80	85	82	82	89	81	83	73

	Block 1 (sites 1, 2, 3)	Block 2 (sites 4, 5, 6)	Block 3 (sites 7, 8, 9)	F-value[3]	P-value[3]
Number of species per plot	15	16	14	1.3	0.36
No. of trees > 0 in. d.b.h.	1,495	1,593	1,483	0.2	0.82
No. of trees ≥ 1.5 in. d.b.h.	524	476	439	1.5	0.32
No. trees ≥ 4.5 in. d.b.h.	176	162	133	58.4	<0.01
Qmd ≥ 1.5 in. d.b.h.	5.9	6.2	6.4	1.3	0.37
Qmd ≥ 4.5 in. d.b.h.	9.3	9.9	10.6	14.5	0.01
Basal area (ft^2/ac) ≥ 1.5 in. d.b.h.	97	97	90	8.9	0.03
Basal area (ft^2/ac) ≥ 4.5 in. d.b.h.	82	85	79	1.2	0.38

	No harvest (sites 1, 6, 8)	Even-aged (sites 3, 5, 9)	Unven-aged (sites 2, 4, 7)	F-value[3]	P-value[3]
Number of species per plot	14	17	16	2.7	0.18
No. of trees > 0 in. d.b.h.	1,413	1,609	1,551	0.6	0.60
No. of trees ≥ 1.5 in. d.b.h.	442	515	483	1.1	0.41
No. trees ≥ 4.5 in. d.b.h.	159	152	161	2.9	0.16
Qmd ≥ 1.5 in. d.b.h.	6.5	5.9	6.1	1.19	0.39
Qmd ≥ 4.5 in. d.b.h.	10.1	10.0	9.8	0.9	0.48
Basal area (ft^2/ac) ≥ 1.5 in. d.b.h.	96	94	94	0.4	0.72
Basal area (ft^2/ac) ≥ 4.5 in. d.b.h.	85	80	81	0.9	0.48

[1] Qmd = quadratic mean d.b.h. (in inches) for trees in the specified size class.
[2] Reported values are per acre except as noted. Metric conversions are 1.5 in. = 4 cm, 4.5 in. = 11 cm, and generally 1 in. = 2.54 cm. Also, (2.47) (no. of trees/ac) = no. trees/ha and (0.2296) (basal area ft^2/ac) = basal area m^2/ha.
[3] For ANOVA of block effects for the indicated attribute based on model [1]. F has (2,4) degrees of freedom.
[4] For ANOVA of treatment effects for the indicated attribute based on model [1]. F has (2,4) degrees of freedom.

Table 5.—*Site, block, and treatment area means for white oak attributes. Treatment means did not differ significantly (α = 0.05) for any listed attribute, although block effects were significant for some attributes.*

Attribute[1,2] (per acre except as noted)	Site 1	2	3	4	5	6	7	8	9
No. of trees > 0 in. d.b.h.	173	138	157	143	137	108	106	122	195
No. of trees ≥ 1.5 in. d.b.h.	130	103	139	113	100	83	61	76	130
No. trees ≥ 4.5 in. d.b.h.	46	41	48	41	42	47	20	24	29
Qmd ≥ 1.5 in. d.b.h.	5.2	5.7	5.5	5.7	6.3	7.2	5.7	5.9	5.3
Qmd ≥ 4.5 in. d.b.h.	7.6	8.2	8.1	8.5	8.8	8.9	8.0	8.9	9.0
Basal area (ft^2/ac) ≥ 1.5 in. d.b.h.	19	17	13	19	22	22	10	14	18
Basal area (ft^2/ac) ≥ 4.5 in. d.b.h.	15	14	18	16	19	20	8	12	14

	Block 1 (sites 1, 2, 3)	Block 2 (sites 4, 5, 6)	Block 3 (sites 7, 8, 9)	F-value[3]	P-value[3]
No. of trees > 0 in. d.b.h.	156	129	141	0.6	0.61
No. of trees ≥ 1.5 in. d.b.h.	156	129	141	0.6	0.61
No. trees ≥ 4.5 in. d.b.h.	45	43	24	50.8	<0.01
Qmd ≥ 1.5 in. d.b.h.	5.5	6.4	5.6	2.7	0.18
Qmd ≥ 4.5 in. d.b.h.	8.0	8.8	8.6	3.2	0.15
Basal area (ft^2/ac) ≥ 1.5 in. d.b.h.	20	21	14	12.7	0.02
Basal area (ft^2/ac) ≥ 4.5 in. d.b.h.	16	18	11	14.8	0.01

	No harvest (sites 1, 6, 8)	Even-aged (sites 3, 5, 9)	Unven-aged (sites 2, 4, 7)	F-value[3]	P-value[3]
No. of trees > 0 in. d.b.h.	135	163	129	1.0	0.44
No. of trees ≥ 1.5 in. d.b.h.	97	123	93	1.5	0.32
No. trees ≥ 4.5 in. d.b.h.	39	40	34	4.1	0.11
Qmd ≥ 1.5 in. d.b.h.	6.1	5.7	5.7	0.5	0.62
Qmd ≥ 4.5 in. d.b.h.	8.5	8.7	8.2	0.8	0.52
Basal area (ft^2/ac) ≥ 1.5 in. d.b.h.	18	21	13	6.4	0.06
Basal area (ft^2/ac) ≥ 4.5 in. d.b.h.	16	17	16	5.3	0.07

[1] Qmd = quadratic mean d.b.h. (in inches) for trees in the specified size class.
[2] Reported values are per acre except as noted. Metric conversions are 1.5 in. = 4 cm, 4.5 in. = 11 cm, and generally 1 in. = 2.54 cm. Also, (2.47) (no. of trees/ac) = no. trees/ha and (0.2296) (basal area ft^2/ac) = basal area m^2/ha.
[3] For ANOVA of block effects for the indicated attribute based on model [1]. F has (2,4) degrees of freedom.
[4] For ANOVA of treatment effects for the indicated attribute based on model [1]. F has (2,4) degrees of freedom.

Table 6.—*Site, block, and treatment area means for black oak attributes. Treatment means did not differ significantly (α = 0.05) for any listed attribute, although block effects were significant for some attributes.*

Attribute[1,2] (per acre except as noted)	Site 1	2	3	4	5	6	7	8	9
No. of trees > 0 in. d.b.h.	77	63	52	42	44	37	101	83	95
No. of trees ≥ 1.5 in. d.b.h.	50	50	40	34	33	21	48	38	51
No. trees ≥ 4.5 in. d.b.h.	42	41	36	25	29	19	30	30	29
Qmd ≥ 1.5 in. d.b.h.	9.8	9.9	10.5	9.5	10.2	12.1	9.3	10.8	9.2
Qmd ≥ 4.5 in. d.b.h.	10.6	10.5	10.9	10.2	10.9	12.5	11.3	11.7	11.4
Basal area (ft^2/ac) ≥ 1.5 in. d.b.h.	126	26	25	19	20	20	22	24	24
Basal area (ft^2/ac) ≥ 4.5 in. d.b.h.	26	25	25	19	20	20	22	25	23

	Block 1 (sites 1, 2, 3)	Block 2 (sites 4, 5, 6)	Block 3 (sites 7, 8, 9)	F-value[3]	P-value[3]
No. of trees > 0 in. d.b.h.	64	41	93	16.9	0.01
No. of trees ≥ 1.5 in. d.b.h.	47	29	46	7.1	0.05
No. trees ≥ 4.5 in. d.b.h.	40	24	29	12.0	0.02
Qmd ≥ 1.5 in. d.b.h.	10.1	10.6	9.8	0.8	0.51
Qmd ≥ 4.5 in. d.b.h.	10.6	11.2	11.5	1.4	0.35
Basal area (ft^2/ac) ≥ 1.5 in. d.b.h.	26	20	24	63.6	<0.01
Basal area (ft^2/ac) ≥ 4.5 in. d.b.h.	25	19	23	50.5	<0.01

	No harvest (sites 1, 6, 8)	Even-aged (sites 3, 5, 9)	Unven-aged (sites 2, 4, 7)	F-value[3]	P-value[3]
No. of trees > 0 in. d.b.h.	66	64	68	0.2	0.85
No. of trees ≥ 1.5 in. d.b.h.	37	41	44	1.0	0.44
No. trees ≥ 4.5 in. d.b.h.	30	31	32	0.16	0.86
Qmd ≥ 1.5 in. d.b.h.	10.9	10.0	9.6	2.1	0.24
Qmd ≥ 4.5 in. d.b.h.	11.6	11.1	10.6	1.7	0.29
Basal area (ft^2/ac) ≥ 1.5 in. d.b.h.	24	23	22	3.1	0.15
Basal area (ft^2/ac) ≥ 4.5 in. d.b.h.	23	22	22	4.0	0.11

[1] Qmd = quadratic mean d.b.h. (in inches) for trees in the specified size class.
[2] Reported values are per acre except as noted. Metric conversions are 1.5 in. = 4 cm, 4.5 in. = 11 cm, and generally 1 in. = 2.54 cm. Also, (2.47) (no. of trees/ac) = no. trees/ha and (0.2296) (basal area ft^2/ac) = basal area m^2/ha.
[3] For ANOVA of block effects for the indicated attribute based on model [1]. F has (2,4) degrees of freedom.
[4] For ANOVA of treatment effects for the indicated attribute based on model [1]. F has (2,4) degrees of freedom.

Table 7.—*Site, block, and treatment area means for scarlet oak attributes. Neither treatment nor block effects were significant (a = 0.05) for any attributes examined.*

Attribute[1,2] (per acre except as noted)	Site 1	2	3	4	5	6	7	8	9
No. of trees > 0 in. d.b.h.	82	49	54	57	35	27	85	56	93
No. of trees ≥ 1.5 in. d.b.h.	60	40	44	46	29	22	66	31	60
No. trees ≥ 4.5 in. d.b.h.	45	31	34	32	21	20	41	24	26
Qmd ≥ 1.5 in. d.b.h.	8.3	9.1	9.0	9.3	9.5	11.7	10.0	11.6	7.8
Qmd ≥ 4.5 in. d.b.h.	9.2	9.9	10.3	10.6	10.6	12.0	11.7	12.7	10.5
Basal area (ft^2/ac) ≥ 1.5 in. d.b.h.	20	18	17	19	13	18	28	22	16
Basal area (ft^2/ac) ≥ 4.5 in. d.b.h.	21	18	18	20	13	18	29	22	18

	Block 1 (sites 1, 2, 3)	Block 2 (sites 4, 5, 6)	Block 3 (sites 7, 8, 9)	F-value[3]	P-value[3]
No. of trees > 0 in. d.b.h.	62	40	78	2.5	0.89
No. of trees ≥ 1.5 in. d.b.h.	48	32	53	1.4	0.35
No. trees ≥ 4.5 in. d.b.h.	37	25	30	1.5	0.33
Qmd ≥ 1.5 in. d.b.h.	8.8	10.1	9.8	0.9	0.49
Qmd ≥ 4.5 in. d.b.h.	9.8	11.1	11.6	3.2	0.15
Basal area (ft^2/ac) ≥ 1.5 in. d.b.h.	18	17	22	3.1	0.16
Basal area (ft^2/ac) ≥ 4.5 in. d.b.h.	19	17	23	2.6	0.19

	No harvest (sites 1, 6, 8)	Even-aged (sites 3, 5, 9)	Unven-aged (sites 2, 4, 7)	F-value[3]	P-value[3]
No. of trees > 0 in. d.b.h.	55	61	63	0.1	0.89
No. of trees ≥ 1.5 in. d.b.h.	38	44	50	0.5	0.64
No. trees ≥ 4.5 in. d.b.h.	30	27	35	0.7	0.56
Qmd ≥ 1.5 in. d.b.h.	10.5	8.8	9.5	1.3	0.36
Qmd ≥ 4.5 in. d.b.h.	11.3	10.5	10.7	0.6	0.58
Basal area (ft^2/ac) ≥ 1.5 in. d.b.h.	20	16	21	3.3	0.14
Basal area (ft^2/ac) ≥ 4.5 in. d.b.h.	21	16	22	3.7	0.12

[1] Qmd = quadratic mean d.b.h. (in inches) for trees in the specified size class.
[2] Reported values are per acre except as noted. Metric conversions are 1.5 in. = 4 cm, 4.5 in. = 11 cm, and generally 1 in. = 2.54 cm. Also, (2.47) (no. of trees/ac) = no. trees/ha and (0.2296) (basal area ft^2/ac) = basal area m^2/ha.
[3] For ANOVA of block effects for the indicated attribute based on model [1]. F has (2,4) degrees of freedom.
[4] For ANOVA of treatment effects for the indicated attribute based on model [1]. F has (2,4) degrees of freedom.

Table 8.—*Site, block, and treatment area means for shortleaf pine attributes. Neither treatment nor block effects were significant (a = 0.05) for any attributes examined.*

Attribute[1,2] (per acre except as noted)	Sites 1	2	3	4	5	6	7	8	9
No. of trees > 0 in. d.b.h.	26	21	15	17	16	36	20	27	34
No. of trees ≥ 1.5 in. d.b.h.	23	16	15	17	16	30	18	18	180
No. trees ≥ 4.5 in. d.b.h.	19	9.6	13	16	14	25	16	10	5.3
Qmd ≥ 1.5 in. d.b.h.	7.1	4.5	8.7	6.8	7.0	6.9	8.9	7.1	5.7
Qmd ≥ 4.5 in. d.b.h.	7.6	5.0	9.0	7.0	7.2	7.0	9.0	7.5	6.4
Basal area (ft^2/ac) ≥ 1.5 in. d.b.h.	9	5	8	8	8	10	11	6	3
Basal area (ft^2/ac) ≥ 4.5 in. d.b.h.	9	5	8	8	8	11	11	6	4

	Block 1 (sites 1, 2, 3)	Block 2 (sites 4, 5, 6)	Block 3 (sites 7, 8, 9)	F-value[3]	P-value[3]
No. of trees > 0 in. d.b.h.	21	23	27	0.6	0.61
No. of trees ≥ 1.5 in. d.b.h.	18	21	18	0.7	0.57
No. trees ≥ 4.5 in. d.b.h.	14	18	10	2.1	0.23
Qmd ≥ 1.5 in. d.b.h.	6.8	6.7	7.2	<0.1	0.96
Qmd ≥ 4.5 in. d.b.h.	7.1	7.1	7.6	0.1	0.92
Basal area (ft^2/ac) ≥ 1.5 in. d.b.h.	7	9	7	0.5	0.65
Basal area (ft^2/ac) ≥ 4.5 in. d.b.h.	7	9	7	0.5	0.65

	No harvest (sites 1, 6, 8)	Even-aged (sites 3, 5, 9)	Unven-aged (sites 2, 4, 7)	F-value[3]	P-value[3]
No. of trees > 0 in. d.b.h.	30	21	19	1.6	0.31
No. of trees ≥ 1.5 in. d.b.h.	24	16	17	3.7	0.12
No. trees ≥ 4.5 in. d.b.h.	18	11	14	2.0	0.25
Qmd ≥ 1.5 in. d.b.h.	7.0	7.1	6.7	<0.1	0.96
Qmd ≥ 4.5 in. d.b.h.	7.3	7.5	7.0	0.1	0.92
Basal area (ft^2/ac) ≥ 1.5 in. d.b.h.	8	6	8	0.4	0.71
Basal area (ft^2/ac) ≥ 4.5 in. d.b.h.	9	7	8	0.3	0.73

[1] Qmd = quadratic mean d.b.h. (in inches) for trees in the specified size class.
[2] Reported values are per acre except as noted. Metric conversions are 1.5 in. = 4 cm, 4.5 in. = 11 cm, and generally 1 in. = 2.54 cm. Also, (2.47) (no. of trees/ac) = no. trees/ha and (0.2296) (basal area ft^2/ac) = basal area m^2/ha.
[3] For ANOVA of block effects for the indicated attribute based on model [1]. F has (2,4) degrees of freedom.
[4] For ANOVA of treatment effects for the indicated attribute based on model [1]. F has (2,4) degrees of freedom.

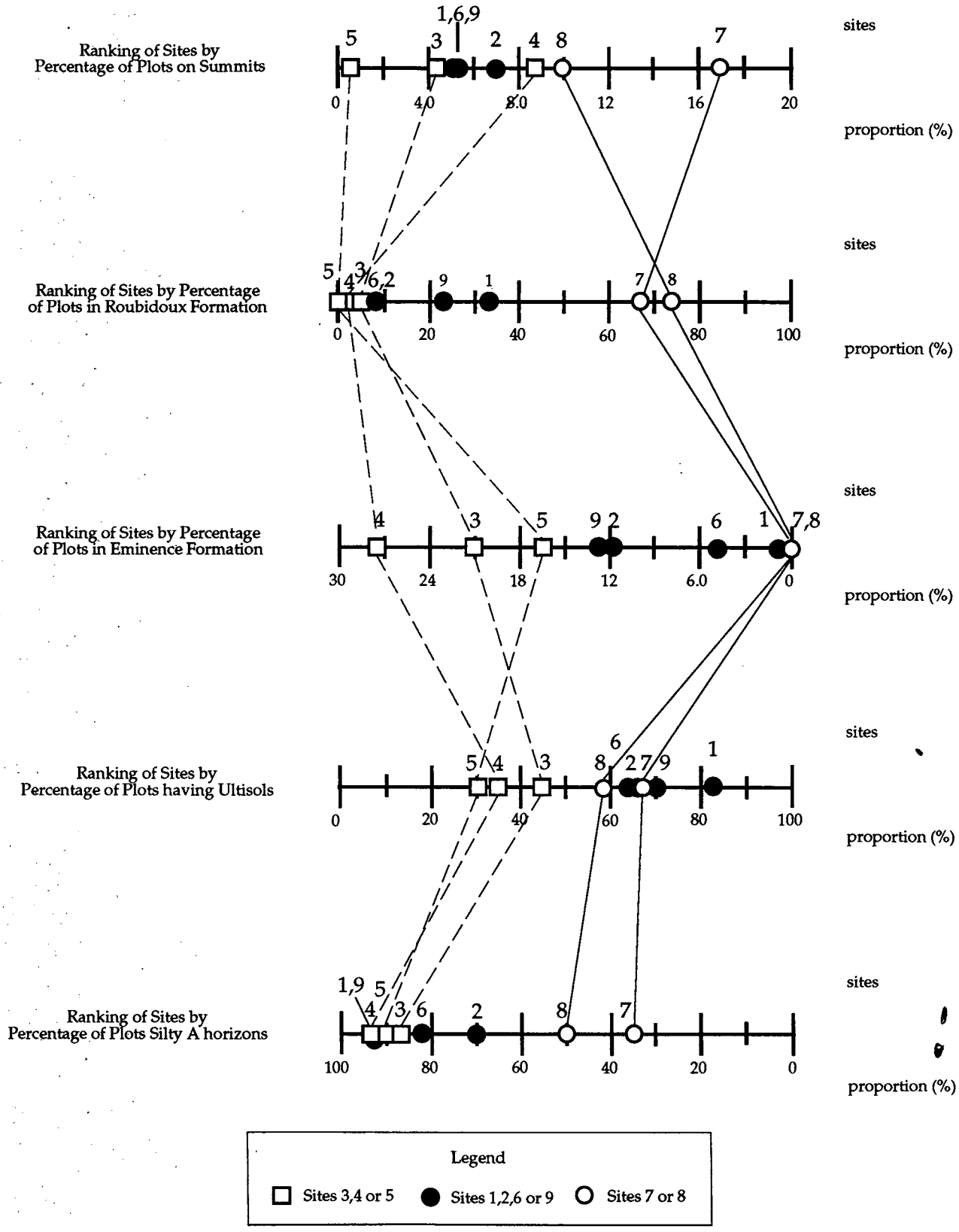

Figure 3.—*Ranking of sites for several key environmental variables. Lines connecting values for sites 3, 4, and 5 and sites 7 and 8 illustrate the similarity of those groups of sites relative to the others.*

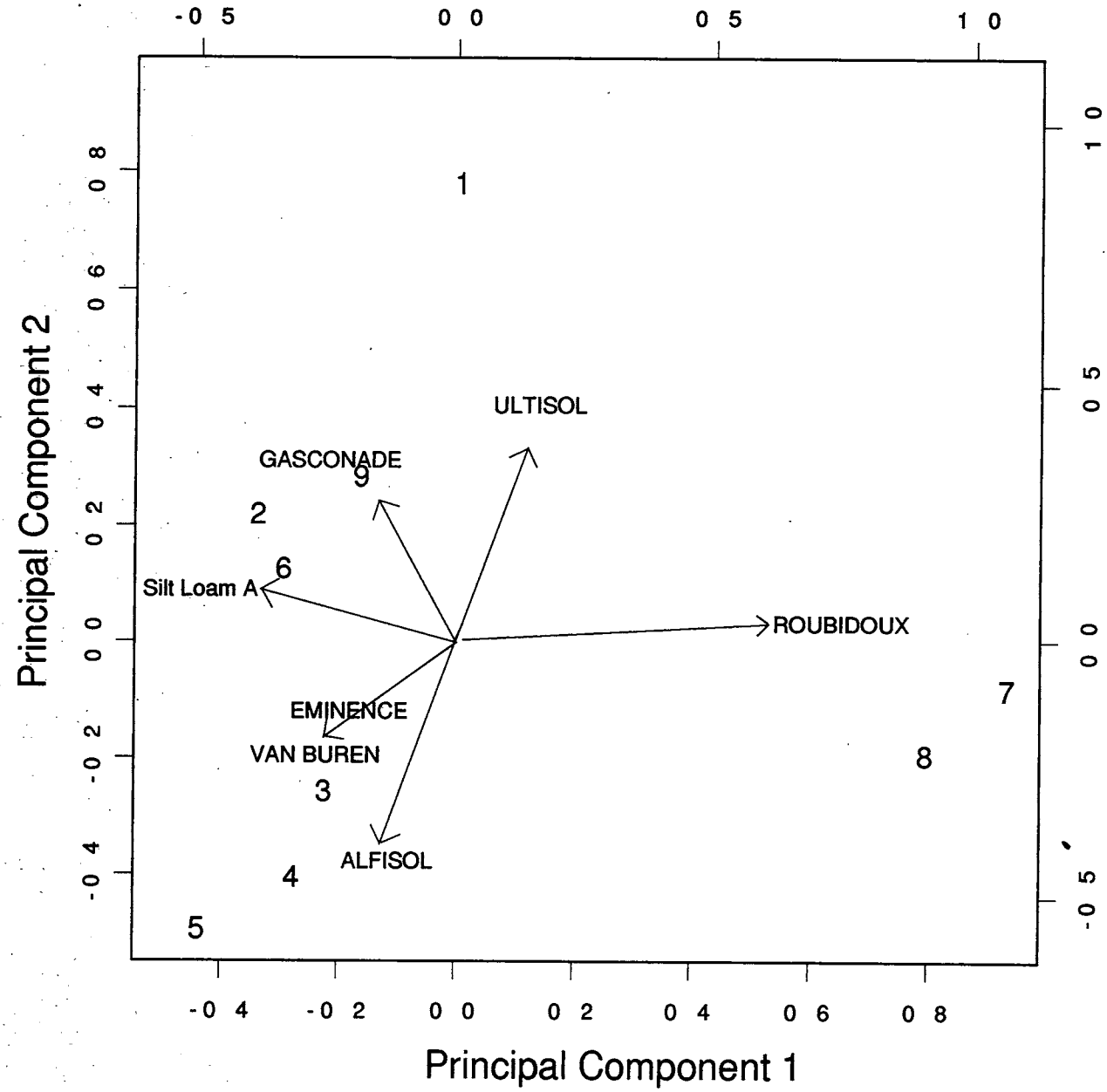

Figure 4.—*Biplot of first two Principal Component axes derived from environmental variables. Numbers correspond to sites. Arrows point toward environmental characteristics that differentiate sites. The labels "ROUBIDOUX," "GASCONADE," and "VAN BUREN" indicate geological strata; "ULTISOL" and "ALFISOL" are important soil orders (i.e., Taxonomic classes); and "Silt Loam A" = silt loam soil textures in the A-horizon.*

variety of soils, and contains more mesic vegetation and glade-savanna complexes than the Hills LTA (Meinert *et al.* 1997).

All of the EAM treatments occurred in sites having more basic soils (Alfisols) and soils with siltier surface soil horizons. No-harvest (NH) treatment areas generally occurred in more acidic soils (Ultisols) and in soils that had greater variation of surface horizon texture (primarily silt loams and loams). Block 2 (sites 4 through 6) appeared to be much more internally uniform in the environmental variables evaluated than block 1 (sites 1 through 3) or block 3 (sites 7 through 9). Block 1 contained site 1, which had somewhat errant properties relative to other sites. Block 3 contained two very similar sites (7 and 8), but one site (9) that contained igneous parent material and outcrops and proportionally less Roubidoux geology.

DISCUSSION

We attribute a portion of the site-level differences in numbers of species, abundances, quadratic mean diameters, and basal area to differences in environmental conditions among sites and to land-use history. Greater numbers of species per acre, greater abundance and basal area of white oak, and fewer scarlet oaks were associated with sites having a greater proportion of base-rich geological strata and soils classified as Alfisols, and they were also associated with greater overall landscape relief and slope steepness. Site 6 appeared to be the only anomaly. Environmental conditions of site 6 were more similar to those of sites 2 through 5, although its woody vegetation characteristics were more similar to those of sites 7 and 8.

Using environmental differences to describe among-site differences in quadratic mean diameter, trees per acre, and total basal area (rather than basal area of specific species) was problematic. Diameter and tree densities are greatly influenced by past management and may not indicate site quality (Reineke 1933). Differences in total basal area can reflect differences in site productivity, but only in fully stocked forests of similar age. Moreover, logging, grazing, and other disturbances can greatly affect total basal area. Land-use histories of all sites prior to Missouri Department of Conservation ownership are generally considered similar. However, the gentler topography of sites 7 and 8 made them more suited for grazing, more susceptible to widespread burning, and more accessible for selective logging than the other sites. These past disturbances may reduce the numbers of trees per unit area, without removing all trees, allowing growth concentrated to fewer trees. This may explain why sites 7 and 8 had fewer but larger trees than the other sites.

Potential Treatment Response Differences

Differences in environmental variables at site-, block-, and treatment-levels prompted us to develop hypotheses about potential differences in woody vegetation responses to proposed silvicultural treatments during the course of the MOFEP experiment. We hypothesize that NH and UAM treatment responses will be more variable and consequently may be more difficult to interpret because these treatments have been delegated to more contrasting sites than the EAM treatments. Moreover, we hypothesize that EAM treatment areas will support a greater abundance of mesic species and have greater growth rates because these treatments were randomly assigned to sites having siltier surface soil textures and a greater proportion of base-rich parents materials.

Effectiveness of Blocking

The goal of blocking in experiments is to create strata that are internally homogenous in conditions thought to affect the experiment so that the response differences to treatments can be identified (Samuals 1989). Blocking is generally considered effective when blocks are internally homogenous and there are significant differences among blocks. Significant pre-treatment differences in woody vegetation variables among blocks suggest that blocking is useful for the MOFEP study. However, our analysis of site-level differences in environmental data suggests that the optimal blocking arrangement has not been achieved, nor can it be, under the current study design. We consider there to be little difference in environmental variables among sites 2 through 6 and between sites 7 and 8 (fig. 3). However, site 1 differs considerably from the remaining sites, but is most similar in soil base saturation to sites 7 and 8 (fig. 3). Site 9 is also unique in that past uplifting from underlying rhyolite (igneous) bedrock has tilted the overlying sedimentary strata. This tilting has caused the overlying sedimentary strata (primarily Gasconade and Eminence) to be more often exposed in different landform positions on site 9 than in the other sites. This essentially increases the parent material heterogeneity of site 9. However, the proportions of each geological strata within site 9 were found to be similar to sites 2 through 6. Therefore, site 9 is more similar to sites 2 through 6 than to sites 7 and 8. Based upon environmental information, improved blocking efficiency may have been achieved by grouping sites 1, 7, and 8. The remaining sites could be blocked in any combination.

Within-Site Variation

The experimental design of MOFEP cutting treatments uses sites as the experimental unit. However, there is considerable variation in both vegetation and environmental characteristics within each site. Each site contains from 16 to 22 distinctly different soil-geo-landform environments, many of which are summarized by Meinert *et al.* (1997). Unpublished data show

differences in woody species abundance and site indices attributable to differences in soil-geo-landforms within sites. For example, black oak is most abundant on acid soils of Roubidoux summits; white oak is more abundant in deep, base-rich soils in Lower Gasconade and Eminence backslopes; and site indices are generally higher for all species in Lower Gasconade backslopes (Kabrick *et al.*, unpublished data). In addition to compositional and productivity differences, we anticipate that soil-geo-landforms will differ in responses to cultural treatments applied during MOFEP. For example, species composition may remain similar on Roubidoux summits regardless of cultural treatment because these soil-geo-landforms favor the xeric and shade intolerant species presently growing on these soil-geo-landforms. However, UAM may favor shade tolerant mesic species on base-rich and moist sites on Lower Gasconade and Eminence backslope positions, causing species composition to change over time. Soil-geo-landform information may become critical for interpreting within-site response heterogeneity.

SUMMARY

Compared to other sites, sites 2 through 5 had greater numbers of species per unit area. Sites 7 and 8 had fewer trees ≥ 1.5 in. (4 cm) d.b.h., less white oak, and more scarlet oak. Block 3 (sites 7, 8, and 9) had fewer trees ≥ 4.5 in. (11 cm) d.b.h., less overall basal area, and less white oak. Block 2 (sites 4, 5, and 6) had less black oak. We found no treatment-level woody vegetation differences.

Greater numbers of species per acre, greater abundance of white oak, and lesser abundance of scarlet oak were associated with sites and blocks that have a greater proportion of base-rich geological strata and a greater proportion of soils classified as Alfisols. We attribute some degree of the observed site and block differences in diameter and trees per unit area to differences in past land-use. We hypothesize: (1) NH and UAM treatment responses will be more variable and more difficult to interpret than EAM treatment responses because the NH and UAM treatments were delegated to more contrasting sites and (2) EAM treatment areas will have greater growth rates because these treatments were delegated to sites having siltier surface soil textures and a greater proportion of base-rich parent materials.

For the variables we examined, the designated blocks were effective in grouping sites with similar vegetational characteristics. However, based on an examination of environmental characteristics, blocks that combined sites 1, 7, and 8; sites 3, 4, and 5; and sites 2, 6, and 9 may improve the effectiveness of blocking.

ACKNOWLEDGMENT

We thank Jenny Grabner, Dennis Meinert, and Tim Nigh for helpful discussions during data analysis and interpretation. We also thank Jenny Grabner for her helpful comments on a previous draft of this manuscript. We gratefully acknowledge the Missouri Department of Conservation for providing the funding and data for this work.

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An Analysis of MOFEP Ground Flora: Pre-treatment Conditions

Jennifer K. Grabner, David R. Larsen, and John M. Kabrick[1]

Abstract.—Similarities and differences in MOFEP ground flora species composition were determined at site, block, and treatment levels. Ground flora data were collected across nine sites on 648 permanent forestry plots; more than 10,300 1-m^2 quadrats were sampled each summer from 1991 through 1995. Approximately 530 species were identified; more than half occurred on fewer than 10 percent of the plots. Highly significant differences among sample years were observed for plot richness, but were regarded as a reflection of improved data quality over the course of the project. Though plots averaged relatively high species diversity, wide ranges from low to high species richness and diversity existed within all sites. Analysis of variance on plot diversity and richness indicated a strong trend of differences between even-aged and control sites. Differences in ground flora species composition and abundance, plot richness, and plot diversity appear strongly correlated with patterns in geology, landform, and soils both within and among the MOFEP sites.

To practice effective ecosystem management, natural resource managers must develop an understanding of relationships among the major components of the systems they are managing. The Missouri Ozark Forest Ecosystem Project (MOFEP) is a large-scale, long-term experiment to investigate effects of even-aged, uneven-aged, and no-harvest management practices on several different components of Missouri's southeastern Ozark forests (Brookshire *et al.* Brookshire and Hauser 1993, Kurzejeski *et al.* 1993).

Understory vegetation is an integral part of any forested community. Herbaceous species have been shown to be useful indicators of site disturbance, health, and potential productivity (Daubenmire 1976, Foti and Devall 1993, Host and Pregitzer 1991). Previous studies have evaluated effects of clearcutting, intermediate, and selective harvesting on understory vegetation in the southern and Midwestern sections of the United States (Crouch 1983, Duffy and Meier 1992, Gove *et al.* 1991, Reader 1987). Many studies, particularly those in the Ozark region, have focused primarily on woody regeneration and wildlife forage production (Crawford 1971 and 1976). To date, there has been no comprehensive evaluation of Missouri's upland Ozark ground flora. MOFEP provides an unparalleled opportunity to thoroughly describe current ground flora conditions in mature second-growth oak/hickory and oak/pine forests in the southeast Missouri Ozarks. The project also provides an opportunity to measure both short and long-term effects of standard forest management practices on ground flora composition and structure.

MOFEP is a large-scale experiment with a randomized block design. As MOFEP researchers prepare for post-treatment phases of data collection and analysis, it is critical to understand the pre-treatment differences and similarities among sites, replication blocks, and treatment groups. The primary objective of this paper is to identify existing pre-treatment differences among sites, treatment classes, and replication blocks with respect to ground flora species composition, plot diversity, and plot richness at the site, block, and treatment levels. A secondary objective is to briefly discuss patterns in the ground flora data in relation to environmental conditions both within and among sites. This preliminary evaluation of MOFEP ground vegetation is not intended as a comprehensive analysis of the entire pre-treatment dataset. Our intention, instead, is to provide baseline information to which future

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investigations of both pre- and post-treatment MOFEP ground flora data can refer.

METHODS

Study Area

Overstory Vegetation

The MOFEP study encompasses nine sites in Carter, Reynolds, and Shannon Counties of southeast Missouri (Brookshire *et al.* 1997, see fig. 1). Sites range in size from 265 to 530 ha, and are primarily composed of mature second-growth oak-hickory and oak-pine forests with relatively closed canopies. Common overstory tree species include black oak (*Quercus velutina* Lam.), white oak (*Quercus alba* L.), scarlet oak (*Quercus coccinea* Muench.), post oak (*Quercus stellata* Wang.), shortleaf pine (*Pinus echinata* Mill.), black hickory (*Carya texana* Buckl.), mockernut hickory (*Carya tomentosa* Nutt.), and pignut hickory (*Carya glabra* Mill.). Flowering dogwood (*Cornus florida* L.), blackgum (*Nyssa sylvatica* Marsh.), and sassafras (*Sassafras albidum* Nutt.) are common understory tree and shrub species. Detailed descriptions of overstory vegetation on MOFEP are provided by Brookshire *et al.* (1997), Kabrick *et al.* (1997), and Pallardy (1995).

Geology and Soils

Soils of the Ozarks are typically highly weathered and occur in a very dissected and weathered landscape. Primary parent materials include residuum, hillslope sediments, loess, and alluvium. Residual soil parent materials are from the Roubidoux, Gasconade, Van Buren, Gunter, and Eminence layers of the stratigraphic column. Sandstone, dolomitic limestone, and chert are the dominant lithologies on all sites, with a small amount of rhyolite expressed in site 9. A detailed description of the soils, geology, and landforms on MOFEP areas is provided by Meinert (1997) and Meinert *et al.* (1997).

Experimental Design

Nine sites were grouped geographically into three replicated blocks; each block contained one even-aged, one uneven-aged, and one no-harvest (control) unit. Treatments were randomly allocated within blocks. Stratified random sampling was used to locate vegetation plots, ensuring at least one plot per stand. From 70 to 76 plots were located in each of the nine sites for a total of 648. More than 90 percent of the vegetation plots were on upland topographic landforms including ridges, shoulder slopes, and backslopes. Upland waterway landforms (floodplains, terraces, alluvial fans, etc.) were probably undersampled due to the existing stand delineations at the time of stratification and plot installation. The MOFEP experimental design is described in detail by Brookshire and Hauser (1993), Kurzejeski *et al.* (1993), and Sheriff and He (1997).

Data Collection

Ground layer vegetation was sampled within the same 0.2-ha circular plots used for MOFEP forestry data collection (Brookshire *et al.* 1997, Jensen 1995). Ground flora data were collected from 16 permanently marked 1-m^2 quadrats in each 0.2-ha plot. Each 0.2-ha plot contained four 0.02-ha subplots. The 1-m^2 quadrats were placed 6 m from the 0.02-ha subplot centers at 45°, 135°, 225°, and 315°. This design yielded a total of 10, 368 quadrats across all nine sites (648 plots x 16 quadrats per plot). See figure 4 in Brookshire *et al.* (1997) for a diagram of the MOFEP vegetation plot design.

Pre-treatment ground flora data collection typically occurred between early June and middle to late August. Sites 7, 8, and 9 were sampled in 1991; 1 through 7 were sampled in 1992; all nine sites were sampled during each of the 1993, 1994, and 1995 seasons. Sites were sampled in the same order each summer to minimize seasonal differences that could potentially confound year to year comparisons within a site. Evaluations of seasonal effects among sites within a sample year have not been completed.

Within the 1-m^2 quadrats, all vascular species with leaves less than a meter above the ground were identified and assigned an estimate of percent foliar coverage. Coverage estimates included plants not rooted in the quadrats but with live foliage hanging over them. Information on canopy closure and ground surface materials was also gathered at each quadrat, including estimates of percent coverage by bare ground, mosses and lichens, leaf litter, rock and gravel, dead wood, and live basal area. For an outline of the sampling protocols used to collect pre-treatment MOFEP ground flora data, see Grabner (1997).

Data Analysis

Calculations

A combination of descriptive statistics and analysis of variance was used for this report to examine MOFEP ground vegetation data at the site, replication block, and treatment levels. A comprehensive species list was developed from the 1991-1995 data; nomenclature follows that of Steyermark (1963) (see appendix). This list includes species life history attributes, native status, average relative abundance, and number of occurrences for each sample year.

Relative abundance was calculated at the plot level by summing 1-m^2 coverages for each species, dividing by the sum of all species coverages for that plot, and multiplying by 100. These values, excluding plots in which the species did not occur, were averaged by plot for each species for the 1993-1995 sampling years. Average relative abundance and the number of 0.2-ha plots on which each species occurred were calculated by site for the 1995 data (see appendix B in Grabner 1997).

In addition, each species was labeled as one of 10 plant types including fern, forb, grass, legume, sedge, shrub, tree, herbaceous vine, and woody vine. Relative abundance was calculated at the plot level for plant types (using 1995 data) by summing species coverages for each type, dividing by the sum of all species coverages in the plot, and multiplying by 100. Species and plant type relative abundances could not be calculated for 1991 or 1992 data because individual coverage estimates were not assigned to woody species (shrubs, trees, and woody vines) during those years.

Species richness was defined as the total number of species identified on each 0.2-ha plot (16 quadrats). Estimates of mean plot richness per site were calculated for all 1991-1995 data. Mean plot richness was also calculated using 1991-1995 data for plots broadly categorized by landtype (e.g., ridges and summits, backslopes, benches, and upland waterways).

Simpson's Index of Diversity and the Shannon-Weiner measure of diversity were calculated at the plot level using 1993-1995 data (1991 and 1992 data were not used for the same reason relative abundances were not calculated for these years). These indices were derived using the following formulas (Krebs 1989):

Simpson's Index of Diversity = $1 - \Sigma(p_i)^2$
Shannon-Weiner Index of Species Diversity = $-\Sigma(p_i)(\log_2 p_i)$

where p_i = proportion of coverage of species$_i$ in a 0.2-ha plot (based on 16 1-m^2 quadrats; =Σ species$_i$ coverages for plot ÷ Σ all species coverages for plot.

Simpson's Index of Diversity has been shown to be more sensitive to changes in common species within a community, while the Shannon-Weiner index is apparently more sensitive to rare species (Krebs 1989). Both measures were analyzed to avoid these biases.

Analysis of Variance Models

Analysis of variance (ANOVA) was performed on mean number of species per plot for 1993-1995 data to evaluate differences among blocks, treatments, and sample years.

$$Y_{ijk} = \mu + \text{block}_i + \text{treatment}_j + \text{year}_T + \text{year*block}_{ik} + \text{year*treatment}_{jk} + \varepsilon_{ijk}$$

where "Y_{ijk}" is the expected value, "μ" is the mean number of species per plot (non-transformed), "block$_i$" is the effect of each of the three replication blocks, "treatment$_j$" is the effect of each of the three treatment groups, "year*block$_{ik}$" is the effect of a year-block interaction, "year*treatment$_{jk}$" is the effect of a year-treatment interaction, and "ε_{ijk}" is the error effect. Mean species richness values were not normally distributed; $\log_{10}$ and natural log (ln) transformations did not effectively normalize the data. Mean, log10-, and ln-transformed values were tested, but no differences in the results of the analyses were found. Only non-transformed plot richness data are presented in this paper. Data from 1991-1992 could not be used in the repeated measures ANOVA because all nine sites were not sampled for those years (see methods).

ANOVA was also used to compare the Simpson's and Shannon-Weiner diversity indices as well as plot richness among replication blocks and treatments for 1993-1995 data. Log_{10} transformations of calculated diversity indices were used to normalize the data. A simple fixed effects model was used for this analysis:

$$Y_{ij} = \mu + \text{block}_i + \text{treatment}_j + \varepsilon_{ij}$$

where "Y_{ij}" is the expected value, "μ" is the mean diversity index or plot richness, "$block_i$" is the effect of each of the three replication blocks, "$treatment_j$" is the effect of each of the three treatment groups, and "ε_{ij}" is the error effect, $N(0,\mu^2)$.

An alpha value of 0.05 was used to test for statistically significant differences for both ANOVA models. Given the low power of the design, however, P-values < 0.2 were considered indicative of potential trends in the data.

RESULTS AND DISCUSSION

General Site Similarities

More than 530 vascular species, representing nearly 275 genera and 85 families, were identified as a result of pre-treatment sampling on MOFEP sites. More than 80 percent were native perennials, and only 25 exotic species were identified (see appendix). Total numbers of species per site (1991-1995) ranged from 309 in site 6 to 381 in site 5, with a mean of 346. Most species were found on two or more sites, with no more than 11 unique to one site (table 1).

Ground flora across the sites was relatively diverse but typically dominated by a few species of woody vines, understory trees, and legumes (fig. 1). The same 5 to 10 species were among the most common across all sites. Tick trefoil (*Desmodium nudiflorum* L.), a legume, was the most common ground flora species on all sites for all sample years. This plant was consistently found in over 90 percent of all MOFEP vegetation plots and had an average relative abundance more than twice that of most other species (see appendix). Flowering dogwood (*Cornus florida* L.), sassafras (*Sassafras albidum* Nutt.), Virginia creeper (*Parthenocissus quinquefolia* L.), summer grape (*Vitis aestivalis* Michx.), black oak (*Quercus velutina* Lam.), and hog peanut (*Amphicarpa bracteata* L.) were also very common (table 2).

Although the species listed in table 2 averaged high relative cover and frequency, most species on all sites occurred in few plots and had low coverages when present. In each site in 1995, approximately 60 percent of all species were found on fewer than 10 percent of the 0.2-ha plots (fig. 2). Similarly skewed occurrence frequency distributions were observed for 1991 - 1994 (see appendix). Our findings are similar to those of Foti and Devall (1993), who studied herbaceous plants in the Ouachita and Ozark-St. Francis National Forests of Arkansas. They estimated that more than half of the 582 species recorded occurred in only 10 to 15 percent of the stands sampled.

Differences Among Sample Years

Our analysis indicated a highly significant year effect for plot richness ($P < 0.005$), but no year-block or year-treatment interactions (table 3). The large effect of sample year on plot richness may be striking, but it is not surprising. The steady increase in mean number of species

Table 1.—*Number of 0.2-ha plots, total number of ground flora species identified in 1-m² quadrats, and number of unique species for each MOFEP site (from 1991-1995 data).*

Site	Block	Treatment	Number of plots	Total number of species	Number of unique species
1	1	No-harvest	76	326	5
2	1	Uneven-aged	73	370	6
3	1	Even-aged	72	334	7
4	2	Uneven-aged	74	365	11
5	2	Even-aged	70	381	10
6	2	No-harvest	71	309	1
7	3	Uneven-aged	71	335	9
8	3	No-harvest	70	343	5
9	3	Even-aged	71	355	10
Means	—	—	72	346	7
Totals	—	—	648	530	64

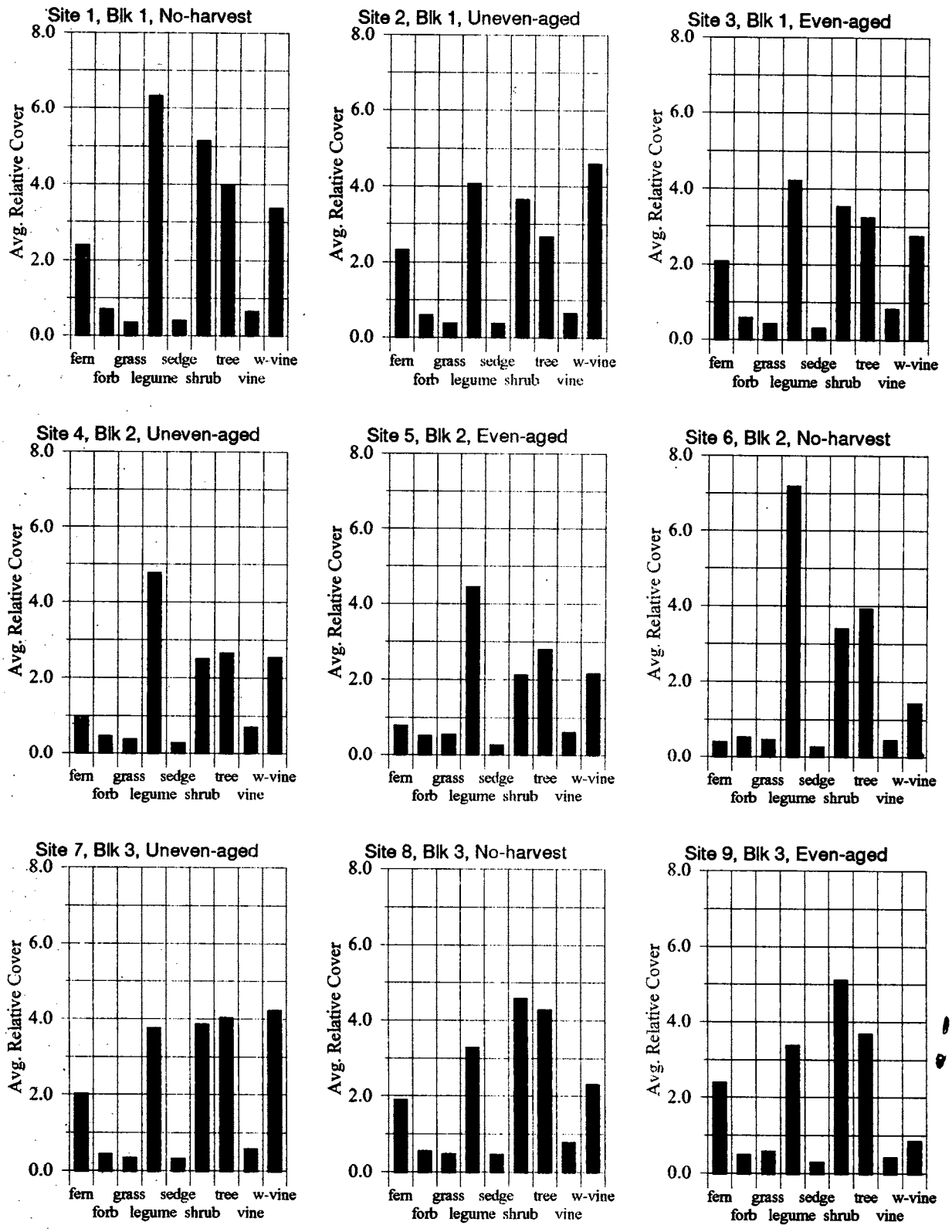

Figure 1.—*Average relative abundance by plant type for all sites in 1995. Note the importance of legumes, shrubs, trees, and woody vines on all sites ("w-vine" = woody vines, "vine" = herbaceous vines).*

Table 2.—*Common ground flora species by site. Rankings were determined by the number of 0.2-ha plots per site in which each species occurred (1995 data only). Replication block and assigned treatments are shown in parentheses below each site number (NH = no-harvest, EA = even-aged, UA = uneven-aged).*

	Site								
	1	2	3	4	5	6	7	8	9
(Block,Treatment)	(1,NH)	(1,UA)	(1,EA)	(2,UA)	(2,EA)	(2,NH)	(3,UA)	(3,NH)	(3,EA)
Species					*Rank*				
Desmodium nudiflorum (tick trefoil)	3	7	1	3	2	1	3	3	2
Cornus florida (dogwood)	4	1	4	1	1	2	5	5	3
Sassafras albidum (sassafras)	2	3	2	2	6	6	2	2	1
Vitis aestivalis (summer grape)	1	2	3	6	5	3	1	6	8
Quercus velutina (black oak)	5	9	6	—	8	4	4	1	4
Quercus alba (white oak)	7	5	5	8	7	5	—	4	6
Amphicarpa bracteata (hog peanut)	10	6	8	5	4	8	—	8	7
Parthenocissus quinquefolia (Virginia creeper)	—	4	9	4	3	10	10	—	—
Nyssa sylvatica (blackgum)	8	—	7	7	9	7	—	—	—
Quercus coccinea (scarlet oak)	—	10	10	9	—	—	9	9	—
Aristolochia serpentaria (Virginia snakeroot)	—	—	—	—	10	—	—	—	—
Vaccinium vacillans (lowbush blueberry)	6	—	—	—	—	—	—	10	—
Vitis spp. (grape)	—	—	—	—	—	9	—	—	—
Carya glabra (pignut hickory)	9	8	—	—	—	—	—	—	—
Carex nigromarginata (sedge)	—	—	—	—	—	—	8	—	5
Vaccinium stamineum (highbush blueberry)	—	—	—	—	—	—	6	7	10
Carya spp. (hickory)	—	—	—	10	—	—	—	—	—
Carya tomentosa (mockernut hickory)	—	—	—	—	—	—	—	—	9
Quercus stellata (post oak)	—	—	—	—	—	—	7	—	—

recorded per plot is, in all likelihood, a direct reflection of annual improvements in skill and training of personnel associated with MOFEP botany data collection. In other words, this trend represents the learning curve of field and supervisory staff involved with the study.

Interestingly, though mean values themselves increased significantly each year, the overall ranking pattern among sites did not change. For 1993-1995, site 5 consistently averaged the highest number of species per 0.2-ha plot, and sites 4 and 9 were ranked second and third, respectively. Sites 2, 3, and 1 were typically in the middle, and sites 6, 7, and 8 were always close together at the bottom (fig. 3). Nearly identical patterns were observed for Simpson's and Shannon-Weiner diversity indices (figs. 4 and 5). Our results are similar to the among-

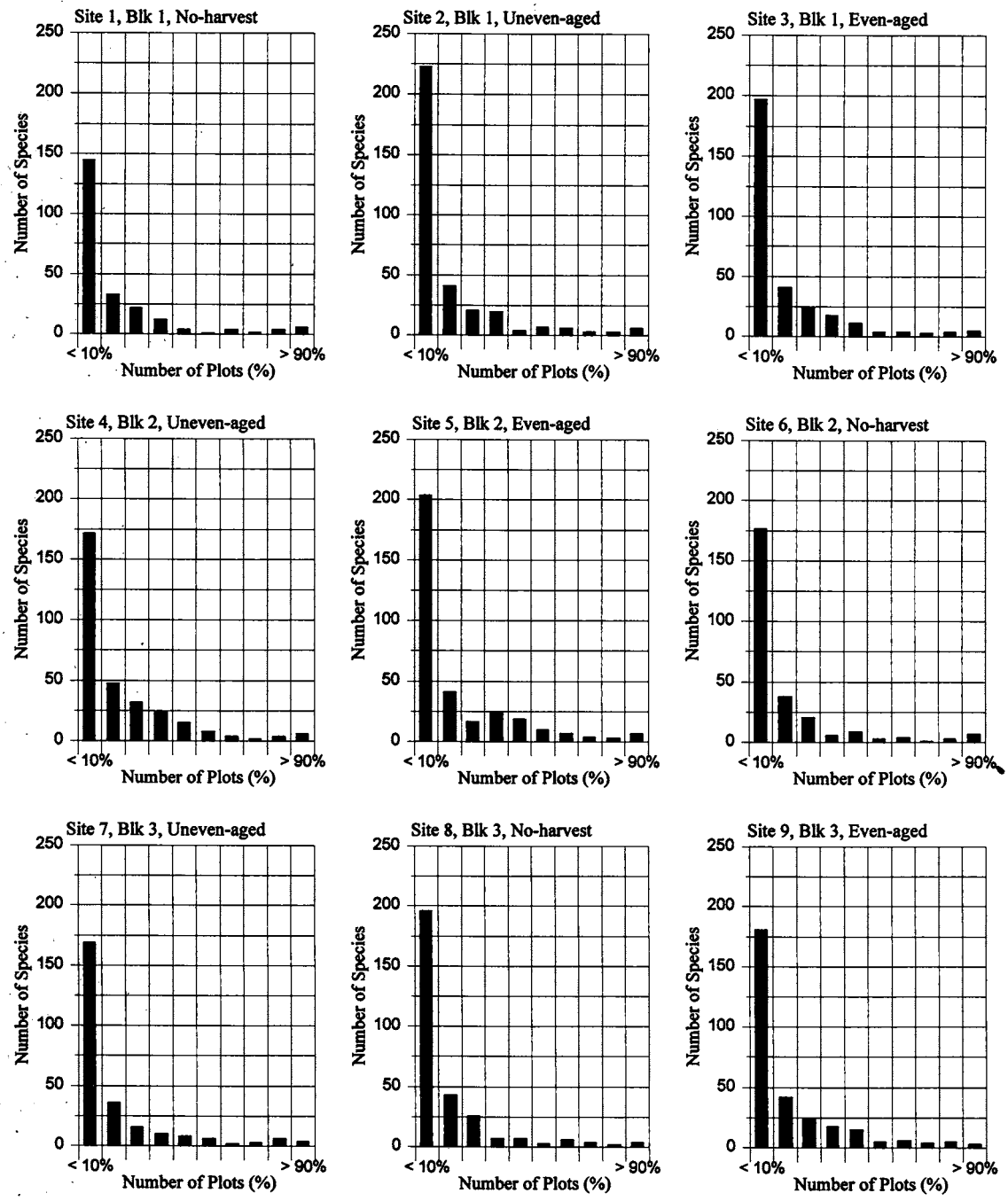

Figure 2.—*Species frequency distributions for all sites in 1995. Values represent the number of ground flora species plotted against the number of plots (out of 648) in which they were found. Note that a large majority of species occurred on fewer than 10 percent of the plots in each site.*

Table 3.—*Repeated measures analysis of variance table of mean number of species per 0.2-ha plot (1993-1995 data, no transformations).*

Source	Pillai's trace	F	Num DF	Den DF	Sum of Squares	Pr(F)
Block	—	6.57	2	—	778.30	0.05
Treatment	—	2.53	2	—	300.07	0.19
Block*Treatment	—	—	4	—	236.81	—
Year	0.97	50.64	2	3	—	0.005
Year*Treatment	0.90	1.63	4	8	—	0.257
Year*Block	0.58	0.83	4	8	—	0.544

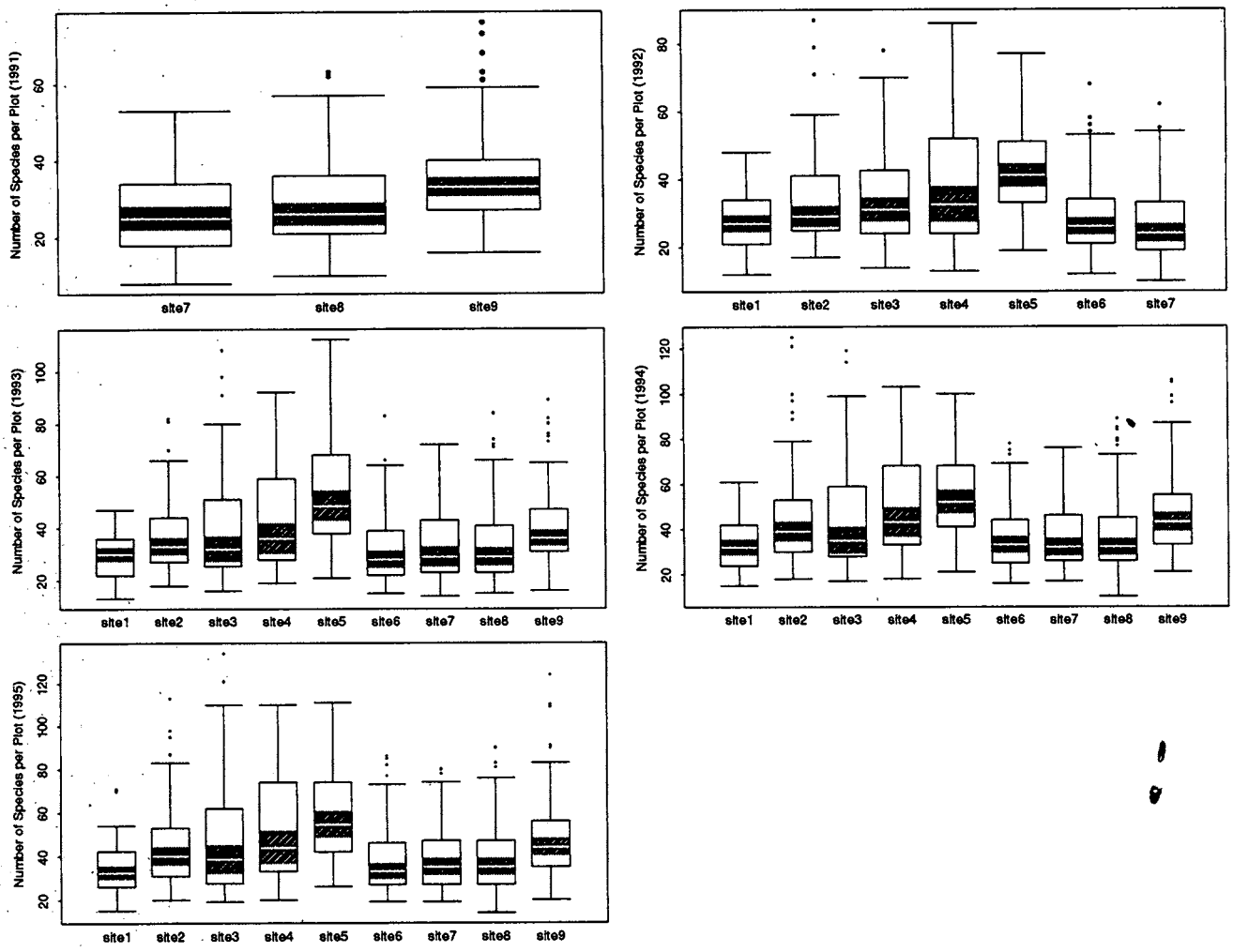

Figure 3.—*Number of ground flora species per 0.2-ha plot for each site (1991-1995). Box plots of several attributes summarized by site from plot-level data. The central (white) bar in each box represents the median. The black bars around the median show the 95 percent confidence interval for the median. The rectangular box indicates the range of 50 percent of the data. Brackets indicate the range of continuous data. Dots beyond the brackets indicate values beyond the range of continuous data.*

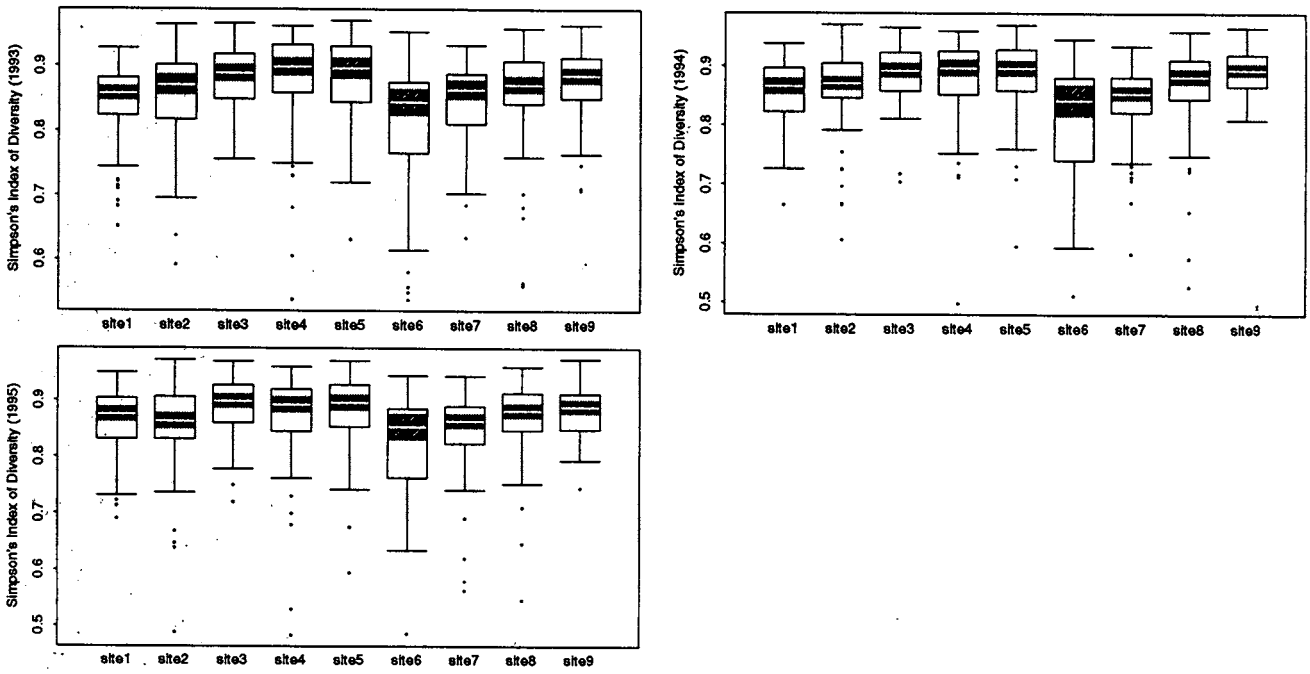

Figure 4.—*Simpson's Index of Diversity by site for 1993-1995 ground flora data. Box plots of several attributes summarized by site from plot-level data. The central (white) bar in each box represents the median. The black bars around the median show the 95 percent confidence interval for the median. The rectangular box indicates the range of 50 percent of the data. Brackets indicate the range of continuous data. Dots beyond the brackets indicate values beyond the range of continuous data.*

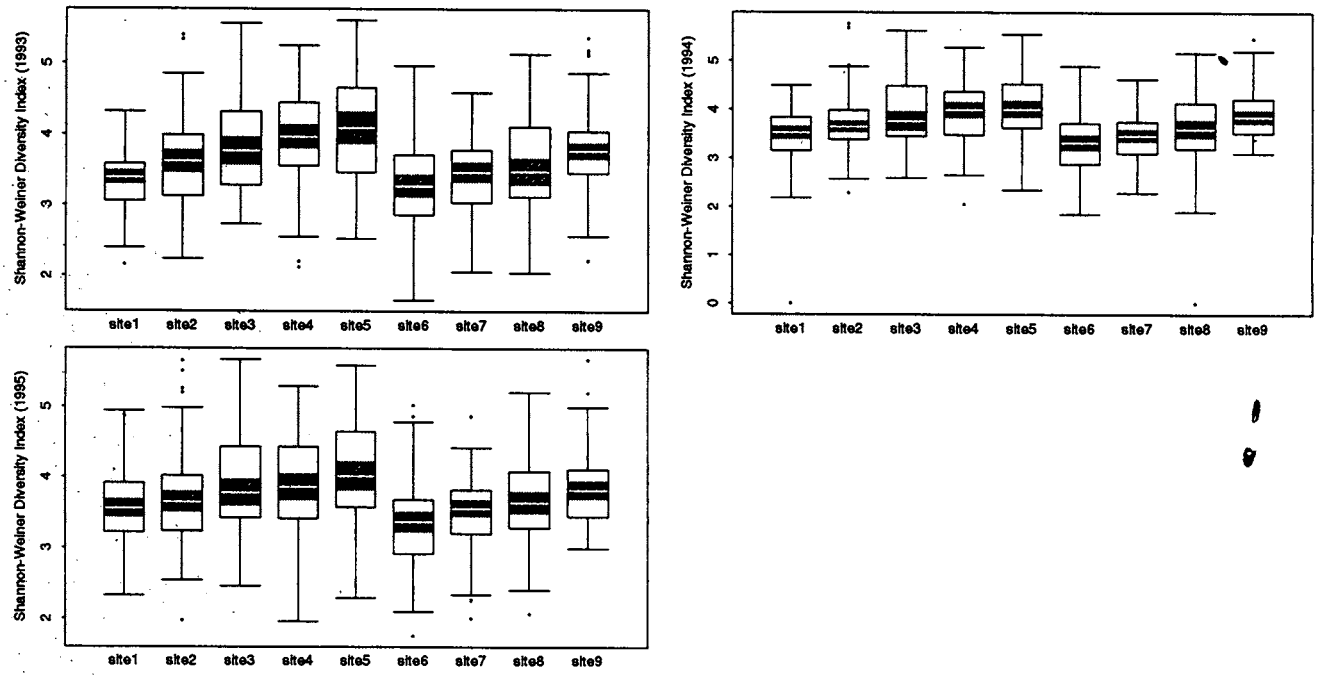

Figure 5.—*Shannon-Weiner Diversity Index by site for 1993-1995 ground flora data. Box plots of several attributes summarized by site from plot-level data. The central (white) bar in each box represents the median. The black bars around the median show the 95 percent confidence interval for the median. The rectangular box indicates the range of 50 percent of the data. Brackets indicate the range of continuous data. Dots beyond the brackets indicate values beyond the range of continuous data.*

site patterns observed by Kabrick *et al.* (1997) for MOFEP woody vegetation.

Consistency in the relative ranking of sites from year to year, combined with the lack of a year-treatment interaction, further supports our assertion that significant year effects do not represent actual temporal variation within sites. In other words, when a MOFEP site is observed from one pre-treatment year to the next, the data give no reason to expect significant differences in average plot diversity or richness other than those created by observer error.

Species Richness, Diversity, and Composition

Block and Treatment-level Analysis of Variance

In keeping with the overall MOFEP experimental design, accurate assessment of post-treatment effects at the site level depends on understanding within and among block pre-treatment conditions. It is important to be aware of block or treatment effects in the data prior to actual treatment implementation.

Analysis of variance indicated no block effects on plot richness or diversity for the 1993-1995 data ($P > 0.2$, tables 4 and 5).

There were no statistically significant treatment effects ($P > 0.05$) on plot-level species diversity as estimated by the Simpson's and Shannon-Weiner Indices of Diversity for 1993, 1994, or 1995. Given the low degrees of freedom, however, a strong trend in treatment differences was apparent ($P < 0.2$) (table 4). Additionally, ANOVA revealed a significant treatment effect on plot species richness in 1995 ($P = 0.047$). Marginally significant differences in plot species richness by treatment class were also visible in the 1994 ($P = 0.062$) and 1993 ($P = 0.067$) data (table 5).

These pre-treatment effects by treatment class appear to reflect inherent differences between control and even-aged sites. As mentioned previously, sites 3, 5, and 9 (even-aged) consistently averaged high plot richness and diversity, while sites 1, 6, and 8 (controls) consistently averaged relatively low values (figs. 3-5).

Species Abundance Patterns Among Sites

Species such as *Desmodium nudiflorum*, *Cornus florida*, *Vitis aestivalis*, and *Sassafras albidum* are always among the 10 most dominant on all sites (table 2). Within this same table, however, differences among sites with respect to their common species become apparent. *Vaccinium stamineum*, for example, was among the 10 most frequently encountered species for each of the block 3 sites (7, 8, and 9), but not for any of the other sites. Similarly, *Carya glabra* was one of the top 10 species in sites 1 and 2 (block 1) but not in any others. Further investigation of

Table 4.—*Analysis of variance table of Simpson's and Shannon-Weiner diversity indices (1993-1995 data, $\log_{10}$ transformations).*

		Simpson's		*Shannon-Weiner*	
Source	**DF**	**Sum of Squares**	**Pr (F)**	**Sum of Squares**	**Pr (F)**
1993					
Block	2	0.00093	0.95	0.031	0.75
Treatment	2	0.060	0.14	0.37	0.12
Error	4	0.036		0.20	
1994					
Block	2	0.0044	0.81	0.013	0.87
Treatment	2	0.060	0.16	0.45	0.08
Error	4	0.040		0.18	
1995					
Block	2	0.0050	0.73	0.0031	0.97
Treatment	2	0.038	0.19	0.24	0.18
Error	4	0.029		0.18	

Table 5.—*Analysis of variance table of mean number of species per 0.2-ha plot (1993-1995 data, no transformations).*

Source	DF	Sum of Squares	Pr(F)
1993			
Block	2	91.6	0.22
Treatment	2	229.6	0.067
Error	4	401.6	
1994			
Block	2	84.7	0.24
Treatment	2	248.7	0.062
Error	4	82.7	
1995			
Block	2	128.7	0.16
Treatment	2	312.7	0.047
Error	4	86.7	

the 1995 data revealed noticeable differences for several species with respect to their abundances among sites (see appendix B, Grabner 1997).

Relationships Between Ground Flora and Soil-Geo-Landform Patterns Among Sites

Though somewhat similar in overall composition and relative dominance of the most common species, important differences in plot diversity, richness, and species abundances were found among the MOFEP sites. We attributed these observed differences to differences in geology, landform, and soil conditions among the sites.

As mentioned previously, the treatment effects revealed by ANOVA appear to reflect differences between the control and even-aged sites. MOFEP control sites (1, 6, and 8) contained a relatively low proportion of vegetation plots in the Lower Gasconade, Gunter, and Eminence geologies. The majority of plots on these sites were in the Roubidoux and Upper Gasconade geologic layers, which are typically associated with more highly weathered, ultic soils. In contrast, the Roubidoux-Upper Gasconade and Lower Gasconade-Eminence layers were fairly evenly represented within the even-aged sites (3, 5, and 9) (table 6). Alfic backslopes, benches, moist floodplains, and variable-depth soil units are common to the Lower Gasconade, Gunter, and Eminence strata, and potentially support a more diverse flora.

Figure 6 illustrates differences in the proportional representation of alfic and ultic landforms within each site. Abundance among sites for several species appears correlated with these types of environmental factors.

For example, sites 2 through 6 contained considerably more plots on alfic ridges and mesic backslopes than did sites 1, 7, and 8. Species often associated with relatively rich mesic to dry-mesic forests such as *Acer saccharum*, *Cimicifuga racemosa*, *Desmodium glutinosum*, *Galium concinnum*, and *Ulmus rubra* were much more abundant on sites 2 through 6 than on sites 1, 7, or 8. Conversely, typical dry acid woodland species such as *Vaccinium stamineum*, *Vaccinium vacillans*, *Quercus stellata*, and *Quercus marilandica* were more abundant on sites 1, 7, and 8 (table 7). These interpretations are supported by Kabrick *et al.* (1997), who showed site 1 (block 1) to be most similar to sites 7 and 8 (block 3) with respect to environmental variables. Collectively, sites 1, 7, and 8 contained a greater proportion of acidic soils than the other sites.

Table 6.—*Proportions by treatment class of 0.2-ha vegetation plots in Roubidoux and Upper Gasconade vs. Lower Gasconade, Gunter, and Eminence geologic strata.*

Treatment	Sites	Roubidoux-Upper Gasconade	Lower Gasconade-Gunter-Eminence
		Proportion of plots	
No-harvest	1, 6, 8	0.85	0.15
Uneven-aged	2, 4, 7	0.65	0.35
Even-aged	3, 5, 9	0.53	0.47

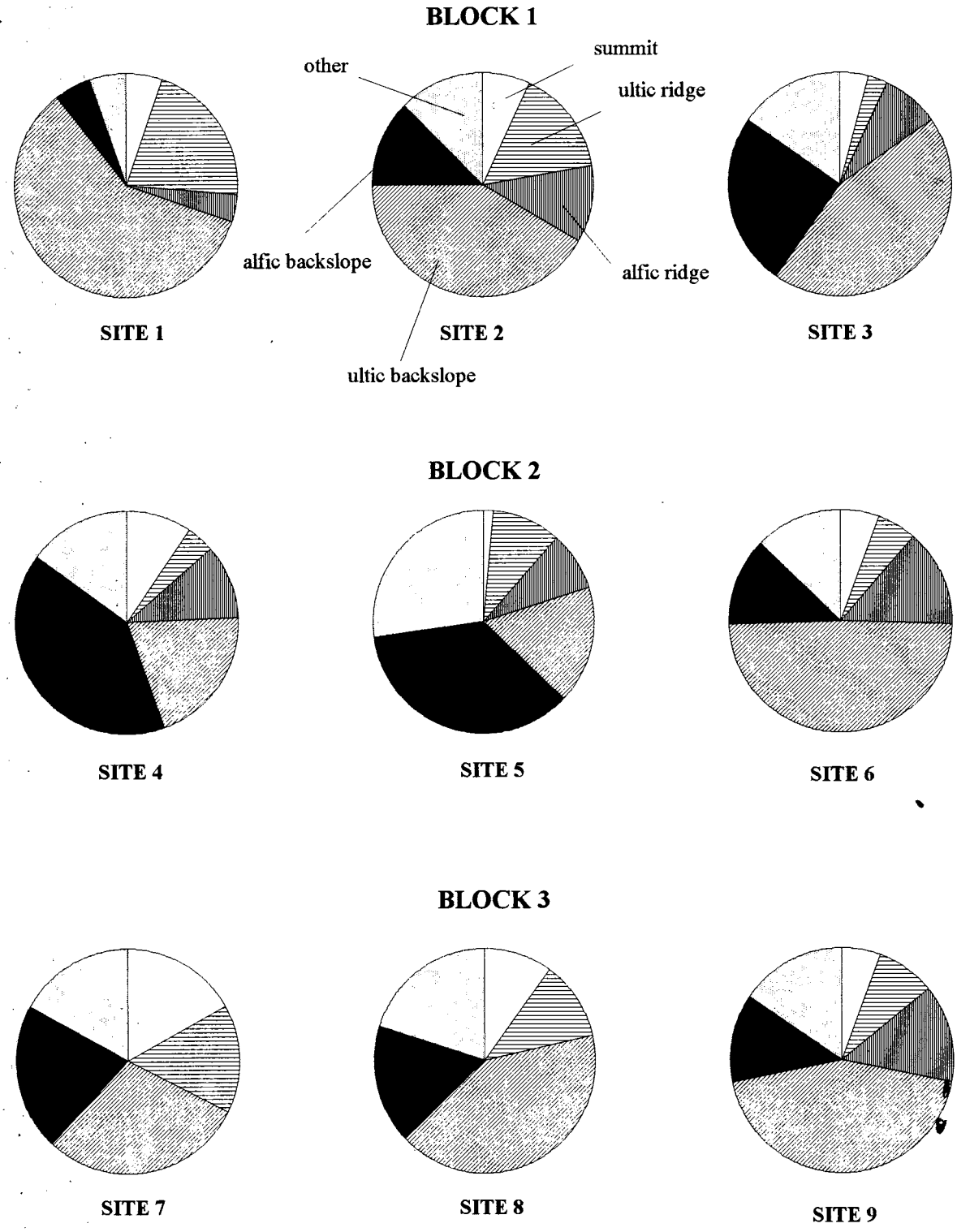

Figure 6.—*Proportions of MOFEP vegetation plots by general soil-landform categories. The "other" category includes glades/glade edges, floodplains, benches, toeslopes, and others. Note the differences in ratios of ultic:alfic plots among sites (particulary 3, 4, & 5 vs. 1, 7, & 8).*

Table 7.—*Ground flora species that differed in frequency among sites. Values are the numbers of 0.2-ha plots in which each species was identified during the 1995 sample year (Bold = values especially high or low relative to others).*

	Site								
	1	2	3	4	5	6	7	8	9
(Block, Treatment)	**(1,NH)**	**(1, UA)**	**(1, EA)**	**(2, UA)**	**(2, EA)**	**(2, NH)**	**(3, UA)**	**(3, NH)**	**(3, EA)**
Species					*Number of plots*				
Acer saccharum	3	8	11	13	7	5	**0**	**0**	**0**
Carya glabra	63	63	52	36	48	48	**19**	**25**	43
Cimicifuga racemosa	**6**	22	11	25	22	19	**0**	**0**	15
Desmodium glutinosum	23	45	36	35	35	20	**0**	**0**	22
Desmodium nuttallii	19	29	14	31	28	20	**42**	**43**	33
Dioscorea quaternata	19	37	32	44	39	16	**8**	**7**	23
Galium concinnum	**3**	25	14	21	21	10	**1**	**3**	13
Hepatica nobilis	4	5	**10**	**19**	6	6	0	0	5
Lespedeza virginica	1	2	4	9	3	4	16	13	10
Passiflora lutea	10	14	13	18	14	16	**0**	**2**	**7**
Polystichum acrostichoides	10	4	4	5	8	8	**0**	**1**	7
Quercus marilandica	2	7	4	0	2	7	**11**	**19**	7
Quercus stellata	13	6	17	20	22	12	**58**	**43**	**32**
Rhus aromatica	**10**	41	46	41	38	**10**	**7**	**7**	23
Ruellia pedunculata	**2**	13	12	23	30	12	**9**	**5**	**10**
Scutellaria incana	4	4	2	12	2	2	**0**	**0**	3
Smilax bona-nox	**0**	23	32	32	26	**7**	**6**	**9**	**9**
Smilax glauca	0	1	0	1	0	1	**22**	**5**	**15**
Ulmus alata	**0**	10	27	21	24	**6**	**1**	**3**	**0**
Ulmus rubra	**0**	31	21	28	34	14	**2**	**5**	**7**
Uvularia grandiflora	14	16	22	22	25	16	**0**	**3**	**7**
Vaccinium stamineum	46	25	34	36	26	26	**62**	**56**	**53**
Vaccinium vacillans	**71**	44	37	43	39	42	**51**	**53**	**52**
Viburnum rufidulum	**3**	12	16	15	23	**8**	**1**	**3**	**2**
Vitis vulpina	**10**	30	22	23	45	27	**8**	**19**	**7**

Within-Site Variation

Understanding year, block, treatment, and site-level relationships is critical for interpreting harvesting effects within the framework of the overall MOFEP design. Equally important, though, is understanding the amount and sources of variation in the plot data from which site-level means were calculated. In 1994 and 1995, the number of species per 0.2-ha plot ranged from 10 to 125 and from 14 to 134, respectively. Similarly, Simpson's Index of Diversity ranged from 0.5 to 0.97 in 1994, and from 0.48 to 0.97 in 1995 (figs. 3 and 4). Not surprisingly, environmental factors such as light, water, and nutrient availability appear to strongly affect plant species distributions and abundance within the MOFEP sites as well as among them. Brief inspection of 1993-1995 data showed noticeable differences in mean numbers of species for plots located in upland waterways, structural benches, ridges and summits, sideslopes with deep soil, and sideslopes with soils ranging from very shallow to moderately deep (fig. 7). The variable depth and upland waterway plots had the highest average richness; ridges and summits had the lowest.

Detailed investigations of the relationships between vegetation and environmental factors using direct and indirect multivariate ordinations are in progress. Preliminary interpretations of both a Two-Way Indicator Species Analysis (TWINSPAN) and a Detrended Correspondence Analysis (DCA) on a subset of the 1995 data support our associations between species abundances and soil-geo-landform patterns at both the site and plot levels (data not shown). Geology and landform appear to be

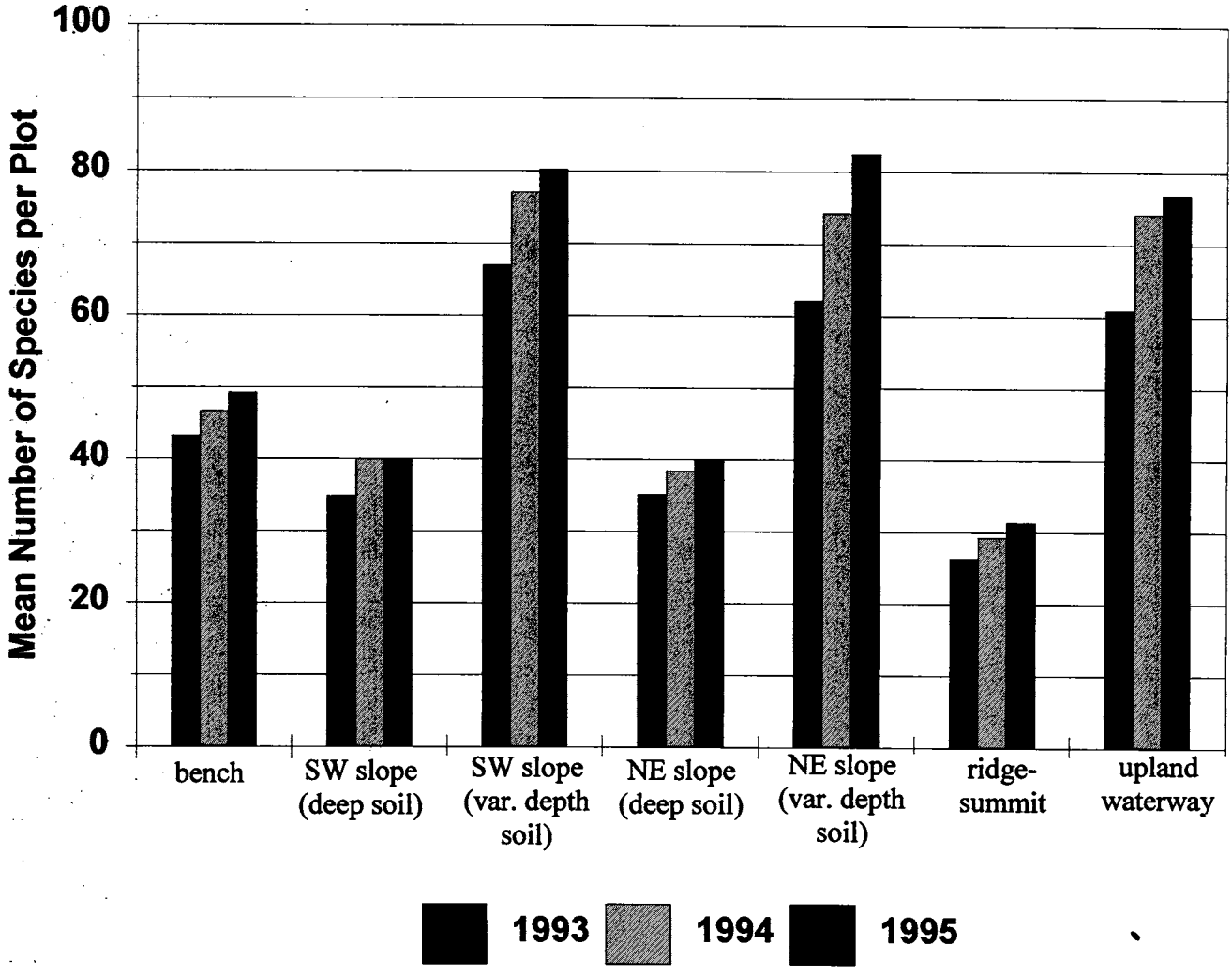

Figure 7.—*Mean plot richness by landtype (1993-1995).*

controlling factors such as soil depth, base saturation, and water availability, which in turn directly affect ground flora species distribution and abundance.

SUMMARY AND CONCLUSIONS

Ground-layer vegetation data were collected across nine sites on 648 0.2-ha plots from 1991 through 1995 as part of the Missouri Ozark Forest Ecosystem Project. More than 300 species were identified on each of the nine sites, with no more than 11 unique to any one site, for a total of over 530 species. A few species of legumes, trees, and woody vines dominated in cover and frequency on all sites. Most species (> 60 percent) occurred on fewer than 10 percent of the sample plots in each site.

There were very large sample year effects on mean plot richness. We regard this as a reflection of improvement in plant identification skill over the course of the study rather than a biological phenomenon. We recommend using the 1994 and 1995 data as the baseline from which to interpret future post-treatment results. Given that the increases in mean plot diversity from year to year were likely due to observer error, we concluded there was no evidence of temporal variation within sites. No year-treatment interaction was detected, and the relative ranking of sites from highest to lowest mean plot richness and diversity was very consistent among years. Sites 5, 4, and 9 consistently averaged the highest plot richness and diversity; sites 6, 7, and 8 typically averaged the lowest.

Though MOFEP sites were found to be somewhat similar in composition (particularly in terms of abundant species), important site and treatment-level differences in species abundance, plot richness, and plot diversity were revealed. Analysis of variance showed even-aged sites (3, 5, and 9) averaged consistently greater plot richness and diversity than did no-harvest sites (1, 6, and 8). Brief inspection of relative cover and frequency data indicated noticeable differences among sites for several species. We attributed these vegetation patterns to differences in geology, landforms, and soil conditions among the sites.

Wide ranges and large variances typify the within-site MOFEP ground flora data. As with among-site patterns, significant amounts of the variation among plots is likely due to differences in geology, landform, and soil factors. When categorized by major landtype, plots in upland waterways averaged more species per plot than did glades, ridges, or sideslopes.

Further analysis of among- and within-site relationships between MOFEP ground flora and soil-geo-landform patterns is in progress.

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APPENDIX

MOFEP Ground Flora: Pre-treatment Species List

ALL CAPS denotes species on Federal or Missouri State Rare and Endangered lists.

Italics indicates non-native species.

Relative abundances were calculated from 1993, 1994, and 1995 MOFEP botany data, and represent the mean relative cover per 0.2-ha plot for each species. As in the paper, these values have been multiplied by 100 to fit them within limited column widths. Average relative abundance values reflect only those plots on which the species occurred.

Number of plots per species per year was calculated from the 1991 - 1995 data by summing the number of 0.2-ha plots on which species occurred in at least one of the sixteen 1-m^2 quadrats.

Species	Family	Type	Number of Plots '91	'92	'93	'94	'95	Avg. Rel. Abundance '93	'94	'95
Acalypha spp.	Euphorbiaceae	nat. ann. forb	0	0	0	2	0	0.00	0.03	0.00
Acalypha virginica	Euphorbiaceae	nat. ann. forb	7	19	6	26	16	0.55	0.07	0.09
Acer negundo	Aceraceae	nat. per. tree	0	0	1	1	1	1.21	0.45	1.17
Acer rubrum	Aceraceae	nat. per. tree	66	304	353	347	353	3.62	3.99	4.40
Acer saccharum	Aceraceae	nat. per. tree	0	30	55	64	47	1.27	1.35	1.47
Achillea millefolium	Asteraceae	ex. perennial forb	2	1	1	1	1	0.16	0.03	0.02
Actaea pachypoda	Ranunculaceae	nat. per. forb	0	0	3	2	1	0.46	0.02	0.46
Actaea rubra	Ranunculaceae	nat. per. forb	0	0	0	1	0	0.00	0.03	0.00
Adiantum pedatum	Polypodiaceae	nat. per. fern	0	5	5	5	5	1.76	1.21	1.40
Aesculus glabra	Hippocastanaceae	nat. per. tree	0	0	0	0	1	0.00	0.00	0.40
Agrimonia parviflora	Rosaceae	nat. per. forb	1	20	21	7	3	0.89	0.51	0.67
Agrimonia pubescens	Rosaceae	nat. per. forb	17	49	96	112	98	0.83	0.88	0.83
Agrimonia rostellata	Rosaceae	nat. per. forb	0	0	0	0	20	0.00	0.00	0.78
Agrimonia spp.	Rosaceae	nat. per. forb	0	0	1	6	17	0.42	0.03	0.12
Agrostis perennans	Poaceae	nat. per. grass	0	0	0	0	2	0.00	0.00	0.13
Allium spp.	Liliacea	nat. per. forb	0	0	1	2	1	0.03	0.04	0.82
Ambrosia artemisiifolia	Asteraceae	nat. ann. forb	5	3	5	9	5	0.24	0.08	0.32
Ambrosia coronopifolia	Asteraceae	nat. per. forb	0	0	0	0	0	0.00	0.00	0.00
Ambrosia trifida	Asteraceae	nat. ann. forb	1	0	0	1	1	0.00	0.48	0.05
Amelanchier arborea	Rosaceae	nat. per. tree	14	53	132	113	127	1.41	1.81	1.35
AMIANTHIUM MUSCITOXICUM	Liliaceae	nat. per. forb	0	0	4	5	5	0.36	0.75	0.24
Amphicarpa bracteata	Fabaceae	nat. per.legume	169	423	550	551	555	6.81	5.93	6.93
Andropogon gerardi	Poaceae	nat. per. grass	18	7	61	60	53	1.33	0.76	0.61
Andropogon scoparius	Poaceae	nat. per. grass	5	20	107	115	115	0.93	0.92	0.91
Andropogon spp.	Poaceae	nat. per. grass	0	5	3	5	2	0.14	0.14	0.72
Andropogon virginicus	Poaceae	nat. per. grass	62	104	9	28	11	0.89	0.73	0.33
Anemone spp.	Ranunculaceae	nat. per. forb	1	0	0	0	0	0.00	0.00	0.00
Anemone virginiana	Ranunculaceae	nat. per. forb	0	1	18	7	10	0.20	0.18	0.25
Anemonella thalictroides	Ranunculaceae	nat. per. forb	8	93	149	123	148	0.25	0.19	0.18
Antennaria plantaginifolia	Asteraceae	nat. per. forb	58	117	150	156	151	0.80	0.72	0.67
Aplectrum hyemale	Orchidaceae	nat. per. forb	2	0	0	0	0	0.00	0.00	0.00
Apocynum cannabinum	Apocynaceae	nat. per. forb	0	3	57	60	72	0.65	0.94	0.87
Apocynum medium	Apocynaceae	nat. per. forb	21	45	38	3	1	1.00	0.47	1.83
Apocynum spp.	Apocynaceae	nat. per. forb	0	17	0	5	1	0.00	0.56	0.06
Aquilegia canadensis	Ranunculaceae	nat. per. forb	0	0	0	1	0	0.00	0.91	0.00
Arabis canadensis	Brassicaceae	nat. bien. forb	0	0	1	0	2	0.06	0.00	0.19
Arabis laevigata	Brassicaceae	nat. bien. forb	0	0	0	2	1	0.00	0.16	0.01
Arabis spp.	Brassicaceae	nat. bien. forb	0	1	0	5	5	0.00	0.07	0.38
Aralia racemosa	Araliaceae	nat. per. forb	0	0	0	3	0	0.00	0.97	0.00
Arctium minus	Asteraceae	ex. bien. forb	0	0	1	0	0	0.93	0.00	0.00
Arisaema atrorubens	Araceae	nat. per. forb	0	0	1	3	3	0.71	0.38	0.39
Arisaema dracontium	Araceae	nat. per. forb	0	0	0	2	1	0.00	0.20	0.02
Aristolochia serpentaria	Aristolochiaceae	nat. per. forb	89	262	385	419	437	0.27	0.27	0.24
Aruncus dioicus pubescens	Rosaceae	nat. per. forb	0	0	2	0	5	1.32	0.00	0.68
Asarum canadense	Aristolochiaceae	nat. per. forb	1	22	6	8	4	1.14	0.99	0.92
Asclepias hirtella	Asclepiadaceae	nat. per. forb	0	0	3	1	1	0.96	0.16	0.02
Asclepias purpurascens	Asclepiadaceae	nat. per. forb	0	0	0	1	4	0.00	0.15	0.33
Asclepias quadrifolia	Asclepiadaceae	nat. per. forb	0	4	56	70	100	0.23	0.23	0.23
Asclepias spp.	Asclepiadaceae	nat. per. forb	0	3	2	4	2	1.11	0.24	0.03

Species	Family	Type	Number of Plots '91	'92	'93	'94	'95	Avg. Rel. Abundance '93	'94	'95
Asclepias tuberosa	Asclepiadaceae	nat. per. forb	0	1	2	3	2	0.40	0.13	0.21
Asclepias verticillata	Asclepiadaceae	nat. per. forb	0	2	10	12	10	0.21	0.19	0.27
Asclepias viridiflora	Asclepiadaceae	nat. per. forb	0	0	3	8	3	0.02	0.48	0.18
Ascyrum hypericoides	Hypericaceae	nat. per. forb	9	8	9	7	30	0.33	0.52	0.36
Asimina triloba	Annonaceae	nat. per. tree	2	17	31	35	31	3.46	3.95	4.00
Asplenium platyneuron	Polypodiaceae	nat. per. fern	23	53	81	80	82	0.27	0.22	0.19
Aster anomalus	Asteraceae	nat. per. forb	23	62	90	121	155	0.40	0.44	0.35
Aster azureus	Asteraceae	nat. per. forb	4	11	44	46	24	0.37	0.33	0.31
Aster cordifolius	Asteraceae	nat. per. forb	0	0	1	0	3	0.43	0.00	0.30
Aster laevis	Asteraceae	nat. per. forb	0	1	17	22	26	0.42	0.68	0.52
Aster lateriflorus	Asteraceae	nat. per. forb	0	0	3	0	4	0.25	0.00	0.54
Aster linariifolius	Asteraceae	nat. per. forb	2	24	20	18	13	0.18	0.29	0.08
Aster novae-angliae	Asteraceae	nat. per. forb	0	1	6	1	2	0.55	1.31	0.92
Aster oblongifolius	Asteraceae	nat. per. forb	0	0	4	5	6	0.53	0.17	0.30
Aster patens	Asteraceae	nat. per. forb	49	100	103	130	128	0.32	0.29	0.27
Aster sagittifolius	Asteraceae	nat. per. forb	0	0	7	7	13	0.48	0.51	0.54
Aster sericeus	Asteraceae	nat. per. forb	2	4	2	7	1	0.20	0.49	0.38
Aster spp.	Asteraceae	nat. per. forb	7	30	29	12	14	0.47	0.11	0.30
Aster turbinellus	Asteraceae	nat. per. forb	0	0	13	20	26	0.27	0.37	0.32
Astragalus mexicanus	Fabaceae	nat. per.legume	0	2	5	1	1	0.84	0.02	1.36
Baptisia leucophaea	Fabaceae	nat. per.legume	15	15	39	44	42	0.99	1.00	0.72
Baptisia spp.	Fabaceae	nat. per.legume	0	0	0	0	0	0.00	0.00	0.00
Berchemia scandens	Rhamnaceae	nat. per. shrub	1	5	9	10	9	4.13	3.53	3.87
Berlandiera texana	Asteraceae	nat. per. forb	0	0	0	1	0	0.00	0.76	0.00
Betula nigra	Betulaceae	nat. per. tree	1	0	0	0	0	0.00	0.00	0.00
Bidens spp.	Asteraceae	nat. ann. forb	0	0	1	2	1	0.02	0.09	0.03
Blephilia ciliata	Lamiaceae	nat. per. forb	0	8	10	3	3	0.39	0.30	0.31
Blephilia hirsuta	Lamiaceae	nat. per. forb	0	5	6	2	3	0.70	0.26	0.15
Blephilia spp.	Lamiaceae	nat. per. forb	1	1	0	0	0	0.00	0.00	0.00
Boehmeria cylindrica	Urticaceae	nat. per. forb	2	2	0	9	1	0.00	0.96	0.32
Boraginaceae family	Boraginaceae	nat. forb	1	0	0	0	0	0.00	0.00	0.00
Botrychium dissectum	Ophioglossaceae	nat. per. fern	2	0	0	0	4	0.00	0.00	0.27
Botrychium spp.	Ophioglossacea	nat. per. fern	0	0	0	4	21	0.00	0.14	0.04
Botrychium virginianum	Ophioglossaceae	nat. per. fern	19	43	104	115	109	0.21	0.63	0.14
Bouteloua curtipendula	Poaceae	nat. per. grass	2	1	4	3	3	0.11	0.84	0.23
Bouteloua spp.	Poaceae	nat. per. grass	0	0	1	0	0	0.02	0.00	0.00
Brachyelytrum erectum	Poaceae	nat. per. grass	14	88	94	154	171	1.15	1.20	0.88
Bromus purgans	Poaceae	nat. per. grass	0	4	78	48	55	0.52	0.19	0.22
Bromus spp.	Poaceae	nat. per. grass	1	29	8	0	6	0.28	0.00	0.05
Bumelia lanuginosa	Sapotaceae	nat. per. tree	7	16	34	50	56	0.99	0.56	0.47
Cacalia atriplicifolia	Asteraceae	nat. per. forb	2	17	27	19	26	1.05	0.91	0.84
Cacalia spp.	Asteraceae	nat. per. forb	0	0	0	0	1	0.00	0.00	0.02
Callitriche terrestris	Callitrichaceae	nat. ann. forb	0	0	0	0	2	0.00	0.00	0.05
Campanula americana	Campanulaceae	nat. ann. forb	0	1	0	3	15	0.00	0.49	0.37
Campsis radicans	Bignoniaceae	nat. per. w-vine	2	6	13	12	11	1.31	0.82	0.88
Carex amphibola	Cyperaceae	nat. per. sedge	0	0	0	7	2	0.00	0.40	0.17
Carex artitecta	Cyperaceae	nat. per. sedge	0	0	0	33	0	0.00	0.31	0.00
Carex blanda	Cyperaceae	nat. per. sedge	0	0	1	34	60	0.30	0.23	0.28
Carex cephalophora	Cyperaceae	nat. per. sedge	0	0	4	51	18	0.30	0.16	0.08
Carex complanata	Cyperaceae	nat. per. sedge	0	0	21	65	64	0.27	0.21	0.27
Carex crawei	Cyperaceae	nat. per. sedge	0	0	2	3	4	0.86	0.04	0.14
Carex digitalis	Cyperaceae	nat. per. sedge	0	0	0	1	4	0.00	0.02	0.76
Carex glaucodea	Cyperaceae	nat. per. sedge	0	0	1	0	2	0.26	0.00	0.06
Carex hirtifolia	Cyperaceae	nat. per. sedge	0	0	1	0	0	0.58	0.00	0.00

Species	Family	Type	Number of Plots '91	'92	'93	'94	'95	Avg. Rel. Abundance '93	'94	'95
Carex laxiculmis	Cyperaceae	nat. per. sedge	0	0	0	0	1	0.00	0.00	0.27
Carex meadii	Cyperaceae	nat. per. sedge	0	0	3	2	2	1.14	0.05	0.13
Carex muhlenbergii	Cyperaceae	nat. per. sedge	0	0	32	0	59	0.45	0.00	0.19
CAREX NIGROMARGINATA	Cyperaceae	nat. per. sedge	0	0	0	319	377	0.00	0.44	0.43
Carex oligocarpa	Cyperaceae	nat. per. sedge	0	0	0	42	49	0.00	0.24	0.14
Carex retroflexa	Cyperaceae	nat. per. sedge	0	0	87	31	65	0.56	0.28	0.31
Carex spp.	Cyperaceae	nat. per. sedge	197	401	396	281	155	0.59	0.26	0.31
Carex umbellata	Cyperaceae	nat. per. sedge	0	0	273	262	316	0.58	0.22	0.26
Carpinus caroliniana	Betulaceae	nat. per. tree	1	4	7	7	15	1.66	2.39	1.50
Carya cordiformis	Juglandaceae	nat. per. tree	3	12	8	21	19	2.13	0.89	1.72
Carya glabra	Juglandaceae	nat. per. tree	64	253	276	393	397	2.85	3.41	3.18
Carya ovata	Juglandaceae	nat. per. tree	0	0	19	2	0	3.06	0.64	0.00
Carya spp.	Juglandaceae	nat. per. tree	13	1	86	251	339	0.36	0.77	0.70
Carya texana	Juglandaceae	nat. per. tree	124	320	501	386	320	4.11	3.73	3.75
Carya tomentosa	Juglandaceae	nat. per. tree	91	166	334	281	336	3.51	3.52	3.75
Cassia fasciculata	Fabaceae	nat. ann.legume	18	16	15	3	10	0.29	0.03	0.29
Cassia marilandica	Fabaceae	nat. per.legume	0	0	2	3	3	0.73	0.18	0.19
Cassia nictitans	Fabaceae	nat. ann.legume	0	1	21	13	8	0.14	0.31	0.21
Cassia spp.	Fabaceae	nat. legume	0	0	0	7	7	0.00	0.06	0.19
Caulophyllum thalictroides	Berberidaceae	nat. per. forb	0	0	0	1	0	0.00	0.55	0.00
Ceanothus americanus	Rhamnaceae	nat. per. shrub	30	60	125	105	92	1.01	0.86	0.78
Celastrus scandens	Celastraceae	nat. per. w-vine	0	0	2	1	7	0.61	0.27	0.65
Celtis laevigata	Ulmaceae	nat. per. tree	0	2	0	3	10	0.00	0.90	0.79
Celtis occidentalis	Ulmaceae	nat. per. tree	4	44	126	146	139	1.25	1.56	1.25
Celtis spp.	Rosaceae	nat. per. tree	31	51	24	22	69	1.32	0.66	0.82
Celtis tenuifolia	Ulmaceae	nat. per. tree	0	0	12	19	7	1.22	1.39	1.28
Cephalanthus occidentalis	Rubiaceae	nat. per. tree	0	0	0	0	1	0.00	0.00	0.70
Cercis canadensis	Fabaceae	nat. per. tree	18	88	138	148	137	2.26	1.85	1.91
Chaerophyllum procumbens	Apiaceae	nat. ann. forb	0	1	0	0	0	0.00	0.00	0.00
Cheilanthes feei	Polypodiaceae	nat. per. fern	0	1	2	2	3	0.15	0.29	0.11
Chenopodium album	Chenopodiaceae	ex. ann. forb	0	0	0	0	1	0.00	0.00	0.10
Chrysanthemum leucanthemum	Asteraceae	ex. peren. forb	0	1	1	0	0	0.37	0.00	0.00
Cicuta maculata	Apiaceae	nat. bien. forb	0	0	0	0	1	0.00	0.00	0.03
Cimicifuga racemosa	Ranunculaceae	nat. per. forb	17	91	107	120	120	4.71	3.73	3.69
Circaea quadrisulcata	Onagraceae	nat. per. forb	0	0	0	1	3	0.00	0.54	0.24
Cirsium altissimum	Asteraceae	nat. per. forb	0	0	16	25	19	0.48	0.42	0.47
Cirsium carolinianum	Asteraceae	nat. bien. forb	0	0	0	0	2	0.00	0.00	0.41
Cirsium discolor	Asteraceae	nat. per. forb	0	0	0	0	1	0.00	0.00	0.15
Cirsium spp.	Asteraceae	perennial forb	0	0	1	3	11	0.03	0.20	0.67
Clematis virginiana	Ranunculaceae	nat. per. vine	1	0	1	0	1	0.05	0.00	0.12
Clitoria mariana	Fabaceae	nat. per.legume	70	122	127	173	165	1.02	0.86	0.71
Cocculus carolinianus	Menispermaceae	nat. per. vine	4	8	5	10	11	0.59	0.46	0.37
Comandra richardsiana	Santalaceae	nat. per. forb	0	3	21	18	16	0.41	0.32	0.23
Convolvulus pellitus	Convolvulaceae	ex. peren. vine	0	0	0	2	0	0.00	0.85	0.00
Convolvulus sepium	Convolvulaceae	nat. per. vine	1	14	6	4	9	0.75	0.94	0.31
Convolvulus spp.	Convolvulaceae	perennial vine	0	3	5	0	1	0.32	0.00	0.02
Corallorhiza odontorhiza	Orchidaceae	nat. per. forb	0	3	0	0	0	0.00	0.00	0.00
Coreopsis lanceolata	Asteraceae	nat. per. forb	0	0	0	2	2	0.00	0.18	0.75
Coreopsis palmata	Asteraceae	nat. per. forb	24	16	46	50	47	0.40	0.31	0.40

Species	Family	Type	Number of Plots '91	'92	'93	'94	'95	Avg. Rel. Abundance '93	'94	'95
Coreopsis pubescens	Asteraceae	nat. per. forb	0	0	0	1	0	0.00	0.31	0.00
Coreopsis spp.	Asteraceae	nat. per. forb	0	1	0	0	3	0.00	0.00	0.06
Coreopsis tripteris	Asteraceae	nat. per. forb	0	3	9	11	13	0.30	0.37	0.25
Cornus drummondi	Cornaceae	nat. per. tree	0	3	3	0	8	0.84	0.00	0.63
Cornus florida	Cornaceae	nat. per. tree	150	437	616	607	635	10.90	10.61	9.25
Cornus spp.	Cornaceae	nat. per. tree	0	4	3	2	3	0.74	0.05	2.29
Corylus americana	Betulaceae	nat. per. tree	10	32	62	57	71	2.46	2.81	2.10
Crataegus spp.	Rosaceae	nat. per. tree	21	52	70	78	73	0.68	0.45	0.49
Crotalaria sagittalis	Fabaceae	nat. ann. forb	0	0	1	1	1	0.08	0.15	0.16
Croton capitatus	Euphorbiaceae	nat. ann. forb	0	5	2	0	0	0.08	0.00	0.00
Croton glandulosus	Euphorbiaceae	nat. ann. forb	1	1	0	0	0	0.00	0.00	0.00
Croton monanthogynus	Euphorbiaceae	nat. ann. forb	0	0	5	4	4	0.28	0.25	0.05
Croton spp.	Euphorbiaceae	nat. ann. forb	0	1	0	0	2	0.00	0.00	0.02
Cryptotaenia canadensis	Apiaceae	nat. per. forb	4	1	3	8	12	0.67	0.50	0.54
Cucurbita pepo	Curcurbitaceae	ex. peren. vine	4	0	0	0	0	0.00	0.00	0.00
Cunila origanoides	Lamiaceae	nat. per. forb	78	163	192	210	208	1.92	1.42	1.52
Cuphea petiolata	Lythraceae	nat. ann. forb	0	1	0	0	0	0.00	0.00	0.00
Cynoglossum officinale	Boraginaceae	ex. bien. forb	0	1	16	3	0	0.50	0.61	0.00
Cynoglossum spp.	Boraginaceae	forb	0	1	1	2	0	0.28	0.30	0.00
Cynoglossum virginianum	Boraginaceae	nat. per. forb	0	7	2	2	4	0.62	0.84	0.57
Cypripedium calceolus	Orchidaceae	nat. per. forb	0	0	0	0	1	0.00	0.00	0.01
Cystopteris fragilis	Polypodiaceae	nat. per. fern	0	0	2	2	3	0.03	0.03	0.03
Danthonia spicata	Poaceae	nat. per. grass	37	81	107	119	120	0.37	0.28	0.27
Daucus carota	Apiaceae	ex. bien. forb	0	2	1	3	1	0.56	0.21	0.25
Delphinium carolinianum	Ranunculaceae	nat. per. forb	0	1	1	0	0	0.05	0.00	0.00
Delphinium tricorne	Ranunculaceae	nat. per. forb	2	2	0	0	0	0.00	0.00	0.00
Desmodium ciliare	Fabaceae	nat. per.legume	0	0	4	7	2	0.45	1.51	1.53
Desmodium cuspidatum	Fabaceae	nat. per.legume	0	1	28	13	20	0.81	0.55	0.60
Desmodium dillenii	Fabaceae	nat. per.legume	0	0	6	0	0	1.07	0.00	0.00
Desmodium glutinosum	Fabaceae	nat. per.legume	23	172	203	204	216	2.28	2.29	2.30
Desmodium laevigatum	Fabaceae	nat. per.legume	54	65	88	115	132	1.17	1.21	1.03
Desmodium marilandicum	Fabaceae	nat. per.legume	8	4	17	12	7	0.62	0.41	0.52
Desmodium nudiflorum	Fabaceae	nat. per.legume	196	479	616	614	622	15.46	15.87	15.61
Desmodium nuttallii	Fabaceae	nat. per.legume	55	64	171	196	259	1.25	1.64	1.42
Desmodium paniculatum	Fabaceae	nat. per.legume	83	33	84	64	45	1.07	0.99	0.61
Desmodium pauciflorum	Fabaceae	nat. per.legume	24	125	67	130	33	0.77	1.11	0.99
Desmodium rigidum	Fabaceae	nat. per.legume	2	0	1	3	0	1.75	0.28	0.00
Desmodium rotundifolium	Fabaceae	nat. per.legume	41	78	106	115	110	1.10	1.13	1.11
Desmodium sessilifolium	Fabaceae	nat. per. forb	0	0	0	0	1	0.00	0.00	0.97
Desmodium spp.	Fabaceae	nat. per.legume	11	10	27	86	128	0.78	0.07	0.09
Diodia teres	Rubiaceae	nat. ann. forb	0	0	0	0	0	0.00	0.00	0.00
Dioscorea quaternata	Dioscoreaceae	nat. per. vine	3	184	201	227	225	1.08	1.16	1.09
Dioscorea spp.	Dioscoreaceae	nat. per. vine	0	0	4	112	61	0.03	0.22	0.16
Dioscorea villosa	Dioscoreaceae	nat. per. vine	59	137	218	131	194	0.78	0.52	0.62
Diospyros virginiana	Ebenaceae	nat. per. tree	20	25	117	114	152	2.58	2.13	1.77
Dodecatheon meadia	Primulaceae	nat. per. forb	0	0	2	0	0	0.19	0.00	0.00
Echinacea pallida	Asteraceae	nat. per. forb	0	1	8	15	13	0.67	0.57	0.52

Species	Family	Type	Number of Plots '91	'92	'93	'94	'95	Avg. Rel. Abundance '93	'94	'95
Echinacea purpurea	Asteraceae	nat. per. forb	0	0	4	3	3	0.71	0.47	0.58
Echinacea spp.	Asteraceae	nat. per. forb	0	0	0	0	4	0.00	0.00	0.07
Elaeagnus umbellata	Elaeagnaceae	ex. peren. tree	1	1	2	3	5	0.52	1.55	2.44
Elephantopus carolinianus	Asteraceae	nat. per. forb	1	1	6	5	9	0.80	1.11	1.07
Elymus canadensis	Poaceae	nat. per. grass	0	1	0	2	4	0.00	0.21	0.02
Elymus spp.	Poaceae	nat. per. grass	0	0	0	9	15	0.00	0.18	0.12
Elymus virginicus	Poaceae	nat. per. grass	11	18	17	18	16	0.24	0.21	0.15
Erechtites hieracifolia	Asteraceae	nat. ann. forb	0	3	9	24	16	0.16	0.54	0.31
Erigeron annuus	Asteraceae	nat. ann. forb	0	0	0	1	1	0.00	0.01	0.03
Erigeron canadensis	Asteraceae	nat. ann. forb	0	0	0	0	1	0.00	0.00	0.46
Eryngium yuccifolium	Apiaceae	nat. per. forb	3	3	10	5	6	0.38	0.63	0.26
Euonymus atropurpureus	Celastraceae	nat. per. tree	1	0	4	0	2	1.19	0.00	0.02
Eupatorium perfoliatum	Asteraceae	nat. per. forb	1	0	1	1	0	0.16	0.01	0.00
Eupatorium purpureum	Asteraceae	nat. per. forb	0	2	6	5	11	0.83	0.84	0.86
Eupatorium rugosum	Asteraceae	nat. per. forb	0	2	35	26	26	0.67	1.66	1.09
Eupatorium spp.	Asteraceae	nat. per. forb	1	1	0	0	9	0.00	0.00	2.06
Euphorbia commutata	Euphorbiaceae	nat. per. forb	0	0	0	3	2	0.00	0.08	0.03
Euphorbia corollata	Euphorbiaceae	nat. per. forb	53	96	150	144	157	0.21	0.24	0.20
Euphorbia dentata	Euphorbiaceae	nat. ann. forb	0	0	1	10	1	0.43	0.08	0.03
Euphorbia heterophyla	Euphorbiaceae	nat. ann. forb	0	0	0	4	1	0.00	0.14	0.06
Euphorbia spp.	Euphorbiaceae	nat. forb	0	0	2	1	0	0.03	0.03	0.00
Evolvulus nuttallianus	Convolvulaceae	nat. per. forb	0	0	1	0	0	0.28	0.00	0.00
Festuca spp.	Poaceae	grass	0	0	0	0	9	0.00	0.00	0.24
Festuca obtusa	Poaceae	nat. per. grass	0	0	0	0	0	0.00	0.00	0.00
Festuca octoflora	Poaceae	nat. ann. grass	0	0	0	0	9	0.00	0.00	0.09
Fimbristylis caroliniana	Cyperaceae	nat. per. sedge	0	0	1	3	3	3.43	0.61	0.95
Fragaria virginiana	Rosaceae	nat. per. forb	10	7	3	2	8	0.50	0.02	0.33
Fraxinus americana	Oleaceae	nat. per. tree	7	49	111	127	95	3.07	2.99	2.64
Fraxinus pennsylvanica	Oleaceae	nat. per. tree	1	12	5	8	59	2.69	2.08	2.83
Fraxinus spp.	Oleaceae	nat. per. tree	13	0	12	6	11	1.71	1.34	0.35
Galactia volubilis	Fabaceae	nat. per.legume	41	10	50	57	99	0.37	0.53	0.30
Galium aparine	Rubiaceae	nat. ann. forb	0	1	1	0	2	2.09	0.00	0.16
Galium arkansanum	Rubiaceae	nat. per. forb	27	77	72	81	78	0.49	0.30	0.48
Galium circaezans	Rubiaceae	nat. per. forb	0	10	143	193	209	0.18	0.14	0.15
Galium concinnum	Rubiaceae	nat. per. forb	16	75	100	108	111	1.18	0.64	0.84
Galium obtusum	Rubiaceae	nat. per. forb	29	106	28	35	21	0.10	0.08	0.13
Galium pilosum	Rubiaceae	nat. per. forb	48	111	119	81	89	0.15	0.11	0.07
Galium spp.	Rubiaceae	nat. per. forb	0	5	3	30	42	0.18	0.06	0.04
Galium tinctorium	Rubiaceae	nat. per. forb	0	0	5	15	7	0.97	0.31	0.07
Galium triflorum	Rubiaceae	nat. per. forb	2	14	19	20	22	0.72	0.38	0.40
Gentiana puberula	Gentianaceae	nat. per. forb	0	0	0	5	3	0.00	0.14	0.10
Geranium maculatum	Geraniaceae	nat. per. forb	0	110	138	122	131	0.64	0.60	0.68
Gerardia flava	Scrophulariaceae	nat. per. forb	1	12	43	35	33	0.61	0.82	0.70
Gerardia grandiflora	Scrophulariaceae	nat. per. forb	0	2	0	0	2	0.00	0.00	0.25
Gerardia pedicularia	Scrophulariaceae	nat. ann. forb	1	0	4	6	9	2.21	1.57	0.52
Gerardia spp.	Scrophulariaceae	nat. per. forb	1	7	1	3	0	1.90	0.15	0.00
Geum canadense	Rosaceae	nat. per. forb	11	32	55	30	39	0.33	0.22	0.38
Geum spp.	Rosaceae	nat. per. forb	0	2	10	80	73	0.14	0.20	0.25
Geum vernum	Rosaceae	nat. per. forb	20	10	1	2	1	0.23	0.06	0.29
Gillenia stipulata	Rosaceae	nat. per. forb	0	5	14	18	15	0.60	0.49	0.50
Gleditsia triacanthos	Fabaceae	nat. per. tree	2	5	3	6	1	1.03	0.21	0.45

Species	Family	Type	Number of Plots '91	'92	'93	'94	'95	Avg. Rel. Abundance '93	'94	'95
Gnaphalium obtusifolium	Asteraceae	nat. bien. forb	0	0	0	2	1	0.00	0.25	0.05
Hackelia virginiana	Boraginaceae	nat. bien. forb	0	0	0	0	0	0.00	0.00	0.00
Hamamelis vernalis	Hamamelidaceae	nat. per. tree	0	0	0	0	0	0.00	0.00	0.00
Hamamelis virginiana	Hamamelidaceae	nat. per. shrub	0	2	0	0	0	0.00	0.00	0.00
Hedeoma pulegioides	Lamiaceae	nat. ann. forb	11	1	2	0	5	0.18	0.00	0.87
Hedera helix	Araliaceae	ex. peren. vine	1	0	0	0	0	0.00	0.00	0.00
Helianthus hirsutus	Asteraceae	nat. per. forb	0	1	186	145	211	0.82	0.74	0.74
Helianthus spp.	Asteraceae	nat. per. forb	0	228	18	14	11	1.00	0.43	0.12
Helianthus strumosus	Asteraceae	nat. per. forb	0	0	125	198	151	0.99	1.10	1.04
Heliopsis helianthoides	Asteraceae	nat. per. forb	0	0	11	24	32	0.29	0.44	0.42
Heliotropium tenellum	Asteraceae	nat. ann. forb	0	0	0	1	0	0.00	0.03	0.00
Hepatica nobilis	Ranunculaceae	nat. per. forb	3	46	48	55	55	0.82	1.00	0.81
Heuchera spp.	Saxifragaceae	nat. per. forb	0	6	0	1	0	0.00	0.30	0.00
Hieracium gronovii	Asteraceae	nat. per. forb	23	61	61	68	66	0.32	0.24	0.17
Houstonia longifolia	Rubiaceae	nat. per. forb	6	8	9	18	14	0.11	0.21	0.05
Houstonia nigricans	Rubiaceae	nat. per. forb	3	9	21	19	20	1.12	1.08	0.67
Houstonia spp.	Rubiaceae	nat. per. forb	0	0	0	1	1	0.00	0.05	0.02
Hybanthus concolor	Violaceae	nat. per. forb	0	25	10	6	7	0.77	0.53	1.96
Hydrangea arborescens	Saxifragaceae	nat. per. tree	3	23	36	37	44	1.91	2.50	2.54
Hydrastis canadensis	Ranunculaceae	nat. per. forb	39	30	15	4	6	0.94	1.25	0.70
Hypericum punctatum	Hypericaceae	nat. per. forb	0	0	1	2	2	0.46	0.61	0.16
Hypericum spathulatum	Hypericaceae	nat. per. shrub	0	0	4	2	0	0.43	0.25	0.00
Hypericum sphaerocarpum	Hypericaceae	nat. per. forb	0	0	2	8	0	0.39	0.33	0.00
Hypericum spp.	Hypericaceae	nat. per. forb	0	0	1	6	3	0.07	0.25	0.14
Hystrix patula	Poaceae	nat. per. grass	0	0	10	1	1	0.26	0.14	0.26
Impatiens capensis	Balsaminaceae	nat. ann. forb	0	0	0	0	3	0.00	0.00	0.07
Ipomaea hederacea	Convolvulaceae	ex. ann. vine	0	0	0	0	2	0.00	0.00	0.76
Ipomoea pandurata	Convolvulaceae	nat. per. vine	22	35	44	44	44	0.56	0.64	0.60
Iris cristata	Iridaceae	nat. per. forb	0	0	2	0	1	1.07	0.00	1.03
Iris spp.	Iridaceae	nat. per. forb	0	0	0	0	1	0.00	0.00	0.41
Juglans nigra	Juglandaceae	nat. per. tree	3	5	11	9	11	0.62	0.31	0.44
Juglans spp.	Juglandaceae	nat. per. tree	0	0	0	3	0	0.00	0.70	0.00
Juncus marginatus	Juncaceae	nat. per. sedge	0	0	0	1	0	0.00	0.02	0.00
Juncus spp.	Juncaceae	nat. per. sedge	0	0	0	2	0	0.00	0.26	0.00
Juniperus virginiana	Cupressaceae	nat. per. tree	6	27	29	27	33	0.66	0.92	0.77
Justicia americana	Acanthaceae	nat. per. forb	3	0	0	0	0	0.00	0.00	0.00
Krigia biflora	Asteraceae	nat. per. forb	22	106	131	137	166	0.43	0.33	0.32
Kuhnia eupatorioides	Asteraceae	nat. per. forb	0	1	7	12	10	0.45	0.41	0.69
Lactuca canadensis	Asteraceae	nat. bien. forb	0	0	1	8	17	0.11	0.41	0.21
Lactuca floridana	Asteraceae	nat. bien. forb	0	0	2	5	8	0.53	0.15	0.24
Lactuca spp.	Asteraceae	nat. bien. forb	3	4	20	6	1	0.27	0.13	0.07
Laportea canadensis	Urticaceae	nat. per. forb	0	5	1	0	0	0.79	0.00	0.00
Lathyrus venosus	Fabaceae	nat. per.legume	0	0	0	0	0	0.00	0.00	0.00
Lechea villosa	Cistaceae	nat. per. forb	0	0	0	1	0	0.00	0.60	0.00
Leersia virginica	Poaceae	nat. per. grass	0	0	0	0	2	0.00	0.00	0.09
Lespedeza capitata	Fabaceae	nat. per.legume	0	0	1	1	0	0.30	0.58	0.00
Lespedeza cuneata	Fabaceae	ex. peren. legume	14	35	12	3	10	0.38	0.46	0.27
Lespedeza hirta	Fabaceae	nat. per.legume	30	55	64	42	68	0.66	1.22	0.86
Lespedeza intermedia	Fabaceae	nat. per.legume	71	84	199	259	242	0.59	0.74	0.68
Lespedeza nuttalii	Fabaceae	nat. per.legume	0	0	2	0	0	0.63	0.00	0.00
Lespedeza procumbens	Fabaceae	nat. per.legume	44	71	77	114	123	0.88	0.69	0.74

Species	Family	Type	Number of Plots '91	'92	'93	'94	'95	Avg. Rel. Abundance '93	'94	'95
Lespedeza repens	Fabaceae	nat. per.legume	99	103	130	161	171	1.11	1.08	0.89
Lespedeza spp.	Fabaceae	nat. per.legume	26	1	19	98	91	0.12	0.06	0.06
Lespedeza stipulacea	Fabaceae	ex. ann. legume	4	82	12	4	6	1.21	0.17	0.75
Lespedeza striata	Fabaceae	ex. ann. legume	1	21	3	3	1	0.40	0.49	0.05
Lespedeza violacea	Fabaceae	nat. per.legume	0	0	102	19	6	0.39	0.30	0.17
Lespedeza virginica	Fabaceae	nat. per.legume	32	73	54	57	62	0.55	0.52	0.49
Liatris aspera	Asteraceae	nat. per. forb	1	3	24	15	13	0.19	0.31	0.31
Liatris cylindracea	Asteraceae	nat. per. forb	0	0	3	5	7	0.83	0.47	0.46
Liatris pycnostachya	Asteraceae	nat. per. forb	1	1	5	1	0	0.28	0.14	0.00
Liatris spp.	Asteraceae	nat. per. forb	1	0	5	2	4	0.14	0.04	0.16
Ligusticum canadense	Apiaceae	nat. per. forb	3	1	41	31	41	0.46	0.43	0.57
Lindera benzoin	Lauraceae	nat. per. tree	4	34	32	32	38	3.16	3.51	5.31
Linum medium	Linaceae	nat. per. forb	0	0	0	0	2	0.00	0.00	0.07
Linum striatum	Linaceae	nat. per. forb	0	0	1	0	0	0.27	0.00	0.00
Lithospermum canescens	Boraginaceae	nat. per. forb	0	8	23	17	26	0.52	0.46	0.69
Lobelia inflata	Campanulaceae	nat. ann. forb	0	0	10	0	5	0.22	0.00	0.66
Lobelia spicata	Campanulaceae	nat. per. forb	1	1	11	24	21	0.28	0.12	0.18
Lobelia spp.	Campanulaceae	nat. forb	0	0	1	0	2	0.50	0.00	0.71
Lonicera spp.	Caprifoliaceae	nat. per. w-vine	0	60	108	110	128	1.36	1.19	1.09
Lysimachia lanceolata	Primulaceae	nat. per. forb	0	2	16	35	52	0.31	0.25	0.31
MALAXIS UNIFOLIA	Orchidaceae	nat. per. forb	0	0	1	0	5	0.05	0.00	0.03
Matelea decipiens	Asclepiadaceae	nat. per. vine	0	0	6	15	17	0.47	0.87	0.63
Matelea spp.	Asclepiadaceae	nat. per. vine	3	7	13	0	0	0.93	0.00	0.00
Menispermum canadense	Menispermaceae	nat. per. vine	0	1	20	31	28	0.39	0.27	0.24
Monarda russeliana	Lamiaceae	nat. per. forb	61	133	183	178	195	0.79	0.79	0.79
Monarda spp.	Lamiaceae	nat. per. forb	0	0	0	1	0	0.00	0.05	0.00
Monotropa hypopithys	Pyrolaceae	nat. per. forb	1	0	1	0	5	0.05	0.00	0.03
Monotropa uniflora	Pyrolaceae	nat. per. forb	2	0	0	1	2	0.00	0.04	0.12
Morus rubra	Moraceae	nat. per. tree	0	10	30	21	31	1.07	0.90	0.38
Muhlenbergia sobolifera	Poaceae	nat. per. grass	13	31	55	45	45	0.71	0.57	0.85
Muhlenbergia spp.	Poaceae	nat. per. grass	0	0	6	7	4	0.30	0.32	0.44
Muhlenbergia tenuiflora	Poaceae	nat. per. grass	0	0	0	0	1	0.00	0.00	0.26
Nyssa sylvatica	Cornaceae	nat. per. tree	95	346	505	505	530	3.51	3.99	3.70
Onosmodium spp.	Boraginaceae	nat. per. forb	0	0	0	6	0	0.00	0.21	0.00
Onosmodium subsetosum	Boraginaceae	nat. per. forb	0	0	1	0	0	0.02	0.00	0.00
Ophioglossum engelmanii	Ophioglossaceae	nat. per. fern	0	0	0	0	1	0.00	0.00	0.17
Osmorhiza claytoni	Apiaceae	nat. per. forb	0	2	0	0	1	0.00	0.00	0.37
Ostrya virginiana	Betulaceae	nat. per. tree	0	15	3	9	6	0.68	2.61	1.60
Oxalis spp.	Oxalidaceae	nat. per. forb	0	8	3	5	2	0.02	0.02	0.02
Oxalis stricta	Oxalidaceae	nat. per. forb	4	4	19	38	33	0.22	0.12	0.10
Oxalis violacea	Oxalidaceae	nat. per. forb	2	0	5	2	6	0.03	0.05	0.17
Oxypolis rigidior	Apiaceae	nat. per. forb	0	1	1	0	1	0.50	0.00	0.43
Panicum anceps	Poaceae	nat. per. grass	0	0	1	2	1	1.85	0.16	1.84
Panicum boscii	Poaceae	nat. per. grass	82	205	308	362	306	0.71	0.77	0.69
Panicum capillare	Poaceae	nat. ann. grass	1	0	0	1	1	0.00	0.39	0.40
Panicum clandestinum	Poaceae	nat. per. grass	1	86	8	2	18	0.56	1.16	0.25
Panicum commutatum	Poaceae	nat. per. grass	65	174	227	224	258	0.36	0.44	0.28
Panicum depauperatum	Poaceae	nat. per. grass	44	24	3	0	2	0.47	0.00	0.05
Panicum dichotomum	Poaceae	nat. per. grass	86	146	196	217	187	0.31	0.29	0.26

Species	Family	Type	Number of Plots '91	'92	'93	'94	'95	Avg. Rel. Abundance '93	'94	'95
Panicum lanuginosum	Poaceae	nat. per. grass	25	14	56	63	47	0.25	0.32	0.35
Panicum laxiflorum	Poaceae	nat. per. grass	2	0	1	1	1	0.47	0.81	0.03
Panicum linearifolium	Poaceae	nat. per. grass	0	0	40	100	129	0.25	0.17	0.22
Panicum oligosanthes	Poaceae	nat. per. grass	0	0	0	0	3	0.00	0.00	0.31
Panicum sphaerocarpon	Poaceae	nat. per. grass	0	1	5	3	37	0.17	1.92	0.44
Panicum spp.	Poaceae	nat. per. grass	24	14	47	109	145	0.10	0.06	0.07
Panicum virgatum	Poaceae	nat. per. grass	3	10	6	16	13	1.47	1.70	0.83
Parietaria pensylvanica	Urticaceae	nat. ann. forb	0	0	0	3	0	0.00	0.06	0.00
Paronychia canadensis	Caryophyllaceae	nat. ann. forb	0	0	1	2	0	1.48	0.17	0.00
Paronychia fastigiata	Caryophyllaceae	nat. ann. forb	0	0	0	1	0	0.00	0.38	0.00
Parthenium hispidum	Asteraceae	nat. per. forb	9	54	17	0	4	0.64	0.00	0.53
Parthenium integrifolium	Asteraceae	nat. per. forb	45	151	173	177	172	0.81	0.90	0.81
Parthenocissus quinquefolia	Vitaceae	nat. per. w-vine	141	391	486	501	532	7.05	7.06	7.41
Passiflora lutea	Passifloraceae	nat. per. vine	14	97	84	85	94	0.26	0.29	0.29
Pedicularis canadensis	Scrophulariaceae	nat. per. forb	2	3	2	2	3	1.17	0.03	0.17
Pellaea atropurpurea	Polypodiaceae	nat. per. fern	1	1	7	14	8	0.22	0.28	0.52
Penstemon pallidus	Scrophulariaceae	nat. per. forb	0	0	1	1	0	0.39	0.03	0.00
Penstemon spp.	Scropulariaceae	nat. forb	0	0	0	0	2	0.00	0.00	0.26
Petalostemon spp.	Fabaceae	nat. per. forb	0	0	0	1	1	0.00	0.02	0.01
Petalostemum candidum	Fabaceae	nat. per. forb	0	0	1	3	3	0.02	0.18	0.40
Petalostemum purpureum	Fabaceae	nat. per. forb	2	1	8	5	9	0.39	0.33	0.21
Phaseolus polystachios	Fabaceae	nat. per.legume	2	69	31	51	18	1.19	3.82	1.35
Phlox divaricata	Polemoniaceae	nat. per. forb	0	20	20	39	29	0.20	0.25	0.17
Phlox pilosa	Polemoniaceae	nat. per. forb	0	0	6	20	16	0.18	0.13	0.13
Phlox spp.	Polemoniaceae	nat. per. forb	3	1	2	1	5	0.10	0.04	0.03
Phryma leptostachya	Phrymaceae	nat. per. forb	7	67	73	165	180	0.47	0.40	0.39
Physalis heterophylla	Solanaceae	nat. per. forb	0	7	10	2	1	0.28	0.08	0.02
Physalis longifolia	Solanaceae	nat. per. forb	0	0	0	1	0	0.00	1.63	0.00
Physalis spp.	Solanaceae	nat. per. forb	0	0	1	10	6	0.01	0.11	0.07
Physalis virginiana	Solanaceae	nat. per. forb	0	0	4	2	31	0.21	0.15	0.19
Physocarpus opulifolius	Rosaceae	nat. per. forb	0	1	0	0	0	0.00	0.00	0.00
Physostegia virginiana	Lamiaceae	nat. per. forb	0	0	2	4	4	0.15	0.51	0.46
Phytolacca americana	Phytolaccaceae	nat. per. forb	0	0	1	0	0	0.20	0.00	0.00
Pilea pumila	Urticaceae	nat. ann. forb	0	1	3	2	17	0.45	0.50	1.05
Pinus echinata	Pinaceae	nat. per. tree	24	83	118	129	179	0.61	0.48	0.44
PLANTAGO CORDATA	Plantaginaceae	nat. per. forb	1	4	0	0	0	0.00	0.00	0.00
Plantago major	Plantaginaceae	ex. ann. forb	1	0	1	1	1	0.19	0.14	0.46
Plantago rugelii	Plantaginaceae	nat. ann. forb	0	0	0	0	2	0.00	0.00	0.23
Plantago spp.	Plantaginaceae	ann. forb	0	3	3	0	1	0.54	0.00	0.01
Plantago virginica	Plantaginaceae	nat. ann. forb	0	0	0	4	2	0.00	0.42	0.74
Poa spp.	Poaceae	peren. grass	0	0	0	1	2	0.00	0.02	0.03
Poa sylvestris	Poaceae	nat. per. grass	0	0	0	0	1	0.00	0.00	0.01
Podophyllum peltatum	Berberidaceae	nat. per. forb	0	4	6	13	12	0.51	0.75	0.94
Polygala senega	Polygolaceae	nat. per. forb	0	0	0	2	3	0.00	0.63	0.43
Polygonatum biflorum	Liliaceae	nat. per. forb	9	32	3	5	1	0.38	0.45	0.02
Polygonum convolvulus	Polygonaceae	ex. ann. vine	0	0	1	0	1	0.03	0.00	0.02
Polygonum scandens	Polygonaceae	nat. per. vine	0	1	4	12	12	0.05	0.07	0.48
Polygonum spp.	Polygonaceae	forb	0	0	0	1	0	0.00	0.03	0.00

Species	Family	Type	Number of Plots '91	'92	'93	'94	'95	Avg. Rel. Abundance '93	'94	'95
Polygonum virginianum	Polygonaceae	nat. per. forb	1	2	2	4	8	0.75	1.68	0.95
Polystichum acrostichoides	Polypodiaceae	nat. per. fern	7	35	42	43	47	0.84	1.08	0.94
Potentilla norvegica	Rosaceae	nat. ann. forb	0	1	0	0	0	0.00	0.00	0.00
Potentilla recta	Rosaceae	ex. peren. forb	0	2	6	1	6	0.27	0.45	0.20
Potentilla simplex	Rosaceae	nat. per. forb	70	145	215	232	240	0.63	0.53	0.59
Potentilla spp.	Rosaceae	peren. forb	0	53	0	0	0	0.00	0.00	0.00
Prenanthes alba	Asteraceae	nat. per. forb	2	4	1	44	18	0.20	0.28	0.36
Prenanthes altissima	Asteraceae	nat. per. forb	2	1	30	14	19	0.34	0.34	0.20
Prenanthes aspera	Asteraceae	nat. per. forb	0	0	0	1	0	0.00	0.12	0.00
Prenanthes spp.	Asteraceae	nat. per. forb	0	1	3	4	17	0.16	0.22	0.17
Prunella vulgaris	Lamiaceae	ex. peren. forb	0	0	4	2	9	0.18	0.17	0.23
Prunus americana	Rosaceae	nat. per. tree	1	0	4	18	52	1.36	0.68	0.99
Prunus serotina	Rosaceae	nat. per. tree	57	163	223	256	266	1.02	0.71	0.78
Prunus spp.	Rosaceae	peren. tree	7	11	40	60	18	0.99	0.73	0.55
Psoralea psoralioides	Fabaceae	nat. per.legume	3	0	36	16	26	1.26	1.20	0.99
Psoralea tenuiflora	Fabaceae	nat. per.legume	0	0	1	1	2	0.79	0.01	0.88
Ptelea trifoliata	Rutaceae	nat. per. tree	0	0	0	1	0	0.00	0.18	0.00
Pteridium aquilinum	Polypodiaceae	nat. per. fern	52	135	175	179	188	4.72	3.56	3.72
Pycnanthemum albescens	Lamiaceae	nat. per. forb	1	7	1	2	8	0.54	0.26	0.42
Pycnanthemum pilosum	Lamiaceae	nat. per. forb	0	0	1	4	2	0.45	1.10	0.12
Pycnanthemum spp.	Lamiaceae	nat. per. forb	0	1	0	0	0	0.00	0.00	0.00
Pycnanthemum tenuifolium	Lamiaceae	nat. per. forb	12	12	9	2	10	0.36	0.16	0.18
Pyrrhopappus carolinianus	Asteraceae	nat. ann. forb	2	1	1	0	0	0.03	0.00	0.00
Pyrus malus	Rosaceae	ex. peren. tree	0	0	0	0	1	0.00	0.00	0.03
Quercus alba	Fagaceae	nat. per. tree	157	413	569	573	573	3.75	4.09	3.87
Quercus coccinea	Fagaceae	nat. per. tree	125	275	413	439	486	1.94	1.85	1.85
Quercus marilandica	Fagaceae	nat. per. tree	25	14	38	45	59	3.00	2.84	2.66
Quercus muehlenbergii	Fagaceae	nat. per. tree	13	40	68	75	75	1.39	1.41	1.12
Quercus rubra	Fagaceae	nat. per. tree	0	0	0	5	5	0.00	0.36	0.49
Quercus shumardii	Fagaceae	nat. per. tree	2	0	0	0	2	0.00	0.00	0.67
Quercus spp.	Fagaceae	nat. per. tree	0	2	3	49	99	0.37	0.10	0.09
Quercus stellata	Fagaceae	nat. per. tree	138	155	212	255	223	5.37	4.78	4.88
Quercus velutina	Fagaceae	nat. per. tree	167	410	553	553	577	3.21	3.35	3.53
Ranunculus abortivus	Ranunculaceae	nat. per. forb	0	0	0	1	0	0.00	0.01	0.00
Ranunculus hispidus	Ranunculaceae	nat. per. forb	1	16	50	58	44	0.36	0.29	0.31
Ranunculus recurvatus	Ranunculaceae	nat. per. forb	0	2	2	4	4	0.18	0.37	0.17
Ranunculus septentrionalis	Ranunculaceae	nat. per. forb	0	0	5	0	15	0.23	0.00	0.23
Ranunculus spp.	Ranunculaceae	nat. per. forb	0	1	1	2	32	0.03	0.35	0.21
Ratibida pinnata	Asteraceae	nat. per. forb	1	1	4	6	9	0.60	0.65	0.59
Rhamnus caroliniana	Rhamnaceae	nat. per. tree	81	166	269	331	374	2.07	1.71	1.35
Rhus aromatica	Anacardiaceae	nat. per. shrub	28	179	218	219	223	3.84	3.74	3.37
Rhus copallina	Anacardiaceae	nat. per. tree	18	11	36	33	34	1.56	1.74	1.27
Rhus glabra	Anacardiaceae	nat. per. tree	2	9	3	4	3	1.99	1.22	1.54
Rhus radicans	Anacardiaceae	nat. per. w-vine	64	206	279	276	302	1.97	1.98	1.79
Rhus spp.	Anacardiaceae	nat. per. tree	0	0	1	0	0	0.51	0.00	0.00
Ribes missouriense	Rosaceae	nat. per. shrub	0	0	0	2	1	0.00	0.11	0.47
Robinia pseudo-acacia	Fabaceae	nat. per. tree	0	1	1	3	4	0.20	1.14	0.25
Rosa carolina	Rosaceae	nat. per. shrub	0	0	114	130	182	0.54	0.45	0.45
Rosa multiflora	Rosaceae	ex. peren.shrub	2	4	16	13	11	0.47	0.63	0.71

Species	Family	Type	Number of Plots '91	'92	'93	'94	'95	Avg. Rel. Abundance '93	'94	'95
Rosa setigera	Rosaceae	nat. per. shrub	0	1	59	58	16	0.45	0.35	0.36
Rosa spp.	Rosaceae	peren. shrub	32	131	17	23	11	0.10	0.08	0.09
Rubus enslenii	Rosaceae	nat. per. w-vine	0	0	140	71	187	1.03	0.90	1.18
Rubus flagellaris	Rosaceae	nat. per. w-vine	0	0	103	171	61	1.51	1.35	1.15
Rubus occidentalis	Rosaceae	nat. per. w-vine	0	0	11	14	12	1.26	1.59	2.31
Rubus pensilvanicus	Rosaceae	nat. per. w-vine	0	0	102	123	112	2.58	2.39	2.63
Rubus spp.	Rosaceae	nat. per. w-vine	87	222	21	40	45	0.41	0.48	0.43
Rubus trivialis	Rosaceae	nat. per. w-vine	0	0	2	0	0	0.11	0.00	0.00
Rudbeckia fulgida	Asteraceae	nat. per. forb	0	0	0	0	4	0.00	0.00	0.19
Rudbeckia hirta	Asteraceae	nat. per. forb	10	5	5	2	14	0.48	0.90	0.41
Rudbeckia missouriensis	Asteraceae	nat. per. forb	0	12	24	18	19	3.27	4.03	4.07
Rudbeckia spp.	Asteraceae	nat. per. forb	1	4	2	6	3	0.37	0.15	0.12
Rudbeckia subtomentosa	Asteraceae	nat. per. forb	1	0	1	0	1	0.27	0.00	0.28
Rudbeckia triloba	Asteraceae	nat. bien. forb	0	0	2	3	0	0.76	0.14	0.00
Ruellia humilis	Acanthaceae	nat. per. forb	0	6	9	14	17	0.63	0.46	0.49
Ruellia pedunculata	Acanthaceae	nat. per. forb	0	44	94	116	116	0.28	0.32	0.27
Ruellia spp.	Acanthaceae	nat. per. forb	0	3	1	8	15	0.11	0.23	0.19
Rumex acetosella	Polygonaceae	ex. peren. forb	0	0	0	0	1	0.00	0.00	0.02
Sabatia angularis	Gentianaceae	nat. bien. forb	1	0	3	0	2	0.10	0.00	0.33
Salvia lyrata	Lamiaceae	nat. per. forb	1	0	6	8	18	0.46	1.01	0.74
Sambucus canadensis	Caprifoliaceae	nat. per. tree	0	0	0	1	2	0.00	0.24	1.10
Sanguinaria canadensis	Papaveraceae	nat. per. forb	0	0	5	1	10	0.49	0.01	0.39
Sanicula canadensis	Apiaceae	nat. bien. forb	30	56	113	106	51	0.73	0.67	0.77
Sanicula gregaria	Apiaceae	nat. per. forb	0	9	2	9	15	0.27	0.25	0.95
Sanicula spp.	Apiaceae	nat. forb	0	1	35	143	189	0.17	0.55	0.51
Sassafras albidum	Lauraceae	nat. per. tree	201	450	606	619	620	7.36	7.65	7.66
Satureja arkansana	Lamiaceae	nat. per. forb	0	1	9	6	8	1.21	0.66	1.17
Schrankia uncinata	Fabaceae	nat. per.legume	6	10	10	4	1	0.36	0.45	0.88
Scirpus spp.	Cyperaceae	nat. per. sedge	0	0	0	0	1	0.00	0.00	0.16
Scleria spp.	Cyperaceae	nat. per. sedge	0	0	15	51	61	0.56	0.66	0.30
Scleria triglomerata	Cyperaceae	nat. per. sedge	0	0	0	32	31	0.00	0.60	0.91
Scutellaria bushii	Lamiaceae	nat. bien. forb	2	4	2	4	5	0.48	0.30	0.19
Scutellaria elliptica	Lamiaceae	nat. bien. forb	0	7	27	3	10	0.24	0.27	0.20
Scutellaria incana	Lamiaceae	nat. per. forb	0	19	49	32	29	0.51	0.29	0.26
Scutellaria nervosa	Lamiaceae	nat. bien. forb	6	3	0	0	0	0.00	0.00	0.00
Scutellaria ovata	Lamiaceae	nat. per. forb	0	17	20	7	16	0.32	0.15	0.53
Scutellaria parvula	Lamiaceae	nat. per. forb	0	1	7	3	3	0.16	0.06	0.02
Scutellaria spp.	Lamiaceae	nat. per. forb	6	25	8	6	4	0.08	0.19	0.02
Senecio aureus	Asteraceae	nat. per. forb	2	3	0	0	2	0.00	0.00	0.11
Senecio obovatus	Asteraceae	nat. per. forb	0	0	3	6	6	0.25	0.58	0.30
Senecio plattensis	Asteraceae	nat. per. forb	1	0	1	0	0	0.23	0.00	0.00
Senecio spp.	Asteraceae	nat. per. forb	0	0	3	2	15	0.19	0.51	0.10
Setaria spp.	Poaceae	ex. ann. grass	0	0	0	0	1	0.00	0.00	0.06
Setaria viridis	Poaceae	ex. ann. grass	0	1	0	0	1	0.00	0.00	0.46
Seymeria macrophylla	Scrophulariaceae	nat. per. forb	0	1	0	0	0	0.00	0.00	0.00
Silene stellata	Caryophyllaceae	nat. per. forb	1	3	5	9	11	0.26	0.14	0.19
Silene virginica	Caryophyllaceae	nat. per. forb	0	0	1	7	7	0.19	0.28	0.21
Silphium asteriscus	Asteraceae	nat. per. forb	0	5	24	56	69	0.54	0.44	0.27
Silphium integrifolium	Asteraceae	nat. per. forb	0	0	3	2	13	0.33	1.01	0.37
Silphium spp.	Asteraceae	nat. per. forb	0	0	0	0	6	0.00	0.00	0.28
Silphium terebinthinaceum	Asteraceae	nat. per. forb	0	18	24	22	21	2.20	2.24	2.74

Species	Family	Type	Number of Plots '91	'92	'93	'94	'95	Avg. Rel. Abundance '93	'94	'95
Sisyrinchium campestre	Iridaceae	nat. per. forb	0	0	0	1	1	0.00	0.04	0.02
Smilacina racemosa	Liliaceae	nat. per. forb	67	177	248	236	265	0.66	0.64	0.71
Smilax bona-nox	Liliaceae	nat. per. w-vine	17	102	137	149	144	2.22	2.16	2.05
Smilax ecirrhata	Liliaceae	nat. per. w-vine	0	0	0	0	1	0.00	0.00	0.23
Smilax glauca	Liliaceae	nat. per. w-vine	37	23	23	40	45	0.66	0.69	0.67
Smilax herbacea	Liliaceae	nat. per. w-vine	0	13	31	1	8	0.73	0.23	0.52
Smilax pulverulenta	Liliaceae	nat. per. w-vine	0	1	26	61	60	0.54	0.50	0.44
Smilax rotundifolia	Liliaceae	nat. per. w-vine	0	1	10	15	29	1.30	0.42	0.76
Smilax spp.	Liliaceae	nat. per. w-vine	3	2	11	42	32	0.11	0.31	0.07
Smilax tamnoides	Liliaceae	nat. per. w-vine	4	46	56	21	26	1.21	0.96	0.90
Solanum americanum	Solanaceae	nat. ann. forb	1	1	0	1	0	0.00	0.02	0.00
Solanum carolinense	Solanaceae	nat. per. forb	4	1	3	4	4	0.51	0.37	0.39
Solanum spp.	Solanaceae	nat. per. forb	1	0	0	6	0	0.00	0.23	0.00
Solidago arguta	Asteraceae	nat. per. forb	5	1	22	1	1	0.46	0.35	0.05
Solidago flexicaulis	Asteraceae	nat. per. forb	4	48	92	49	93	0.73	0.50	0.54
Solidago hispida	Asteraceae	nat. per. forb	11	50	155	145	126	0.58	0.59	0.46
Solidago juncea	Asteraceae	nat. per. forb	0	1	6	2	2	0.46	0.58	0.17
Solidago nemoralis	Asteraceae	nat. per. forb	0	0	0	3	20	0.00	0.30	0.28
Solidago petiolaris	Asteraceae	nat. per. forb	0	0	15	77	9	0.63	0.57	0.69
Solidago radula	Asteraceae	nat. per. forb	19	0	26	30	10	0.47	0.29	0.34
Solidago spp.	Asteraceae	nat. per. forb	54	269	222	76	62	0.71	0.42	0.35
Solidago ulmifolia	Asteraceae	nat. per. forb	0	0	9	206	248	0.52	0.81	0.77
Sorghastrum nutans	Poaceae	nat. per. grass	0	1	4	12	9	0.79	0.48	0.79
Sorghum halepense	Poaceae	ex. peren.grass	0	0	2	1	1	0.18	0.12	0.54
Specularia perfoliata	Campanulaceae	nat. ann. forb	0	0	0	0	1	0.00	0.00	0.01
Sphenopholus obtusata	Poaceae	nat. per. grass	0	0	0	0	1	0.00	0.00	0.07
Sporobolus asper	Poaceae	nat. per. grass	1	0	0	6	13	0.00	0.60	1.14
Sporobolus spp.	Poaceae	nat. per. grass	2	0	0	0	3	0.00	0.00	0.03
Sporobolus vaginiflorus	Poaceae	nat. ann. grass	0	0	0	3	2	0.00	0.03	0.27
Staphylea trifolia	Staphyleaceae	nat. per. tree	0	2	2	2	3	2.08	4.14	2.38
Strophostyles leiosperma	Fabaceae	nat. ann.legume	0	3	8	0	0	0.39	0.00	0.00
Strophostyles umbellata	Fabaceae	nat. per.legume	0	0	0	8	3	0.00	0.36	0.28
Stylosanthes biflora	Fabaceae	nat. per.legume	12	10	37	49	53	0.21	0.15	0.17
Symphoricarpos orbiculatus	Caprifoliaceae	nat. per. shrub	37	72	110	107	110	1.81	1.71	1.69
Taenidia integerrima	Apiaceae	nat. per. forb	0	4	9	10	13	0.49	0.43	0.36
Tephrosia virginiana	Fabaceae	nat. per.legume	62	67	102	100	104	1.51	1.71	1.47
Thalictrum dioicum	Ranunculaceae	nat. per. forb	0	0	1	1	3	0.15	0.30	0.40
Thaspium barbinode	Apiaceae	nat. per. forb	0	33	24	44	14	0.72	0.69	0.54
Thaspium spp.	Apiaceae	nat. per. forb	0	1	3	8	40	0.20	0.06	0.47
Thaspium trifoliatum	Apiaceae	nat. per. forb	8	62	56	56	32	0.63	0.49	0.46
Thelypteris hexagonoptera	Polypodiaceae	nat. per. fern	0	18	14	4	8	2.39	7.02	4.53
Tradescantia longipes	Commelinaceae	nat. per. forb	0	0	0	4	3	0.00	0.03	0.17
Tragia cordata	Euphorbiaceae	nat. per. vine	0	0	1	4	3	0.23	0.17	0.14
Tridens flavus	Poaceae	nat. per. grass	2	3	1	1	0	0.33	0.02	0.00
Trifolium pratense	Fabaceae	ex. bien.legume	0	0	0	0	1	0.00	0.00	0.21
Trillium spp.	Liliaceae	nat. per. forb	0	0	0	2	4	0.00	0.09	0.17
Triosteum angustifolium	Caprifoliaceae	nat. per. forb	4	0	0	1	2	0.00	0.02	0.30
Triosteum aurantiacum	Caprifoliaceae	nat. per. forb	0	2	0	1	1	0.00	0.42	0.02
Triosteum spp.	Caprifoliaceae	nat. per. forb	2	0	0	1	1	0.00	0.14	0.02
Triphora trianthophora	Orchidaceae	nat. per. forb	0	0	0	1	4	0.00	0.03	0.08

Species	Family	Type	Number of Plots '91	'92	'93	'94	'95	Avg. Rel. Abundance '93	'94	'95
Ulmus alata	Ulmaceae	nat. per. tree	8	49	93	59	92	1.36	1.06	0.85
Ulmus americana	Ulmaceae	nat. per. tree	2	74	31	45	49	1.26	1.47	1.35
Ulmus rubra	Ulmaceae	nat. per. tree	15	113	134	129	142	2.35	2.67	2.31
Ulmus spp.	Ulmaceae	nat. per. tree	6	3	14	70	44	0.59	0.69	0.28
Uniola latifolia	Poaceae	nat. per. grass	4	12	12	11	17	1.33	1.22	1.05
Uvularia grandiflora	Liliaceae	nat. per. forb	0	43	109	120	125	0.47	0.52	0.51
Vaccinium arboreum	Ericaceae	nat. per. shrub	0	0	87	107	72	3.04	3.29	2.25
Vaccinium spp.	Ericaceae	nat. per. shrub	192	369	125	14	14	8.17	1.22	0.24
Vaccinium stamineum	Ericaceae	nat. per. shrub	0	0	316	343	364	5.53	4.80	4.62
Vaccinium vacillans	Ericaceae	nat. per. shrub	0	0	357	422	432	6.10	5.79	6.47
Verbena canadensis	Verbenaceae	nat. per. forb	0	0	0	2	2	0.00	0.02	0.33
Verbena simplex	Verbenaceae	nat. per. forb	0	1	1	0	2	2.36	0.00	0.02
Verbena spp.	Verbenaceae	nat. per. forb	1	0	0	0	0	0.00	0.00	0.00
Verbena urticifolia	Verbenaceae	nat. per. forb	5	2	5	1	1	2.08	0.67	0.66
Verbesina helianthoides	Asteraceae	nat. per. forb	14	35	72	88	83	1.39	1.36	1.23
Verbesina virginica	Asteraceae	nat. per. forb	0	0	0	1	0	0.00	3.82	0.00
Vernonia altissima	Asteraceae	nat. per. forb	0	0	2	8	7	0.78	0.64	0.62
Vernonia baldwini	Asteraceae	nat. per. forb	6	32	90	112	74	0.72	0.60	0.70
Vernonia crinita	Asteraceae	nat. per. forb	2	7	17	20	14	0.51	0.53	0.53
Vernonia spp.	Asteraceae	nat. per. forb	0	4	4	8	0	0.28	0.33	0.00
Veronicastrum virginicum	Scrophulariaceae	nat. per. forb	1	1	2	3	4	0.23	0.16	0.11
Viburnum rufidulum	Caprifoliaceae	nat. per. tree	5	34	61	74	89	1.01	0.61	0.61
Viburnum spp.	Caprifoliaceae	nat. per. tree	0	0	6	0	1	0.96	0.00	0.59
Vicia americana	Fabaceae	nat. per. forb	0	0	0	0	1	0.00	0.00	0.21
Vicia caroliniana	Fabaceae	nat. per.legume	13	11	16	21	26	0.24	0.21	0.08
Vicia spp.	Fabaceae	peren. legume	0	0	0	3	2	0.00	0.18	0.04
Viola pedata	Violaceae	nat. per. forb	0	1	25	27	27	0.19	0.12	0.10
Viola sagittata	Violaceae	nat. per. forb	0	5	6	6	12	0.15	0.22	0.14
Viola sororia	Violaceae	nat. per. forb	0	2	140	157	192	0.41	0.47	0.56
Viola spp.	Violaceae	nat. per. forb	73	229	68	202	167	0.30	0.09	0.07
Viola striata	Violaceae	nat. per. forb	0	3	7	6	7	1.42	2.86	2.15
Viola triloba	Violaceae	nat. per. forb	0	18	232	169	248	0.33	0.20	0.25
Viola viarum	Violaceae	nat. per. forb	0	1	37	89	20	0.16	0.19	0.06
Vitis aestivalis	Vitaceae	nat. per. w-vine	187	480	348	574	600	2.85	3.74	3.41
Vitis spp.	Vitaceae	nat. per. w-vine	23	33	463	446	405	2.67	0.23	0.12
Vitis vulpina	Vitaceae	nat. per. w-vine	4	1	36	117	191	0.57	0.81	1.01
Woodsia obtusa	Polypodiaceae	nat. per. fern	0	0	1	0	1	0.23	0.00	0.02
Zizia aptera	Apiaceae	nat. per. forb	3	0	1	0	0	0.27	0.00	0.00
Zizia aurea	Apiaceae	nat. per. forb	0	3	0	0	1	0.00	0.00	1.30
Zizia spp.	Apiaceae	nat. per. forb	0	1	2	0	2	0.15	0.00	0.24
None	none	none	58	118	64	59	45	0.00	0.00	0.00
Forb	Unknown	unknown forb	66	150	55	161	300	0.30	0.17	0.09
Grass	Unknown	unknown grass	23	39	21	58	49	0.50	0.13	0.19
Legume	Fabaceae	unkn. legume	7	17	13	31	33	0.22	0.07	0.05
Woody	Unknown	peren. tree	5	33	27	121	85	0.61	0.09	0.13
Composite	Asteraceae	unknown forb	0	6	11	5	26	0.69	0.05	0.33
Fern	Polypodiaceae	fern	2	3	2	13	1	0.11	0.09	0.02
Mint	Lamiaceae	unknown forb	3	3	1	2	0	0.03	0.16	0.00
Unknown	Unknown	unknown	37	31	0	10	1	0.00	0.82	0.03
Unknown vine	Unknown	unknown vine	2	9	4	5	17	0.31	0.15	0.07

Acorn Production on the Missouri Ozark Forest Ecosystem Project Study Sites: Pre-treatment Data

Larry D. Vangilder[1]

Abstract.—In the pre-treatment phase of a study to determine if even- and uneven-aged forest management affects the production of acorns on the Missouri Forest Ecosystem Project (MOFEP) study sites, acorn production was measured on the nine study sites by randomly placing from 2 to 6 plots in each of four ecological land type (ELT) groupings (N=130 plots). A split-plot multivariate analysis of variance revealed that the production of sound, mature acorns varied significantly among years, blocks, and ELT's. In addition, a significant year by "treatment" effect was observed. When years were combined to examine between subjects effects, ELT was shown to have a significant effect on acorn production. ELT also affected average sound, mature acorn production per 1,000 m^2 of oak canopy area with ridgetops being the most productive. Given the variability observed in acorn production during the 3 years of this study, it is clear that only very long term data on acorn production will provide the information needed to meet the study's objectives.

Oak mast is a very important source of fall and winter food for many species of wildlife (Dickson 1990, Goodrum *et al.* 1971, Perry 1991, Rogers *et al.* 1990, Smith and Scarlett 1987). Poor mast years have been shown to result in lowered reproductive success and/or reduced numbers of squirrels (*Sciurus* spp.) (Barkalow *et al.* 1970, Nixon and McClain 1969), white-tailed deer (*Odocoileus virginianus*) (Rogers *et al.* 1990, Wentworth *et al.* 1992), black bears (*Ursus americanus*) (Rogers 1976), and red-headed woodpeckers (*Melanerpes erythrocephlus*) (Smith and Scarlett 1987). Acorns are also important in the regeneration of oak trees (Cecich 1992). Because of the importance of mast in the ecology of the Ozark forest, a study is being conducted to determine if and how even- and uneven-aged forest management affect the production of acorns on the MOFEP study sites. This paper present 3 years of acorn production data from the pre-treatment phase of the MOFEP experiment (Sheriff and He 1997).

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METHODS

Acorn Collection Methods

Methods of hard mast collection were modified from Myers (1979) and Christisen and Kearby (1984) and are similar to those being used in another ongoing study of hard mast production in the Missouri Ozarks that began in 1989 (Schroeder and Vangilder 1997). Because of the extreme variability of acorn production among individual trees, species, and years (Christisen and Kearby 1984), and because of the impracticality of sampling acorns from individual trees in a closed canopy forest, I chose to determine the number of acorns falling to the ground on a plot of land rather than the number of acorns falling to the ground under an individual tree. In addition, repeated measures of the acorn production of an individual tree through the entire course of the MOFEP experiment (Sheriff and He 1997) would not be possible because of natural tree mortality and tree mortality due to treatment. Therefore, a plot of land that will remain intact throughout the entire course of the experiment was the correct sampling unit. A 4 X 5 grid of 20 traps was systematically placed in a 7.7 X 8.7 m spacing to sample acorn production in plots. To estimate acorn production, each plot was 38.5 X 53 m in size (2,002

m^2). Each cone-shaped trap was 0.73 m in diameter and constructed from 6-mil plastic. Traps were suspended above ground on three 1.52-m pieces of 0.95-cm reinforcement rod. The 20 traps sampled 8.37 m^2 of the plot.

From 1993 through 1995, mast was collected weekly from each plot beginning in August and ending when no mast was collected from any plot (January or February). Hard mast from each trap was placed in small paper grocery sacks and labeled with the site, plot, and trap number. Weekly collections were air-dried by hanging sacks on clotheslines indoors. When air dry, the nuts from each sack were identified to species and weighed, and their maturity class was determined (Christisen and Kearby 1984). Five maturity classes were identified with classes 4 and 5 considered mature (Christisen and Kearby 1984). Soundness of each nut was determined by cutting the nut open to determine whether any of the fruit remained. Nuts in which more than half the fruit remained were considered sound.

Placement of Acorn Plots

I chose to use stratified random sampling to decide where to place the acorn plots. Thirteen different ecological land types (Miller 1981) occurred under the original ELT designations. However, three ELT's made up almost 90 percent of the total land area of the sites. South and west slopes (ELT 17), north and east slopes (ELT 18), and ridgetops (ELT 11) were the most frequent ELT's. The next most common ELT's were broad ridges (ELT 15) and upland waterways (ELT 5). Thus, each of the nine MOFEP sites was divided into four ELT groupings: ridgetops (ELT's 11 and 15), south and west slopes (ELT 17), north and east slopes (ELT 18), and a group containing all the other ELT's (this group is subsequently called "other"). Each site was originally targeted to receive at least 12 plots. Plots were randomly assigned to each ELT grouping roughly in proportion to the area that each of the groups made up on each of the sites. Under the original ELT designation, one site (Site 1) had only the three major ELT groups (no "other" ELT's). On Site 1, I chose to establish two plots in areas that upon field examination were known to be in one of the "other" ELT's even though the "other" ELT had not been designated as such. As a result of this sampling scheme, 130 plots were placed on the nine study sites (fig. 1). Because upland waterways (ELT 5) (Miller 1981) dominated the "other" ELT group, most acorn plots in the "other" ELT group were actually on upland waterways (ELT 5).

Measurement of Trees on Plots

Each tree greater than or equal to 11.4 cm diameter at breast height (d.b.h.) was measured, identified to species, and marked with a uniquely numbered metal tag. The canopy position and condition of each tree were also recorded. In addition, the distance and azimuth of each tree to the center of the plot was recorded so that a map of the trees on each plot could be made. For tree measurement, the outside edge of the plot was considered to be a distance of 9.144 m out from the outside line of traps. This distance was chosen because a preliminary analysis of the data from the 648 permanent plots (Brookshire *et al.* 1997) indicated that only 22 of 9,664 trees in these plots had crown radii greater than 9.144 m. Plot size for the purpose of tree measurement was 42.118 m by 53.818 m or 2,266.7 m^2. The above measurements were taken from January-March 1995. The crown diameter of each marked tree was measured parallel to the long and short axes of the plot from February to April 1996. These two measurements were averaged and the average was divided by 2 to determine the average radius of the crown of each tree. Scientific nomenclature for trees follow Settergren and McDermott (1974).

Statistical Analysis

Analysis of Variance Approach

The number of sound, mature acorns per plot for each of the 3 years of the study was used as the dependent variable in a multivariate analysis of variance. Because the number of acorns per plot was "count" data, the data were transformed using a square root transformation ($\sqrt{(x+1)}$) (Snedecor and Cochran 1967: 325). The design was a repeated measures (year), split-plot (ELT) design (MODEL 3, Sheriff and He 1997). For analysis of oak tree d.b.h., average canopy area of oaks, and average sound, mature acorn production per 1,000 m^2 of oak crown area, a split-plot repeated measures design was used (MODEL 2, Sheriff and He 1997). Although there were 130 acorn plots, there were only three blocks, three treatments, and four ELT's; therefore, the sample size for each year for sound, mature acorns per plot

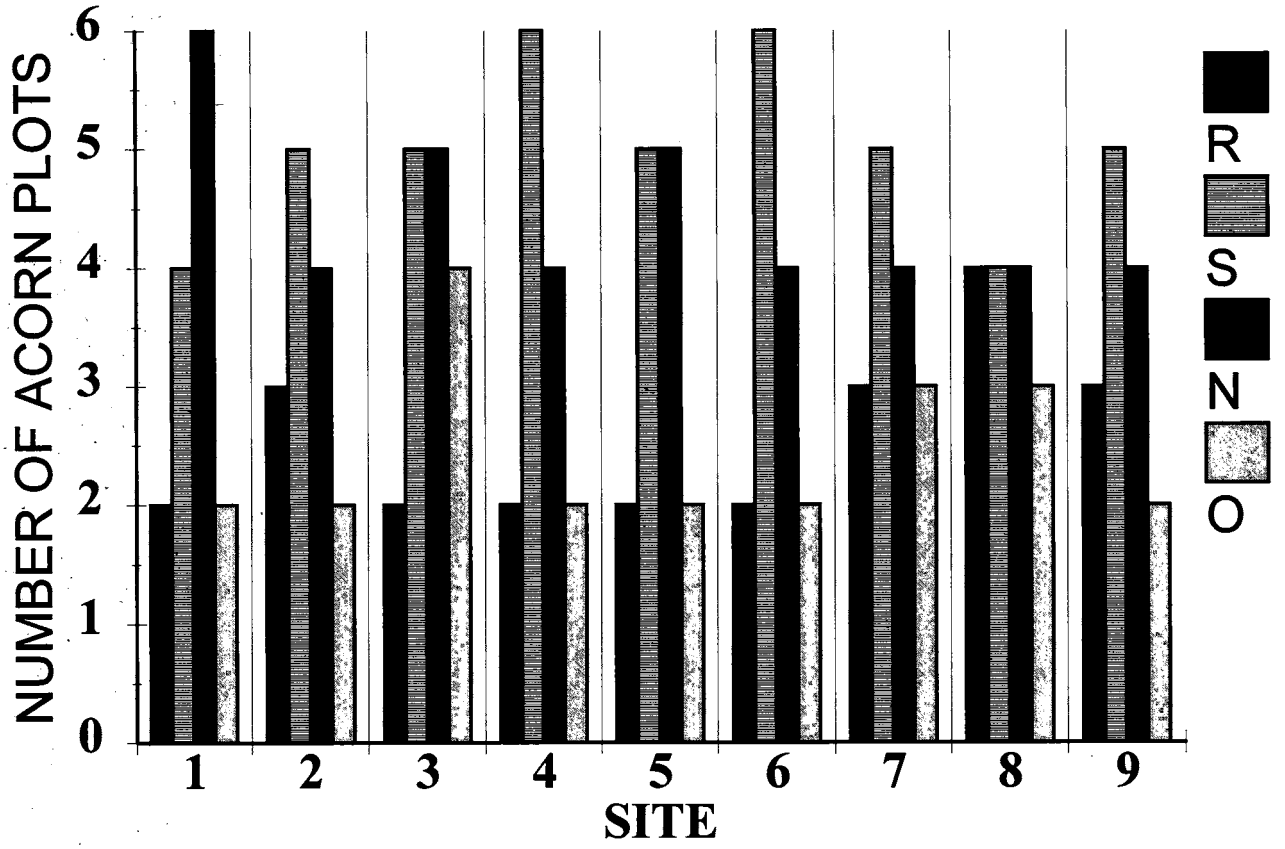

Figure 1.—*Number of acorn plots placed on each MOFEP study site by ELT grouping. R=ridgetop, S=south and west slope, N=north and east slope, and O="other."*

was 36. An average number of acorns per plot for the plots that belonged to each of the 36 block, treatment, and ELT combinations was used in the multivariate analysis. A similar procedure was used for oak tree d.b.h. and average canopy area of oak trees. For average sound, mature acorn production per 1,000 m^2 of oak crown area, sound, mature acorn production was averaged across the 3 years of the study for each plot. This average for each plot was then divided by the total crown area of oaks (m^2) in that plot divided by 1,000. Pairwise comparisons of oak tree d.b.h., average canopy area of oak trees, and average sound, mature acorn production per 1,000 m^2 of oak crown area were made with Fisher's Protected Least Significant Difference test (Huitema 1980: 82-86). The significance level for all statistical tests was set at α=0.1.

Sampling Approach

For each year, the total number of sound, mature acorns produced was estimated for each of the nine MOFEP sites by summing the four separate estimates for each strata. Similarly, for each year, the variance of each estimate for each site was also calculated by summing the four variance estimates for each strata (Cochran 1977: 89-96). Each estimate of the total production of sound, mature acorns per site and the lower and upper bounds of the 95 percent confidence interval of the estimate were then converted to estimates of sound, mature acorns per hectare by dividing the total estimate and the lower and upper bounds of the 95 percent confidence interval by the number of hectares in each site.

To determine whether stratification by ELT helped reduce the sampling variance of acorn production estimates, the percent gain in

efficiency was calculated by comparing the variance of each estimate as calculated above with the variance of each estimate when calculated as if the sample had been a simple random sample (Cochran 1977: 136-138).

Acorns were also divided into two groups: those from red oak group trees and those from white oak group trees. Data were then examined by site, year, and species group to determine what proportion of the sound mature acorn production came from red oak group trees.

The proportion of sound, mature acorns of all mature acorns from each group that fell into traps was also determined for each site and year.

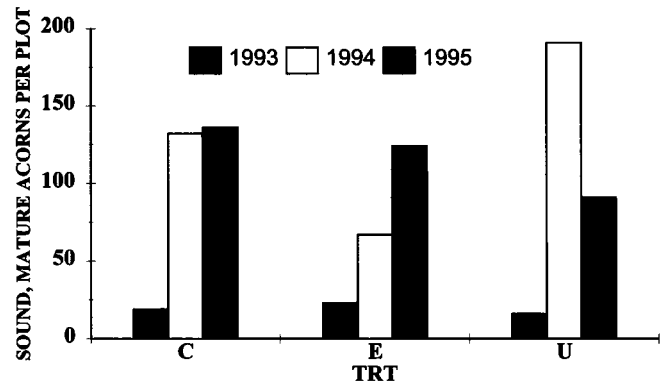

Figure 2.—*Number of sound, mature acorns per plot by year and treatment (trt) (C=control, E=even-aged, U=uneven-aged) on the MOFEP study sites.*

RESULTS

Analysis of Variance Approach

Acorns

A multivariate analysis of variance revealed a significant YEAR X TREATMENT interaction (P=0.0386) (table 1). In 1994, the number of sound, mature acorns per plot appeared differentially higher on sites designated to receive the uneven treatment when compared with the other year and treatment combinations (fig. 2). An alternative explanation for the YEAR X TREATMENT interaction is that the number of sound, mature acorns per plot was differentially lower on sites designated to receive the even-aged treatments. A significant YEAR X BLOCK X ELT interaction (P=0.0201) for the number of sound, mature acorns per plot was also detected (table 1). The number of sound, mature acorns per plot did not differ consistently across the year, block, and ELT combinations (fig. 3).

When between subjects effects were examined, a significant ELT effect was revealed (P=0.0001) (table 2). The mean number of sound, mature

Table 1.—*Multivariate analysis of variance table for a split-plot, repeated measures design with the dependent variables being the number of sound, mature acorns per plot (transformed by √(x+1)) for 1993, 1994, and 1995 and the independent variables being the fixed effects of BLOCK, TREATMENT, AND ELT. Pillai's trace was used as the multivariate test criterion. The numerator (Num DF) and denominator (Den DF) degrees of freedom are shown for each effect. The sample size is 36 (3 BLOCKS X 3 TREATMENTS X 4 ELTS). The YEAR X BLOCK X TREATMENT sum of squares and cross products (SSCP) matrix (ERROR A) was used to test the YEAR X BLOCK and YEAR X TREATMENT interaction SSCP matrices. The ERROR B SSCP matrix was used to test the remainder of the effects.*

Effect	Pillai's Trace	Num DF	Den DF	Pr>F
YEAR	282.12	2	11	0.0001
ERROR B				
YEAR X BLOCK	1.83	4	8	0.2172
YEAR X TREATMENT	4.27	4	8	0.0386
YEAR X BLOCK X TREATMENT (ERROR A)				
YEAR X ELT	2.56	6	24	0.0467
YEAR X BLOCK X ELT	2.66	12	24	0.0201
YEAR X TREATMENT X ELT	0.50	12	24	0.8930
ERROR B				

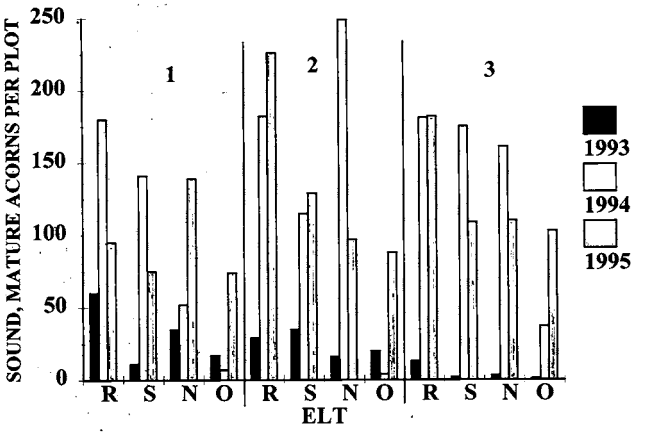

Figure 3.—*Number of sound, mature acorns per plot by year, block (1,2,3) and ELT grouping (R=ridgetop, S=south and west slope, N=north and east slope, and O="other") on the MOFEP study sites.*

acorns produced per plot was higher on ridgetops than any other ELT group (P≤0.0347) (table 3). South and west and north and east slopes did not differ in acorn production (P=0.6142), but both south and west and north and east slopes produced significantly more sound, mature acorns per plot than did the "other" ELT group (P≤0.0004) (table 3).

Trees

A total of 11,020 trees ≥ 11.4 cm d.b.h. were measured on the 130 acorn plots. The most frequent trees on the plots were white oak (*Quercus alba*) (28.2 percent), scarlet oak (*Quercus coccinea*) (16.5 percent), black oak (*Quercus velutina*) (15.4 percent), and shortleaf pine (*Pinus echinata*) (9.3 percent). Post oak (*Quercus stellata*) (5.5 percent) was the only other species of oak that made up more the 1 percent of the total individuals. Other species that made up more than 1 percent of the total trees were black hickory (*Carya texana*) (5.5 percent), mockernut hickory (*Carya tomentosa*) (5.2 percent), pignut hickory (*Carya glabra*) (5.2 percent), blackgum (*Nyssa sylvatica*) (1.7 percent), and flowering dogwood (*Cornus florida*) (1.3 percent).

A split-plot analysis of variance revealed no significant BLOCK or TREATMENT effects for mean d.b.h. of oak (*Quercus* spp.) trees ≥ 11.4 cm d.b.h. (table 4). However, the effect of ELT was significant (table 4). Mean d.b.h. of oak trees was significantly lower in the "other" ELT group than in the other three ELT groups (P≤0.0580) (fig. 4). Mean d.b.h. of oak trees on south and west slopes was lower than on ridgetops (P=0.0063) (fig. 4).

A split-plot analysis of variance revealed a significant BLOCK but no significant TREATMENT effect for mean canopy area of oak trees ≥ 11.4 cm d.b.h. (table 5). The mean canopy area in block 3 (Peck Ranch) was significantly higher (P < 0.0221) than in block 1 (fig. 5). The effect of ELT was also significant (table 5). Mean canopy area of oak trees was significantly

Table 2.—*Multivariate analysis of variance table for between subject effects for a split-plot, repeated measures design with the dependent variable being the sum of the number of sound, mature acorns per plot (transformed by √(x+1)) for 1993-1995 divided by the square root of 3 and the independent variables being the fixed effects of BLOCK, TREATMENT, AND ELT. The sample size is 36 (3 BLOCKS X 3 TREATMENTS X 4 ELTS). The BLOCK X TREATMENT effect (ERROR A) was used to test the BLOCK and TREATMENT effects. ERROR B was used to test the remainder of the effects.*

Effect	DF	Mean Square	F Value	Pr>F
BLOCK	2	14.07	1.07	0.4258
TREATMENT	2	15.94	1.21	0.3890
BLOCK X TREATMENT (ERROR A)	4	13.21		
ELT	3	141.55	21.20	0.0001
BLOCK X ELT	6	2.63	0.39	0.8689
TREATMENT X ELT	6	7.68	1.15	0.3925
ERROR B	12	6.68		

Table 6.—*Analysis of variance table for a split-plot design with the dependent variable being the average sound, mature acorn production per 1,000 m² of oak canopy area (PCAN) and the independent variables being the fixed effects of BLOCK, TREATMENT, AND ELT. The sample size is 36 (3 BLOCKS X 3 TREATMENTS X 4 ELTS). The BLOCK X TREATMENT effect (ERROR A) was used to test the BLOCK and TREATMENT effects. ERROR B was used to test the remainder of the effects.*

Effect	DF	Mean Square	F Value	Pr>F
BLOCK	2	303.88	0.46	0.6620
TREATMENT	2	309.47	0.47	0.6575
BLOCK X TREATMENT (ERROR A)	4	663.39		
ELT	3	1213.12	5.43	0.0136
BLOCK X ELT	6	122.80	0.55	0.7616
TREATMENT X ELT	6	246.95	1.11	0.4136
ERROR B	12	223.37		

Table 7.—*Means from a split-plot analysis of variance for the effect of ELT on the average sound, mature acorn production per 1,000 m² of oak canopy area (PCAN). The critical value for the Fisher's Protected Least Significant Difference at α=0.10 with 12 degrees of freedom is 1.782.*

		t-value (Pr > |T|) of indicated comparison		
ELT	Mean PCAN	S	N	O
Ridgetop	53.57	2.26(.0430)	1.91 (0.0802)	4.02 (0.0017)
South and West Slopes (S)	37.63		0.35 (0.7312)	1.76 (0.1043)
North and East Slopes (N)	40.11			2.11 (0.0567)
Other (O)	25.25			

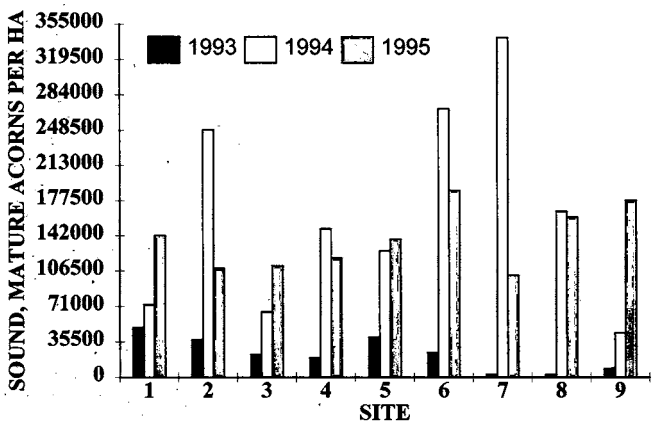

Figure 7.—*Sound, mature acorn production (acorns per hectare) by year and MOFEP site.*

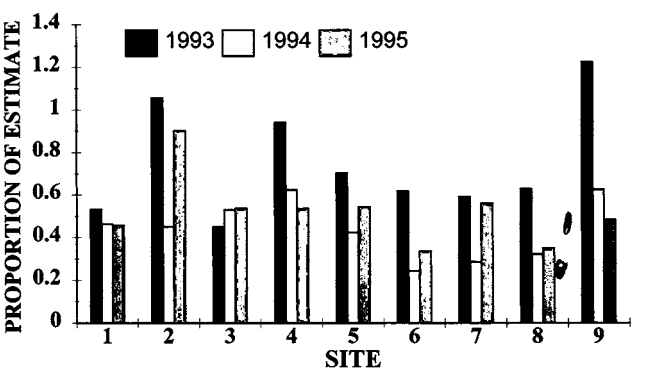

Figure 8.—*The proportion of the sound, mature acorn production estimate that the half-width of the 95 percent confidence interval made up for each year and MOFEP site.*

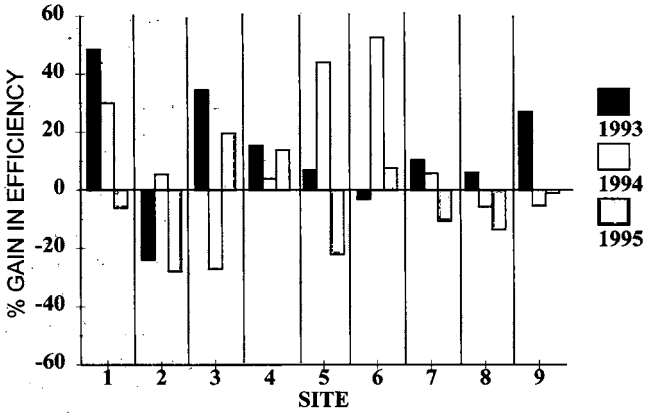

Figure 9.—*The percent gain in efficiency (reduction in variance) that results from stratification by ELT grouping when compared with the variance that would have resulted from a simple random sample by year and MOFEP site.*

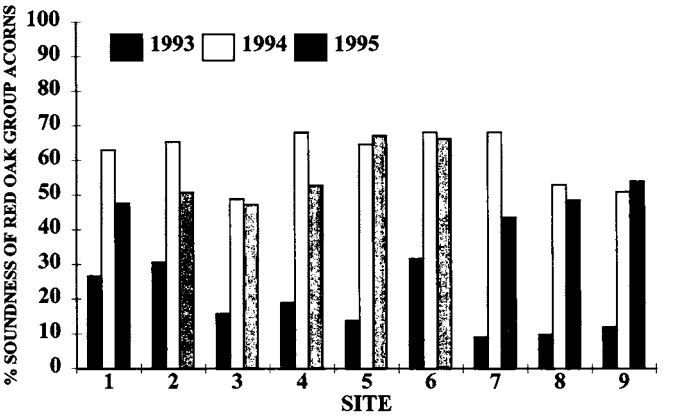

Figure 11.—*Percent soundness of red oak group acorns by year and MOFEP site.*

(fig. 10). In 1994, virtually all sound, mature production came from red oak group trees (>0.96 on all sites) (fig. 10).

Soundness of red oak group acorns ranged from 9 percent on site 7 in 1993 to 68 percent on site 6 in 1994 (fig. 11), and soundness of white oak group acorns ranged from 6 percent on site 7 in 1993 to 83 percent on site 9 in 1995 (fig. 12).

DISCUSSION

Production of sound, mature acorns varied considerably among treatments (sites), years, blocks, and ELT's. Such variation has been reported in a number of other studies (Christisen 1955, Dickson 1990, Goodrum *et al.* 1971, Schroeder and Vangilder 1997). In the current study, because the treatments had not been applied, the significant YEAR X TREATMENT interaction was no doubt the result of random variation in acorn production among the sites. The significant interaction illustrates the importance of collecting pre-treatment data. Although ideally, pre-treatment data should have been collected over a longer time period, the 3 years of pre-treatment data that were collected will help in the interpretation of post-treatment data.

Stratification by ELT group was a very important aspect of this study. With a simple random

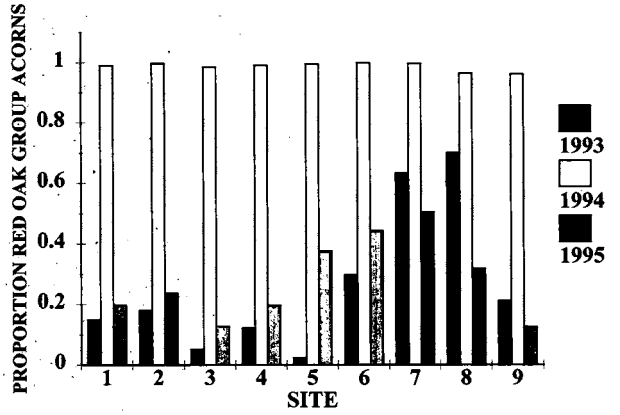

Figure 10.—*The proportion that red oak group acorns made up of the total sound, mature acorn production by year and MOFEP site.*

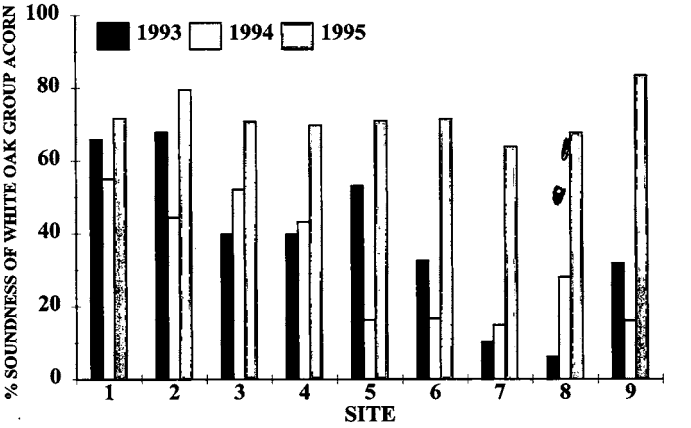

Figure 12.—*Percent soundness of white oak group acorns by year and MOFEP site.*

sample, important ELT effects could not have been detected. The production of sound, mature acorns, d.b.h. of oak trees, and mean canopy area of oak trees differed significantly among ELT's. In particular, sound, mature acorn production, d.b.h. of oak trees, and mean canopy area of oak trees were lower on plots in the "other" ELT group (primarily upland waterways) than on plots in the other three ELT groups. In addition, the analysis of variance of PCAN indicated that this difference in sound, mature acorn production among ELT's was due not only to the difference in the canopy area of oak trees among ELT's, but also to some inherent difference in productivity among ELT's. In other words, an "other" plot would produce fewer acorns than a ridgetop plot even when both plots had exactly the same amount of total canopy area of oaks.

Other measures of the canopy area of oaks have also been shown to be correlated with average acorn production in other studies (Goodrum *et al.* 1971, Schroeder and Vangilder 1997). Christisen (1955) reported that large-crowned oaks tended to produce more acorns than smaller crowned oaks.

Estimates of sound, mature acorns per hectare varied considerably among years and sites in this study. Other studies have also reported high levels of variability. Schroeder and Vangilder (1997) reported that average acorn production (N=5 years) ranged from 956 to 86,518 sound, mature acorns per hectare on 43 plots in the Missouri Ozarks. The maximum number of sound, mature acorns per hectare ranged from 27,000 to 106,000 on four study areas in Missouri from 1973 to 1976, while the minimum number of sound, mature acorns per hectare ranged from 2,500 to 6,000 (Christisen and Kearby 1984). Dickson (1990) reported that production of sound, mature acorns from 1959 to 1977 ranged from 5.4 to 637.5 kg/ha on an upland white oak-black oak-northern red oak site in the Sylamore Experimental Forest in the Ozarks of Arkansas. In a stream bottom white oak-black oak-northern red oak site on Sylamore, production ranged from 0.0 to 122.8 kg/ha. These relatively unproductive stream bottoms are similar to the "other" ELT group (upland waterways) in this study. One hypothesis that might account for lower average acorn production in "upland waterways" is that freezing temperatures in the spring occur there more often than higher up on slopes or ridgetops. If these freezing temperatures occur during flowering, many of the oak flowers will be destroyed and fewer acorns will be produced. In the spring, a hard frost may occur in these "upland waterways" (also called hollow bottoms) while the temperature will be well above freezing on the ridgetop (personal observation).

Variation about acorn production estimates was also quite high in some years on some sites. In 1993, on site 9 variation about the acorn production estimate was extremely high. An estimate of the number of plots needed to produce 95 percent confidence limits within 10 percent of the mean estimate (given the estimate and variance observed in 1993 on site 9) was 153 (Snedecor and Cochran 1967: 58). Although the required sample size might be slightly lower if stratification were taken into account, this rough calculation shows that, especially in years of low acorn abundance, the number of plots needed to get 95 percent confidence limits within 10 percent of the estimate is impractically large.

Almost all production of sound, mature acorns came from red oak group trees in 1994. In the other years, white oak group acorns made up a much higher proportion of the production. Dickson (1990) found that in 4 of the 19 years of his study almost no white oak acorns were produced. In another year, no red oak acorns were produced while production of white oak acorns was high. Dickson (1990) speculated that the asynchrony of acorn production between white oak and red oak group trees might be related to freezing temperatures in the spring, which might limit white oak acorn production in the subsequent fall but not limit red oak acorn production until the next fall (red oak group acorns take 2 years to develop). Sork *et al.* (1993) found that acorn crop size was correlated with spring temperatures during the season of maturation.

Soundness of acorns was also highly variable among species groups and among years in this study. Other studies have reported similar results. During the 4-year study reported by Christisen and Kearby (1984), soundness of acorns averaged 27 percent and ranged from 8 to 46 percent across the four areas studied. They also found that species differences were not consistent from area to area or from year to year. Soundness of white oak group acorns ranged from 13 to 42 percent across areas, while black oak group acorns (black and scarlet oak only) ranged from 11 to 50 percent. In an

earlier study, Christisen (1955) reported that more than 50 percent of the acorns in two study areas in the Ozarks were damaged by insects.

Although not many firm conclusions can be drawn from 3 years of acorn production data, the results are similar to those observed in other studies. Because of the long-term nature of the MOFEP experiment, the potential for detecting patterns (if patterns exist) in sound, mature acorn production through time is great. In addition, the effects of forest management on sound, mature acorn production will be measured quantitatively for the first time.

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Abundance and Production of Berry-producing Plants on the MOFEP Study Sites: The Soft Mast Study Pre-harvest Conditions (1994-1995)

Debby K. Fantz and David A. Hamilton[1]

Abstract.—We surveyed the permanent Missouri Ozark Forest Ecosystem Project (MOFEP) forest vegetation cluster plots in 1994 and 1995 to determine pre-treatment frequency of occurrence, amount of vegetative cover, and number of berries for plants that produce soft mast. Mean percentage occurrence of selected plants for each site ranged from 0.1 to 33.0 for *Vaccinium* sp., and from 0 to 8.6 for *Rubus* sp. Mean percentage vegetative cover (0-1 m) for each site ranged from <0.1 to 1.1 for *Vaccinium* sp., and from 0 to 0.3 for *Rubus* sp. Mean numbers of berries for each site ranged from 0 to 20.3 for *Vaccinium* sp., and from 0 to 1.2 for *Rubus* sp. Generally, few soft mast plants were found, they provided little vegetative cover, and they rarely produced fruit in the pre-treatment plots. Some significant differences were detected, mainly due to year and block effects.

Natural resource agencies involved in forest management are continually being challenged to justify traditional silvicultural practices, especially the use of clearcutting in even-aged forest management systems. Some environmental advocacy groups have been increasingly successful in persuading natural resource management agencies to replace clearcutting with uneven-aged forest management and non-traditional cutting practices. However, the effects of these timber management practices on wildlife species and habitats, including the abundance of plants producing soft mast (soft fruit) and the production of soft mast, have not adequately been examined.

Plants that produce soft mast provide food for a variety of wildlife species. The abundance of both soft and hard mast can dramatically influence the population dynamics of some wildlife species, including gray squirrels (*Sciurus carolinensis*), eastern chipmunks (*Tamias striatus*), and black bears (*Ursus americanus*) (Beeman and Pelton 1977, Cherry and Deardon 1975, Gorman and Roth 1989, Gurnell 1983, Nixon and McClain 1969, Nixon *et al.* 1975, Rogers 1976). The needs of wildlife for consistent and dependable food sources, and for cover requirements, were the primary concerns of wildlife managers that led to the eventual acceptance of even-aged forest management as an important wildlife management tool in forested landscapes. The need to achieve a balance of timber age- and size-classes, to provide sustained forage, and to limit large-scale conversion of hardwood forests to pine plantations helped to shape management programs on public forests in Missouri, which had been largely based on even-aged silvicultural systems (Evans 1974).

Some concern exists among wildlife managers that uneven-aged silvicultural systems will not provide habitat conditions that will meet the needs of wildlife species dependent upon early successional plant fruits or vegetation structure because of limited canopy removal and rapid canopy closure of small openings following timber harvests. Past research has convincingly shown the relationship between increasing amounts of crown closure and decline in wildlife forage.

In one study in the Ozarks of Arkansas, clearcuts in upland hardwood stands initially produced four times as much wildlife forage as selective cuts (Crawford and Harrison 1971). Likewise, soft mast production was higher in even-aged managed forests than in uneven-aged forests in the Adirondack Mountains, and in regenerating stands of red pine (*Pinus resinosa*)

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and 9- to 16-year-old regenerating aspen (*Populus* sp.) in Minnesota than in uneven-aged stands or those unmanaged (Costello 1992, Noyce and Coy 1990). None of these studies had pre-treatment data.

In Missouri, a few studies were conducted that measured various aspects of fruit production in forested habitats (Murphy and Crawford 1970, Murphy and Ehrenreich 1965). In an early study of fruit-producing trees and shrubs in Missouri's Ozark forests, abundance of fruiting plants and the percentage producing fruit were both influenced by crown cover of overstory trees (Murphy and Ehrenreich 1965). None of the fruiting species had a high percentage of plants with fruit, perhaps because of the relative lack of substantial openings in the forest. No studies of soft mast production have been conducted in Missouri for either even-aged or uneven-aged forest management systems.

The Missouri Ozark Forest Ecosystem Project (MOFEP) is a comprehensive research project designed to examine the landscape-scale effects of forest management practices (even- and uneven-aged management) on selected flora, fauna, and abiotic components of the southern Missouri oak-hickory (*Quercus* sp. - *Carya* sp.) forest (Brookshire *et al.* 1997, Sheriff and He 1997). One component of MOFEP is a study to determine if even- and uneven-aged forest management practices have a landscape-scale effect on the abundance of plants producing soft mast and on the production of soft mast of selected species on MOFEP sites. The development of such a long-term study of the impacts of these silvicultural practices in Missouri oak-hickory forests represents a unique opportunity to gather information about the abundance and production of berry-producing plants resulting from these treatments.

This paper reports on the pre-treatment (1994-1995) abundance and production of seven focal soft mast producing species: *Vaccinium arboreum* (farkleberry), *V. stamineum* (deerberry), *V. vacillans* (lowbush blueberry), *Rubus enslenii* (dewberry), *R. flagellaris* (dewberry), *R. occidentalis* (black raspberry), and *R. pensilvanicus* (high-bush blackberry). Common names follow Steyermark (1963).

METHODS

Field Sampling

We surveyed the MOFEP permanent forest vegetation cluster plots for selected plants that produce soft mast (Appendix A). The permanent forest vegetation cluster plot sampling design included 645 permanent 1/2-acre plots in 1993 and 1994, and 648 permanent 1/2-acre plots in 1995. Each 1/2-acre plot contains four 1/20-acre subplots, four 1/100-acre subplots, and sixteen 1-m^2 quadrats (Brookshire *et al.* 1997). These plots occur on 12 ecological landtypes (ELT); most are on southwest-facing slopes (ELT17) (40 percent) and northeast-facing slopes (ELT18) (33 percent).

We conducted a pilot study during the summer of 1993 to evaluate methods of estimating soft mast production and to determine when fruits ripen. Measurements were taken on seventeen 1/2-acre plots and 272 1-m^2 quadrats within six sites in 4- to 6-year-old clearcuts next to MOFEP sites on Deer Run State Forest and Peck Ranch Conservation Area in Shannon and Carter Counties. We measured the frequency of occurrence of soft mast plants in these plots, estimated their percentage vegetative cover, and counted and weighed berries.

Information on plant species producing soft mast within the MOFEP permanent forest vegetation cluster plots was collected between mid-May and mid-October in 1994 and from late May to late September in 1995. We used a two-tiered approach to data collection that used the intensive efforts of the MOFEP botany crews that measure herbaceous and small woody vegetation in each of the 1-m^2 quadrats (≤1 m tall), and the MOFEP tree measurement crews that measure woody vegetation appropriate to plots and subplots (1/2-acre plots: d.b.h. ≥4.5 inches, 1/20-acre subplots: d.b.h. ≥1.5 inches and <4.5 inches, 1/100-acre subplots: d.b.h. <1.5 inches and ≥1 m tall). We sampled berry production in all plots identified by the forest vegetation crews as containing fruit-bearing species during the preceding field season. Therefore, our 1994 sampling occurred on plots identified in the 1993 forest vegetation data as containing soft mast species, and our 1995

sampling was based on the 1994 forest vegetation data. The 1-m² quadrats were sampled first and then the 1/2-acre plots and 1/20-acre subplots. No sampling was done in the 1/100-acre subplots because we believed that most vegetation in these plots was immature and would produce few or no berries (woody vegetation; d.b.h. <1.5 inches and ≥1 m tall). Information for the three plots added in 1995 was not included in our analysis.

1-m² Quadrat Sampling

Within plots known to have soft mast producers, all soft mast plants within the 1-m² quadrats (even those that grow beyond 1 m in height) were recorded. Between mid-May and mid-September 1994, we sampled all 1-m² quadrats within plots identified by the 1993 forest vegetation data as containing soft mast species. Between late May and late August 1995, we sampled all 1-m² quadrats within plots identified by the 1994 forest vegetation data as containing soft mast species.

Sampling was based on the fruiting periods of two core plant genera, *Vaccinium* and *Rubus*. During the 1993 pilot year, we determined that *Vaccinium* sp. fruit before *Rubus* sp. Therefore, plots containing any *Vaccinium* sp. were sampled first and all soft mast plants were recorded. Then plots containing any *Rubus* sp. were sampled and all soft mast plants were recorded. Plots were sampled only once (some plots containing *Vaccinium* sp. also contained *Rubus* sp.; these plots were not resampled). Plots containing other soft mast species that had not been surveyed for *Vaccinium* or *Rubus* were sampled last.

Within the 1-m² quadrats, we estimated percentages for litter; down, dead, and woody material; moss; bare ground; rock; total herbaceous cover; and total vegetative cover. All soft mast species were identified, their percentage vegetative cover from 0-1 m and 1-2 m in height was estimated, and numbers of plants and berries were counted. Numbers of berries were divided according to seven condition classes: flowers, green, red, ripe, dry, damaged and missing (berry stem present). A sample of ripe berries from outside, but adjacent to, the plot was collected and weighed, and an average weight per berry was calculated. Soft mast plants rooted outside the quadrat that provided vegetative cover within the quadrat were also recorded.

1/2-Acre Plot and 1/20-Acre Subplot Sampling

Trees with a d.b.h. greater than 4.5 inches were sampled within pre-selected 1/2-acre plots, and trees with a d.b.h. from 1.5 to 4.5 inches were sampled within pre-selected 1/20-acre subplots. Analysis and discussion of the 1/2-acre plot and 1/20-acre subplot data are beyond the scope of this report and will be presented in a subsequent paper.

Statistical Analysis

Mean percentage occurrence, mean percentage vegetative cover, and mean number of berries between sites and years were calculated for seven species: *Vaccinium arboreum, V. stamineum, V. vacillans, Rubus enslenii, R. flagellaris, R. occidentalis,* and *R. pensilvanicus.* We surveyed 9,104 of 10,320 1-m² forest vegetation quadrats for soft mast plants in 1994 and 9,280 of 10,320 1-m² quadrats in 1995. Quadrats not sampled within a year were assumed to have no soft mast species. Multivariate repeated measures analysis of variance (with year as the repeated factor) (SAS 1989) was used to examine the effect of year, treatment, and block, and their interactions on the pre-treatment conditions of these seven species. We used 0.10 as the alpha level for our analysis.

RESULTS

General

We surveyed 9,104 (88 percent) of the 10,320 1-m² forest vegetation quadrats for soft mast plants in 1994 and 9,280 (90 percent) of the 10,320 1-m² quadrats in 1995. The forest vegetation crews identified 40 of the soft mast target species (+2 plants we identify only to genera) in 1993, 38 target species (+2 plants we identify only to genera) in 1994, and 39 target species (+2 plants we identify only to genera) in 1995 (Appendix A). *Vaccinium arboreum, V. stamineum, V. vacillans, Rubus enslenii, R. flagellaris,* and *R. pensilvanicus* were found on all nine sites, and *R. occidentalis* was found on eight sites during 1993, 1994, and 1995. *Rubus trivialis* was found only in two quads in two plots on Site 1 in 1993; it is therefore, not considered in the analysis. All 12 ELT's were surveyed, but numbers of plots within individual ELT's were not equal. Most quadrats were on southwest-facing slopes (42 percent) and northeast-facing slopes (32 percent).

Mean Percentage Occurrence - *Vaccinium* sp. and *Rubus* sp.

Mean percentage occurrence for *Vaccinium* sp. for each site ranged from 0.5 (*V. arboreum*) to 33.0 (*V. vacillans*) in 1994, and from 0.1 (*V. arboreum*) to 32.2 (*V. vacillans*) in 1995 (table 1). *V. vacillans* had the greatest mean percentage occurrence on all sites for both years, followed by *V. stamineum* then *V. arboreum*, except on site 7 where *V. stamineum* had a larger mean percentage occurrence than *V. vacillans* in 1994 and 1995. The *Rubus* sp. did not exhibit such clear trends. The mean percentage occurrence for *Rubus* sp. for each site ranged from 0.0 (*R. occidentalis*) to 5.8 (*R. flagellaris*) in 1994, and from 0.0 (*R. occidentalis*) to 8.6 (*R. enslenii*) in 1995 (table 2). *Rubus occidentalis* consistently had the lowest mean percentage occurrence per site in both years (except for site 2 in 1994 and site 5 in 1995), and was not found on three sites (block 3, the Peck Ranch sites) in 1994 and two sites in 1995. The other three species were found on all sites in both years. *Rubus flagellaris* was the dominant plant in 1994, but *R. enslenii* was dominant in 1995. However, we

Table 1.—*Mean percentage occurrence of* Vaccinium *sp. for each MOFEP site and all sites combined by year (data from MOFEP forest vegetation study). Yearly means for all sites combined represent means of means, and standard deviations (s.d.) are based on nine sites.*

Site	*V. arboreum*		*V. stamineum*		*V. vacillans*	
	1994	1995	1994	1995	1994	1995
1	1.3	1.5	5.4	6.9	33.0	32.2
2	2.5	1.2	4.1	2.8	13.8	16.1
3	1.0	1.0	5.1	4.4	11.7	13.8
4	1.3	0.9	5.4	5.0	13.2	14.5
5	0.5	0.1	3.6	3.6	8.5	9.7
6	1.1	0.6	4.8	3.1	15.4	18.0
7	2.9	1.6	19.2	17.1	12.2	15.1
8	2.9	1.7	10.0	16.1	22.1	18.6
9	2.0	1.4	14.3	11.0	23.6	28.4
All sites	1.7	1.1	8.0	7.8	17.1	18.5
(s.d.)	(0.90)	(0.52)	(5.42)	(5.59)	(7.71)	(7.23)

Table 2.—*Mean percentage occurrence of* Rubus *sp. for each MOFEP site and all sites combined by year (data from MOFEP forest vegetation study). Yearly means for all sites combined represent means of means, and standard deviations (s.d.) are based on nine sites.*

Site	*R. enslenii*		*R. flagellaris*		*R. occidentalis*		*R. pensilvanicus*	
	1994	1995	1994	1995	1994	1995	1994	1995
1	1.4	2.2	3.3	2.0	0.1	0.2	0.8	0.9
2	0.9	2.7	3.0	1.1	1.5	1.1	0.9	1.5
3	0.8	4.0	4.3	0.4	0.1	0.1	0.4	1.0
4	1.9	3.5	2.1	0.8	0.3	0.1	1.9	2.2
5	2.1	8.6	2.8	0.1	0.2	0.2	5.5	3.0
6	0.2	2.2	1.2	0.2	0.1	0	1.5	0.9
7	1.1	0.6	1.0	0.9	0	0.1	4.7	4.9
8	0.3	1.9	3.0	0.5	0	0.1	1.8	2.1
9	1.7	5.9	5.8	1.2	0	0	3.4	4.3
All sites	1.1	3.5	3.0	0.8	0.2	0.2	2.3	2.3
(s.d.)	(0.68)	(2.42)	(1.49)	(0.59)	(0.46)	(0.35)	(1.79)	(1.50)

suspect that crews had difficulty distinguishing *R. flagellaris* from *R. enslenii* and, therefore, these trends may change if they are combined into one dewberry category. Mean percentage occurrences for *Vaccinium* sp. and *Rubus* sp. by year, block, and treatment type are presented in tables 3 and 4. Block 3 tended to have higher estimates, but no trends were detected for treatment types.

Significant differences were detected for block (*V. stamineum, V. arboreum, R. pensilvanicus*), treatment (*V. arboreum, R. enslenii*), year (*V. arboreum, R. flagellaris, R. enslenii*), and year x treatment (*R. flagellaris, R. enslenii*) (tables 5-9). A significant year and year x treatment effect was detected for *Vaccinium* sp. and *Rubus* sp. combined (table 10). No significant effects were detected for *V. vacillans* or *R. occidentalis*.

Mean percentage occurrence by ELT also was calculated. Mean values for *Vaccinium* sp. ranged from 0 to 26.6 in 1994, and 0 to 27.8 in 1995 (table 11). Mean values for *Rubus* sp. ranged from 0 to 13.5 in 1994, and from 0 to 16.7 in 1995 (table 12). For *Vaccinium* sp., southwest-facing slopes (ELT17) consistently had higher mean percentage occurrences when compared to northeast-facing slopes (ELT 18), but *Rubus* sp. estimates were mostly higher for northeast-facing slopes (ELT 18) when compared to southwest-facing slopes (ELT 17). A brief description of ELT's is presented in Appendix B. No repeated measures analysis of variance was conducted on the ELT data.

Table 3.—*Mean percentage occurrence of* Vaccinium *sp. and* Rubus *sp. by block, year, and combined years (data from MOFEP forest vegetation study). Standard deviations (s.d.) are based on 2 years of three sites.*

	Block 1			Block 2			Block 3		
Species	**1994**	**1995**	**Comb.(s.d.)**	**1994**	**1995**	**Comb. (s.d.)**	**1994**	**1995**	**Comb. (s.d.)**
V. arboreum	1.6	1.2	1.4 (0.57)	0.9	0.5	0.7 (0.43)	2.6	1.6	2.1 (0.65)
V. stamineum	4.9	4.7	4.8 (1.38)	4.6	3.9	4.2 (0.95)	14.5	14.7	14.6 (3.57)
V. vacillans	19.5	20.7	20.1 (9.77)	12.4	14.1	13.2 (3.56)	19.3	20.7	20.0 (5.91)
R. enslenii	1.0	3.0	2.0 (1.24)	1.4	4.7	3.1 (2.89)	1.0	2.8	1.9 (2.05)
R. flagellaris	3.6	1.1	2.4 (1.49)	2.0	0.3	1.2 (1.07)	3.2	0.9	2.1 (2.02)
R. occidentalis	0.5	0.5	0.5 (0.62)	0.2	0.1	0.1 (0.90)	0	0.1	<0.1 (0.05)
R. pensilvanicus	0.7	1.1	0.9 (0.38)	2.9	2.0	2.5 (1.62)	3.3	3.8	3.5 (1.33)

Table 4.—*Mean percentage occurrence of* Vaccinium *sp. and* Rubus *sp. by treatment type, year, and combined years (data from MOFEP forest vegetation study). Standard deviations (s.d.) are based on 2 years of three sites.*

	Treatment type								
	Even-aged			Uneven-aged			Control		
	1994	**1995**	**Comb. (s.d.)**	**1994**	**1995**	**Comb. (s.d.)**	**1994**	**1995**	**Comb. (s.d.)**
V. arboreum	1.1	0.8	1.0 (0.69)	2.2	1.2	1.7 (0.79)	1.7	1.3	1.5 (0.76)
V. stamineum	7.7	6.3	7.0 (4.53)	9.6	8.3	8.9 (7.21)	6.8	8.7	7.7 (4.71)
V. vacillans	14.6	17.3	16.0 (8.14)	13.1	15.3	14.2 (1.39)	23.5	22.9	23.2 (7.58)
R. enslenii	1.5	6.2	3.8 (2.96)	1.3	2.2	1.8 (1.12)	0.6	2.1	1.4 (0.93)
R. flagellaris	4.3	0.6	2.4 (2.30)	2.0	0.9	1.5 (0.89)	2.5	0.9	1.7 (1.28)
R. occidentalis	0.1	0.1	0.1 (0.08)	0.6	0.4	0.5 (0.62)	0.1	0.1	0.1 (0.06)
R. pensilvanicus	3.1	2.8	2.9 (1.95)	2.5	2.9	2.7 (1.69)	1.4	1.3	1.3 (0.57)

Table 5.—*Results of repeated measures analysis of variance examining the effect of year, block, treatment, and their interactions on mean percentage occurrence of* Vaccinium stamineum *on MOFEP sites during 1994-1995.*

Between Site Effects				
Source	**df**	**Mean square**	**F-value**	**P**
Treatment	2	5.7579	0.64	0.58
Block	2	203.6156	22.47	<0.01
Error (Blk X Trt)	4	9.0614		

Within Site Effects					
Source	**Pillai's Trace**	**F-value**	**Numerator df**	**Denominator df**	**P**
Year	0.011	0.0444	1	4	0.84
Yr X Trt	0.3639	1.1444	2	4	0.40
Yr X Blk	0.0368	0.0764	2	4	0.93

Table 6.—*Results of repeated measures analysis of variance examining the effect of year, block, treatment, and their interactions on mean percentage occurrence of* Vaccinium arboreum *on MOFEP sites during 1994-1995.*

Between Site Effects				
Source	**df**	**Mean square**	**F-value**	**P**
Treatment	2	0.8789	24.34	<0.01
Block	2	2.7155	75.20	<0.01
Error (Blk X Trt)	4	0.0361		

Within Site Effects					
Source	**Pillai's Trace**	**F-value**	**Numerator df**	**Denominator df**	**P**
Year	0.7916	15.192	1	4	0.02
Yr X Trt	0.4587	1.6946	2	4	0.29
Yr X Blk	0.5086	2.0704	2	4	0.24

Table 7.—*Results of repeated measures analysis of variance examining the effect of year, block, treatment, and their interactions on mean percentage occurrence of* Rubus pensilvanicus *on MOFEP sites during 1994-1995.*

Between Site Effects				
Source	**df**	**Mean square**	**F-value**	**P**
Treatment	2	4.428	1.81	0.27
Block	2	10.5079	4.31	0.10
Error (Blk X Trt)	4	2.4402		

Within Site Effects					
Source	**Pillai's Trace**	**F-value**	**Numerator df**	**Denominator df**	**P**
Year	0.0011	0.0045	1	4	0.95
Yr X Trt	0.1647	0.3943	2	4	0.70
Yr X Blk	0.5106	2.0866	2	4	0.24

Table 8.—*Results of repeated measures analysis of variance examining the effect of year, block, treatment, and their interactions on mean percentage occurrence of* Rubus flagellaris *on MOFEP sites during 1994-1995.*

Between Site Effects				
Source	**df**	**Mean square**	**F-value**	**P**
Treatment	2	1.5076	1.18	0.40
Block	2	2.1936	1.72	0.29
Error (Blk X Trt)	4	1.2759		

Within Site Effects					
Source	**Pillai's Trace**	**F-value**	**Numerator df**	**Denominator df**	**P**
Year	0.9201	46.0414	1	4	<0.01
Yr X Trt	0.7645	6.4919	2	4	0.06
Yr X Blk	0.2092	0.5289	2	4	0.63

Table 9.—*Results of repeated measures analysis of variance examining the effect of year, block, treatment, and their interactions on mean percentage occurrence of* Rubus enslenii *on MOFEP sites during 1994-1995.*

Between Site Effects				
Source	**df**	**Mean square**	**F-value**	**P**
Treatment	2	10.5093	5.64	0.07
Block	2	2.5232	1.35	0.36
Error (Blk X Trt)	4	1.8621		

Within Site Effects					
Source	**Pillai's Trace**	**F-value**	**Numerator df**	**Denominator df**	**P**
Year	0.9066	38.8408	1	4	<0.01
Yr X Trt	0.8239	9.3546	2	4	0.03
Yr X Blk	0.4663	1.7477	2	4	0.28

Table 10.—*Results of repeated measures analysis of variance examining the effect of year, block, treatment, and their interactions on mean percentage occurrence of* Vaccinium *sp. and* Rubus *sp. combined on MOFEP sites during 1994-1995.*

Between Site Effects				
Source	**df**	**Mean square**	**F-value**	**P**
Treatment	2	48.7126	0.31	0.75
Block	2	565.1224	3.65	0.13
Error (Blk X Trt)	4	154.9775		

Within Site Effects					
Source	**Pillai's Trace**	**F-value**	**Numerator df**	**Denominator df**	**P**
Year	0.8306	19.6145	1	4	0.01
Yr X Trt	0.7782	7.0163	2	4	0.05
Yr X Blk	0.4469	1.6159	2	4	0.31

Table 11.— *Mean percentage occurrence of* Vaccinium *sp. for each MOFEP ELT by year (data from MOFEP forest vegetation study).*

ELT	*V. arboreum* 1994	*V. arboreum* 1995	*V. stamineum* 1994	*V. stamineum* 1995	*V. vacillans* 1994	*V. vacillans* 1995
05	0.4	0.6	4.8	5.4	4.4	7.1
06	0	0	0	0	0	0
07	2.1	0	3.1	5.2	9.4	10.4
11	0.8	0.8	7.8	7.9	7.9	8.3
15	0	0	8.8	11.3	6.3	6.3
17	2.9	1.9	10.0	8.9	25.1	27.8
18	0.9	0.2	6.4	6.9	15.3	16.2
19	1.0	1.6	3.9	2.6	4.9	5.6
20	0	0	2.3	3.1	7.8	7.0
21	4.7	6.3	9.4	15.6	26.6	18.8
22	2.1	0	2.1	6.3	12.5	12.5
23	2.1	1.4	14.6	13.2	4.9	6.9

Table 12.— *Mean percentage occurrence of* Rubus *sp. for each MOFEP ELT by year (data from MOFEP forest vegetation study).*

ELT	*R. enslenii* 1994	*R. enslenii* 1995	*R. flagellaris* 1994	*R. flagellaris* 1995	*R. occidentalis* 1994	*R. occidentalis* 1995	*R. pensilvanicus* 1994	*R. pensilvanicus* 1995
05	2.0	8.7	5.6	1.8	0	0	7.5	7.7
06	0	0	3.1	3.1	0	0	0	0
07	9.4	12.5	13.5	5.2	0	0	11.5	13.5
11	1.6	3.2	3.0	1.9	0.8	0.6	1.8	1.8
15	0	1.3	2.5	1.3	0	0	0	0
17	0.8	2.3	2.2	0.5	0.2	0.1	1.5	1.7
18	1.1	3.9	2.9	0.7	0.1	0.1	2.3	2.1
19	2.0	6.3	2.6	0	1.0	0.7	3.0	1.3
20	0.8	10.2	8.6	1.6	0	0.8	0	0
21	0	0	0	0	0	0	3.1	1.6
22	0	0	8.3	0	0	0	10.4	16.7
23	0	2.8	1.4	0	0	0	3.5	2.8

Mean Percentage Vegetative Cover - *Vaccinium* sp. and *Rubus* sp.

Mean percentage cover (0-1 m) for *Vaccinium* sp. for each site ranged from <0.1 (*V. arboreum*) to 0.9 (*V. stamineum, V. vacillans*) in 1994 and from <0.1 (*V. arboreum*) to 1.1 (*V. vacillans*) in 1995 (table 13). *V. vacillans* had the greatest mean percentage cover (0-1 m) on all sites for both years, except for site 7 in 1994, and sites 7 and 8 in 1995 (*V. stamineum* had the greater mean percentage cover). *V. arboreum* had the lowest 0-1 m mean percentage cover values for all sites in both years. Mean percentage cover from 1 to 2 m indicated that *V. arboreum* tends to grow taller than *V. stamineum* or *V. vacillans*.

The *Rubus* species did not exhibit clear trends for 0- to 1-m mean percentage covers. Ranges were from 0 (*R. occidentalis*) to 0.3 (*R. pensilvanicus*) in 1994 and 1995 (tables 14-15). *R. occidentalis* tended to have the lowest 0- to 1-m mean percentage cover and *R. pensilvanicus* the highest for both years. *R. enslenii* and *R. flagellaris* did not grow above 1 m in 1994 or 1995, but *R. occidentalis* and *R. pensilvanicus* did on some sites. Estimates of mean percentage cover for *Vaccinium* sp. and *Rubus* sp. by year, block, and treatment type are presented in tables 16-17. Block 3 tended to have higher mean percentage cover estimates, but no trends were detected for treatment types.

Table 13.—*Mean percentage cover (0-1 m and 1-2 m) of* Vaccinium *sp. for each MOFEP site and all sites combined by year (data from MOFEP forest vegetation study). Yearly means for all sites combined represent means of means.*

	V. arboreum				*V. stamineum*				*V. vacillans*			
	0-1 m		1-2 m		0-1 m		1-2 m		0-1 m		1-2 m	
Site	94	95	94	95	94	95	94	95	94	95	94	95
1	0.1	0.1	<0.1	<0.1	0.2	0.3	0	0	0.9	1.1	0	0
2	0.1	<0.1	0.1	0.1	0.2	0.1	<0.1	<0.1	0.5	0.6	0	0
3	<0.1	<0.1	0	0	0.3	0.3	<0.1	<0.1	0.3	0.4	0	0
4	<0.1	<0.1	<0.1	<0.1	0.2	0.2	0	<0.1	0.4	0.4	0	0
5	<0.1	<0.1	<0.1	<0.1	0.2	0.2	<0.1	0	0.4	0.3	0	0
6	<0.1	<0.1	<0.1	<0.1	0.2	0.1	0	0	0.5	0.5	0	<0.1
7	0.1	<0.1	<0.1	<0.1	0.9	0.8	<0.1	<0.1	0.3	0.4	0	<0.1
8	0.1	<0.1	<0.1	<0.1	0.4	0.8	0	<0.1	0.6	0.5	0	<0.1
9	0.1	<0.1	0.1	0.1	0.7	0.6	<0.1	<0.1	0.9	1.0	0	<0.1
All sites	0.1	<0.1	<0.1	<0.1	0.4	0.4	<0.1	<0.1	0.5	0.6	0	<0.1

Table 14.—*Mean percentage cover (0-1 m and 1-2 m) of* Rubus *sp. for each MOFEP site and all sites combined for 1994 (data from MOFEP forest vegetation study). Yearly means for all sites combined represent means of means.*

	R. enslenii		*R. flagellaris*		*R. occidentalis*		*R. pensilvanicus*	
Site	0-1 m	1-2 m	0-1 m	1-2 m	0-1 m	1-2 m	0-1 m	1-2 m
1	<0.1	0	0.1	0	<0.1	0	<0.1	0
2	<0.1	0	0.1	0	0.1	<0.1	0.1	0
3	<0.1	0	0.1	0	<0.1	0	<0.1	0
4	<0.1	0	<0.1	0	<0.1	0	0.1	<0.1
5	<0.1	0	0.1	0	<0.1	0	0.3	<0.1
6	<0.1	0	<0.1	0	<0.1	0	0.1	0
7	<0.1	0	<0.1	0	0	0	0.2	<0.1
8	<0.1	0	0.1	0	0	0	0.1	<0.1
9	<0.1	0	0.2	<0.1	0	0	0.1	<0.1
All sites	<0.1	0	0.1	<0.1	<0.1	<0.1	0.1	<0.1

Table 15.—*Mean percentage cover (0-1 m and 1-2 m) of* Rubus *sp. for each MOFEP site and all sites combined for 1995 (data from MOFEP forest vegetation study). Yearly means for all sites combined represent means of means.*

	R. enslenii		*R. flagellaris*		*R. occidentalis*		*R. pensilvanicus*	
Site	0-1 m	1-2 m	0-1 m	1-2 m	0-1 m	1-2 m	0-1 m	1-2 m
1	<0.1	0	<0.1	0	<0.1	0	0.1	<0.1
2	0.1	0	<0.1	0	0.1	<0.1	0.1	<0.1
3	0.1	0	<0.1	0	<0.1	0	0.1	<0.1
4	<0.1	0	<0.1	0	<0.1	0	0.1	<0.1
5	0.2	0	<0.1	0	<0.1	<0.1	0.2	0
6	<0.1	0	<0.1	0	0	0	<0.1	0
7	<0.1	0	<0.1	0	<0.1	0	0.3	<0.1
8	<0.1	0	<0.1	0	<0.1	0	0.1	<0.1
9	0.1	0	<0.1	0	0	0	0.1	<0.1
All sites	0.1	0	<0.1	0	<0.1	<0.1	0.1	<0.1

Table 16.—*Mean percentage cover (0-1 m and 1-2 m) of* Vaccinium *sp. and* Rubus *sp. by block and year (data from MOFEP forest vegetation study).*

	Block 1				Block 2				Block 3			
	0-1 m		1-2 m		0-1 m		1-2 m		0-1 m		1-2 m	
	94	95	94	95	94	95	94	95	94	95	94	95
V. arboreum	0.1	0.1	<0.1	0.1	<0.1	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1
V. stamineum	0.2	0.2	<0.1	<0.1	0.2	0.1	<0.1	<0.1	0.7	0.7	<0.1	<0.1
V. vacillans	0.6	0.7	0	0	0.4	0.4	0	<0.1	0.6	0.6	0	<0.1
R. enslenii	<0.1	0.1	0	0	<0.1	0.1	0	0	<0.1	<0.1	0	0
R. flagellaris	0.1	<0.1	0	0	<0.1	<0.1	0	0	0.1	<0.1	<0.1	0
R. occidentalis	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	0	<0.1	0	<0.1	0	0
R. pensilvanicus	<0.1	0.1	0	<0.1	0.1	0.1	<0.1	<0.1	0.1	0.2	<0.1	<0.1

Table 17.—*Mean percentage cover (0-1 m and 1-2 m) of* Vaccinium *sp. and* Rubus *sp. by treatment type and year (data from MOFEP forest vegetation study).*

	Treatment type											
	Even-aged				Uneven-aged				Control			
	0-1 m		1-2 m		0-1 m		1-2 m		0-1 m		1-2 m	
Species	94	95	94	95	94	95	94	95	94	95	94	95
V. arboreum	<0.1	<0.1	<0.1	<0.1	0.1	<0.1	0.1	0.1	0.1	<0.1	<0.1	<0.1
V. stamineum	0.4	0.3	<0.1	<0.1	0.4	0.4	<0.1	<0.1	0.3	0.4	0	<0.1
V. vacillans	0.5	0.6	0	<0.1	0.4	0.5	0	<0.1	0.7	0.7	0	<0.1
R. enslenii	<0.1	0.1	0	0	<0.1	<0.1	0	0	<0.1	<0.1	0	0
R. flagellaris	0.1	<0.1	<0.1	0	0.1	<0.1	0	0	0.1	<0.1	0	0
R. occidentalis	<0.1	<0.1	0	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	0	0
R. pensilvanicus	0.1	0.1	<0.1	<0.1	0.1	0.2	<0.1	<0.1	<0.1	0.1	<0.1	<0.1

Significant differences were detected for block (*V. stamineum, V. arboreum*), treatment (*R. enslenii*), year (*V. arboreum, R. flagellaris, R. enslenii*), and year x treatment (*R. enslenii*) for 0- to 1-m coverage (tables 18-21). A significant block effect was detected for *Vaccinium* sp. and *Rubus* sp. combined (table 22). No significant effects were detected for *V. vacillans, R. occidentalis* or *R. pensilvanicus*. No repeated measures analysis of variance was conducted on the 1-2 m coverage data.

Mean Number of Berries - *Vaccinium* sp. and *Rubus* sp.

Mean numbers of berries per square meter for *Vaccinium* sp. for each site ranged from 0 (all three species) to 6.3 (*V. stamineum*) in 1994, and from 0 (*V. arboreum, V. stamineum*) to 20.3 (*V. arboreum*) in 1995 (table 23). *V. stamineum* tended to have the highest mean number of berries in both years. In 1995, only three *V. arboreum* plants with berries were found on site 7. One plant had two berries, one had one berry, and the third had 1,440 berries. Because of the unusually high number of berries on one plant, *V. arboreum* was not included for statistical analysis. Mean numbers of berries per square meter for *Rubus* sp. for each site ranged from 0 (all four species) to 0.4 (*R. pensilvanicus*) in 1994, and from 0 (all four species) to 1.2 (*R. pensilvanicus*) in 1995 (table 24). No berries were found on *R. occidentalis* plants in 1994 or 1995. Mean numbers of berries for *Vaccinium* sp. and *Rubus* sp. by year, block, and treatment type are presented in tables 25 and 26. Block 3 had a higher mean number of berries, but no trends were detected for treatment types.

Significant differences were detected for block (*V. stamineum, Vaccinium sp.*), year (*V. vacillans, Vaccinium sp., R. pensilvanicus, R. flagellaris, Rubus* sp.), and year x treatment (*V. vacillans, R. flagellaris*) tables 27-32). No repeated measures analysis of variance was conducted for *V. arboreum, R. enslenii,* or *R. occidentalis*.

Table 18.—*Results of repeated measures analysis of variance examining the effect of year, block, treatment, and their interactions on mean percentage cover (0-1 m) for* Vaccinium stamineum *on MOFEP sites during 1994-1995.*

Between Site Effects				
Source	**df**	**Mean square**	**F-value**	**P**
Treatment	2	0.007	0.51	0.64
Block	2	0.5184	37.53	<0.01
Error (Blk X Trt)	4	0.0138		

Within Site Effects					
Source	**Pillai's Trace**	**F-value**	**Numerator df**	**Denominator df**	**P**
Year	0.00003	0.0001	1	4	0.99
Yr X Trt	0.3528	1.0904	2	4	0.42
Yr X Blk	0.1267	0.2901	2	4	0.76

Table 19.—*Results of repeated measures analysis of variance examining the effect of year, block, treatment, and their interactions on mean percentage cover (0-1 m) for* Vaccinium arboreum *on MOFEP sites during 1994-1995.*

Between Site Effects				
Source	**df**	**Mean square**	**F-value**	**P**
Treatment	2	0.0005	1.47	0.33
Block	2	0.0057	17.81	0.01
Error (Blk X Trt)	4	0.0003		

Within Site Effects					
Source	**Pillai's Trace**	**F-value**	**Numerator df**	**Denominator df**	**P**
Year	0.6841	8.6606	1	4	0.04
Yr X Trt	0.2019	0.5061	2	4	0.64
Yr X Blk	0.5512	2.456	2	4	0.20

Table 20.—*Results of repeated measures analysis of variance examining the effect of year, block, treatment, and their interactions on mean percentage cover (0-1 m) for* Rubus enslenii *on MOFEP sites during 1994-1995.*

Between Site Effects				
Source	**df**	**Mean square**	**F-value**	**P**
Treatment	2	0.0057	5.87	0.06
Block	2	0.0003	0.27	0.77
Error (Blk X Trt)	4	0.001		

Within Site Effects					
Source	**Pillai's Trace**	**F-value**	**Numerator df**	**Denominator df**	**P**
Year	0.894	33.7179	1	4	<0.01
Yr X Trt	0.8481	11.1696	2	4	0.02
Yr X Blk	0.1637	0.3914	2	4	0.70

Table 21.—*Results of repeated measures analysis of variance examining the effect of year, block, treatment, and their interactions on mean percentage cover (0-1 m) for* Rubus flagellaris *on MOFEP sites during 1994-1995.*

Between Site Effects				
Source	**df**	**Mean square**	**F-value**	**P**
Treatment	2	0.0014	1.36	0.36
Block	2	0.0022	2.03	0.25
Error (Blk X Trt)	4	0.0011		

Within Site Effects					
Source	**Pillai's Trace**	**F-value**	**Numerator df**	**Denominator df**	**P**
Year	0.7917	15.2007	1	4	0.02
Yr X Trt	0.5435	2.3815	2	4	0.21
Yr X Blk	0.181	0.4421	2	4	0.67

Table 22.—*Results of repeated measures analysis of variance examining the effect of year, block, treatment, and their interactions on mean percentage cover (0-1 m) for all* Vaccinium *sp. and* Rubus *sp. combined on MOFEP sites during 1994-1995.*

Between Site Effects				
Source	**df**	**Mean square**	**F-value**	**P**
Treatment	2	0.0114	0.06	0.94
Block	2	1.0546	5.82	0.07
Error (Blk X Trt)	4	0.1813		

Within Site Effects					
Source	**Pillai's Trace**	**F-value**	**Numerator df**	**Denominator df**	**P**
Year	0.0286	0.1176	1	4	0.75
Yr X Trt	0.2521	0.674	2	4	0.56
Yr X Blk	0.3938	1.2993	2	4	0.37

Table 23.—*Mean number of berries per square meter for* Vaccinium *sp. for each MOFEP site by year (data from the MOFEP soft mast study).*

	V. arboreum		*V. stamineum*		*V. vacillans*	
Site	**1994**	**1995**	**1994**	**1995**	**1994**	**1995**
1	0	0	0	2.8	0.1	1.5
2	0	0	0	0. 9	0	0.3
3	0	0	0.8	3.4	0.1	0.3
4	0	0	0	0	0.1	<0.1
5	0	0	0	1.4	0	2.2
6	0	0	0.1	0.4	0	3.0
7	0	20.3	4.4	13.9	0.6	1.8
8	0	0	1.4	8.3	0.7	3.4
9	0	0	6.3	4.3	0.2	0.8

Table 24.—*Mean number of berries per square meter for* Rubus *sp. for each MOFEP site by year (data from the MOFEP soft mast study).*

Site	*R. enslenii* 1994	*R. enslenii* 1995	*R. flagellaris* 1994	*R. flagellaris* 1995	*R. occidentalis* 1994	*R. occidentalis* 1995	*R. pensilvanicus* 1994	*R. pensilvanicus* 1995
1	0	0.4	<0.1	0	0	0	0	0.4
2	0	0	0	0	0	0	0	0.3
3	0	0	0	<0.1	0	0	0	0.4
4	0	0	0	0	0	0	0	0.6
5	0	<0.1	<0.1	0.6	0	0	0.4	1.2
6	0	0	0	<0.1	0	*	0	0
7	0	0.3	0	0.2	*	0	0.1	1.2
8	0	<0.1	0	0.1	*	0	0	0
9	0.1	<0.1	0	0.9	*	*	0	0.3

* species was not present within 1 -m^2 quadrats on that site for that year.

Table 25.—*Mean number of berries per square meter for* Vaccinium *sp. and* Rubus *sp. by block and year (data from the MOFEP soft mast study).*

	Block 1 1994	Block 1 1995	Block 2 1994	Block 2 1995	Block 3 1994	Block 3 1995
V. arboreum	0	0	0	0	0	6.8
V. stamineum	0.3	2.4	<0.1	0.6	4.0	8.8
V. vacillans	0.1	0.7	<0.1	1.8	0.5	2.0
R. enslenii	0	0.1	0	<0.1	<0.1	0.1
R. flagellaris	<0.1	<0.1	<0.1	0.2	0	0.4
R. occidentalis	0	0	0	0	0	0
R. pensilvanicus	0	0.3	0.1	0.6	<0.1	0.5

Table 26.—*Mean number of berries per square meter for* Vaccinium *sp. and* Rubus *sp. by treatment type and year (data from the MOFEP soft mast study).*

	Treatment type					
	Even-aged 1994	Even-aged 1995	Uneven-aged 1994	Uneven-aged 1995	Control 1994	Control 1995
V. arboreum	0	0	0	6.8	0	0
V. stamineum	2.4	3.0	1.5	4.9	0.5	3.9
V. vacillans	0.1	1.1	0.2	0.7	0.3	2.6
R. enslenii	<0.1	<0.1	0	0.1	0	0.1
R. flagellaris	<0.1	0.5	0	<0.1	<0.1	<0.1
R. occidentalis	0	0	0	0	0	0
R. pensilvanicus	0.1	0.6	<0.1	0.7	0	0.1

Table 27.—*Results of repeated measures analysis of variance examining the effect of year, block, treatment, and their interactions on mean number of berries for* Vaccinium stamineum *on MOFEP sites during 1994-1995.*

Between Site Effects				
Source	**df**	**Mean square**	**F-value**	**P**
Treatment	2	1.5863	0.29	0.77
Block	2	64.5901	11.66	0.02
Error (Blk X Trt)	4	5.54		

Within Site Effects					
Source	**Pillai's Trace**	**F-value**	**Numerator df**	**Denominator df**	**P**
Year	0.4838	3.749	1	4	0.12
Yr X Trt	0.2005	0.5016	2	4	0.64
Yr X Blk	0.313	0.9113	2	4	0.47

Table 28.—*Results of repeated measures analysis of variance examining the effect of year, block, treatment, and their interactions on mean number of berries for* Vaccinium vacillans *on MOFEP sites during 1994-1995.*

Between Site Effects				
Source	**df**	**Mean square**	**F-value**	**P**
Treatment	2	1.7615	3.98	0.11
Block	2	1.1264	2.54	0.19
Error (Blk X Trt)	4	0.4428		

Within Site Effects					
Source	**Pillai's Trace**	**F-value**	**Numerator df**	**Denominator df**	**P**
Year	0.8536	23.3228	1	4	<0.01
Yr X Trt	0.6945	4.5457	2	4	0.09
Yr X Blk	0.4191	1.443	2	4	0.34

Table 29.—*Results of repeated measures analysis of variance examining the effect of year, block, treatment, and their interactions on mean number of berries for* Vaccinium staminium *and* V. vacillans *combined on MOFEP sites during 1994-1995.*

Between Site Effects				
Source	**df**	**Mean square**	**F-value**	**P**
Treatment	2	0.2451	0.03	0.97
Block	2	77.8554	10.54	0.03
Error (Blk X Trt)	4	7.3882		

Within Site Effects					
Source	**Pillai's Trace**	**F-value**	**Numerator df**	**Denominator df**	**P**
Year	0.6256	6.6824	1	4	0.06
Yr X Trt	0.2445	0.6473	2	4	0.57
Yr X Blk	0.2673	0.7296	2	4	0.54

Table 30.—*Results of repeated measures analysis of variance examining the effect of year, block, treatment, and their interactions on mean number of berries for* Rubus pensilvanicus *on MOFEP sites during 1994-1995.*

Between Site Effects				
Source	**df**	**Mean square**	**F-value**	**P**
Treatment	2	0.1757	1.00	0.45
Block	2	0.0581	0.33	0.74
Error (Blk X Trt)	4	0.1761		

Within Site Effects					
Source	**Pillai's Trace**	**F-value**	**Numerator df**	**Denominator df**	**P**
Year	0.7352	11.1074	1	4	0.03
Yr X Trt	0.4355	1.543	2	4	0.32
Yr X Blk	0.0459	0.0961	2	4	0.91

Table 31.—*Results of repeated measures analysis of variance examining the effect of year, block, treatment, and their interactions on mean number of berries for* Rubus flagellaris *on MOFEP sites during 1994-1995.*

Between Site Effects				
Source	**df**	**Mean square**	**F-value**	**P**
Treatment	2	0.0976	3.85	0.12
Block	2	0.048	1.89	0.26
Error (Blk X Trt)	4	0.0253		

Within Site Effects					
Source	**Pillai's Trace**	**F-value**	**Numerator df**	**Denominator df**	**P**
Year	0.6470	7.3329	1	4	0.05
Yr X Trt	0.6935	4.5261	2	4	0.09
Yr X Blk	0.5680	2.6292	2	4	0.19

Table 32.—*Results of repeated measures analysis of variance examining the effect of year, block, treatment, and their interactions on mean number of berries for* Rubus pensilvanicus, R. enslenii, *and* R. flagellaris *combined on MOFEP sites during 1994-1995.*

Between Site Effects				
Source	**df**	**Mean square**	**F-value**	**P**
Treatment	2	0.3601	1.15	0.40
Block	2	0.1295	0.41	0.69
Error (Blk X Trt)	4	0.3143		

Within Site Effects					
Source	**Pillai's Trace**	**F-value**	**Numerator df**	**Denominator df**	**P**
Year	0.7579	12.5247	1	4	0.02
Yr X Trt	0.3427	1.0426	2	4	0.43
Yr X Blk	0.1952	0.4849	2	4	0.65

V. stamineum and *R. pensilvanicus* tended to have the higher percentage of plants with berries in both years (tables 33 and 34). Block 3 tended to have more plants with berries, but no trends were detected for treatment types (tables 35 and 36).

DISCUSSION

Generally, few soft mast plants were found, they provided little vegetative cover, and they rarely produced fruit in the MOFEP pre-treatment plots. Numerous previous studies identified a direct relationship between the amount of sunlight reaching the forest floor, and the abundance of fruiting plants and their production of fruit. Since the amount of upper canopy cover is the primary determinant of light intensity and duration, it is not unexpected that there were few soft mast plants and limited production of fruit in the pre-treatment forest sites at MOFEP.

In Minnesota, pin cherry (*Prunus pensylvanica*), raspberry (*Rubus strigosus*), blackberry (*Rubus allegheniensus*), and dogwood (*Cornus* sp.) were more abundant and had higher fruit biomass along edges of forested stands where crown

Table 33.—*Percent of 1-m² quadrats with berries (number of quadrats with berries/number of quadrats where that species was found) for* Vaccinium *sp. for each MOFEP site and all sites combined by year.*

	V. arboreum		*V. stamineum*		*V. vacillans*	
Site	1994	1995	1994	1995	1994	1995
1	0	0	0	9.6	0.5	3.6
2	0	0	0	9.7	0	3.0
3	0	0	12.1	17.1	1.3	3.5
4	0	0	0	0	0.7	0.7
5	0	0	0	2.9	0	8.4
6	0	0	4.2	7.7	0	2.9
7	0	23.1	9.2	17.0	4.0	9.3
8	0	0	14.9	18.9	5.0	12.1
9	0	0	3.2	12.5	1.9	3.3
all	0	4.4	6.8	13.3	1.4	4.7

Table 34.—*Percent of 1-m² quadrats with berries (number of quadrats with berries/number of quadrats where that species was found) for* Rubus *sp. for each MOFEP site and all sites combined by year.*

	R. enslenii		*R. flagellaris*		*R. occidentalis*		*R. pensilvanicus*	
Site	1994	1995	1994	1995	1994	1995	1994	1995
1	0	5.8	2.1	0	0	0	0	20.0
2	0	0	0	0	0	0	0	14.3
3	0	0	0	5.6	0	0	0	20.0
4	0	0	0	0	0	0	0	18.8
5	0	5.3	3.2	3.4	0	0	17.4	32.0
6	0	0	0	3.7	0	0	0	0
7	0	15.6	0	15.0	0	0	6.3	15.0
8	0	4.2	0	11.1	0	0	0	0
9	6.3	8.6	0	16.7	0	0	0	11.1
all	1.8	5.2	0.8	8.6	0	0	6.3	17.9

Table 35.—*Percent of 1-m² quadrats with berries (number of quadrats with berries/number of quadrats where that species was found) for* Vaccinium *sp. and* Rubus *sp. by block, year, and combined years.*

	Block 1			Block 2			Block 3		
	1994	1995	Comb.	1994	1995	Comb.	1994	1995	Comb.
V. arboreum	0	3.0	1.5	0	0	0	0	8.3	4.5
V. stamineum	3.5	11.0	7.6	1.0	2.4	1.8	8.8	13.2	11.5
V. vacillans	<1.0	2.6	1.6	<1.0	3.0	1.7	3.1	5.0	4.2
R. enslenii	0	2.5	1.9	0	2.4	<1.0	3.2	9.9	5.7
R. flagellaris	<1.0	5.6	1.5	1.5	2.7	2.2	0	15.8	9.1
R. occidentalis	0	0	0	0	0	0	0	0	0
R. pensilvanicus	0	13.0	6.9	6.3	18.6	12.7	1.6	7.6	4.6

Table 36.—*Percent of 1-m² quadrats with berries (number of quadrats with berries/number of quadrats where that species was found) for* Vaccinium *sp. and* Rubus *sp. by treatment type, year, and combined years.*

	Treatment type								
	Even-aged			Uneven-aged			Control		
	1994	1995	Comb.	1994	1995	Comb.	1994	1995	Comb.
V. arboreum	0	0	0	0	11.5	5.8	0	0	0
V. stamineum	4.4	10.7	8.1	6.0	11.5	9.2	8.3	11.1	9.9
V. vacillans	1.3	3.1	2.3	1.5	3.3	2.5	1.2	4.2	2.8
R. enslenii	3.6	5.1	4.2	0	5.5	3.2	0	4.9	2.6
R. flagellaris	<1.0	10.1	5.9	0	6.4	2.8	1.3	5.6	2.7
R. occidentalis	0	0	0	0	0	0	0	0	0
R. pensilvanicus	5.2	17.1	11.1	1.9	12.3	7.9	0	6.1	2.8

closure of overstory trees was lower (Noyce and Coy 1990). In an earlier study, Arimond (1979) found that production of fruits important to black bears in Minnesota (blueberry, raspberry, and pin cherry) was significantly higher in forested stands with low densities of overstory trees (<800 trees/ha). These stands included clearcuts, strip-cuts, and selection cuts.

In New York's Adirondack Mountains, raspberry and pin cherry abundance was highest in even-aged managed habitats cut less than 16 years before sampling (Costello 1992). Non-managed habitats had the lowest abundance of these species, recognized as important black bear foods in New York. Berry counts for raspberry ranged from 54,000 berries/ha to 733,000 berries/ha and averaged 382,000 berries/ha in even-aged stands.

In sharp contrast, in Missouri on MOFEP plots during 1994 and 1995, there was no black raspberry production, and the highest mean blackberry production figure was only 6,000 berries/ha on block 2 in 1995. The highest berry yields among our selected species were for *V. stamineum*, which produced an average of 232 berries/ha on block 2 in 1994 at the low end and 88,000 berries/ha on block 3 in 1995, the highest yield overall. In our 1993 pilot study on clearcuts adjacent to MOFEP sites, we found an average of 656,000 blackberries/ha in 4- to 6-year-old clearcuts, and 111,000 blackberries/ha in 7- to 10-year-old clearcuts.

Some significant differences exist between blocks, years, and treatments, based on measurements of abundance of soft mast plants and production of berries on the MOFEP sites. Block differences are attributed to block 3 (the Peck Ranch sites). This block is physiographically different from blocks 1 and 2. Significant differences between blocks supports the use of the randomized block design for the MOFEP

experiment by attributing some differences in results to local geographic variation. As expected, there were a few differences due to year effect, primarily related to increased berry production across the board in 1995 and perhaps associated with the slight difference between sampling periods between years. Few treatment type effects were observed during this pre-treatment measurement effort, and though a few effects were statistically significant, it appears that they may be small and easily overcome if there are substantial responses due to actual treatment.

There may be small, negative bias of the sampling plan. Quadrats that we sampled were those that contained soft mast plants the previous year. Out of a total of 10,320 quadrats, 1,216 (12 percent) were not sampled in 1994 and 1,040 (10 percent) were not sampled in 1995. We assumed that no soft mast plants existed within these quadrats, but some new plants may have emerged. This may have resulted in lower calculated means, but we believe this to be of minor consequence. These plants would be very small and would not produce fruit until several years old.

The MOFEP experiment provides an excellent opportunity to examine the effects of forest management practices on soft mast. This pre-treatment research shows a framework for a successful project examining the effects of silvicultural treatments on the abundance of soft mast plants and production of soft mast. Following cutting, data for control sites will be compared with even- and uneven-aged sites to determine if differences exist between treatment types.

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Appendix A.—*Presence of soft mast species within the permanent MOFEP forest vegetation cluster plot 1-m² quadrats by site during 1993-1995 (data from MOFEP forest vegetation study). An X indicates presence of that species within the 3-year period.*

Species	Site 1	2	3	4	5	6	7	8	9
Amelanchier arborea	X	X	X	X	X	X	X	X	X
Asimina triloba	—	X	X	X	X	X	X	X	X
Ceanothus americanus	X	X	X	X	X	X	X	X	X
Celtis sp.	X	X	X	X	X	X	X	X	X
Celtis occidentalis	X	X	X	X	X	X	X	X	X
Cornus drummondi	X	X	—	X	—	—	—	—	—
Cornus florida	X	X	X	X	X	X	X	X	X
Corylus americana	X	X	X	X	X	X	X	X	X
Crataegus sp.	X	X	X	X	X	X	X	X	X
Diospyros virginiana	X	X	X	X	X	X	X	X	X
Fragaria virginiana	X	X	—	—	—	—	—	X	—
Lindera benzoin	—	X	X	X	X	X	X	X	X
Morus sp.	—	X	X	X	X	—	X	X	X
Morus rubra	—	X	X	X	X	X	X	X	X
Nyssa sylvatica	X	X	X	X	X	X	X	X	X
Phytolacca americana	—	—	—	—	—	—	X	—	—
Prunus americana	X	X	X	X	X	X	X	X	X
Prunus serotina	X	X	X	X	X	X	X	X	X
Rhamnus caroliniana	X	X	X	X	X	X	X	X	X
Rhus aromatica	X	X	X	X	X	X	X	X	X
Rhus copallina	—	X	—	X	X	—	X	X	X
Rhus glabra	—	X	—	—	X	X	X	X	—
Ribes missouriense	—	X	X	—	—	X	—	—	—
Rosa sp.	X	X	X	X	X	X	—	X	X
Rosa carolina	X	X	X	X	X	X	X	X	X
Rosa multiflora	X	X	X	X	X	—	X	X	X
Rosa setigera	X	X	X	X	X	X	X	X	X
Rubus sp.	X	X	X	X	X	X	X	X	X
Rubus enslenii	X	X	X	X	X	X	X	X	X
Rubus flagellaris	X	X	X	X	X	X	X	X	X
Rubus occidentalis	X	X	X	X	X	X	X	X	—
Rubus pensilvanicus	X	X	X	X	X	X	X	X	X
Rubus trivialis	X	—	—	—	—	—	—	—	—
Sambucus canadensis	—	X	—	—	—	X	—	X	—
Sassafras albidum	X	X	X	X	X	X	X	X	X
Smilacina racemosa	X	X	X	X	X	X	X	X	X
Smilax sp.	X	X	X	X	X	X	X	X	X
Smilax bona-nox	X	X	X	X	X	X	X	X	X
Smilax glauca	X	X	X	X	—	X	X	X	X
Smilax herbacea	X	X	X	X	X	X	X	X	X
Smilax pulverulenta	X	X	X	X	X	X	X	X	X
Smilax rotundifolia	X	X	X	X	X	X	X	X	X
Smilax tamnoides	X	X	X	X	X	X	X	X	X
Symphoricarpos orbiculatus	X	X	X	X	X	X	X	X	X
Vaccinium sp.	X	X	X	X	X	X	X	X	X
Vaccinium arboreum	X	X	X	X	X	X	X	X	X
Vaccinium stamineum	X	X	X	X	X	X	X	X	X
Vaccinium vacillans	X	X	X	X	X	X	X	X	X
Viburnum rufidulum	X	X	X	X	X	X	X	X	X
Vitis sp.	X	X	X	X	X	X	X	X	X

Appendix B.—*Description of ecological landtypes (ELT's) associated with the MOFEP permanent forest vegetation cluster plots (Brookshire and Hauser 1993, Randy Jensen personal communication).*

ELT	Land form	Aspect	Percent slope	Soil series	Vegetation community
5	Upland waterway	Neutral	0-4	Midco	Dry bottomland forest
6	Upland waterway	Neutral	0-4	Midco	Dry-mesic bottomland forest
7	Toe slope	All	0-14	Viraton	Mesic forest
11	Ridge	Neutral	0-8	Clarksville Poynor Gepp	Dry chert forest
15	Flat	Neutral	0-8	Viburnum	Dry chert forest
17	Side slope	South and West	8-99	Clarksville Poynor Gepp	Dry chert forest
18	Side slope	North and East	8-99	Clarksville Poynor Gepp	Dry-mesic chert forest Dry-mesic sand forest
19	Side slope	South and West	8-99	Bardley	Glade savanna
20	Side slope	North and East	8-99	Bardley	Dry mesic limestone forest
21	Side slope	All	5-99	Gasconade Rockland	Dolomite glade Limestone glade
22	Side slope	All	5-99	Gasconade Rockland	Xeric limestone forest
23	Side slope	All	5-99	Gasconade Rockland	Dry limestone forest

Patterns of Genetic Variation in Woody Plant Species in the Missouri Ozark Forest Ecosystem Project

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Abstract.—We quantified current patterns of genetic variation of three woody plant species—*Carya tomentosa* (Juglandaceae), *Quercus alba* (Fagaceae), and *Sassafras albidum* (Lauraceae)—distributed throughout the nine Missouri Ozark Forest Ecosystem Project (MOFEP) study sites and evaluated the data in light of the MOFEP experimental design. Genetic variation was estimated using electrophoretically detected isozymes as genetic markers. Results indicate that population level genetic diversity estimates were within the range typical of woody plant species but a comparison of levels of genetic variation of *Q. alba* at MOFEP with other *Quercus* species indicates that levels were somewhat low. Each species showed significant differences among sites for the genetic diversity measures or inbreeding coefficient. *C. tomentosa* and *Sassafras albidum* showed significant differences due to ELT. Unexpectedly high levels of inbreeding coefficients were documented in all three species. Two of the species, *Q. alba* and *Sassafras albidum*, showed a significant impact of year of acquisition on measures of genetic diversity and inbreeding. We found differences among the management treatment classes for *Sassafras albidum* only. We conclude that the pattern of genetic diversity and inbreeding is heterogeneous across MOFEP study sites with land use history of specific sites being at least one of the contributing factors. Nonetheless, this heterogeneity has not created any excessive biases for the experimental design of the management treatment experiment of MOFEP.

"...every human action, every aspect of forest management, has ecological and genetic effects, and we must try to determine what those effects are if we are to maintain healthy ecosystems." (Ledig 1992)

Maintenance of genetic variation has been a major concern to conservation biologists and forest managers because the amount of variation determines the ability of a population to respond to environmental change (Ellstrand and Elam 1993, Fisher 1939). Moreover, the existing quality of genetic variation determines the fitness of populations because it provides the diversity of phenotypic traits that are needed to meet the vicissitudes of current and future environmental conditions (Ledig 1992). Because global warming, atmospheric pollution, and habitat alteration are real threats to living organisms, populations that are genetically depauperate will be less able to respond to environmental changes (Ledig 1992). Unfortunately, consideration of this factor is not always a part of forest management. The Missouri Ozark Forest Ecosystem Project (MOFEP) offers a unique opportunity to examine the current status of genetic variation in Missouri forests.

Genetic variation often is described with three statistical parameters: polymorphism (P), heterozygosity (H), and allelic diversity (A) (Hamrick and Godt 1989, Hamrick *et al.* 1992). Polymorphism is equal to the proportion of total loci that have a common allele with a maximum frequency of 95 percent (P_{95}) or the proportion of

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loci that have two or more alleles in the sample examined with no criteria for the frequency of the common allele (P_{NC}). Heterozygosity can be quantified in two ways: observed heterozygosity (H_O), the proportion of heterozygous individuals per locus averaged across loci; and expected heterozygosity (H_E), which uses the allele frequencies to calculate the expected frequency of heterozygotes when the population is at Hardy-Weinberg equilibrium. H_O is a useful index of heterozygosity because several studies have indicated a positive relationship between fitness components and observed heterozygosity (Mitton and Grant 1984). H_E is a commonly used index of genetic diversity (Hamrick and Godt 1989, Hamrick *et al.* 1992). Allelic diversity is the average number of alleles across all loci (A) or the average considering only polymorphic loci (A_P). All of these measures can be estimated for individual subpopulations and for the entire sampled population. In general, we expect species with low gene flow, high inbreeding, or narrow geographic ranges to have low values for genetic diversity indices and species with high gene flow to have high values (Hamrick and Godt 1989, Hamrick *et al.* 1992). In most studies of forest tree species, the values are relatively high in comparison to annual plants or herbaceous perennial species (Hamrick and Godt 1989, Hamrick *et al.* 1992).

Most population genetic models assume that populations are at equilibrium, that all have equal likelihood of gene flow, and that selection has had no impact on patterns of genetic variation (Hartl and Clark 1989, Slatkin 1985). Yet, populations that exist within a heterogeneous landscape, such as the Missouri Ozarks, may not satisfy these assumptions: gene flow may not be equal among all populations and local selection by microhabitat may create heterogeneity in patterns of diversity. In particular, the assumption that populations are at equilibrium may be questionable for second-growth forests such as those in the Ozarks. The particular land use history of Missouri Ozark forests may have had an especially severe and prolonged impact on genetic variation. Evidence suggests that much of the Ozarks was managed by indigenous groups through deliberate, episodic fires (Guyette and Dey 1997). More recently, in the 1880's, the southern Ozarks experienced extensive clearcutting for timber (Cunningham and Hauser 1989). Photographs of that era indicate a naked landscape extending for large areas (Sork, personnal observation). Subsequent to clearcutting, the site was managed for grazing of sheep and cattle with the use of occasional fires to prevent forest reestablishment (Cunningham and Hauser 1989). The few populations remaining could have suffered a loss of genetic variation if these populations experienced a significant reduction in population size, known as a genetic bottleneck (Hartl and Clark 1989). Typically, genetic bottlenecks are also accompanied by high inbreeding coefficients when the population increases in size. Starting in 1925, the Missouri Department of Conservation purchased sites of land for the purpose of forest management. Thus, the sites of MOFEP have different years of acquisition and land use histories.

The overall goal of this study was to quantify the current patterns of genetic variation of selected woody plant species distributed throughout the Missouri Ozark Forest Ecosystem Project (MOFEP) study sites. As part of MOFEP, this study used its experimental design (Sheriff and He 1997). To represent woody plants, we selected three study species that exhibited a range of pollination and seed dispersal modes and growth forms: *C. tomentosa* (Juglandaceae), *Quercus alba* (Fagaceae), and *Sassafras albidum* (Lauraceae). Genetic variation was estimated using electrophoretically detected isozymes as genetic markers. The specific objectives of this paper were: (1) to quantify the mean amount of genetic variation per population for the three woody plant study species, using several genetic diversity measures and the inbreeding coefficient; (2) to examine whether these measures of genetic diversity differ significantly among sites or between two microhabitat types, using a model independent of the MOFEP design; (3) to explore possible influence of land use history, as indicated by year of land acquisition by the Missouri Department of Conservation, on genetic diversity and inbreeding measures; and (4) to evaluate MOFEP experimental design using pretreatment data on genetic diversity and inbreeding.

MATERIALS AND METHODS

Study Species

We selected two canopy tree species and one understory shrub species to be the focal study species. These three species were chosen because their wide distribution among MOFEP study sites and in the region (Braun 1950) make them ideal representatives of temperate

forest woody species. These species also represent a range of pollination and dispersal modes. The first species is *Carya tomentosa* Nuttell (Juglandaceae) (common name = mockernut hickory), which is a monoecious, canopy tree that is tetraploid (Stone 1961). Pollen is wind dispersed; squirrels and gravity are responsible for seed movement. The second species is *Q. alba* L. (Fagaceae) (common name = white oak), which also is a canopy species. Plants are monoecious, the flowers are wind pollinated, and the seeds are dispersed by gravity, mammals, and birds. The availability of genetic information on *Q. alba* (Sork, unpublished data) and other oak species (Huang 1992, Sork *et al.* 1993) allows us to compare the structure of the MOFEP study site with other locations in the United States. The third species is *Sassafras albidum* (Nuttell) Nees (Lauraceae), which in the Ozarks is generally a shrub or small tree. The plants are generally dioecious with insect-pollinated flowers. Fruiting is largely confined to forest gaps and edges in this shade intolerant species. The seeds are dispersed by birds.

Study Site

The Missouri Ozark Forest Ecosystem Project study area incorporates one wildlife area and four State forests that are located in the Ozark Mountains of south-central Missouri: Deer Run State Forest (Reynolds County), Paint Rock, Cardavera, and Carr Creek State Forests (Shannon County), and Peck Ranch Wildlife Area (Carter County). In the MOFEP design, these forests are divided into nine sites, each of which is assigned to one of three forest management treatments (even-aged, uneven-aged, and no harvest; Kurzejeski *et al.* 1992, Brookshire *et al.* 1977, Sheriff and He 1997). The entire MOFEP study area is divided into stands that are classified according to ecological land type (ELT).

Before 1880, most of these Ozark forests were dominated by continuous *Pinus echinata* (shortleaf pine) communities, but intensive harvesting (1880 to 1920) followed by repeated burning and grazing altered the landscape to produce the oak-hickory and oak-pine communities found there today (Cunningham and Hauser 1989). In the Ozarks, *Q. alba* shares the canopy with other species of oaks, including *Q. stellata*, *Q. velutina*, *Q. coccinea*, and with *Pinus echinata*, and *C. tomentosa* (Kurzejeski *et al.* 1992). Forest stands that were sampled range in elevation from 182 to 275 m and were within 37°00' N and 37°15' N, and 91°07' W and 91°00' W (U.S. Topographic Maps, 7.5 minute series: Fremont Mo., Van Buren North Mo., Stegall Mountain Mo., Powder Mill Ferry Mo., and Exchange Mo). Distances between populations range from 0.2 km to 24 km.

Sampling Procedure

Sampling for this study was conducted in 1993 and 1994. In July 1993, leaf samples from *C. tomentosa* and *Sassafras albidum* were collected. In June and July 1994, leaf samples were collected from *Q. alba*. In both years, we sampled 36 stands located throughout the MOFEP study area. Using a hierarchical sampling design, we collected mature leaf tissue from nine sites, two microhabitats within each site, (ELT 17, north- and northeast-facing slopes, and ELT 18, south- and southwest-facing slopes), and two forest stands within each ELT. Within a stand, 48 juvenile and adult trees were sampled within an area approximately 1 ha in size. We consider this sample of individuals within a stand as representative of the local population. Trees were sampled along two to three transects within the midslope region and were separated by at least 7 to 10 m to minimize sampling of related individuals. From each individual, the diameter at breast height (d.b.h.) was measured and two to three leaves were collected. Leaves were kept on ice for up to 3 days until they were transported to the University of Missouri-St. Louis and stored in a -70°C freezer.

Laboratory Analysis

All leaf samples were analyzed using standard horizontal starch gel electrophoresis procedures (Kephart 1990, Sork *et al.* 1992). Mature leaf tissue was ground into a fine powder in a mortar using liquid nitrogen and a pestle. Protein from each sample was extracted using a phosphate extraction buffer (Mitton *et al.* 1979), fortified with 10 percent (w/v) polyvinylpyrrolidone to inactivate phenolics, which tend to bind proteins. The crude extract was absorbed onto 4 mm x 6 mm Whitman #3 chromatography paper wicks and stored at -70°C until electrophoresis. Gels used in electrophoresis consisted of 10 percent starch (Sigma S-4501).

After surveying 20 enzymes on various combinations of five gel/electrode buffer systems, we selected various buffer combinations and enzymes for each species (table 1). For analyses

Table 1.—*List of enzymes, gel/electrode buffer systems, and number of alleles observed for 36 subpopulations of three woody plant species found in the MOFEP study area in southern Missouri. Numbers for gel/electrode buffer systems refer to recipes in Soltis* et al. *(1983) or modifications of those recipes. System 8 modifications followed Rieseberg and Soltis (1989), while system 6 gel buffer contained 0.055 M citric acid and 0.190 M tris.*

Enzymes (Abbreviation-locus)	Gel/electrode buffer system	Number of alleles
	Carya tomentosa	
Aspartate aminotransferase (AAT-2)	7	3
Diaphorase-2 (DIA-2)	7	2
Fluorescent esterase (FES-1)	8	2
Leucine aminopeptidase (LAP-1)	6	1
Malate dehydrogenase (MDH-1)	4	1
Menadione reductase-1 (MNR-1)	6	1
Menadione reductase-2 (MNR-2)	6	2
Peroxidase (PER-1)	6	2
Peroxidase (PER-3)	6	2
Phosphoglucoisomerase-1 (PGI-1)	6	1
Phosphoglucoisomerase-2 (PGI-2)	6	4
Phosphoglucoisomerase-3 (PGI-3)	6	4
Shikimate dehydrogenase (SKDH-1)	4	2
	Quercus alba	
Colormetric esterase (CES)	6	3
Fluorescent esterase (FES-1)	8	3
Fluorescent esterase (FES-2)	8	1
Fluorescent esterase (FES-3)	8	1
Fluorescent esterase (FES-4)	8	3
Fructose 1,6-diphosphatase (F16)	4	3
Malate dehydrogenase (MDH-1)	4	1
Menadione reductase-1 (MNR-1)	6	3
Peroxidase (PER-1)	6	3
Peroxidase (PER-3)	6	3
Phosphoglucoisomerase (PGI-1)	8	1
Phosphoglucoisomerase (PGI-2)	8	4
Shikimate dehydrogenase (SKDH-1)	4	2
	Sassafras albidum	
Aspartate aminotransferase (AAT-2)	7	3
Aspartate aminotransferase (AAT-3)	7	3
Diaphorase-2 (DIA-1)	7	2
Diaphorase-2 (DIA-2)	7	2
Menadione reductase-1 (MNR-2)	6	1

done on all 36 populations of each species, we selected a subset of putative loci: 9 loci for *C. tomentosa*, 10 loci for *Q. alba*, and 5 loci for *Sassafras albidum*. Although we could have increased the number of loci in the first two species, we concentrated our efforts on loci that are polymorphic in at least one population because those loci are more useful in identifying patterns of genetic differences among populations. This decision reduced the time and expense of running additional gels and staining for apparently monomorphic loci for more than 1,700 genotypes per species. However, we acknowledge that the bias toward polymorphic loci biases genetic diversity measures upward.

Statistical Analysis

We calculated standard measures of genetic diversity using BIOSYS-1 (Swofford and Selander 1981) for *Q. alba* and *Sassafras albidum* and our own programs for the tetraploid species, *C. tomentosa*. The measures we used were: percent of polymorphic loci (P_{95} and P_{NC}), number of alleles per polymorphic locus (A_p), and observed and expected heterozygosities (H_O and H_E) for polymorphic loci. We calculated inbreeding coefficients for each individual population based on the formula: $F_{IS} = 1 - (H_O/H_E)$.

We tested whether these five measures of genetic diversity and the inbreeding coefficient differed among site or ELT, using a two-way fixed effects analysis of variance model. For this analysis, we treated sites as fixed effects because they were not randomly sampled from the Ozarks but represent the only sites available for this study. We transformed P_{95}, P_{NC}, H_O, and H_E using an arc sine square root transformation to satisfy the equal variances assumption of ANOVA. Even after transformations, P_{95} and P_{NC} did not satisfy the normality assumption well because the data were not continuously distributed, but the data did approximate a normal distribution with one mode around the mean. We present the results anyway both here and with models described below because ANOVA can be quite robust. Nonetheless, our discussion will emphasize other measures of genetic diversity.

We used year of acquisition by the Missouri Department of Conservation as a measure of impact of land use history. Although we do not know the exact chronology of land use history of each site, once the MDC purchased a site, the forests were protected from fire and were managed to promote tree regeneration. Thus, year of acquisition represents the number of years of forest management. Because this variable created unequal sample sizes, we conducted a nonparametric Kruskal-Wallis k-sample test using the F-values generated by an ANOVA model based on ranks. Each species was analyzed separately.

To address our final goal of the pre-treatment study, we examined our genetic diversity and inbreeding measures, using the experimental design of the MOFEP project (Brookshire *et al.* 1997, Sheriff and He 1997). The ANOVA model included block and management treatment as the main effects. Both terms were tested over the interaction term. The model was run separately for each species. For the sake of simplicity, we did not include ELT in this model because variation due to ELT was tested in the ANOVA model above when we examined site and ELT. However, in future analyses of post-treatment data, ELT can be incorporated into the model.

In our statistical models, we indicate levels of significance, which start at 0.10. While we will cautiously interpret any findings with a probability level greater than 0.05, we want to minimize risk of Type II error (that is, the probability that we accept our null hypothesis of no differences when differences truly exist). To evaluate the risk of Type II error, we conducted a power analysis on all variables with nonsignificant treatment effects within the MOFEP experimental design, using the block by treatment interaction as the error term. For this analysis, we set alpha = 0.05. In general, to avoid a Type II error, one needs a high degree of power.

RESULTS

Variation Across Site and ELT

The average levels of genetic variation and inbreeding per population differed across the three species (table 2). *C. tomentosa*, a tetraploid species, had higher values of the five genetic diversity measures and inbreeding coefficient than the other two species. *S. albidum* had higher values for all five genetic diversity indices and the inbreeding coefficient than *Q. alba*. We caution about comparisons among species because the differences may be due, at least in part, to the differences in number of loci

Table 2.—*Species means (with 1 standard error in parentheses) for population measures of genetic variation and inbreeding. Thirty-six populations were sampled for each species with equal sampling of the nine MOFEP sites. The measures of genetic variation were: polymorphism at 95 percent level (P_{95}); polymorphism with no criterion (P_{NC}); allelic diversity of polymorphic loci (A_P); observed heterozygosity (H_O); expected heterozygosity based on Hardy-Weinberg expectations (H_E); and inbreeding coefficient (F_{IS}).*

	No. loci	Mean no. inds. per population	P_{95}	P_{NC}	A_P	H_O	H_E	F_{IS}
Carya tomentosa	9	41.0	0.710 (0.019)	0.811 (0.009)	3.26 (0.109)	0.315 (0.008)	0.484 (0.011)	0.348 (0.009)
Quercus alba	10	47.3	0.331 (0.012)	0.497 (0.013)	1.17 (0.004)	0.098 (0.002)	0.105 (0.002)	0.059 (0.018)
Sassafras albidum	5	42.6	0.689 (0.028)	0.856 (0.025)	2.55 (0.037)	0.188 (0.011)	0.259 (0.010)	0.267 (0.038)

sampled. Nonetheless, H_O, H_E, and F_{IS} should be not be too biased by sample size because these values are based on means across polymorphic loci. Thus, for the two diploid species, we cautiously conclude that the *S. albidum*, an understory shrub, may have higher genetic diversity and higher inbreeding than *Q. alba*, a canopy tree.

The ANOVA models, which analyzed variation within the six genetic diversity and inbreeding measures across sites and between ELT's, indicated slightly different patterns among the three species (table 3). *S. albidum* was the species that indicated the most genetic diversity variables with significant differences across sites. For example, when we compare the pattern of variation in H_E across sites for the three species (fig. 1), we see that *S. albidum* had much greater variation. In terms of the inbreeding coefficient, *C. tomentosa* and *Q. alba* showed significant variation due to site (table 3, fig. 1). An examination of the variation in mean F_{IS} for *S. albidum* (fig. 1) revealed that this species also varied greatly across sites but that the standard errors were sufficiently high to prevent statistical significance. In general, the three species did not show the same pattern across sites for either H_E or F_{IS} (fig. 1).

In general, we observed a significant effect due to ELT in very few models (table 3). Both *C. tomentosa* and *S. albidum* were significantly different for H_E (table 3), although in opposite directions (fig. 2). *C. tomentosa*, the only species that showed significant differences between ELT's for the inbreeding coefficient (table 3), showed greater inbreeding on south- and west-facing slopes (fig. 2). *C. tomentosa* and *Q. alba* tended to have higher values of H_E and F_{IS} on south- and west-facing slopes, while *S. albidum* showed the opposite pattern to those two species (fig. 2).

Impact of Year of Acquisition

The nonparametric analyses of the effect of year of acquisition on genetic diversity and inbreeding measures indicated that two of the species, *Q. alba* and *S. albidum*, showed significant differences for at least some of the measures (table 4). *Q. alba* had three variables that were either significant or almost significant, and *S. albidum* had two variables that had P-values less than 10 percent (table 4). A comparison of the pattern in H_E across years shows that *Q. alba* and *C. tomentosa* had a similar trend of decreasing values with year (fig. 3). In spite of some dramatic differences in mean inbreeding across years for *Q. alba* (fig. 3), *S. albidum* is the only species that showed a trend toward significance for this variable (table 4). Interestingly, *Q. alba*, a canopy tree, and *S. albidum*, an understory tree, showed opposite patterns across years (fig. 3).

Analysis of MOFEP Design

In general, our analyses revealed that none of the three species show strong differences among management treatment classes (table 5). For *C. tomentosa*, A_P is significant but the overall model is not unless we remove block. This result is due to reduced allelic diversity in

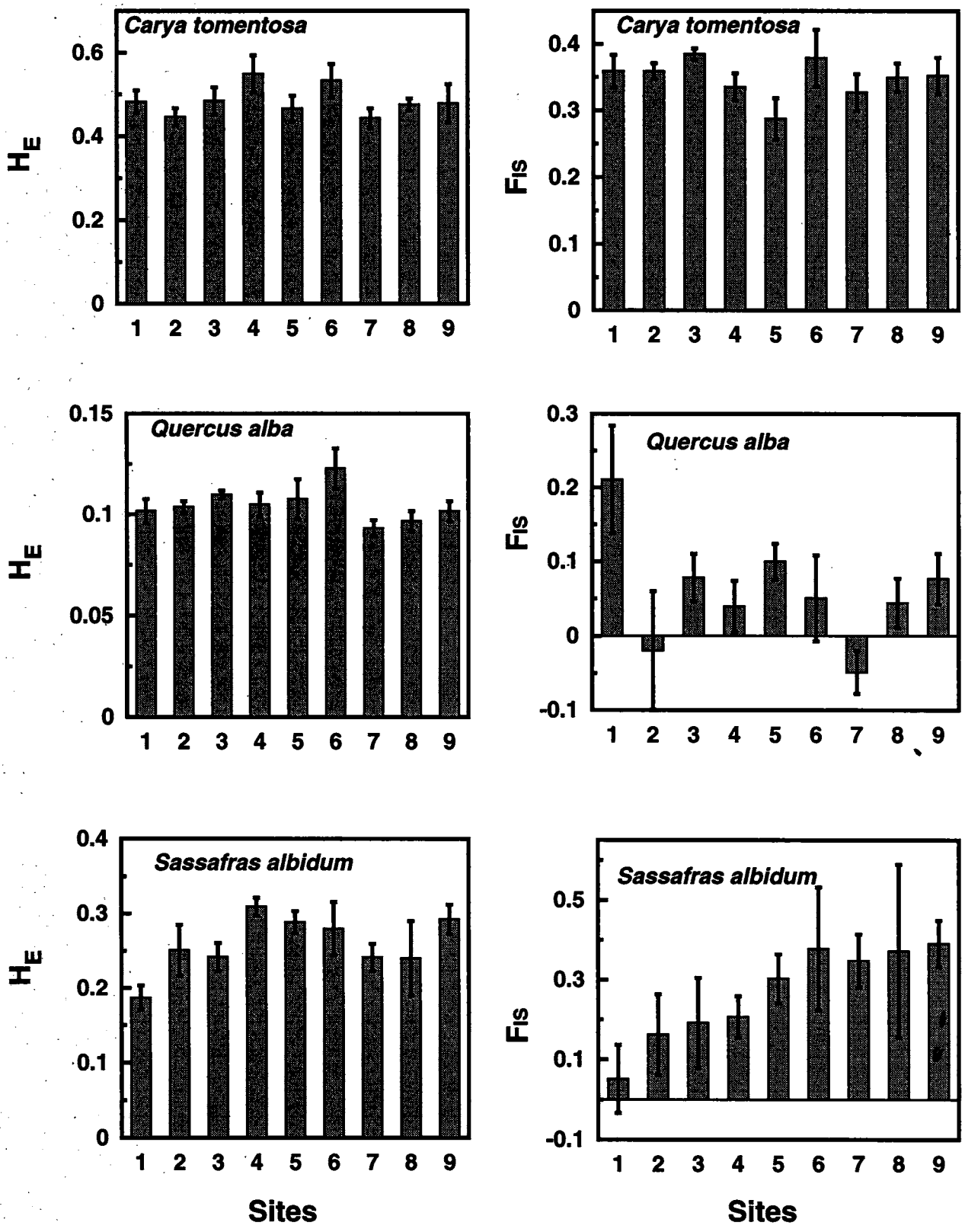

Figure 1.—*Mean (+/- 1 SE) H_E and F_{IS} of four populations per each of nine sites of MOFEP study area in south-central Missouri for* Carya tomentosa, Quercus alba, *and* Sassafras albidum.

Table 3.—*Summary of F-values from six separate two-way fixed ANOVA models estimating the effect of site and ELT on five measures of genetic diversity and the inbreeding coefficient (see table 2 for description of variables). A total of 36 populations distributed throughout MOFEP study plot are used. The degrees of freedom for the error term of each source of variation is 18.*

Source	DF	P_{95} [a]	P_{NC} [a]	A_P	H_O [a]	H_E [a]	F_{IS}
			Carya tomentosa				
Model	17	0.90	2.68*	0.88	1.72	1.53	7.89***
Site	8	0.98	2.18†	0.79	1.36	1.41	5.21**
ELT	1	0.05	0.27	0.29	1.83	4.63*	5.02*
Site x ELT	8	0.92	3.49*	1.05	2.07	1.26	10.93***
			Quercus alba				
Model	17	0.91	1.55	1.33	2.03†	1.34	1.90†
Site	8	1.28	1.25	0.73	2.89*	1.85	2.59*
ELT	1	0.08	0.54	0.00	0.12	0.19	0.03
Site x ELT	8	0.64	1.97	2.10†	1.40	0.98	1.45
			Sassafras albidum				
Model	17	1.64	2.86*	1.00	0.87	3.19**	1.27
Site	8	2.93*	5.65***	1.34	0.80	3.23*	1.22
ELT	1	2.30	1.71	0.11	1.64	10.26**	0.03
Site x ELT	8	0.27	0.22	0.77	0.84	2.28†	1.47

[a] variables were arc sine square root transformed

† $P < 0.10$ * $P < 0.05$ ** $P < 0.01$ *** $P < 0.001$

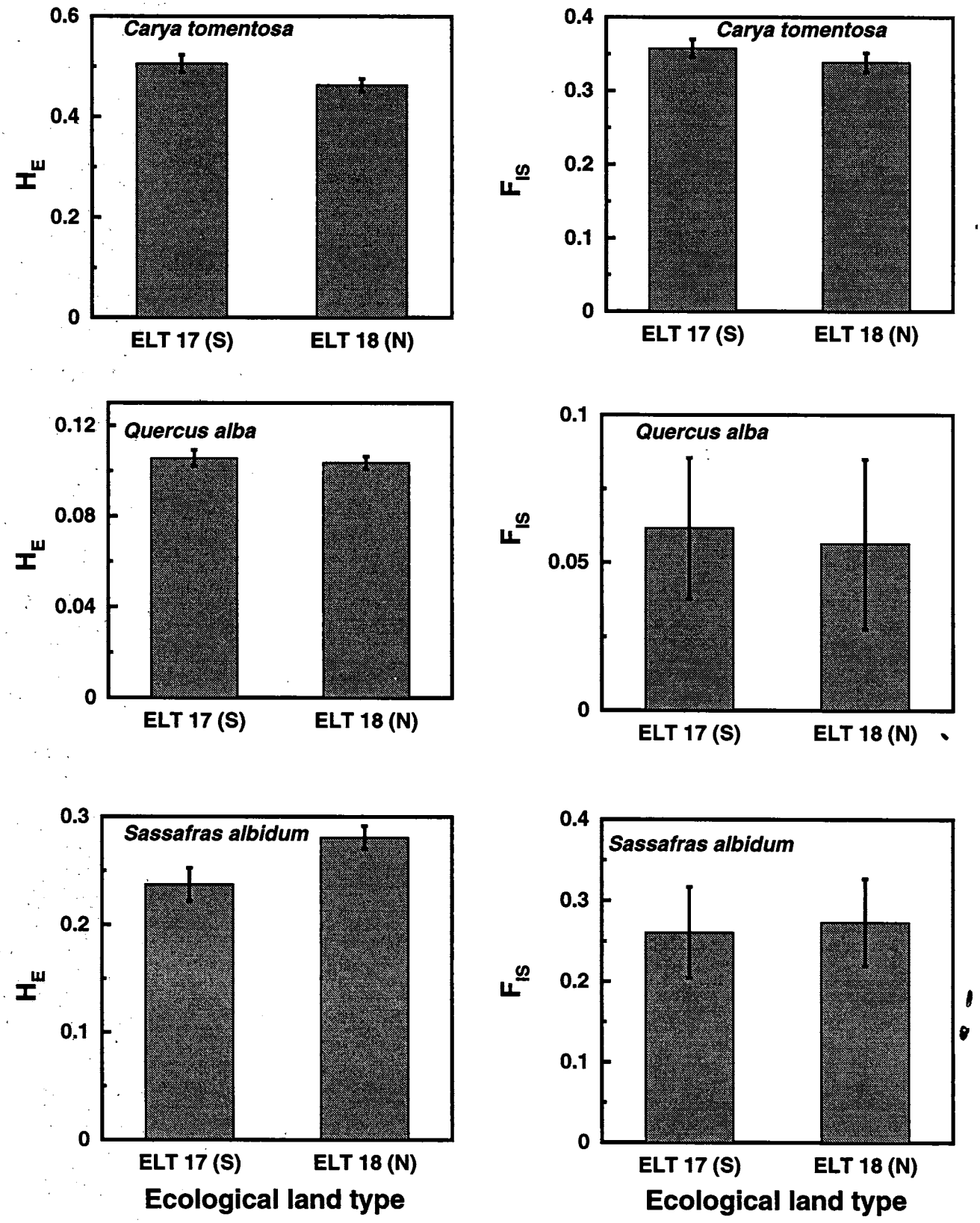

Figure 2.—*Mean (+/- 1 SE)* H_E *and* F_{IS} *of subpopulations found in each of two ELT 17 (south- to west-facing slope) and ELT 18 (north- to east-facing slope) in the MOFEP study area for* Carya tomentosa, Quercus alba, *and* Sassafras albidum.

Table 4.—*Summary of F-values from Kruskal-Wallis non-parametric tests using year of acquisition as the class variable and six dependent genetic variables (see table 2 for description of variables). Models were run separately for each species. (Results for* Q. alba *are taken from Koop 1996.)*

	DF	P_{95}	P_{NC}	A_P	H_O	H_E	F_{IS}
Carya tomentosa	3, 32	0.52	1.47	0.67	1.03	1.27	0.46
Quercus alba	3, 32	2.59†	1.41	0.37	2.59†	5.43**	0.96
Sassafras albidum	3, 32	1.48	12.46***	1.97	1.54	1.87	2.89†

† P < 0.10 * P < 0.05 **P < 0.01 *** P < 0.001

the sites assigned to the even-aged management class (fig. 4). *Q. alba* does not have any genetic variability that is significantly different across treatment classes (table 5); however, mean inbreeding coefficients across treatment classes show a great deal of variation (fig. 4), with the even-aged treatment showing the lowest values. These means are significantly different across treatments in an ANOVA model that treats treatment class and site nested within treatment as fixed effects (ANOVA, df = 2,27, F = 4.65, P < 0.05), which illustrates the potential for Type II error of this experiment. *S. albidum* has two variables with P-values less than 10 percent: P_{95} and P_{NC} (table 5). In this case, polymorphism is highest in the even-aged treatment and lowest in the control treatment (fig. 4). In general, the pattern of variation across treatment classes does not show the same trend across species.

The power analysis of our treatment effect revealed that for most variables our power was very low. For almost all variables tested, the power was less than 0.30. The exceptions were: for *Q. alba*, the power of detecting a treatment effect of F_{IS} was 0.60, and for *S. albidum*, the power of detecting a treatment effect for H_E = 0.65, for H_O = 0.78, and for P_{95} = 0.87.

Table 5.—*Summary of F-values from six separate two-way mixed ANOVA models estimating the effect of species and future management treatment on five measures of genetic diversity and inbreeding coefficient (see table 2 for description of variables). As described in table 3, the following variables were transformed:* P_{95}, P_{NC}, H_O, H_E.

Source	DF	P_{95}	P_{NC}	A_P	H_O	H_E	F_{IS}
			Carya tomentosa				
Model	8, 27	1.04	1.27	0.79	1.01	1.17	1.27
Block	2, 4	0.52	0.73	2.08	5.29†	1.93	0.90
Treatment	2, 4	0.06	1.63	15.75*	0.02	0.31	0.46
Error (B X T)	4, 27	1.61	1.17	0.16	0.55	1.10	1.52
			Quercus alba				
Model	8, 27	1.49	0.98	0.57	2.66*	1.92†	2.35*
Block	2, 4	2.16	0.71	1.35	0.59	3.48	0.84
Treatment	2, 4	1.60	0.50	0.73	0.18	0.80	2.76
Error (B X T)	4, 27	1.03	1.22	0.56	3.84*	1.22	1.68
			Sassafras albidum				
Model	8, 27	3.53**	7.11***	1.49	0.82	1.87	1.10
Block	2, 4	4.26†	8.92*	2.76	3.25	6.64*	7.96*
Treatment	2, 4	4.51†	6.19†	1.05	3.68	2.94	0.43
Error (B X T)	4, 27	1.31	1.66	1.03	0.37	0.65	0.42

† P < 0.10 * P < 0.05 ** P < 0.01 *** P < 0.001

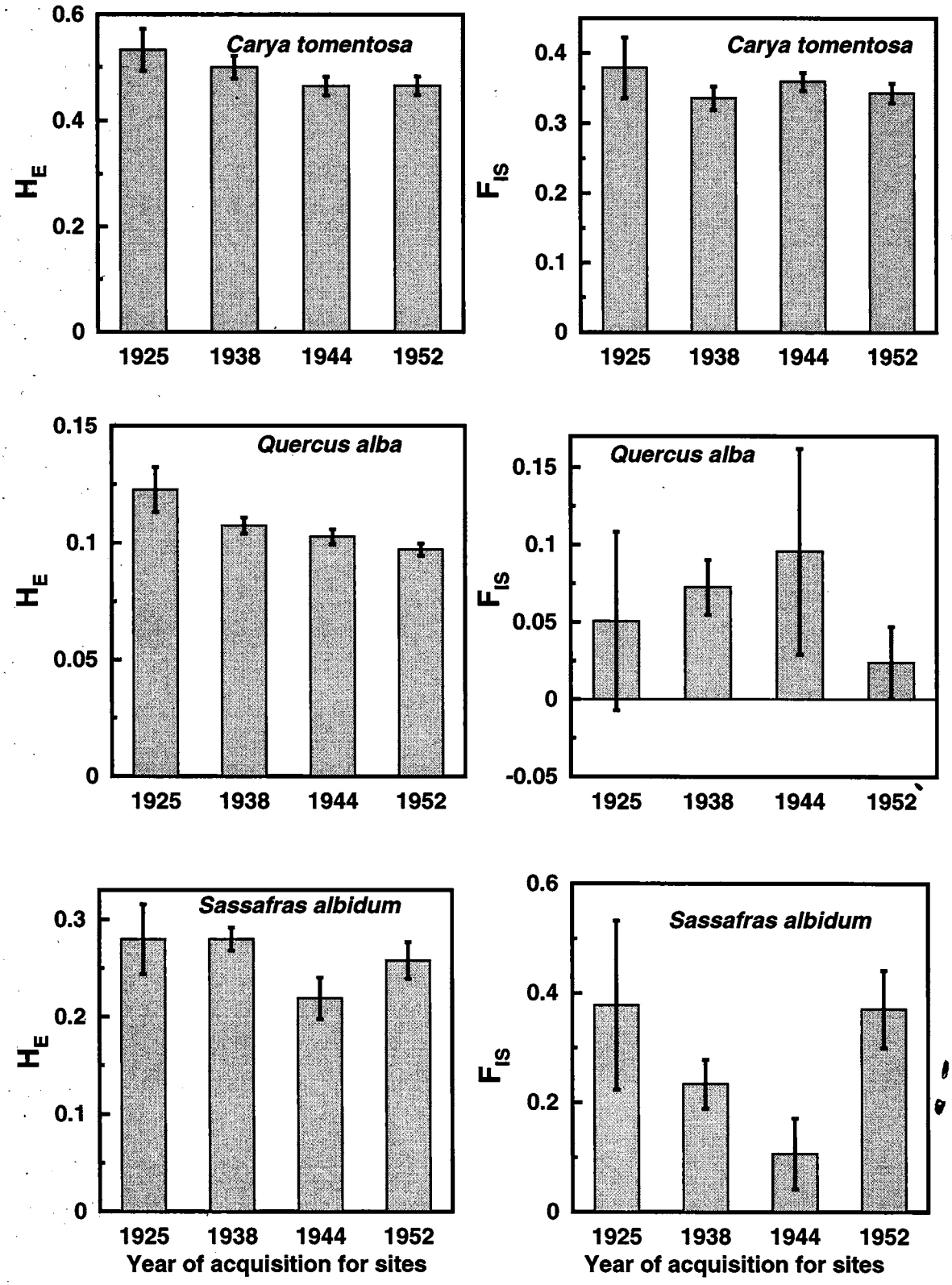

Figure 3.—*Mean (+/- 1 SE) H_E and F_{IS} of populations found in sites with different years of acquisition by the Missouri Department of Conservation for* Carya tomentosa, Quercus alba, *and* Sassafras albidum. *Site 6 was purchased in 1925, sites 3-5 were purchased in 1938, sites 1 and 2 were purchased in 1944, and sites 7-9 were purchased in 1952.*

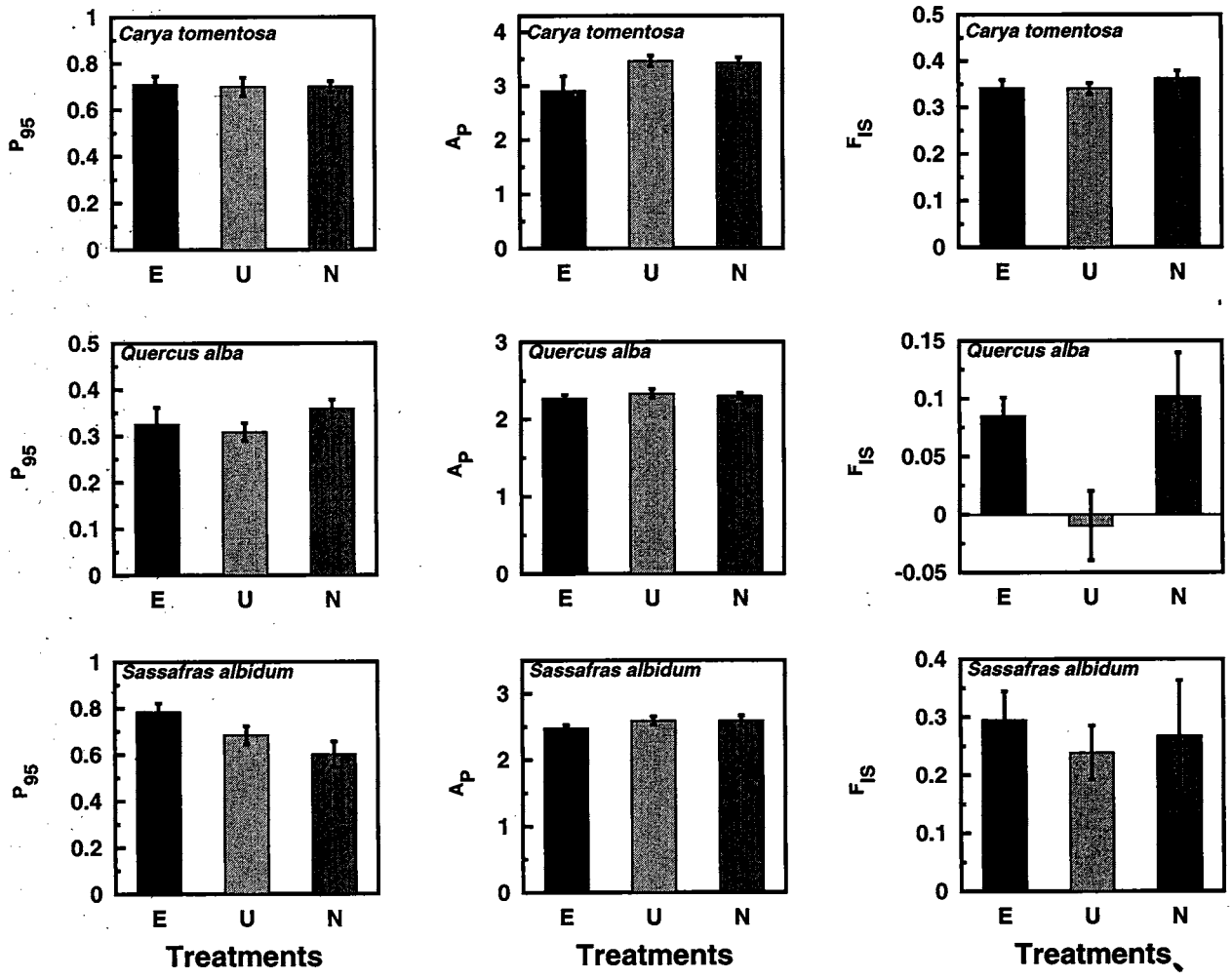

Figure 4.—*Mean (+/- 1 SE) P_{95}, A_P, and F_{IS} of 12 populations per each of three management treatments (even-aged (E), uneven-aged (U), and no harvest (N)), which are part of the MOFEP experimental design.*

DISCUSSION

The genetic variation of the three study species is within the range of expectations for woody plant species as indicated by a summary of the literature by Hamrick and Godt (1989), who estimated that the average values of P (no criteria) across all loci to be 50.0 percent, A to be 1.79, and H_E to be 0.149. Both *C. tomentosa* and *S. albidum* have values much higher than these means, but a precise comparison is not feasible for either of these species. For *C. tomentosa*, a comparison is not valid because the values of Hamrick and Godt (1989) are based on diploid data. Tetraploids, like *C. tomentosa*, should have much higher values than would diploid species because they have twice as many alleles. In fact, several studies have reported higher genetic diversity for tetraploids than for their diploid congeners: *Avena* sp. (Allard *et al.* 1993), *Antennaria* sp. (Bayer 1989), *Prunus* sp. (Beaver *et al.* 1995), and *Heuchera* sp. (Ness *et al.* 1989). A notable exception is a tetraploid variety of *Turnera ulmifolia*, which has less diversity than diploid congeners, possibly due to founder events (Shore 1991). A comparison with the literature is hampered for *S. albidum* because of the small number of loci for which we could obtain electrophoretic resolution. Because the five loci we used were all highly polymorphic, they may yield a higher estimate of diversity than if we had included more loci. For both of these species, it would be useful to sample populations at sites outside the Ozarks to make comparisons about whether the values we report here are typical or atypical for the species.

A useful way to compare genetic diversity of Ozark woody plants with the published literature is through *Q. alba*. Our estimates of P, A, and H are based on averages across polymorphic loci that should give higher estimates than the approach of Hamrick and Godt (1989). Nonetheless, our estimate of P (49.7 percent) is close to their average (50 percent). Moreover, we observed allelic diversity of 1.17 and expected heterozygosity of 0.105, which are much lower than the values stated above. We infer that the lower than expected levels of genetic diversity found in *Q. alba* may indicate that Ozark woody plants have slightly less genetic variation than similar species found elsewhere. An analysis of other woody plant species in the Ozarks will be necessary before we can conclude whether reduced genetic diversity is restricted to *Q. alba* or applies to other species.

The pattern of genetic variation of populations within each species is very heterogeneous across the MOFEP landscape. The null hypothesis for outcrossing long-lived species is that measures of P, H, and A will vary randomly across populations. For *C. tomentosa* and *Q. alba*, that expectation is generally true: both species had only one measure that was significant or almost significant. In contrast, P_{95}, P_{NC}, and, H_E were significantly different across sites for *S. albidum*. Differences in genetic diversity across MOFEP sites may be due to uneven gene flow within this landscape or they could be due to independent founder events. Our analyses also revealed that microhabitat was associated with variation in genetic diversity in *C. tomentosa* and *S. albidum*. In the case of *C. tomentosa*, northern and northeastern aspects had greater expected heterozygosity, while in *S. albidum* the pattern was the opposite. These sets of findings about the distribution of genetic variation across sites and ELT's indicate that genetic diversity can be influenced by landscape features. They also indicate that the manner in which landscape influences genetic diversity is species-specific.

Our analysis of heterogeneity across sites and ELT's was also extended to the population levels of inbreeding as measured by $F_{IS} = 1 - H_O/H_E$. We caution that estimates of inbreeding based on this formula will differ from inbreeding estimates based on the F-statistic formulas (e.g., Davis *et al.* 1991; Weir and Cockerham 1984; Wright 1951, 1965). Therefore, we will not compare the values reported here to those of the literature. However, we will point out that all three species have significant inbreeding coefficients using F-statistic formulas of Davis and others (1991): *C. tomentosa* $F_{IS} = 0.316$, *S. albidum* $F_{IS} = 0.234$ (Sork, unpublished data), and *Q. alba* $F_{IS} = 0.103$ (Koop 1995). Thus, each of these species demonstrates significant inbreeding, and it is worthwhile to investigate whether inbreeding is heterogeneous within the MOFEP landscape.

Inbreeding can be the result of self-pollination or mating with relatives. Because *C. tomentosa* and *Q. alba* are known to be outcrossing species that rarely self-pollinate and *S. albidum* is dioecious, which prevents self-pollination, we conclude that any inbreeding we observe is most likely due to mating with relatives. Mating with relatives is possible when seed dispersal is sufficiently restricted that half-sibs become established within the vicinity of the mother and grow up with some likelihood of mating with each other. *C. tomentosa* showed significant variation in F_{IS} due to site, ELT, and the interaction term. *Q. alba* showed significant effects due to site only. Thus, of the three species, *C. tomentosa* showed the most heterogeneity in its level of inbreeding. Of the three species, *C. tomentosa* also has the most restricted seed dispersal because it has large nuts that are likely to be dispersed by terrestrial rodents who do not carry nuts far (Sork, personal observation). In contrast, *Q. alba* is dispersed by both birds and rodents, and *S. albidum* has berries that are dispersed mostly by birds. It is possible that restricted seed dispersal is a contributing factor to overall high level of inbreeding of *C. tomentosa* and to the high heterogeneity in inbreeding. However, one must be cautious in drawing conclusions about dispersal mode because this study does not replicate species within a mode. Thus, the high heterogeneity in F_{IS} of *C. tomentosa* may be due to its restricted seed dispersal mechanism or to one or more other species-specific factors.

One obvious factor of the MOFEP landscape that might contribute to the heterogeneity in genetic diversity or inbreeding is the land use history of these sites. Our analysis of year of acquisition by the Missouri Department of Conservation was the approach we used to address this question. Although the various sites probably differ in many others ways (e.g., soils, Kabrick *et al.* 1997), year of acquisition represents the time at which each site began to be managed for forest instead of grassland. In effect, year of acquisition is probably a year of

release for any woody plant species that were suppressed by fire and grazing, and it represents a shift in the type of local ecosystem. Our findings indicate that this shift is associated with different levels of local genetic diversity in two of the species we examined. For *Q. alba*, we found significant differences for H_E such that the populations that were managed for forest longer have greater genetic diversity. *C. tomentosa*, a co-occurring canopy species, showed the same trend, but it was not significant. Such data provide preliminary evidence of a relationship between management and genetic diversity.

Our findings also revealed a highly significant difference in inbreeding level across year of acquisition for *S. albidum*. This pattern does not correlate directly with year of acquisition as we observed for heterozygosity in the two canopy species. However, this pattern does show an inverse relationship with *Q. alba* (see fig. 3) that suggests that land use history may be influencing inbreeding as well. Thus, factors that may promote inbreeding for *S. albidum* may be the same factors that retard inbreeding for the other species. The lack of an overall pattern in the extent to which genetic diversity measures and inbreeding levels vary across sites and year of acquisition illustrates that not all woody plant species will respond similarly to management regimes. In all likelihood, *C. tomentosa* and *Q. alba* were suppressed by the grassland management regime. In contrast, *S. albidum*, which does well in open areas, may not have been suppressed under those conditions. For each of the woody plant species, the impact of management may have been slightly different. Nonetheless, the data are highly suggestive that the change in management contributed to the creation of a mosaic of patterns of genetic diversity for many species.

The final goal of our study was to evaluate the MOFEP experimental design using our pre-treatment data. Of greatest concern is whether the genetic patchiness of the MOFEP landscape might have any impact on the analysis of management treatments that are currently being implemented. Of the five genetic diversity parameters, H_E is the most important one to monitor because it is the best measure of genetic diversity due to its wide use across studies. Moreover, this measure shows more continuous variation than P and A, which makes it more amenable to ANOVA. None of the species had significant treatment effects for this variable although we found that *S. albidum* has two genetic parameters (P_{95}, P_{NC}) that were almost significant. If we use these parameters in the post-treatment analyses, these results will need to be taken into account.

As we evaluate the models for significant treatment effects, we need to address the concern of falsely accepting a null hypothesis (Type II error). For example, when we visually analyze the means across data (fig. 4), *Q. alba* shows some dramatic differences in F_{IS} across management treatments and *S. albidum* shows some differences. At least two factors can contribute to a Type II error. The first is that the power of our test is weak. Indeed, results from the power analysis indicated that we had low power on most of the variables we examined. The best way to increase power without adding new sites is to reduce the variance within site by sampling more stands per site. We will consider this approach in the post-treatment study.

A second factor that can contribute to a Type II error would be an inappropriately designed ANOVA model. Given this possibility, we analyzed the *Q. alba* F_{IS} data using a different ANOVA model (eliminate block and consider site as a fixed effect nested within treatment) and found that management treatment is significant. We discuss this example to point out the MOFEP experimental design may create a Type II error for some variables and some species. Not only does the randomized block have very few degrees of freedom for the error term (df = 4) but the blocks do not always help the model because there may be significant heterogeneity within them. In the post-treatment analysis of data, it will be important to examine the data with several models and with an awareness of means and variances across treatment classes to avoid overly conservative analysis of findings. Nonetheless, after considering the results of all of the ANOVA models (table 5) and the patterns in the data (fig. 4), we conclude that differences among pre-treatment classes do not reflect strong biases that will hamper the impact of future management treatments or interpretation of post-treatment data.

The fact that the Ozark landscape reflects a mosaic of genetic patterns illustrates the benefits of evaluating an ecosystem before initiating an experimental treatment. Few studies actually measure the pre-existing conditions of an experiment. It is fascinating that land use history may have influenced patterns of genetic

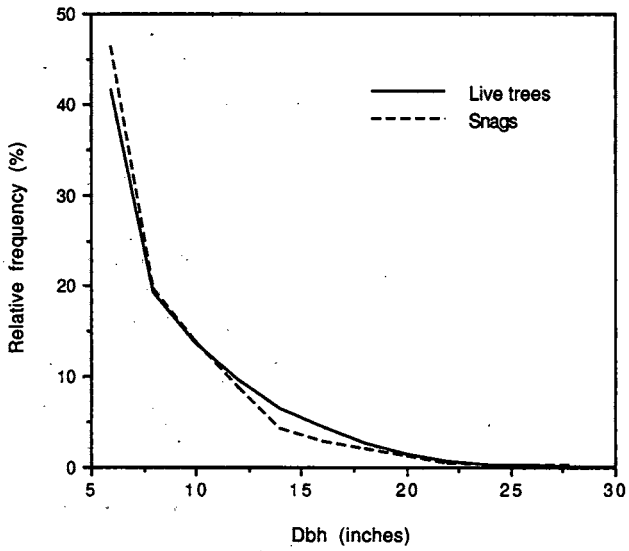

Figure 1.—*Relative frequency of number of snags and live trees by d.b.h. class for all nine MOFEP sites combined. Note the strong similarity in diameter distributions for snags and live trees.*

generally expect little change in the relative size distribution of snags for the no-harvest treatment. Intermediate thinning operations as part of the even-aged and uneven-aged treatments may eventually reduce relative snag densities by harvesting declining trees before they die, particularly trees in the commercial size classes. In the short term, however, thinning practices may have the opposite impact on the relative proportion of snags. At sites 2 through 5 (even- and uneven-aged harvest treatments), loggers exercised their option to simply girdle rather than fell many culls and submerchantable trees that were marked for removal. This will result in a large relative increase in the number of snags while temporarily delaying inputs of dead wood to the forest floor. Treatments that affect the number and size distribution of snags should eventually be reflected in differences in the quantity of down wood, because large volumes of down wood result when snags (or portions thereof) fall to the forest floor.

CONCLUSIONS

Analyses of the pre-treatment MOFEP data revealed no statistically significant ($P \geq 0.05$) differences in the number of snags or the basal area of snags by treatment class. Nor were treatment class differences observed in the volume of down wood or the percentage of the ground area covered by down wood. This is the desired condition before implementation of the treatments. For those same forest attributes, the block effect (assignment of sites to blocks based on spatial proximity) was not significant. Sites 6, 7, and 8 stand out in having more snags and higher snag basal areas than the other sites. In general, snag and down wood attributes observed for the MOFEP sites were consistent with those reported for other sites in the region. The volume of down wood is expected to increase on all sites after treatment. We suspect that the ratio of snags to live trees (in composite or by d.b.h. class) will be a reasonably sensitive indicator of changes in snag conditions over time.

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Determination of the Ecological and Geographic Distributions of *Armillaria* Species in Missouri Ozark Forest Ecosystems

Johann N. Bruhn, James J. Wetteroff, Jr., Jeanne D. Mihail, and Susan Burks[1]

Abstract.—Armillaria root rot contributes to oak decline in the Ozarks. Three *Armillaria* species were detected in Ecological Landtypes (ELT's) representing south- to west-facing side slopes (ELT 17), north- to east-facing side slopes (ELT 18), and ridge tops (ELT 11). *Armillaria mellea* was detected in 91 percent of 180 study plots; was detected with equal frequency in all three ELT's; and was ubiquitous in block 3. *Armillaria gallica* was detected in 64 percent of the study plots; was detected least frequently in block 3; and was detected least frequently on ELT 17 in block 3. The distribution of *A. tabescens* remains incompletely resolved; it is the least abundant species and the most difficult to survey. *Armillaria mellea* was much more frequently associated with oak mortality than were *A. gallica* or *A. tabescens*, based on isolations from dying or recently killed trees. If these three species compete for substrate, oak decline levels may be influenced by landscape patterns of *Armillaria* species co-occurrence. We hypothesize that oak decline will be most severe in block 3, and especially on ELT 17, where *A. mellea* most often occurs in the absence of *A. gallica*.

Armillaria (Fr.:Fr.) Staude is a white-rot wood decay fungus genus (Fungi, Agaricales) comprising about 40 species worldwide (Volk and Burdsall 1995, Watling *et al.* 1991). Due to similarities in the morphology of *Armillaria* mushrooms, mycelial fans, and rhizomorphs, all annulate North American *Armillaria* were widely thought to belong to a single highly variable species (*Armillaria mellea*) until the late 1970's. Following Hintikka's (1973) description of a mating test for distinguishing *Armillaria* species using pedigreed single-basidiospore isolates, great progress has been made in clarifying biological, ecological and taxonomic issues concerning *Armillaria* species (Korhonen 1995). The name *Armillaria mellea* (Vahl:Fr.) Kummer now clearly represents a single *Armillaria* species, the type species of the entire genus (Watling *et al.* 1991). The exact number of *Armillaria* species in North America remains uncertain due to insufficient study. Unfortunately, much of the *Armillaria* literature well into the 1980's is of limited value because the correct identity of the *Armillaria* species studied was never established. This is the initial report of the first formal study of the *Armillaria* species influencing forest structure in upland Ozark oak-hickory forests. The three *Armillaria* species encountered were *A. gallica* Marxmüller & Romagnesi, *A. mellea*, and *A. tabescens* (Scop.) Emel.

A portion of the energy derived by *Armillaria* mycelia from wood decay (Garraway *et al.* 1991) is spent on sexual reproduction of airborne basidiospores on mushroom gills. Each spore that successfully germinates to colonize a suitable woody substrate (food base) generally mates with another sexually compatible germling to form a genetically unique individual ("genet," *sensu* Harper 1977) that may become established in the landscape as an agent of wood decomposition and perhaps of root disease and forest decline (Anderson and Kohn 1996, Guillaumin *et al.* 1991).

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Genets of all *Armillaria* species are functionally territorial, enlarging through sequential colonization of woody food bases by branching, cord-like rhizomorph systems and/or growth across root contacts and grafts (Gregory *et al.* 1991, Morrison *et al.* 1991, Redfern and Filip 1991). Rhizomorph growth is fueled with energy and nutrients derived from food base decay (Anderson and Ullrich 1982, Garrett 1956, Rishbeth 1972) and from the soil through which the rhizomorphs grow (Morrison 1975). *Armillaria* rhizomorph production is generally increased when using hardwood compared with conifer food bases (Redfern and Filip 1991). Because *Armillaria* species do not produce asexual spores, *Armillaria* genets are potentially continuous in the forest floor. *Armillaria* genets are also potentially long-lived and can achieve great size (Anderson and Kohn 1996, Bruhn *et al.* 1997, Korhonen 1978, Legrand *et al.* 1996, Rishbeth 1991, Shaw and Roth 1976, Smith *et al.* 1992), especially when compared with most vegetation.

Armillaria species differ in host preference and virulence; genets of the same species can also differ in virulence. Studies elsewhere of *Armillaria* species that also occur in the Ozarks have concluded that *A. mellea* is much more virulent than either *A. gallica* or *A. tabescens* (Gregory *et al.* 1991, Guillaumin *et al.* 1993, Redfern and Filip 1991, Rishbeth 1991). *Armillaria mellea* and *A. gallica* are generally considered to be much more common than *A. tabescens* (which can be locally abundant). *Armillaria mellea* is capable of attacking and killing a wide variety of hardwoods and a smaller range of conifers (mainly non-resinous species). *Armillaria gallica* is more restricted to colonizing dying or dead material and causing butt rot of hardwoods. In western Europe, *A. tabescens* is considered the least virulent of the three species, largely restricted to hardwood stumps. A notable exception is primary parasitism by *A. tabescens* of exotic *Eucalyptus* species in southwest France. North American *A. tabescens* has a large host range and may be somewhat more virulent than European *A. tabescens* (Sinclair *et al.* 1987). However, Rhoads (1925, 1956) indicated that exotic and cultivated tree species were much more susceptible than native tree species to North American *A. tabescens*, especially when planted on land previously cleared of oak forest.

Armillaria species (and genet) distributions are related to long-term vegetation and Ecological Land Type (ELT) characteristics (Bruhn *et al.* 1994, Korhonen 1978, Rishbeth 1982). The mechanisms by which neighboring *Armillaria* genets of the same or different species interact to allocate space among themselves are not yet clear. Where the perimeters of *Armillaria* genets meet or overlap, genets may interact as a result of niche overlap and competitive exclusion (Leibold 1995, Mohammed and Guillaumin 1989). Genets of different *Armillaria* species may circumvent each other as a result of different colonization strategies (Legrand *et al.* 1996). Nevertheless, the activity levels of *Armillaria* genets adjust to changes in the environment (*e.g.*, climate, defoliation, vegetation management) that affect the supply of food bases and the vulnerability of potential hosts (Bruhn *et al.* 1994, Lonsdale and Gibbs 1996, Wargo 1996, Wargo and Harrington 1991). The spatial arrangements and ecological attributes of *Armillaria* genets help shape long-term forest community structure in response to perturbations (Lundquist 1993, Worrall and Harrington 1988), because each extant combination of genets contributes differently to the regulation of stand structure and composition.

Armillaria species are often implicated as opportunistic root parasites contributing to forest declines incited by various stress events (Bauce and Allen 1992, Clinton *et al.* 1993, Houston 1992, Johnson and Law 1989, Kile *et al.* 1991, Wargo 1996). Both excess moisture and drought during the growing season are capable of inciting *Armillaria* root disease (e.g., Lonsdale and Gibbs 1996, Wargo and Harrington 1991). Rhoads (1956) found that droughty acidic sites predisposed trees to attack in Florida, whereas poorly drained soils on former oak sites predisposed grape plants to attack in Missouri (Rhoads 1925). A study of oak decline in upland Ozark forests showed that the growth rates of trees that eventually died did not recover following severe drought (compared to similar trees that remained healthy), and that growth of declining trees was further depressed with each succeeding drought (Dwyer *et al.* 1995). This scenario is consistent with a combined *Armillaria* + drought etiology. A relationship has been recognized between predisposing stress events (e.g., drought, late frost, defoliation), Armillaria root disease, and oak decline and mortality in the Missouri Ozarks (Johnson and Law 1989, Law and Gott 1987), though the identities of the *Armillaria* species involved and the nature and extent of their involvement and interactions were not determined. The black/

scarlet oak cover type occupies approximately 2 x 10^6 ha in Missouri. Affecting over 7.2 x 10^5 ha on the Mark Twain National Forest alone, oak decline has been most severe on Captina silt loam soils situated on broad ridges and moderately severe on Clarksville silt loam soils with west aspects (Law and Gott 1987). If predictions of greater climatic instability including more frequent summer droughts prove correct (Joyce *et al.* 1990, Kraüchi 1993, Rind *et al.* 1990), the resultant physiological stress to forest trees could heighten levels of *Armillaria* root disease and associated forest decline.

The shortage of previous knowledge about *Armillaria* distributions and activities in upland Ozark forests is related to the lack of attention paid to this geographic region by mycologists in the past and the difficulty of distinguishing the annulate *Armillaria* species in the field. Once the distributions and behaviors of Ozark *Armillaria* species are clarified, it will be possible to devise silvicultural programs that consider this pivotal genus of forest fungi.

Objectives

The goal of our study is to use ecological characteristics to explain the pre-treatment geographic distributions and behavioral patterns of all *Armillaria* species occurring in the nine MOFEP sites. Characteristics to be considered include forest vegetation cover and ELT variables describing geo-landform, soils, and climate. Data describing these variables for the permanent vegetation plots are gradually becoming available (Chen *et al.* 1997, Kabrick *et al.* 1997, Meinert *et al.* 1997). As a result, the pre-treatment distribution of *Armillaria* species with respect to oak decline occurrence and severity will be clarified.

Our initial research objectives are:

1. to identify all *Armillaria* species occurring in the nine MOFEP sites before treatment;
2. to test the hypotheses that each *Armillaria* species is initially uniformly distributed: (a) among the three silvicultural treatments, (b) among the three blocks of sites, and (c) among ELT's characterized by ridgetops, south- to west-facing side slopes, and north- to east-facing side slopes; and
3. to formulate hypotheses based on field observations concerning the pre-treatment relationship of each *Armillaria* species to the occurrence of oak decline.

METHODS

Experimental Design

MOFEP is designed to evaluate the responses of forest vegetation (and other forest life-forms) to even-aged (EAM), uneven-aged (UAM), and no-harvest (NHM) management. Over 600 permanent 0.2-ha study plots (fig. 4 in Brookshire *et al.* 1997) have been established in nine sites of approximately 400 ha each. The nine sites are arranged in three blocks of three sites each. One site in each block has been allocated to each of the three types of management (fig. 1 in Brookshire *et al.* 1997). Approximately 10 percent of each EAM and UAM site have been set aside from harvest. Within each site, plots were allocated to ELT's approximately in proportion to site land area represented by each ELT. Three upland ELT's (designated 11, 17, and 18) dominate the study sites (Miller 1981). These three ELT's can be roughly described as ridgetops, south- to west-facing side slopes, and north- to east-facing side slopes, respectively (fig. 2 in Brookshire *et al.* 1997). Overstory vegetation associated with these three ELT's is mostly mature second-growth oak, hickory, and shortleaf pine. Logging has not occurred in any of the nine sites for at least 40 years. Experimental cutting in the EAM and UAM sites began in the spring of 1996.

Because we plan to build on this *Armillaria* distribution study with studies of responses of *Armillaria* species and vegetation to silvicultural treatments, we anticipated need for at least six study plots (per ELT per site) that receive the treatment assigned to that site. Permanent vegetation plots representing each of the three dominant upland ELT's in each of the nine MOFEP sites were randomly selected for this study (fig. 5 in Brookshire *et al.* 1997). Because 11 of our originally selected plots are located in stands subsequently reserved from treatment (designated OG, "old growth"), and to include all permanent vegetation plots in which weather data are being collected (Chen *et al.* 1997), we now have *Armillaria* distribution data for 180 plots rather than the 162 plots originally selected (table 1). Of these, 64 plots received silvicultural treatment in 1996 (table 1). Although it would be difficult to confirm the absence of an *Armillaria* species from a study plot, we assume that the inability to detect a particular *Armillaria* species in the vicinity of a plot constitutes strong evidence that the species is ecologically much less influential than if it

Table 1.—*Distribution of* Armillaria *study plots among statistical blocks, forest sites, silvicultural systems, ecological land types, and type of harvest activity*

Block	Site	Silvic. system[1]	Harvest treatment[1]	ELT[2]	Total plots[3]	Harvested plots[3]
1	1	NHM	—	11	6	0
			—	17	6	0
			—	18	7	0
	2	UAM	S	11	7	7
			S	17	6	3
			S	18	8	5
	3	EAM	I	11	6	2
			I	17	8	1
			C	17	8	1
			I	18	6	4
			C	18	6	1
2	4	UAM	S	11	6	6
			S	17	7	5
			S	18	6	6
	5	EAM	I	11	7	4
			C	17	8	1
			I	18	8	1
			C	18	8	3
	6	NHM	—	11	6	0
			—	17	6	0
			—	18	7	0
3	7	UAM	S	11	7	5
			S	17	8	4
			S	18	6	2
	8	NHM	—	11	6	0
			—	17	6	0
			—	18	6	0
	9	EAM	C	11	6	1
				17	6	0
			C	18	8	2

[1] Silvicultural system: NHM indicates no-harvest management (—); UAM indicates uneven-aged management by single-tree and group selection (S); EAM indicates even-aged management by clearcutting (C) and thinning (I). None of the six ELT 17 *Armillaria* study plots in site 9 received harvest treatment in 1996.
[2] Ecological landtype, based on slope and aspect: ridges (ELT 11), south- and west-facing side slopes (ELT 17), and north- and east-facing side slopes (ELT 18).
[3] Total plots are the number of plots examined for *Armillaria* in the site. Harvested plots are the number of plots examined for *Armillaria* harvested by the indicated treatment.

were abundant enough for us to detect its presence. Thus, our experimental hypothesis was:

H_0 : Each *Armillaria* species occurs with equal frequency irrespective of MOFEP block, ELT, or proposed silvicultural treatment.

This hypothesis was evaluated separately for *A. gallica* and *A. mellea* using the GLM algorithms of the SAS statistical package to perform analysis of variance (ANOVA). MOFEP block, ELT, and silvicultural treatment served as classification variables. The response variable was the transformed proportion of plots within a site in which the *Armillaria* species of interest was found. The transformation used was the arcsin of the square root of the calculated proportion (Steel and Torrie 1980). Because of the small number of plots per site, the response variable was weighted by the inverse of its variance: $[p(1-p)/n]^{-1}$. The treatment*block interaction was used as "error a," to evaluate the significance of differences among treatments and blocks. The treatment*ELT*block interaction was used as "error b," to evaluate significance of differences among ELT's and the treatment*ELT interaction. Occurrence data for *A. tabescens* will be analyzed after additional field isolates are collected and identified.

Because the ANOVA above combines the 5 to 8 binomial presence/absence data for each ELT/site combination into a single proportion, its ability to detect ELT differences is severely limited. Because of the pre-harvest timing of this evaluation, the silvicultural treatments can be set aside to examine the distributions of *A. gallica* and *A. mellea* among ELT's in each of the three blocks of sites using contingency table analysis of the raw data. We used the general association statistic (GA) of the Cochran-Mantel-Haenszel test (Agresti 1990) for this purpose.

Sampling

Each entire 0.2-ha plot was thoroughly searched at least once, depending on what was collected and what could be observed. The forest floor was scanned carefully for fruiting of *A. mellea* and *A. tabescens* during at least one visit when each species was known to be fruiting on the site. When fruiting was found on a plot, at least one collection was made representing each mushroom morphology type (based on color and stature) encountered. Fruiting at the base of trees was collected preferentially. During every visit, any imminent or recent tree mortality was noted and evaluated for presence of mycelial fans, and these were always collected. Living trees with abnormally few live leaves (and many of these abnormally small and chlorotic) were categorized as "dying." Dead trees retaining fine twig structure and any dead leaves were categorized as "recent-dead" (table 2). During at least one visit, all woody debris, stumps, and dead trees were carefully examined for presence of rhizomorphs. Several rhizomorph samples were collected from each plot whenever possible. Evaluation of a plot was considered complete only after it had been searched thoroughly for all these forms of evidence. The locations of all field collections were mapped for use in ensuing studies of the spatial relationships between *Armillaria* populations, tree vegetation, and oak decline.

Field estimation of an *Armillaria* genet's pathogenicity requires careful consideration of available evidence, including (1) the condition of the woody substrates from which isolates are taken, and (2) the source tissues of the isolate (Gregory *et al.* 1991, Morrison *et al.* 1991). The presence of an *Armillaria* mycelial fan in the root collar cambial region of a dying or recently killed tree constitutes strong evidence of pathogenicity, because mycelial fans represent lethal colonization of the invaded root cambium tissue. Mycelial fans under the bark of long-dead trees may represent necrotrophic colonization unrelated to pathogenicity. Although rhizomorphs are the organs of root infection, rhizomorphs alone are not strong evidence of pathogenicity. Rhizomorphs on root surfaces are either non-pathogenic or have not had appropriate opportunity (e.g., through host stress) to demonstrate their pathogenicity. Because *Armillaria* species fruit well on the forest floor and on woody debris in proximity to living trees, fruiting near a tree is not strong evidence of pathogenicity. Based on these considerations, all of the above structures were used to determine the presence/absence within plots of each *Armillaria* species, but only the presence of a mycelial fan in the root collar of a dying or recently killed tree was interpreted as strong evidence of pathogenicity.

Sample Analysis

Armillaria field isolates representing each study plot were derived from (1) mycelial fans on dying

Table 2.—*Sources of MOFEP* Armillaria *study isolates*[1].

Substrate	Source	*Armillaria* species *gallica*	*Armillaria* species *mellea*
Healthy			
red oaks (subgenus *Erythrobalanus*)			
	mycelial fan or wood	0	0
	mushroom	0	8
	rhizomorph	0	0
white oaks (subgenus *Leucobalanus*)			
	mycelial fan or wood	0	0
	mushroom	0	2
	rhizomorph	0	0
hickories (*Carya* species)			
	mycelial fan or wood	0	0
	mushroom	0	1
	rhizomorph	0	0
other hardwoods[2]			
	mycelial fan or wood	0	0
	mushroom	0	1
	rhizomorph	2	0
pine (*Pinus echinata*)			
	mycelial fan or wood	0	0
	mushroom	0	0
	rhizomorph	0	0
Total (healthy)		2	12
Dying or Recent-dead			
red oaks			
	mycelial fan or wood	3	32
	mushroom	0	41
	rhizomorph	5	1
white oaks			
	mycelial fan or wood	2	1
	mushroom	0	2
	rhizomorph	0	0
hickories			
	mycelial fan or wood	0	0
	mushroom	0	0
	rhizomorph	0	0
other hardwoods[2]			
	mycelial fan or wood	0	0
	mushroom	0	0
	rhizomorph	0	0
pine			
	mycelial fan or wood	1	0
	mushroom	0	0
	rhizomorph	0	3
Total (dying or recent-dead)		11	80
Debris or Dead ≥ 2 yrs			
red oaks			
	mycelial fan or wood	3	39
	mushroom	0	68
	rhizomorph	29	2
white oaks			
	mycelial fan or wood	1	4
	mushroom	0	20
	rhizomorph	13	0
hickories			
	mycelial fan or wood	1	0
	mushroom	0	2
	rhizomorph	21	0
other hardwoods[2]			
	mycelial fan or wood	3	3
	mushroom	0	22
	rhizomorph	59	0
pine			
	mycelial fan or wood	1	0
	mushroom	0	0
	rhizomorph	1	0
Total (debris or dead ≥ 2 yrs)		132	160
Total (all 3 categories)		145	252

[1] The 89 isolates not represented include: *A. gallica* - 15 rhizomorph isolates from unidentifiable woody debris, 1 isolate from a bait potato, and 1 fan isolate with incomplete data; *A. mellea* - 39 forest floor mushroom isolates, 1 fan isolate with incomplete data, and 1 isolate from unidentifiable woody debris; *A. tabescens* - all 31 isolates.

[2] Other hardwoods includes dogwood, red maple, unidentifiable oak, sassafras, and black walnut.

or dead trees, (2) rhizomorphs from dying or dead trees or woody debris on the forest floor, and/or (3) mushrooms. It was necessary to culture *Armillaria* isolates from field samples because reliable species and especially genet identifications are based on tests applied to pure cultures. Initial isolations were made by transferring fungal tissue to petri dishes containing 2-percent (w/v) water agar with 200 micrograms per milliliter streptomycin sulfate. Mushroom caps were torn radially, and internal cap trama tissue for isolation was taken from just above the gills. Mycelial fan isolates were derived using sections of colonized root with intact bark, by sterilizing the bark surface with 20-percent household bleach (1.05-percent NaOCl) and carefully removing a window of bark to expose the fan. Rhizomorph isolates were obtained by soaking 5+-cm rhizomorph lengths in 20-percent household bleach for 7 minutes, blotting them dry in a clean paper towel, and culturing from 1-mm-long sections. Bacterial contamination was eliminated using van Tieghem cells (Tuite 1969). Working cultures were maintained in petri dishes containing 2-percent (w/v) malt extract medium solidified with 2-percent (w/v) agar. Isolates were preserved for long-term storage in sterile distilled water (Richter and Bruhn 1989). The Center for Forest Mycology Research, USDA Forest Products Laboratory, Madison, WI, and the Field Museum of Natural History, Botany Department, Chicago, IL, as well as our own laboratory, serve as permanent repositories for representative *Armillaria* cultures and/or voucher mushroom specimens.

Field isolates were first identified to genet through vegetative incompatibility tests conducted in petri dishes on 3-percent (w/v) malt extract agar (MEA) (Guillaumin *et al.* 1996). Each genet was then identified to species by at least one of several means. The traditional means of determining *Armillaria* species identity is by mating tests in which single-basidiospore (haploid) isolates obtained from a mushroom representing an unidentified field genet are mated in petri dish culture with single-basidiospore "tester" isolates of known species identity (Guillaumin *et al.* 1991). For this purpose, we have used a set of tester isolates identified and provided to us by Dr. James B. Anderson (Dept. of Botany, University of Toronto). In compatible matings, characteristic morphological changes occur as the tester isolate becomes converted to a diploid condition. Although single-basidiospore isolates may be derived for some genets through *in vitro* fruiting of field isolates (Darmono *et al.* 1993, Garraway *et al.* 1991), other means of identification are required for the preponderance of genets that do not readily fruit in culture. In so-called "diploid-haploid" pairing tests, tester isolates are paired with unidentified field isolates (presumed diploid). Conversion of the haploid tester isolate to diploid morphology occurs if the paired isolates are conspecific , (Korhonen 1978, Rizzo and Harrington 1992).

Because both types of mating test are time consuming and laborious, we also evaluated more efficient methods of speciation. All MOFEP isolates of our *Armillaria* species could be distinguished on the basis of their growth rate and culture morphology either or both (1) after 7 weeks incubation on 1.5-percent (w/v) MEA in the dark at 33°C, or (2) after 7 weeks incubation on tannic acid agar (Davidson *et al.* 1938) at 24°C in the dark. We also found it possible to distinguish nearly all of our MOFEP isolates on the basis of their esterase and polyphenoloxidase enzyme complements. Having developed these two supplementary systems for *Armillaria* isolate identification, we learned in late 1994 of a much faster new technique for *Armillaria* isolate speciation using RFLP and PCR analysis of genetic patterns in the intergenic spacer (IGS) region of the ribosomal RNA operon (Harrington and Wingfield 1995). We currently rely on either diploid-haploid pairings or PCR analysis of the ribosomal RNA operon to speciate field isolates.

Considering the potentially very large sizes of *Armillaria* genets (e.g., Shaw and Roth 1976, Smith *et al.* 1992), we evaluated the possibility that any of the detected genets might occupy a territory large enough to span more than one study plot. To do this, we conducted somatic compatibility tests between isolates representing all genets of each species occurring on neighboring plots. These tests involved 71 plots, and included 40 genets of *A. gallica* from 36 plots, 60 genets of *A. mellea* from 41 plots, and 7 genets of *A. tabescens* from 6 plots.

RESULTS

Sample Collection

Establishment of the large collection of MOFEP *Armillaria* field isolates required for this initial study is nearly complete. All of the 485 field isolates obtained in 1993-1995 from 180 of the

permanent MOFEP plots have been identified as representing 431 genets belonging to three *Armillaria* species (140 genets of *A. gallica*, 261 genets of *A. mellea*, and 30 genets of *A. tabescens*). No genet was encountered on more than one of our study plots. As many as four genets and three species have been recovered from individual plots.

Armillaria gallica was collected mostly as rhizomorphs (90 percent of collections), seldom as mycelial fans (9 percent); we have not yet found *A. gallica* fruiting in the study plots. *Armillaria mellea* has been collected rarely as rhizomorphs (2 percent), and mostly as mycelial fans (27 percent) or mushrooms (70 percent); *A. mellea* fruited well October 11-22, 1993, August 24 to September 13, 1994, and October 3-11, 1995. *Armillaria tabescens* has never been collected as rhizomorphs, but mostly as mycelial fans (52 percent) or mushrooms (48 percent); *A. tabescens* fruited well mid-August to September 8, 1993 and August 26 to September 7, 1994, but poorly in mid-October 1995. Final evaluation of *A. tabescens* distribution is postponed pending collection of additional field data during a year favorable for fruiting.

Isolates of *A. gallica*, *A. mellea*, and *A. tabescens*, respectively, were derived from mycelial fans at the root crowns of 5, 33, and 3 declining or recently killed hardwood trees (table 2, *A. tabescens* data not shown). This represents 4 percent, 13 percent, and 10 percent, respectively, of the isolates included in table 2 (*A. tabescens* data not shown). *Armillaria mellea* appears to be quite virulent, *A. tabescens* appears to be intermediate in virulence, and *A. gallica* appears to be relatively avirulent (though probably capable of butt rot).

Armillaria Species Distributions

Results of our 3-year survey clearly portray the pre-treatment distributions of *A. gallica* and *A. mellea* in MOFEP's upland forests (table 3).

Table 3.—*Frequencies of detection of* Armillaria gallica *and* A. mellea *on 180 randomly selected 0.2-ha permanent vegetation plots, by ELT within the nine MOFEP sites*[1].

Species	ELT[2]	Status	Site[3]									
			1	2	3	4	5	6	7	8	9	Total
A. gallica	11	Present	6	6	3	4	7	5	3	3	3	40
		Absent	0	1	3	2	0	1	4	3	2	16
	17	Present	3	3	5	4	5	5	1	0	2	28
		Absent	3	3	3	3	3	1	7	6	4	33
	18	Present	6	8	5	6	6	5	4	2	4	46
		Absent	1	0	1	0	2	1	2	4	3	14
A. mellea	11	Present	4	7	5	6	4	5	7	6	6	50
		Absent	2	0	1	0	2	1	0	0	0	6
	17	Present	6	5	7	6	6	5	8	5	6	54
		Absent	0	1	1	1	2	1	0	1	0	7
	18	Present	7	6	4	6	8	7	6	6	8	58
		Absent	0	2	1	0	0	0	0	0	0	3

[1] Tabular values are the numbers of plots for which evaluation is complete in which the specified *Armillaria* species has been detected (present) or has not been detected (absent).
[2] Ecological land type, based on slope and aspect: ridges (ELT 11), south- and west-facing side slopes (ELT 17), and north- and east-facing side slopes (ELT 18).
[3] Sites 1-3 comprise statistical block 1; sites 4-6 comprise statistical block 2; sites 7-9 comprise statistical block 3. Sites 1, 6, and 8 will remain uncut; sites 2, 4, and 7 are receiving uneven-aged management; sites 3, 5, and 9 are receiving even-aged management.

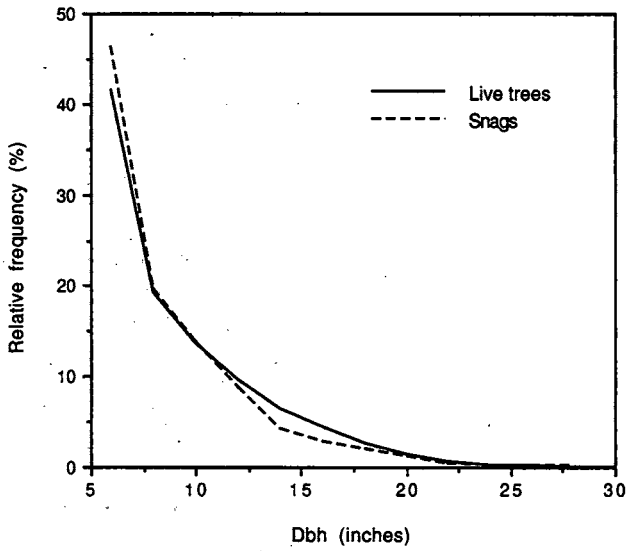

Figure 1.—*Relative frequency of number of snags and live trees by d.b.h. class for all nine MOFEP sites combined. Note the strong similarity in diameter distributions for snags and live trees.*

generally expect little change in the relative size distribution of snags for the no-harvest treatment. Intermediate thinning operations as part of the even-aged and uneven-aged treatments may eventually reduce relative snag densities by harvesting declining trees before they die, particularly trees in the commercial size classes. In the short term, however, thinning practices may have the opposite impact on the relative proportion of snags. At sites 2 through 5 (even- and uneven-aged harvest treatments), loggers exercised their option to simply girdle rather than fell many culls and submerchantable trees that were marked for removal. This will result in a large relative increase in the number of snags while temporarily delaying inputs of dead wood to the forest floor. Treatments that affect the number and size distribution of snags should eventually be reflected in differences in the quantity of down wood, because large volumes of down wood result when snags (or portions thereof) fall to the forest floor.

CONCLUSIONS

Analyses of the pre-treatment MOFEP data revealed no statistically significant ($P \geq 0.05$) differences in the number of snags or the basal area of snags by treatment class. Nor were treatment class differences observed in the volume of down wood or the percentage of the ground area covered by down wood. This is the desired condition before implementation of the treatments. For those same forest attributes, the block effect (assignment of sites to blocks based on spatial proximity) was not significant. Sites 6, 7, and 8 stand out in having more snags and higher snag basal areas than the other sites. In general, snag and down wood attributes observed for the MOFEP sites were consistent with those reported for other sites in the region. The volume of down wood is expected to increase on all sites after treatment. We suspect that the ratio of snags to live trees (in composite or by d.b.h. class) will be a reasonably sensitive indicator of changes in snag conditions over time.

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Determination of the Ecological and Geographic Distributions of *Armillaria* Species in Missouri Ozark Forest Ecosystems

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Abstract.—Armillaria root rot contributes to oak decline in the Ozarks. Three *Armillaria* species were detected in Ecological Landtypes (ELT's) representing south- to west-facing side slopes (ELT 17), north- to east-facing side slopes (ELT 18), and ridge tops (ELT 11). *Armillaria mellea* was detected in 91 percent of 180 study plots; was detected with equal frequency in all three ELT's; and was ubiquitous in block 3. *Armillaria gallica* was detected in 64 percent of the study plots; was detected least frequently in block 3; and was detected least frequently on ELT 17 in block 3. The distribution of *A. tabescens* remains incompletely resolved; it is the least abundant species and the most difficult to survey. *Armillaria mellea* was much more frequently associated with oak mortality than were *A. gallica* or *A. tabescens*, based on isolations from dying or recently killed trees. If these three species compete for substrate, oak decline levels may be influenced by landscape patterns of *Armillaria* species co-occurrence. We hypothesize that oak decline will be most severe in block 3, and especially on ELT 17, where *A. mellea* most often occurs in the absence of *A. gallica*.

Armillaria (Fr.:Fr.) Staude is a white-rot wood decay fungus genus (Fungi, Agaricales) comprising about 40 species worldwide (Volk and Burdsall 1995, Watling *et al.* 1991). Due to similarities in the morphology of *Armillaria* mushrooms, mycelial fans, and rhizomorphs, all annulate North American *Armillaria* were widely thought to belong to a single highly variable species (*Armillaria mellea*) until the late 1970's. Following Hintikka's (1973) description of a mating test for distinguishing *Armillaria* species using pedigreed single-basidiospore isolates, great progress has been made in clarifying biological, ecological and taxonomic issues concerning *Armillaria* species (Korhonen 1995). The name *Armillaria mellea* (Vahl:Fr.) Kummer now clearly represents a single *Armillaria* species, the type species of the entire genus (Watling *et al.* 1991). The exact number of *Armillaria* species in North America remains uncertain due to insufficient study. Unfortunately, much of the *Armillaria* literature well into the 1980's is of limited value because the correct identity of the *Armillaria* species studied was never established. This is the initial report of the first formal study of the *Armillaria* species influencing forest structure in upland Ozark oak-hickory forests. The three *Armillaria* species encountered were *A. gallica* Marxmüller & Romagnesi, *A. mellea*, and *A. tabescens* (Scop.) Emel.

A portion of the energy derived by *Armillaria* mycelia from wood decay (Garraway *et al.* 1991) is spent on sexual reproduction of airborne basidiospores on mushroom gills. Each spore that successfully germinates to colonize a suitable woody substrate (food base) generally mates with another sexually compatible germling to form a genetically unique individual ("genet," *sensu* Harper 1977) that may become established in the landscape as an agent of wood decomposition and perhaps of root disease and forest decline (Anderson and Kohn 1996, Guillaumin *et al.* 1991).

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Genets of all *Armillaria* species are functionally territorial, enlarging through sequential colonization of woody food bases by branching, cord-like rhizomorph systems and/or growth across root contacts and grafts (Gregory *et al.* 1991, Morrison *et al.* 1991, Redfern and Filip 1991). Rhizomorph growth is fueled with energy and nutrients derived from food base decay (Anderson and Ullrich 1982, Garrett 1956, Rishbeth 1972) and from the soil through which the rhizomorphs grow (Morrison 1975). *Armillaria* rhizomorph production is generally increased when using hardwood compared with conifer food bases (Redfern and Filip 1991). Because *Armillaria* species do not produce asexual spores, *Armillaria* genets are potentially continuous in the forest floor. *Armillaria* genets are also potentially long-lived and can achieve great size (Anderson and Kohn 1996, Bruhn *et al.* 1997, Korhonen 1978, Legrand *et al.* 1996, Rishbeth 1991, Shaw and Roth 1976, Smith *et al.* 1992), especially when compared with most vegetation.

Armillaria species differ in host preference and virulence; genets of the same species can also differ in virulence. Studies elsewhere of *Armillaria* species that also occur in the Ozarks have concluded that *A. mellea* is much more virulent than either *A. gallica* or *A. tabescens* (Gregory *et al.* 1991, Guillaumin *et al.* 1993, Redfern and Filip 1991, Rishbeth 1991). *Armillaria mellea* and *A. gallica* are generally considered to be much more common than *A. tabescens* (which can be locally abundant). *Armillaria mellea* is capable of attacking and killing a wide variety of hardwoods and a smaller range of conifers (mainly non-resinous species). *Armillaria gallica* is more restricted to colonizing dying or dead material and causing butt rot of hardwoods. In western Europe, *A. tabescens* is considered the least virulent of the three species, largely restricted to hardwood stumps. A notable exception is primary parasitism by *A. tabescens* of exotic *Eucalyptus* species in southwest France. North American *A. tabescens* has a large host range and may be somewhat more virulent than European *A. tabescens* (Sinclair *et al.* 1987). However, Rhoads (1925, 1956) indicated that exotic and cultivated tree species were much more susceptible than native tree species to North American *A. tabescens*, especially when planted on land previously cleared of oak forest.

Armillaria species (and genet) distributions are related to long-term vegetation and Ecological Land Type (ELT) characteristics (Bruhn *et al.* 1994, Korhonen 1978, Rishbeth 1982). The mechanisms by which neighboring *Armillaria* genets of the same or different species interact to allocate space among themselves are not yet clear. Where the perimeters of *Armillaria* genets meet or overlap, genets may interact as a result of niche overlap and competitive exclusion (Leibold 1995, Mohammed and Guillaumin 1989). Genets of different *Armillaria* species may circumvent each other as a result of different colonization strategies (Legrand *et al.* 1996). Nevertheless, the activity levels of *Armillaria* genets adjust to changes in the environment (*e.g.*, climate, defoliation, vegetation management) that affect the supply of food bases and the vulnerability of potential hosts (Bruhn *et al.* 1994, Lonsdale and Gibbs 1996, Wargo 1996, Wargo and Harrington 1991). The spatial arrangements and ecological attributes of *Armillaria* genets help shape long-term forest community structure in response to perturbations (Lundquist 1993, Worrall and Harrington 1988), because each extant combination of genets contributes differently to the regulation of stand structure and composition.

Armillaria species are often implicated as opportunistic root parasites contributing to forest declines incited by various stress events (Bauce and Allen 1992, Clinton *et al.* 1993, Houston 1992, Johnson and Law 1989, Kile *et al.* 1991, Wargo 1996). Both excess moisture and drought during the growing season are capable of inciting *Armillaria* root disease (e.g., Lonsdale and Gibbs 1996, Wargo and Harrington 1991). Rhoads (1956) found that droughty acidic sites predisposed trees to attack in Florida, whereas poorly drained soils on former oak sites predisposed grape plants to attack in Missouri (Rhoads 1925). A study of oak decline in upland Ozark forests showed that the growth rates of trees that eventually died did not recover following severe drought (compared to similar trees that remained healthy), and that growth of declining trees was further depressed with each succeeding drought (Dwyer *et al.* 1995). This scenario is consistent with a combined *Armillaria* + drought etiology. A relationship has been recognized between predisposing stress events (e.g., drought, late frost, defoliation), Armillaria root disease, and oak decline and mortality in the Missouri Ozarks (Johnson and Law 1989, Law and Gott 1987), though the identities of the *Armillaria* species involved and the nature and extent of their involvement and interactions were not determined. The black/

scarlet oak cover type occupies approximately 2 x 10^6 ha in Missouri. Affecting over 7.2 x 10^5 ha on the Mark Twain National Forest alone, oak decline has been most severe on Captina silt loam soils situated on broad ridges and moderately severe on Clarksville silt loam soils with west aspects (Law and Gott 1987). If predictions of greater climatic instability including more frequent summer droughts prove correct (Joyce *et al.* 1990, Kraüchi 1993, Rind *et al.* 1990), the resultant physiological stress to forest trees could heighten levels of *Armillaria* root disease and associated forest decline.

The shortage of previous knowledge about *Armillaria* distributions and activities in upland Ozark forests is related to the lack of attention paid to this geographic region by mycologists in the past and the difficulty of distinguishing the annulate *Armillaria* species in the field. Once the distributions and behaviors of Ozark *Armillaria* species are clarified, it will be possible to devise silvicultural programs that consider this pivotal genus of forest fungi.

Objectives

The goal of our study is to use ecological characteristics to explain the pre-treatment geographic distributions and behavioral patterns of all *Armillaria* species occurring in the nine MOFEP sites. Characteristics to be considered include forest vegetation cover and ELT variables describing geo-landform, soils, and climate. Data describing these variables for the permanent vegetation plots are gradually becoming available (Chen *et al.* 1997, Kabrick *et al.* 1997, Meinert *et al.* 1997). As a result, the pre-treatment distribution of *Armillaria* species with respect to oak decline occurrence and severity will be clarified.

Our initial research objectives are:

1. to identify all *Armillaria* species occurring in the nine MOFEP sites before treatment;
2. to test the hypotheses that each *Armillaria* species is initially uniformly distributed: (a) among the three silvicultural treatments, (b) among the three blocks of sites, and (c) among ELT's characterized by ridgetops, south- to west-facing side slopes, and north- to east-facing side slopes; and
3. to formulate hypotheses based on field observations concerning the pre-treatment relationship of each *Armillaria* species to the occurrence of oak decline.

METHODS

Experimental Design

MOFEP is designed to evaluate the responses of forest vegetation (and other forest life-forms) to even-aged (EAM), uneven-aged (UAM), and no-harvest (NHM) management. Over 600 permanent 0.2-ha study plots (fig. 4 in Brookshire *et al.* 1997) have been established in nine sites of approximately 400 ha each. The nine sites are arranged in three blocks of three sites each. One site in each block has been allocated to each of the three types of management (fig. 1 in Brookshire *et al.* 1997). Approximately 10 percent of each EAM and UAM site have been set aside from harvest. Within each site, plots were allocated to ELT's approximately in proportion to site land area represented by each ELT. Three upland ELT's (designated 11, 17, and 18) dominate the study sites (Miller 1981). These three ELT's can be roughly described as ridgetops, south- to west-facing side slopes, and north- to east-facing side slopes, respectively (fig. 2 in Brookshire *et al.* 1997). Overstory vegetation associated with these three ELT's is mostly mature second-growth oak, hickory, and shortleaf pine. Logging has not occurred in any of the nine sites for at least 40 years. Experimental cutting in the EAM and UAM sites began in the spring of 1996.

Because we plan to build on this *Armillaria* distribution study with studies of responses of *Armillaria* species and vegetation to silvicultural treatments, we anticipated need for at least six study plots (per ELT per site) that receive the treatment assigned to that site. Permanent vegetation plots representing each of the three dominant upland ELT's in each of the nine MOFEP sites were randomly selected for this study (fig. 5 in Brookshire *et al.* 1997). Because 11 of our originally selected plots are located in stands subsequently reserved from treatment (designated OG, "old growth"), and to include all permanent vegetation plots in which weather data are being collected (Chen *et al.* 1997), we now have *Armillaria* distribution data for 180 plots rather than the 162 plots originally selected (table 1). Of these, 64 plots received silvicultural treatment in 1996 (table 1). Although it would be difficult to confirm the absence of an *Armillaria* species from a study plot, we assume that the inability to detect a particular *Armillaria* species in the vicinity of a plot constitutes strong evidence that the species is ecologically much less influential than if it

Table 1.—*Distribution of* Armillaria *study plots among statistical blocks, forest sites, silvicultural systems, ecological land types, and type of harvest activity*

Block	Site	Silvic. system[1]	Harvest treatment[1]	ELT[2]	Total plots[3]	Harvested plots[3]
1	1	NHM	—	11	6	0
			—	17	6	0
			—	18	7	0
	2	UAM	S	11	7	7
			S	17	6	3
			S	18	8	5
	3	EAM	I	11	6	2
			I	17	8	1
			C	17	8	1
			I	18	6	4
			C	18	6	1
2	4	UAM	S	11	6	6
			S	17	7	5
			S	18	6	6
	5	EAM	I	11	7	4
			C	17	8	1
			I	18	8	1
			C	18	8	3
	6	NHM	—	11	6	0
			—	17	6	0
			—	18	7	0
3	7	UAM	S	11	7	5
			S	17	8	4
			S	18	6	2
	8	NHM	—	11	6	0
			—	17	6	0
			—	18	6	0
	9	EAM	C	11	6	1
				17	6	0
			C	18	8	2

[1] Silvicultural system: NHM indicates no-harvest management (—); UAM indicates uneven-aged management by single-tree and group selection (S); EAM indicates even-aged management by clearcutting (C) and thinning (I). None of the six ELT 17 *Armillaria* study plots in site 9 received harvest treatment in 1996.
[2] Ecological landtype, based on slope and aspect: ridges (ELT 11), south- and west-facing side slopes (ELT 17), and north- and east-facing side slopes (ELT 18).
[3] Total plots are the number of plots examined for *Armillaria* in the site. Harvested plots are the number of plots examined for *Armillaria* harvested by the indicated treatment.

were abundant enough for us to detect its presence. Thus, our experimental hypothesis was:

H_0 : Each *Armillaria* species occurs with equal frequency irrespective of MOFEP block, ELT, or proposed silvicultural treatment.

This hypothesis was evaluated separately for *A. gallica* and *A. mellea* using the GLM algorithms of the SAS statistical package to perform analysis of variance (ANOVA). MOFEP block, ELT, and silvicultural treatment served as classification variables. The response variable was the transformed proportion of plots within a site in which the *Armillaria* species of interest was found. The transformation used was the arcsin of the square root of the calculated proportion (Steel and Torrie 1980). Because of the small number of plots per site, the response variable was weighted by the inverse of its variance: $[p(1-p)/n]^{-1}$. The treatment*block interaction was used as "error a," to evaluate the significance of differences among treatments and blocks. The treatment*ELT*block interaction was used as "error b," to evaluate significance of differences among ELT's and the treatment*ELT interaction. Occurrence data for *A. tabescens* will be analyzed after additional field isolates are collected and identified.

Because the ANOVA above combines the 5 to 8 binomial presence/absence data for each ELT/site combination into a single proportion, its ability to detect ELT differences is severely limited. Because of the pre-harvest timing of this evaluation, the silvicultural treatments can be set aside to examine the distributions of *A. gallica* and *A. mellea* among ELT's in each of the three blocks of sites using contingency table analysis of the raw data. We used the general association statistic (GA) of the Cochran-Mantel-Haenszel test (Agresti 1990) for this purpose.

Sampling

Each entire 0.2-ha plot was thoroughly searched at least once, depending on what was collected and what could be observed. The forest floor was scanned carefully for fruiting of *A. mellea* and *A. tabescens* during at least one visit when each species was known to be fruiting on the site. When fruiting was found on a plot, at least one collection was made representing each mushroom morphology type (based on color and stature) encountered. Fruiting at the base of trees was collected preferentially. During every visit, any imminent or recent tree mortality was noted and evaluated for presence of mycelial fans, and these were always collected. Living trees with abnormally few live leaves (and many of these abnormally small and chlorotic) were categorized as "dying." Dead trees retaining fine twig structure and any dead leaves were categorized as "recent-dead" (table 2). During at least one visit, all woody debris, stumps, and dead trees were carefully examined for presence of rhizomorphs. Several rhizomorph samples were collected from each plot whenever possible. Evaluation of a plot was considered complete only after it had been searched thoroughly for all these forms of evidence. The locations of all field collections were mapped for use in ensuing studies of the spatial relationships between *Armillaria* populations, tree vegetation, and oak decline.

Field estimation of an *Armillaria* genet's pathogenicity requires careful consideration of available evidence, including (1) the condition of the woody substrates from which isolates are taken, and (2) the source tissues of the isolate (Gregory *et al.* 1991, Morrison *et al.* 1991). The presence of an *Armillaria* mycelial fan in the root collar cambial region of a dying or recently killed tree constitutes strong evidence of pathogenicity, because mycelial fans represent lethal colonization of the invaded root cambium tissue. Mycelial fans under the bark of long-dead trees may represent necrotrophic colonization unrelated to pathogenicity. Although rhizomorphs are the organs of root infection, rhizomorphs alone are not strong evidence of pathogenicity. Rhizomorphs on root surfaces are either non-pathogenic or have not had appropriate opportunity (e.g., through host stress) to demonstrate their pathogenicity. Because *Armillaria* species fruit well on the forest floor and on woody debris in proximity to living trees, fruiting near a tree is not strong evidence of pathogenicity. Based on these considerations, all of the above structures were used to determine the presence/absence within plots of each *Armillaria* species, but only the presence of a mycelial fan in the root collar of a dying or recently killed tree was interpreted as strong evidence of pathogenicity.

Sample Analysis

Armillaria field isolates representing each study plot were derived from (1) mycelial fans on dying

Table 2.—*Sources of MOFEP* Armillaria *study isolates*[1].

Substrate	Source	*Armillaria* species *gallica*	*Armillaria* species *mellea*
Healthy			
red oaks (subgenus *Erythrobalanus*)			
	mycelial fan or wood	0	0
	mushroom	0	8
	rhizomorph	0	0
white oaks (subgenus *Leucobalanus*)			
	mycelial fan or wood	0	0
	mushroom	0	2
	rhizomorph	0	0
hickories (*Carya* species)			
	mycelial fan or wood	0	0
	mushroom	0	1
	rhizomorph	0	0
other hardwoods[2]			
	mycelial fan or wood	0	0
	mushroom	0	1
	rhizomorph	2	0
pine (*Pinus echinata*)			
	mycelial fan or wood	0	0
	mushroom	0	0
	rhizomorph	0	0
Total (healthy)		2	12
Dying or Recent-dead			
red oaks			
	mycelial fan or wood	3	32
	mushroom	0	41
	rhizomorph	5	1
white oaks			
	mycelial fan or wood	2	1
	mushroom	0	2
	rhizomorph	0	0
hickories			
	mycelial fan or wood	0	0
	mushroom	0	0
	rhizomorph	0	0
other hardwoods[2]			
	mycelial fan or wood	0	0
	mushroom	0	0
	rhizomorph	0	0
pine			
	mycelial fan or wood	1	0
	mushroom	0	0
	rhizomorph	0	3
Total (dying or recent-dead)		11	80
Debris or Dead ≥ 2 yrs			
red oaks			
	mycelial fan or wood	3	39
	mushroom	0	68
	rhizomorph	29	2
white oaks			
	mycelial fan or wood	1	4
	mushroom	0	20
	rhizomorph	13	0
hickories			
	mycelial fan or wood	1	0
	mushroom	0	2
	rhizomorph	21	0
other hardwoods[2]			
	mycelial fan or wood	3	3
	mushroom	0	22
	rhizomorph	59	0
pine			
	mycelial fan or wood	1	0
	mushroom	0	0
	rhizomorph	1	0
Total (debris or dead ≥ 2 yrs)		132	160
Total (all 3 categories)		145	252

[1] The 89 isolates not represented include: *A. gallica* - 15 rhizomorph isolates from unidentifiable woody debris, 1 isolate from a bait potato, and 1 fan isolate with incomplete data; *A. mellea* - 39 forest floor mushroom isolates, 1 fan isolate with incomplete data, and 1 isolate from unidentifiable woody debris; *A. tabescens* - all 31 isolates.

[2] Other hardwoods includes dogwood, red maple, unidentifiable oak, sassafras, and black walnut.

or dead trees, (2) rhizomorphs from dying or dead trees or woody debris on the forest floor, and/or (3) mushrooms. It was necessary to culture *Armillaria* isolates from field samples because reliable species and especially genet identifications are based on tests applied to pure cultures. Initial isolations were made by transferring fungal tissue to petri dishes containing 2-percent (w/v) water agar with 200 micrograms per milliliter streptomycin sulfate. Mushroom caps were torn radially, and internal cap trama tissue for isolation was taken from just above the gills. Mycelial fan isolates were derived using sections of colonized root with intact bark, by sterilizing the bark surface with 20-percent household bleach (1.05-percent NaOCl) and carefully removing a window of bark to expose the fan. Rhizomorph isolates were obtained by soaking 5+-cm rhizomorph lengths in 20-percent household bleach for 7 minutes, blotting them dry in a clean paper towel, and culturing from 1-mm-long sections. Bacterial contamination was eliminated using van Tieghem cells (Tuite 1969). Working cultures were maintained in petri dishes containing 2-percent (w/v) malt extract medium solidified with 2-percent (w/v) agar. Isolates were preserved for long-term storage in sterile distilled water (Richter and Bruhn 1989). The Center for Forest Mycology Research, USDA Forest Products Laboratory, Madison, WI, and the Field Museum of Natural History, Botany Department, Chicago, IL, as well as our own laboratory, serve as permanent repositories for representative *Armillaria* cultures and/or voucher mushroom specimens.

Field isolates were first identified to genet through vegetative incompatibility tests conducted in petri dishes on 3-percent (w/v) malt extract agar (MEA) (Guillaumin *et al.* 1996). Each genet was then identified to species by at least one of several means. The traditional means of determining *Armillaria* species identity is by mating tests in which single-basidiospore (haploid) isolates obtained from a mushroom representing an unidentified field genet are mated in petri dish culture with single-basidiospore "tester" isolates of known species identity (Guillaumin *et al.* 1991). For this purpose, we have used a set of tester isolates identified and provided to us by Dr. James B. Anderson (Dept. of Botany, University of Toronto). In compatible matings, characteristic morphological changes occur as the tester isolate becomes converted to a diploid condition. Although single-basidiospore isolates may be derived for some genets through *in vitro* fruiting of field isolates (Darmono *et al.* 1993, Garraway *et al.* 1991), other means of identification are required for the preponderance of genets that do not readily fruit in culture. In so-called "diploid-haploid" pairing tests, tester isolates are paired with unidentified field isolates (presumed diploid). Conversion of the haploid tester isolate to diploid morphology occurs if the paired isolates are conspecific , (Korhonen 1978, Rizzo and Harrington 1992).

Because both types of mating test are time consuming and laborious, we also evaluated more efficient methods of speciation. All MOFEP isolates of our *Armillaria* species could be distinguished on the basis of their growth rate and culture morphology either or both (1) after 7 weeks incubation on 1.5-percent (w/v) MEA in the dark at 33°C, or (2) after 7 weeks incubation on tannic acid agar (Davidson *et al.* 1938) at 24°C in the dark. We also found it possible to distinguish nearly all of our MOFEP isolates on the basis of their esterase and polyphenoloxidase enzyme complements. Having developed these two supplementary systems for *Armillaria* isolate identification, we learned in late 1994 of a much faster new technique for *Armillaria* isolate speciation using RFLP and PCR analysis of genetic patterns in the intergenic spacer (IGS) region of the ribosomal RNA operon (Harrington and Wingfield 1995). We currently rely on either diploid-haploid pairings or PCR analysis of the ribosomal RNA operon to speciate field isolates.

Considering the potentially very large sizes of *Armillaria* genets (e.g., Shaw and Roth 1976, Smith *et al.* 1992), we evaluated the possibility that any of the detected genets might occupy a territory large enough to span more than one study plot. To do this, we conducted somatic compatibility tests between isolates representing all genets of each species occurring on neighboring plots. These tests involved 71 plots, and included 40 genets of *A. gallica* from 36 plots, 60 genets of *A. mellea* from 41 plots, and 7 genets of *A. tabescens* from 6 plots.

RESULTS

Sample Collection

Establishment of the large collection of MOFEP *Armillaria* field isolates required for this initial study is nearly complete. All of the 485 field isolates obtained in 1993-1995 from 180 of the

permanent MOFEP plots have been identified as representing 431 genets belonging to three *Armillaria* species (140 genets of *A. gallica*, 261 genets of *A. mellea*, and 30 genets of *A. tabescens*). No genet was encountered on more than one of our study plots. As many as four genets and three species have been recovered from individual plots.

Armillaria gallica was collected mostly as rhizomorphs (90 percent of collections), seldom as mycelial fans (9 percent); we have not yet found *A. gallica* fruiting in the study plots. *Armillaria mellea* has been collected rarely as rhizomorphs (2 percent), and mostly as mycelial fans (27 percent) or mushrooms (70 percent); *A. mellea* fruited well October 11-22, 1993, August 24 to September 13, 1994, and October 3-11, 1995. *Armillaria tabescens* has never been collected as rhizomorphs, but mostly as mycelial fans (52 percent) or mushrooms (48 percent); *A. tabescens* fruited well mid-August to September 8, 1993 and August 26 to September 7, 1994, but poorly in mid-October 1995. Final evaluation of *A. tabescens* distribution is postponed pending collection of additional field data during a year favorable for fruiting.

Isolates of *A. gallica*, *A. mellea*, and *A. tabescens*, respectively, were derived from mycelial fans at the root crowns of 5, 33, and 3 declining or recently killed hardwood trees (table 2, *A. tabescens* data not shown). This represents 4 percent, 13 percent, and 10 percent, respectively, of the isolates included in table 2 (*A. tabescens* data not shown). *Armillaria mellea* appears to be quite virulent, *A. tabescens* appears to be intermediate in virulence, and *A. gallica* appears to be relatively avirulent (though probably capable of butt rot).

Armillaria Species Distributions

Results of our 3-year survey clearly portray the pre-treatment distributions of *A. gallica* and *A. mellea* in MOFEP's upland forests (table 3).

Table 3.—*Frequencies of detection of* Armillaria gallica *and* A. mellea *on 180 randomly selected 0.2-ha permanent vegetation plots, by ELT within the nine MOFEP sites*[1].

Species	ELT[2]	Status	Site[3]									
			1	2	3	4	5	6	7	8	9	Total
A. gallica	11	Present	6	6	3	4	7	5	3	3	3	40
		Absent	0	1	3	2	0	1	4	3	2	16
	17	Present	3	3	5	4	5	5	1	0	2	28
		Absent	3	3	3	3	3	1	7	6	4	33
	18	Present	6	8	5	6	6	5	4	2	4	46
		Absent	1	0	1	0	2	1	2	4	3	14
A. mellea	11	Present	4	7	5	6	4	5	7	6	6	50
		Absent	2	0	1	0	2	1	0	0	0	6
	17	Present	6	5	7	6	6	5	8	5	6	54
		Absent	0	1	1	1	2	1	0	1	0	7
	18	Present	7	6	4	6	8	7	6	6	8	58
		Absent	0	2	1	0	0	0	0	0	0	3

[1] Tabular values are the numbers of plots for which evaluation is complete in which the specified *Armillaria* species has been detected (present) or has not been detected (absent).
[2] Ecological land type, based on slope and aspect: ridges (ELT 11), south- and west-facing side slopes (ELT 17), and north- and east-facing side slopes (ELT 18).
[3] Sites 1-3 comprise statistical block 1; sites 4-6 comprise statistical block 2; sites 7-9 comprise statistical block 3. Sites 1, 6, and 8 will remain uncut; sites 2, 4, and 7 are receiving uneven-aged management; sites 3, 5, and 9 are receiving even-aged management.

ANOVA detected significant distributional differences among the three statistical blocks for both *A. gallica* ($P = 0.036$) and *A. mellea* ($P = 0.046$) (table 4). Though *A. mellea* was common on all three ELT's in all nine sites (table 3), it was nearly ubiquitous in block 3 (i.e., sites 7-9, the Peck Ranch) compared with blocks 1 and 2. *Armillaria mellea* was detected in 86, 88, and 98 percent of the study plots in blocks 1, 2, and 3, respectively (table 5). In contrast, *A. gallica* was much less commonly detected in block 3 than in blocks 1 and 2. *Armillaria gallica* was detected in 75, 78, and 39 percent of the same study plots in blocks 1, 2 and 3, respectively (table 5). The distribution record for *A. tabescens* is only complete for the no-harvest management treatment (sites 1, 6, and 8), where *A. tabescens* was found in 39, 39, and 18 percent of the study plots in blocks 1, 2, and 3, respectively. ANOVA detected no differences in *Armillaria* species occurrence among treatments or ELT's.

When the distributions of *A. gallica* and *A. mellea* among the three study ELT's were examined for each block using contingency table analysis of the raw presence/absence data, the Cochran-Mantel-Haenszel test detected no difference in the frequencies with which *A. mellea* was detected on the three study ELT's (block 1: GA = 0.327, df = 2, $P = 0.849$; block 2: GA = 4.248, df = 2, $P = 0.120$; block 3: GA = 1.950, df = 2, $P = 0.377$). Significant differences were detected in the frequencies with which *A. gallica* was detected on the three study ELT's in blocks 1 and 3 (block 1: GA = 6.989, df = 2, $P = 0.030$; block 2: GA = 2.551, df = 2, $P = 0.279$; block 3: GA = 7.138, df = 2, $P = 0.028$). In block 1, *A. gallica* occurred on only 55 percent of south- to west-facing side slope plots, 79 percent of ridgetop plots, and 90 percent of north- to east-facing side slope plots. In block 3, *A. gallica* occurred on only 15 percent of south- to west-facing side slope plots, compared with 50 percent of ridgetop plots, and 53 percent of north- to east-facing side slope plots.

Table 4.—*Analysis of variance table for evaluating distribution of* Armillaria gallica *and* A. mellea *among MOFEP plots relative to block, silvicultural treatment, and ELT.*

Species	Source of variation[1]	df[2]	Type III SS[3]	F[4]	Pr > F[5]
A. gallica	Block	2	39.3	8.5	0.036
	Treatment	2	5.0	1.1	0.423
	Error a (Treatment*Block)	4	9.3	.	.
	ELT	2	0.7	0.2	0.839
	Treatment*ELT	4	13.6	1.7	0.222
	Error b (Treatment*ELT*Block)	12	24.5	.	.
A. mellea	Block	2	73.5	7.4	0.046
	Treatment	2	6.1	0.6	0.588
	Error a (Treatment*Block)	4	20.0	.	.
	ELT	2	19.1	0.2	0.844
	Treatment*ELT	4	38.8	0.2	0.947
	Error b (Treatment*ELT*Block)	12	664.5	.	.

[1] Silvicultural treatment: even-aged management, uneven-aged management, or no-harvest management; ELT, ecological landtype based on slope and aspect: ridges, south- and west-facing side slopes, or north- and east-facing side slopes.
[2] df: degrees of freedom.
[3] Type III SS: sums of squares values associated with the indicated sources of variation.
[4] F: F-statistic associated with the indicated source of variation.
[5] Pr > F: the probability of observing an F-statistic of greater magnitude by random chance.

Table 5.—*Distribution of* Armillaria gallica *and* A. mellea *among the three study ELTs*[1], *in each block.*

Species	Status	Block 1			Block 2			Block 3		
		11	17	18	11	17	18	11	17	18
A. gallica	Present	15	11	19	16	14	17	9	3	10
	Absent	4	9	2	3	7	3	9	17	9
A. mellea	Present	16	18	17	15	17	21	19	19	20
	Absent	3	2	3	3	4	0	0	1	0

[1] Ecological landtype, based on slope and aspect: ridges (ELT 11), south- to west-facing side slopes (ELT 17), and north- to east-facing side slopes (ELT 18).

DISCUSSION

We have confirmed the presence of three *Armillaria* species on a stratified sample of the permanent vegetation study plots located in all nine MOFEP sites over the period 1993-1995. This represents the first demonstration of the occurrence of *A. gallica* and *A. mellea* (in the strict sense) in the Ozarks; *A. tabescens* was previously reported from southern Missouri by Rhoads (1925). The distribution of *A. tabescens* has proven more difficult to finalize than those of *A. gallica* or *A. mellea*, because *A. tabescens* (1) produces few or no rhizomorphs in the forest floor, (2) causes little mortality that would provide mycelial fans, (3) fruits less predictably than *A. mellea*, and (4) appears to be the least abundant of the three species. Depending on conditions for fruiting, we expect to complete the "pre-treatment" distribution record for *A. tabescens* over the next year or two, in conjunction with logging damage documentation. Because *Armillaria* genet establishment is a very slow process (in contrast to genet response to environmental change), we feel safe in assuming that genets detected in the next year or two will still reflect pre-operational distributions.

As the study progressed, it became apparent that an effective survey for all three species should involve a different search strategy for each species. Although *A. gallica* apparently did not fruit and was rarely virulent enough to provide mycelial fans on recently killed trees, it produced the vast majority of the rhizomorphs that were collected. *Armillaria mellea* fruited regularly in mid to late autumn, was commonly collected as mycelial fans from recently killed trees, but was rarely collected as rhizomorphs. Fruiting of *A. mellea* was associated with the advent of cold autumn nights as well as adequate moisture. *Armillaria tabescens* has taken the longest time to survey, in part because it appears to be the least common. Fruiting provided the majority of records for this species, which was recovered infrequently as mycelial fans and never as rhizomorphs. The timing and abundance of *A. tabescens* fruiting was quite unpredictable from year to year, apparently depending mainly on abundant moisture in mid to late summer. It can fruit in late summer if moisture is abundant, later in the autumn with *A. mellea*, or hardly at all. Both *A. mellea* and *A. tabescens* fruited exceptionally well in 1993, one of the wettest years on record. Dry weather in late August and September 1995 was apparently responsible for delayed and greatly diminished fruiting by *A. tabescens*. In general, annual fruiting of each species was restricted to a single 2- to 3-week window of time, and these windows did not necessarily overlap. Based on these considerations, we placed highest survey priority on searching for fruiting from mid-August through late-October, and focused on rhizomorph, mycelial fan, and decay collections when fruiting was not occurring. The differences among these three species in the relative abundance with which they produce rhizomorphs, mycelial fans, and mushrooms underscore major differences in their biologies and the need to search for them differently.

Armillaria mellea was the most widely distributed of the three species, detected in 91 percent of all plots examined. *Armillaria gallica* was detected in 64 percent of the plots examined, and *A. tabescens* was the least frequently detected species, although the survey of its

distribution is incomplete. No pre-treatment differences were detected in the distributions of either *A. gallica* or *A. mellea* among the sets of sites assigned to each silvicultural treatment, but significant differences were detected for both species among the three blocks of sites. Both *A. gallica* and *A. mellea* were frequently detected in blocks 1 and 2, but *A. mellea* was nearly ubiquitous in block 3 (the Peck Ranch) where *A. gallica* was detected on fewer than half of the studied plots. Further, no differences were detected in the distribution of *A. mellea* among the three study ELT's in any of the three blocks, whereas *A. gallica* was less frequently detected on south- to west-facing side slope plots in blocks 1 and (especially) 3 than on either ridgetop plots or north- to east-facing side slope plots. It therefore appears that *A. mellea* occurs in the absence of *A. gallica* most frequently in block 3, and especially on south- to west-facing side slopes.

If south- to west-facing side slopes in blocks 1 and (especially) 3 are generally drier, warmer, and/or rockier than the rest of the MOFEP sites, the *A. gallica* distributional differences may be explained by conditions for rhizomorph growth. Seasonal drying can affect *Armillaria* rhizomorph growth in upper soil layers. It has been shown that cellulose and lignin degradation rates in forest soils increase with rising soil moisture and temperature (Donnelly *et al.* 1990). Working with *A. gallica* and *A. mellea*, Morrison (1976) encountered few rhizomorphs below 30 cm depth, and found few rhizomorphs in the upper 5 cm of the soil at a dry site, whereas rhizomorphs were most abundant in the upper 5 cm of the soil at a moist site. It seems reasonable to anticipate that rhizomorph growth would generally be less robust on exposed south- to west-facing side slopes than on more protected north- to east-facing side slopes. The distribution of *A. mellea* appears to be less affected by ELT variables, perhaps because *A. mellea* is less dependent on rhizomorph spread than is *A. gallica*.

Our sample of 180 of the 0.2-ha MOFEP vegetation plots represents the rich variety of interactions occurring within MOFEP forest communities among stand structure, ELT, silvicultural treatment effects, and local patterns of *Armillaria* genet distribution. Studies elsewhere have shown that forest floor maps of genet distribution often indicate little or no map overlap of *Armillaria* genets belonging to species with similar "colonization strategies," but frequent overlap of genets belonging to *Armillaria* species with different colonization strategies (e.g., Bruhn *et al.* 1997; Kile *et al.* 1991; Legrand *et al.* 1996; Rizzo and Harrington 1993; Smith *et al.* 1992, 1994). Different colonization strategies can result from differences in virulence or host preference. The unique genetic potential of each *Armillaria* genet is expressed only within that genet's boundary, but when genets of the same or different *Armillaria* species occupy the same landscape they may influence each other's behavior in areas of genet contact. For example, Mohammed and Guillaumin (1989) found that when *A. gallica* and *A. mellea* occupied the same substrate, *A. mellea* inhibited *A. gallica*, without being inhibited in return by *A. gallica*. Since all three MOFEP *Armillaria* species are hardwood-specializing fungi, and *A. gallica* is by far the most prolific producer of rhizomorphs, *A. mellea* and *A. tabescens* may often have less access to food base resources suitable for all three species within the boundaries of competing *A. gallica* genets. Thus, as a result of niche overlap (Leibold 1995), *A. gallica* may mitigate the root disease activity of a co-occurring *A. mellea* or *A. tabescens* genet. Bruhn *et al.* (1997) found small *A. mellea* genets to occur commonly within larger *A. gallica* genets, suggesting that *A. mellea* had sole access to certain food base resources perhaps due to its greater virulence. The small size of the *A. mellea* genets may reflect their isolation by the surrounding *A. gallica* genet.

From the above discussion, it appears that south- to west-facing side slopes in MOFEP block 3 should have the highest risk of oak decline associated with *Armillaria* root disease in the MOFEP sites. Our long-term objectives involve mapping of representative spatial patterns of *Armillaria* genet distributions in selected study plots, experimental testing of *Armillaria* species interactions under selected sets of field conditions, and modeling of temporal and spatial projections of forest structure (e.g., Larsen 1997) including decline. Ultimately, we are interested in explaining the interactions among *Armillaria* populations and MOFEP forest structure, as influenced by MOFEP experimental silvicultural treatments.

Silvicultural operations can affect residual forest development in unexpected ways when interactions with the fungal and insect components of forest communities are not anticipated. The relative contributions of even-aged *vs.*

uneven-aged management to the risk of decline are not clear. Comparisons of these two systems from the standpoint of decline exacerbation should focus attention on the frequency of stand entry, the spatial and size distributions of stumps created (i.e., new *Armillaria* food bases), the extent of forest floor disturbance, and aboveground residual tree damage. We are documenting harvest effects on our study plots by mapping and characterizing stumps, residual stem injuries, and vehicle paths. Belowground root damage along vehicle paths is also being characterized. Although root wounds are not always necessary for host infection by *A. tabescens* (Rhoads 1956), they have been found to increase host vulnerability (Weaver 1974), probably in part because *A. tabescens* rhizomorph growth through soil rarely if ever occurs. It has also been shown that damaged roots are more vulnerable to *A. mellea* invasion than uninjured roots, and that this effect is not limited to the point of injury (Popoola and Fox 1996). Root collar and basal stem injuries may have similar physiological effects on host vulnerability to *Armillaria* root disease and/or butt rot. Maps of the juxtaposition of stumps, vehicle paths, residual trees, and *Armillaria* genets will provide unprecedented opportunities to interpret forest community dynamics.

Starkey *et al.* (1989) associated the risk of oak decline in southern upland hardwood forests with acute summer drought, recent or repeated spring defoliation, stand maturity, predominance of red oak group species, low site index, and xeric site conditions. Dwyer *et al.* (1995) found that oak decline in the Ozarks affected stressed trees regardless of age. Nevertheless, silvicultural options for maintaining healthy stands are more satisfactory than options for dealing with declining ones. Partial cutting in declining stands for any reason often results in acceleration of decline, and regeneration of declining stands can be complicated by the impaired condition of trees needed as vigorous seed or sprout sources (Starkey *et al.* 1989). As species composition shifts away from the red oak group in declining stands, managers will have to decide whether or not to augment natural hardwood regeneration by encouraging or planting shortleaf pine. In young high risk stands prior to the advent of decline, partial cuttings may reduce stress and shift species composition toward more resistant species (e.g., white oak, shortleaf pine, etc.). Shortening the rotation age may reduce stand vulnerability to decline if it reduces physiological stress levels.

Although *Armillaria* species are certainly not the only organisms that contribute to mortality or decline in the Ozarks, they are of particular interest because of the spatial stability of *Armillaria* genets (i.e., their long-term relationship with forest structure), and their pivotal role in mediating the influences of stress events and the activities of stress agents (Wargo 1996). Other relevant organisms and diseases include oak wilt, Hypoxylon canker of oak, the two-lined chestnut borer, and defoliating insects (e.g., the looper complex and gypsy moth). Oak wilt disease is widely distributed in the Ozarks (Jones and Bretz 1958). The oak wilt pathogen (*Ceratocystis fagacearum*) is a primary parasite capable of infecting and killing healthy oaks. Oak wilt is most severe in stands approaching pure red oak species composition, where root grafts connect a high proportion of the most susceptible trees (Bruhn *et al.* 1991). Because oak wilt epidemiology is independent of host stress (at least with red oak species), oak wilt and oak decline are not causally related. Hypoxylon canker of oak (caused by *Hypoxylon atropunctatum*) has been associated with other factors causing oak decline and mortality (Bassett and Fenn 1984, Law and Gott 1987). Bassett and Fenn (1984) showed that the pathogen occurs in branches and boles of healthy oaks without causing disease until the advent of stress; they were not able to cause disease with artificial inoculations. They isolated the pathogen with equal frequency from non-diseased branches and boles of healthy black or red oaks and white oaks, suggesting that the greater observed incidence of disease on black or red oaks was due to differences in susceptibility or exposure to drought. Although the two-lined chestnut borer (*Agrilus bilineatus*) is most often a secondary colonizer of severely stressed or dying trees, it can occasionally build to population levels capable of accelerating mortality. Borer activity in the Ozarks is commonly associated with formation of mortality pockets in conjunction with oak wilt, *Armillaria* root disease, and/or Hypoxylon canker (Law and Gott 1987). Although the gypsy moth has not yet arrived in the Ozarks, a very high proportion of Ozark land area supports forest stands comprising very high densities of tree species preferred by the gypsy moth (Liebhold *et al.* 1997).

It seems appropriate to close this consideration of relevant Ozark forest pathogens and insect pests with a brief mention of annosus root disease of shortleaf pine, caused by

Heterobasidion annosum. Once found widely distributed in the Ozarks (Berry and Dooling 1962), *Heterobasidion annosum* has become all but forgotten with the encroachment of oaks onto logged-over upland Ozark pine forest sites (Johnson and Law 1989) and the de-emphasis on pine regeneration. A substantial portion of the Ozark land area currently supporting black/scarlet oak forest was previously dominated by more drought-tolerant shortleaf pine (Law and Gott 1987). Although annosus and *Armillaria* root diseases share some important features (Sinclair *et al.* 1987), in the Ozarks annosus root disease does not noticeably affect hardwoods and pine is not appreciably affected by *Armillaria* root disease. Although the distribution and intensity of annosus root rot in preceding pine forests are unknown, there are no records of "pine decline" corresponding to more recent records of oak decline. It seems plausible that shortleaf pine is ecologically better adapted to the more stressful upland Ozark sites than are members of the red oak subgenus. Perhaps oak decline functions to shift forest vegetation on these sites toward greater compatibility with the long-term local environment.

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Effects of Selected Timber Management Practices on Forest Birds in Missouri Oak-Hickory Forests: Pre-treatment Results

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Abstract.—Our goal is to understand the repercussions of two different forest management techniques on Neotropical migrant birds in the heavily forested landscape of the Missouri Ozarks. Our objectives are to determine breeding densities of forest birds under even-aged and uneven-aged management regimes and to determine the effects of these practices on songbird demographics. Our methods included spot mapping, nest monitoring, and mist-netting and banding. Analyses of our pre-treatment data show some variation both spatially and temporally, but do suggest that we have adequate baseline data for future comparisons. The data will allow us to see the immediate avian response to cutting, although decades and subsequent cutting cycles will be needed to evaluate the complete response. They also will allow us to examine avian population demographics on a scale that is unsurpassed for migrant songbirds.

Recent concerns about possible declines in populations of Neotropical migrant birds led to two major international symposia (the Manomet Symposium published as Hagan and Johnston [1992] and the Estes Park Meeting published both as Finch and Stangel [1993] and Martin and Finch [1995]) and to the development of the Neotropical Migratory Bird Conservation Program (also known as Partners in Flight). Three major factors have been cited as possible causes of these purported declines: winter habitat limitation, stopover habitat limitation during migration, and habitat loss and fragmentation in the breeding grounds. Although declines in wintering populations have been documented (Faaborg and Arendt 1992), the role of winter habitat limitation in causing overall population declines in most species is very controversial (see Rappole and McDonald [1994] and Latta and Baltz [1997] for an introduction to the problem). The role of stopover habitat loss in causing population-wide declines is even more difficult to document, although habitat loss can be at least locally critical for birds dealing with barriers such as the Gulf of Mexico and the Great Lakes (Moore and Simons 1992, Ewert and Hamas 1996).

In contrast, numerous studies have shown that fragmented breeding habitats have lower species diversity and reduced breeding success among those species that still occur. Primarily due to increased nest predation and cowbird parasitism (Robinson 1996, Thompson 1996), it appears that many fragmented regions have populations of migrant birds living in population "sinks" that exist only because of regular "rescue" from population "sources" (Donovan *et al.* 1995a, 1995b). It appears that potential source regions for forest migrants in the Midwest are those areas that still contain large areas of forest with little non-forest habitat, including such areas as the Missouri Ozarks, northern Wisconsin and Minnesota, and, perhaps, southern Indiana (Robinson *et al.* 1995).

If the Missouri Ozarks are crucial to maintaining populations of migrant birds across a large area of the Midwest, it is critical that we understand what habitat manipulations such as

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timber management might do to the demography of migrant birds within this region. Several studies in central Missouri have shown that those species of migrants that required the interior of mature forest responded negatively to forest fragmentation by avoiding forest fragments even though many of those fragments were hundreds of times larger than the typical breeding territory (Hayden *et al.* 1985), by occurring at reduced densities on the smallest of those fragments where they did occur (Wenny *et al.* 1993), by having reduced pairing success on smaller fragments (Gibbs and Faaborg 1990, Van Horn *et al.* 1995), and by showing reduced nesting success of those nests that occurred as fragments got smaller in size (Donovan *et al.* 1995a). Data supported both nest predation and cowbird parasitism as mechanisms causing these patterns (Donovan *et al.* 1995a, O'Conner and Faaborg 1993) and it was clear that most bird populations on these fragments were not producing enough offspring to replace the mortality of the adults.

As our data on fragmented populations grew, we realized that knowledge about populations in this fragmented situation was of limited value for providing management guidelines for the heavily forested Ozarks of southern Missouri. This region is not characterized by large gaps between populations, great amounts of edge, or small tracts of forest surrounded by fields or pastures. Rather, the Ozarks are 80 percent or more forested; when disturbance does occur, it is the cutting of a small portion of a large tract of forest. While such cutting may negatively affect the migrants that require mature forest, patterns of avian demography that apply to a landscape of agriculture with isolated woodlots do not transfer to a landscape of woodlands with isolated openings (Donovan *et al.* 1996).

At the time we developed our ideas with regard to MOFEP (the late 1980's), forest management studies had collected primarily correlational information to examine species-habitat relationships. Only Thompson and Fritzell (1990) had conducted experiments on forest-bird interactions in Missouri, and their study was within the fragmented region of central Missouri. When the idea for MOFEP was developed (Kurzejeski *et al.* 1993), we were enthusiastic because we felt that an experimental approach would allow us to better understand all of the interactions occurring with birds during timber management and it would permit us to better assess the impacts of management decisions on avian populations in the future.

OBJECTIVES

The overall, long-term objectives of the MOFEP bird study are:

1. To determine differences in breeding densities of some common forest songbirds in forest managed by the even-aged method, the uneven-aged method, and forests with no timber harvest.
2. To determine rates of nest parasitism, nest predation, and reproductive success for these songbirds in forests managed by the even-aged method, the uneven-aged method, and forests with no timber harvest.

At the end of the pre-treatment phase of MOFEP, comparison of the data from all of the study sites over a 5-year period allows us to understand how bird populations and nesting success may vary over both time and space. It also allows us a detailed look at the spatial distribution of various species within the study sites. The distributional data can be used as a template to see the precise effects of the different treatment practices on bird distributions within each study site, whereas the density and reproduction summaries from each area can provide information on the demographic consequences of management practices within the scale of the study area.

MATERIALS AND METHODS

The MOFEP sites have been described in detail elsewhere in this volume (Brookshire *et al.* 1997). We were able to do all of our sampling activities on all nine sites for 5 years before treatment (1991-1995); we anticipate intensive studies on these sites for at least 3 years post-treatment (1997-1999).

We selected five forest-dwelling species as focal species (ovenbird [*Seiurus aurocapillus*], worm-eating warbler [*Helmitheros vermivorus*], Kentucky warbler [*Oporornis formosus*], wood thrush [*Hylocichla mustelina*], and Acadian flycatcher [*Empidonax virescens*]). These were selected because:

1. they are territorial and vocal, thus allowing estimates of their densities via spot mapping;

2. their nests are generally accessible for monitoring of reproductive success;
3. we had comparable data on abundance and demography of these species from fragmented habitats in prior or concurrent studies.

Data also were gathered on 13 additional species of Neotropical migrant forest birds (e.g., yellow-throated vireo [*Vireo flavifrons*]), five Neotropical migrant species that are associated with forest edge or second growth (e.g., blue-winged warbler [*Dendroica pinus*]), and three permanent resident species (e.g., Carolina wren [*Thryothorus ludovicianus*]). To date, data for these species have not been analyzed but are available for future study. For example, sample sizes for second-growth habitat species were very small, but should increase following treatment, at which time the comparative nature of the pre-treatment datasets should increase their value despite their small size.

To facilitate study, each of the nine study areas was laid out in a grid system for orientation and subdivision. Grid lines run E-W and N-S and were approximately 300 m apart. Trees along grid lines were permanently marked with orange paint. Junctions were flagged and identified as to location on the grid. Differences in size posed a problem for equalizing effort among the nine study areas. To standardize, more or less, the area actually studied on the various study sites, exterior edges of sites 1 through 4, 6, 7, and 9 were excluded from study during the pre-treatment phase of the project. The entire area of sites 5 and 8 was studied. As a result, the amount of area studied in each of the nine sites ranged from 287 to 353 ha (table 1).

Bird densities were determined through spot-mapping (Robbins 1970). Each study area was divided into seven spot mapping plots, each of which was approximately 45 ha in size. Each plot was visited 10 times at 2 to 3 working-day intervals (excluding weekends) from mid-May through the end of June. Mappers used enlarged topographic maps of the spot-map plots to orient themselves and marked all detections of birds on their maps, along with the path used in making the map. Workers were instructed to use a different route across the plot from the one used in the prior visit. One map was produced each day a spot-map plot was visited; most maps took 3 to 4 hours to complete.

Table 1—*Amount of each study area surveyed via spot mapping and searched for nests, 1991-1995.*

Site	Number of hectares in the study area
1	335
2	315
3	287
4	321
5	313
6	323
7	318
8	339
9	353

To determine densities, composite maps were compiled for each species. To locate territories, we looked for clusters of observations (≥3). In addition to the density data for each plot each year, a file of territory locations will be maintained that will be used to ascertain bird response to treatments; at some point, all this will be put into a GIS system.

To determine reproductive success, as well as parasitism and predation rates, we located and monitored nests while spot mapping and by deliberate searching from mid-May through July. Nest locations were recorded on the enlarged topographic maps and marked on-site by flagging. Nests were monitored every 3 to 5 days until nest fate was determined. This produced reproductive data and a permanent record of nest locations. Daily survival rates were calculated using the methods of Mayfield (1961, 1975) as modified and categorized by the protocol for the BBIRD program.

Birds also were captured in mist nets and banded to examine movements and return rates. Thirteen mist net lines, each containing 12 nets (36 mm mesh) set 50 m apart, were placed systematically throughout each study area on the east-west grid lines. Net lines (and net locations) also were marked on the topographic maps to ensure consistent placement of nets on an annual basis. Such consistent placement also was aided by the use of aluminum nails put into a tree to attach one end of each net. This also reduced the number of net poles that had to be carried up and down the Ozark slopes. Each net line was run for two

consecutive mornings from dawn to noon. All birds captured in the nets were identified, aged, sexed, banded with U.S. Fish and Wildlife Service bands, and released.

We used 25 to 27 field assistants each summer to conduct the bird study. This was done as an Undergraduate Research Internship through the University of Missouri-Columbia, which offered the students a stipend, research credit, and a chance to do independent projects.

Statistical methodology used to analyze avian density data and nest survival data is contained in Littell *et al.* (1996). The analytical approach used for the mist netting capture/recapture data is documented in Pollock *et al.* (1990).

PRE-TREATMENT RESULTS AND DISCUSSION

Spot Mapping

During 1991-1993 and 1995, each spot-map plot was visited 10 times. In 1994, due to weather and personnel problems, each spot-map plot was run nine times. We were able to compute densities (number of territories per 100 ha) of the five focal species on a scale we feel is unmatched by any other study (table 2). Ovenbird and Acadian flycatcher were the most abundant species, and Kentucky warblers occurred only in low densities.

Both ovenbird and worm-eating warbler had significant patterns of density variation by study site (block effect of tables 3 and 4), as did all birds combined (table 8). The Acadian flycatcher showed significantly increasing populations through the study (a year effect, table 6). The worm-eating warbler, Kentucky warbler, wood thrush, and all birds combined had significant relationships between both year and study site (year*block; tables 4, 5, 7, and 8). The finding of significance in analyses involving block effects suggests that developing MOFEP with a block design was a wise decision. The lack of significant relationships between density of birds and assigned treatment suggests that these study sites will serve adequately for post-treatment analysis.

Nest Monitoring

Even with a large crew, it was difficult to find nests. During 1991-1995, we found the nests of 27 species of birds, of which 23 (85 percent) were Neotropical migrants. We have amassed a dataset with nearly 1,800 nests overall (table 9). Of these, approximately 880 nests proved useful for extraction of information on reproductive success. In addition to the impressive number of nests and nests found at the egg stage, it is noteworthy that cowbird parasitism rates were exceptionally low in the Ozarks, ranging from 1.3 to 3.6 percent annually. These figures are minuscule compared to parasitism rates in mid-Missouri, Illinois, and elsewhere in the Midwest (Robinson 1996).

To date, we have been able to conduct only two major analyses of our nest success data. In an attempt to see if our study sites were uniform in nest success characteristics, we computed daily nest survival rates for all nests of all species by year in each of the treatment groups (table 10). Despite a range of values from 0.945 in blocks 7-8-9 in 1991 to 0.970 in block 1-2-3 in 1991, the mean of the three treatment groups over the 5-year sample differed by only 0.01. These values were subjected to analysis of variance, for each year, to test for block or treatment effects (table 11). No block effects were observed, but a treatment effect was noted in 1995, although the difference in nest success rates in the treatment groups was small (table 11). We also subjected the combined daily nest success rate data to repeated measure analysis, with year as the repeated factor (table 12). No year, block, or treatment effects were found. As a result, we feel the data provide useful results to compare with the post-treatment data we will gather in the future.

We also have computed annual variation in daily nest success rates for the four focal species for which we had adequate data (excluding the Kentucky warbler) for the study area blocks. Daily nest survival rates for ovenbirds ranged from 0.917 in block 4-5-6 in 1993 to 1.000 for block 1-2-3 in 1994 (for only five nests; table 13). The mean daily nest survival rate for ovenbird nests for all years combined was 0.949(+/-0.007 SE). For this species, block 4-5-6 shows consistently low nest success rates, but the smaller sample sizes by species confound statistical comparison.

Daily nest survival rates for the worm-eating warbler ranged from 0.879 to 1.0 in different years and blocks (table 14), although the mean daily nest success rates over the 5-year period were more consistent between blocks for this

Table 2.—*Densities (number of territories per 100 ha) of ovenbirds, worm-eating warblers, Kentucky warblers, wood thrushes, and Acadian flycatchers on the MOFEP study areas, 1991-1995.*

Year	Study area	Ovenbird	Worm-eating warbler	Kentucky warbler	Wood thrush	Acadian flycatcher
1991	1	33.73	17.91	0.30	5.27	26.07
1992	1	26.37	11.94	0.60	5.37	26.17
1993	1	25.77	20.40	0.00	6.87	27.46
1994	1	33.08	21.79	3.28	8.66	31.14
1995	1	28.66	18.21	0.30	3.88	32.70
Mean(SE)		29.52(3.71)	18.05(3.77)	0.90(1.35)	6.01(1.82)	28.71(3.03)
1991	2	35.00	22.86	3.17	6.67	29.74
1992	2	29.34	16.19	1.90	7.62	29.13
1993	2	29.61	19.37	0.95	5.05	26.98
1994	2	34.92	21.90	6.35	7.06	34.29
1995	2	38.31	24.60	4.13	4.44	37.75
Mean(SE)		33.44(3.87)	20.98(3.28)	3.30(2.09)	6.17(1.36)	31.58(4.36)
1991	3	23.00	21.84	0.70	2.09	27.87
1992	3	16.03	16.03	0.35	1.39	30.84
1993	3	20.64	21.69	0.00	3.14	31.71
1994	3	22.30	25.09	4.18	8.01	34.76
1995	3	21.60	25.09	1.05	9.41	35.66
Mean(SE)		20.71(2.76)	21.95(3.70)	1.26(1.68)	4.81(3.65)	32.17(3.14)
1991	4	43.09	19.63	1.25	4.36	26.79
1992	4	34.67	17.34	0.62	1.56	31.96
1993	4	29.98	23.36	0.62	2.18	33.10
1994	4	28.91	18.03	0.62	2.49	27.73
1995	4	24.87	19.31	3.66	0.31	29.80
Mean(SE)		32.30(6.97)	19.53(2.33)	1.35(1.32)	2.18(1.48)	29.88(2.69)
1991	5	47.71	19.49	1.92	6.07	24.28
1992	5	46.30	20.55	1.17	6.18	25.18
1993	5	47.63	23.00	1.28	3.35	23.24
1994	5	49.26	21.09	1.46	3.83	31.52
1995	5	40.19	20.77	2.68	5.75	23.96
Mean(SE)		46.22(3.53)	20.98(1.28)	1.70(0.62)	5.04(1.34)	25.64(3.36)
1991	6	43.34	21.37	2.79	16.10	30.96
1992	6	38.03	19.84	0.31	16.14	28.79
1993	6	42.44	17.13	0.00	13.70	21.98
1994	6	40.34	16.10	0.00	11.24	30.86
1995	6	38.29	20.12	0.00	10.53	33.44
Mean(SE)		40.49(2.39)	18.91(2.20)	0.62(1.22)	13.54(2.63)	29.21(4.36)
1991	7	16.35	13.52	0.00	2.20	17.92
1992	7	17.61	14.56	2.52	3.14	21.07
1993	7	12.74	14.15	0.94	5.56	20.02
1994	7	13.98	11.68	0.00	5.35	17.13
1995	7	10.38	13.52	0.31	2.83	22.01
Mean(SE)		14.21(2.87)	13.49(1.10)	0.75(1.06)	3.82(1.54)	19.63(2.07)
1991	8	8.55	13.42	0.29	2.65	17.40
1992	8	7.18	14.16	2.95	4.42	23.30
1993	8	6.78	16.81	1.18	5.25	25.07
1994	8	9.26	14.50	0.00	3.54	20.53
1995	8	6.39	10.62	0.29	3.24	21.77
Mean(SE)		7.63(1.22)	13.90(2.23)	0.94(1.21)	3.82(1.02)	21.61(2.90)
1991	9	15.01	20.02	0.00	5.10	20.96
1992	9	15.81	20.77	0.57	8.33	34.84
1993	9	11.40	19.12	1.56	6.94	34.75
1994	9	14.98	15.30	0.00	5.84	27.48
1995	9	13.19	16.01	0.09	6.18	30.88
Mean(SE)		14.08(1.78)	18.24(2.45)	0.44(0.67)	6.48(1.23)	29.78(5.80)

Table 3.—*Multivariate repeated measurement analysis (year as repeated variable) of ovenbird densities on the MOFEP study areas, 1991-1995.*

Between site effects				
Source	**df**	**Mean square**	**F**	**P-value**
Block	2	2897.9	11.09	0.0233*
Treatment	2	4.9	0.02	.9813
Error	4	261.3		

Within site effects					
Source	**Pillai's Trace Statistic**	**F**	**Numerator df**	**Denominator df**	**P-value**
Year	0 .985	16.3	4	1	0.184
Year*Block	1.738	3.3	8	4	.131
Year*Treatment	1.231	.8	8	4	.636

* Significant

Table 4.—*Multivariate repeated measurement analysis (year as repeated variable) of worm-eating warbler densities on the MOFEP study areas, 1991-1995.*

Between site effects				
Source	**df**	**Mean square**	**F**	**P-value**
Block	2	118.9	16.50	0.012*
Treatment	2	93.1	6.46	.056
Error	4	7.2		

Within site effects					
Source	**Pillai's Trace Statistic**	**F**	**Numerator df**	**Denominator df**	**P-value**
Year	.948	4.5	4	1	0.337
Year*Block	1.865	6.9	8	4	.040*
Year*Treatment	1.407	1.2	8	4	.464

* Significant

Table 5.—*Multivariate repeated measurement analysis (year as repeated variable) of Kentucky warbler densities on the MOFEP study areas, 1991-1995.*

Bewteen site effects				
Source	**df**	**Mean square**	**F**	**P-value**
Block	2	4.6	1.42	0.343
Treatment	2	3.8	1.17	.398
Error	4	3.2		

Within site effects					
Source	**Pillai's Trace Statistic**	**F**	**Numerator df**	**Denominator df**	**P-value**
Year	.981	12.8	4	1	0.206
Year*Block	1.895	9.0	8	4	.025*
Year*Treatment	1.681	2.6	8	4	.183

* Significant

Table 6.—*Multivariate repeated measurement analysis (year as repeated variable) of Acadian flycatcher densities on the MOFEP study areas, 1991-1995.*

Between site effects				
Source	**df**	**Mean square**	**F**	**P-value**
Block	2	196.243	2.49	0.198
Treatment	2	30.452	.39	.702
Error	4	78.709		

Within site effects					
Source	**Pillai's Trace Statistic**	**F**	**Numerator df**	**Denominator df**	**P-value**
Year	1.000	1,043.0	4	1	0.023*
Year*Block	1.560	1.8	8	4	.304
Year*Treatment	1.439	1.3	8	4	.431

* Significant

Table 7.—*Multivariate repeated measurement analysis (year as repeated variable) of wood thrush densities on the MOFEP study areas, 1991-1995.*

Between site effects				
Source	**df**	**Mean square**	**F**	**P-value**
Block	2	18.5	0.27	0.774
Treatment	2	53.5	.79	.515
Error	4	67.9		

Within site effects					
Source	**Pillai's Trace Statistic**	**F**	**Numerator df**	**Denominator df**	**P-value**
Year	.944	4.2	4	1	0.348
Year*Block	1.968	31.2	8	4	.002*
Year*Treatment	1.839	5.7	8	4	.055

* Significant

Table 8.—*Multivariate repeated measurement analysis (year as repeated variable) of densities for all birds combined on the MOFEP study areas, 1991-1995.*

Between site effects				
Source	**df**	**Mean square**	**F**	**P-value**
Block	2	6,421.048	10.5	0.026*
Treatment	2	147.475	0 .2	.797
Error	4	611.949		

Within site effects					
Source	**Pillai's Trace Statistic**	**F**	**Numerator df**	**Denominator df**	**P-value**
Year	0 .835	1.3	4	1	0.575
Year*Block	1.925	12.9	8	4	.013*
Year*Treatment	1.204	0 .8	8	4	.660

* Significant

Table 9.—*Total number of nests, number of nests with eggs, and number of nests that were parasitized, 1991-1995.*

Year	Total found *Number*	With eggs *Number*	Parasitized *Number (Percent)*
1991	353	149	2 (1.3)
1992	323	173	6 (3.5)
1993	398	197	7 (3.6)
1994	269	197	4 (2.0)
1995	423	250	6 (2.4)

Table 10.—*Daily survival rates for all nests in each block of study areas, 1991-1995.*

Year	Study area block 1-2-3	4-5-6	7-8-9	Overall
1991	0.970 (40)[1]	0.950 (55)	0.945 (44)	0.956 (139)
1992	0.963 (40)	0.952 (66)	0.953 (40)	0.956 (146)
1993	0.962 (55)	0.964 (97)	0.955 (32)	0.962 (184)
1994	0.968 (35)	0.953 (79)	0.966 (61)	0.960 (175)
1995	0.967 (65)	0.963 (87)	0.960 (81)	0.963 (233)
Mean [SE]	0.966 [0.003]	0.956 [0.007]	0.956 [0.008]	0.959 [0.003]

[1]( )=Number of nests

Table 11.—*Analysis of variance for block or treatment effects in daily survival rates for nests of all species combined, 1991-1995.*

Year	Source	df	Mean square	F	P-value
1991	Block	2	0.0005	3.14	0.151
	Treatment	2	.0005	2.95	.163
	Error	4	.0002		
1992	Block	2	.0002	1.83	.272
	Treatment	2	.0005	3.87	.116
	Error	4	.0001		
1993	Block	2	.0003	.92	.470
	Treatment	2	.0007	2.01	.249
	Error	4	.0004		
1994	Block	2	.0002	.77	.521
	Treatment	2	.0001	.39	.699
	Error	4	.0003		
1995	Block	2	.0001	2.83	.171
	Treatment	2	.0003	15.73	.013*
	Error	4	.0000		

*Significant

Table 12.—*Multivariate repeated measurement analysis (year as repeated variable) of daily survival data for all species combined, 1991-1995.*

Between site effects				
Source	**df**	**Mean square**	**F**	**P-value**
Block	2	0.0007	1.91	0.261
Treatment	2	.0006	1.51	.324
Error	4	.0004		

Within site effects					
Source	**Pillai's Trace Statistic**	**F**	**Numerator df**	**Denominator df**	**P-value**
Year	0 .874	1.735	4	1	0.510
Year*Block	1.268	.867	8	4	.601
Year*Treatment	1.480	1.422	8	4	.389

Table 13.—*Daily survival rates for ovenbird nests in each block of study areas, 1991-1995.*

	Study area block			
Year	**1-2-3**	**4-5-6**	**7-8-9**	**Overall**
1991	0.939 (6)[1]	0.940 (13)	0.958 (4)	0.942 (23)
1992	0.968 (5)	0.944 (11)	0.972 (3)	0.956 (19)
1993	0.971 (6)	0.917 (11)	0.943 (2)	0.943 (19)
1994	1.000 (5)	0.928 (15)	0.983 (4)	0.957 (24)
1995	0.976 (3)	0.938 (14)	0.944 (6)	0.947 (23)
Mean [SE]	0.971 [0.022]	0.933 [0.011]	0.960 [0.017]	0.949 [0.007]

[1]( )=Number of nests

species than for the ovenbird. The mean daily nest survival rate for worm-eating warbler nests for all years combined was 0.957 (+/-0.026 SE).

The wood thrush showed daily nest survival rates ranging from 0.914 to 0.977 (table 15), but the mean values of the treatment blocks were remarkably similar. The mean overall daily survival rate for all years combined was 0.961 (+/-0.008 SE).

Daily nest survival rates for the Acadian flycatcher ranged from 0.924 to 0.979 (table 16), with block 1-2-3 showing consistently higher success rates than the other treatment blocks. The mean overall daily nest survival rate for this species was 0.959 (+/-0.004 SE).

To date, we have computed only preliminary estimates of the source/sink status of these populations by year and treatment block. Because these estimates rely heavily on measures of both adult and juvenile mortality, both of which are not accurately known for this area, they can be difficult to calculate. A study by Donovan *et al.* (1995a) that used a subset of MOFEP nests during 1991-1992 showed that ovenbird and wood thrush populations produced young at a rate that qualified for source status, but not all treatment blocks in all years show this trend. For example, a subset of wood thrush nests analyzed by Anders *et al.* (1997) for the years 1994 and 1995 showed lower nest success and possible sink status for this species at that time.

Mist Netting

Of the 13 mist net lines designated per study area, 11 were run in 1991, 12 in 1992 and 1993, and all 13 in 1994 and 1995. The increased intensity of netting in the latter years reflected our operating more concurrent net lines at that time, in part because of the low capture rates discovered in the earlier part of the study. We caught 41 species of birds in the

Table 14.—*Daily survival rates for worm-eating warbler nests in each block of study areas, 1991-1995.*

Year	Study area block 1-2-3	4-5-6	7-8-9	Overall
1991	0.960 (8)[1]	0.949 (2)	0.926 (12)	0.940 (22)
1992	0.962 (8)	0.945 (13)	0.978 (5)	0.958 (26)
1993	0.949 (7)	0.949 (2)	0.879 (5)	0.923 (14)
1994	0.946 (5)	0.985 (9)	1.000 (4)	0.983 (18)
1995	0.965 (5)	0.987 (9)	1.000 (4)	0.980 (18)
Mean [SE]	0.956 [0.008]	0.963 [0.021]	0.957 [0.053]	0.957 [0.026]

[1]( )=Number of nests

Table 15.—*Daily survival rates for wood thrush nests in each block of study areas, 1991-1995.*

Year	Study area block 1-2-3	4-5-6	7-8-9	Overall
1991	0.914 (4)[1]	0.957 (15)	0.973 (5)	0.953 (24)
1992	0.970 (7)	0.956 (13)	0.938 (6)	0.957 (26)
1993	0.977 (10)	0.977 (18)	0.943 (6)	0.973 (34)
1994	0.960 (3)	0.953 (10)	0.961 (14)	0.958 (27)
1995	0.961 (8)	0.953 (14)	0.971 (22)	0.964 (44)
Mean [SE]	0.956 [0.025]	0.959 [0.010]	0.957 [0.016]	0.961 [0.008]

[1]( )=Number of nests

Table 16.—*Daily survival rates for Acadian flycatcher nests in each block of study areas, 1991-1995.*

Year	Study area block 1-2-3	4-5-6	7-8-9	Overall
1991	0.979 (19)[1]	0.924 (15)	0.930 (15)	0.954 (49)
1992	0.962 (12)	0.954 (15)	0.954 (14)	0.956 (41)
1993	0.947 (20)	0.972 (27)	0.961 (9)	0.964 (56)
1994	0.966 (12)	0.962 (22)	0.959 (10)	0.962 (44)
1995	0.965 (26)	0.955 (22)	0.956 (16)	0.960 (64)
Mean [SE]	0.964 [0.011]	0.953 [0.018]	0.952 [0.013]	0.959 [0.004]

[1]( )=Number of nests

nets, of which 31 (76 percent) were Neotropical migrants. The red-eyed vireo (*Vireo olivaceus*) was the most caught species, with the Acadian flycatcher next most abundant (table 17). Only three cowbirds were captured in 5 years of netting. Captures varied by treatment block (table 18), but given the annual variation in total captures (708 birds in 1995 vs. 1,425 in 1994), it is difficult to determine what this variation means.

Capture rates per net line were low, which is typical of breeding season netting in mature forest. After mid-July, they were even lower, and it was common to catch no birds in mist net lines run after this time. This precipitated our concentrating the netting effort in late June and early July in 1994 and 1995. Although the 1994 totals suggested this was a wise move, the lack of captures in 1995 was puzzling. Results from a radio-tracking study of wood thrush

Table 17.—*Numbers of the five focal species, two commonly caught species, and other birds caught in mist nets, 1991-1995.*

	Species							
Year	Ovenbird	Worm-eating warbler	Kentucky warbler	Acadian flycatcher	Wood thrush	Red-eyed vireo	Scarlet tanager	Other
1991	64	90	37	110	82	239	46	274
1992	50	41	10	120	97	238	81	332
1993	64	47	18	115	62	244	74	262
1994	94	92	19	120	90	412	106	492
1995	49	30	17	108	27	196	45	236

Table 18.—*Numbers of birds (all species) caught in mist nets and banded in each study area and block, 1991-1995.*

Study area	1991	1992	1993	1994	1995	Totals
1	86	133	108	129	70	526
2	195	116	160	228	102	801
3	119	110	65	212	71	577
Block total	400	359	333	569	243	1,904
4	88	116	67	145	48	464
5	103	71	87	95	46	402
6	81	100	91	148	61	481
Block total	272	287	245	388	155	1,347
7	75	95	110	163	101	544
8	83	96	81	151	124	535
9	112	132	117	154	85	600
Block total	270	323	308	468	310	1,679
Totals	942	969	886	1,425	708	4,930
No. recaptured	—	24	70	104	65	263
Percent recaptured		2.5	7.9	7.3	9.2	5.3

(Anders *et al.* 1997) and several intern projects suggest that the forest birds move into the denser cover of clearcuts and riparian vegetation later in the breeding season, which may account for our lower capture rates in late July.

Recapture rates of previously banded birds also were low, although they increased annually (table 18). The low value in 1992 reflects a smaller pool of banded birds from which recaptures could occur.

The mist netting data were subjected to capture/recapture analysis using program JOLLY (Pollock *et al.* 1990). Unfortunately, we did not have enough data for any of the individual species to obtain species-specific estimates, so we tried to combine the data. The attempted groupings were: (1) all birds, regardless of species, and (2) a "guild" approach, combining the five focal species plus red-eyed vireo, scarlet (*Piranga olivacea*) and summer (*P. rubra*) tanagers, and indigo bunting (*Passerina cyanea*). Even after grouping, however, the data were too sparse to obtain reasonable estimates at the study area or block level. The only two groupings of the data that were successfully run through the program were for all study areas combined. Given the number of species that were represented in these analyses, assumptions of homogeneous capture and survival probabilities across individuals and among

species would be more than suspect. Therefore, models of population dynamics cannot be developed using these data.

Although the banding results have been disappointing in many ways, this aspect of the study will not be abandoned. Our dataset represents one of the largest breeding ground banding efforts in North America. With the addition of harvest treatments and the expected increase in nettable birds, the MOFEP bird banding effort may achieve more definitive results in the future.

CONCLUSIONS AND PREDICTIONS

MOFEP is designed to be a long-term experiment. Our goal during 1991 through 1995 was to understand the spatial and temporal variation in avian characteristics of our study sites so that we could truly measure the effects of the forest treatments that will occur on them; we feel we are in an excellent position to do that during the coming years.

At the time we developed our protocol for MOFEP, we had some ideas about how the different timber harvest practices might affect bird communities following the treatments, but these were general hunches. During the pre-treatment phase of MOFEP, several papers were published that improved our ability to predict which species will be most affected by the conditions that will occur post-treatment. Thompson *et al.* (1992) surveyed birds in forests with and without clearcutting elsewhere in the Ozarks, while Annand and Thompson (1997) surveyed species in a variety of forest regeneration types. Wenny *et al.* (1993) provided detailed measures of habitat preferences of two of the focal species. All of these studies provide insight into how different species may respond to different treatments. In a more general way, Thompson (1993) modeled how birds with negative responses to the creation of edge may respond differently to the even-aged and uneven-aged harvest techniques tested in MOFEP.

These articles suggest that forest interior species living in the three study sites receiving even-aged treatments should lose the percentage of territories located in stands that were harvested. This percentage varies by species, but, for example, was 15 percent for ovenbirds on study site 5. It is possible some sort of edge effect might reduce densities in forest around the clearcuts, but this remains to be seen. If site faithfulness prevails, it is possible that densities of birds in the uncut forest might increase, at least for awhile. For even-aged management, the negative effects of forest management on forest interior birds should be confined to the cut areas and their immediate vicinity.

Sites with even-aged treatments also must be studied for the potential positive effects that clearcuts will have on second-growth habitat species that invade clearings sometime in the first year or two after cutting. Species such as prairie warbler (*Dendroica discolor*), yellow-breasted chat (*Icteria virens*), and indigo bunting, to name just a few, will become abundant in these sites where they were rare or nonexistent before. There is some evidence that these species have much lower parasitism and nest predation rates in the Ozarks than elsewhere in Missouri, which may mean that these clearcuts are important source habitats for these species. Although the positive benefit of these clearcuts may take longer to measure, it is very possible that it will be quite pronounced for certain species.

The effects of uneven-aged treatment will be harder to predict, in part because less work has been done on this management technique, and because it involves more subtle changes in vegetation structure without the addition of large areas of a new habitat. The results of Annand and Thompson (1997) suggest that abundances of hooded warbler (*Wilsonia citrea*) will go up dramatically following uneven-aged treatment, while densities of worm-eating warbler and black-and-white warbler (*Mniotilta varia*) may increase somewhat. It is less clear if the increase in edge caused by the many clearings associated with uneven-aged management will reduce nesting success of the remaining species appreciably. In general, the Ozarks have low densities of cowbirds, so parasitism rates will be lower than in more fragmented regions. The data of Annand and Thompson (1997) also suggest that densities of Acadian flycatcher and ovenbird will be reduced in areas with uneven-aged management. Given that as many as 70 percent of ovenbird territories may occur where at least some trees are removed in an area with uneven-aged management, negative effects on these forest interior species could be measurable. It is quite possible, though, that there may be a 1- or 2-year time lag in some of these effects, because some birds may return to territories where they previously

occurred despite the loss of trees, while subsequent males may be unwilling to use these areas for establishing breeding territories because of their changed vegetation structure.

Although we can make some quantitative predictions of possible effects based on the area of mature forest that is harvested, and some qualitative predictions from prior studies in different habitats, the beauty of MOFEP is the combination of its experimental design, its large scale, and long-term nature. Over the next 3 years and more, we should be able to measure in detail the distributional shifts of forest birds in response to the cuts, the addition of new birds in clearcuts and, perhaps, group and single tree openings, and the demographic effects of the two management schemes on all the birds common in these forests. With the strength of our 5 years of preliminary data, we and subsequent researchers should have a chance to gain unprecedented insight into the effects of these forest management techniques on the demography of migrant and resident birds. The pre-treatment data will allow us to see the immediate avian response to cutting, although decades and subsequent cutting cycles will be needed to evaluate the complete response. If the Ozarks truly are a population source region for other parts of the Midwest, we should be able to design a management plan that maintains the integrity of this resource for future generations of both songbirds and humans.

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Pre-treatment Conditions of Herpetofaunal Communities on Missouri Ozark Forest Ecosystem Project (MOFEP) Sites, 1992-1995

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Abstract.—I examined the species composition, species richness, and relative abundance of herpetofaunal communities on southwest-facing and northeast-facing slopes on the MOFEP sites. For the landscape-scale investigations, herpetofaunal communities on southwest-facing slopes were relatively similar, averaged 23.4 species/site, and had relative abundance estimates ranging from 14.4 to 38.2 captures/100 trap days. Communities on northeast-facing slopes were also relatively similar, averaged 23.2 species/site, and had relative abundance estimates ranging from 14.7 to 41.1 captures/100 trap days. For the small-scale investigations, herpetofaunal community similarity indices ranged from 0.56 to 0.77 and relative abundance estimates ranged from 15.9 to 29.7 captures/100 trap days.

Natural resource management agencies are increasingly expected to manage for the entire spectrum of wildlife species. The public is interested in nongame species and the conservation of plant and animal communities of native habitats (MO Department of Conservation 1990). This increasing public interest encourages resource management agencies to examine the effects of their management practices on nongame animal communities. In Missouri, forest management agencies are under fire to justify traditional silvicultural practices. We already have information on the advantages and disadvantages of silvicultural practices to several game species, but we lack much information about the effects of forest management practices on less obvious, yet abundant vertebrates, such as amphibians and reptiles.

Herpetofauna are worthy subjects for research examining the effects of forest management because they make up a significant portion of biomass in forest ecosystems (Gibbons 1988), are non-migratory or short-distance migrants, and are sensitive to abiotic changes in the environment. In Hubbard Brook studies in the eastern deciduous forest ecosystem, salamanders alone make up 2.6 times the biomass of birds and are equal in biomass to mammals (Burton and Likens 1975). Unlike birds and mammals that can quickly move from a changed environment or undergo annual migrations, most forest herpetofauna occupy small home ranges (e.g., redback salamanders occupy 10 to 20 m^2 territories, Kleeberger and Werner 1982) and reside in a small area throughout the year. Many herpetofaunal species are not likely to or cannot move from an area that has been drastically impacted by changes in the environment. Also, because all amphibians require water or moist environments for breeding and respiration, they are likely to be most impacted by the changes in soil moisture, surface temperature, and vegetation that result from forest management.

Previous research on herpetofaunal communities in Missouri has described the animal species and numbers present in different habitat types in central Missouri (Clawson and Baskett 1982, Clawson *et al.* 1984). Researchers in other portions of the United States have evaluated the effects of clearcutting on herpetofaunal communities (Ash 1988, Blymer and McGinnes 1977, Bury 1983, deMaynadier and Hunter 1995, Dupuis *et al.* 1995, Enge and Marion 1986, Pais *et al.* 1988, Petranka *et al.*

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1993, Petranka *et al.* 1994, Pough *et al.* 1987, Welsh 1990), but information on the effects of forest management practices on the herpetofaunal communities of Ozark oak-hickory forests is lacking.

This study examines the effects of standard Missouri Department of Conservation (MDC) forest management practices, even- and uneven-aged silviculture, on herpetofaunal communities inhabiting southern Missouri's Ozark oak-hickory forests on MDC property. I have two objectives for this research. First, I want to determine if even-aged and uneven-aged forest management has landscape-scale effects on the species composition, species richness, and relative abundance of herpetofaunal communities inhabiting MOFEP sites during 1992-2001. Secondly, I will determine if even-aged forest management has a small-scale effect on the species composition, species richness, and relative abundance of herpetofaunal communities inhabiting stands to be cut, and adjacent uncut forest (50 m and 200 m from clearcut boundary edge) on MOFEP sites during 1992-2001. The information presented in this paper describes the pre-treatment conditions of herpetofaunal communities studied during 1992-1995. For further information concerning the genesis and development of MOFEP, see Brookshire *et al.* (1997).

METHODS

Sampling Design

The overall design of MOFEP is described elsewhere (Sheriff and He 1997). To meet the objective of examining the landscape-scale effect of even- and uneven-aged forest management on the species composition, species richness, and relative abundance of herpetofaunal communities, 12 herpetofaunal sampling arrays were randomly placed on southwest-facing slopes (ecological land type (ELT) 17) and northeast-facing slopes (ELT 18) on each site. Of the 12 arrays, six were placed on ELT 17 landscapes and six were placed on ELT 18 landscapes (see fig. 5, Brookshire *et al.* 1997). Twelve arrays were used per site because I believed that two technicians could check all 12 arrays within the average work day. Southwest-facing and northeast-facing slopes were sampled because they make up 68 to 83 percent of the area within the sites.

To meet the objective of examining the small-scale effect of even-aged forest management on herpetofaunal communities within a clearcut, and 50 m and 200 m from the edge of clearcuts, two stands within each even-aged treatment site were randomly selected for sampling. A sampling array was randomly placed within each stand to be clearcut. Additional arrays were placed 50 m and 200 m from the treatment stand boundary. The three arrays associated with a clearcut stand were on the same slope type (either southwest- or northeast-facing). Only two designated even-aged treatment stands per site were sampled because few designated clearcut stands could meet the criteria allowing me to place two additional arrays 50 m and 200 m from the clearcut edge and remain on the same slope-type as the clearcut.

Field Sampling Methods

The species composition, species richness, and relative abundance of herpetofaunal communities on the MOFEP study sites were sampled using arrays modified from the Jones (1981) design (fig. 1). Arrays were composed of three, 7.5-m x 0.75-m drift fences of aluminum flashing buried 10 cm in the ground. Wings of the array were placed 120 degrees apart. The pitfall trap at the junction of the drift fences was a 19-liter plastic bucket. Funnel traps, made from aluminum window screening, were placed along the sides and at the distant ends of the drift fences. The small ends of funnel trap openings were 6 to 8 cm in diameter.

I selected a modified Jones' array as the sampling technique because it is well-suited for long-term research projects. Many collaborating research projects are simultaneously occurring on MOFEP sites (Brookshire *et al.* 1997). I needed a technique that would not disrupt or preclude other researchers from sampling at that same point where I was sampling for amphibians and reptiles. After installation of the array, the area at and surrounding the sample point is relatively undisturbed. Array sampling is also a passive sampling technique. As such, I can use hundreds of technicians over the course of this long-term research and not fear that their varying abilities to see, hear, and grab animals will bias samples among sites and years. Array sampling also allows repeated sampling at the same point over many days,

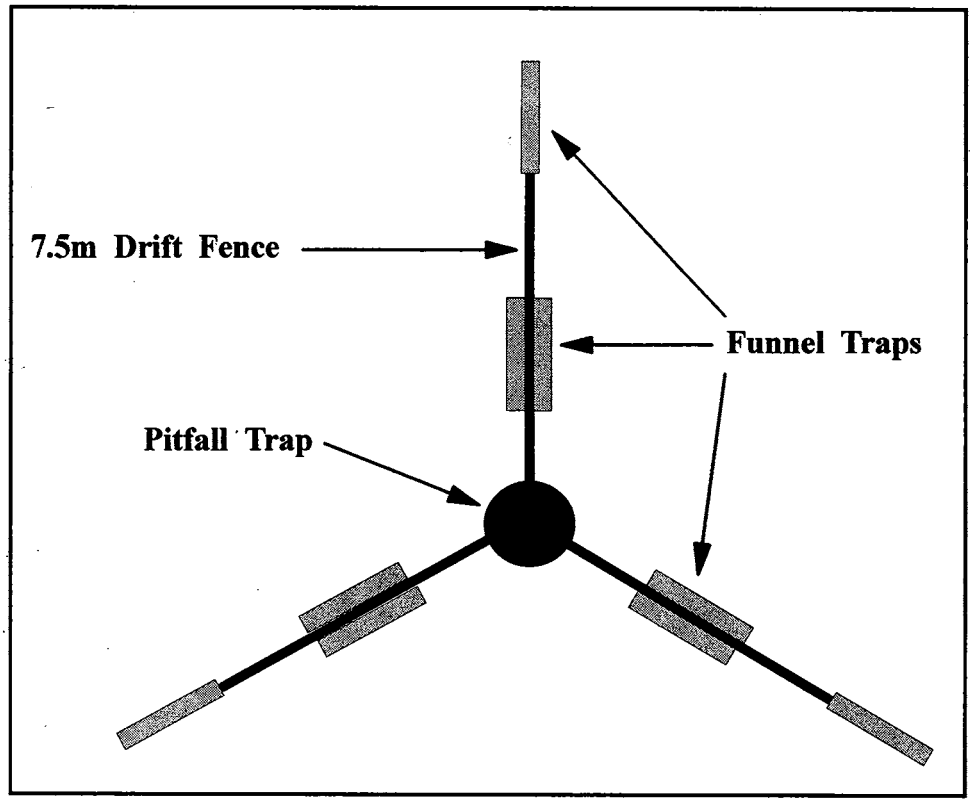

Figure 1.—*The design of a MOFEP herpetofaunal sampling array with pitfall trap, drift fences, and funnel traps.*

months, and years. Most importantly, array sampling is one of the best techniques for sampling the widest spectrum of species within a community (Corn 1994). Array sampling does undersample some groups of amphibians and reptiles, such as treefrogs and box turtles, yet it allows for the capture of individuals from almost every species present in the upland forest region.

Arrays were open for sampling during 20 March - 2 July and 19 August - 28 October 1992 (165 trap days); 4 March - 2 July and 30 August - 30 October 1993 (174 trap days); 25 February - 1 July and 29 August - 2 November 1994 (183 trap days); and 27 February - 30 June and 29 August - 2 November 1995 (184 trap days). During periods when sampling did not occur, pitfall traps were filled with rocks and sticks, and funnel traps were removed from arrays. All arrays on a site were checked for captured animals approximately every 3 days. The nine sites were grouped into three blocks of three sites each (randomized block design) to account for the influence of location on observed results (Sheriff and He 1997). All arrays within a block were checked on the same day.

Captured individuals were identified to species, measured for snout-vent length, toe clipped or ventral scale clipped with a unique mark, and released approximately 5 to 7 m from the traps. Turtles were marked by filing notches in marginal scutes. During 1993, 1994, 1995, and the latter part of 1992, American toads (refer to appendix A for a list of scientific names) and central newts were given a batch mark unique for the sampling year. All other species were given unique individual marks.

Data Analysis

Differences in species composition of herpetofaunal communities among sites during the 4-year pre-treatment period were qualitatively and quantitatively described. Species were considered widespread in distribution if captured at 83 to 100 percent of the arrays within a slope-type (southwest- or northeast-facing) on a site. If a species was captured at ≤ 33 percent of the arrays, I considered them to be local in distribution or infrequently captured. Indices of similarity (Jaccard 1901) in species composition were calculated among the nine sites for each slope-type. An index near 1.00

meant the species composition between sites was very similar.

The species richness of each site was computed as the number of species caught for a given site, year, and slope-type. A repeated measures analysis of variance (SAS 1989) with year as the repeated factor was used to examine the effect of year, treatment, block, and their interactions on the species richness of herpetofaunal communities within southwest- and northeast-facing landscapes during the pre-treatment period. An effect was considered to be significant if the P-value in the test was ≤ 0.05. The normality of model residuals was analyzed using the SAS (1989) univariate procedure (Z. He personal communication).

Relative abundance estimates for each array were derived by summing the number of captures at each array for each year and dividing by the total number of trap days (number of days the arrays were open for sampling) for that year. One trap day was defined as one array operating for one day. I defined trap days as such because all 10 traps within an array (1 pitfall and 9 funnel traps) were not independent of one another. Mean annual relative abundance estimates (n=6) for each slope-type within each site were calculated. Repeated measures analysis of variance with year as the repeated factor (SAS 1989) was used to detect any differences in relative abundance estimates within a slope-type during the 4-year pre-treatment period due to year, treatment, block, and their interactions. I considered a factor significant if the P-value was ≤ 0.05. The normality of model residuals was analyzed using the SAS (1989) univariate procedure (Z. He personal communication). Relative abundance estimates were also calculated for each species by site and slope-type. Species relative abundance estimates were qualitatively compared among sites and years.

Some of the above-mentioned summaries and analyses were also used to examine the effect of distance to designated clearcut stands on herpetofaunal communities within clearcut stands, and 50 m and 200 m from the clearcut stand boundary. Similarity indices were used to examine similarities in species composition between communities during the pre-treatment period. Because of the potential for a lack of independence between distance categories at a designated clearcut, paired t-tests (SAS 1989) of mean differences in relative abundance estimates within years and between distance categories were used to determine if mean differences were different from zero. Relative abundances of individual species among years and within distance from clearcut categories (within designated clearcuts, and 50 m and 200 m from designated clearcuts) were qualitatively evaluated.

RESULTS

General

During 1992-1995, 22,306 specimens from 43 species were captured at the 126 arrays on the MOFEP sites.

Landscape-scale Effects of Forest Management: Pre-treatment Conditions

Herpetofaunal Communities on Southwest-facing Slopes (ELT 17)

Species Composition.—Forty species were captured at arrays on southwest-facing slopes (table 1). Of these, 8 were salamanders, 9 were frogs or toads, 5 were lizards, 1 was a turtle, and 17 were snakes. Seven species (spotted salamanders; American toads; five-lined, broadhead, and ground skinks; and redbelly and smooth earth snakes) were widespread in distribution on the sites (table 1). Eight other species (dark-sided salamander, four-toed salamander, Blanchard's cricket frog, timber rattlesnake, speckled kingsnake, northern water snake, rough green snake, and rough earth snake) were relatively local in distribution or infrequently captured (table 1).

The species composition of communities among sites was very similar. Jaccard's similarity indices of the species composition between sites averaged 0.76, yet ranged from 0.59 for sites 8 and 9, to 0.88 for sites 3 and 7 (table 2). The mean indices for sites within treatments were 0.73 for no-harvest, 0.76 for even-aged, and 0.72 for uneven-aged sites. The mean indices for sites within blocks were 0.83 for block 1, 0.75 for block 2, and 0.71 for block 3 sites.

Species Richness.—The number of species on southwest-facing slopes per site/year ranged from 18 to 30 during 1992-1995 (table 3). The mean number of species per site/year was 23.4 species. On average, the number of species

Table 1.—*The percent of arrays (N=6) within each site at which a species was captured on southwest-facing slopes on the MOFEP sites during 1992-1995. Scientific names for species are in appendix A.*

	MOFEP site								
Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
Salamanders									
Cave	17	17	17	67	33	33	—	—	50
Central newt	100	83	100	100	100	100	100	100	50
Dark-sided	17	17	17	33	33	17	—	—	33
Four-toed	17	—	—	17	17	—	—	17	33
Marbled	100	83	50	67	67	67	83	100	67
Redback	100	83	100	100	83	100	100	67	50
Slimy	100	100	100	100	67	33	67	100	100
Spotted	100	100	100	100	100	100	100	100	100
Frogs/Toads									
American toad	100	100	100	100	100	100	100	100	100
Blanchard's cricket	—	—	—	—	—	17	—	—	—
E. Narrowmouth	50	—	17	17	—	—	17	17	—
Gray treefrog	67	17	—	—	17	33	—	—	17
Green frog	100	83	100	100	83	83	100	83	50
Pickerel frog	83	83	67	83	67	83	50	83	33
S. Leopard frog	67	50	33	17	17	33	33	17	—
Spring peeper	83	50	83	67	100	100	100	83	33
Woodhouse's toad	33	50	67	67	33	17	—	—	50
Lizards									
Broadhead skink	83	100	100	100	100	100	100	100	100
Coal skink	83	83	100	83	83	83	83	100	67
Fence lizard	67	67	83	67	100	83	100	100	100
Five-lined skink	100	100	100	100	100	100	100	100	100
Ground skink	100	100	100	100	100	100	100	100	100
Snakes									
Copperhead	100	100	83	100	100	100	67	50	100
Black rat	17	17	33	50	17	17	33	50	—
E. Garter	50	50	50	50	—	67	33	67	33
E. Hognose	33	50	33	50	17	67	33	—	17
E. Yellowbelly racer	33	50	50	—	—	17	67	33	50
Midland brown	33	—	17	17	17	—	33	67	33
N. Redbelly	83	100	100	100	100	100	100	100	100
N. Water	17	17	33	—	—	—	17	—	17
Prairie ringneck	83	100	100	67	67	100	67	33	67
Red milk	—	—	17	—	17	67	33	33	—
Rough earth	17	—	—	—	—	33	33	—	17
Rough green	17	—	17	17	—	17	17	17	—
Smooth earth	100	100	100	100	100	100	100	100	100
Speckled kingsnake	—	—	—	17	—	—	—	—	—
Timber rattlesnake	—	—	—	—	—	17	—	—	17
W. Ribbon	—	17	—	—	—	50	—	33	—
W. Worm	83	33	17	33	67	83	17	50	67
Turtles									
Three-toed box	17	50	—	17	33	—	—	—	17

Table 2.—*Jaccard's indices of similarity in species composition of herpetofaunal communities observed on southwest-facing slopes on MOFEP sites during 1992 - 1995. Indices near 1.00 are most similar.*

	MOFEP sites								
MOFEP sites	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
1	—	0.83	0.86	0.86	0.81	0.77	0.81	0.73	0.84
2		—	0.80	0.75	0.82	0.81	0.69	0.67	0.78
3			—	0.83	0.82	0.81	0.88	0.79	0.71
4				—	0.82	0.69	0.72	0.74	0.74
5					—	0.73	0.67	0.69	0.75
6						—	0.75	0.69	0.72
7							—	0.84	0.69
8								—	0.59
9									—

Table 3.—*Number of species captured on southwest-facing slopes on MOFEP sites during 1992-1995.*

	Year			
MOFEP site	**1992**	**1993**	**1994**	**1995**
1	29	24	26	22
2	24	22	27	21
3	21	26	25	24
4	24	23	27	19
5	22	18	23	23
6	30	21	25	23
7	21	22	26	20
8	20	20	26	24
9	23	23	23	25

captured on a site varied by six during the 4-year period.

Species richness values did not differ among sites due to treatment or block effects (table 4). The interactions of year x treatment and year x block also did not influence species richness among sites. However, year did have a significant effect on species richness in repeated measures analysis. Species richness values for 1994 were not normally distributed. I do not have an explanation for why the richness values for 1994 were different from other years. When the values for 1994 were omitted from the repeated measures analysis of variance, then year (P=0.49), treatment (P=0.41), block (P=0.48), year x treatment (P=0.19), and year x block (P=0.29) did not affect species richness values.

Table 4.—*Results of repeated measures analysis of variance examining the effect of year, block, treatment, and their interactions on species richness on southwest-facing slopes on MOFEP sites during 1992-1995.*

	Between site effect			
Source	**Degrees of freedom**	**Mean square**	**F-value**	**P**
Treatment	2	5.4	1.07	0.42
Block	2	7.2	1.42	0.34
Error (Blk x Trt)	4	5.1		

	Within Site Effect				
Source	**Pillai's Trace**	**F-value**	**Numerator df**	**Denominator df**	**P**
Year	0.98	35.18	3	2	0.03
Year x Block	1.17	1.42	6	6	0.34
Year x Treatment	1.44	2.59	6	6	0.14

Relative Abundance.—Mean relative abundance estimates/site for herpetofaunal communities on southwest-facing slopes ranged from 14.4 to 38.2 captures/100 trap days for the MOFEP sites (table 5). The difference in relative abundance estimates among years for a site ranged from 2.6 captures/100 trap days for site 7, to 17.2 captures/100 trap days for site 2. In repeated measures analysis of variance, year, treatment, and block did not affect estimates (table 6). The interactions year x treatment and year x block also had no effect on relative abundance (table 6).

Table 5.—*Mean relative abundance estimates (s.e.) for amphibian and reptile communities on southwest-facing slopes on MOFEP sites during 1992-1995. Estimates are defined as the number of captures/ 100 trap days.*

MOFEP site	Year 1992	1993	1994	1995
1	30.8 (3.8)	28.9 (4.7)	35.0 (5.1)	29.1 (7.2)
2	34.0 (7.0)	16.8 (1.8)	23.4 (2.3)	26.1 (4.8)
3	22.1 (2.8)	21.5 (1.6)	25.6 (2.0)	14.4 (2.5)
4	18.0 (2.9)	26.8 (2.9)	22.6 (1.5)	19.2 (2.9)
5	25.6 (4.0)	21.8 (3.6)	14.5 (1.5)	20.3 (3.6)
6	35.3 (1.8)	27.1 (2.8)	21.5 (2.6)	31.3 (1.0)
7	21.4 (1.7)	21.3 (2.2)	22.7 (3.4)	23.9 (0.9)
8	28.7 (2.6)	26.2 (4.1)	30.7 (6.5)	25.0 (3.1)
9	38.2 (5.2)	26.1 (5.2)	28.6 (2.4)	33.2 (2.4)

Relative abundance estimates for individual species on southwest-facing slopes were generally small (for mean relative abundance estimates for individual species by site, refer to appendix B). Herpetofaunal species trapped in greater numbers (≥1.0 captures/100 trap days) on all sites included American toads, ground skinks, and smooth earth snakes. These species will likely be candidates for a closer examination of the effects of forest management on individual species following post-treatment. Three other species (spotted salamander, five-lined skink, and redback salamander) are also likely to be examined. These species did not occur in as great numbers as American toads, ground skinks, or smooth earth snakes, but did occur in moderate numbers (typically ≥ 0.5 captures/100 trap days) and were located on all sites in most years. All other species captured were either infrequently caught or captured in such small numbers that statistical analyses would be difficult.

Herpetofaunal Communities on Northeast-facing Slopes (ELT 18)

Species Composition.—Forty-three species were captured at arrays on northeast-facing slopes (table 7). Of these 43 species, 9 were salamanders, 10 were frogs or toads, 6 were lizards, 17 were snakes, and 1 was a turtle. Six of the seven species that were widespread in distribution on southwest-facing slopes were also widespread on northeast-facing slopes. On

Table 6.—*Results of repeated measures analysis of variance examining the effect of year, block, treatment, and their interactions on herpetofaunal relative abundance on southwest-facing slopes on MOFEP sites during 1992-1995.*

Source	Between site effect: Degrees of freedom	Mean square	F-value	P
Treatment	2	124.5	1.74	0.29
Block	2	37.2	0.52	0.63
Error (Blk x Trt)	4	71.6		

Source	Within site effect: Pillai's Trace	F-value	Numerator df	Denominator df	P
Year	0.75	1.98	3	2	0.35
Year x Block	1.42	2.44	6	6	0.15
Year x Treatment	0.88	0.79	6	6	0.61

Table 7.—*The percent of arrays (N=6) within each site at which a species was captured on northeast-facing slopes on the MOFEP sites during 1992-1995. Scientific names for species are in Appendix A.*

	MOFEP site								
Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
Salamanders									
Cave	17	17	33	67	17	33	—	67	17
Central newt	100	100	100	100	100	100	83	83	50
Dark-sided	—	17	33	33	67	33	—	—	17
Four-toed	—	—	—	17	17	—	—	33	17
Marbled	100	83	50	50	83	67	83	50	17
Redback	100	67	100	100	83	100	100	100	67
Slimy	100	100	83	100	83	33	83	83	100
Spotted	100	100	100	100	100	100	100	100	100
Tiger	17	—	—	—	—	—	—	17	—
Frogs/Toads									
American toad	100	100	100	100	100	100	100	100	100
Blanchard's cricket	—	—	—	—	—	33	—	17	—
Bullfrog	—	—	—	—	—	—	—	17	—
E. Narrowmouth	33	—	—	—	—	—	—	—	—
Gray treefrog	50	17	—	—	50	50	17	50	—
Green frog	100	83	100	83	83	100	100	100	17
Pickerel frog	67	100	67	50	83	100	33	100	—
S. Leopard frog	100	50	17	33	67	33	50	67	—
Spring peeper	83	67	50	67	100	100	100	100	33
Woodhouse's toad	67	67	67	67	—	50	—	—	17
Lizards									
Broadhead skink	100	100	100	100	100	100	100	100	83
Coal skink	67	83	83	67	100	83	83	83	100
Fence lizard	33	50	67	67	67	50	50	83	100
Five-lined skink	100	100	100	83	83	100	100	100	100
Ground skink	100	100	100	100	100	83	100	100	100
Six-lined racerunner	—	—	—	—	—	—	—	17	—
Snakes									
Copperhead	100	100	83	83	100	83	83	100	100
Black rat	17	33	17	50	17	—	17	17	—
E. Garter	83	50	50	33	83	17	50	33	17
E. Hognose	17	33	33	17	67	33	33	33	—
E. Yellowbelly racer	33	17	33	17	33	—	33	33	17
Midland brown	—	50	—	—	—	—	33	50	67
N. Redbelly	83	50	100	100	100	100	100	67	100
N. Water	—	17	—	—	—	—	—	—	—
Prairie ringneck	83	83	50	67	67	67	83	50	50
Red milk	33	—	—	—	33	17	33	17	33
Rough earth	—	—	17	—	—	17	17	—	50
Rough green	—	—	17	—	33	—	17	—	—
Smooth earth	100	100	100	100	100	100	100	100	100
Speckled kingsnake	17	17	—	—	—	—	17	—	—
Timber rattlesnake	—	—	—	17	17	—	—	—	17
W. Ribbon	17	17	—	17	17	67	17	17	17
W. Worm	67	17	67	—	17	83	50	17	50
Turtles									
Three-toed box	50	17	—	17	33	33	—	—	33

northeast-facing slopes, the copperhead replaced the redbelly snake as a widespread species. The list of species (Blanchard's cricket frog, tiger salamander, eastern yellowbelly racer, six-lined racerunner, timber rattlesnake, dark-sided salamander, eastern narrowmouth toad, four-toed salamander, speckled kingsnake, red milk snake, northern water snake, rough green snake, and bullfrog) that were local in distribution or infrequently captured on northeast-facing slopes was similar to that for southwest-facing slopes.

Jaccard's similarity indices between sites averaged 0.74, and ranged from 0.64 between sites 8 and 9 to 0.85 between sites 4 and 5 (table 8). The mean indices for sites within treatments were 0.75 for no-harvest, 0.73 for even-aged, and 0.74 for uneven-aged sites. The mean indices for sites within blocks were 0.77 for block 1, 0.79 for block 2, and 0.69 for block 3 sites.

Species Richness.—The mean number of species per site/year on northeast-facing slopes ($\bar{x}$=23.2) was essentially identical to the mean for southwest-facing slopes. The range in number of species per site/year (range = 18 to 29) was also nearly identical to that of southwest-facing slopes (table 9). Herpetofaunal communities on northeast-facing slopes tended to vary a little less in the number of species captured among years within sites ($\bar{x}$ difference = 4.4 species) than southwest-facing slopes. Year, treatment, block, and the interactions of year x treatment and year x block in repeated measures analysis of variance did not affect species richness (table 10).

Table 9.—*Number of species captured on northeast-facing slopes on MOFEP sites during 1992-1995.*

MOFEP site	Year 1992	1993	1994	1995
1	26	25	26	25
2	21	23	26	24
3	20	23	22	23
4	20	24	25	20
5	27	29	24	21
6	23	22	21	20
7	25	25	19	24
8	28	22	27	23
9	20	21	21	18

Relative Abundance.—Mean relative abundance estimates/year ranged from 14.7 captures/100 trap days to 41.1 captures/100 trap days (table 11). The difference in estimates among years on a site ranged from 5.0 captures/100 trap days for site 2 to 14.2 captures/100 trap days for site 4. In repeated measures analysis of variance, year, treatment, and block did not affect herpetofaunal relative abundance during the pre-treatment period (table 12). The interactions of year x treatment and year x block also had no effect on herpetofaunal relative abundance (table 12).

Estimates of relative abundance for individual species were typically small (see appendix C for mean species relative abundance estimates) by site. Species that occurred in greater numbers (typically with relative abundance estimates ≥ 1.0 captures/100 trap days) included American toad, ground skink, and smooth earth

Table 8.—*Jaccard's indices of similarity in species composition of herpetofaunal communities observed on northeast-facing slopes on MOFEP sites during 1992 - 1995. Indices near 1.00 are most similar.*

MOFEP sites	MOFEP sites 1	2	3	4	5	6	7	8	9
1	—	0.83	0.72	0.74	0.78	0.78	0.78	0.76	0.65
2		—	0.77	0.80	0.78	0.78	0.78	0.72	0.70
3			—	0.79	0.77	0.76	0.76	0.68	0.68
4				—	0.85	0.74	0.65	0.68	0.76
5					—	0.78	0.78	0.76	0.75
6						—	0.72	0.71	0.74
7							—	0.76	0.67
8								—	0.64
9									-

Table 10.—*Results of repeated measures analysis of variance examining the effect of year, block, treatment, and their interactions on herpetofaunal species richness on northeast-facing slopes on MOFEP sites during 1992-1995.*

Source	Between site effect Degrees of freedom	Mean square	F-value	P
Block	2	2.7	0.12	0.89
Treatment	2	7.7	0.33	0.73
Error (Blk x Trt)	4	23.1		

Source	Within site effect Pillai's Trace	F-value	Numerator df	Denominator df	P
Year	0.78	2.39	3	2	0.31
Year x Block	1.53	3.30	6	6	0.09
Year x Treatment	1.31	1.89	6	6	0.23

Table 11.—*Mean relative abundance estimates (s.e.) for amphibian and reptile communities on northeast-facing slopes on MOFEP sites during 1992-1995. Estimates are defined as the number of captures/ 100 trap days.*

MOFEP site	Year 1992		1993		1994		1995	
1	35.6	(4.4)	38.0	(3.0)	41.1	(12.3)	33.2	(4.7)
2	22.8	(3.5)	19.3	(3.7)	21.8	(2.1)	17.8	(2.1)
3	15.7	(1.9)	20.0	(1.3)	20.4	(2.9)	14.7	(1.7)
4	17.5	(2.3)	31.7	(4.6)	27.4	(5.1)	18.5	(2.0)
5	25.1	(4.0)	27.7	(2.3)	16.6	(2.3)	22.4	(3.3)
6	33.2	(4.7)	25.0	(1.3)	27.2	(2.8)	27.3	(4.8)
7	25.6	(2.6)	26.0	(5.2)	21.0	(2.1)	30.7	(4.5)
8	30.6	(5.4)	28.8	(4.8)	27.7	(3.3)	24.5	(3.0)
9	30.2	(3.5)	24.5	(3.0)	27.3	(3.3)	34.6	(4.6)

Table 12.—*Results of repeated measures analysis of variance examining the effect of year, block, treatment, and their interactions on herpetofaunal relative abundance on northeast-facing slopes on MOFEP sites during 1992-1995.*

Source	Between site effect Degrees of freedom	Mean square	F-value	P
Treatment	2	238 .5	1.99	0.25
Block	2	27.9	0.23	0.80
Error (Blk x Trt)	4	119.7		

Source	Within site effect Pillai's Trace	F-value	Numerator df	Denominator df	P
Year	0.29	0.28	3	2	0.84
Year x Block	0.97	0.94	6	6	0.53
Year x Treatment	0.71	0.55	6	6	0.76

snake. These species, which also occurred in greater numbers on southwest-facing slopes, will likely be good candidates for examining the effects of forest management following post-treatment. Spotted salamanders, redback salamanders, and five-lined skinks occurred in moderate numbers (typically ≥ 0.5 captures/ 100 trap days) on all sites and in most years, and will also be examined for effects of forest management.

Small-Scale Effects (the Effect of Distance) of Clearcutting: Pre-treatment Conditions

Herpetofaunal Communities on Southwest-facing Slopes (ELT 17)

Species Composition.—During the pre-treatment period, a total of 37 species were captured on southwest-facing slopes associated with research examining the effect of distance from an even-aged treatment stand (within a clearcut, 50 m, and 200 m from a clearcut edge; see appendix D for list of species captured). This total is just three species fewer than the total number of species captured on southwest-facing slopes used to examine the landscape-scale (compartment level) effect of forest management. Of these 37 species, 8 were salamanders, 8 were frogs or toads, 6 were lizards, and 15 were snakes.

Jaccard's similarity indices (SI) among the communities representing three different distances (within, 50 m, and 200 m) from the designated clearcuts were virtually identical (SI=0.76 for within a designated clearcut vs. 50 m from a clearcut edge, SI=0.77 for 50 m from clearcut vs. 200 m from a clearcut, and SI=0.77 for within a designated clearcut vs. 200 m from a clearcut edge). Twelve species were captured at every distance and during every year (spotted salamander, American toad, coal skink, five-lined skink, broadhead skink, central newt, slimy salamander, redback salamander, ground skink, fence lizard, redbelly snake, and smooth earth snake). These species were widespread in distribution on southwest-facing slopes. An additional 13 species were captured at each of the three distance categories, but were not captured every year (cave salamander, marbled salamander, gray treefrog, green frog, spring peeper, southern leopard frog, Woodhouse's toad, copperhead, eastern yellowbelly racer, hognose snake, midland brown snake, prairie ringneck snake, and western worm snake). These 13 additional species were also widespread in distribution, yet not as abundant or as likely to be trapped.

Species Richness.—Even though a total of 37 species were captured on southwest-facing slopes, the number of species captured per distance category/year ranged from 18 to 24 species. Within distance categories, the difference in number of species trapped among years ranged from 2 for areas 200 m from designated clearcuts to 6 for areas within designated clearcuts.

Relative Abundance.—Herpetofaunal community relative abundance estimates ranged from 15.90 to 29.70 captures/100 trap days (table 13). Paired t-tests comparing annual differences in mean relative abundance estimates between communities within clearcuts vs. communities 50 m from clearcuts and between communities 50 m from clearcuts vs. communities 200 m from clearcuts suggested no differences in estimates between categories. The trend in relative abundance estimates for the three communities during the 4-year period is the same. Relative abundance estimates were high in 1992, dropped in 1993, and gradually rose during 1994 and 1995 (table 13).

Relative abundance estimates for individual species in communities at the three distances from designated clearcuts were typically small (see appendix D for relative abundance estimates of individual species). Species that were captured in relatively greater numbers (typically ≥ 1.0 captures/100 trap days) and in all years were slimy salamander, American toad, five-lined skink, ground skink, and smooth earth snake. These species are likely candidates for further species-specific analyses following post-treatment.

Herpetofaunal Communities on Northeast-facing Slopes (ELT 18)

Species Composition.—A total of 37 species also were captured on northeast-facing slopes used to examine the effects of distance from clearcut on herpetofaunal communities (see appendix E for complete list of species that were captured). This total was six species fewer than the number of species captured on northeast-facing slopes used for examining the compartment-level effect of forest management. Of the 37 species captured, 8 were salamanders, 8 were frogs or toads, 6 were lizards, one was a turtle, and 14 were snakes.

Table 13.—*Overall relative abundance estimates (s.e.) for herpetofaunal communities within, and 50 m and 200 m from designated clearcut stands during 1992-1995. Relative abundance is defined as number of captures/ 100 trap days.*

	Southwest-facing slopes			
	Year			
Distance	**1992**	**1993**	**1994**	**1995**
Within clearcut	29.29 (13.24)	20.88 (2.21)	22.77 (4.42)	23.73 (9.92)
50 m from clearcut	29.70 (6.13)	15.90 (2.03)	16.58 (0.66)	19.02 (7.67)
200 m from clearcut	19.60 (0.73)	16.67 (2.07)	18.21 (2.65)	21.74 (7.07)

	Northeast-facing slopes			
	Year			
Distance	**1992**	**1993**	**1994**	**1995**
Within clearcut	28.48 (7.30)	18.97 (2.18)	21.86 (3.94)	22.10 (4.18)
50 m from clearcut	21.41 (6.30)	18.01 (2.21)	18.03 (3.72)	21.56 (10.02)
200 m from clearcut	23.03 (6.54)	27.39 (3.77)	22.22 (1.46)	23.91 (5.43)

Table 14.—*P values for paired t-tests examining the mean difference in relative abundance estimates between herpetofaunal communities captured within designated clearcuts vs. communities 50 m from clearcuts, and between communities 50 m from clearcuts vs. communities 200 m from clearcuts. The hypothesis tested was that the mean difference was not different from zero.*

	Southwest-facing slopes			
	Year			
Comparison	**1992**	**1993**	**1994**	**1995**
Within vs. 50 m	0.97	0.07	0.31	0.36
50 m vs. 200 m	0.25	0.81	0.67	0.08

	Northeast-facing slopes			
	Year			
Comparison	**1992**	**1993**	**1994**	**1995**
Within vs. 50 m	0.25	0.84	0.007*	0.94
50 m vs. 200 m	0.16	0.08	0.50	0.67

* Means were significantly different at $P \leq 0.05$.

Jaccard's similarity indices indicated a greater difference in species composition between the community at 200 m from the designated clearcut and the communities within the designated clearcut and 50 m from the clearcut. Similarity indices were 0.70 for communities within vs. 50 m from designated clearcuts, 0.61 for communities at 50 m vs. 200 m from clearcuts, and 0.56 for communities within vs. 200 m from clearcuts. Ten species were captured at every distance category and during every year of the pre-treatment period. These species were spotted salamander, American toad, five-lined skink, broadhead skink, central newt, slimy salamander, redback salamander, ground skink, redbelly snake, and smooth earth snake. Eight other species were as widely distributed as the previously mentioned species, but were not trapped every year (marbled salamander, green frog, pickerel frog, spring peeper, coal skink, fence lizard, copperhead, prairie ringneck snake).

snake. These species, which also occurred in greater numbers on southwest-facing slopes, will likely be good candidates for examining the effects of forest management following post-treatment. Spotted salamanders, redback salamanders, and five-lined skinks occurred in moderate numbers (typically ≥ 0.5 captures/ 100 trap days) on all sites and in most years, and will also be examined for effects of forest management.

Small-Scale Effects (the Effect of Distance) of Clearcutting: Pre-treatment Conditions

Herpetofaunal Communities on Southwest-facing Slopes (ELT 17)

Species Composition.—During the pre-treatment period, a total of 37 species were captured on southwest-facing slopes associated with research examining the effect of distance from an even-aged treatment stand (within a clearcut, 50 m, and 200 m from a clearcut edge; see appendix D for list of species captured). This total is just three species fewer than the total number of species captured on southwest-facing slopes used to examine the landscape-scale (compartment level) effect of forest management. Of these 37 species, 8 were salamanders, 8 were frogs or toads, 6 were lizards, and 15 were snakes.

Jaccard's similarity indices (SI) among the communities representing three different distances (within, 50 m, and 200 m) from the designated clearcuts were virtually identical (SI=0.76 for within a designated clearcut vs. 50 m from a clearcut edge, SI=0.77 for 50 m from clearcut vs. 200 m from a clearcut, and SI=0.77 for within a designated clearcut vs. 200 m from a clearcut edge). Twelve species were captured at every distance and during every year (spotted salamander, American toad, coal skink, five-lined skink, broadhead skink, central newt, slimy salamander, redback salamander, ground skink, fence lizard, redbelly snake, and smooth earth snake). These species were widespread in distribution on southwest-facing slopes. An additional 13 species were captured at each of the three distance categories, but were not captured every year (cave salamander, marbled salamander, gray treefrog, green frog, spring peeper, southern leopard frog, Woodhouse's toad, copperhead, eastern yellowbelly racer, hognose snake, midland brown snake, prairie ringneck snake, and western worm snake). These 13 additional species were also widespread in distribution, yet not as abundant or as likely to be trapped.

Species Richness.—Even though a total of 37 species were captured on southwest-facing slopes, the number of species captured per distance category/year ranged from 18 to 24 species. Within distance categories, the difference in number of species trapped among years ranged from 2 for areas 200 m from designated clearcuts to 6 for areas within designated clearcuts.

Relative Abundance.—Herpetofaunal community relative abundance estimates ranged from 15.90 to 29.70 captures/100 trap days (table 13). Paired t-tests comparing annual differences in mean relative abundance estimates between communities within clearcuts vs. communities 50 m from clearcuts and between communities 50 m from clearcuts vs. communities 200 m from clearcuts suggested no differences in estimates between categories. The trend in relative abundance estimates for the three communities during the 4-year period is the same. Relative abundance estimates were high in 1992, dropped in 1993, and gradually rose during 1994 and 1995 (table 13).

Relative abundance estimates for individual species in communities at the three distances from designated clearcuts were typically small (see appendix D for relative abundance estimates of individual species). Species that were captured in relatively greater numbers (typically ≥ 1.0 captures/100 trap days) and in all years were slimy salamander, American toad, five-lined skink, ground skink, and smooth earth snake. These species are likely candidates for further species-specific analyses following post-treatment.

Herpetofaunal Communities on Northeast-facing Slopes (ELT 18)

Species Composition.—A total of 37 species also were captured on northeast-facing slopes used to examine the effects of distance from clearcut on herpetofaunal communities (see appendix E for complete list of species that were captured). This total was six species fewer than the number of species captured on northeast-facing slopes used for examining the compartment-level effect of forest management. Of the 37 species captured, 8 were salamanders, 8 were frogs or toads, 6 were lizards, one was a turtle, and 14 were snakes.

Species Richness.—Species richness on northeast-facing slopes appeared to be more variable by distance category and year than on southwest-facing slopes. The number of species captured per distance category/year ranged from 13 to 22 species. Also, within distance categories, the difference in number of species captured among years ranged from three for communities within clearcuts to nine for communities 50 m from designated clearcuts.

Relative Abundance.—Relative abundance estimates for northeast-facing slope communities ranged from 18.01 to 28.48 captures/100 trap days (table 13). Results of paired t-tests of the difference in means revealed that relative abundance estimates between communities within designated clearcuts vs. communities 50 m from clearcuts during 1994 were different (table 14). This significant difference was due to an unusually small amount of variation for that mean difference ($\bar{x}$ = 3.82, s.e. = 0.31) and the small sample size (n = 3) in the comparison. I do not think the relative abundances for those two distance categories were really different. The trend in relative abundance estimates during 1992-1995 is the same for communities within clearcuts and 50 m from clearcuts, but differs for the community at 200 m from clearcuts. As with southwest-facing slope communities, relative abundance estimates for communities within clearcuts and 50 m from clearcuts were high in 1992, fell in 1993, and rose in 1994 and 1995 (table 13). The relative abundance estimates for the communities at 200 m differ by rising in 1993 and falling to the 1992 level in 1994 and 1995 (table 13).

As with relative abundance estimates for individual species on southwest-facing slopes, the relative abundance estimates for individual species on northeast-facing slopes were small (see appendix E). Eight species were captured in relatively greater numbers than other species and during every year. These species (central newt, redback salamander, slimy salamander, spotted salamander, American toad, five-lined skink, ground skink, and smooth earth snake) will likely be examined for abundance trends following treatment.

DISCUSSION

A number of studies have documented that amphibian populations, especially salamander populations, are positively correlated with forest stand age. Researchers have noted that in young forest stands, typically clearcuts ≤ 10 years old, salamander populations are very low or salamanders are not captured (Ash 1988, Blymer and McGinnes 1977, Dupuis *et al.* 1995, Petranka *et al.* 1993, Welsh 1990). As the forest matures, salamander populations rebound (Welsh 1990). Yet populations in mature forest that is 50 to 80 years old are still only at levels 20 to 50 percent of salamander populations occupying old-growth forest (Dupuis *et al.* 1995, Petranka *et al.* 1994). Some researchers speculate that in the eastern deciduous forest ecosystem, 50 to 70 years is needed for amphibian communities to recover from the perturbation of habitat (Petranka *et al.* 1993).

Researchers so far have concluded that the silvicultural technique is not necessarily to blame for the greatly reduced numbers of amphibians after cutting. It is the resulting environment that is hostile to amphibian existence and reproduction (Dupuis *et al.* 1995, Welsh 1990). Stands that have been recently cut have higher temperatures and reduced levels of soil- and ground-level moisture (Blymer and McGinnes 1977, Dupuis *et al.* 1995). Recently cut stands also have reduced amounts of decomposed, down, dead woody material on the forest floor (Petranka *et al.* 1994). This warmer, drier habitat with little usable cover is not conducive to amphibian communities. After cutting, salamanders probably die from the heat and dry environment (Petranka *et al.* 1993) or retreat underground for years until ground-level conditions are more favorable (Petranka *et al.* 1994). While underground, salamanders probably starve and cannot reproduce because of the lack of moisture (Petranka *et al.* 1994).

I expect to see a change in species composition of herpetofaunal communities and a reduction of amphibian numbers on some portions of MOFEP sites following the first entry cutting that occurred during 1996. Forty-two of the 126 sample points on the MOFEP study sites experienced extreme habitat disturbance of some form due to silvicultural operations. What is yet to be determined is if this disturbance translates into landscape-scale or edge-effect changes in species composition, species richness, and relative abundance estimates.

Herpetofaunal communities on MOFEP sites were similar in species composition, species richness, and relative abundance during the pre-treatment period. The species composition, species richness, and relative abundance of

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Appendix A.—*Common and scientific names for amphibians and reptiles captured on the MOFEP sites during 1992-1995.*

Common name	Scientific name
Salamanders	
Cave	*Eurycea lucifuga*
Central newt	*Notophthalmus viridescens*
Dark-sided	*Eurycea longicauda*
Four-toed	*Hemidactylium scutatum*
Marbled	*Ambystoma opacum*
Redback	*Plethodon serratus*
Slimy	*Plethodon glutinosus*
Spotted	*Ambystoma maculatum*
Tiger	*Ambystoma tigrinum*
Frogs/Toads	
American toad	*Bufo americanus*
Blanchard's cricket	*Acris crepitans*
Bullfrog	*Rana catesbiana*
Eastern narrowmouth	*Gastrophryne carolinensis*
Gray treefrog	*Hyla chrysoscelis*
Green frog	*Rana clamitans*
Pickerel frog	*Rana palustris*
Southern leopard	*Rana utricularia*
Spring peeper	*Pseudacris crucifer*
Woodhouse's toad	*Bufo woodhousii*
Lizards	
Broadhead skink	*Eumeces laticeps*
Coal skink	*Eumeces anthracinus*
Fence lizard	*Sceloporus undulatus*
Five-lined skink	*Eumeces fasciatus*
Ground skink	*Scincella lateralis*
Six-lined racerunner	*Cnemidophorus sexlineatus*
Snakes	
Copperhead	*Agkistrodon contortrix*
Black rat	*Elaphe obsoleta*
Eastern garter	*Thamnophis sirtalis*
Eastern hognose	*Heterodon platirhinos*
Eastern yellowbelly racer	*Coluber constrictor*
Midland brown	*Storeria dekayi*
Northern redbelly	*Storeria occipitomaculata*
Northern water	*Nerodia sipedon*
Prairie ringneck	*Diadophis punctatus*
Pygmy rattlesnake	*Sistrurus miliarius*
Red milk	*Lampropeltis triangulum*
Rough earth	*Virginia striatula*
Rough green	*Opheodrys aestivus*
Smooth earth	*Virginia valeriae*
Speckled kingsnake	*Lampropeltis getula*
Timber rattlesnake	*Crotalus horridus*
Western ribbon	*Thamnophis proximus*
Turtles	
Three-toed box	*Terrapene carolina*

Appendix B.—*Mean pre-treatment period relative abundance estimates (s.e.) for species captured on southwest-facing slopes on the MOFEP sites during 1992-1995. Relative abundance estimates are defined as the number of captures/100 trap days.*

	MOFEP sites								
Species	1	2	3	4	5	6	7	8	9
Salamanders									
Cave	0.05 (0.05)	0.05 (0.03)	0.03 (0.03)	0.32 (0.16)	0.05 (0.03)	0.20 (0.14)	—	—	0.19 (0.04)
Central newt 1.32 (0.16)	0.51 (0.16)	0.84 (0.26)	1.57 (0.48)	3.76 (1.31)	3.59 (0.86)	0.50 (0.12)	0.80 (0.30)	0.07 (0.02)	
Dark-sided	0.02 (0.02)	0.02 (0.02)	0.02 (0.02)	0.05 (0.03)	0.05 (0.05)	0.29 (0.09)	—	—	0.23 (0.11)
Four-toed	0.03 (0.03)	—	—	0.02 (0.02)	0.03 (0.03)	—	—	0.02 (0.02)	0.17 (0.08)
Marbled	0.68 (0.14)	0.34 (0.10)	0.16 (0.08)	0.17 (0.05)	0.28 (0.07)	0.54 (0.11)	0.19 (0.08)	0.97 (0.19)	0.30 (0.08)
Redback	2.80 (0.78)	4.93 (1.18)	3.41 (0.62)	1.45 (0.43)	2.03 (0.44)	1.33 (0.56)	3.20 (0.23)	1.42 (0.36)	0.14 (0.06)
Slimy	3.06 (0.29)	2.69 (0.72)	1.19 (0.13)	2.05 (0.25)	0.36 (0.14)	0.12 (0.06)	0.22 (0.13)	0.58 (0.16)	9.98 (1.04)
Spotted	2.23 (0.42)	0.57 (0.15)	1.03 (0.21)	1.86 (0.64)	1.43 (0.32)	1.98 (0.88)	0.89 (0.18)	2.43 (0.58)	0.74 (0.27)
Frogs/Toads									
American toad 7.03 (0.57)	4.20 (0.74)	3.94 (0.64)	4.19 (0.57)	2.53 (0.34)	7.06 (1.10)	5.38 (0.92)	6.92 (0.78)	6.01 (1.11)	
Blanchard's cricket	—	—	—	—	—	0.03 (0.03)	—	—	—
E. Narrowmouth	0.08 (0.08)	—	0.02 (0.02)	0.02 (0.02)	—	—	0.07 (0.07)	0.02 (0.02)	—
Gray treefrog 0.24 (0.10)	0.02 (0.02)	—	—	0.02 (0.02)	0.05 (0.05)	—	—	0.02 (0.02)	
Green frog	1.30 (0.43)	0.38 (0.11)	0.56 (0.19)	0.68 (0.17)	0.18 (0.08)	0.52 (0.18)	0.37 (0.16)	0.73 (0.22)	0.27 (0.15)
Pickerel frog 0.34 (0.14)	0.17 (0.07)	0.31 (0.13)	0.28 (0.08)	0.38 (0.19)	0.37 (0.18)	0.10 (0.06)	0.92 (0.38)	0.05 (0.03)	
S. Leopard frog	0.42 (0.27)	0.07 (0.07)	0.07 (0.04)	0.03 (0.03)	0.02 (0.02)	0.05 (0.05)	0.07 (0.04)	0.02 (0.02)	—
Spring peeper 0.24 (0.10)	0.17 (0.06)	0.21 (0.18)	0.18 (0.10)	0.59 (0.23)	1.41 (0.44)	0.50 (0.20)	0.33 (0.08)	0.07 (0.05)	
Woodhouse's toad	0.09 (0.06)	0.07 (0.04)	0 .14 (0.03)	0.07 (0.04)	0.03 (0.03)	0.03 (0.03)	—	—	0.07 (0.07)
Lizards									
Broadhead skink	0.52 (0.17)	1.23 (0.18)	0.67 (0.18)	0.70 (0.19)	0.86 (0.19)	1.11 (0.36)	0.77 (0.21)	1.35 (0.41)	0.86 (0.29)
Coal skink	0.53 (0.18)	0.42 (0.07)	0.47 (0.07)	0.40 (0.10)	0.56 (0.21)	0.25 (0.11)	0.82 (0.07)	0.42 (0.12)	0.37 (0.12)
Fence lizard	1.11 (0.22)	0.48 (0.18)	0.43 (0.07)	0.17 (0.07)	0.54 (0.18)	0.57 (0.07)	0.74 (0.25)	0.97 (0.07)	1.06 (0.18)
Five-lined skink	1.36 (0.22)	1.44 (0.19)	1.39 (0.18)	0.90 (0.16)	1.36 (0.28)	1.31 (0.19)	1.11 (0.15)	1.42 (0.19)	2.21 (0.23)
Ground skink 2.97 (0.36)	2.97 (0.37)	2.17 (0.44)	3.22 (0.57)	2.33 (0.13)	4.15 (0.55)	3.46 (0.34)	5.03 (0.58)	3.98 (0.40)	
Snakes									
Copperhead	0.76 (0.39)	0.43 (0.20)	0.46 (0.23)	0.57 (0.24)	0.41 (0.21)	0.35 (0.29)	0.22 (0.13)	0.21 (0.10)	0.49 (0.19)
Black rat	0.02 (0.02)	0.02 (0.02)	0.07 (0.05)	0.07 (0.04)	0.02 (0.02)	0.03 (0.03)	0.05 (0.03)	0.09 (0.04)	—
E. Garter	0.12 (0.06)	0.18 (0.10)	0.10 (0.04)	0.09 (0.04)	—	0.17 (0.10)	0.09 (0.06)	0.14 (0.06)	0.05 (0.03)
E. Hognose	0.05 (0.03)	0.07 (0.04)	0.10 (0.07)	0.10 (0.04)	0.05 (0.03)	0.15 (0.07)	0.09 (0.002)	—	0.02 (0.02)
E. Yellowbelly racer	0.07 (0.02)	0.12 (0.05)	0.14 (0.03)	—	—	0.02 (0.02)	0.17 (0.05)	0.09 (0.04)	0.12 (0.07)
Midland brown	0.05 (0.05)	—	0.05 (0.03)	0.02 (0.02)	0.02 (0.02)	—	0.07 (0.04)	0.12 (0.04)	0.17 (0.06)
N. Redbelly	1.07 (0.31)	0.87 (0.20)	0.82 (0.25)	0.96 (0.26)	0.80 (0.08)	1.04 (0.35)	0.61 (0.17)	0.52 (0.12)	1.37 (0.27)
N. Water	0.02 (0.02)	0.02 (0.02)	0.05 (0.03)	—	—	—	0.02 (0.02)	—	0.02 (0.02)
Prairie ringneck	0.48 (0.08)	0.69 (0.22)	0.36 (0.07)	0.22 (0.11)	0.10 (0.04)	0.43 (0.09)	0.19 (0.10)	0.09 (0.04)	0.26 (0.09)
Red milk	—	—	0.05 (0.05)	—	0.02 (0.02)	0.10 (0.07)	0.05 (0.03)	0.09 (0.09)	—
Rough earth 0.05 (0.03)	—	—	—	—	0.05 (0.03)	0.07 (0.04)	—	0.02 (0.02)	
Rough green 0.02 (0.02)	—	0.02 (0.02)	0.02 (0.02)	—	0.03 (0.03)	0.02 (0.02)	0.02 (0.02)	—	
Smooth earth 1.40 (0.24)	1.59 (0.43)	1.50 (0.35)	1.10 (0.10)	1.34 (0.20)	1.03 (0.27)	2.26 (0.44)	1.48 (0.28)	1.84 (0.40)	
Speckled kingsnake	—	—	—	0.02 (0.02)	—	—	—	—	0.02 (0.02)
Timber rattlesnake	—	—	—	—	—	0.02 (0.02)	—	—	0.03 (0.03)
W. Ribbon	—	0.03 (0.03)	—	—	—	0.12 (0.02)	—	0.07 (0.04)	—
W. Worm	0.19 (0.08)	0.14 (0.03)	0.02 (0.02)	0.07 (0.05)	0.19 (0.06)	0.17 (0.02)	0.02 (0.02)	0.08 (0.08)	0.22 (0.05)
Turtles									
Three-toed box	0.05 (0.03)	0.14 (0.06)	—	0.03 (0.03)	0.05 (0.03)	—	—	—	0.03 (0.03)

Appendix C.—*Mean pre-treatment period relative abundance estimates (s.e.) for species captured on northeast-facing slopes on the MOFEP sites during 1992-1995. Relative abundance estimates are defined as the number of captures/ 100 trap days.*

	MOFEP sites								
Species	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
Salamanders									
Cave	0.02 (0.02)	0.02 (0.02)	0.07 (0.05)	0.12 (0.09)	0.03 (0.03)	0.07 (0.05)	—	1.08 (0.23)	0.03 (0.03)
Central newt 3.09 (0.39)	0.59 (0.11)	1.12 (0.31)	1.91 (0.82)	5.13 (1.09)	5.48 (1.15)	0.23 (0.04)	0.53 (0.17)	0.07 (0.02)	
Dark-sided	—	0.02 (0.02)	0.16 (0.04)	0.05 (0.03)	0.42 (0.23)	0.07 (0.04)	—	—	0.12 (0.03)
Four-toed	—	—	—	0.07 (0.04)	0.02 (0.02)	—	—	0.05 (0.03)	0.03 (0.03)
Marbled	1.73 (0.13)	0.33 (0.09)	0.14 (0.08)	0.23 (0.04)	0.24 (0.03)	0.45 (0.18)	0.88 (0.45)	0.55 (0.16)	0.05 (0.05)
Redback	8.16 (0.73)	0.33 (0.03)	2.19 (0.73)	4.04 (1.18)	2.22 (0.59)	6.44 (0.97)	1.41 (0.43)	3.68 (0.70)	1.17 (0.23)
Slimy	2.20 (0.39)	2.25 (0.55)	0.24 (0.09)	1.81 (0.26)	0.26 (0.06)	0.05 (0.05)	1.23 (0.16)	2.47 (0.66)	8.68 (0.22)
Spotted	4.78 (0.57)	3.22 (0.47)	1.13 (0.36)	1.90 (0.52)	2.06 (0.74)	1.93 (0.45)	1.48 (0.29)	2.95 (0.68)	0.57 (0.24)
Tiger	0.02 (0.02)	—	—	—	—	—	—	0.02 (0.02)	—
Frogs/Toads									
American toad7.35 (0.74)	5.91 (0.53)	5.32 (0.47)	5.31 (0.30)	2.99 (0.55)	4.94 (0.64)	7.10 (0.93)	6.44 (0.53)	5.62 (0.61)	
Blanchard's cricket	—	—	—	—	—	0.05 (0.05)	—	0.02 (0.02)	—
Bullfrog	—	—	—	—	—	—	—	0.03 (0.03)	—
E. Narrowmouth	0.05 (0.03)	—	—	—	—	—	—	—	—
Gray treefrog 0.12 (0.04)	0.02 (0.02)	—	—	0.07 (0.04)	0.08 (0.08)	0.03 (0.03)	0.05 (0.03)	—	
Green frog	1.69 (0.52)	0.59 (0.11)	0.64 (0.23)	0.78 (0.26)	0.35 (0.13)	0.69 (0.08)	0.50 (0.13)	0.28 (0.07)	0.02 (0.02)
Pickerel frog 0.19 (0.07)	0.39 (0.11)	0.23 (0.10)	0.19 (0.05)	0.20 (0.12)	0.41 (0.17)	0.05 (0.03)	1.27 (0.36)	—	
S. Leopard frog	0.44 (0.20)	0.12 (0.06)	0.02 (0.02)	0.05 (0.03)	0.14 (0.06)	0.05 (0.03)	0.07 (0.02)	0.11 (0.07)	—
Spring peeper 0.40 (0.12)	0.19 (0.09)	0.28 (0.12)	0.24 (0.10)	0.97 (0.19)	1.93 (0.66)	0.42 (0.12)	0.50 (0.21)	0.09 (0.04)	
Woodhouse's toad	0.10 (0.04)	0.14 (0.06)	0.17 (0.04)	0.14 (0.06)	—	0.07 (0.05)	—	—	0.02 (0.02)
Lizards									
Broadhead skink	0.46 (0.11)	0.78 (0.14)	0.62 (0.16)	0.71 (0.16)	0.79 (0.13)	0.98 (0.30)	1.38 (0.45)	0.72 (0.21)	0.87 (0.10)
Coal skink	0.28 (0.14)	0.27 (0.19)	0.28 (0.13)	0.14 (0.05)	0.37 (0.18)	0.18 (0.11)	0.55 (0.10)	0.50 (0.23)	0.62 (0.29)
Fence lizard	0.14 (0.03)	0.28 (0.07)	0.09 (0.002)	0.11 (0.06)	0.19 (0.05)	0.07 (0.05)	0.82 (0.23)	0.57 (0.12)	0.92 (0.37)
Five-lined skink	0.89 (0.26)	0.83 (0.22)	0.66 (0.13)	0.72 (0.26)	0.77 (0.11)	0.82 (0.32)	1.58 (0.35)	0.95 (0.15)	2.01 (0.33)
Ground skink 0.96 (0.26)	1.35 (0.23)	1.42 (0.19)	2.27 (0.35)	2.34 (0.33)	0.83 (0.18)	3.35 (0.67)	2.40 (0.33)	3.47 (0.90)	
Six-lined racerunner	—	—	—	—	—	—	—	0.03 (0.03)	—
Snakes									
Copperhead	0.50 (0.12)	0.39 (0.15)	0.39 (0.18)	0.55 (0.16)	0.52 (0.11)	0.27 (0.13)	0.44 (0.21)	0.36 (0.14)	0.57 (0.09)
Black rat	0.03 (0.03)	0.05 (0.03)	0.02 (0.02)	0.07 (0.02)	0.02 (0.02)	—	0.05 (0.05)	0.02 (0.02)	—
E. Garter	0.14 (0.04)	0.16 (0.08)	0.11 (0.09)	0.07 (0.04)	0.19 (0.07)	0.02 (0.02)	0.21 (0.08)	0.05 (0.05)	0.02 (0.02)
E. Hognose	0.05 (0.03)	0.09 (0.06)	0.10 (0.04)	0.03 (0.03)	0.14 (0.05)	0.05 (0.03)	0.12 (0.06)	0.07 (0.02)	—
E. Yellowbelly racer	0.05 (0.05)	0.02 (0.02)	0.05 (0.05)	0.02 (0.02)	0.07 (0.04)	—	0.05 (0.03)	0.07 (0.05)	0.02 (0.02)
Midland brown	—	0.07 (0.04)	—	—	—	—	0.05 (0.03)	0.07 (0.02)	0.14 (0.03)
N. Redbelly	0.44 (0.20)	0.24 (0.07)	0.78 (0.20)	0.55 (0.17)	0.99 (0.14)	0.61 (0.07)	0.75 (0.09)	0.33 (0.05)	1.44 (0.23)
N. Water	—	0.02 (0.02)	—	—	—	—	—	—	—
Prairie ringneck	0.33 (0.07)	0.33 (0.08)	0.14 (0.06)	0.26 (0.16)	0.17 (0.05)	0.21 (0.05)	0.40 (0.05)	0.22 (0.10)	0.19 (0.11)
Red milk	0.05 (0.03)	—	—	—	0.05 (0.03)	0.02 (0.02)	0.05 (0.03)	0.02 (0.02)	0.05 (0.05)
Rough earth —	—	0.03 (0.03)	—	—	0.02 (0.02)	0.03 (0.03)	—	0.10 (0.10)	
Rough green —	—	0.07 (0.04)	—	0.07 (0.02)	—	0.02 (0.02)	—	—	
Smooth earth 1.81 (0.28)	1.14 (0.25)	0.97 (0.11)	1.31 (0.43)	0.97 (0.09)	0.89 (0.19)	2.35 (0.28)	1.13 (0.13)	2.06 (0.50)	
Speckled kingsnake	0.02 (0.02)	0.02 (0.02)	—	—	—	—	0.02 (0.02)	—	—
Timber rattlesnake	—	—	—	0.03 (0.03)	0.02 (0.02)	—	—	—	0.02 (0.02)
W. Ribbon	0.05 (0.05)	0.07 (0.04)	—	0.02 (0.02)	0.02 (0.02)	0.17 (0.06)	0.02 (0.02)	0.05 (0.03)	0.02 (0.02)
W. Worm	0.15 (0.07)	0.02 (0.02)	0.12 (0.06)	—	0.02 (0.02)	0.20 (0.14)	0.10 (0.06)	0.03 (0.03)	0.07 (0.02)
Turtles									
Three-toed box	0.11 (0.06)	0.02 (0.02)	—	0.05 (0.03)	0.05 (0.03)	0.05 (0.03)	—	—	0.05 (0.03)

Appendix D.—*Mean pre-treatment period relative abundance estimates (s.e.) for each species by distance from designated clearcuts on southwest-facing slopes on MOFEP sites during 1992-1995. Mean relative abundance estimates are defined as the number of captures/100 trap days.*

Species	Distance from designated clearcuts		
	Within clearcuts	50 m from clearcut	200 m from clearcut
Salamanders			
Cave	0.35 (0.21)	0.09 (0.05)	0.19 (0.07)
Central newt	0.75 (0.30)	1.16 (0.43)	1.11 (0.33)
Dark-sided	0.05 (0.05)	—	0.23 (0.11)
Four-toed	—	—	0.14 (0.05)
Marbled	0.09 (0.05)	0.05 (0.05)	0.15 (0.10)
Redback	0.65 (0.21)	0.89 (0.24)	0.83 (0.26)
Slimy	1.73 (0.33)	0.87 (0.32)	1.38 (0.27)
Spotted	1.08 (0.33)	0.67 (0.20)	0.77 (0.31)
Frogs/Toads			
American toad	5.87 (0.84)	3.74 (0.93)	3.72 (0.69)
Blanchard's cricket	—	0.05 (0.05)	—
Gray treefrog	0.09 (0.09)	0.05 (0.05)	0.05 (0.05)
Green frog	0.52 (0.28)	0.34 (0.10)	0.42 (0.04)
Pickerel frog	—	0.19 (0.11)	0.19 (0.14)
S. Leopard frog	0.05 (0.05)	0.14 (0.14)	0.05 (0.05)
Spring peeper	0.15 (0.09)	0.42 (0.11)	0.14 (0.05)
Woodhouse's toad	0.14 (0.09)	0.10 (0.10)	0.05 (0.05)
Lizards			
Broadhead skink	1.71 (0.20)	1.37 (0.62)	0.51 (0.13)
Coal skink	0.48 (0.10)	0.65 (0.17)	0.88 (0.31)
Fence lizard	0.52 (0.16)	0.91 (0.29)	1.44 (0.26)
Five-lined skink	1.52 (0.13)	1.47 (0.20)	1.25 (0.44)
Ground skink	3.00 (0.41)	2.76 (0.52)	2.66 (0.65)
Six-lined racerunner	—	—	0.05 (0.05)
Snakes			
Copperhead	0.63 (0.35)	1.07 (0.47)	0.24 (0.13)
Black rat	0.10 (0.06)	—	0.05 (0.05)
E. Garter	—	0.05 (0.05)	0.05 (0.05)
E. Hognose	0.10 (0.06)	0.05 (0.05)	0.05 (0.05)
E. Yellowbelly racer	0.14 (0.05)	0.05 (0.05)	0.14 (0.09)
Midland brown	0.10 (0.06)	0.27 (0.17)	0.14 (0.09)
N. Redbelly	1.21 (0.45)	0.80 (0.07)	0.65 (0.18)
Prairie ringneck	0.34 (0.17)	0.24 (0.12)	0.23 (0.09)
Pygmy rattlesnake	—	0.05 (0.05)	—
Red milk	—	0.05 (0.05)	0.10 (0.06)
Rough earth	0.05 (0.05)	0.10 (0.10)	—
Smooth earth	2.34 (0.60)	1.22 (0.33)	0.94 (0.19)
Timber rattlesnake	0.05 (0.05)	—	—
W. Ribbon	—	—	0.05 (0.05)
W. Worm	0.15 (0.15)	0.24 (0.14)	0.19 (0.08)

Appendix E.—*Mean pre-treatment period relative abundance estimates (s.e.) for each species by distance from designated clearcuts on northeast-facing slopes on MOFEP sites during 1992-1995. Mean relative abundance estimates are defined as the number of captures/100 trap days.*

Species	Distance from designated clearcuts		
	Within clearcuts	50 m from clearcut	200 m from clearcut
Salamanders			
Cave	—	—	0.10 (0.10)
Central newt	2.27 (0.51)	1.91 (0.28)	2.74 (0.21)
Dark-sided	—	—	0.05 (0.05)
Four-toed	0.05 (0.05)	0.05 (0.05)	—
Marbled	0.09 (0.05)	0.05 (0.05)	0.23 (0.09)
Redback	1.61 (0.24)	0.99 (0.09)	1.57 (0.46)
Slimy	2.44 (0.39)	0.78 (0.32)	1.51 (0.23)
Spotted	1.48 (0.54)	1.27 (0.47)	1.90 (0.52)
Frogs/Toads			
American toad	4.54 (0.76)	4.64 (0.82)	4.51 (0.49)
Blanchard's cricket	—	0.05 (0.05)	—
Gray treefrog	—	—	0.05 (0.05)
Green frog	0.42 (0.20)	0.23 (0.09)	0.48 (0.17)
Pickerel frog	0.15 (0.10)	0.05 (0.05)	0.15 (0.10)
S. Leopard frog	—	0.10 (0.06)	0.05 (0.05)
Spring peeper	0.42 (0.04)	0.76 (0.27)	0.24 (0.05)
Woodhouse's toad	—	0.05 (0.05)	—
Lizards			
Broadhead skink	0.66 (0.06)	0.38 (0.07)	1.64 (0.12)
Coal skink	0.15 (0.10)	0.18 (0.07)	0.29 (0.19)
Fence lizard	0.28 (0.05)	0.59 (0.41)	0.61 (0.21)
Five-lined skink	1.78 (0.28)	1.53 (0.44)	1.73 (0.39)
Ground skink	2.79 (0.40)	3.28 (0.54)	2.80 (0.28)
Six-lined racerunner	—	—	0.05 (0.05)
Snakes			
Copperhead	0.58 (0.17)	0.25 (0.19)	0.29 (0.12)
Black rat	—	—	0.10 (0.10)
E. Garter	—	—	0.14 (0.05)
E. Hognose	—	0.14 (0.05)	0.05 (0.05)
E. Yellowbelly racer	—	0.05 (0.05)	0.05 (0.05)
Midland brown	0.05 (0.05)	—	0.05 (0.05)
N. Redbelly	1.04 (0.19)	0.93 (0.33)	0.90 (0.28)
N. Water	—	0.05 (0.05)	—
Prairie ringneck	0.19 (0.07)	0.19 (0.08)	0.10 (0.06)
Red milk	—	—	0.05 (0.05)
Rough green	—	—	0.09 (0.05)
Smooth earth	1.52 (0.47)	1.12 (0.21)	1.45 (0.18)
Timber rattlesnake	0.09 (0.05)	—	—
W. Worm	—	—	0.05 (0.05)
Turtles			
Three-toed box	0.05 (0.05)	—	—

Appendix D.—*Mean pre-treatment period relative abundance estimates (s.e.) for each species by distance from designated clearcuts on southwest-facing slopes on MOFEP sites during 1992-1995. Mean relative abundance estimates are defined as the number of captures/100 trap days.*

Species	Distance from designated clearcuts		
	Within clearcuts	50 m from clearcut	200 m from clearcut
Salamanders			
Cave	0.35 (0.21)	0.09 (0.05)	0.19 (0.07)
Central newt	0.75 (0.30)	1.16 (0.43)	1.11 (0.33)
Dark-sided	0.05 (0.05)	—	0.23 (0.11)
Four-toed	—	—	0.14 (0.05)
Marbled	0.09 (0.05)	0.05 (0.05)	0.15 (0.10)
Redback	0.65 (0.21)	0.89 (0.24)	0.83 (0.26)
Slimy	1.73 (0.33)	0.87 (0.32)	1.38 (0.27)
Spotted	1.08 (0.33)	0.67 (0.20)	0.77 (0.31)
Frogs/Toads			
American toad	5.87 (0.84)	3.74 (0.93)	3.72 (0.69)
Blanchard's cricket	—	0.05 (0.05)	—
Gray treefrog	0.09 (0.09)	0.05 (0.05)	0.05 (0.05)
Green frog	0.52 (0.28)	0.34 (0.10)	0.42 (0.04)
Pickerel frog	—	0.19 (0.11)	0.19 (0.14)
S. Leopard frog	0.05 (0.05)	0.14 (0.14)	0.05 (0.05)
Spring peeper	0.15 (0.09)	0.42 (0.11)	0.14 (0.05)
Woodhouse's toad	0.14 (0.09)	0.10 (0.10)	0.05 (0.05)
Lizards			
Broadhead skink	1.71 (0.20)	1.37 (0.62)	0.51 (0.13)
Coal skink	0.48 (0.10)	0.65 (0.17)	0.88 (0.31)
Fence lizard	0.52 (0.16)	0.91 (0.29)	1.44 (0.26)
Five-lined skink	1.52 (0.13)	1.47 (0.20)	1.25 (0.44)
Ground skink	3.00 (0.41)	2.76 (0.52)	2.66 (0.65)
Six-lined racerunner	—	—	0.05 (0.05)
Snakes			
Copperhead	0.63 (0.35)	1.07 (0.47)	0.24 (0.13)
Black rat	0.10 (0.06)	—	0.05 (0.05)
E. Garter	—	0.05 (0.05)	0.05 (0.05)
E. Hognose	0.10 (0.06)	0.05 (0.05)	0.05 (0.05)
E. Yellowbelly racer	0.14 (0.05)	0.05 (0.05)	0.14 (0.09)
Midland brown	0.10 (0.06)	0.27 (0.17)	0.14 (0.09)
N. Redbelly	1.21 (0.45)	0.80 (0.07)	0.65 (0.18)
Prairie ringneck	0.34 (0.17)	0.24 (0.12)	0.23 (0.09)
Pygmy rattlesnake	—	0.05 (0.05)	—
Red milk	—	0.05 (0.05)	0.10 (0.06)
Rough earth	0.05 (0.05)	0.10 (0.10)	—
Smooth earth	2.34 (0.60)	1.22 (0.33)	0.94 (0.19)
Timber rattlesnake	0.05 (0.05)	—	—
W. Ribbon	—	—	0.05 (0.05)
W. Worm	0.15 (0.15)	0.24 (0.14)	0.19 (0.08)

Appendix E.—*Mean pre-treatment period relative abundance estimates (s.e.) for each species by distance from designated clearcuts on northeast-facing slopes on MOFEP sites during 1992-1995. Mean relative abundance estimates are defined as the number of captures/100 trap days.*

Species	Distance from designated clearcuts		
	Within clearcuts	50 m from clearcut	200 m from clearcut
Salamanders			
Cave	—	—	0.10 (0.10)
Central newt	2.27 (0.51)	1.91 (0.28)	2.74 (0.21)
Dark-sided	—	—	0.05 (0.05)
Four-toed	0.05 (0.05)	0.05 (0.05)	—
Marbled	0.09 (0.05)	0.05 (0.05)	0.23 (0.09)
Redback	1.61 (0.24)	0.99 (0.09)	1.57 (0.46)
Slimy	2.44 (0.39)	0.78 (0.32)	1.51 (0.23)
Spotted	1.48 (0.54)	1.27 (0.47)	1.90 (0.52)
Frogs/Toads			
American toad	4.54 (0.76)	4.64 (0.82)	4.51 (0.49)
Blanchard's cricket	—	0.05 (0.05)	—
Gray treefrog	—	—	0.05 (0.05)
Green frog	0.42 (0.20)	0.23 (0.09)	0.48 (0.17)
Pickerel frog	0.15 (0.10)	0.05 (0.05)	0.15 (0.10)
S. Leopard frog	—	0.10 (0.06)	0.05 (0.05)
Spring peeper	0.42 (0.04)	0.76 (0.27)	0.24 (0.05)
Woodhouse's toad	—	0.05 (0.05)	—
Lizards			
Broadhead skink	0.66 (0.06)	0.38 (0.07)	1.64 (0.12)
Coal skink	0.15 (0.10)	0.18 (0.07)	0.29 (0.19)
Fence lizard	0.28 (0.05)	0.59 (0.41)	0.61 (0.21)
Five-lined skink	1.78 (0.28)	1.53 (0.44)	1.73 (0.39)
Ground skink	2.79 (0.40)	3.28 (0.54)	2.80 (0.28)
Six-lined racerunner	—	—	0.05 (0.05)
Snakes			
Copperhead	0.58 (0.17)	0.25 (0.19)	0.29 (0.12)
Black rat	—	—	0.10 (0.10)
E. Garter	—	—	0.14 (0.05)
E. Hognose	—	0.14 (0.05)	0.05 (0.05)
E. Yellowbelly racer	—	0.05 (0.05)	0.05 (0.05)
Midland brown	0.05 (0.05)	—	0.05 (0.05)
N. Redbelly	1.04 (0.19)	0.93 (0.33)	0.90 (0.28)
N. Water	—	0.05 (0.05)	—
Prairie ringneck	0.19 (0.07)	0.19 (0.08)	0.10 (0.06)
Red milk	—	—	0.05 (0.05)
Rough green	—	—	0.09 (0.05)
Smooth earth	1.52 (0.47)	1.12 (0.21)	1.45 (0.18)
Timber rattlesnake	0.09 (0.05)	—	—
W. Worm	—	—	0.05 (0.05)
Turtles			
Three-toed box	0.05 (0.05)	—	—

Pre-harvest (1994-1995) Conditions of the Missouri Ozark Forest Ecosystem Project Small Mammal Communities

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Abstract.—We conducted a capture-recapture study on northeast-facing slopes to determine the pre-treatment landscape-scale effect of even- and uneven-aged silvicultural treatments upon the species composition, species richness, and relative abundance of small mammals on Missouri Ozark Forest Ecosystem Project (MOFEP) sites. Similarity indices of species composition between sites ranged from 0.29 to 1.00, with an overall mean index of 0.64. Species richness estimates ranged from two to six species per site per year. Overall small mammal relative abundance estimates ranged from 0.93 (s.e. = 0.35) to 6.54 (s.e. = 0.06) individuals per 100 trap nights per site. Year, treatment, block, and their interactions did not affect species richness or relative abundance estimates.

The effects of various silvicultural practices on many game species are well documented, but information on the nongame fauna is lacking. Clearcutting, for example, may alter the species composition and abundance of small mammals because of extreme habitat changes associated with the removal of the forest overstory. Natural resource management agencies are increasingly interested in examining the effects of their silvicultural practices on nongame animal communities. The Missouri Ozark Forest Ecosystem Project (MOFEP) is a comprehensive research project designed to examine the landscape-scale effects of forest management practices (even- and uneven-aged management) on selected flora, fauna (including small mammals), and abiotic components of the southern Missouri oak-hickory (*Quercus* sp. - *Carya* sp.) forest (Brookshire *et al.* 1997, Sheriff and He 1997).

In other portions of the United States, researchers have evaluated the effects of timber management on small mammal communities and have reported varied results, which emphasize the importance of site-specific and plant community differences to small mammal community changes after timber harvest. In northeastern forest ecosystems, some researchers have reported no significant changes or only minimal changes in the number and composition of small mammals following clearcutting (Brooks and Healy 1988, Healy and Brooks 1988, Krull 1970). Others have concluded that the small mammal community is generally resilient to clearcutting, but responses vary by species (Clough 1987, Healy and Brooks 1988, Kirkland 1977, Lovejoy 1975, Monthey and Soutiere 1985, Yahner 1992). Krull (1970) found lower densities of small mammals in clearcuts, and reported that there are slightly more, but not statistically significant more, mice (*Peromyscus* sp.) in forest habitat than in clearcut areas. Yahner (1992) reported that clearcutting increased populations of white-footed mice (*P. leucopus*) and southern red-backed voles (*Clethrionomys gapperi*) in an oak-aspen (*Quercus* sp. - *Poplar* sp.) forest in central Pennsylvania.

Small mammal studies in the Pacific Northwest have compared clearcuts with forested stands (Corn *et al.* 1988; Gashwiler 1959, 1970; Hooven and Black 1976; Tevis 1956). Although there is considerable treatment variation among the studies (for example: burning, herbicide use), there are some similar trends. Corn *et al.* (1988) stated that, in general, populations of deer mice (*P. maniculatus*), creeping voles (*Microtus oregoni*), and Townsend's chipmunks

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(*Tamias townsendii*) increase after logging, whereas southern red-backed voles and Trowbridge's shrews (*Sorex trowbridgii*) decline. Ream and Gruell (1980) reported that in Rocky Mountain coniferous forests, deer mice were most abundant in clearcuts about 5 years after logging. Corn *et al.* (1988) reported that deer mice were about three times more abundant in recent (<10 years old) clearcuts than in young (30 to 80 years) stands, and Hooven and Black (1976) concluded that populations of mice (*Peromyscus* sp.) and Oregon creeping voles (*M. oregoni*) increased after logging and slash burning on clearcuts.

Studies in Canada have been conducted on uncut, selectively cut, and clearcut boreal forests. Clearcutting in northern Ontario produced a dramatic change in the composition of the small mammal community, but there appeared to be little change in overall small mammal density (Martell and Radvanyi 1977). Deer mice increased on clearcuts (when compared with uncut stands) and predominated in the small mammal community by the end of the second summer after cutting. Martell (1983) reported that the small mammal community in both clearcut and strip-cut stands changed over the first 3 years after logging from one dominated by southern red-backed voles to one dominated by deer mice, and then remained relatively stable for 13 years. That shift was not apparent in selectively cut stands where the composition of the small mammal community was similar between uncut and selectively cut stands 4 to 23 years after harvest. Relatively little change occurred in total numbers of small mammals after logging. Sullivan (1979), working in British Columbian coniferous forests, concluded that densities of deer mice in forested and clearcut areas were similar, but slightly higher on clearcuts.

Many of these studies specifically addressed changes in *Peromyscus* sp. populations following logging. Most concluded that there are more deer mice on logged areas compared with adjacent forested habitat (Ahlgren 1966; Gashwiler 1959, 1970; Hooven and Black 1976; Martell and Radvanyi 1977; Tevis 1956; Verme and Ozoga 1981; Yahner 1992). Clearcut areas produce large quantities of seeds, fruits, and insects (Ahlgren 1966, Hooven 1973, Tevis 1956). Deer mice are considered a pioneering species, and these foods are a large proportion of their diet (Hamilton 1941, Whitaker 1966).

Information on the landscape-scale effects of forest management practices on the small mammal communities of Ozark oak-hickory forests is lacking. Only one known study has examined the stand-level effects of even-aged forest management on small mammal communities in Midwest oak-hickory forests. Root *et al.* (1990) noted that white-footed mice numbers were largely unaffected by even-aged cuts (up to 6 years after clearcutting) in central Missouri. They reported that clearcuts generally had greater numbers of white-footed mice, yet population trends were similar between clearcut and control areas. Clearcutting did not appear to affect overall population fluctuations of white-footed mice.

The research objectives of the MOFEP small mammal study are to determine if even- and uneven-aged silvicultural treatments have a landscape-scale, short-term (2 and 3 years after cutting) effect on species composition, species richness, and relative abundance of small mammal communities inhabiting MOFEP sites. The objective of the pre-treatment portion of the study is to document the condition of small mammal communities before any silvicultural treatments are applied. This paper reports on the pre-treatment status of small mammal communities occupying northeast-facing slopes during 1994-1995.

METHODS

Field Sampling

We randomly selected two locations on northeast-facing slopes (ecological landtype (ELT) 18) on each of the 9 MOFEP sites. At each location, a 12x12 station grid (144 stations per grid) was laid out, with 25 m between stations (7.6-ha grid, two grids per site). We sampled only on northeast-facing slopes because we believed these locations would contain more small mammals due to the moister environment on northeast-facing slopes. Only two grids were sampled per site for several reasons. First, the number of northeast-facing slopes that were large enough to contain a 7.6-ha grid was limited on several sites. Secondly, we estimated that one person could check, rebait, and reset all traps within two, 7.6-ha grids within an average workday. We selected 7.6 ha as a grid size to fit upon available northeast-facing slopes and to attempt to maximize the number of available traps within a grid. We placed one

Sherman small mammal live trap (8 x 9 x 23 cm) at each station and baited traps with a mixture of peanut butter and rolled oats. Trapping occurred during April and May of 1994 and 1995. We trapped during April and May because results from an earlier small mammal trapping effort in the south central Missouri Ozarks suggested that late March, April, and May were the most successful months for capturing small mammals (Murray 1991). We selected spring as our sampling season because small mammals may be most active or most likely to be captured during April and May, and our capture probabilities might be greatest then. Grids within each block of three sites were simultaneously sampled during a 6-night trapping period (six grids sampled per trapping period). Block 1 (sites 1, 2, and 3) was sampled on April 6-12, 1994 and April 12-18, 1995; block 2 (sites 4, 5, and 6) was sampled on May 4-10, 1994 and May 10-16, 1995; and block 3 (sites 7, 8, and 9) was sampled on May 18-24, 1994 and May 24-30, 1995. Trapping was not conducted during Missouri's annual spring firearms turkey season in late April. Traps were disinfected with a dilute bleach solution between trapping periods as a precautionary measure against possible exposure to hantavirus.

Traps were checked for captured animals and rebaited once daily. Captured animals were identified to species, individually marked by toe-clipping (except chipmunks and wood rats were individually marked with nontoxic, waterproof markers), and released at the point of capture. We recorded species, identification number, trap station number, age of individual (adult or juvenile), and whether the animal was captured for the first time or was a recapture. Dead animals were noted.

Statistical Methods

Differences in species composition of small mammal communities between sites and years were qualitatively evaluated. Coefficients of similarity (Jaccard 1901) in species composition were calculated between sites for the pre-treatment period to examine how sites differed between proposed treatment sites and blocks.

Species richness within small mammal communities was defined as the number of species caught on a site within a year. Multivariate repeated measures analysis of variance (with year as the repeated factor) (SAS 1989) was used to examine the effect of year, treatment, block, and their interactions on species richness of small mammal communities on northeast-facing slopes during the pre-treatment period. The normality of model residuals was tested (SAS 1989) after fitting the model (Z. He personal communication). We used 0.05 as the alpha level for our analysis.

We attempted to estimate densities by grid and year from the capture/recapture data using population modeling programs. However, numbers of captures and recaptures per grid were too small to produce reliable population estimates with the population models. Recapture rates were 49 percent for individuals captured in 1994 and 24 percent for 1995. Therefore, we calculated relative abundance estimates instead of density estimates. Small mammal relative abundance was defined as the number of individuals captured per grid per 100 trap nights. Relative abundance estimates for each grid were calculated by dividing the total number of individuals captured on that grid by the total number of trap nights per grid (864 trap nights). In 1994, on grid 1 of site 6, we experienced only 549 trap nights due to raccoon (*Procyon lotor*) trap raiding problems. Relative abundance estimates were averaged by site for each year. Multivariate repeated measures analysis of variance was used to detect differences in relative abundance estimates due to year, treatment, block, and their interactions. The normality of model residuals was tested (SAS 1989) after fitting the model (Z. He personal communication)

Peromyscus sp. dominated the sample in abundance and occurrence. Because relative abundance estimates for other species were so small, we combined data for *Peromyscus* sp. by grid per year and examined the effect of year, treatment, block, and their interactions on the relative abundance of only *Peromyscus* sp.

RESULTS

General

We captured, marked, and released 372 individual animals (726 total captures) of six species in 1994, and 473 individual animals (670 total captures) of eight species in 1995. The most often trapped species were white-footed mice (54 percent and 38 percent of individuals captured in 1994 and 1995, respectively) and

deer mice (35 percent and 52 percent of individuals captured in 1994 and 1995, respectively).

Species Composition

Eight species of small mammals were captured on northeast-facing slopes during 1994-1995 (table 1). One species was a shrew (Elliot's short-tailed shrew, *Blarina hylophaga*), two were squirrels, (eastern chipmunk, *Tamias striatus*; southern flying squirrel, *Glaucomys volans*), and the remaining five species were members of the mice and rat family (woodland vole, *Microtus pinetorum*; eastern woodrat, *Neotoma floridana*; golden mouse, *Ochrotomys nuttalli*; white-footed mouse, *Peromyscus leucopus*; deer mouse, *Peromyscus maniculatus*). Common names follow Schwartz and Schwartz (1981).

Our sample consisted of two principal species (white-footed mouse, deer mouse) that were captured on all grids at all sites during both years (table 1). If captured within a site, eastern chipmunks tended to be consistently caught in both years. The remaining five species were sporadic, localized captures within sites and between years.

Jaccard's similarity indices of species composition among sites ranged from 0.29 for sites 3 and 5, and 3 and 7, to 1.00 for comparisons between sites 2 and 4, 5 and 7, 2 and 8, and 4 and 8 (table 2). The overall mean index between sites was 0.64. The mean index within each block of sites also was 0.64. Mean indices within treatments were not as consistent. The mean indices for control and uneven-aged treatment sites were 0.68 and 0.67, respectively. The mean index for even-aged treatment sites was 0.49. This mean was greatly influenced by the dissimilarity in communities between sites 3, 5, and 7.

Species Richness

Species richness estimates ranged from two species for site 7 during 1994, to six species for site 8 during 1995 (table 1). The number of species on each site typically did not vary more than by one species between years. This small difference is not surprising because so few species were captured on the sites. Only eight species were captured in all. We believe that the difference in species richness will never be great because of the small number of species we could possibly capture. We determined that year, treatment, block, and the interactions of year x treatment and year x block had no significant influence on species richness during the pre-treatment period (table 3).

Relative Abundance

Overall small mammal relative abundance estimates ranged from 0.93 individuals per 100 trap nights (s.e. = 0.35) for site 5 in 1994 to 6.64 individuals per 100 trap nights (s.e. = 0.06) for site 1 in 1994 (table 1). Year, treatment, block, and the interactions of year x treatment and year x block had no significant effect upon relative abundance estimates (table 4). The difference between 1994 and 1995 estimates within sites ranged from 0.23 individuals per 100 trap nights for site 4, to 4.34 individuals per 100 trap nights for site 7 (table 1). Generally, relative abundance estimates increased slightly from 1994 to 1995.

Most relative abundance estimates of individual species on the sites were small and had large standard errors (table 1). The only somewhat reasonable estimates were those for white-footed and deer mice, although for some sites, estimates had extremely high standard errors (sites 1, 2, 5, and 9). Estimates of relative abundance for all other species were small and may not be valuable for examining the effects of forest management practices on an individual species basis.

If we examine the relative abundance estimates of just *Peromyscus* sp., and lump white-footed and deer mice captures, then year, treatment, and the interaction of year x treatment still had no significant effect on relative abundance estimates (table 5). However, the year x block interaction was significant and block nearly significant. While block 2 relative abundance estimates of *Peromyscus* sp. remained about the same from 1994 to 1995, block 1 estimates decreased and block 3 estimates increased. This interaction was probably influenced by the high relative abundance estimates for sites 1 in 1994 and 7 in 1995. The localized annual variation in *Peromyscus* sp. numbers may make interpretation of treatment effects challenging after treatment.

Table 1.—*Mean small mammal relative abundance estimates (s.e.) on northeast-facing slopes for MOFEP sites during 1994 and 1995. Relative abundance was defined as the number of individuals captured per 100 trap nights. N = 2 for each estimate.*

Site/Year	Species								
	Elliot's short-tailed shrew	Southern flying squirrel	Woodland vole	Eastern wood rat	Golden mouse	Deer mouse	White-footed mouse	Eastern chipmunk	All species
1 - 1994	0.06 (0.06)	—	—	—	0.17 (0.17)	2.20 (0.58)	4.05 (0.69)	0.06 (0.06)	6.64 (0.06)
1 - 1995	—	—	0.06 (0.06)	—	0.17 (0.06)	1.33 (0.64)	0.87 (0.17)	—	2.43 (0.81)
2 - 1994	0.12 (0.00)	—	—	0.23 (0.23)	—	1.22 (0.87)	1.27 (0.23)	0.06 (0.06)	2.89 (0.81)
2 - 1995	—	—	—	—	0.06 (0.06)	1.33 (0.87)	0.98 (0.52)	0.12 (0.12)	2.49 (1.56)
3 - 1994	0.06 (0.06)	—	—	—	—	1.45 (0.06)	1.50 (0.35)	—	3.01 (0.35)
3 - 1995	—	0.06 (0.06)	—	0.12 (0.00)	0.06 (0.06)	2.26 (0.64)	1.50 (0.58)	—	3.99 (1.22)
4 - 1994	0.23 (0.12)	—	—	—	—	0.35 (0.00)	0.75 (0.17)	0.12 (0.00)	1.45 (0.06)
4 - 1995	—	—	—	0.12 (0.12)	0.06 (0.06)	0.98 (0.41)	0.41 (0.06)	0.12 (0.12)	1.68 (0.64)
5 - 1994	—	—	—	—	—	0.23 (0.00)	0.64 (0.29)	0.06 (0.06)	0.93 (0.35)
5 - 1995	—	—	—	—	—	0.98 (0.41)	0.52 (0.17)	0.06 (0.06)	1.56 (0.64)
6 - 1994	0.06 (0.06)	—	—	—	—	0.98 (0.29)	1.67 (0.51)	0.42 (0.31)	3.14 (1.05)
6 - 1995	—	—	—	—	—	1.68 (0.17)	1.68 (0.64)	0.46 (0.23)	3.82 (1.04)
7 - 1994	—	—	—	—	—	0.35 (0.12)	0.87 (0.41)	—	1.22 (0.29)
7 - 1995	—	—	—	—	—	2.95 (0.75)	2.43 (0.93)	0.17 (0.06)	5.56 (1.62)
8 - 1994	0.06 (0.06)	—	—	—	—	0.69 (0.12)	0.81 (0.12)	0.35 (0.00)	1.91 (0.17)
8 - 1995	0.06 (0.06)	—	—	0.12 (0.12)	0.06 (0.06)	1.97 (0.93)	1.22 (0.17)	0.35 (0.12)	3.76 (1.33)
9 - 1994	—	—	—	—	—	0.41 (0.17)	0.46 (0.23)	0.17 (0.06)	1.04 (0.00)
9 - 1995	—	—	—	0.06 (0.06)	—	0.87 (0.29)	0.93 (0.58)	0.12 (0.12)	1.97 (1.04)

Table 2.—*Jaccard's indices of similarity* in species composition of small mammal communities observed on northeast-facing slopes on MOFEP sites during 1994-1995. Pairs of sites with indices near 1.00 are most similar.*

Site	1	2	3	4	5	6	7	8	9
1		0.71	0.50	0.71	0.50	0.67	0.50	0.71	0.43
2			0.71	1.00	0.50	0.67	0.50	1.00	0.67
3				0.71	0.29	0.43	0.29	0.71	0.43
4					0.50	0.67	0.50	1.00	0.67
5						0.75	1.00	0.50	0.75
6							0.75	0.67	0.60
7								0.50	0.75
8									0.67
9									

* Similarity index = $\frac{a}{a+b+c}$

where:

a = the number of species present on Site A that are also present on Site B
b = the number of species absent on Site A that are present on Site B
c = the number of species present on Site A that are absent on Site B

Table 3.—*Results of repeated measures analysis of variance of species richness values for small mammal communities on northeast-facing slopes of MOFEP sites during 1994-1995.*

Between Subject Effects

Source	df	Mean square	F-value	P
Treatment	2	1.06	0.61	0.51
Block	2	0.89	0.52	0.63
Error (Blk x Trt)	4	1.72		

Within Subject Effects

Source	Pillai's trace	F-value	Numerator df	Denominator df	P
Year	0.20	1.00	1	4	0.37
Yr x Trt	0.18	0.44	2	4	0.67
Yr x Blk	0.33	1.00	2	4	0.44

Table 4.—*Results of repeated measures analysis of variance of relative abundance estimates of small mammals on northeast-facing slopes of MOFEP sites during 1994-1995.*

Between Subject Effects

Source	df	Mean square	F-value	P
Treatment	2	3.62	2.60	0.19
Block	2	3.34	2.40	0.21
Error (Blk x Trt)	4	1.39		

Within Subject Effects

Source	Pillai's trace	F-value	Numerator df	Denominator df	P
Year	0.17	0.82	1	4	0.42
Yr x Trt	0.29	0.81	2	4	0.51
Yr x Blk	0.57	2.63	2	4	0.19

Table 5.—*Results of repeated measures analysis of variance of relative abundance estimates of Peromyscus sp. on northeast-facing slopes of MOFEP sites during 1994-1995.*

Between Subject Effects

Source	df	Mean square	F-value	P
Treatment	2	4.84	2.27	0.14
Block	2	7.13	3.34	0.07
Error (Blk x Trt)	13	2.13		

Within Subject Effects

Source	Pillai's trace	F-value	Numerator df	Denominator df	P
Year	0.11	1.56	1	13	0.23
Yr x Trt	0.21	1.75	2	13	0.21
Yr x Blk	0.43	4.90	2	13	0.03

DISCUSSION

Small mammal communities on the MOFEP sites were similar in species composition and species richness during the 2-year pre-treatment period. Although similarity indices in species composition ranged as low as 0.29, the communities only differed by one to four species. The small number of possible species to capture on the sites greatly influenced the magnitude of the similarity indices. All sites were occupied by white-footed and deer mice, and eastern chipmunks occurred on most sites. The remaining five species were sporadic, localized captures, and therefore would not be good indicator species for determining the landscape-scale effects of forest management.

Small mammal communities were also similar in overall relative abundance during 1994-1995. Sites did not significantly differ in overall small mammal relative abundance between years or between treatment and block assignments. The nearly significant block effect on *Peromyscus* sp. only supports the use of the randomized block design for the MOFEP experiment by attributing some of the variation in results to local geographic variation. We did observe a significant year by block interaction in lumped *Peromyscus* sp. relative abundance. This interaction principally was the result of the nearly significant block effect and the yet unexplained annual variation in relative abundance on two sites. This type of annual variation in small mammal numbers is not unusual. Small mammal numbers may fluctuate annually in response to a variety of density-dependent and density-independent factors. Other researchers have determined that annual population fluctuations were not dependent on treatment type (Krull 1970, Root *et al.* 1990, Yahner 1992). Yahner (1992) reported significantly lower numbers of individuals during a drought year that presumably reduced the availability of terrestrial arthropods as a food resource. Krull (1970) found irregular yearly fluctuations of white-footed mice densities that occurred despite the effects of earlier habitat manipulation of northern hardwood stands. Petticrew and Sadleir (1974) found that deer mice densities in coniferous stands in British Columbia varied more between years than between habitat types. Root *et al.* (1990) stated that white-footed mice numbers will fluctuate regardless of whether a site has been cut or not. Unless we observe huge sustained changes in animal numbers following treatment, these natural population variations will make determining the influence of treatments on small mammal numbers challenging. Collaboration with other MOFEP researchers, especially those working on the hard mast study, may provide insight into the variation we observed.

Logging affects the vegetative structure and species composition of forests, and can have a major influence on microclimates available to resident small mammals. Physical barriers are created or removed, more sunlight reaches the ground, the range of ground surface temperatures increases, and moisture regimes are altered. Eventually, the increase in light and moisture results in abundant growth of forbs, grasses, and shrubs, which provide more favorable habitat for some small mammal species (Ream and Gruell 1980).

Researchers have reported a successional sequence of small mammal species in response to the availability of food and cover following logging (Ream and Gruell 1980). Most species were adversely affected immediately following logging, but over the long term, populations of most small mammals increased (some species decreased). In general, habitat change associated with an even-aged cut was more dramatic than change associated with a selective cut. Extreme habitat modification associated with clearcuts resulted in the decline of some small mammal species and increases in others. Less pronounced changes were associated with uneven-aged cuts because selective cutting resulted in an insufficient change in the environment to significantly alter the composition of the small mammal community or total numbers of small mammals (Martell 1983).

The MOFEP experiment provides a unique opportunity to examine the effects of forest management on small mammal communities because it is concerned with the landscape-scale effects of management, rather than the smaller forest stand-scale other researchers have studied. The experiment also provides the opportunity to examine conditions of small mammal communities before treatment, rather than solely after treatment. Unlike many other studies, MOFEP gives us the opportunity to examine responses of small mammal communities for many decades. It is hoped that the results of this pre-treatment research will provide a good springboard for the comparison of post-treatment conditions, and ultimately, help us discern the long-term, landscape-scale effects of forest management on small mammal communities.

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The Distribution and Abundance of Leaf Litter Arthropods in MOFEP Sites 1, 2, and 3

Jan Weaver and Sarah Heyman[1]

Abstract.—In June 1993, we collected 144 leaf litter samples from 36 plots (4 samples/plot) located in MOFEP forest sites 1, 2 and 3. Half of the plots were placed randomly on northeast-facing stands (ELT 18), and half randomly placed on southwest-facing stands (ELT 17). Arthropods were extracted using Tullgren funnels, and then sorted into morpho-species, counted, and measured. Out of 126 usable samples, we found 22 orders of arthropods, 547 morpho-species, 40,000 individuals, and 30 g of arthropod biomass. ANOVA showed richness, numbers, and mass were higher on northeast- than on southwest-facing plots, but diversity was lower. Diversity, and to a lesser extent, numbers and richness, were lower in site 1.

Theoretically, 90 percent of a forest's Net Primary Production returns to the soil. There, microbial and fungal activity break down the organic debris of the forest into nutrients that can be cycled back into the ecosystem. Although capable of performing this operation by themselves, the microbes and fungi are aided by the fauna living in the leaf litter and the top few centimeters of soil. Mites and collembola, whose combined weight may be less than 2 g/m^2 (Cornaby *et al.* 1974) can be directly responsible for 15 to 28 percent of annual litter breakdown, 1 percent of the potassium release, and 12 percent of the calcium release in a forest (Gist and Crossley 1974). Indirectly they may be responsible for much more nutrient cycling because their feeding breaks litter into smaller fragments, increasing the surface area available for decomposition and leaching, and innoculating the litter fragments with fungi and microorganisms that continue the decomposition (Barbosa and Wagner 1989, Gist and Crossley 1974). Seastedt (1984) estimated the indirect effect of invertebrates on litter decay at 45 to 71 percent, depending on the species of leaf litter (dogwood, tulip poplar, or white oak). The dependence of microbes on invertebrates to aid decomposition may be chemical as well as mechanical. The Collembola *Tomocerus* and *Folsomia* have been shown to ingest clay in greater amounts when consuming *Quercus* leaves. The clay apparently detoxifies the polyphenols and increases the rate of microbial decomposition (Coleman and Crossley 1996).

The leaf litter fauna also play an important role in the forest food web. The soil/litter component of the forest contains half again as much carbon as the standing forest. This large carbon reserve, along with the relatively high assimilation efficiency of invertebrates—20 to 90 percent (Coleman and Crossley 1996), enables the development of long food chains in detrital food webs. These long chains, in turn, allow the concentration of nutrients needed by animals higher on the food chain. Sodium increases two to three times between trophic transfers (Coleman and Crossley 1996), and the calcium necessary for vertebrate bones and egg shells is sequestered by Oribatid mites, Millipedes, and snails from their feeding on fungi, and by spiders from their feeding on these organisms. More directly, the density of leaf litter invertebrates positively influences the population density of animals higher on the food chain (Smith and Shugart 1987, Stenger 1958).

OBJECTIVES OF THIS STUDY

We sampled in Missouri Ozark forests to characterize the pre-treatment leaf litter arthropod

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community of forests undergoing logging as part of the Missouri Ozark Forest Ecosystem Project (MOFEP). By estimating the numbers, mass, richness, and diversity of this community, and by identifying dominant species and studying their distributions, we hoped to establish ecological markers of ecosystem structure. These markers could then be used to evaluate the impact of logging or other disturbances on the ecosystem.

MODIFICATIONS OF THE MOFEP EXPERIMENTAL DESIGN

Because of its high species diversity, large population size, and high variability, the leaf litter community could not be sampled with the same thoroughness over as large an area as other taxa in MOFEP. Consequently, we decided to use a different sampling and analytical approach. Although the MOFEP experimental design consists of three treatments, each replicated three times in nine forest sites, our study uses only three sites; one to investigate each treatment. Without replicating the treatments at the site level, we cannot discuss the forest-level impact of logging on leaf litter communities. However, we will be able to compare pre- and post-treatment samples to see if variability in these communities over time is related to treatment applications.

MATERIALS AND METHODS

Sampling Dates

Leaf litter samples were collected in the first week of June 1993. Although we also collected samples in June 1994 and 1995, we have not completed analysis of those samples. This paper will cover data only from 1993.

Sampling Scheme

Plots were initially randomly located and resampled yearly. There were 12 plots in each of the three sites: six on Northeast (NE)-facing stands (ELT18), and six on Southwest (SW)-facing stands (ELT17). Sample locations are shown in figure 5 of Brookshire *et al.* (1997), a foldout map included with this proceedings. Each plot was 5 x 5 m, and was marked semi-permanently with 25-cm pieces of PVC pipe driven into the ground at the bottom and upper left corners of the plot. In addition, two trees within a few meters of the downhill pipe were marked with paint and their positions relative to the pipe were recorded in case the pipe disappeared. Samples were collected from four randomly selected points within each plot each year (4 x 36 =144 samples total). Sampling was without replacement.

Sampling Protocol

Once the sample point was located, a 3-pound coffee can with a diameter of 15.5 cm (area = 0.02 m^2) was plunged into the litter and pressed down. A sharp knife was used to cut the litter and small twigs from around the can, and this debris was brushed away from the can perimeter. Larger sticks were broken off or gently removed from underneath the can. A gallon-size clear plastic bag with a label indicating date and location of sample was readied, the can was lifted, and the litter was grasped in one hand and then scooped into the waiting bag. Spiders, beetles or cockroaches escaping from within the sample perimeter were stunned by slapping them with a flat palm, and then placed in the bag. All litter down to, but not including, finely divided leaf litter and soil was collected. Stones, large clumps of soil (>10 mm), or sticks (of a size to poke holes in the bag) were not placed in the bag, but were examined for arthropods before being discarded.

Sample Extraction

We used a Tullgren Funnel to extract arthropods from the litter. The extraction equipment consisted of:

1. paint buckets (1 and 2 gallon);
2. a funnel made out of aluminum flashing with a large end diameter of 30 cm, a small end diameter of 3 cm, a length of 20 cm, and an angle of approximately 45°;
3. a circular piece of 1/2 in. hardware cloth 23 cm in diameter;
4. an inverted funnel-shaped lamp support made out of aluminum flashing with a large end diameter of 26 cm, a small end diameter of 22 cm, a length of 18 cm, and four 3.5- x13-cm screened openings in the upper half;
5. a polarized clamp lamp with a white plastic shade from SNAPIT (Leviton Co., Cable Electric Products, Inc., PO Box 6767, Providence RI 02940) fitted with a 25-watt bulb;
6. a 100-ml plastic container filled with 40 ml of 70 percent ethanol.

The plastic container sat in the bottom of the bucket, which supported the funnel, the screen was laid in the funnel, the lamp support was placed large side down in the funnel, and the clamp lamp was placed over the lamp support. The lamp support held the light away from the sample and prevented the larger and more active arthropods from walking out of the funnel. The screened openings in the funnel support helped prevent the sample from becoming too hot. Leaf litter was spread over the surface of the screen before setting it in the funnel.

Samples were processed the day they were collected, usually within 6 hours. Until processing, samples were kept in a Styrofoam ice chest. Leaf litter was unbagged onto the screen while the screen rested on a plate; then the screen was carefully placed in the funnel and litter that had fallen onto the plate was tipped on the piled litter. The leaf litter was heated and dried by the 25-watt bulb suspended 10 to 15 cm above it. The temperature inside the funnel was approximately 40° C. The samples remained in the funnels for 42 to 46 hours. Arthropods moved down through the litter as the sample dried and fell through the screen supporting the sample into the container of 70 percent ethanol.

Sampling Efficiency

To evaluate the efficiency of the Tullgren funnels, one leaf litter sample from each plot (collected in 1995) was hand-sorted under a dissecting microscope after it had been extracted, and the numbers and kinds of arthropods found were recorded.

Sample Analysis

The sample containers were returned to the lab, and the number, length, and morpho-species of individuals over 0.2 mm were determined and recorded. Species identifications were not made; instead, different kinds of individuals were identified by their morphology, or body shape, and given a unique number so that their distribution across samples could be determined. Although specimens are being sent to specialists for ultimate identifications, for the purposes of this work it was sufficient to be able to simply distinguish one kind of morpho-species from another (Oliver and Beattie 1993). The only exception to this generalization is that the Diptera, Coleoptera, and Oribatid mites all have larva that look different from the adult forms, so the richness of these groups may have been overestimated because some species were counted twice. On the other hand, the larval forms usually live in different microhabitats, eat different food, and are eaten by different animals. So although larvae and adults are connected through time, they were functionally different species within the parameters of this study. Individuals less than 0.2 mm were too small and numerous for us to reliably sort them into morpho-species. However, these were sorted into orders and their total numbers were estimated by counting individuals in a subsample.

To keep track of the morpho-species across multiple samples, each new species was sketched and specimens were preserved in a reference collection maintained in our laboratory at the University of Missouri. Individuals in new samples were compared to sketches of previously recorded morpho-species and/or compared to individuals in the reference collection before being assigned to a morpho-species.

The number and length of each morpho-species found in a sample were entered into a computer database. In addition, each morpho-species was assigned a six-letter code that allowed species within a sample to be sorted by taxonomic categories. The first letter of the code designated the phylum, the second the class, the third the order, the fourth the family, the fifth and sixth the genus and species, respectively. The letter Z was used whenever the taxonomic category was unknown. This made it possible to sort the data into various taxonomic categories for further analysis and to update the code for a particular species as identifications were made.

Once data from individual samples were entered, the numbers, mass, richness, and diversity for each sample were determined. Numbers and richness were derived directly by counting the number of individuals and morpho-species in a particular sample. To determine mass, the average length for each morpho-species in a sample was converted to milligrams using regression equations specific to its taxonomic group. This value was multiplied by the number of individuals of that morpho-species, and then masses of all morpho-species in a sample were summed to find the sample mass.

The equations for mite and Collembola mass were determined in our lab by a student technician. Live mites and Collembola were chilled (to reduce movement) and then individually weighed on a Cahn 28 Electrobalance. After checking to make sure the animal was still alive, the technician preserved it in 70 percent ethanol and measured its length using an ocular micrometer. Equations for the other groups were taken from Sage (1982). The number of animals used (n) and the R^2 and probability for each regression are listed with its equation. All equations are for wet/fresh weight with length expressed in mm and mass espressed in mg.

1. Mites ($n = 22$, $R^2 = 0.88$, $p < 0.001$)
   $\text{mass} = 10^{(0.99081 + 2.5103 \times \text{Log10 (length)})}$

2. Other Arachnids (spiders, pseudoscorpions, *etc.* $n = 39$, $R^2 = 0.91$, $p < 0.001$)
   $\text{mass} = 1000 \exp(0.459 (\text{length}) - 0.007 (\text{length})^2 - 6.504)$

3. Collembola ($n = 23$, $R^2 = 0.88$, $p < 0.001$)
   $\text{mass} = 10^{(-1.3233 + 2.1211 \times \text{Log10 (length)})}$

4. Other Insects (beetles, ants, bugs, thrips, *etc.* $n = 153$, $R^2 = 0.87$, $p < 0.001$)
   $\text{mass} = 1000 \exp(0.369 (\text{length}) - 0.004 (\text{length})^2 - 6.973)$

5. Soft Bodied Larvae (ants, flies, moths, butterflies, *etc.* $n = 27$, $R^2 = 0.96$, $p < 0.001$)
   $\text{mass} = 1000 \exp(0.355 (\text{length}) - 0.004 (\text{length})^2 - 7.622)$

6. Hard Bodied Larvae/Myriapods (beetles, centipedes, millipedes, *etc.* $n = 9$, $R^2 = 0.84$, $p < 0.001$)
   $\text{mass} = 1000 \exp(0.735 (\text{length}) - 0.16 (\text{length})^2 - 10.783)$

The diversity index used was the inverse Simpson's index, $1/\sum pi^2$ (Hill 1973) where pi is the proportion of species i in the sample. Therefore, samples dominated by one or a few species have lower diversities than samples in which individuals are more uniformly distributed among species. Richness, on the other hand, is weighted towards rare species because every species counts the same regardless of whether it is represented by 1 or 100 individuals. All other diversity indices fall somewhere between these two measures (Hill 1973) so they represent the end points of a continuum of diversity measures. Together, the two estimates give a more complete picture of a community's diversity than using a single index.

Plot Data

In 1996, plots were visited to gather environmental data on them. Plot 4 in site 1 and plot 6 in site 2 could not be located during this trip so there are no data from them. The aspect was determined for each plot, as opposed to the aspect of the stand it was in; the percent slope and soil pH were also determined. To measure soil pH, 2 to 5 cc of soil were collected from the center and four corners of each plot and physically mixed in a plastic bag. Then 5 g of soil were mixed with 10 drops of millipore water to make a paste. ColorpHast indicator sticks were inserted into this paste and compared to a standard chart to obtain soil pH.

Data Analysis

We analyzed the distribution and influence of plot aspect (compass orientation), percent slope, and pH on community characteristics and species populations using Pearson correlation with Bonferroni-adjusted family probabilities. To perform correlation analysis on aspect, we converted the azimuth to eight classes: 1(338-22°), 2(23-67°), 3(293-337°), 4(68-112°), 5(248-292°), 6(113-137°), 7(203-247°), and 8(138-202°), with class 1 being the northernmost and class 8 being the southernmost. Although this is not a widely used method of classifying aspect, the categories we selected were adequate to highlight general trends.

We used ANOVA to analyze the distributions of community characteristics and species populations by site and aspect. For aspect, we used both the plot aspect (compass orientation of a plot) and the stand aspect (the compass orientation of the stand a plot was located in). For plot aspect, classes 1 to 4 (293°-112°) were designated NE-facing and classes 5 to 8 (113°-292°) were designated SW-facing. This allowed us to assess the influence of plot environmental conditions vs. stand environmental conditions. We also used ANOVA to check how uniformly the plot variables percent slope and pH were distributed by compartment and aspect.

RESULTS

Forest Floor Arthropods

Of the 144 samples collected in 1993, 18 had to be discarded because they were knocked over, dried out, or contaminated with fungus. However, each plot was represented by at least one sample. The 126 remaining samples contained 40,000 individuals over 0.2 mm in length, had a mass of approximately 30 g, included 547 morpho-species, and had an overall diversity value of 28.1. The average number of individuals per sample was 323, the average biomass was 235 mg, the average richness was 55 morpho-species, and the average diversity value was 15.8. The average number of individuals per square meter was 16,150 (average sample number x 50), and the average mass was 11.7 g/m^2. Because neither richness or diversity increases arithmetically with area, their values per square meter can't be estimated by multiplying the average values by 50.

Figure 1 shows the average number of individuals per square meter, the total mass per square meter, and the total number of morpho-species for each of 22 arthropod taxa found in the leaf litter. Based on numbers alone, the Diptera (adult and larval flies, mostly Cecidomyidae), Collembola (springtails), and Acari (Oribatid, Mesostigmatid, and Prostigmatid mites) were the most important members of the community. If mass were considered, the Hymenoptera (mostly ants), Diptera, Orthoptera (two species of cockroaches), and the Acari were the most important members of the community. If richness were considered, then Diptera, Coleoptera (adult and larval beetles), Aranea (mostly Gnaphosid spiders), and Acari dominated. The overall dominants in the community (at least 50 individuals/m^2, 50 mg/m^2, and 50 species) were the Diptera, Coleoptera, Aranea, Acari, and the Hymenoptera. The Lepidoptera (almost all larval) and Collembola could be considered subdominants.

In our evaluations of sampling efficiency, an average of 18.5 arthropods remained in litter extracted in the Tullgren funnels in 1995. If the average number of arthropods in a 1995 sample is comparable to the average of the 1993 samples, then approximately 5.7 percent of arthropods are missing from the leaf litter samples once they are processed. This percentage of individuals was within the limits of the samples' standard errors for numbers and mass (assuming the average mass of an individual is 1 mg), so we do not believe these missing arthropods affected results for numbers or

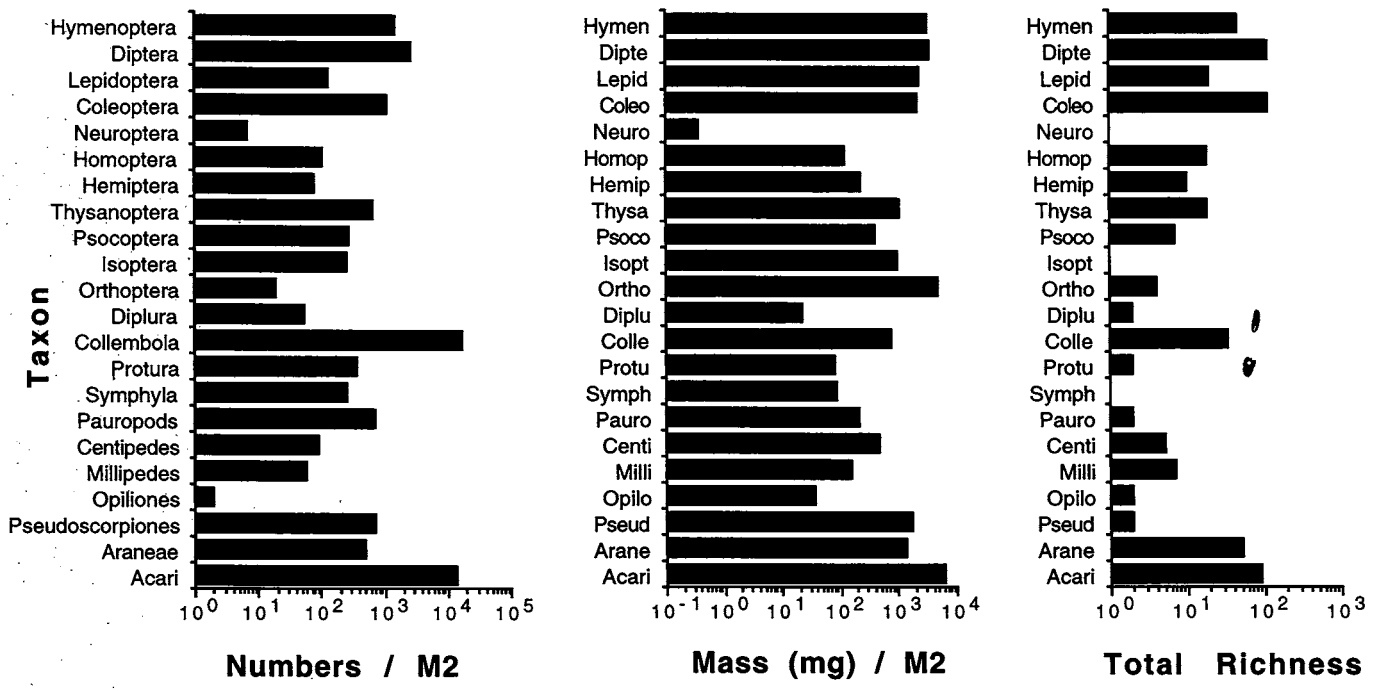

Figure 1.—*Average numbers per square meter, mass per square meter, and total richness for 22 arthropod taxa found in 126 leaf litter samples.*

mass. Richness would be more sensitive to missing arthropods if they also represented missing species, but in most cases, the arthropods were members of a common group. Diversity would be less sensitive, since this measure is weighted more heavily towards common species. Interestingly, there were a large number of snails, about four per sample, a much higher value than we normally found in extracted samples. If this value is representative, a typical square meter of forest floor would have more than 200 snails.

Community Characteristics

Table 1 contains data on aspect(s), slope, and pH for each plot, along with the average (based on 1 to 4 samples per plot) numbers (N), mass (M), richness (R), and diversity (D) of its arthropod community. In eight cases, the orientation of the plot was markedly different from the stand orientation, with four plots shifting from NE to SW and four shifting from SW to NE. Using Pearson correlation coefficients with Bonferroni family probability rates, richness was highly correlated with both numbers ($r = 0.765$, $p < 0.001$, family: N, M , R, D), and mass ($r = 0.443$, $p = 0.041$), but diversity was not correlated with any of the other community characteristics (Wilkinson 1989). Only number was significantly correlated with any of the plot variables—numbers decreased as slope increased ($r = -0.570$, $p = 0.003$, family: N, plot class, slope, pH).

Table 2 contains means and standard errors for community characteristics, plot variables, and 10 numerically dominant species. Data were averages of average sample values for a plot, and represent N, M, R, and D for a 0.02 m^2 sample. There is a set of values for all plots, for NE and SW plots, and for site 1, 2, and 3 plots. The numerically dominant species accounted for 47 percent of the individuals found in all plots; therefore, it is not surprising that overall diversity (28.1) was relatively low compared to the richness (547). From the table, it is clear that NE plots had higher numbers, mass, and richness, but lower diversity than the SW plots. NE plots also had less steep slopes and a higher pH than SW plots. Four of the 10 dominant species, *Onychiurus ramosus*, *Folsomia stella*, the box mite, and *Hypogastrura brevis*, had at least 1.5 times as many individuals on NE plots as on SW plots, and may account for the higher numbers and mass on NE plots.

There were also marked differences among sites. Site 1 had lower numbers, mass, richness, and diversity than sites 2 and 3. It also had steeper slopes and a lower pH. Of dominant species, it had markedly fewer *H. brevis* and more *Pseudosinella* sp. 367. Site 2 had a higher mass and more *Hypogastrura brevis*, while site 3 was distinguished by having more *O. ramosus*.

These patterns were tested using ANOVA, and the results are shown in table 3. We tried three models: the first included the interaction of site and plot aspect as well as their main effects, the second looked only at main effects of site and plot aspect, and the third used stand aspect instead of plot aspect to examine the relative influence of local (plot aspect) versus general (stand aspect) conditions. Numbers, mass, and richness varied strongly ($p < 0.05$) and diversity varied weakly ($0.05 < p < 0.1$) with plot aspect. There was a weak effect of site on numbers and richness and a strong effect on diversity. There was no interaction between site and plot aspect for the community variables. When the same data were analyzed using stand aspect, differences between aspect became weaker or disappeared.

As a check on the uniformity of the plots' physical and chemical characteristics, we performed ANOVA on percent slope and pH by site and aspect. Slope was steeper on SW plots than on NE plots, and pH was lower in site 1 than in sites 2 and 3. The plot locations were selected randomly so it seems unlikely we happened to randomly locate plots on more steep slopes in SW-facing stands than in NE-facing stands, but it also seems unlikely that SW stands would tend to be steeper. With regard to pH, it is possible that sites or aspects could influence pH. In any case, these differences in physical and chemical characteristics will have to be considered in evaluating treatment differences among plots.

For dominant species, only *O. ramosus*, *Lepidocyrtus* sp. 149, and the box mite showed a strong response to aspect, appearing to prefer NE to SW plots and/or stands, and both *Folsomia stella* and Pseudoscorpiones sp. 97 were weakly responsive to plot aspect. None of the species showed significant differences in distribution with site. The relative lack of response of some species may have been due to the high variability in their distributions. For

Table 1.—*Plot variables and community characteristics for 36 plots. Plot compass, plot aspect, slope, and pH are from June 1996 (except for plots 1.4 and 2.6, which could not be located on that trip). Arthropod numbers, mass, richness, and diversty are from June 1993. Arthropod values are sample averages per plot.*

Site Plot	Stand aspect	Plot compass	Plot aspect[1]	Plot class	Percent slope	pH	# Samples	Number of arthropods	Mass(mg)	Richness	Inverse Simpson's diversity
1.1	S	210	S	7	22	4.0	4	212	77	39	10.9
1.2	N	355	N	1	23	4.5	2	252	180	46	11.4
1.3	N	115	S	6	27	4.5	4	341	113	50	10.7
1.4	S	.	S	.	.	.	4	234	93	43	10.1
1.5	S	105	N	4	35	4.7	2	342	180	63	12.4
1.6	N	270	S	5	36	5.0	4	233	117	50	12.4
1.7	N	330	N	3	26	5.5	4	178	110	43	13.5
1.8	S	205	S	7	48	4.5	4	246	164	52	15.5
1.9	N	10	N	1	30	4.5	4	348	267	63	14.5
1.10	N	30	N	2	25	4.5	4	251	904	55	14.3
1.11	S	190	S	8	33	3.5	4	171	44	37	11.8
1.12	S	150	S	8	45	4.0	4	313	155	61	18.6
2.1	S	190	S	8	30	4.7	4	228	213	51	17.0
2.2	S	120	S	6	20	5.5	4	410	724	64	16.5
2.3	S	85	N	4	20	5.5	4	515	705	60	11.6
2.4	N	315	N	3	24	5.0	4	567	39	63	11.5
2.5	N	2	N	1	12	5.5	4	700	202	73	18.8
2.6	S	.	S	.	.	.	1	304	195	63	19.3
2.7	N	5	N	1	27	4.0	4	428	252	59	15.2
2.8	N	45	N	2	33	5.0	4	274	87	52	17.2
2.9	N	35	N	2	25	5.5	2	321	263	62	16.1
2.10	S	245	S	7	43	5.0	2	156	154	49	21.0
2.11	S	255	S	5	45	5.5	4	126	49	36	13.5
2.12	N	340	N	1	37	6.0	4	279	269	58	18.1
3.1	N	60	N	2	30	5.0	4	390	196	56	10.9
3.2	N	65	N	2	18	5.7	4	448	691	66	12.0
3.3	N	110	N	4	16	6.0	4	433	478	60	6.2
3.4	S	295	N	3	30	4.5	4	390	196	56	10.9
3.5	N	90	N	4	20	5.0	4	293	156	60	22.6
3.6	S	110	N	4	16	5.0	2	457	72	60	17.5
3.7	N	120	S	6	30	6.0	2	477	315	67	18.5
3.8	N	115	S	6	27	5.7	3	207	83	50	18.3
3.9	S	270	S	5	34	4.0	1	243	64	63	25.4
3.10	S	135	S	6	35	5.5	4	321	91	59	20.3
3.11	S	170	S	8	21	5.0	4	297	147	56	18.4
3.12	S	250	S	5	24	4.0	4	249	50	39	13.2

[1]Aspects were grouped into the following classes: 1=338-22°, 2=23-67°, 3=293-337°, 4=68-112°, 5=248-292°, 6=113-137°, 7=203-247°, and 8=138-202°.

Table 2.—*Means and standard errors for community characteristics, plot variables, and numbers of numerically dominant species. Means are for average plot values, (plot values have an area of = 0.02 m²), for all plots, for northeast (NE) and southwest(SW) plots, and for sites 1, 2, and 3. Standard errors are shown in parentheses below each mean.*

Characteristic/Variable		All plots (n = 36)	NE plots (n = 18)	SW plots (n = 18)	Site 1 (n = 12)	Site 2 (n = 12)	Site 3 (n = 12)
Numbers	mean	323	381	264	260	359	350
	standard error	(21)	(30)	(21)	(18)	(49)	(27)
Mass (mg)		235	311	158	200	292	211
		(35)	(55)	(37)	(66)	(62)	(56)
Richness		55	58	51	50	57	58
		(1.5)	(1.6)	(2.3)	(2.6)	(2.7)	(2.2)
Diversty (inverse Simpson's)		15.2	14.1	16.2	13.0	16.3	16.2
		(0.7)	(0.9)	(1.0)	(0.7)	(0.9)	(1.6)
Slope (percent)		28	25	32	31	29	25
		(1.4)	(1.6)	(2.1)	(2.5)	(2.8)	(2.0)
pH		4.9	5.1	4.8	4.5	5.3	5.1
		(0.1)	(0.1)	(0.2)	(0.1)	(0.1)	(0.2)
Onychiurus ramosus (n) Collembola		41.9	54.6	29.3	36.2	38.7	50.9
		(5.2)	(8.0)	(5.2)	(9.0)	(6.9)	(10.8)
Tomocerus lamelliferous (n) Collembola		21.3	22.6	20.1	25.1	22.4	16.5
		(2.6)	(3.5)	(4.0)	(4.4)	(5.9)	(2.8)
Mesostigmatid mite sp. 154 (n)		18.4	18.6	18.1	16.7	18.9	19.5
		(1.4)	(1.9)	(2.1)	(2.2)	(2.4)	(2.7)
Tomocerus elongatus (n) Collembola		15.1	14.7	15.5	13.8	16.4	15.1
		(1.3)	(1.9)	(2.0)	(1.7)	(2.7)	(2.5)
Lepidocyrtus sp. 149 (n) Collembola		13.1	13.5	12.7	13.7	10.4	15.1
		(1.5)	(2.7)	(1.6)	(2.4)	(2.0)	(3.4)
Folosomia stella (n) Collembola		11.3	18.2	4.5	10.8	15.1	8.1
		(3.5)	(6.7)	(1.2)	(3.6)	(9.9)	(2.9)
Oribatid mite sp. 329 (n) (Euphthricaridae - box mite)		8.3	10.1	6.4	6.2	10.2	8.3
		(0.8)	(1.4)	(0.8)	(0.9)	(1.9)	(1.4)
Hypogastrura brevis (n) Collembola		8.1	11.6	4.6	2.6	15.8	5.9
		(2.8)	(5.3)	(1.3)	(0.6)	(7.8)	(1.8)
Pseudosinella sp. 367 (n) Collembola		7.6	8.0	7.2	10.0	6.9	5.9
		(0.9)	(1.3)	(1.4)	(1.4)	(2.0)	(1.3)
Pseudoscorpiones sp. 97 (n)		5.6	6.6	4.6	4.8	5.6	6.5
		(0.5)	(0.7)	(0.8)	(0.9)	(0.8)	(1.2)

Table 3.—*ANOVA of community characteristics, plot variables, and dominant species on compartment and aspect. Weakly significant values (0.05 < p < 0.10) are underlined, strongly significant values (p < 0.05) are underlined and set in boldface. F-values and p-values are ordered for site, aspect, and site x aspect effects as indicated in the first entry of the table.*

Variable		Model 1		Model 2		Model 3	
		Site	**df = 2**	**Site**	**df = 2**	**Site**	**df = 2**
		Plot aspect	**df = 1**	**Plot aspect**	**df = 1**	**Stand aspect**	**df = 1**
		S x PA	**df = 2**	**Error**	**df = 32**	**Error**	**df = 32**
		Error	**df = 30**				
Numbers	Site	F = 2.7	p = 0.085	F = 2.3	p = 0.115	F = 2.7	p = 0.080
	Aspect	F = 9.7	p = **0.004**	F = 9.1	p = **0.005**	F = 3.1	p = 0.089
	S x A	F = 2.0	p = 0.147				
Mass (mg)		F = 0.5	p = 0.610	F = 0.4	p = 0.645	F = 0.7	p = 0.515
		F = 4.4	p = **0.045**	F = 4.5	p = **0.041**	F = 1.8	p = 0.188
		F = 0.6	p = 0.573				
Richness		F = 2.4	p = 0.108	F = 2.6	p = 0.088	F = 3.1	p = 0.061
		F = 5.0	p = **0.033**	F = 5.2	p = **0.029**	F = 2.6	p = 0.117
		F = 0.2	p = 0.815				
Diversity		F = 3.3	p = 0.052	F = 3.6	p = **0.039**	F = 2.8	p = 0.078
(Inverse Simpson's)		F = 4.0	p = 0.054	F = 3.9	p = 0.058	F = 0.9	p = 0.353
		F = 2.1	p = 0.146				
Slope (percent)		F = 1.6	p = 0.224	F = 1.6	p = 0.216	F = 1.6	p = 0.213
		F = 6.5	p = **0.016**	F = 6.9	p = **0.013**	F = 3.2	p = 0.083
		F = 0.1	p = 0.920				
pH		F = 4.7	p = **0.017**	F = 5.1	p = **0.012**	F = 7.5	p = **0.002**
		F = 1.6	p = 0.215	F = 1.7	p = 0.204	F = 8.7	p = **0.006**
		F = 0.2	p = 0.835				
Onychiurus ramosus (n)		F = 0.9	p = 0.426	F = 0.9	p = 0.424	F = 0.9	p = 0.414
		F = 6.7	p = **0.015**	F = 6.9	p = **0.013**	F = 7.5	p = **0.010**
		F = 0.5	p = 0.612				
Tomocerus lamelliferous (n)		F = 0.7	p = 0.487	F = 0.9	p = 0.404	F = 0.9	p = 0.419
		F = 0.3	p = 0.594	F = 0.3	p = 0.599	F < 0.1	p = 0.829
		F = 2.6	p = 0.091				
Mesostigmatid mite sp. 154 (n)		F = 0.3	p = 0.731	F = 0.4	p = 0.707	F = 0.4	p = 0.700
		F < 0.1	p = 0.950	F < 0.1	p = 0.947	F < 0.1	p = 0.893
		F = 0.1	p = 0.940				
Tomocerus elongatus (n)		F = 0.3	p = 0.752	F = 0.3	p = 0.718	F = 0.3	p = 0.745
		F = 0.2	p = 0.684	F = 0.2	p = 0.682	F = 0.3	p = 0.573
		F = 1.8	p = 0.186				
Lepidocyrtus sp. 149 (n)		F =0.9	p = 0.429	F = 0.8	p = 0.438	F = 0.9	p = 0.408
		F = 0.1	p = 0.730	F = 0.1	p = 0.721	F = 4.5	p = **0.042**
		F = 1.7	p = 0.197				
Folsomia stella (n)		F = 0.2	p = 0.824	F = 0.2	p = 0.785	F = 0.3	p = 0.720
		F = 3.5	p = 0.071	F = 3.6	p = 0.066	F = 2.5	p = 0.125
		F = 0.4	p = 0.688				
Oribatid mite sp. 329 (n)		F = 1.4	p = 0.258	F = 1.6	p = 0.223	F = 2.6	p = 0.093
		F = 4.5	p = **0.042**	F = 4.1	p = 0.051	F = 11.2	p = **0.002**
		F = 2.2	p = 0.129				
Hypogastrura brevis (n)		F = 1.7	p = 0.199	F = 1.9	p = 0.166	F = 2.1	p = 0.134
		F = 1.2	p = 0.279	F = 1.1	p = 0.305	F < 0.1	p = 0.851
		F = 2.3	p = 0.118				
Pseudosinella sp. 367 (n)		F = 1.6	p = 0.225	F = 1.8	p = 0.180	F = 1.7	p = 0.200
		F = 0.3	p = 0.559	F = 0.4	p = 0.553	F < 0.1	p = 0.898
		F = 1.9	p = 0.172				
Pseudoscorpiones sp. 97 (n)		F = 0.8	p = 0.444	F = 0.8	p = 0.473	F = 0.8	p = 0.449
		F = 3.3	p = 0.077	F = 3.3	p = 0.078	F = 0.9	p = 0.358
		F = 1.5	p = 0.239				

example, although *Hypogastrura brevis* was more than twice as abundant in site 2 than in 1 and 3, and on NE than on SW stands, its standard error values were 23 to 49 percent of the mean value.

DISCUSSION

Although there is a large and varied literature on leaf litter communities, we have as yet found no studies directly comparable to ours with respect to the ecological community investigated, the methods used, and the members of the community sampled. Hoekstra *et al.* (1995), sampling leaf litter communities in coastal redwood, found 11,500 individuals/m^2 in old-growth forest, 22,000 individuals/m^2 in mature second-growth forest, and 3,500 individuals/m^2 in cut forest (these values for area were derived from their volume estimates). These numbers are comparable to the 16,150 individuals/m^2 we estimate are present in our second-growth Ozark forest. Seastedt and Crossley (1981), sampling in Appalachian forest, found 98,900 to 133,500 individuals/m^2. However, their samples included soil as well as litter, and they counted animals smaller than 0.2 mm, which we did not. We did estimate the number of individuals in this size class for all our samples and adding them would easily double our population estimates. This still does not put us in the range of Seastedt and Crossley's numbers, but their inclusion of soil as well as litter might account for the difference. Moulder and Reichle (1972) estimated the macroarthropod density in oak forest at 514/m^2. They also estimated biomass at 8.6 g/m^2. A similar suite of taxa from our study gave values of 2,212 individuals/m^2. Because Moulder and Reichle were investigating spider prey, it is likely that we included more small individuals than they did, so our population estimate would be larger. Their estimate of mass, however, is roughly consistent with ours, 11.7 g/m^2. We found no estimates of richness for the total arthropod community, though several studies estimated richness for particular groups.

The significant correlation between richness and mass that we found in our community is consistent with Tilman (1996) and Tilman *et al.*'s (1996) finding that in grassland communities, plant mass and productivity (but not numbers) are increased by species richness of the plant community. The authors hypothesize that increased richness increases the redundancy in the system, allowing different plant species to exploit variability in local conditions over time while ensuring constancy of primary production and therefore of plant biomass. Didham *et al.* (1996) make a similar argument for the decomposer community of the forest floor. Decomposition is only weakly related to numbers but can experience dramatic declines when richness decreases. A large number of leaf litter arthropod species may mean that all or most of the available niches and microhabitats are being utilized, thus increasing the transfer of resources from microbes and fungi to arthropods. When particular species are lost, their niches are no longer used, and resources in the food chain may be routed through other channels in the community, including being leached into lower soil layers where they may no longer be available to any members of the community. A similar argument may account for the relation of richness to numbers.

The lack of correlation between diversity and any of the other community characteristics in our study was rather surprising. Tilman and Tilman *et al.* found their diversity measures (like the Shannon-Weiner index) correlated with mass. The discrepancy could be due to the different communities investigated, the different taxa sampled, or to our use of the inverse Simpson's index. What our results do suggest is that the factors that dictate how evenly resources are shared differ from the factors that dictate how many species there are. For example, extreme environmental conditions, like drought, flooding, soil pH, percent slope, or even a food-rich environment will be advantageous to the particular species adapted to them. These species will garner a larger share of the available resources, effectively reducing evenness and therefore the value of the inverse Simpson's index. However, these extreme conditions might not be severe enough to actually exclude other species, which might continue at very low population levels. Thus, richness would remain relatively constant while diversity went down.

Only numbers correlated significantly with any of the physical/chemical characteristics of plot, being negatively correlated with a plot's slope. Numbers may go down on steeper slopes because of the physical instability of the habitat. Runoff is likely to be swifter and have more energy to shift leaf litter, soil, and stones. As a result, it may be harder for most species to establish themselves and generate large populations.

The ANOVA showed that numbers, richness, and mass were higher and diversity lower on NE plots than on SW plots. A number of factors could account for this result. For the MOFEP sites, annual tree growth is slightly higher on NE stands, 0.61 m^2/ha vs. 0.59 m^2/ha (Jensen 1995), tree basal area is greater, there is more litter cover, and there is less bare soil and rock (Grabner 1995). Because soil moisture is higher on NE stands, microbial and fungal growth must also be higher. With a higher plant productivity, greater and more uniform litter cover and a higher rate of breakdown by microbes and fungi, the NE plots ought to be able to support a larger and richer arthropod community. These results are consistent with those of Mudrick *et al.* (1994) and Seastedt and Crossley who found higher numbers of microarthropods on north-facing forest slopes. Interestingly, the larger arthropod populations of NE plots in our study did not seem to be translated into larger vertebrate populations, at least for reptiles and amphibians. In the same MOFEP sites that were sampled for leaf litter arthropods, reptile and amphibian numbers were consistently lower on NE stands than on SW stands (Renken 1995).

The differences for community characteristics among sites are harder to account for, because the three sites were considered roughly equivalent. One explanation may be the lower pH of soils in site 1. The activity of bacteria and actinomycetes falls rapidly at pH values below 5.5 though fungi function well at all pH levels (Brady 1974). If the lower pH of site 1 caused the decomposer resource base to be reduced to fungi, only those species that specialized on fungi would do well. As a consequence, their numbers would increase relative to species dependent on bacteria and actinomycete food chains, leading to a reduction in the diversity value. There might also be an overall decrease in numbers and richness. What is not clear is why mass did not also decrease. Unfortunately, this explanation of pH effect appears to be contradicted by the fact that SW plots had higher diversities than NE plots even though they had lower pH values.

Two other factors complicate the generalized picture of the leaf litter community. Although there was a significant effect when plot aspect was used, there was little or no effect on numbers, mass, richness, and diversity when stand aspect was used. In other words, the orientation of the plot or local environment was important, but not the orientation of the stand or general environment. This suggests that disturbances would have to be on or near a plot to have much impact, so an activity like logging may have little direct influence on the leaf litter community outside of the area where trees are actually removed. The second factor is the fact that SW-facing plots in this study had significantly steeper slopes than NE-facing plots. Because numbers were negatively correlated with degree of slope, differences between northeast and southwest plots might be due to steepness as well as, or instead of, things like primary plant productivity or fungal growth. These two factors, along with pH, will have to be taken into account when evaluating the impact of the logging treatments.

The Collembola, or springtails, were key species in this community. This group of primitive wingless insects typically forms large populations in the soil and leaf litter. The common name "springtail" comes from the ability of many species to spring out of harm's way using a furcula, a forked, tail-like structure held under the body until the animal is disturbed, when it is then flipped down and back propelling it upward and forward. Collembola are generally fungivorous, though they occasionally engulf leaf litter and even nematodes when they are abundant (Coleman and Crossley 1996). Some species feed selectively on different types of fungi and may thereby affect the speed and direction of forest successions. They are also a significant prey species for a variety of predators (Coleman and Crossley 1996, van Straalen *et al.* 1985) including toads, frogs, and salamanders as well as arthropod predators, like spiders, beetles, and ants.

A preliminary search of the literature uncovered relatively little information on the particular species found at the MOFEP sites, but various species of the genera *Tomocerus* (Takeda 1981) and *Lepidocyrtus* (Seipel 1994) have been described as epigeic, or surface dwellers, on leaf litter. They are characterized by relatively long legs, long antennae, a long furcula, large eyes, a pigmented integument, and in the case of *Lepidocyrtus* species, distinctive dark and light markings. Therefore, our three species, *Tomocerus lamelliferous*, *Tomocerus elongatus*, and *Lepidocyrtus* sp. 149, probably constitute a group of active, surface dwelling Collembola in our community. Three soil dwelling species, *Onychiurus ramosus*, *Folsomia stella* , and *Pseudosinella* sp. 367, were characterized by

reduced legs, antenna, furcula, eyes, and pigmentation. The remainung species, *Hypogastrura brevis*, is an intermediate form, with reduced legs, antenna and furcula like the soil dwelling group, but distinct eyes and pigmentation like the litter surface group. These different kinds of Collembola in one community may be a good indicator of the quality of the leaf litter community. The more active species can exploit small and scattered patches of litter, while the soil species colonize deeper and more continuous layers of litter. Together, they may be more effective at converting the fungi into biomass for animals higher on the food chain.

Only *Onychiurus ramosus* showed a strong difference in its distribution, being more abundant on NE plots. An important factor might be that the litter appears to be distributed more uniformly on NE stands (Grabner 1995). *Onychiurus ramosus* in particular is poorly adapted to cross open spaces, so it may be able to build larger populations where the litter cover is relatively continuous. *Folsomia stella*, another deep litter species, and *Lepidocyrtus* sp. 149, a surface litter species, were also more abundant on NE plots or stands. *Folsomia stella* may be more abundant on NE plots for the same reason *Onychiurus ramosus* is, but it is not clear why *Lepidocyrtus* should show a preference. If the different cutting treatments affect the distribution and depth of leaf litter significantly, there may be a shift in dominance among deep litter and surface litter species.

The Oribatid mite in the family Euphthiricaridae also preferred NE plots. It is a specialist on downed dead wood, and because of the higher plant productivity on NE stands, there is likely to be more woody material. However, it is not likely to respond rapidly to changes in availability of its resource. In general, the Oribatid mites are slow growing, slowly reproducing K-selected species (Coleman and Crossley 1996), so it might take years for an environmental disturbance to shift their population numbers significantly.

Because forest food webs may have many links, they may be buffered against changes in the prey populations. Therefore, dominant generalist predators may not be very good indicators of environmental change. Both the Mesostigmatid mite and the Pseudoscorpion probably feed on anything they can overpower, so their numbers may not fluctuate much even with significant changes in the arthropod community. The Pseudoscorpion, a miniature scorpion-shaped arachnid without the tail, was somewhat more abundant on NE plots. It may be able to respond more rapidly to changes in numbers or mass than the Mesostigmatid mite, or it may be specialized on species that do better on NE plots.

CONCLUSIONS

There were 22 orders of arthropods and 547 morpho-species in the leaf litter samples collected from MOFEP sites 1, 2, and 3. In terms of numbers, mass, and richness, the community was dominated by Diptera (adults and larvae, mostly Cecidomyidae), Coleoptera (adults and larvae), Araanea (mostly Gnaphosid spiders), and Acari (oribatid, mesostigmatid and prostigmatid mites). The numbers, mass, and richness of arthropod leaf litter communities were significantly higher on NE- than on SW-facing plots, while diversity (inverse Simpson's index) was significantly lower. There were also differences among the forest sites we sampled, but only strongly for diversity. Because some of the physical features of the plots varied with plot aspect (NE plots had less steep slopes and higher pH than SW plots) and with site (site 1 had a lower pH than sites 2 and 3), aspect and site effects may be confounded by slope and pH. When stand aspect was used instead of plot aspect, differences for numbers, mass, and richness became weaker or disappeared, which suggests that local (as in arthopod sampling plot) conditions may be more important in shaping leaf litter communities than general (as in stand) conditions. Of the 547 morpho-species identified, 10 contained 47 percent of the individuals found. Seven of these were Collembola, primitive, wingless insects specialized on fungi. These could be sorted into the active surface-dwelling species capable of traversing open spaces between patches of litter, and the less mobile soil/humus-dwelling species limited to deeper and more extensive litter patches. The other dominants included a mite specialist on woody material (Euphthiricaridae), and a mesostigmatid mite and a pseuodoscorpion (both predatory). Three of the Collembola, the Euphthiricarid mite, and the Pseudoscorpion were either somewhat or significantly more numerous on NE plots.

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Estimating Pre-treatment Variation in the Oak Leaf-chewing Insect Fauna of the Missouri Ozark Forest Ecosystem Project (MOFEP)

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Abstract.—We describe spatial and temporal variation in the insect herbivore communities associated with the MOFEP, prior to application of contrasting cutting regimes. No pre-treatment differences were found in total insect density on either black (*Quercus velutina*) or white oak (*Q. alba*) during 1993-1995. There was great seasonal variation in insect abundance on both host species as well as high variation across years for white oak. White oak on north- and east-facing slopes tended to have more insects than white oak on south- and west-facing slopes. Sites under the auspices of the Missouri Department of Conservation for a longer time had higher insect densities than more recently acquired sites.

The goal of the Missouri Forest Ecosystem Project (MOFEP) is to determine the effects of alternative forest management schemes on long-term forest productivity, genetic structure of plant populations, and biodiversity of the communities under management. Treatments (even-aged versus uneven-aged management, plus controls; see Brookshire *et al.* 1997 for explanation of the MOFEP treatments and design) were begun in 1996. During 1993-1995, sampling was carried out to quantify any differences that might exist among replicates, so that potential true effects produced by the treatments could be distinguished from conditions existing prior to treatment application.

One of the major components of these Ozark forested communities, in terms of their ecological, economic, and conservation role, are the insect herbivores that feed on oaks. The majority of leaf-feeding insects on Missouri oaks are larvae of Lepidoptera (moths and butterflies) (Marquis and Whelan 1994). As herbivores, they have potential growth impact on their hosts. Non-outbreak population levels cause enough damage to reduce growth of saplings (Marquis and Whelan 1994), while outbreak levels can have negative impacts on growth and survivorship of trees (Rexrode 1971, Coffelt *et al.* 1993) and can potentially influence ecosystem processes such as nutrient cycling (Parker and Patton 1975). The resultant economic impact could be substantial because timber harvesting and processing in Missouri generate $3 billion in economic activity annually (T. Robison, personal communication). Oaks are also important as food for wildlife (Brezner 1972, White 1995), but their economic contribution in this form has yet to be estimated.

From a conservation standpoint, Lepidoptera, and butterflies in particular, have come under increasing scrutiny as the abundance of many species declines (e.g., Thomas and Mallorie 1985, Hill 1995, Legge *et al.* 1996). Lepidoptera can be used as indicator species for changes in habitat quality because their populations are intimately tied to the abundance of their host plant, and host plant decimation is often synonomous with habitat destruction (e.g., Eberhardt and Thomas 1991, Sparrow *et al.* 1994). In Missouri, these insects represent a major component of the State's biodiversity and natural heritage: at least 300 species have been documented on oaks in the Eastern United States and 200 on white oak alone in Missouri (Tietz 1972, Covell 1984). Additionally, these insects are important because they serve as hosts for a number of parasitoids, both insects and nematodes. In so doing, they could serve to maintain a reservoir population of parasitoids that might be used to control invading exotic

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insect pests such as the European gypsy moth, *Lymantria dispar.*

The goal of this project was to describe variation in the abundance of the leaf-chewing insect fauna among replicate sites of the MOFEP project during the 3 years before harvesting treatments were applied. Two host plant species were chosen for study, black (*Quercus velutina*) and white (*Q. alba*) oaks. These two species dominate the canopy of most MOFEP upland stands. Limited resources prevented us from sampling more host species. We chose to include all leaf-chewing insect species, and not a subset of that fauna, because preliminary sampling in 1989-1992 suggested that species' abundances of leaf-chewing insects fluctuate unpredictably (RJM, unpublished data). Thus, a study that focused on only common species in one year would have no estimates of abundances of previously rare species that had become common. High diversity of the leaf-chewing guild (at least 200 species) prevented us from sampling other herbivore guilds associated with black and white oak. However, numbers of galling and sap-sucking insects in the MOFEP region, and throughout Missouri, appear to be low (Marquis and Whelan 1994).

Our overall objective here is to describe pre-treatment variation (years 1993-1995) in the abundance of the leaf-chewing insect herbivores associated with *Quercus alba* and *Q. velutina* at the MOFEP sites. In this paper, we first describe the initial sampling undertaken to establish the sample size chosen for the 3 years of pre-treatment sampling. Second, we analyze the pre-treatment data to determine whether sites assigned to different treatments actually demonstrated differences before treatments were applied. Third, we present analysis of the spatial variation in herbivore abundances irrespective of the original sampling design to understand possible sources of background heterogeneity among the study sites, including potential biases inherent in our sampling. Fourth, we discuss whether we are currently undersampling or oversampling in light of the patterns observed. To do so, we use power analysis to predict the minimum difference produced by treatments that we would be able to establish as statistically significant. Finally, we make recommendations about post-treatment sampling. We present results for total insect numbers sampled in the understory and analyze abundances of a subset of species to illustrate the variety of individual species patterns. Results of analyses of herbivore community composition and canopy sampling will be presented separately.

METHODS

General Census Methods

To determine insect abundance, leaves were searched both top and bottom, as were associated branches and the main stem of the tree. Chewing insects encountered were classified to morpho-species. Each census person was given a training period in identification prior to actual sampling, and had a list of descriptions for all morpho-species known to be encountered. At no time were leaves collected. All insects were left intact on the plant unless individuals were unknown. In that case, unknowns were taken back to the laboratory for rearing and photographing. Each unknown was given its own unique sample number and description, and this information was entered into a database. Photographs were taken, and the insect was observed through development until it could be verified as a previously-recognized species or classified as a species new to our inventory. Photos were used in the field to help with identification when necessary.

Preliminary Sampling to Establish Adequate Sample Size

Preliminary sampling was conducted in early September 1992 to determine the sample size necessary to adequately estimate the mean and variance in total numbers of insects per tree per stand and per site, and species composition per site. Ten trees per stand were sampled in site 6 for each of three north-facing slopes and three south-facing slopes for both black and white oak. The mean and variance in total numbers of insects per leaf area per tree were plotted for each stand and across stands for each tree species. The number of new species encountered with increasing number of stands sampled was plotted to determine how the number of insects species found in a site increased with increasing number of stands sampled. The total number of species per site was compared with species accumulation curves for each stand and each host plant. This preliminary sampling then served to determine sample size for all subsequent sampling in years 1993-1995, described below. For this analysis and all subsequent analyses, insect abundance was expressed on a leaf area basis. Average leaf

area per tree species was estimated based on a sample of 200 undamaged, fully expanded leaves per species, with a maximum of five leaves per tree.

1993-1995 Censuses

Overall MOFEP Design

The MOFEP design (see figure 2 in Brookshire *et al.* 1997) includes nine sites of approximately 400 ha each. Each of these sites has been assigned to either a control, even-aged, and uneven-aged treatment. Sites are blocked by geographic proximity and other general characteristics (Sheriff and He 1997).

Tree Attributes

Ground-level censusing (0.5 to 2.5 m) was conducted from a mixture of saplings and low-hanging branches of sub-canopy to canopy trees.

Leaf and Tree Sample Size

When available, we censused a minimum of 3,000 white oak leaves and 1,200 black oak leaves per stand distributed among five white and five black oak trees. More trees were added when necessary to complete the minimum leaf sample. Leaves were counted either in the May (1993 and 1994) or June census (1995).

Stand Sample Size

Sampling was stratified within sites by ecological land type (ELT; see Brookshire *et al.* 1997). From 1993 to 1995, we sampled three stands on south- and west-facing slopes (ELT 17) and three stands on north- and east-facing slopes (ELT 18) per site. The same trees and the same stands were censused each year and across years. Dead individuals were replaced with nearby neighbors to maintain a comparable sample size. Sampled trees were spread over approximately a 0.5- to 1.0-acre area per stand.

Stand Selection

Stands (six per site) were selected randomly from those available in control and uneven-aged sites. To maintain consistency in timing of cutting, stands sampled in even-aged sites were chosen randomly from those likely to be cut in the second round of cutting (year 2006).

Number of Samples

Due to changes in herbivore abundance and composition through the year (Marquis and Whelan 1994), trees were censused four times per year: April-May, late June, late July, and August-September. Each census required 2 weeks to complete. At each census, sites were always censused in the same order for each of the 3 years: 6, 5, 4, 3, 2, 1, 7, 8, 9.

Statistical Analysis

For data collected in years 1993-1995, repeated measures analysis of variance (ANOVA) (Littell *et al.* 1991, p. 130, 282, von Ende 1993) was first used to test for pre-treatment differences among sites as they were assigned to treatments, for block effects as designated in the original design (Brookshire *et al.* 1997), and for the relative importance of ELT, census, and year on insect density (number of insects per leaf area per tree). All but block, treated as a random effect, were considered to be fixed. ELT was considered to be nested within treatment in a split-block design. Separate analyses were run for white oak and black oak. Profile analyses (Littell *et al.* 1991, von Ende 1993) were run to determine during which censuses and years temporal effects were significant. These same analyses were conducted for the five most common herbivore species on white and black oak separately in the May censuses to illustrate individual species patterns.

In a separate repeated measures ANOVA, we tested for initial differences in sites irrespective of the original experimental design described in Brookshire *et al.* 1997. The goal was to determine the degree to which sites were equal replicates. In this analysis, ELT was included to allow statistical comparison of any observed site effect with that of ELT. ELT was considered to be crossed with site, and the effects of both ELT and site were considered to be fixed. An interaction term between ELT and site was included to determine if the effect of ELT was consistent across sites.

Results for both repeated measures models are presented as between subjects effects (effects of treatments across or among trees) and within subjects effects (how treatments interacted with time to influence values obtained for individual trees). Because black oak was not represented in all north- and east-facing slopes sampled,

Type IV SS were used to calculated F- and P-values for effects of ELT on abundances of insects on this tree species. In all other cases, Type III SS were used. A result was considered to be statisticaly significant at P = 0.05 unless otherwise specified.

Possible site effects might occur due to seasonal changes taking place within the course of a census. Because 2 weeks are required to complete an entire census, later censused stands and sites could have different insect numbers than stands and sites visited at the beginning of the spring census. Such seasonal changes occur most rapidly during the April-May census, when there is a change in insect species composition and numbers associated with the completion of leaf expansion (RJM and JL, unpublished data). Accordingly, the April-May censuses were timed by phenology rather than calendar date to take into account the fact that leafing and insect activity vary by years. For both oak species, we tested whether species diversity varied by site for the spring censuses of 1993-1995 using ANOVA on the Shannon-Weiner Diversity Index (Poole 1974).

Finally, we caculated a power analysis (Zar 1984) to determine the minimum detectable difference for each census in insect density given the observed variation. The mean square error for block by treatment term from the ANOVA for each separate census was used, with $\alpha = 0.05$ and power $(1-\beta) = 0.95$.

RESULTS

Preliminary Sampling

Estimates of the mean number of insects per tree per square meter of leaf area and standard deviation of that estimate appear to stabilize at approximately five to six trees at all six stands sampled for both white (fig. 1) and black oak (not shown). For this particular sample, differences in mean values between north- and south-facing slopes were not consistent for either white or black oak (unpublished data).

To determine the number of sampled stands necessary to characterize the variation in insects numbers at a site, the above estimates of the mean number of insects per tree for six trees at each of six stands were used to calculate a mean value per stand. Means and standard deviation values for site 6 appear to stabilize after three to four stands were sampled for

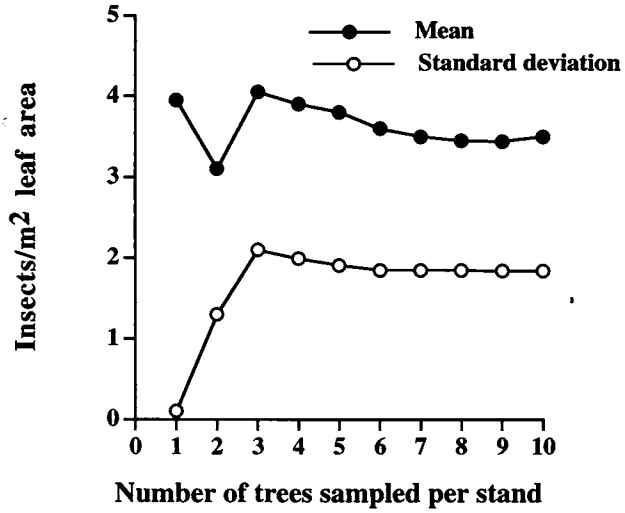


Figure 1.—*One example, chosen randomly from the six patterns available for white oak, showing the relationship between the estimate of the mean and standard deviation of the number of insects per square meter leaf area with increasing number of trees sampled in a stand. Data are from six stands in site 6 collected in September 1992.*

both white and black oak (fig. 2). Finally, number of new species encountered with increasing number of trees sampled per site appears to stabilize at about 30 to 35 trees for each host plant species (fig. 3).

Together, these results suggested that a sample of five trees per species per stand and six stands per site would be adequate to characterize the variation in insect numbers and species composition within a site. Because there was some evidence of differences among stands located on different slope positions, three stands were located on north- and east-facing slopes (ELT 18) and three were located on south- and west-facing slopes (ELT 17).

Sampling 1993-1995

There were no significant main or interaction effects involving treatment and block for number of insects per leaf area on either white or black oak (table 1). ELT had a significant impact (P = 0.001) on insect density on white oak and a significant interaction with year and census (both P = 0.001) (table 1). When differences were significant, there were more insects on trees on north- and east-facing slopes (ELT

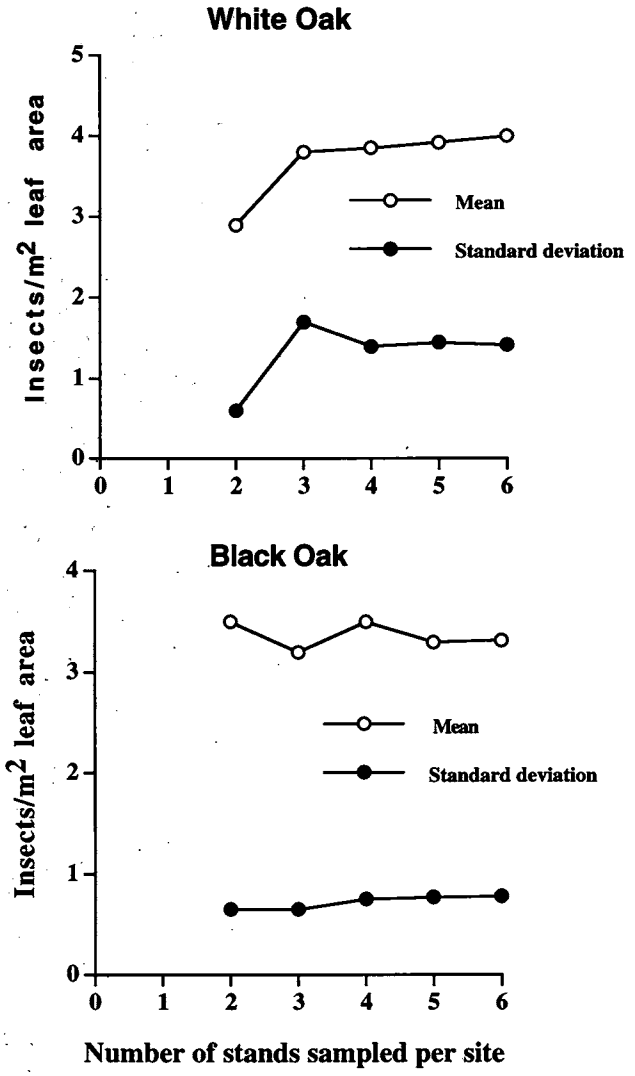


Figure 2.—*The relationship between the estimate of number of insects per tree per stand and its standard deviation and increasing number of stands sampled in site 6 (September 1992) for both white and black oak.*

18) than on trees on south- and west-facing slopes (ELT 17) (fig. 4). Stand as a main effect was a marginally significant predictor of insect abundance in white oak (P = 0.11) but not in black oak (P = 0.31). There was, however, a significant interaction between stand and census for both white and black oak P = 0.012 and 0.013, respectively), demonstrating a stand effect for some censuses in both species, and a significant year by stand interaction (P = 0.014) in black oak (table 1). There were significant interactions of block with census for white oak (P = 0.052) and year for black oak (P = 0.069).

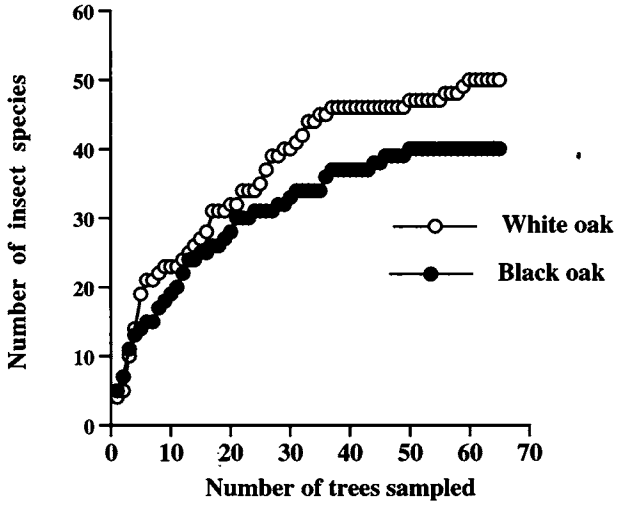


Figure 3.—*The relationship between number of trees sampled and number of species of leaf-chewing insects encountered in site 6 for both white and black oak.*

Profile analysis for white oak (table 2) showed that the effect of ELT increased from 1993 to 1994, and then again from 1994 to 1995, irrespective of season (i.e., the interaction effect between ELT and year was significant for both contrasts) (fig. 4). The effect of ELT on insects feeding on white oak was also greater later in the season across all years: its effect increased from June to July (significant ELT effect), and then again from July to August censuses, but not from May to June (table 2, fig. 4).

Insect densities, summed over all sites and all censuses, varied significantly across years (table 1), but more so for white than black oak (fig. 5). For white oak, total numbers of insects found on trees in 1994 and 1995 were twice that in 1993; for black oak, totals in 1995 were 15 percent and 22 percent less than in 1993 and 1994, respectively (fig. 5). Seasonal pattern also varied by year. Seasonal variation in white oak showed two patterns: either high abundance in the spring and fall (1993) or an increase in abundance in spring to fall (1994 and 1995) (fig. 6). In contrast, seasonal pattern of insect abundance on black oak was consistent across years; abundance was highest in the spring (and 50 to 100 percent greater than white oak spring abundances), lowest in the midsummer, then increased again in the fall (fig. 6).

Table 1.—*Repeated measures ANOVA testing possible pre-treatment effects on number of insects per leaf area per tree. F-approximations are based on the Pillai's Trace test statistic. MS_{den} is the denominator used in calculating the F-statistic for the between subjects effects. Ndf and Ddf are numbers of degrees of freedom in the numerator and denominator, respectively, for calculating the F-statistic for within subjects effects. Stand is nested within treatment, block, and ELT.*

Between subjects

		Quercus alba				*Quercus velutina*			
Source	**MS_{den}**	**df**	**MS**	**F**	**P**	**df**	**MS**	**F**	**P**
Treat (T)	MS_{TxB}	2	49.92	0.29	0.762	2	235.8	1.18	0.396
Block (B)	MS_{TxB}	2	453.4	2.68	0.185	2	552.4	2.76	0.176
T X B (whole plot error)		4	169.4			4	399.7		
ELT (E)	MS_{Stand}	1	2,081	14.42	0.001	1	4.46	0.06	0.814
T X E	MS_{Stand}	2	1.67	0.01	0.989	2	61.1	0.77	0.471
Stand	MS_{E}	42	144.4	1.30	0.110	34	79.4	1.11	0.313
Error (subplot)		298	110.9			267			

Within subject

	Quercus alba			*Quercus velutina*		
Source	**Ndf/Ddf**	**F**	**P**	**Ndf/Ddf**	**F**	**P**
Year(Y)	2/297	133.7	0.001	2/266	6.62	0.002
Census (C)	3/296	68.7	0.001	3/265	157.1	0.001
Y X C	6/293	86.1	0.001	6/262	37.17	0.001
Y X T	4/8	0.63	0.656	4/8	1.82	0.190
Y X B	4/8	1.29	0.350	4/58	3.34	0.069
Y X E	2/41	9.14	0.001	2/33	0.145	0.250
Y X Stand	84/596	0.88	0.757	68/534	1.45	0.014
Y X T X E	4/84	1.62	0.178	4/68	0.80	0.527
C X T	6/6	0.64	0.701	6/6	0.39	0.867
C X B	6/6	4.20	0.052	6/6	1.51	0.315
C X E	3/40	8.03	0.001	3/32	1.40	0.262
C X Stand	126/894	1.34	0.012	102/801	1.36	0.013
C X T X E	6/82	0.66	0.677	6/66	1.28	0.279
Y X C X Stand	252/1788	1.16	0.057	204/1602	1.17	0.064
Y X C X T[1]	—	0.51	0.889	—	0.61	0.811
Y X C X B[1]	—	0.85	0.599	—	1.98	0.074
Y X C X E	6/37	0.63	0.703	6/29	0.75	0.613
Y X C X T X E	12/76	0.66	0.785	12/60	0.62	0.817

[1]Insufficient degrees of freedom to calculate values in MANOVA; univariate results are reported.

Analysis of abundance of the five most common species of the May census showed that changes in individual species abundances were not necessarily consistent with those of the entire community (table 3). Like the entire community, all species varied significantly across years (P = 0.001). However, some patterns at the species level contradicted those at the community level. For white oak, for example, there was a "pre-treatment" and ELT effect on abundance of one species, two species varied significantly by block, and three species showed significant variation in abundance by stand. For black oak, one species varied significantly by ELT, two showed significant variation by block, and four of five species varied significantly by stand.

The contribution of geographic scale for insect density differed between white and black oak (table 4). As in the previous analysis (table 1), ELT had a significant effect on overall insect abundance on white oak but not on black oak. However, this second analysis revealed that there was a marginally significant ELT by census interaction (P = 0.08) and a significant census by site by ELT interaction for black oak (P = 0.024). Both suggest a significant ELT effect in black oak, but the effect appears in

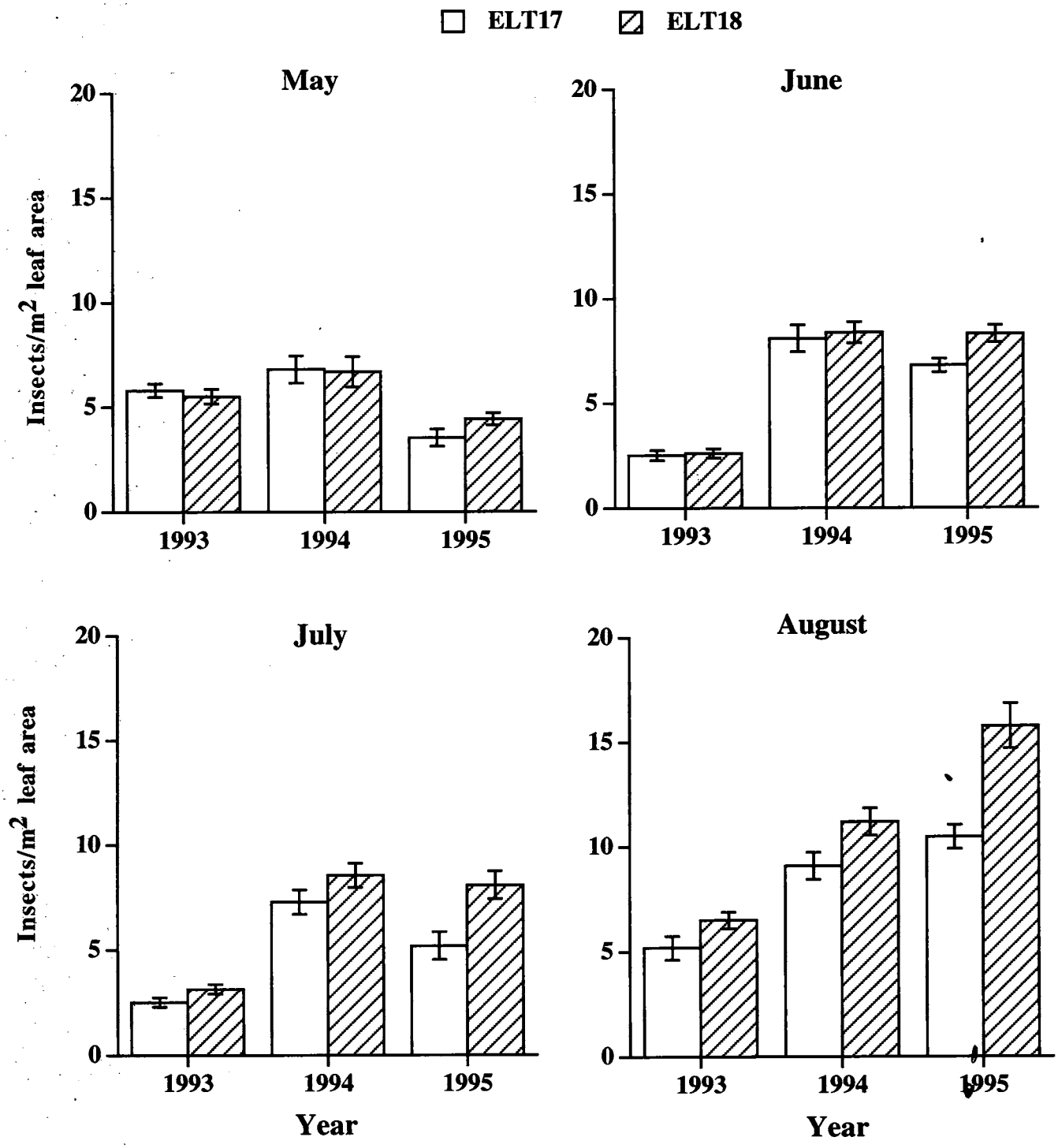


Figure 4.—*Effect of ELT, year, and census on the mean (± SE) number of insects per leaf area on white oak.*

Table 2.—*Profile analysis for* Quercus alba *for the effect of either year or census ("Time") and ELT X Time interaction ("ELT X Time") over the time periods indicated on insect density per tree.*

Source	F	P
Contrast variable: Year 1 - Year 2		
Time	171.6	0.001
ELT X Time	18.4	0.001
Contrast variable: Year 2 - Year 3		
Time	2.4	0.123
ELT X Time	5.4	0.026
Contrast variable: May -June		
Time	14.9	0.001
ELT X Time	1.0	0.323
Contrast variable: June - July		
Time	5.0	0.026
ELT X Time	3.4	0.073
Contrast variable: July - August		
Time	180.5	0.001
ELT X Time	4.5	0.040

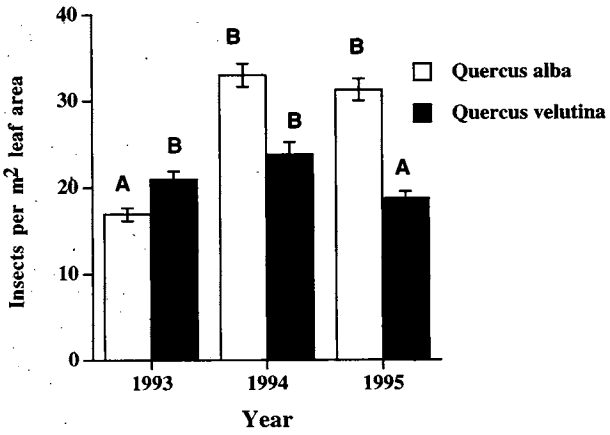


Figure 5.—*Annual variation in the mean (± SE) number of insects per leaf area on white and black oak.*

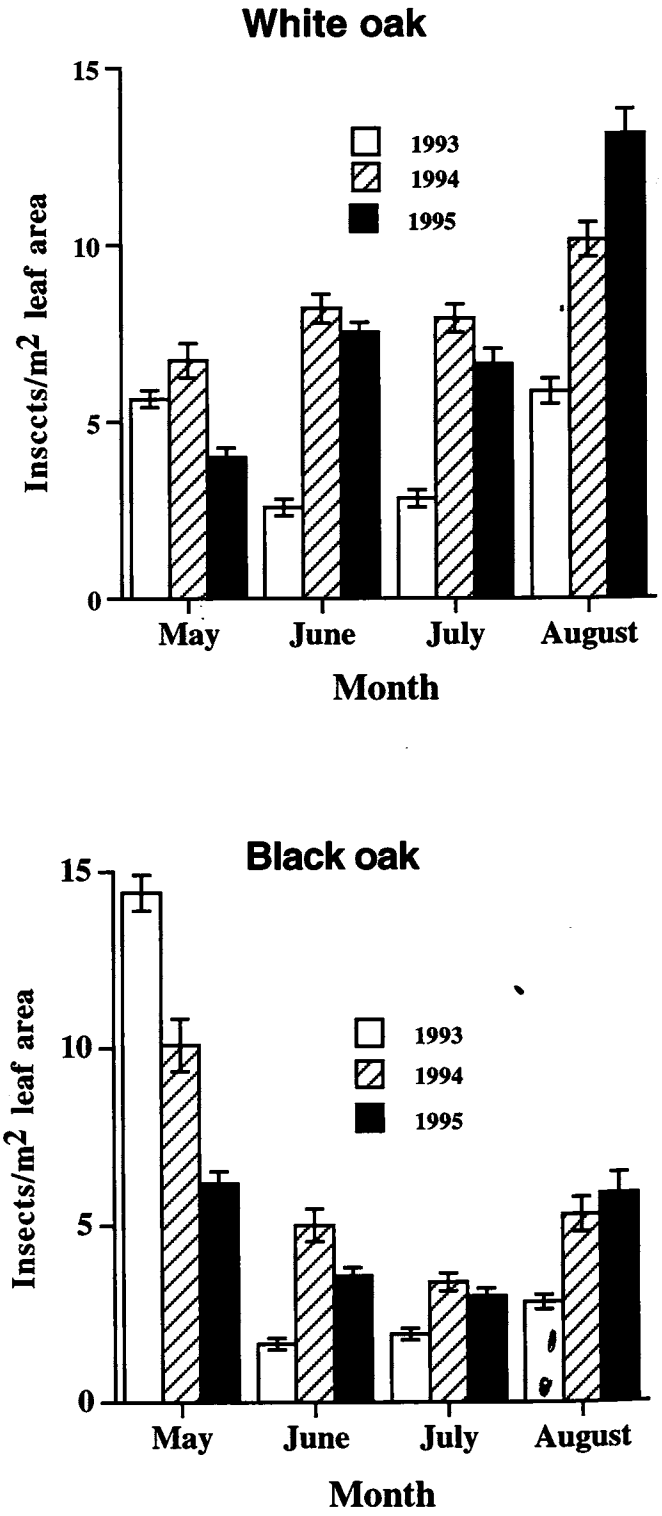


Figure 6.—*Seasonal variation by year in the mean (± SE) number of insects per leaf area in white oak and black oak.*

Table 3.—*Repeated measures ANOVA testing possible pre-treatment effects on numbers of the five most common insect species per leaf area per tree. Analysis is the same as reported in table 1. N.S. = non-significant at P>0.10.*

	Quercus alba				
Factor	***Lithophane antennata***	***Chionodes* sp.**	***Telphusa latifasciella***	***Spargonothis pettitana***	***Dichomeris ligulella***
ELT (E)	N.S.	N.S.	N.S.	N.S.	0.005
Treatment (T)	N.S.	N.S.	N.S.	N.S.	0.017
Block (B)	0.080	N.S.	N.S.	N.S.	0.019
Stand (S)	N.S.	0.061	0.023	N.S.	0.003
T X E	N.S.	N.S.	N.S.	N.S.	N.S.
Year (Y)	0.001	0.001	0.001	0.001	0.001
Y X E	N.S.	N.S.	N.S.	N.S.	0.020
Y X T	N.S.	N.S.	N.S.	N.S.	N.S.
Y X B	N.S.	N.S.	N.S.	N.S.	0.003
Y X S	0.003	0.006	N.S.	N.S.	N.S.
Y X T X E	N.S.	N.S.	0.031	N.S.	N.S.

	Quercus velutina				
Factor	***Chionodes* sp.**	***Telphusa latifasciella***	**unidentified Tortricidae**	***Spargonothis pettitana***	***Dichomeris ligulella***
ELT (E)	0.068	N.S.	N.S.	N.S.	N.S.
Treatment (T)	N.S.	N.S.	N.S.	N.S.	N.S.
Block (B)	N.S.	N.S.	0.078	N.S.	0.054
Stand (S)	0.035	0.006	0.016	N.S.	0.013
T X E	N.S.	N.S.	N.S.	N.S.	N.S.
Year (Y)	0.001	0.001	0.001	0.001	0.001
Y X E	N.S.	N.S.	N.S.	N.S.	N.S.
Y X T	N.S.	N.S.	N.S.	N.S.	N.S.
Y X B	N.S.	0.040	N.S.	N.S.	0.066
Y X S	0.002	0.004	N.S.	N.S.	0.009
Y X T X E	N.S.	N.S.	N.S.	N.S.	N.S.

only some sites for the August-September census. As in white oak, when differences occurred, there were more insects on black oak trees of north- and east-facing slopes (ELT 18) than on trees of south- and west-facing slopes (ELT 17) (25 percent more averaged across all sites in August censuses; not shown).

Site had a significant main effect for black oak (P = 0.005) and a significant site by census interaction for white oak P = 0.002). The site effect in black oak is due in part to consistently higher and lower insect numbers in site 6 and site 2, respectively (fig. 7). The other contributing factor to the site effect is the great range in insect numbers across sites for black oak during the May censuses of 1993 and 1995 (fig. 7, significant year by census by site interaction, patterns by year not shown). The decline in values corresponds to the order in which sites were sampled (sites are listed in sampling order). The significant site by census interaction in white oak is due to a similar pattern: a range in site values occurs only in May, but again corresponds to the order in which sites were sampled (fig. 8). May is when the insect species composition changes most rapidly, and total insect numbers decline over a very short time period as leaves become fully expanded (RJM and JL, unpublished data). However, diversity (Shannon-Weiner index) did not decline as sites were sampled in May for either black or white oak (P > 0.15 for both species and all years). Site differences in insect abundance in May on both black and white oak correspond to the time of acquisition of the sites by the MDC (fig. 9), with those sites under control of the MDC longer having greater insect

Table 4.—*Repeated measures ANOVA for the effect of geographic scale on number of insects per leaf area per tree. F-approximations are based on the Pillai's Trace test statistic. Ndf and Ddf are number of degrees of freedom in the numerator and denominator, respectively, for calculating the F-statistic. Stand is nested within site and ELT.*

Between subjects

	Quercus alba			*Quercus velutina*		
Source	**df**	**F**	**P**	**df**	**F**	**P**
Site (S)	8	1.42	0.221	8	3.70	0.005
ELT (E)	1	14.8	0.001	1	0.08	0.779
S X E	8	0.73	0.666	8	0.88	0.547
Stand	36	1.26	0.151	28	1.10	0.333
Error	298			267		

Within subject

	Quercus alba			*Quercus velutina*		
Source	**Ndf/Ddf**	**F**	**P**	**Ndf/Ddf**	**F**	**P**
Year(Y)	2/297	133.7	0.001	2/266	8.34	0.001
Census(C)	3/296	68.7	0.001	3/265	172.7	0.001
Y X C	6/293	86.1	0.001	6/262	40.22	0.001
Y X S	16/72	1.82	0.045	16/56	2.27	0.012
Y X E	2/35	8.97	0.001	2/27	1.91	0.168
Y X Stand	72/596	0.85	0.796	56/534	1.52	0.012
Y X S X E	16/72	1.17	0.310	16/56	0.80	0.683
C X S	24/108	2.26	0.002	24/84	0.96	0.532
C X E	3/34	8.26	0.001	3/26	2.51	0.081
C X Stand	108/894	1.31	0.023	84/801	1.10	0.253
C X S X E	24/108	0.72	0.818	24/84	1.82	0.024
Y X C X S	48/216	1.53	0.022	48/168	1.58	0.018
Y X C X E	6/31	0.66	0.680	6/23	1.02	0.436
Y X C X Stand	216/1708	1.16	0.060	168/1602	1.14	0.110
Y X C X S X E	48/216	0.64	0.960	48/168	0.86	0.720

numbers (table 5) (r = -0.78 and -0.85, for P = 0.012 and 0.004 for white and black oak, respectively).

Power Analysis

Based on our present estimates of variation, we have enough statistical power to conclude that a twofold to sixfold increase in total insect density would be significant at P = 0.05 (table 6). Power varies by census and year: in some cases a relatively small change (5.7 insects per m^2) would be significant, while in others the differences would have to be much larger (30-50 insects per m^2) to state that a treatment effect had occurred.

DISCUSSION

We found no evidence of differences by treatment for either white or black oak in the total number of insects prior to application of the actual treatments. The lack of treatment effect suggests that there are no pre-treatment differences among sites that later could be misinterpreted as treatment effects (although one of the common species, *Dichomeris ligulella*, shows such a pre-treatment difference on white oak, but not on black oak).

We found no significant main effect of block as proscribed in the original design. However, there were significant interactions of block with census (white oak) and year (black oak). The fact that block does account for some of the variation is support for keeping the block effect (as originally designed) in the model.

Spatial variation in insect numbers existed unrelated to the original blocking. Trees varied in the number of insects depending on the stand, but the stand effect was variable both by year (black oak) and by census (white and black oak). Individual species were more likely to

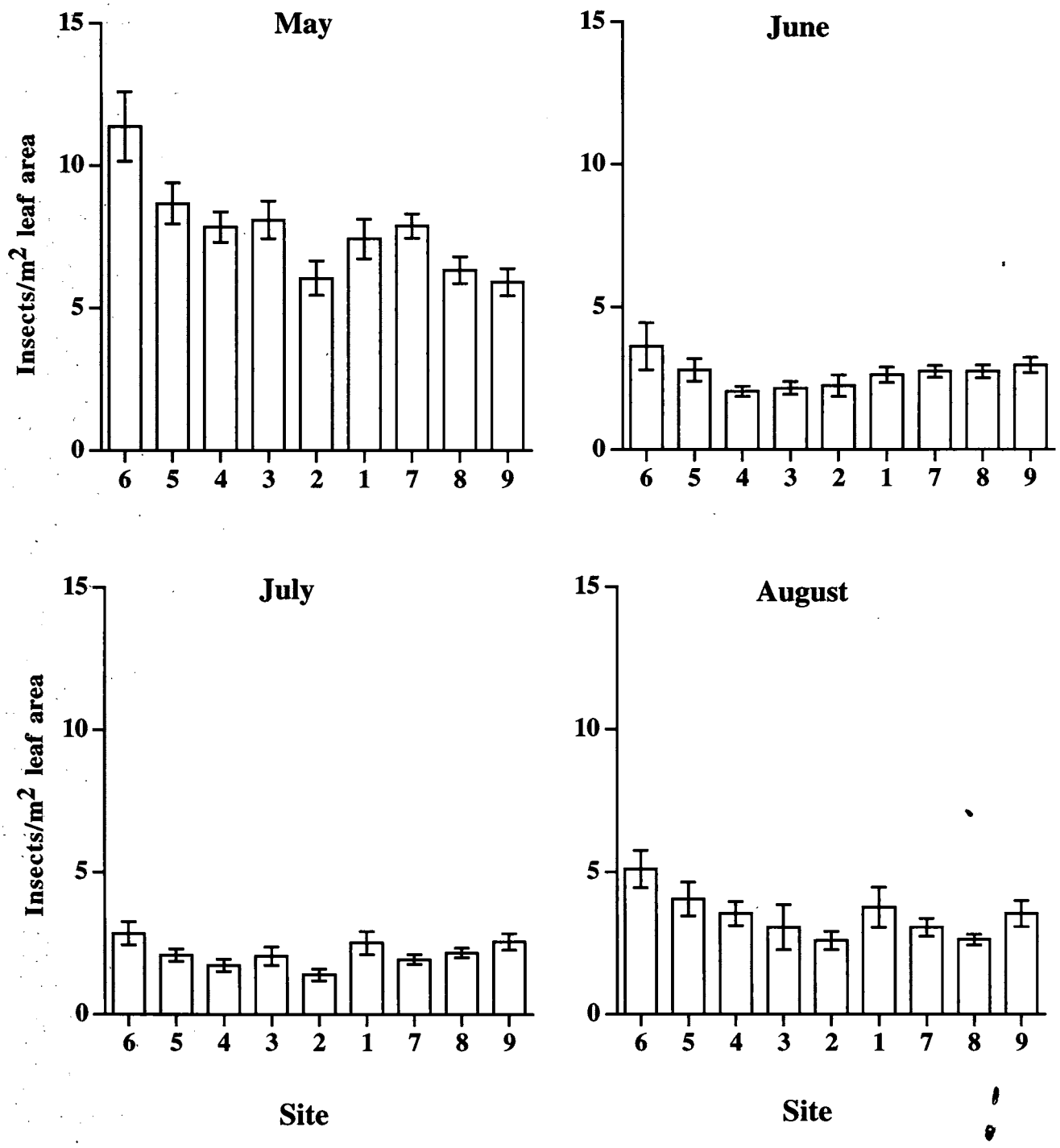


Figure 7.—*Effect of site on estimates in the mean (± SE) number of insects per leaf area for each census across years for black oak. Sites are shown in the order they were sampled.*

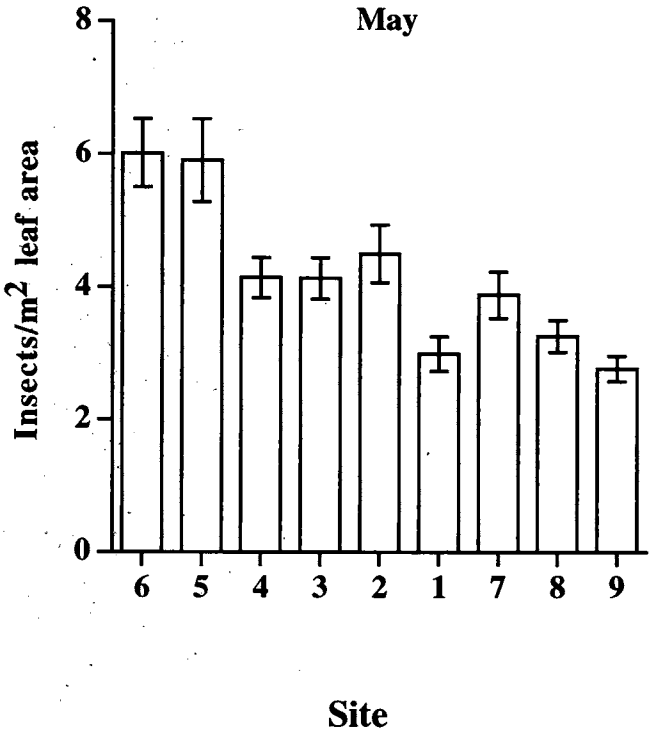
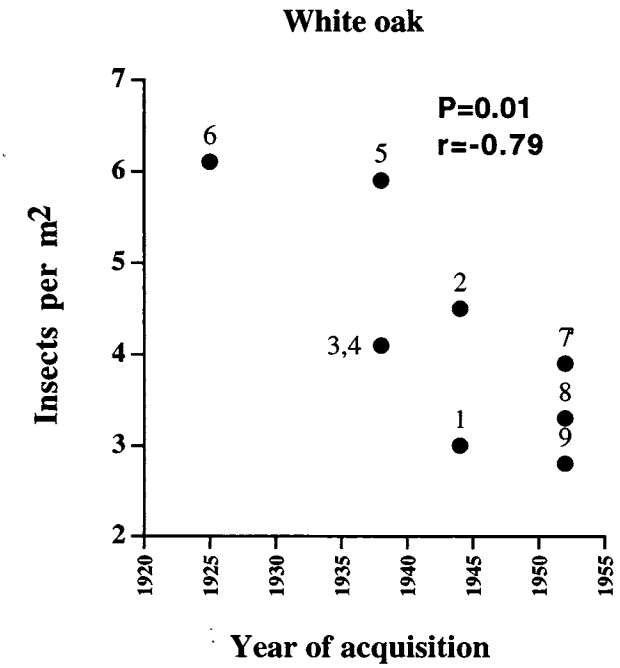


Figure 8.—*Effect of site on estimates in the mean (± SE) number of insects per leaf area for May censuses on white oak. Sites are shown in the order they were sampled.*

vary by stand than did the community as a whole. Stands differed in the number of insects depending on their slope position (ELT), more so for white than black oak. The ELT effect was consistent across sites (no significant ELT by site interaction), and thus appeared to be independent of site, despite the fact that sites vary in soil type (MOFEP unpublished data). Finally, both white oak (for 3 years) and black oak trees (for 2 years) varied in the total numbers of insects in the May census, depending on the site in which they were located. The fact that diversity did not change across sites in the spring censuses suggests that the significant site effect for both oak species is not a sampling artifact due to loss of species (and therefore insect numbers) as the census proceeded. Why the site effect is greatest for the spring census is not clear. Perhaps microsite differences in climate are greatest early in the spring, leading to differences in phenology. For both oak species, there is a strong relation between numbers of insects per site and the time those sites came under the auspices (and protection



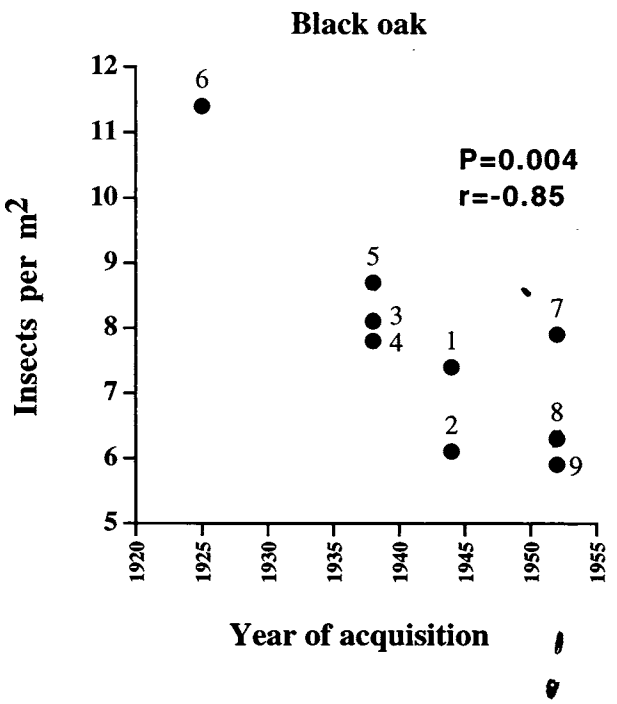


Figure 9.— *The relationship between year of acquisition of a site under the auspices of the Missouri Department of Conservation and the mean density of insects in May censuses (calculated over the years 1993-1995) for both white and black oak. Each point is labeled with its corresponding site number.*

Table 5.—*Relation between year of incorporation of site and the mean number of insects per square meter leaf area (± SE) for white and black oak averaged over the May censuses of 1993-1995.*

Year of acquisition	Site	*Quercus alba*	*Quercus velutina*
1925	6	6.1 ± 0.5	11.4 ± 1.2
1938	5	5.9 ± 0.6	8.7 ± 0.7
1938	4	4.1 ± 0.3	7.8 ± 0.5
1938	3	4.1 ± 0.3	8.1 ± 0.7
1944	2	4.5 ± 0.4	6.1 ± 0.6
1944	1	3.0 ± 0.3	7.4 ± 0.7
1952	7	3.9 ± 0.4	7.9 ± 0.8
1952	9	2.8 ± 0.2	5.9 ± 0.5
1952	8	3.3 ± 0.2	6.3 ± 0.5

from grazing and fire) of the Missouri Department of Conservation. The reason why numbers of insects on black oak are unusually low in site 2 and unusually high in site 6 across censuses and years is unclear (fig. 7). At this time, we also do not know what factors cause the observed stand effects.

Based on our results, we make the following suggestions about future sampling:

1. Present sample size (number of trees per stand or number of stands per site) should be maintained. We now have sufficient statistical power to distinguish "relatively small" treatment effects, but reduction of sample size would jeopardize the power that is available. Increased sampling (more stands per site) should be considered.

2. Because black and white oaks dominate the canopy, we suggest that sampling should continue on both species. Moreover, spatial and temporal variation is different for the two host plants, suggesting that results from one species cannot be extrapolated necessarily to other oak species.

3. The significant effect of ELT suggests that stratified sampling by ELT should continue.

4. Relatively high numbers of insects can occur at any time of the year. In addition, species turnover among the four censuses is relatively high. Taken together, we recommend continued sampling for four times a year.

Table 6.—*Minimum detectable difference (Zar 1984) for each census in the number of chewing insects per square meter leaf area given the observed variation (mean square error for block by treatment term in the ANOVA) for $\alpha = 0.05$ and power $(1-\beta) = 0.95$. Percent increase in actually observed values that the difference would represent is given in parentheses.*

Census	*Quercus alba*		*Quercus velutina*	
May 1993	13.9	(246)	45.6	(315)
June 1993	8.7	(337)	5.7	(345)
July 1993	7.8	(302)	7.3	(380)
August 1993	5.7	(97)	14.2	(500)
May 1994	37.5	(556)	49.0	(205)
June 1994	8.5	(103)	26.8	(534)
July 1994	30.5	(386)	7.2	(211)
August 1994	28.2	(278)	18.4	(347)
May 1995	12.5	(313)	11.8	(190)
June 1995	10.3	(137)	7.6	(212)
July 1995	31.3	(471)	9.1	(303)
August 1995	41.3	(314)	21.9	(369)

5. Because of the year-to-year variation in total insect numbers and abundance of individual species, we recommend conducting post-treatment sampling every year.

6. Individual insect species exhibit idiosyncratic patterns compared to overall community patterns. Such individual species differences suggest that sampling by insect species should continue, because effects of forestry management on overall insect abundance will entail individual species' responses to the treatments. In addition, a number of our species are known to go through population irruptions (e.g., *Symmerista albifrons, Heterocampa gutivitta, Diapheromera femorata, Lochmaeus manteo, Sabine stimulea, Psilocorsis quercicella, Melanoplus* sp.). Ignoring changes in these particular species for which previous information on their population biology is available might seriously reduce our ability to understand treatment effects.

7. Estimates of amount of leaf area consumption (based on laboratory feeding trials) should be made to translate insect abundance into damage estimates. Given that it is important to know the relative economic impacts of alternative forest managements regimes, estimates of leaf damage will be of more use in estimating treatment effects on tree growth than will estimates of insect numbers. Consumption rates then can be

used to translate estimates of insects numbers from past censuses into leaf damage.

Finally, we make a plea for future integration of sampling and analysis among projects under the MOFEP auspices. As an example of the understanding that might arise from such an integration, we present a path diagram (see Li 1975 and Schemske and Horvitz 1988) in figure 10, which relates herbivorous insect abundance to tree growth, and moderating factors that may directly and indirectly modify this interaction. It is highly likely that many studied taxa and processes will have their own independent, direct effect on tree growth. Thus, in figure 10, insect populations, soil characteristics, tree pathogens, and tree genetic diversity all are shown to have a direct effect on tree growth. However, the impact of insect herbivores on tree growth can be understood thoroughly only by considering the additional indirect effects of the factors listed above (including bird populations) on insect populations. These indirect effects may be as important in determining the relationship among variables as the direct effects. Knowing these indirect effects will require cooperative planning and coordinated sampling for estimation of the path coefficients. Path diagrams like this one could be drawn for each studied taxon and process. In turn, we will want to estimate the coefficients for these path diagrams under each of the treatments to understand how the treatments affect the underlying relationships. Our biggest challenge will be to integrate our efforts so that we can understand the underlying processes that might lead to treatment effects.

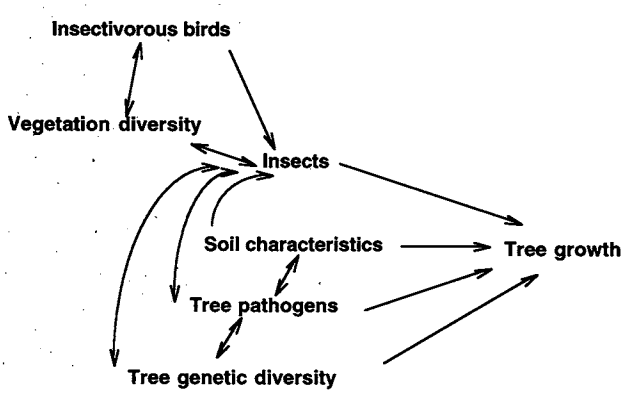


Figure 10.—*Path diagram linking the factors likely to both directly and indirectly affect the impact of herbivorous insects on tree growth in MOFEP.*

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Simulated Long-term Effects of the MOFEP Cutting Treatments

David R. Larsen[1]

Abstract.—Changes in average basal area and volume per acre were simulated for a 35-year period using the treatments designated for sites 4, 5, and 6 of the Missouri Ozark Forest Ecosystem Project. A traditional growth and yield model (Central States TWIGS variant of the Forest Vegetation Simulator) was used with Landscape Management System Software to simulate and display changes over time. Both the even-aged and uneven-aged treatments exhibited decreasing average basal area per acre and increasing average standing volume per acre over the 35-year period. The no-harvest treatment exhibited both increasing average basal area and increasing average standing volume per acre. The even-aged treatment produced the greatest average yield per acre, the uneven-aged treatment produced an intermediate average yield per acre, and the no harvest treatment produced the least average yield per acre. Tools used to visualize the model output are illustrated.

The Missouri Ozark Forest Ecosystem Project (MOFEP) was designed to investigate relations between common forest management practices and other components of the forest ecosystem (see Brookshire *et al.* 1997). Forest response to silvicultural treatment at Missouri Ozark Forest Ecosystem Project can be predicted in many ways. In this paper I used a traditional growth model to simulate growth response of MOFEP sites to uneven-aged, even-aged, and no-harvest treatments. I graphically displayed simulation output using recently developed stand and landscape visualization software, and I compared the outputs to illustrate differences in mean response of the MOFEP sites. This methodology has general applicability for simulating forest change under a wide variety of scenarios and is complimentary with other landscape scale disturbance models being applied in the Ozarks (e.g., Shifley *et al.* 1997).

The software used for the projections presented in this paper are bundled in the Landscape Management System (LMS)[2] (McCarter *et al.* 1996), a generalized software system for the display and manipulation of spatial data on a landscape scale. This software provides an interface to the Forest Vegetation Simulator (FVS) Central States variant (Bush 1995), and the Stand Visualization System (SVS) (McGoughy and McCarter 1995) and Landscape viewer (UVIEW) (McGoughy 1996). These tools were used to simulate MOFEP stand development for a 35-year period and visualize stand and landscape structure.

LANDSCAPE MANAGEMENT SYSTEM

Landscape Management System (LMS) is a computer program which integrates landscape-level spatial information, stand-level inventory data, and distance-independent individual-tree growth models to project changes through time. A long-standing problem with software developed for specific tasks is the difficulty of interfacing one program's output to another program's input. LMS is a flexible, extensible system for connecting growth models with analysis, and visualization tools. LMS follows the philosophy that many good tools exist, but they are difficult to use together. The Landscape Management System provides a collection of translation tools that allow the movement of data from one program to another and provides an interface through a Microsoft Windows® environment.

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[2] This software was developed by Dr. Chadwick D. Oliver, Jim B. McCarter and the silviculture group at the University of Washington.

The configuration of LMS used in this analysis included the LMS 1.5, Central States variant of the Forest Vegetation Simulator (FVS), Stand Visualization System (SVS), and the UVIEW Landscape visualization system. Additionally, links and macros are provided to process model output with EXCEL® spreadsheet and ACCESS® database system, which are part of the Microsoft Office® package. The three major component programs (FVS, SVS, and UVIEW) used in this analysis are discussed below.

FOREST VEGETATION SIMULATOR

The Forest Vegetation Simulator (FVS) framework is now the dominant forest modeling tool used by the Forest Service. It started as the Prognosis stand growth model developed by the Forest Service Intermountain Forest Experiment Station (Wykoff *et al.* 1982). This model was built as a distance-independent individual-tree growth model for Idaho, western Montana, eastern Washington, and eastern Oregon. The software developed for the model is of late 1970's vintage, retaining the concept of card image files and specific column input. Despite the age of the Prognosis program, it is very flexible and allows local calibration, and complicated management regimes, and it provides a facility to submit large batch runs. Because of these features and the flexibility of the distance-independent individual tree growth model, the Forest Service began making variants of the model by modifying the internal equations for other geographic regions. The user interface has also been expanded and improved.

There are now 22 variants of the model, which span geographically from Alaska to California and east to the Rocky Mountains. Recently, the equations developed for the TWIGS (Miner *et al.* 1988) growth model were incorporated into the FVS framework, extending the FVS variant coverage east to include the Lake States, Central States, and the Northeast USA. The specific equations used in each variant are described in documents available with the software (Bush 1995).

STAND VISUALIZATION SYSTEM

The Stand Visualization System (SVS) is a program developed by the Cooperative for Forest Systems Engineering, a group that includes both Forest Service and university scientists working on a number of forest systems engineering problems. SVS is a DOS program that reads a flat ASCII file containing tree records and draws these trees on a representative acre (McGoughy and McCarter 1995). Trees can be displayed in three basic configurations: map, profile, and three-dimensional views. Additionally, each view can be drawn in wire frame, solid, and realistic tree images. The program also allows viewing the stand structure with two-dimensional graphs that illustrate diameter, height, crown-ratio, and species classes.

SVS contains a "tree designer" that allows the program to be used in regions other than the one for which the program was originally designed. A complete set of tree images was designed for Missouri species in the FVS Central States TWIGS variant.

UVIEW

UVIEW is a forest landscape visualization tool also developed by the Cooperative for Forest Systems Engineering. This program uses a digital elevation model (DEM), a stand map, and the stand inventory to produce a three-dimensional image of the management area landscape (McGoughy 1996). As forest conditions change, trees of the appropriate size are drawn within each stand boundary but at a lower resolution than the SVS viewer. The user can move the viewing position or the point of focus within the image as desired. This tool is effective for evaluating the aesthetic aspects of a particular forest management treatment.

METHODS

Software Data Structure

The software used for analysis was built on the premise that foresters are managing a collection or portfolio of stands on a landscape. A variety of data are needed to describe the management units.

- Stand data including stand identifiers, site index, age, ecological land type, aspect, slope percentage, elevation.
- A stand inventory made up of individual tree records describing species, diameter, height, crown ratio, and the number of trees per acre each sample tree represents.
- A digital elevation model (DEM), which is a standard method of describing the surface of a particular part of the Earth through a grid of elevation values.

- A stand map, which allows the connection of specific forest characteristics to specific locations on the landscape.

MOFEP Data

During the initial phase of MOFEP, stands were laid out with methods typically used by Missouri Department of Conservation foresters based on slope, aspect, and operability by logging equipment. MOFEP stands were approximately 10 acres in size resulting in between 70 and 73 stands per site. Plot-level data were used to describe stand conditions within each MOFEP site. Plots falling on or adjacent to stand boundaries were rejected. For stands that did not include an inventory plot, a plot from a similar stand was chosen to represent initial stand conditions.

Data from the 1992 inventory were used to define initial stand conditions for all trees ≥ 4.5 in. d.b.h. Variables included species, diameter at breast height, and expansion factor (trees per acre represented by the sample tree). Tree height and crown ratio, measured on a subset of trees, were used where available and estimated from crown ratio equations for the remaining trees.

Analysis

To initialize the analysis, the 1992 MOFEP stand conditions were entered into the LMS program. For this analysis, three sites were chosen to illustrate the treatment classes found in the MOFEP study: site 4 (an uneven-aged management unit), site 5 (an even-aged management unit), and site 6 (a no-harvest unit) (see figs. 1 and 2 in Brookshire *et al.* 1997). The FVS growth model predicts in 5-year time steps, and treatments cannot be conveniently implemented midcycle within the model. Consequently the treatments implemented in the field during the summer of 1996 were applied by the model in year 1997 of the simulation. The first simulated treatments were applied to individual stands as specified in the cutting information provided at the 1995 MOFEP investigators meeting. Distance-independent individual tree growth models do not allow clustered stand treatments, so the uneven-aged management was simulated as 70 percent retention removed proportionally (equal thinning in all diameter classes), with 60 trees per acre (TPA) regeneration. Even-aged management was implemented as either harvest with 300 TPA regeneration or thinning from below to 100 TPA without regeneration.

All stands in the three sites were grown to the year 2027 (35 years). In years 2007 and 2017, stands were treated in a manner similar to the 1997 treatment subject to the following constraints: previously untreated stands are treated first, riparian exclusion stands are not treated, and harvests in the even-aged management unit are dispersed as much as possible. Changes in stands for each site was predicted and the projected basal area and volume were summarized by species over time. Additionally, yield (cut volume plus standing volume) was calculated for each compartment.

RESULTS

A series of computer-generated figures are used to illustrate the possible outputs from the LMS program. Figure 1 illustrates a three-dimensional view of site 4, stand 14 in year 2027. Figure 2 shows the profile of the same stand, and figure 3 illustrates the two-dimensional graphical abilities of the SVS program. Figure 4 illustrates output from the UVIEW program, a landscape view of site 4 in year 2027.

The two treated sites exhibited similar basal area per acre and board foot volume profiles over time. Both treatments slightly reduced residual basal area and increased standing volume over time (figs. 5 and 6).

In the uneven-aged treatment site (4), basal area by species tended to remain relatively constant while faster growing species such as black oak (*Quercus, velutina* Lam.), scarlet oak (*Quercus coccinea* Muenchh.), shortleaf pine (*Pinus echantia* Mill.), and white oak (*Quercus alba* L.) increased in volume (fig. 5A). In this site, the uneven-aged treatment favored scarlet oak in volume increment.

In the even-aged treatment site (5), basal area and volume by species remained relatively constant. White oak volume was favored slightly by this treatment method (figs. 5B and 6B).

The no-harvest treatment site (6) initially had the greatest basal area and volume per acre (figs. 5C and 6C). Both values continued to

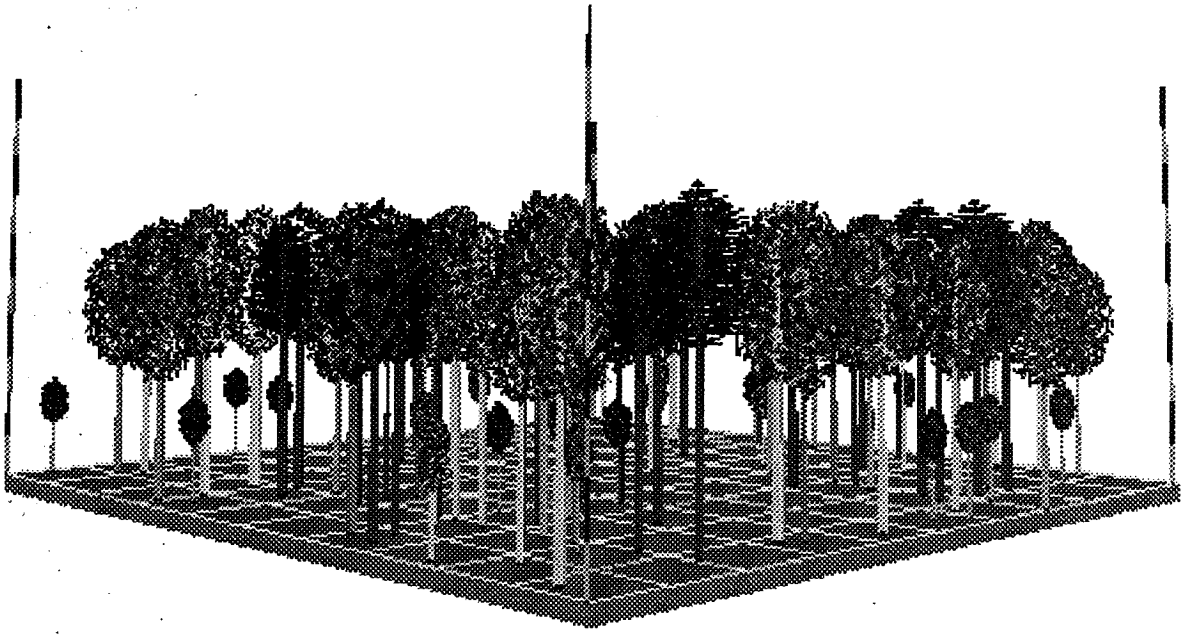


Figure 1.—*Example of output from the Stand Visualization System (SVS) program showing a three-dimensional view of site 4, stand 14, in 2027.*

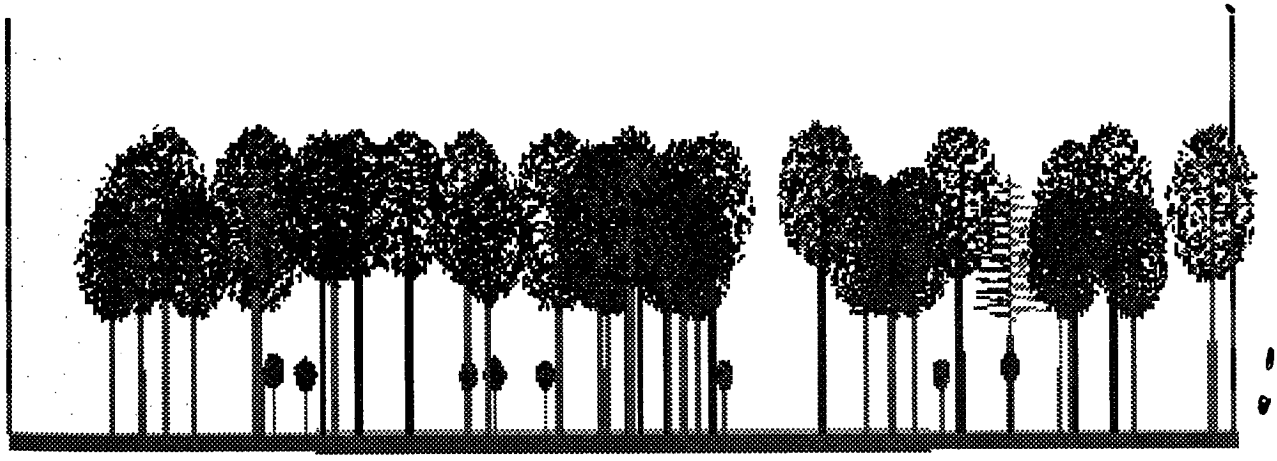


Figure 2.—*Example of profile output for site 4, stand 14, in year 2027 from the SVS program.*

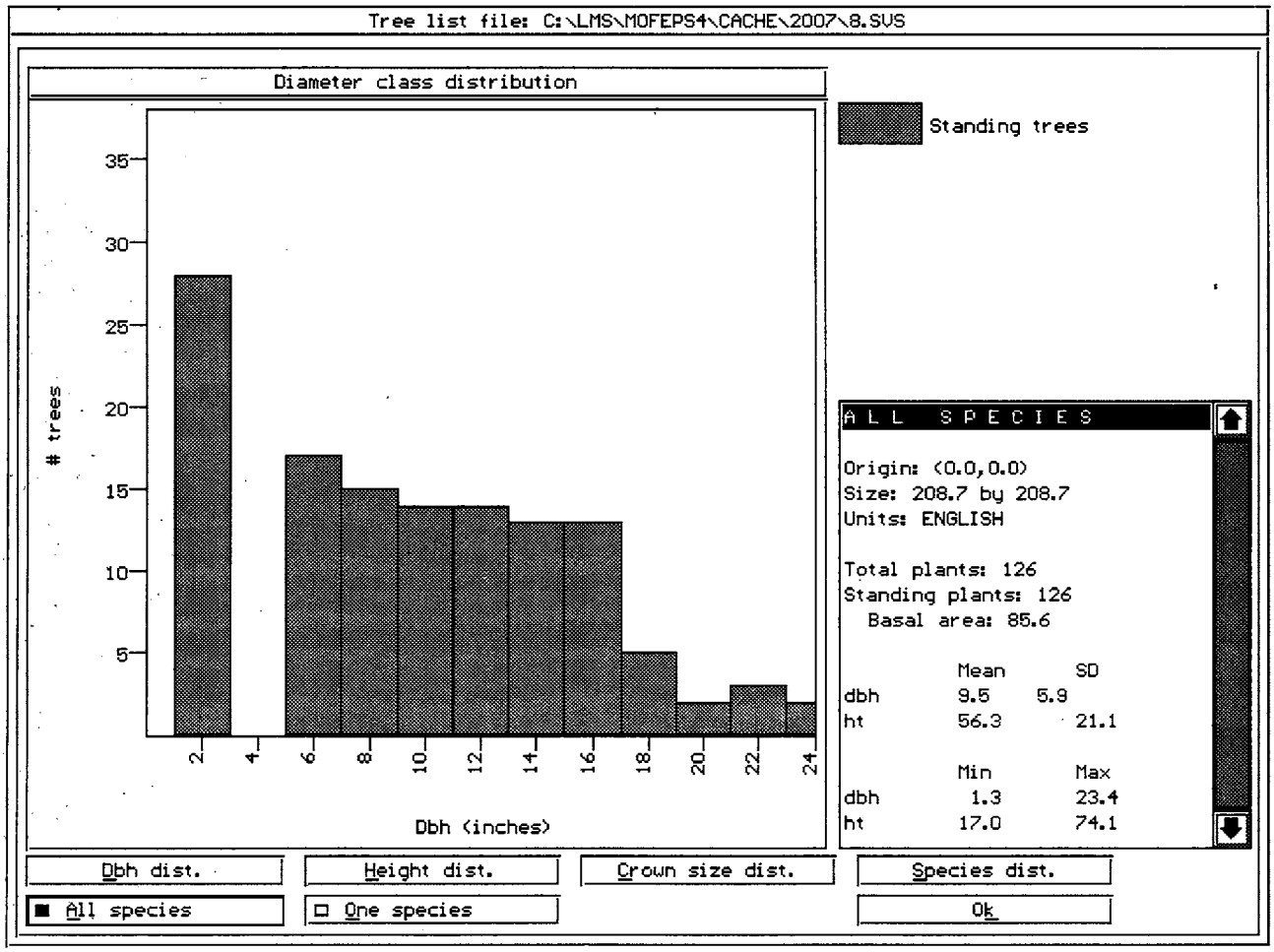


Figure 3.—*Graph of the diameter distribution for site 4, stand 14, in year 2027.*

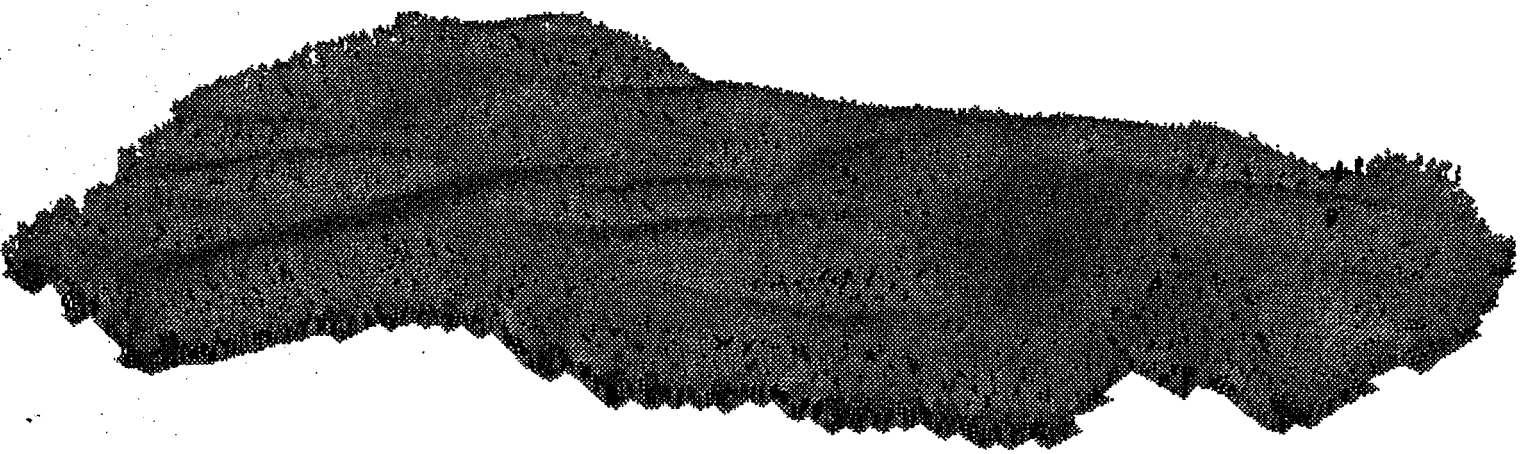
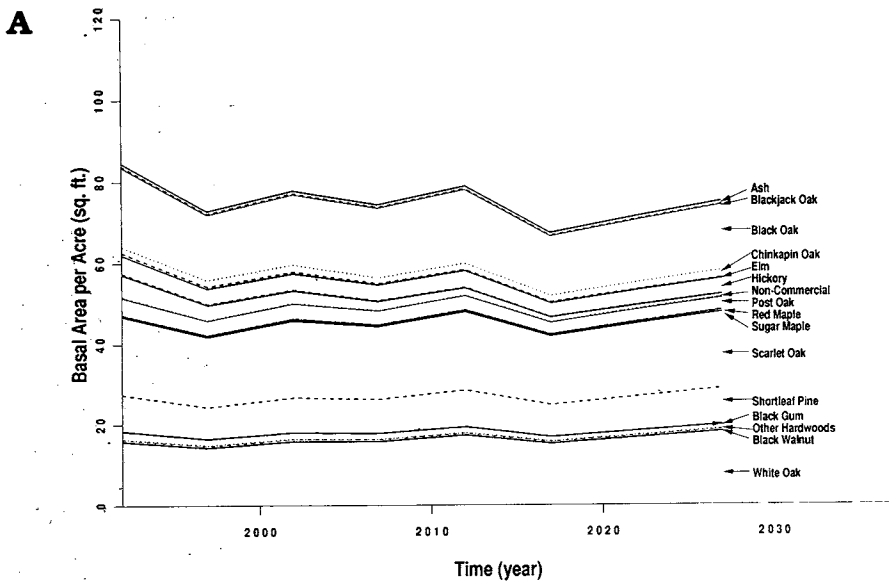
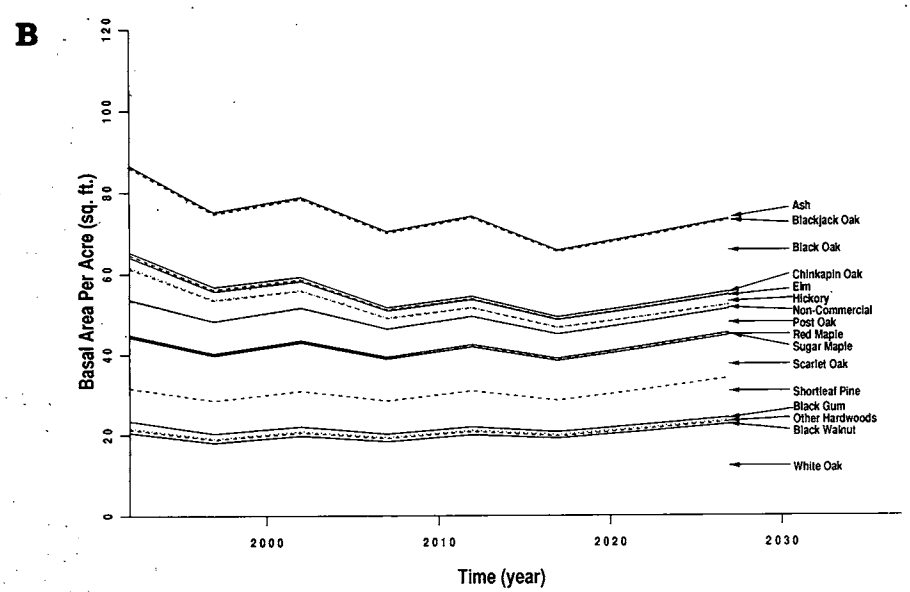


Figure 4.—*Example of landscape output from UVIEW for site 4 in year 2027.*





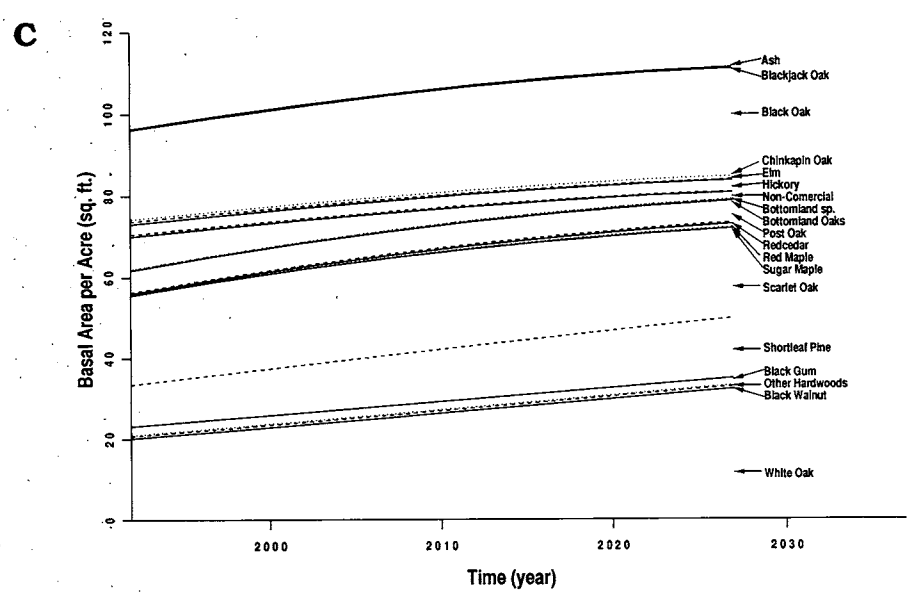
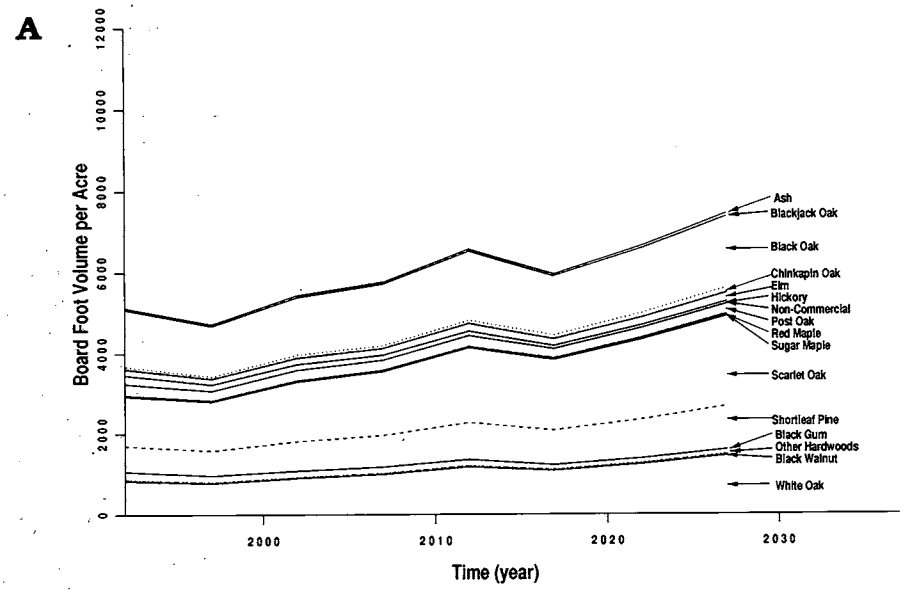
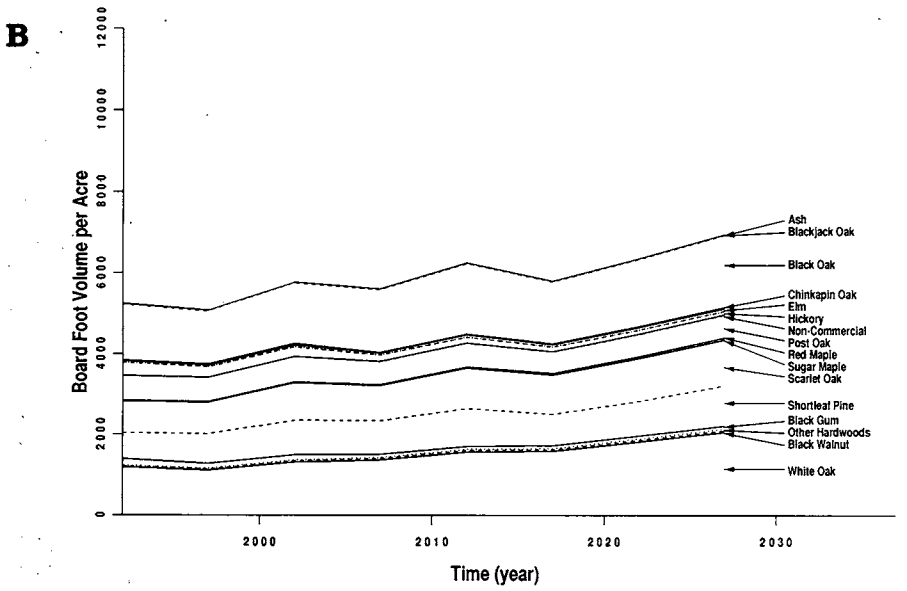


Figure 5.—*(A) Average basal area per acre for site 4 over time. The graph is a cumulative graph; the top line is the total average basal area per acre at each time. The difference between two adjacent lines is the basal area contribution of the species indicated on the upper line.*

(B) Average basal area per acre for site 5 over time.

(C) Average basal area per acre for site 6 over time.





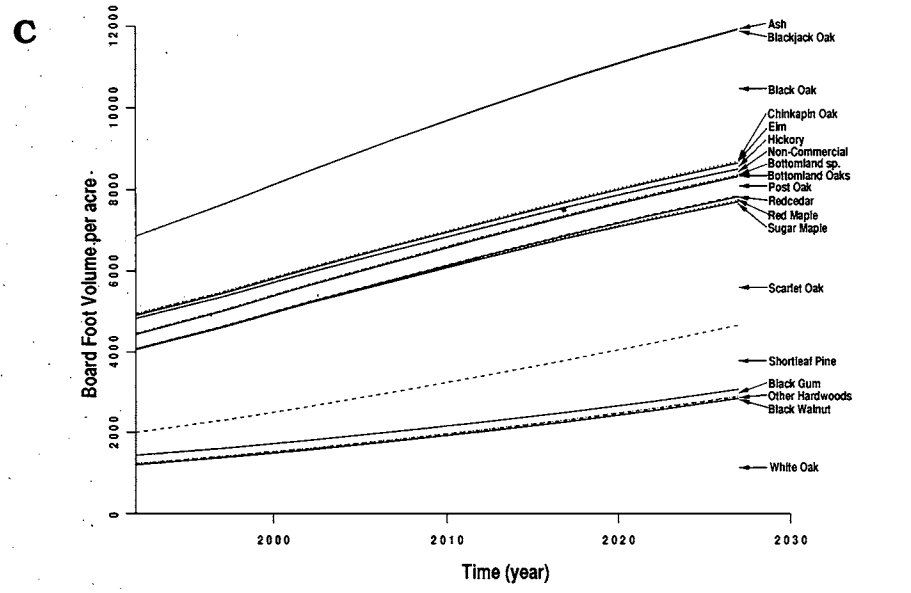


Figure 6.—*(A) Average volume per acre for site 4 over time. The graph was constructed like the basal area graph and can be interpreted in a similar way.*

(B) Average volume per acre for site 5 over time.

(C) Average volume per acre for site 6 over time.

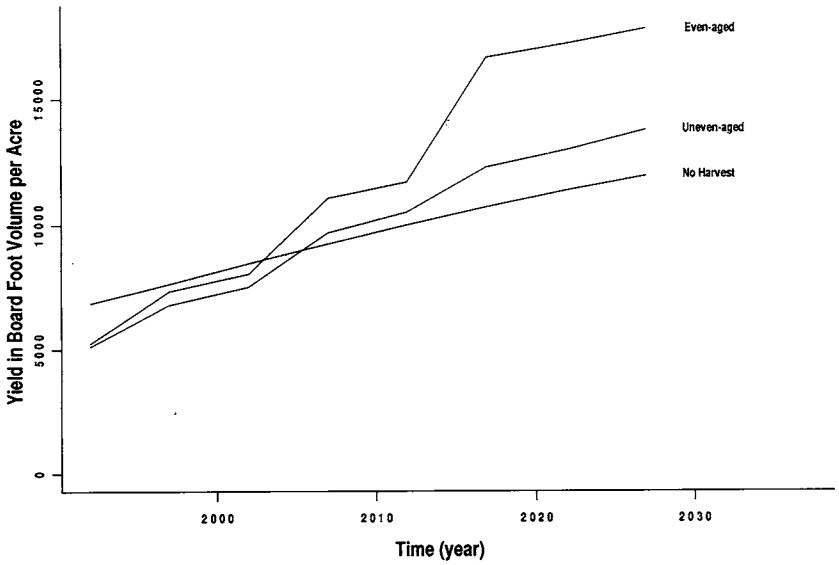


Figure 7.—*Average yield per acre for each site. Yield is standing volume plus cut volume.*

increase during the growth simulation period. The greater stand densities resulting from no thinning tended to favor basal area increases in black oak and white oak and to disfavor non-commercial species. Black oak, scarlet oak, shortleaf pine, and white oak increased in volume relative to other species. This treatment resulted in the greatest standing volume at the end of the projection period.

To evaluate the volume production by site and treatment, total volume yield was calculated for the 35-year simulation period (fig. 7). Total yield for each site includes cut volume plus the current standing volume. Figure 7 illustrates that the no-harvest treatment produced the least total yield over the 35-year simulation. The uneven-aged treatment produced intermediate yields and the even-aged treatment produced the greatest yield per acre over time.

DISCUSSION AND CONCLUSION

Assuming that the representations of the treatments and the projections in this analysis are reasonably accurate, uneven-aged and even-aged management produced equivalent average basal area and average standing volume per acre. The no-harvest treatment produced the largest average standing volume. In terms of average yield per acre, the even-aged treatment produced the greatest yield over time, the uneven-aged treatment produced an intermediate yield, and the no-harvest treatment produced the lowest average yield per acre over the simulation period.

Although projections of forest change are seldom precise they are useful for comparing the anticipated outcomes of alternative management practices. As with all predictions, the variance of the estimates increases exponentially with the length of prediction time. However, this applies to all the predictions equally. These projections are reasonable estimates of the average outcome of stands like these over the next 35 years. They serve to illustrate the likely changes in tree growth due to stand density over that period.

This paper also illustrates several of the currently available tools for projecting forest growth for the Missouri Ozarks and some of the ways this information can be used. These tools provide a framework for both growth and yield estimates as well as a way to visualize the changes in forest structure on the landscape due to silvicultural treatments. Growth analysis of the MOFEP treatment indicate the both even-aged and uneven-aged treatment will maintain equivalent basal area and volume per acre averages. The no-harvest treatment will maintain the largest standing volume but the least total yield over time.

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Synthesis and Integration of Pre-treatment Results from the Missouri Ozark Forest Ecosystem Project

Wendy K. Gram, Victoria L. Sork, and Robert J. Marquis[1]

Abstract.—Integrating results across disciplines is a critical component of ecosystem management and research. The common research sites, landscape-scale experimental design, and breadth of research subjects in Missouri Ozark Forest Ecosystem Project provide circumstances conducive for addressing multidisciplinary questions. Our objectives were to (1) summarize the treatment and block effects for pre-treatment studies, (2) identify potential relationships among taxa at different scales by comparing site and ecological landtype (ELT) patterns of diversity and relative abundance, and (3) explore abundance patterns of taxa across year of Missouri Department of Conservation land acquisition classes. We found few pre-treatment effects, but block 3 frequently was different from blocks 1 and 2. Many potential interactions were identified, most of which were between species from different taxonomic groups. Our results suggest that many relationships within an ecosystem are apparent only among species at fine spatial scales. Future analyses will include use of multivariate and spatially explicit models.

A distinct advantage of adopting a multidisciplinary experimental approach to studying the effects of forest management practices on ecosystem sustainability is the opportunity for integration. The Missouri Ozark Forest Ecosystem Project (MOFEP) includes more than 15 individual research studies that are conducted within the same nine experimental sites during the same time period (Brookshire *et al.* 1997). These studies focus on biotic and abiotic characteristics of the ecosystem, and all projects include both pre-and post-treatment data collection to evaluate the effects of three different forest management treatments on the organisms or elements of interest (Sheriff and He 1997). The common research sites, landscape-scale experimental design, and breadth of research subjects in MOFEP provide an ideal opportunity for integrating research results across disciplines, a critical component of ecosystem management (Christensen *et al.* 1996, Ehrlich 1986, Jones and Lawton 1995, Larsen *et al.* 1997).

Traditional management strategies have emphasized control of single groups of organisms such as forest trees, migratory birds, and game species (Christensen *et al.* 1996), but the current shift to ecosystem management, which emphasizes long-term sustainability of ecosystem diversity and function, has prompted research on the effects of management protocols on all aspects of an ecosystem, both physical and biological (Brookshire *et al.* 1997, Franklin 1996, Kurzejeski *et al.* 1993, Levin 1992). As with the analysis of any complicated biological community, results from research on isolated parts of a system are not ecologically independent and may not completely reflect the ecosystem as a whole. Synthesis of results from research on different parts of the Ozark forest ecosystem provides an assessment of the MOFEP experimental design and, eventually, will lead to development of a model depicting the effects of the treatments on an intact ecosystem. Incorporated in this ecosystem model will be numerous relationships among biotic and abiotic elements that control ecosystem diversity and function, the ultimate goal of long-term ecosystem sustainability (Christensen *et al.* 1996).

Determining the appropriate scale of analysis is a primary question in synthesizing MOFEP research results and identifying potential

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interactions (Shifley *et al.* 1995). The major experimental scale of MOFEP is the site (Sheriff and He 1997), stratified by ecological landtype (ELT; Miller 1981). MOFEP includes nine sites that comprise three replicates in a randomized complete block design with three treatments (Brookshire and Hauser 1993, Sheriff and He 1997). Combined data from the pre-treatment phase of the project provide an opportunity to characterize differences and general trends among sites. Although MOFEP is designed to test hypotheses at the landscape level, it may be necessary to evaluate data at finer scales to identify potential multidisciplinary interactions that are important in maintaining ecosystem integrity.

Many factors may contribute to variation across sites. Because recent studies have shown that land-use history can influence modern forest characteristics (Foster 1992, Orwig and Abrams 1994), we include a preliminary examination of this factor in this paper. All the sites in MOFEP are owned by the Missouri Department of Conservation (MDC), but various sites were purchased at different times between 1925 and 1952 (MDC, personal communication). Under MDC, sites were managed for forests (Cunningham and Hauser 1989). Land use of each site prior to MDC acquisition included logging disturbance, fire suppression, and grazing, but the precise land-use history is unknown. For the purposes of this study, we use year of acquisition by MDC as an indicator of recent land-use history. Because two MOFEP studies found significant differences due to land-use history (Marquis and Le Corff 1997, Sork *et al.* 1997), we evaluated associations among abundance patterns of taxa across year of land acquisition classes.

Within the MOFEP experimental design, pre-treatment data have been collected on the distribution and abundance of a wide variety of organisms and environmental characteristics. Our objectives are to (1) summarize the treatment and block effects for pre-treatment studies, (2) identify potential relationships among taxa at different scales by comparing site and ELT patterns of diversity and relative abundance, and (3) explore abundance patterns of taxa across year of MDC land acquisition classes.

METHODS

Data for this paper were obtained from 12 investigations presented at the 1997 MOFEP Symposium (for details on data collection, see the individual papers in this volume), including studies of woody plant genetic structure, snags and down wood, berry-producing plants, acorn production, surface soils, and seven studies of taxonomic groups at various levels (woody vegetation, ground flora, small mammals, leaf-chewing insects, forest interior birds, herpetofauna, and *Armillaria* distribution). When necessary, we calculated site and ELT-level summary statistics from additional data provided by investigators.

We compiled a summary of pre-treatment Analysis of Variance (ANOVA) results found in 12 MOFEP investigations to present treatment and block effects. We summarized the main effects of treatment and block and their interactions assigning significance at $P < 0.1$. From each study, we included density or abundance, diversity, species richness, and genetic inbreeding coefficient F_{IS} as dependent variables, based on the variables reported by the investigators. The woody vegetation study (Kabrick *et al.* 1997) reported results for multiple measures of density and volume. To avoid counting these highly correlated variables, we included only results for density (number of trees per acre). Similarly, Sork *et al.* (1997) reported results for six measures of woody plant genetic structure, but, for the three species studied, we included only one measure of genetic diversity (expected heterozygosity H_E) and a measure of inbreeding (F_{IS}).

To identify general trends among study sites, we analyzed variation in species richness and density or relative abundance of five taxonomic groups (woody vegetation, ground flora, small mammals, herpetofauna, and forest interior birds) among sites with one-way ANOVA. We also tested for site differences in mean plot diversity (Simpson's diversity index or genetic diversity as measured by expected heterozygosity H_E) with ground flora, woody vegetation, small mammals, herpetofauna, and H_E of three tree species. We performed correlation analyses between taxonomic groups to look for similar abundance patterns across sites. Because individual species within a taxonomic group

may exhibit different abundance patterns among sites, we analyzed variation among sites in density/relative abundance of 24 individual species from seven different taxonomic groups (see Appendix A) with one-way ANOVA.

To identify potential interactions among individual species, we performed correlation analyses on density or relative abundance of 24 species from seven different taxonomic groups by site and of 17 species from five taxonomic groups (see Appendix A) by site stratified by ELT (only including the most common ELT's, south- and west-facing slopes or ELT 17 and north- and east-facing slopes or ELT 18). To illustrate patterns among both taxonomic groups and species, we present some of the results in scatter plots.

Patterns among taxonomic groups also were correlated across year of MDC acquisition to explore the potential effect of land-use history on taxa abundance patterns. The experimental sites were acquired over a 28-year period; site 6 was purchased in 1925, sites 3, 4, and 5 in 1938, sites 1 and 2 in 1944, and sites 7, 8, and 9 (which make up replicate block 3) in 1952 (MDC, personal communication). We analyzed data on ground flora, woody vegetation, small mammals, herpetofauna relative abundance, and genetic inbreeding coefficient F_{IS} for three tree species. Because we have only four classes of land-use history, we use the correlations to detect trends. Differences among sites in geology and soil characteristics also confound interpretation of the effects of land-use history on species abundance and distribution. To illustrate the patterns with year of MDC acquisition, we present some of the results in histograms.

RESULTS

Treatment and Block Effects

Treatment main effects only were reported for three of 57 variables from 10 studies, including *Rubus enslenii* abundance (Fantz and Hamilton 1997), ground flora species richness (Grabner *et al.* 1997), and density of the moth caterpillar *Dichomeris ligulella* on white oak (*Quercus alba*) (Marquis and Le Corff 1997). Fantz and Hamilton (1997) and Grabner *et al.* (1997) found that sites assigned to even-aged treatment were different from sites assigned to uneven-aged and unmanaged treatments for *Rubus enslenii* and ground flora species richness, whereas Marquis and Le Corff (1997) found that sites assigned to uneven-aged treatment were different for *Dichomeris ligulella*. Investigators found treatment interaction effects for two variables. Acorn production and density of the moth caterpillar *Telphusa latifasciella* on white oak showed significant treatment interaction effects with year and year by ELT, respectively (Marquis and Le Corff 1997, Vangilder 1997).

Twelve studies tested data for block effects (table 1). Summarizing results from these studies, we found a significant block main effect for 19 of 57 variables, with block 3 different from blocks 1 and 2 in 13 of these cases. Although 38 variables did not exhibit significant block effects, eight of these variables had significant block interaction effects (see individual papers mentioned in table 1 for interaction terms).

Diversity and Abundance Patterns Among Sites

We did not find a general trend among sites for species richness (ANOVA, $F_{8, 36} = 0.1$, $P = 0.99$; fig. 1a) or diversity (ANOVA, $F_{8, 54} = 0.2$, $P = 0.99$; fig. 1b); in fact, within a taxonomic group, differences among sites were uncommon. We also did not find a general trend among sites for density/abundance of taxonomic group species (ANOVA, $F_{8, 27} = 0.1$, $P = 0.99$; fig. 1c), but select taxonomic groups showed variability among sites. Ground flora and herpetofauna were negatively correlated (Pearson's $r_7 = -0.71$, $P < 0.05$), indicating a potential relationship between ground flora cover and abundance of reptiles and amphibians.

The 24 species examined did not exhibit a common abundance pattern among sites (ANOVA, $F_{8, 207} = 0.2$, $P = 0.99$), but we found 25 significant correlations between species pairs. At $P < 0.05$, we would expect by chance to find only 14 significant correlations with 276 pairwise tests. The significant correlations, 20 of which were between species from different taxonomic groups, represent potential interactions between species that may warrant further investigation. For example, shortleaf pine (*Pinus echinata*) and wood thrush (*Hylocichla mustelina*) density were positively correlated

Table 1.—*Summary of block effects across 12 MOFEP investigations. (Note: The sampling and design of the ANOVAs differed across investigations, but all included a block main effect.)*

MOFEP Investigation	Block main effect SIG	Block main effect NS	3 different from 1 & 2	2 different from 1 & 3	1 different from 2 & 3	Source of data (this volume)
Woody vegetation						Kabrick *et al.*
Total tree density	x		x			
Quercus alba density	x		x			
Quercus coccinea density		x				
Quercus velutina density	x			x		
Pinus echinata density		x				
Woody plant genetic structure						Sork *et al.*
Carya tomentosa H_E		x				
Quercus alba H_E		x				
Sassafras albidum H_E	x				x[1]	
C. tomentosa F_{IS}		x				
Q. alba F_{IS}		x				
S. albidum F_{IS}	x		x[2]			
Ground flora						Grabner *et al.*
Species richness		x				
Diversity		x				
Snags and down wood						Shifley *et al.*
Snag abundance		x				
Down wood abundance		x				
Armillaria distribution						Bruhn et al.
A. gallica abundance	x		x			
A. mellea abundance	x		x			
Oak leaf-chewing insects						Marquis & Le Corff
Insect density on *Q. alba* [3]		x				
Insect density on *Q. velutina*		x				
Lithophane antennata on *Q. alba*	x			x		
Chionodes sp. on *Q. alba*		x				
Telphusa latifasciella on *Q. alba*		x				
Spargonothis pettitana on *Q. alba*		x				
Dichomeris ligulella on *Q. alba* [3]	x			x		
Chionodes sp. on *Q. velutina*		x				
Telphusa latifasciella on *Q. velutina* [3]		x				
Tortricidae sp. on *Q. velutina*	x			x		
Spargonothis pettitana on *Q. velutina*		x				
Dichomeris ligulella on *Q. velutina* [3]	x		x			
Forest interior birds						Clawson *et al.*
Ovenbird density	x		x			
Worm-eating warbler density	x		x			
Kentucky warbler density		x				
Wood thrush density		x				

(table continued on next page)

(table continued)

MOFEP Investigation	Block main effect SIG	Block main effect NS	3 different from 1 & 2	2 different from 1 & 3	1 different from 2 & 3	Source of data (this volume)
Acadian flycatcher density [3]		x				
Small mammals						Fantz & Renken
Species richness		x				
Total mammal abundance		x				
Peromyscus sp. abundance [3]		x				
Herpetofaunal community						Renken
Species richness		x				
Total amphibian and reptile abundance [3]		x				
Surface soils						Spratt
Carbon in A-horizon soil		x				
Total sulfur in A-horizon soil		x				
Organic sulfur in A-horizon soil		x				
Organic sulfur production	x		x			
Cellulose mineralization rate	x				x	
Lignin mineralization		x				
Exchangeable potassium		x				
Exchangeable magnesium	x		x			
Berry-producing plants						Fantz & Hamilton
Vaccinium arboreum abundance	x		x			
V. stamineum abundance	x		x			
V. vacillans abundance		x				
Rubus occidentalis abundance		x				
R. pensilvanicus abundance		x				
R. flagellaris abundance		x				
R. enslenii abundance		x				
Acorn production						Vangilder
Acorn density [3]		x				
Oak tree diameter at breast height (d.b.h.)		x				
Oak tree canopy area	x		x			
Totals	19	38	13	4	2	

[1] Block 1 > 2 but 1 = 3 and 2 = 3
[2] Block 3 > 1 but 1 = 2 and 2 = 3.
[3] Significant block interaction effect.

(Pearson's $r_7 = 0.84$, $P < 0.05$; fig. 2a), and sassafras (*Sassafras albidum*) relative abundance was negatively correlated with spotted salamander (*Ambystoma maculatum*) relative abundance (Pearson's $r_7 = -0.85$, $P < 0.05$; fig. 2a).

Stratifying site by ELT, we found six significant correlations in 136 pairwise tests on ELT 17 (south- and west-facing slopes), including negative relationships between shortleaf pine density and sassafras genetic inbreeding coefficient F_{IS} (Pearson's $r_7 = -0.81$, $P < 0.05$; fig. 2b), and smooth earth snake (*Virginia valeriae*) relative abundance and white oak density (Pearson's $r_7 = -0.79$, $P < 0.05$; fig. 2b). On ELT 18 (north- and east-facing slopes), we also found six significant correlations in 136 pairwise tests, but none of the significant correlations were between the same species as in ELT 17. For example, sassafras relative abundance was positively correlated with ground skink

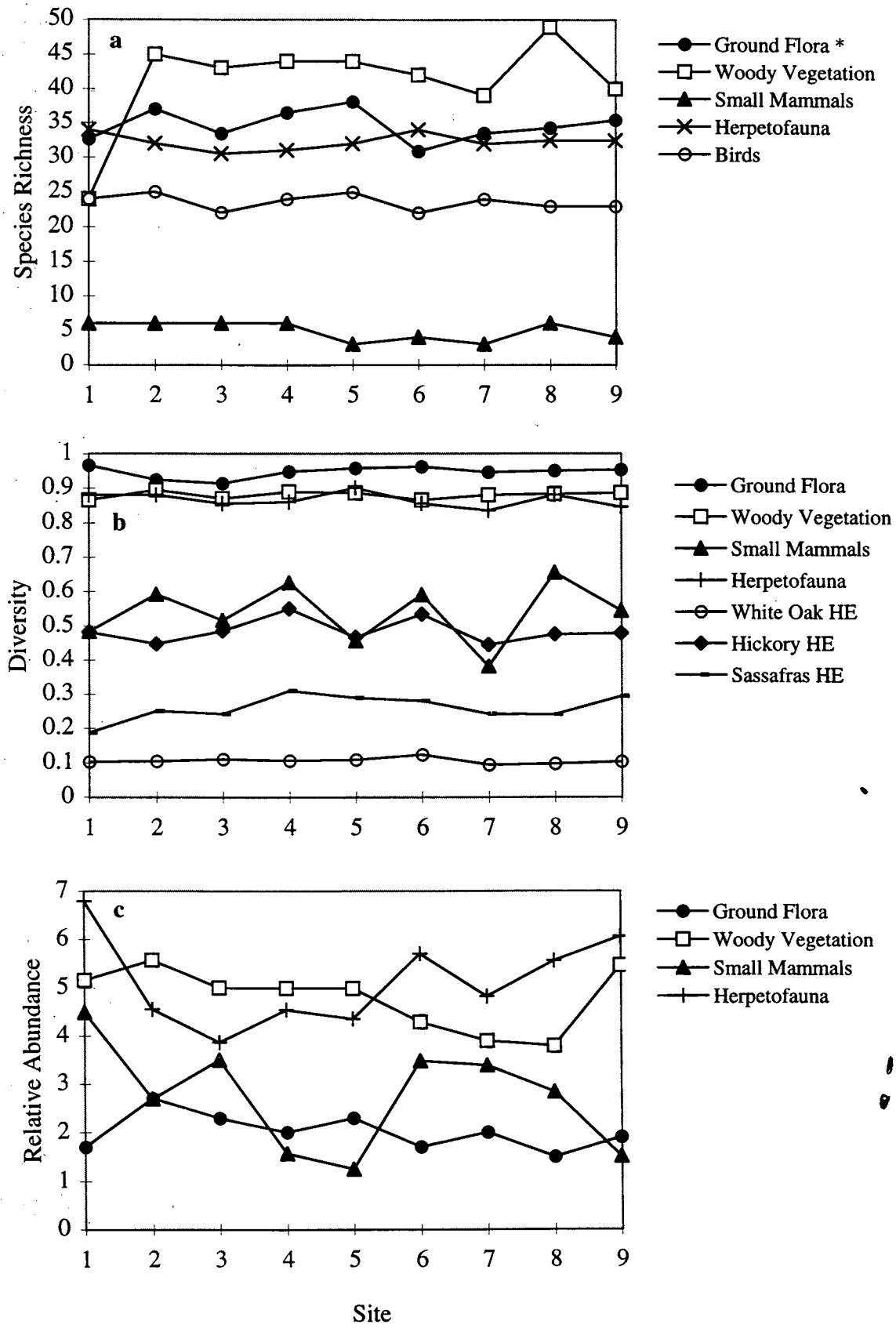

Figure 1.—*Scatter plots of (a) species richness, (b) diversity using Simpson's diversity index, and (c) relative abundance in each experimental site for select taxa. Points are connected only to visually discern patterns among sites and taxa.*
** species richness x 0.1.*

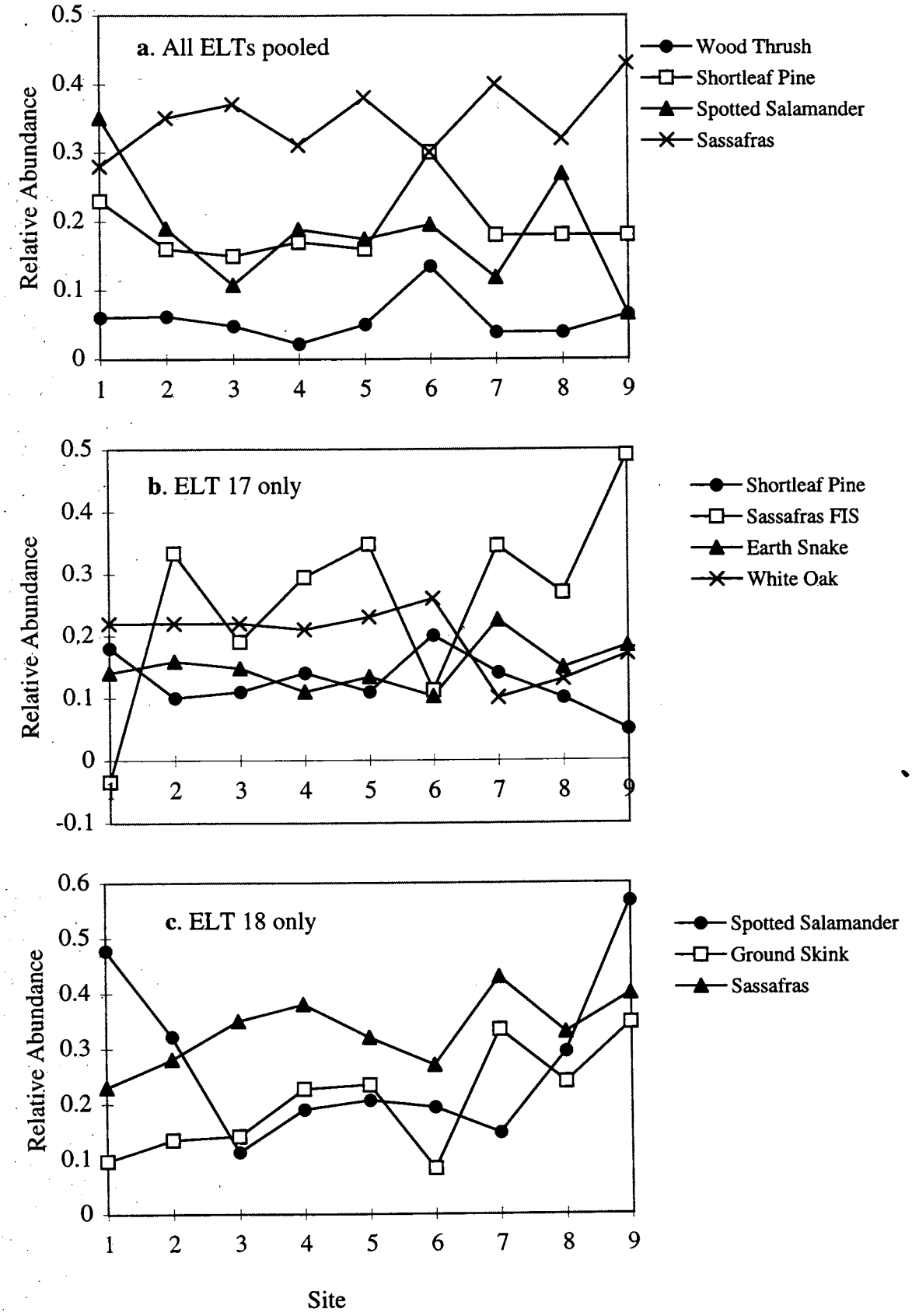

Figure 2.—*Scatter plots of relative abundance in each experimental site (a) for all ELTs combined, (b) for ELT 17, and (c) for ELT 18 for select species from individual MOFEP studies. Points are connected only to visually discern patterns among sites and taxa.*

(*Scincella lateralis*) relative abundance (Pearson's $r_7 = 0.87$, $P < 0.05$; fig. 2c) and negatively correlated with spotted salamander relative abundance (Pearson's $r_7 = -0.78$, $P < 0.05$; fig. 2c). In ELT 17 and 18, five and four, respectively, of the six significant correlations were between species from different taxonomic groups. Furthermore, many of the significant correlations found in ELT 17 and 18 were not significant at the overall site level (three correlations from ELT 17 and none from ELT 18 were significant at the site level).

Patterns by Year of Land Acquisition by MDC

We found high correlations (Pearson's $r > 0.85$) between six groups, but two correlations were particularly noteworthy. Woody vegetation density was strongly correlated with ground flora cover (Pearson's $r_2 = 0.95$, $P < 0.05$; fig. 3), and woody vegetation was negatively correlated with sassafras inbreeding coefficient F_{IS} (Pearson's $r_2 = -0.99$, $P < 0.05$; see also Sork *et al.* 1997). In general, species that were significantly correlated in patterns of density/abundance by site were also correlated by year of acquisition by MDC.

DISCUSSION

Synthesis of the MOFEP results indicated that treatment class was rarely a significant main effect in the pre-treatment data. These findings will facilitate interpretation of the effects of each management protocol although the pre- versus post-treatment analyses planned in the MOFEP experimental design do not require treatment class similarity prior to treatment. Because the MOFEP randomized block design has low statistical power (high probability of Type II error) due to only three replicates of each treatment class, it may have been difficult to detect statistical differences among treatments (Sheriff and He 1997). It is unlikely that studies that found similar means among pre-treatment classes were affected by low statistical power. Studies that showed apparently different means among pre-treatment classes that were not statistically different, however, may be suffering from Type II error (not rejecting a null hypothesis when it is false). In reviewing the investigations included in this paper, we found that some studies clearly did not have pre-treatment differences and other studies may have had pre-treatment differences that were not detectable statistically because of high variance around sampling means and low statistical power.

Given the scale of the MOFEP project, further replication of sites is not feasible. However, we can reduce some problems associated with low replication by increasing sampling within sites

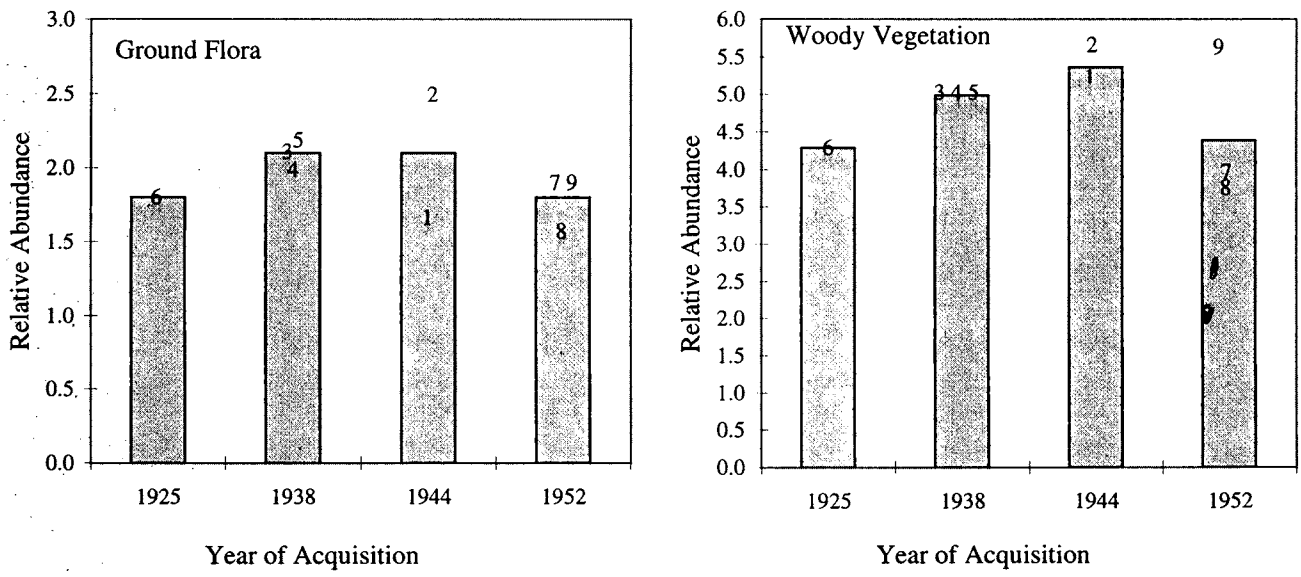

Figure 3.—*Mean relative abundance of ground flora and woody vegetation in sites with different years of acquisition by the Missouri Department of Conservation. Site 6 was purchased in 1925, sites 3, 4, and 5 in 1938, sites 1 and 2 in 1944, and sites 7, 8, and 9 (which make up replicate block 3) in 1952. Numbers near bars indicate the mean of the corresponding site.*

for individual investigations within the framework of the universal randomized block design (e.g., sample more leaves per tree, more trees per plot, or more plots per site). For example, Marquis and Le Corff (1997), before determining their sampling protocol, statistically evaluated the sample sizes necessary to adequately estimate the mean and variance in insect density. Retrospective power analyses or calculation of confidence intervals (Steidl *et al.* 1997) for pretreatment studies also would facilitate statistical evaluation of the sampling design of each investigation and may suggest sampling changes that would increase statistical power during future phases of the project.

Differences among blocks were found in a third of the studies, with block 3 most commonly different from blocks 1 and 2. Geographically, block 3 is located south of blocks 1 and 2 in the Peck Ranch Wildlife Area, and the three sites in block 3 were acquired by MDC after all other sites were acquired. Blocks 1 and 2, on the other hand, are adjacent to each other in Carr Creek and Cardareva State Forests (block 1) and Cardareva, Paint Rock and Deer Run State Forests (block 2); sites 3 and 4 are continuous yet located in different blocks. It is not clear that variability among sites is smaller within blocks 1 and 2 than within different blocks, suggesting that the blocking groups may not be optimal (see also Kabrick *et al.* 1997, Shifley *et al.* 1997). Two sites in block 3 (sites 7 and 8) are sharply different from all other sites in soil texture, stoniness, subsoil acidity, and geological strata (Kabrick *et al.* 1997). Sites 7 and 8 also have longer and less steep slopes than other sites (Meinert *et al.* 1997). The distinct geographical and physical characteristics of sites 7 and 8 may account for the dominant block effect in MOFEP studies. Thus, some results indicate that a different blocking design might have been preferable, but that overall, the randomized block experimental design and the assignment of blocks is satisfactory.

We did not find differences among sites for pretreatment patterns of species richness and diversity within most taxonomic groups, preventing detection of interactions among taxonomic groups. Because taxonomic groups consist of ecologically different species, it is likely that community-level measures, such as species richness and diversity, conceal relationships among individual species. When comparing density/relative abundance, however, we found differences among sites within taxonomic groups and for individual species, but we did not find a general trend across sites. Variability across sites detected in density/abundance measures suggests that these measures may best illustrate interactions among ecosystem elements. We detected few potential relationships among taxonomic groups, except between ground flora cover and herpetofauna relative abundance. When comparing patterns of species' density/abundance, we identified 25 potential interactions and 80 percent of these interactions were between species from different taxonomic groups. Direct and indirect interactions are usually species-dependent, and our results suggest that it is necessary to look at the species level to identify these potential interactions. The predominance of intertaxa correlations confirms the importance of integrating data among taxa because it is likely that some of these relationships influence widespread ecosystem processes.

When we stratified site by ELT, we found additional relationships among species that may be apparent only on an ecologically fine scale. It is particularly notable that few of the significant correlations identified on the site level existed when site was stratified by ELT. In addition, correlations between organisms on ELT 17 were not found on ELT 18. The most appropriate scale for determining potential interactions is probably dependent on the size, ecological constraints, and mobility of the species or elements of interest. In general, plants may be more closely associated with an ELT than animals, and specialist herbivorous insects may be more dependent on a specific ELT (which contains its host plant) than insectivorous birds. Furthermore, relationships among organisms can vary in different landscapes, vertically in the forest, by time, or by season, indicating that stratification may be necessary to reveal the scope of interactions present in an ecosystem. For example, oak herbivores vary extensively in species presence and density among months (Marquis and Le Corff 1997). A more complete understanding of ecosystem processes will develop from an increased awareness of many small-scale interactions that, when combined with other interactions, explain the more complex, multivariate interactions.

Land-use history is an example of a factor that may influence patterns of species distribution and abundance (Foster 1992, Orwig and Abrams 1994). Unfortunately, unequal sample sizes among year of acquisition classes and the

confounding effects of geological and soil differences make it difficult to attribute any specific association directly to land-use history. Nonetheless, we found a statistically significant correlation between ground flora cover and woody vegetation density when compared by year of acquisition that was not evident when compared by site alone. These results suggest that patterns of species succession in plant communities may be directly related to land-use history. MOFEP investigators of tree genetic structure and oak herbivore communities found statistically significant patterns by year of MDC acquisition in their data analyses (Marquis and Le Corff 1997, Sork *et al.* 1997). Notably, the patterns among the studies that examined the relation of year of acquisition were different, suggesting that land-use history may have dissimilar effects on current patterns of diversity, abundance, and genetic structure of different species. Although these results are not conclusive, they do suggest that land-use history is a factor worth considering in future analyses.

Patterns we have identified in this preliminary analysis of the pre-treatment data may represent direct interactions among species, indirect interactions that are mediated by unknown factors, or spurious relationships that have no ecological significance. Some relationships appear ecologically plausible, such as the inverse relationship between ground flora cover and herpetofauna relative abundance, whereas other interactions are less likely to be ecologically significant, such as the positive correlation between wood thrush and shortleaf pine density. Indirect interactions often are the most difficult to recognize and may require extensive investigation to uncover the mediating factors. Our next step is to further evaluate potential relationships among species with spatially explicit statistical analyses and modeling. By using geographic information systems (GIS) and geostatistic tools, we plan to address questions focused on the spatial dependence of different organisms within the MOFEP landscape relative to different ecosystem attributes such as soil characteristics and geo-landform properties (Cressie 1993, Goodchild *et al.* 1993). With information about relationships among species and environmental characteristics at different spatial scales, we can build on existing landscape-level models that involve simulation over time of ecological attributes related to the location and configuration of specific areas (Baker 1989, Sklar and Costanza 1991). For example, investigators have used various habitat suitability models (e.g., cartographic and Bayesian models) to predict species abundance, herbivory effects, and lek sites relative to elevation, water resources, and vegetation type (Hyman *et al.* 1991, Milne *et al.* 1989, Nisbet and Reed 1983). We will also rely on multivariate regression and correlation analyses to identify interactions that may not be spatially dependent. Thus, our future goals involve integrating the MOFEP data to create predictive models of ecosystem processes.

To fully integrate components of the Ozark forest ecosystem, multidisciplinary studies are necessary to address questions about the effects of disturbance on ecosystem integrity and the specific interactions that maintain various ecosystem functions. It is very likely that these multidisciplinary studies will identify critical components of the ecosystem that individual studies do not find, particularly for processes that affect more than one trophic level. As we gain more information about the parts of an ecosystem, we will be better equipped to put the parts together to understand the complexities of ecosystems as a unit, and, thus the impacts of management on the functioning of these ecosystems.

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Appendix A.—*List of species (and their taxonomic groups) used in species correlation analyses*

Armillaria Distribution
Armillaria gallica
A. mellea

Woody Vegetation
Quercus alba (white oak)
Q. velutina (black oak)
Q. coccinea (scarlet oak)
Pinus echinata (shortleaf pine)

Forest Interior Birds[1]
Seiurus aurocapillus (ovenbird)
Helmitheros vermivorous (worm-eating warbler)
Oporornis formosus (Kentucky warbler)
Hylocichla mustelina (wood thrush)
Empidonax virescens (Acadian flycatcher)

Woody Plant Genetic Structure
Carya tomentosa F_{IS} (mockernut hickory genetic inbreeding coefficient)
Quercus alba F_{IS} (white oak genetic inbreeding coefficient)
Sassafras albidum F_{IS} (sassafras genetic inbreeding coefficient)

Small Mammals[1]
Peromyscus maniculatus (deer mouse)
P. leucopus (white-footed mouse)

Herpetofauna
Ambystoma maculatum (spotted salamander)
Bufo americanus (American toad)
Scincella lateralis (ground skink)
Virginia valeriae (smooth earth snake)

Ground Flora
Cornus florida (flowering dogwood)
Desmodium nudiflorum (tick trefoil)
Sassafras albidum (sassafras)
Vitis aestivalis (summer grape)

[1] Groups of species not included in the correlation by site stratified by Ecological Landtype (ELT).

Initiating Long-Term Soil Productivity Research in Missouri

Felix Ponder, Jr.

Abstract.—Management practices necessary for sustaining long-term soil productivity (LTSP) of forest lands are being defined from a network of coordinated, long-term experiments established in various ecosystems across the United States and British Columbia according to the same basic study plan. The study was established in the Ozark Region of southeastern Missouri in Shannon County in 1995. It is being led by Forest Service Research, with cooperation from the Mark Twain National Forest, Missouri's Department of Conservation and Department of Natural Resources, the Natural Resources Conservation Service, and the University of Missouri. The impacts of treatments on soil productivity and site quality will be periodically evaluated over the life of the regenerating stands at the study site. This report summarizes some of the pre-treatment data, mortality, and nutrient concentrations in herbaceous vegetation.

Results from long-term soil productivity (LTSP) studies are necessary for the development of land management practices that will sustain forest productivity in the Central Hardwood Region. Sustaining or increasing the productivity of forest land is also essential because the acreage of commercial forest is declining due to environmental constraints, increased recreational uses, and other uses while demands for timber products are increasing. Also of concern are the effects of heavy equipment (Woodbury 1930) and whole-tree harvesting (Hornbeck and Kropelin 1982) on soil productivity. The use of heavy equipment and whole-tree harvesting affect soil porosity and soil organic matter, which are believed to be the primary properties controlling forest productivity and the most impacted by forest harvesting activities. The LTSP program is based on three specific questions:

1. Are management practices degrading the long-term productivity of the land?
2. What are the principal soil processes involved?
3. Can detrimental effects be overcome by mitigation?

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The answers to these questions when used in conjunction with the latest soil survey information will provide a foundation of scientific knowledge to highlight site limitations and to provide interpretations for sustainable use over extensive areas.

High public interest in forest health and in the ability of forests to sustain their inherent productivity has resulted in legislation (USDA Forest Service 1983) and policies (U.S. Code of Federal Regulations 1985) that ensure research and monitoring (USDA Forest Service 1987) of management systems to prevent the impairment of the land's productivity. The 1990 National Research Council (NRC) identified critical areas of forestry research in the U.S. that needed to be strengthened, and the 1995 NRC's Forestry Research and Educational Initiative Implementation Committee recommended an initiative to focus on soil properties, processes, and plant-growth relationships as fundamental to sustaining managed forest ecosystems.

The summation of these concerns, policies, and legislation about the impacts of management activities on National Forest lands led to the initiation of a joint National Forest System/ Forest Service Research study to "evaluate timber management impacts on long-term soil productivity." The study plan calls for three levels of organic matter removal (bole only, total

tree, and total aboveground biomass) and three levels of compaction (none, medium, and severe). The objectives of the program are to: (1) quantify the effects of soil disturbance from management activities on long-term soil productivity; (2) validate soil monitoring standards developed in compliance with the National Forest Management Act of 1976, which requires research and monitoring of Federal lands to safeguard the productivity of forest soils; (3) learn more about the fundamental relationships between soil properties, long-term productivity, and forest management practices; and (4) evaluate the potential for mitigating the adverse effects of disturbance.

Evidence of this interest and cooperation is exhibited in the Forest Service LTSP study that was installed in 1995 on Missouri Department of Conservation land in the Ozark Region of southeastern Missouri in Shannon County. The study is being led by Forest Service Research, with cooperation from the Mark Twain National Forest, Missouri's Departments of Conservation and Natural Resources, the USDA Natural Resources Conservation Service, and the University of Missouri. The cooperative research effort is designed to: (1) to establish experiments that focus on key soil and site properties affected by management, rather than focusing on operational practices, (2) institutionalizing the effort so the study will be maintained, measured, and reported on through a rotation (80 to 100 years), and (3) establishing the study on the most important soil-species combination. Relating changes in growth potential of the regenerating stand to changes in site organic matter and soil porosity caused by treatments will permit us to estimate the magnitude of damage to forest productivity that has been generated by disturbance.

THE STUDY SITE

The site selection team included representatives from the cooperating agencies. The installation of the LTSP study involved choosing a forest type in the Central Hardwood Region, selecting a productivity gradient within the region, identifying individual sites, and applying treatments. The initial productivity gradient for the study included sites in Missouri, Illinois, and Indiana; the installations in those States represented low, medium, and high productive sites, respectively. However, because of budget constraints and the high cost of installation and maintenance, there are no plans to install the study in Illinois and Indiana.

The Missouri LTSP study is located in the southeastern Missouri Ozarks on the Carr Creek State Forest (Missouri Department of Conservation) in Shannon County. Before the site was selected, several preliminary soil surveys were made to locate the study area on relatively uniform soils. Soil pits were dug and soils were described and analyzed with cooperation from the Missouri Department of Natural Resources, the Natural Resources Conservation Service, the Mark Twain National Forest, and the University of Missouri. Field examination included estimation of depths to restrictive layers as well as horizon thicknesses, textures, and gravel content. Mean annual precipitation in the area is 112 cm (44 in.), and mean annual temperature is 13.3°C (56°F). The site occupies the upper sideslopes of two ridges with northeastern aspects. At the beginning of the study, the site was covered by a well-stocked, mature, second-growth oak-hickory forest. Site index ranges from 74 to 80 based on black oak (*Quercus velutina* Lam.) at 50 years (Hahn 1991). The oak-hickory timber type is the major timber type in the Central Hardwood Region, occurring over a variety of soils, relief, and stand conditions.

The sloping topography (20 to 28 percent slopes) has small shallow streams that contain exposed cobbles and stones. The area is underlain mainly by Ordovician dolomite, and areas of Cambrian dolomite and Precambrian igneous rocks are also present (Missouri Geological Survey 1979). The weathering of the Ordovician and Cambrian dolomite has resulted in a deep mantle of cherty residuum (Gott 1975). Soils derived from this residuum are primarily of the Clarksville series (loamy skeletal mixed mesic Typic Paleudults). Water drains freely through the soils into subsurface channels.

EXPERIMENTAL DESIGN

The LTSP study consists of nine treatments derived from combinations of three levels of organic matter removal and three levels of soil compaction:

Organic Matter Removal	Soil Compaction
Merchantable boles removed (bole only, **BO**)	No compaction (**None**)
All living vegetation removed (whole tree, **WT**)	Intermediate compaction (**Medium**)
All living vegetation removed plus forest floor, exposing mineral soil (whole tree + forest floor, **WT + FF**)	Severe compaction (**Severe**)

Severe compaction is defined as 80 percent of the difference between the hypothetical growth-limiting bulk density (Daddow and Warrington 1983) and the bulk density of the uncompacted soil. Medium soil compaction is intermediate between severe compaction and no compaction. Each of the nine treatment combinations was replicated three times. The national study plan suggests that supplementary treatments and an uncut control area be included when space and other resources are available. Consequently, physical and chemical plot variables are also being measured in an uncut area adjacent to plots in the present study.

The nine treatment combinations of organic matter removal and compaction treatments create a gradient in organic matter removal and compaction that covers most of the harvest-related disturbances found operationally. These nine treatments are shown in table 1.

Treatment plots are artificially regenerated with tree species normally managed on the site. Competing vegetation will be eliminated chemically and/or mechanically on one-half of each plot by the third year. The contrasting treatments will be used to measure net primary productivity, study how weeds may affect soil recovery rates from compaction, and determine the impact of weed diversity on tree growth and soil properties. Effects will be analyzed statistically after years three and five, and then at 5-year intervals thereafter by analysis of variance and by regression using soil, vegetation, and climatic variables.

Plot Layout and Pre-treatment Measurements

After determining that the key soil properties did not vary significantly across the selected area, we established preliminary plot boundaries. Three replicates of nine treatment plots approximately 0.4 ha (1 ac) in size were laid out randomly in the summer of 1993. Four-meter-wide buffer strips were included around all plots. All treatment plots are separated from residual forest by a cleared area that approximates or exceeds the height of bordering trees.

The pre-harvest inventory of the overstory, understory, herbaceous layer, and dead and downed woody material was completed in the summer of 1993 by the Missouri Forest Ecosystem Project (MOFEP) forester and the botany crew of the Missouri Department of Conservation. Overstory measurements were made on 0.2-ha (0.5-ac) circular plots. All trees living and dead standing 11.5 cm (4.5 in.) d.b.h. and greater were identified and d.b.h. was measured. All live saplings between 3.8 cm (1.5 in.) and 11.2 cm (4.4 in.) d.b.h. were identified and measured on four circular 0.02-ha (0.05-ac) plots located 17.25 m (56.4 ft) from the center

Table 1.—*LTSP treatments including the nine combinations of organic matter and soil compaction.*

	Organic matter removal		
Compaction	**Bole only**	**Whole tree**	**Whole tree + Forest floor**
None	BO None	WT None	WT + FF None
Medium	BO Medium	WT Medium	WT + FF Medium
Severe	BO Severe	WT Severe	WT + FF Severe

point in each cardinal direction (N, S, E, and W). Understory woody vegetation 1.3 cm (0.5 in.) but less than 3.8 cm (1.5 in.) d.b.h. and greater than 1 m (3.3 ft) tall was measured on 0.004-ha (0.01-ac) plots that were located within sapling plots. Dead and downed woody material greater than 5 cm (2 in.) in diameter and 0.6 m (2 ft) long was inventoried (species, maximum diameter, length, and decomposition class) along each of four line intercept transects 17.25 m (56.4 ft) in length. Herbaceous vegetation was identified and counted on four 1-m^2 (11-ft^2) plots that were located 6.1 m (20 ft) from the sapling plot center along NE, SE, SW, and NW transects: a total of 16 herbaceous plots were sampled within each 0.2-ha (0.5-ac) plot.

Biomass samples were collected for overstory canopy trees, understory saplings, ground vegetation, and leaf litter/humus layer. A total of 54 trees were selected, felled, and weighed in the field during the spring of 1994. Twenty-six saplings (d.b.h. < 10 cm) and 28 midstory and overstory trees (d.b.h. > 10 cm) were selected and total tree biomass was measured. Total height, d.b.h., basal diameter, and specific crown dimensions were measured on each tree. Trees with merchantable logs were sectioned in appropriate lengths; others were cut to 2-m lengths. Sawdust samples and wood disks were collected from the end of each log section. Fresh weights of all tree logs and crown portions were measured in the field. Some merchantable logs were too large to be weighed in the field (scale limit = 500 lb). Thus, detailed log dimensions were taken to estimate volume; weight was later predicted from laboratory samples. Fresh weights of all sawdust samples, wood disks, and crown subsamples were measured separately. Woody and herbaceous ground covers were clipped separately. Samples were collected before leaf drop in the fall of 1993. Leaf litter/humus samples were collected, and leaf litter was separated from humus material. All samples were dried at 105°C for 72 hours or until a constant weight was achieved. Each sample (sawdust, leaf litter, leaf, crown components, woody and herbaceous ground covers, and humus) was then ground to a fine powder in a Wiley Mill and analyzed for macronutrient and micronutrient content. Inventory and sampling procedures are further described in Ponder and Mikkelson (1995).

In addition to soil pits, soil samples were collected with a two-person power-driven coring device. Four intact cores (7.6 cm dia. x 40 cm long) (3 in. diameter x 16 in. long) of soil per plot were collected and partitioned by soil horizon for determination of bulk density, pH, organic matter content, hydraulic conductivity, and macronutrient content (Soil Survey Staff 1984, Page *et al.* 1982, Black 1965).

Timber Harvesting

Trees and biomass were removed according to protocols in the national LTSP study plan (Powers *et al.* 1989) by means that minimized soil disturbance. Trees were harvested over a 4-month period in 1994, beginning in February and ending in May. On plots designated as uncompacted, merchantable trees were directionally felled and removed with a skyline cable logging system. Merchantable trees on remaining plots, plot borders, and the area within the study boundary were directionally felled and removed with a skidder that traveled only on designated paths within the plots and in plot borders. Remaining crowns, unmerchantable trees, dead and live snags, dead and down wood, leaf litter layer, and other debris were removed manually according to protocols. Depending on the treatment, on some plots, it was necessary to replace these materials (except the leaf/litter layer) after compaction was completed.

Post-harvest Treatment

Tree crowns were retained on bole only (BO) plots. On plots where whole trees (WT) and the leaf/litter layer (WT & FF) were removed, total aboveground biomass was removed. All understory vegetation was clipped and removed, and the forest floor was raked away to the mineral soil. Skidders and tractors were permitted on compacted plots, but not on uncompacted plots. A 14-ton vibrating sheep-foot roller was used to treat compacted plots. Severely compacted plots were compacted until there was no change in bulk density after roller passes. Soil bulk density measurements were taken after the roller made one, three, five, and eight passes over the severely compacted treatment. Changes in bulk density usually ceased after five passes. Medium compacted plots received three passes.

All plots were planted to 1-0 red oak (*Quercus rubra* L.), white oak (*Quercus alba* L.), and shortleaf pine (*Pinus echinata* Mill.) in a 6:6:1 ratio using hoedads. Several measurements were recorded for all seedlings including root

collar diameter, root volume, and number of large (>1.0 mm) lateral roots. A 1-meter-radius (3 ft) area was sprayed with glyphosate around each seedling to control competing weeds and to help seedlings become established. Beginning in the second growing season and completed by the end of the third growing season, half of each plot will be kept weed-free until crown closure to permit planted trees to grow freely. The other half of the plot has been allowed to develop naturally into a more complex community of trees and other vegetation. Net primary productivity in these two plant communities will provide direct measures of productivity as influenced by the degree of soil disturbance.

Soil moisture blocks were installed at 10, 20, and 30 cm (4, 8, and 12 in.) deep between rows in the upper and lower halves of all plots in the unsprayed treatment. Soil temperature-moisture cells were installed in the upper and lower halves of weed-free plots in treatment combinations of no soil compaction, severe soil compaction, bole only removed, and whole tree plus forest floor removed at the same depths and between the same rows.

Survival, height, diameter, and crown width of planted trees will be measured at the first, second, third, and fifth year after planting and at 5-year intervals thereafter. Herbaceous or ground flora samples will be sampled on the same schedule for weight, composition, and nutrient element content. Herbaceous samples on 2.3 m^2 (25 ft^2) plots placed across the upper and lower slopes of each plot will be clipped, put into bags, air-dried before being oven dried, weighed, ground in a Wiley mill, and analyzed at the Ohio Research Analytical Laboratory for elemental analyses.

Preliminary Results and Discussion

The 1997 growing season will be the second complete growing season for the Missouri study; several of the older LTSP studies will be entering their seventh growing season. Soil compaction is a major component of the LTSP study. Bulk densities on the Missouri site were comparatively high before compaction treatments were applied (table 2). Soil bulk density generally increased with depth and number of passes. However, only mean bulk density measurements at the 22.9- to 30.5-cm depth were different ($\alpha = 0.05$) from other depths for five passes. Arriving at the moderate level of compaction was difficult because once the soil was compacted, we could not uncompact it and start over. We could only try to compact the severe level more.

Wood (stem only and whole tree) represents the majority of the biomass on the site. The Missouri plots averaged 77, 159, and 207 Mg/ ha of biomass removed for bole only, whole tree, and whole tree plus forest floor removed, respectively.

The amount of nutrients in the biomass on the Missouri site is shown in table 3. Harvesting the whole tree removed considerably more nutrients than harvesting only the merchantable part of the tree. Undoubtedly, the unmerchantable tree components and forest floor had a large concentration of nutrients. The large amount of manganese, iron, and aluminum in the total aboveground removed treatment suggests that removing the aboveground biomass removes a significant amount of these nutrients. This may also mean that these nutrients are either accumulating in the litter or

Table 2.—*Mean soil bulk density measurements following compaction with a 14-ton vibrating sheep-foot roller.*

Depth[1] (cm)	Number of passes with compactor: 0		2		3		5	
	Bulk density (g/cm³)							
0 - 7	1.26	(± 0.28)[2]	1.40	(± 0.20)	1.53	(± 0.12)	1.32	(± 0.09)
8 - 15	1.41	(± 0.23)	1.66	(± 0.25)	1.76	(± 0.19)	1.89	(± 0.08)
16 - 23	1.49	(± 0.20)	1.92	(± 0.17)	1.77	(± 0.12)	1.88	(± 0.15)
24 - 31	1.63	(± 0.29)	1.84	(± 0.04)	1.84	(± 0.04)	2.12	(± 0.39)

[1] 2.54 cm = 1 inch.
[2] Standard deviation

Table 3.—*Nutrients removed by different harvesting treatments from the Missouri LTSP study site.*

Nutrients	Harvesting treatments: Bole only		Whole tree		Total above ground	
	- - - - - - - - - - - - kg/ha - - - - - - - - - - - -					
Macronutrients						
Nitrogen	195.3	(± 58.8)[1]	540.0	(± 166.8)	810.8	(± 238.7)
Phosphorus	9.1	(± 2.3)	25.0	(± 8)	48.3	(± 17)
Potassium	108.7	(± 33.5)	255.6	(± 79)	284.9	(± 91)
Calcium	774.2	(± 238)	2,303.1	(± 474	2,819.2	(± 588.3)
Magnesium	19.9	(± 4)	52.6	(± 16.3)	81.2	(± 28)
Micronuturients						
Manganese	7.1	(± 2.2)	18.0	(± 5.6)	49.4	(± 15.3)
Iron	1.0	(± 0.3)	2.6	(± 08)	17.5	(± 5.4)
Zinc	0.5	(± 0.2)	1.6	(± 0.6)	2.6	(± 0.9
Aluminum	2.1	(± 0.7	7.6	(± 2.5)	81.1	(± 22)
Sodium	0.5	(± 0.3)	1.1	(± 0.8)	1.6	(± 0.6)
Copper	0.1	(± 0.1)	0.3	(± 0.2)	0.6	(± 0.3)
Boron	0.4	(± 0.2)	1.1	(± 04)	1.5	(± 0.6)

[1] Standard deviation

they are more abundant in the understory and herbaceous layers. This warrants further study.

Many more nutrients were removed in the harvest of hardwoods (red oak, *Quercus rubra*, white oak, *Q. alba*, and hickory (*Carya* spp.) than in the harvest of shortleaf pine of similar weight (Mikkelson and Ponder 1995). Also, the comparison showed that large amounts of nutrients are in crown materials.

The number of planted seedlings that died after two growing seasons differed slightly among treatments (table 4). The number of dead seedlings was lowest in the whole tree plus forest floor removed treatment. Nearly half of the dead seedlings in the uncompacted bole only treatment were in one plot. The plot was the first plot planted, and it was planted at the end of a dry weather period. Seedlings in the plot were watered once before rain ended the dry period.

Large numbers of seedlings in all plots suffered damage from rabbits and pack rats during the winter after planting. Stems of many seedlings appeared to have been cut off 3 to 5 cm (1 to 2 in.) above the root collar. The damage appeared to be greatest near debris piles along the edge of plots. Many of the pins and flags used to identify seedlings were also missing. Nevertheless, nearly all of the damaged seedlings produced new stems in the spring of the second year and growth appeared normal.

Table 4.—*The total number of planted and mean number of dead seedlings on LTSP plots in Missouri 2 years after planting.*

Biomass removed	Compaction: None: Seedlings planted	None: No. of dead seedlings	Medium: Seedlings planted	Medium: No. of dead seedlings	Total above ground: Seedlings planted	Total above ground: No. of dead seedlings
Bole only	1,021	94 (± 76)[1]	999	40 (± 28)	691	34 (± 12)
Whole tree	967	49 (± 51)	1,306	65 (± 32)	1,433	65 (± 42)
Whole tree + forest floor	910	29 (± 21)	1,160	36 (± 17)	950	33 (± 19)

[1] Standard deviation

Plastic tree protectors were placed around all seedlings in the second year. Although preliminary observations showed that some of the protectors were missing, overall, fewer seedlings were damaged. Damaged seedlings occured where protectors were missing or had been partially destroyed.

Trends in treatment differences for nutrient concentrations in herbaceous vegetation were not apparent after year one, but both N and Al differed ($\alpha = 0.05$) between treatments after year two (table 5). Data for the 2 years showed that in year two N, K, and Ca decreased and Fe, Zn, and Al increased compared to year one.

Summary

While preliminary results can be interesting, it will be a number of years before trends and real differences can be rigorously tested and substantiated. The results will help us better understand how organic matter and compaction impact the behavior of ecosystems and how these properties of soil productivity can be manipulated to sustainability of our Nation's forests.

This is a long-term study that has been established in several ecosystems. Thirty-nine LTSP installations currently are operational in the United States, and another three are in early establishment stages in central Idaho (Powers and Fiddler, in press, 1997). Four others were installed in interior British Columbia by the B. C. Ministry of Forests and several others are planned. In all, nearly 4 dozen common-protocol installations will exist by the end of 1997 (fig. 1).

Table 5.—*Mean concentration of nutrients in herbaceous vegetation in plots of the Missouri long-term soil productivity study for year one and year two after site preparation and artificial regeneration.*

Treatment		Nutrient element						
		N	P	K	Ca	Fe	Zn	Al
Biomass removed	Compaction							
		Percent	- - - - - - - - -		*ppm*	- - - - - - - - -		
				Year one				
Bole only	None	1.3a[1]	748a	576a	12,051a	77a	49a	87a
Bole only	Medium	1.3a	753a	657a	20,219a	78a	43a	60a
Bole only	Severe	1.6a	821a	680a	16,739a	90a	41a	67a
Whole tree	None	1.5a	798a	554a	17,332a	76a	43a	78a
Whole tree	Medium	1.4a	1,015a	681a	26,017a	71a	33a	98a
Whole tree	Severe	1.6a	806a	670a	16,745a	83a	43a	74a
Whole tree + forest floor	None	1.4a	833a	648a	12,597a	93a	41a	72a
Whole tree + forest floor	Medium	1.4a	868a	676a	25,750a	78a	39a	82a
Whole tree + forest floor	Severe	1.3a	798a	615a	18,925a	79a	41a	74a
				Year two				
Bole only	None	1.6a	1,251a	732a	11,822a	93ab	99a	55b
Bole only	Medium	1.1b	1,031a	462a	13,179a	56b	67b	58b
Bole only	Severe	1.1b	899a	782a	11,262a	90ab	59b	111ab
Whole tree	None	0.9b	853a	522a	9,839a	71ab	45b	73b
Whole tree	Medium	1.1b	1,162a	536a	11,726a	90ab	54b	70b
Whole tree	Severe	1.2ab	930a	470a	11,481a	80ab	63b	90ab
Whole tree + forest floor	None	0.9b	783a	417a	10,429a	157a	63b	146ab
Whole tree + forest floor	Medium	1.2ab	1,357a	428a	12,358a	156a	53b	218a
Whole tree + forest floor	Severe	0.9b	777a	569a	11,603a	70ab	57b	96ab

[1] Values in a column for a year are not significantly different ($\alpha = 0.05$) when followed by the same letters.

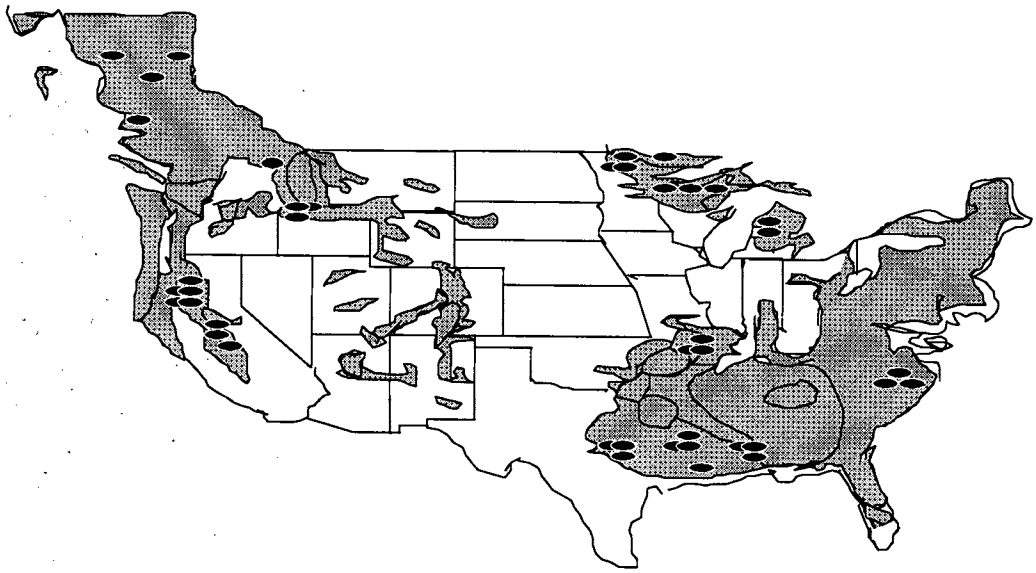

Figure 1.—General range of commercial forest in the United States and British Columbia. Ovals indicate individual LTSP installations.

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Our job at the North Central Forest Experiment Station is discovering and creating new knowledge and technology in the field of natural resources and conveying this information to the people who can use it. As a new generation of forests emerges in our region, managers are confronted with two unique challenges: (1) Dealing with the great diversity in composition, quality, and ownership of the forests, and (2) Reconciling the conflicting demands of the people who use them. Helping the forest manager meet these challenges while protecting the environment is what research at North Central is all about.

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