HERBACEOUS PRODUCTIVITY AND SPECIES COMPOSITION ASSOCIATED WITH HARVEST INTENSITIES IN A SOUTHERN MICHIGAN MIXED HARDWOOD FOREST [1/]

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Herbaceous productivity and species composition were measured in an uneven-aged, mixed hardwood stand before and one year after receiving four different intensities of harvest cuttings. Productivity was significantly higher in the harvested areas (153 $g/m^2/yr$) than in the uncut areas (37 $g/m^2/yr$), but no significant differences occurred between clearcut, shelterwood and group selection harvest cuts. Resulting slash deposits created heterogenous micro-environmental patterns throughout the study area, irrespective of cutting treatment. Whereas species composition and diversity remained unchanged in control areas, they increased in the harvested areas. In addition to 29 resident species, eight new invading species were observed after canopy removal. Herbaceous production estimates are contrasted with other reported studies.

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INTRODUCTION

The impact of commercial logging upon the herbaceous understory in the eastern deciduous forests has been largely neglected. Instead, most post-cutting studies have concentrated on tree reproduction (Boivin 1971; Wendel and Trimble 1968; Metzger and Tubb 1971; Minckler and Woerheide 1965). However, there is a need to examine shifts in herbaceous productivity and species composition after a site has been logged. The rapid growth of early successional species may be important in preventing early nutrient loss (Marks and Bormann 1972). The herbs become competitors with the newly established tree species. Also, many herbaceous species growing in forest openings have food value for wildlife (McGaffey and Creed 1969).

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Herbaceous response to canopy removal can be examined in several ways. Mueller-Dombois (1965) inventoried a number of different sites ranging in age from the oldest to the most recently logged. Data collected this way, however, only describes changes in broad terms since site differences, rather than time, may account for species differences. Of greater usefulness are such studies as reported by Dryness (1973) where vegetative development was followed for seven years after logging on a Pacific Northwest site. By successively sampling permanent plots, total plant cover was found to increase from 15% in the first year to 49% in the second year, and to 79% in the fifth year after slash burning. The number of plant species also increased dramatically during the same period. Residual herbs were dominant during the first two years but a cover of invading herbs surpassed these by the third year. Dryness did not estimate herbaceous net productivity in terms of dry weight. Though productivity estimates have been made for eastern deciduous forests (Eber 1972; Siccama, Bormann, and Likens 1970; Whittaker and Woodwell 1969; Whittaker 1966, 1968), none have been made for recently logged areas.

Furthermore, canopy removal undoubtedly changes many micro-environmental factors which affect herbaceous productivity. Slash that often covers extensive portions of cutting sites can create sheltered microsites that have different micro-environmental parameters than more exposed sites. While influence of such micro-environmental heterogeneity should be recognized in any post-cutting studies, little documentation of such is available. The objective of this study was to record such changes and document the herbaceous productivity and species diversity associated with the amount of tree canopy removed.

METHODS

Site Description

The site is a 17.6 ha (44 acre) stand of oak and mixed hardwoods in the Fred Russ Experimental Forest, a property of Michigan State University, located in southwestern Michigan. Basal area averaged 31.2 m^2/ha (136 ft^2/A) with *Quercus rubra* L., *Quercus alba* L., *Quercus velutina* Lam., *Acer saccharum* Marsh. and *Prunus serotina* Ehrh. the major tree species. The topography is level except for one minor depression leading to an adjoining swamp (Fig 1).

Kalamazoo and Oshtemo are the two major soil series present. Both have similar soil properties, being well-drained typic hapludalfs which have developed in gravelly loam and sandy loam material. The Oshtemo soils differ from the Kalamazoo soils in thickness and amount of clay in the B2T horizon. This horizon has a thickness of 20-31 cm and is a sandy loam in the Oshtemo and 25-56 cm and a sandy clay loam to clay loam in the Kalamazoo. Annual precipitation over 30 years averaged 1092 mm (43 in.). Rainfall during May 1 to September 15 averages 417 mm, but during the two growing seasons of the study, rainfall was 317 mm (1971) and 376 mm

(1972). While spring vegetative growth begins between April 20 and May 1, trees are not in full leaf until about May 15 and much of the herbaceous growth does not appear before May 30. Termination of the growing season was assumed to be September 15 since most species are then in a state of senescence.

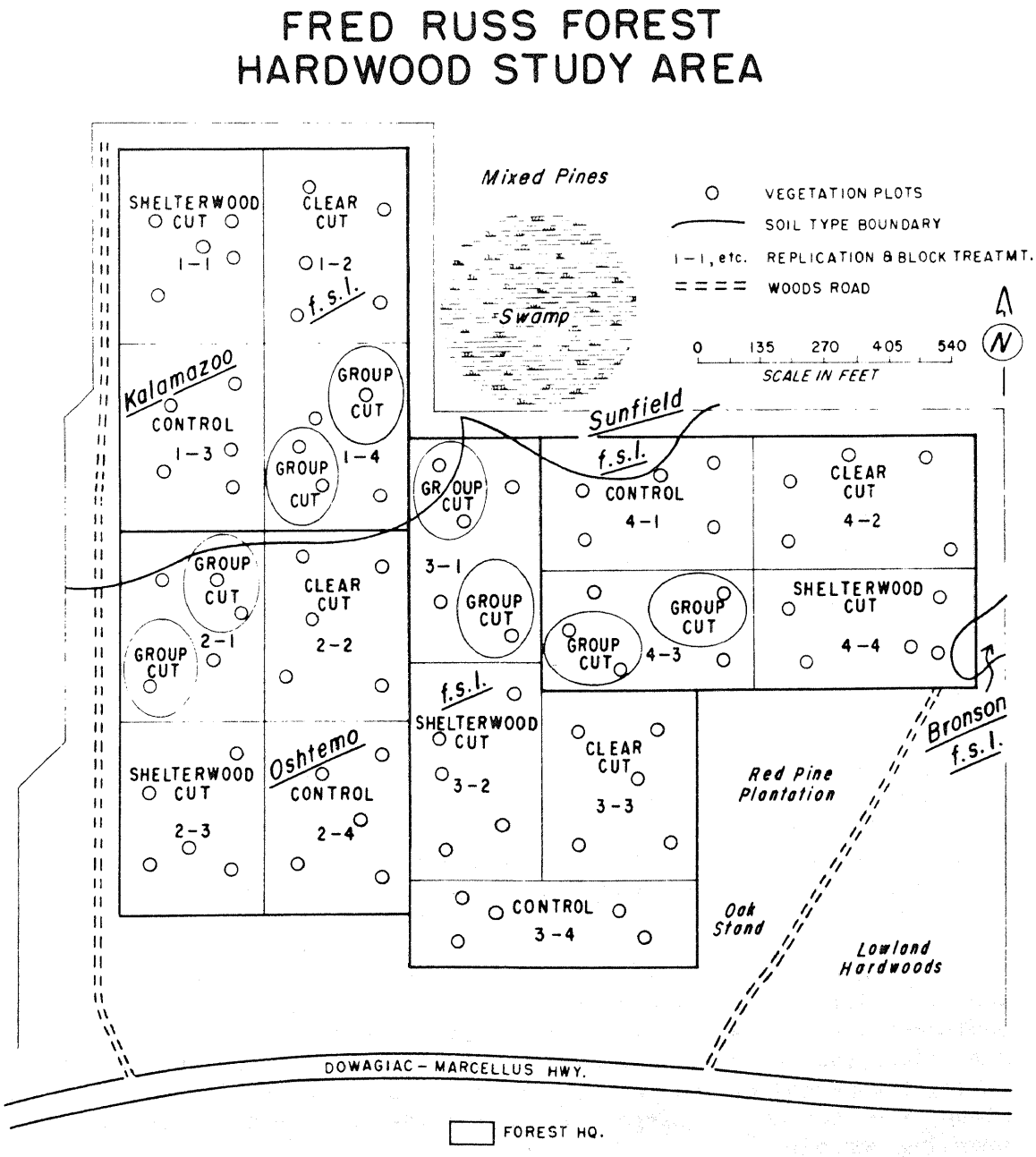

Figure 1. Arrangement of plots in the Fred Russ Forest hardwood study area.

Plot Establishment and Canopy Removal

The stand was divided into 16 rectangular areas, each 1.1 ha in size (Fig 1). Four treatments, of varying crown densities, were arranged in a randomized block design. The treatments were: control, in which all trees were left uncut (31.2 m^2/ha basal area); shelterwood, in which 20-25 large trees (6.2 m^2/ha basal area) were left uncut; group selection, in which all trees were removed within a 0.25 ha area; and clearcut, in which all trees were removed. Commercial cutting operations were conducted from October to December 1971. Permanent plots were established and the herbaceous vegetation surveyed before and after canopy removal. Five 3m x 3m plots were randomly located in each treatment area during the summer of 1971 (Fig 1). After canopy removal, microsite conditions became more heterogeneous due to extensive slash deposits. Plots under slash deposits had no herbaceous growth while those in the open had luxuriant growth. To compensate for the increased heterogeneity, 64 of the original 80 plots were expanded from 3m x 3m to 20m x 20m and then subsampled.

Productivity Measurements

A visual estimate of leaf area similar to that used by Cristofolini (1970) was made with the aid of a portable m^2 frame and templates (Fig 2). The circular .01 m^2 or rectangular .02 m^2 template was placed directly on the plant leaves and total leaf area of each species within the frame was recorded. To test the accuracy of this technique, leaf area as measured by the templates was compared to values obtained by placing a square centimeter grid over the foliage and counting the number of squares occupied. Template accuracy varied according to species; large, broadleaf species being more accurately measured than small, multi-leaf species such as the grasses. Based on these observed errors, corrections were made in original field estimates of leaf area to more closely approximate values obtained by the grid method.

Leaf area was converted into dry weight using regression equations developed for the 29 most abundant species (Appendix I). The remaining species, 7 percent of the total leaf area, were not abundant enough to permit equation development. Above-ground plant parts were harvested after leaf area had been recorded. Plant parts were oven dried at 85° C for 48 hours, and the dry weight regressed on leaf area.

Leaf area was recorded once during the pre-cutting season of 1971 and twice during the post-cutting season of 1972 (June 12 - July 7 and September 5 - September 15). Above ground annual net productivity (gm/m^2) was calculated by using only the species leaf area value that occurred during the period of its peak standing biomass. Peak biomass was determined by selecting the largest value recorded in the two post-cutting sampling periods.

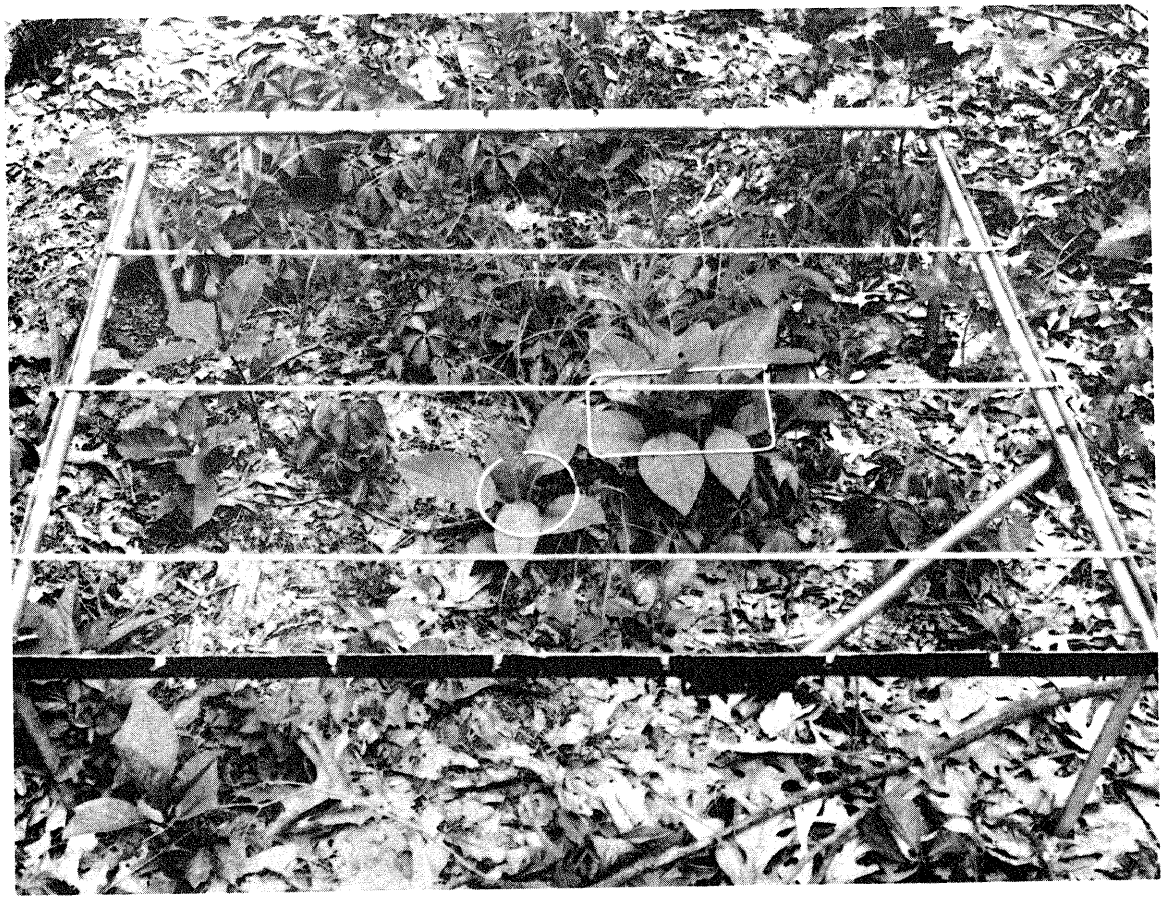

Figure 2. Portable m^2 sampling frame with .01 m^2 and .02 m^2 templates used in estimating leaf area.

Species Composition Measurements

Shifts in species composition were estimated from leaf area measurements of each species in one 3m x 3m permanent plot located in each treatment area. Measurements were made the year before and the year after cutting. None of these plots were modified after cutting. Members of *Poaceae* were recorded as one multi-species group. *Geum canadensis* Jacq. and *Sanicula canadensis* L. were considered as one species group as was *Polygonatum biflorum* (Walter) Ell. and *Smilacina racemosa* (L.) Desf. Voucher specimens are located in the Department of Forestry, Michigan State University.

Species diversity was also calculated for the 37 most abundant species using both the Shannon-Wiener function (H') and Simpson's index (D). Fourteen additional plots ranging in productivity from 11 gm/m^2 to 507 gm/m^2 were selected in treatment areas for comparing diversity calculations with productivity values.

RESULTS

Productivity

Leaf area estimates for the 1971 growing season showed that herbaceous productivity did not differ between treatment and control areas before cutting. During the 1972 growing season net above-ground herbaceous productivity differed significantly ($P<.05$) for all cut areas (142.6 gm/m^2) and the uncut control areas (34.4 gm/m^2). However, there were no significant differences ($P<.05$) between the various cutting treatments (Table 1). Productivity values are probably underestimated since the leaf areas of the least abundant species were not converted to a dry weight basis. Assuming that these miscellaneous species had a leaf area-dry weight ratio equal to the average leaf area-dry weight ratio for the 29 most abundant species, productivity values would be increased by 7% resulting in productivity of 152.6 gm/m^2 in cut areas and 36.8 gm/m^2 in control areas.

Sampling each plot twice during the growing season provided the opportunity to observe different seasonal patterns of species productivity. Species were grouped according to the period when maximum standing biomass was observed, i.e., early or late summer (Table 2). In the first group, biomass was greater in the late summer. The second group showed greater biomass in early summer. The third group had approximately the same biomass at both sampling periods. A variety of growth patterns is thus evident, and in order to achieve accurate productivity estimates, each species must be sampled during the period of its peak biomass. Compare in table 2 the mean dry weight for all species in the first sample period (68.3 gm/m^2) with the second sample period (130.8 gm/m^2) to that of the mean annual dry weight (142.6 gm/m^2) as determined by using the maximum standing biomass value found for each species. The error inherent in a single sampling period is easily seen.

Table 1. Mean herbaceous leaf area (gm/m^2) by cutting treatments.

Group Selection	Shelterwood	Clear Cut	Control	Level of Significance
153.4	138.9	135.3	34.4	.05

Figures underlined are not significantly different.

Table 2. Mean plant weight (gm/m^2) of selected species at peak biomass for two sampling periods, 1972.

Species	Mean weight and standard error June 12 - July 7		Mean weight and standard error Sept. 5 - Sept. 24	
Increasing Biomass				
*+ *Phytolacca americana*	6.00	(.93)	33.25	(3.75)
*+ *Poaceae* (species group)	18.71	(5.50)	26.10	(4.50)
*+ *Conyza canadensis*	2.52	(.72)	12.74	(2.33)
*+ *Circaea quadrisulcata*	3.10	(.65)	8.17	(1.26)
+ *Geranium robertianum*	1.90	(.37)	5.95	(.74)
Rubus spp.	.97	(.57)	3.14	(.58)
+ *Cirsium* spp.	1.00	(.46)	3.87	(.83)
Quercus rubra	1.75	(.46)	3.14	(.53)
Oxalis stricta	.00	(.00)	3.13	(.73)
Geum canadensis and *Sanicula canadensis*	.36	(.12)	2.79	(.68)
Ulmus spp.	1.13	(.30)	2.99	(.32)
Sassafras albidum	.96	(.31)	1.92	(.54)
Physalis subglabrata	.20	(.08)	1.72	(.60)
Hedeoma pulegioides	.00	(.00)	1.73	(.73)
Cornus florida	.26	(.10)	.78	(.41)
Acer rubrum	.09	(.04)	.26	(.06)
Polygonatum biflorum and *Smilacina racemosa*	.12	(.06)	.38	(.14)
Decreasing Biomass				
*+ *Parthenocissus quinquefolia*	13.20	(1.38)	7.69	(.69)
* *Podophyllum peltatum*	2.88	(.55)	.48	(.25)
Viola spp.	1.84	(.28)	1.26	(.16)
* *Galium circaezans*	5.58	(1.33)	3.34	(1.27)
Osmorrhiza claytonii	1.57	(.17)	1.26	(.19)
Quercus alba	.44	(.13)	.22	(.06)
Amelanchier spp.	.43	(.11)	.20	(.07)
Phryma leptostachya	.19	(.06)	.43	(.16)
Constant Biomass				
Ribes spp.	1.23	(.34)	1.76	(.43)
Toxicodendron radicans	.39	(.14)	.45	(.15)
Acer saccharum	.42	(.17)	.67	(.17)
Tovara virginiana	.31	(.21)	.51	(.14)
Prunus serotina and *Prunus virginiana*	.73	(.11)	.52	(.10)
Total	68.30		130.84	

* These species comprise 76% of the standing crop June 12 - July 7.

\+ These species comprise 75% of the standing crop September 5 - 24.

Changes in Species Abundance

Canopy removal caused a significant shift in the abundance of some species. However, no difference in the pattern of shifting was noted among the various types of canopy removal and data from all these areas were combined (Table 3).

Parthenocissus quinquefolia (L.) Planch. dominated the herbaceous layer the year before cutting (1971) with 64% of the total leaf area.[1/] Four other major species, *Ulmus rubra* Muhl., *Viola* spp., *Osmorrhiza claytonii* (Michx.) C. B. Clark and *Circaea quadrisulcata* Maxim., accounted for 18% of the leaf area. The remaining 18% of the leaf area was distributed among 32 other species. After cutting, *P. quinquefolia* still remained the largest component (32%) of the total leaf area. However, *Phytolacca americana* L. and *C. quadrisulcata* became major dominants, increasing to a total of 20% of the total leaf area. Four other species, *O. claytonii*, *Tovara virginiana* (L.) Raf., *U. rubra* and *Q. rubra*, contributed another 14%. Resident species, those present in one or more plots before cutting, and invading species, those not present in any plots before cutting, increased their proportion of total leaf area at the expense of *P. quinquefolia* which decreased 32% after canopy removal. Total mean leaf area rose from 7,194 cm^2/m^2 in 1971, to 11,714 cm^2/m^2 in 1972, an increase of 63%. Over 43% of this increase is attributed to resident species.

In contrast to cutting treatment areas, species composition remained relatively unchanged in control areas (Table 4). During the two growing seasons, *P. quinquefolia* was the single dominant species. Resident species which had significant changes in leaf areas were *Cornus florida* L., *Podophyllum peltatum* L., *G. canadensis* and *S. canadensis*. Similar shifts have been described for a mature undisturbed *Acer saccharum* - *Fagus grandifolia* stand and it was concluded that the changes were non-directional (Schneider 1966). None of the invading species found in treatment areas were present in control areas.

Species Diversity

Canopy removal increased mean diversity in all treatment areas, H'=2.48 in 1971 to 3.38 in 1972. Also, the mean number of species per plot doubled, 4.5/m^2 in 1971 to 8.7/m^2 in 1972. Since only eight new species were found in the 1972 survey, increasing the total number of species from 29 to 37, this increase in diversity is not primarily due to these new species. Spatial patterns of the resident species have also shifted, distributing these species more uniformly over all plots and influencing the equitability component of the diversity index. Resident species (numbers 1, 5, 7, 16, 17, 22, 23, 24, 26 and 28) occupied more quadrats after cutting (Fig 3). These species have been successful in invading newly available sites created by canopy removal.

[1/] Percentage values calculated from Tables 3 and 4.

Table 3. Changes in mean leaf area (percent of 1 m^2) for each species in harvest cutting treatment areas between the years 1971 and 1972.

	Species	Mean leaf area and standard error - 1971	Mean leaf area and standard error - 1972	Difference 1971-1972	"T" sig.[1/]	Changes in proportion 1971 to 1972
Herbs						
1	Circaea quadrisulcata	3.86 (.98)	10.81 (1.92)	6.95	**	+ 3.8
+ 2	Cirsium spp.	.00 (.00)	.34 (.32)	.34		+ .2
+ 3	Conyza canadensis	.00 (.00)	2.05 (.68)	2.05	**	+ 1.7
4	Galium circaezans	.51 (.20)	1.26 (.38)	.76		+ .4
5	Geranium robertianum	1.40 (.67)	2.51 (.46)	1.11		+ .3
6	Geum canadensis and Sanicula canadensis	.65 (.20)	2.61 (.57)	1.96	**	+ 1.5
+ 7	Hedeoma pulegioides	.00 (.00)	.29 (.14)	.29		+ .2
8	Hydrophyllum canadense	.00 (.00)	.01 (.01)	.01		
+ 9	Lactuca saligna L.	.00 (.00)	.71 (.21)	.71	**	+ .6
10	Osmorrhiza claytonii	2.25 (.33)	3.61 (.91)	1.36		
+11	Oxalis stricta	.00 (.00)	1.25 (.33)	1.25	**	+ 1.1
12	Parthenocissus quinquefolia	46.51 (4.49)	37.94 (3.74)	-8.57		-32.2
13	Phryma leptostachya	1.31 (.35)	.94 (.28)	- .37		- 1.0
+14	Physalis subglabrata	.00 (.00)	.17 (.08)	.17	*	+ .1
+15	Phytolacca americana	.00 (.00)	12.55 (1.93)	12.55	**	+10.6
16	Poaceae (species group)	.62 (.30)	3.04 (.54)	2.42	**	+ 1.7
17	Podophyllum peltatum	.26 (.15)	3.57 (.99)	3.30	**	+ 2.6
+18	Polygonatum biflorum and Smilacina racemosa	.22 (.09)	1.09 (.45)	.87		+ .6
19	Polygonatum sagittatum	.00 (.00)	1.24 (.63)	1.24	**	+ 1.1
20	Toxicodendron radicans	.85 (.25)	1.02 (.27)	.17		- .3
21	Tovara virginiana	1.76 (.80)	4.19 (1.23)	2.43		+ 1.2
22	Viola spp.	3.80 (.83)	3.38 (.47)	- .41		- 2.4

Table 3. (Continued)

Species	Mean leaf area and standard error - 1971	Mean leaf area and standard error - 1972	Difference 1971-1972	"T" sig.1/	Changes in proportion 1971 to 1972
Trees					
23 *Acer rubrum*	.33 (.11)	.56 (.16)	.23		+ .1
24 *Acer saccharum*	1.03 (.24)	3.28 (.63)	2.25	**	+ 1.4
25 *Carya cordiformis*	.23 (.13)	.00 (.00)	- .23		- .3
26 *Cornus florida*	.66 (.33)	2.72 (.77)	-2.06		+ .2
27 *Ostrya virginiana*	.00 (.00)	.40 (.26)	.40		+ .3
28 *Prunus serotina*	.18 (.08)	1.10 (.19)	.92	**	+ .3
29 *Prunus virginiana*	.68 (.22)	1.05 (.38)	.37		
30 *Quercus alba*	.13 (.05)	.10 (.04)	- .03		- .1
31 *Quercus rubra*	.13 (.06)	4.59 (.66)	4.46	**	+ 3.7
32 *Sassafras albidum*	.17 (.07)	1.73 (.68)	1.56	*	+ 1.2
33 *Ulmus rubra*	3.06 (.80)	3.82 (.63)	.76		- 1.0
Shrubs					
34 *Crataegus* spp.	.04 (.03)	.08 (.08)	.04		
35 *Ribes* spp.	.54 (.15)	1.19 (.50)	.65	*	+ .9
36 *Rubus* spp.	.02 (.20)	1.94 (.56)	1.92	**	+ 1.6
37 *Viburnum lentago*	.71 (.22)	.00 (.00)	- .71	**	- 1.0

1/ Test of significance between 1971 and 1972 means

\+ Invading species

* = .05

** = .01

Table 4. Changes in mean leaf area (percent of 1 m^2) for each species in control areas between the years 1971 and 1972.

	Species	Mean leaf area and standard error - 1971	Mean leaf area and standard error - 1972	Difference 1971-1972	"T" sig.[1/]	Changes in proportion 1971 to 1972
Herbs						
1	Circaea quadrisulcata	10.89 (2.35)	7.39 (1.71)	-3.50		- 1.2
+ 2	Cirsium spp.					
+ 3	Conyza canadensis					
4	Galium circaezans	.14 (.14)	.06 (.06)	- .08		- .2
5	Geranium robertianum	2.33 (1.16)	.67 (.26)	-1.66		- 1.5
6	Geum canadensis and Sanicula canadensis	1.67 (.48)	2.56 (.68)	.89		+ 1.9
+ 7	Hedeoma pulegioides					
8	Hydrophyllum canadense	4.17 (1.96)	2.00 (.83)	-2.17		- 1.6
+ 9	Lactuca saligna					
10	Osmorrhiza claytonii	2.53 (.70)	1.58 (.32)	- .95		- .5
+11	Oxalis stricta					
12	Parthenocissus quinquefolia	57.39(10.57)	43.56 (7.34)	-13.83		+ .1
13	Phryma leptostachya	.42 (.31)	.64 (.26)	.22		+ .5
+14	Physalis subglabrata					
+15	Phytolacca americana					
16	Poaceae (species group)	.11 (.11)	.03 (.03)	- .08		- .1
17	Podophyllum peltatum	.00 (.00)	2.06 (.72)	2.06	**	+ 3.0
18	Polygonatum biflorum and Smilacina racemosa	.91 (.14)	.22 (.15)	- .69		+ .1
+19	Polygonatum sagittatum					
20	Toxicodendron radicans	.14 (.14)	.00 (.00)	- .14		- .2
21	Tovara virginiana	.69 (.69)	1.06 (.64)	.37		+ .7
22	Viola spp.	2.28 (.76)	1.55 (.41)	- .87	*	- .3

Table 4. (Continued)

	Species	Mean leaf area and standard error - 1971	Mean leaf area and standard error - 1972	Difference 1971-1972	"T" sig.[1]	Changes in proportion 1971 to 1972
Trees						
23	Acer rubrum	.06 (.06)	.06 (.04)	.00		
24	Acer saccharum	.69 (.27)	1.00 (.31)	.31		+ .7
25	Carya cordiformis	.28 (.19)	.00 (.00)	- .28		- .3
26	Cornus florida	1.69 (.94)	2.86 (1.30)	1.17		+ 2.3
27	Ostrya virginiana					
28	Prunus serotina	.97 (.37)	.11 (.09)	- .86		- .9
29	Prunus virginiana	.75 (.45)	.14 (.09)	- .61		- .6
30	Quercus alba	.28 (.17)	.17 (.12)	- .11		- .1
31	Quercus rubra					
32	Sassafras albidum					
33	Ulmus rubra	1.56 (.48)	.92 (.36)	- .64	*	- .4
Shrubs						
34	Crataegus spp.					
35	Ribes spp.	1.67 (.49)	1.06 (.44)	- .61		- .3
36	Rubus spp.					
37	Viburnum lentago	.58 (.30)	.00 (.00)	- .58		- .6

[1] Test of significance between 1971 and 1972 means

+ Invading species

* = .05

** = .01

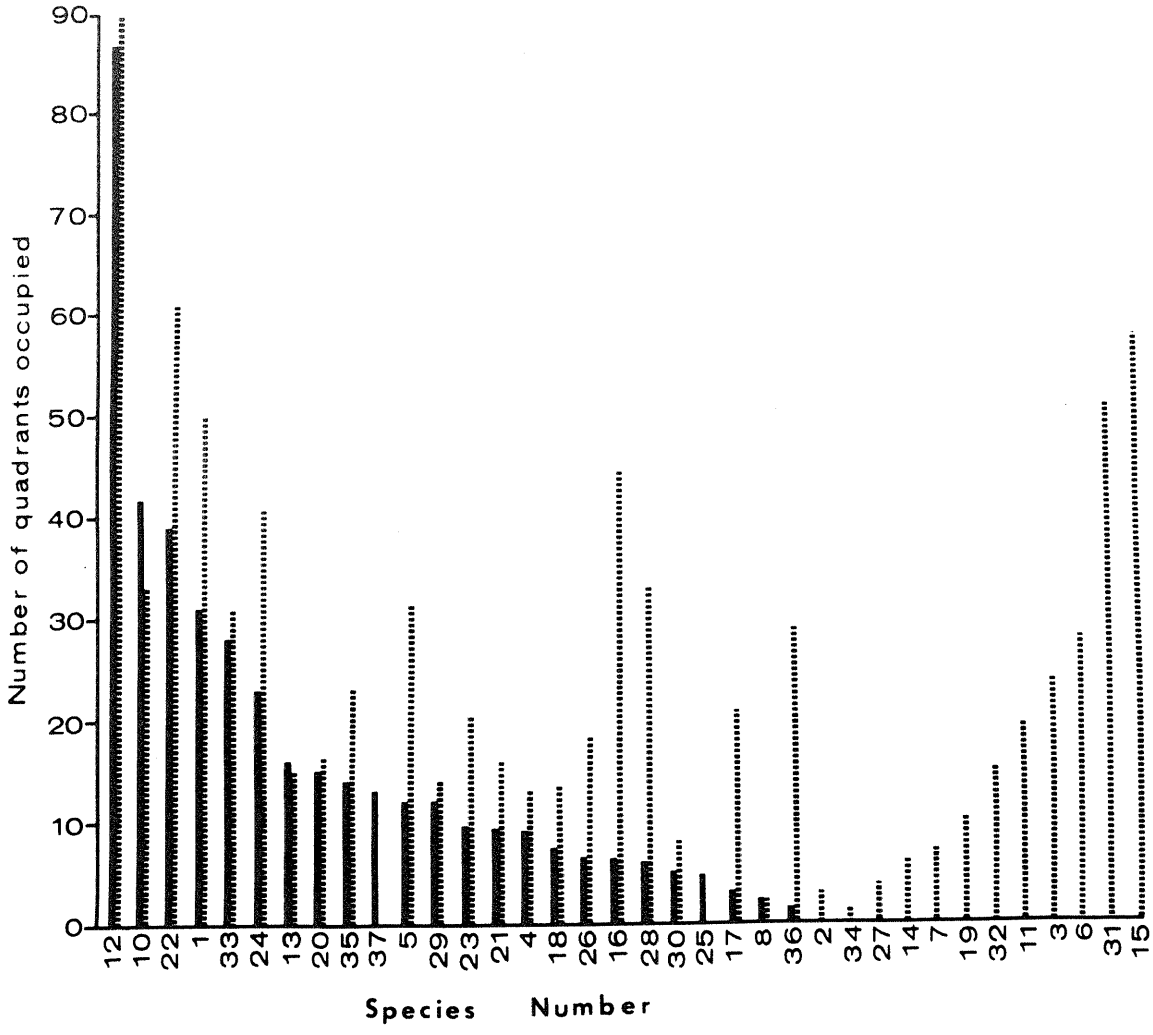

Figure 3. Number of quadrats occupied by species in harvest cutting treatment areas during 1971 (black line) and 1972 (dash line). Refer to Table 2 for species names.

Mean diversity in the control areas remained stable, H'=2.27 in 1971 and 2.26 in 1972. While these areas had a slight increase in number of species per plot, 4.1/m^2 in 1971 to 4.9/m^2 in 1972, this small shift is probably due to new random establishments of resident species.

The relationship between diversity and productivity in areas of canopy removal is shown in table 5. The number of species per plot increased with increasing productivity up to 229 gm/m^2, peaking at 17 species and then decreasing to 12 species at higher productivity (Table 5). The two diversity indices follow a similar pattern, the highest diversity being found in intermediate productivity plots (132 to 299 gm/m^2). Some of the lowest diversity values are found in the two most productive plots.

These plots still contained a large number of species but productivity is concentrated in one species, *P. americana*. This results in the low evenness values (J) and explains why diversity indices are so low.

Table 5. Changes in evenness and three measures of diversity; number of species, Shannon-Weiner function, and Simpson's index, in relation to changes in net productivity (gm/m^2).

Dry Weight $gm.m^{-2}$	Number of Species	Shannon-Weiner function (H')	Simpson's index (D)	Evenness H'/H' max. (J)
11	5	1.827	.732	.786
19	5	1.901	.732	.822
40	6	1.339	.844	.518
50	6	2.973	.634	1.150
75	9	2.485	.749	.784
106	11	1.551	.548	.409
132	12	3.033	.435	.846
165	16	3.651	.915	.913
196	14	2.727	.786	.716
229	17	4.362	.918	1.067
292	11	1.458	.569	.348
303	12	2.641	.784	.736
425	10	1.192	.321	.359
507	12	1.538	.448	.429

DISCUSSION

Our data show that canopy removal causes increases in herbaceous productivity and shifts in species composition within the herb strata. However, the amount of increased productivity and shifts in species composition did not vary according to the intensity of canopy removal. Slash deposits probably had a more profound influence on the herbaceous microenvironment than did types of canopy removal. In and around slash deposits microenvironmental conditions were shadier, cooler and more humid than in exposed sites (Appendix II). Herbaceous productivity recorded near or under slash deposits was extremely low as compared to the exposed sites.

The slash appeared to be randomly distributed across all treatment areas which in turn caused a random pattern of herbaceous productivity and species composition. Clearcut areas had larger amounts of slash than group selection or shelterwood areas but this was concentrated in a few large piles. Thus it is probable the slash deposits, not the degree of canopy removal, exerts the dominant influence on herbaceous productivity and species composition. Conceivably, manipulation of slash deposits could be a useful tool in creating microsites which would encourage desirable understory species and discourage their competitors.

Net herbaceous productivity at Fred Russ Forest was compared with other forest ecosystems of various ages, densities and locations (Table 6). The uncut control areas of Fred Russ Forest had a productivity value of 37 $gm/m^2/yr$. This value is slightly lower than for sites in Tennessee and Nova Scotia and much higher than in New England, California, Louisiana and Germany. The cutting treatment areas had an average productivity of 153 $gm/m^2/yr$. This figure is high compared to partially cut stands in Louisiana but low compared to a one-year-old abandoned field.

These comparisons suggest that herbaceous productivity at Fred Russ Forest was above average before canopy removal. It must still be determined if this high productivity had a direct influence upon the number of new invading species appearing the year after cutting. Dryness (1970) suggests that areas of high productivity may more fully occupy a site with less available space for invading species. By counting the number of species not observed in both of two time periods, one year before cutting and seven years after cutting, shifts in species composition were shown. In an unproductive site, 11 species were not observed in both periods while in a highly productive site only five species were not observed in both periods.

At Fred Russ Forest, little change in species composition occurred. Only eight principle invading species were observed and all 29 of the resident species were found after cutting. Many resident species are thriving in the cutting areas, and these species successfully invaded new microsites created by cutting (Fig 3). These data agree with those of Dryness and suggest that sites of high productivity will have little species change, while sites of low productivity may have a large species change, after cutting.

Table 6. Comparisons of above ground net herbaceous productivity ($gm/m^2/yr$) between Russ Forest and other ecosystems. All data concerns only the herbaceous strata.

Ecosystem	Above-ground productivity ($gm/m^2/yr$)
1. Russ Forest (control areas), 80 yrs., 31 m^2 h^{-1}	37
2. Mixed hardwood forest (Oak Ridge, Tenn.), 4 yr. old opening	45 (1)
3. Red-white oak forest (Smoky Mts., Tenn.), climax stand, 22 m^2 h^{-1}	35 (2)
4. Red oak forest (Smoky Mts., Tenn.), climax stand, 24 m^2 h^{-1}	52 (2)
5. Dense hardwood (N. Brunswick-Nova Scotia)	51 (3)
6. Open mixed hardwood-conifer (Nova Scotia)	44 (3)
7. Fagetum forest (West Germany), 120 yrs. dense	1 (4)
8. Oak-pine woodland (Brookhaven, N.Y.), 56 yrs., 16 m^2 h^{-1}	2 (5)
9. Pine-oak woodland (St. Catalina Mts., Calif.), climax stand, 26 m^2 h^{-1}	3 (6)
10. Sugar maple, beech, birch forest (Hubbard Brook, N.H.), 67 yrs., 23 m^2 h^{-1}	10-16 (max. 29) (7)
11. Pine-hardwood forest (Louisiana) evenage plantation, 17 m^2 h^{-1}	10 (8)
12. Russ Forest (cutover areas)	153
13. Pine-hardwood forest after elimination of hardwoods (Louisiana)	62 (8)
14. Oldfield first year after abandonment (Georgia)	494 (9)

1. Cristofolini 1970
2. Whittaker 1966
3. Telfer 1971
4. Eber 1972
5. Whittaker and Woodwell 1969
6. Whittaker and Woodwell 1969
7. Siccama et al. 1970
8. Blair 1971
9. Odum 1960

Although an increase in both species diversity and productivity was observed in cutting areas, as compared to uncut control areas, the relation between the two is complex. Margalef (1969) suggests these two parameters vary in an inverse logarithmic relationship, and Odum (1971) feels that while productivity affects species diversity, the two are not related in any simple manner. Odum cites examples of very productive communities with both high diversity (coral reef) or low diversity (a temperate estuary). We observed a decrease in diversity on the most productive and least productive plots, and this serves to support Odum's position that the relationship between diversity and productivity is unclear and should not be loosely generalized.

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Appendix I. Regression equations converting leaf area (cm x 10^2) to dry weight (gm).

	Regression equation (Y=wgt.(gm), X=leaf area (cm x 10^2)[5/]	Coefficient of variation	Mean sample weight and standard errors	Standard error of single measurement at mean sample weight	Sample size
1 *Podophyllum peltatum* L.	Y = .01 + .78X	.59	3.8 (.37)	1.48	15
2 *Conyza canadensis* (L.) Cronq.[1/]	Y = 6.84 + 3.56X	.84	19.0 (2.76)	11.07	15
3 *Cirsium* spp.	Y = -1.07 + 1.46X	.76	4.14 (0.4)	1.53	14
4 *Phytolacca americana* L.	Y = 3.07 + 1.35X	.75	41.0 (5.65)	26.23	20
5 *Quercus alba* L.	Y = .14 + .42X	.79	2.6 (.26)	.99	12
6 *Geum canadensis* Jacq.[2/]	Y = 1.16 + .99X	.59	7.5 (.72)	1.11	14
7 *Ulmus* spp.	Y = .30 + .65X	.96	12.4 (.52)	2.46	21
8 *Galium circaezans* Michx.	Y = - .40 + 1.58X	.69	10.5 (1.25)	3.56	8
9 *Acer rubrum* L.	Y = - .78 + .53X	.91	1.8 (.1)	.47	24
10 *Oxalis stricta* L.	Y = -2.05 + 1.47X	.95	10.3 (.76)	2.50	10
11 *Prunus serotina* Ehrh.[3/]	Y = .28 + .47X	.84	3.2 (.14)	.92	27
12 *Hedeoma pulegioides* (L.) Pers.	Y = - .50 + 2.36X	.96	11.8 (.71)	2.38	10
13 *Cornus florida* L.	Y = -1.70 + .66X	.87	7.2 (.56)	2.63	21
14 *Poaceae* (species group)	Y = -3.05 + 3.34X	.88	8.31 (.77)	2.56	10
15 *Acer saccharum* Marsh.	Y = -1.80 + .86X	.87	4.17 (.35)	1.53	18
16 *Rubus* spp.	Y = -2.00 + .93X	.95	5.26 (.28)	1.20	18
17 *Osmorrhiza claytonii* (Michx.) C. B. Clark	Y = .74 + .27X	.53	2.46 (.28)	1.30	19
18 *Ribes* spp.	Y = -1.45 + 1.26X	.72	11.52 (2.15)	7.73	12
19 *Toxicodendron radicans* L.	Y = - .45 + .46X	.66	3.87 (.48)	2.10	19
20 *Physalis subglabrata* Mackenz. & Bush	Y = .49 + .69X	.95	8.70 (.79)	2.52	9
21 *Parthenocissus quinquefolia* (L.) Planch.	Y = .85 + .25X	.95	11.64 (.57)	3.09	28
22 *Viola* spp.	Y = - .46 + .52X	.76	2.54 (.24)	1.09	24

Appendix I. (Continued)

	Regression equation (Y=wgt.(gm), X=leaf area (cm x 10^2)[5/]	Coefficient of variation	Mean sample weight and standard errors	Standard error of single measurement at mean sample weight	Sample size
23 *Phryma leptostachya* L.	Y = - .99 + .67X	.83	3.51 (.95)	2.61	14
24 *Polygonatum biflorum* (Walter) Ell.[4/]	Y = - .77 + .66X	.64	3.52 (.55)	2.33	17
25 *Circaea quadrisulcata* (Maxim.) Franch. & Sav.	Y = 1.13 + .66X	.98	10.10 (.84)	3.99	21
26 *Tovara virginiana* (L.) Raf.	Y = -1.40 + .94X	.88	7.72 (.50)	2.28	20
27 *Geranium robertianum* L.	Y = - .78 + .65X	.93	13.46 (1.02)	4.79	21
28 *Quercus rubra* L.	Y = .14 + .42X	.79	2.6 (.26)	.99	12
29 *Sassafras albidum* (Nutt.) Nees	Y = -1.70 + .66X	.87	7.2 (.56)	2.63	21

1/ Includes *Euerigeon annuus* L.

2/ Includes *Sanicula canadensis* L.

3/ Includes *Prunus virginiana* L.

4/ Includes *Smilacina racemosa* (L.) Desf.

5/ Regression equations significant at .01 level except that for *Galium circaezans* which is significant at .05 level.

Appendix II. Environmental parameters recorded by treatment areas [1,2].

Parameter	Clearcut	Shelterwood	Group Selection	Control
Light (gm. cal./cm^2)	29.8 (12.95)	25.1 (8.62)	17.1 (9.36)	4.0 (3.02)
Temp. max. (c)	31.00 (6.98)	32.7 (7.15)	31.6 (8.83)	24.3 (4.73)
Rel. humidity max. (%)	94.4 (11.61)	90.4 (12.62)	92.6 (5.94)	88.7 (5.37)
Rel. humidity min. (%)	38.4 (21.75)	33.4 (13.35)	47.4 (24.2)	77.1 (35.62)

[1] Means accompanied by standard errors.

[2] All means underlined not significantly different at .05 level.