

## GRADIENTS OF TREE SPECIES COMPOSITION

### IN THE CENTRAL HARDWOOD REGION<sup>1/</sup>

Julian J.N. Campbell<sup>2/</sup>

---

Abstract.-- This study uses DECORANA ordination to show the major gradients of tree species composition in available data from Appalachian and Mid-Western regions. The major gradient in upland forests is related to soil pH and bedrock, with a weak east-west trend. Perpendicular to this is a gradient from ridges and south slopes to north slopes and bottoms, with some latitudinal trend. Most successions include increases in species of moister sites. A third independent gradient is related to swampy conditions, and distinct streamside samples had to be ordinated separately. Major gradients within swamp and streamside forests are also related to soil pH.

Keywords: forests, E. North America, ordination, soil pH.

---

#### INTRODUCTION

Since the pioneering work of Whittaker (1956), Bray and Curtis (1957) and others, gradient analysis has been widely applied in eastern forests, but rarely to whole States or Forest Regions (e.g., Brush et al. 1980, Rogers 1981). In this paper, I use data from many sources for an analysis of the whole 'Central Hardwood Region'. This region has four broad zones, following Braun (1950): Oak-Chestnut (without montane Spruce-Fir); Mixed Mesophytic and the Allegheny Section of Hemlock-Northern Hardwoods; Western Mesophytic and Beech-Maple; Oak-Hickory and Maple-Basswood (without extensions of Southern Bottomland Forest). Available data do not accurately represent this whole area, and differences in measurement increase 'noise' in the results. However, the strong environmental relationships emphasized below cannot be explained away in terms of sampling biases. With reference to detailed local studies, these results form a general model of composition patterns that suggests important new avenues of research in the region.

---

<sup>1/</sup>Paper presented at the Sixth Central Hardwood Forest Conference, Knoxville TN, February 24-26, 1987.

<sup>2/</sup>School of Biological Sciences, University of Kentucky, Lexington, Kentucky 40506.

<sup>3/</sup>Details of the data base, with all references, may be got from the author.

#### METHODS<sup>3/</sup>

I extracted all quantitative data on tree species composition from the following sources (\* with over 50 samples): Braun (1950)\*, Curtis (1959), Voight & Mohlenbrock (1964); American Journal of Botany, American Midland Naturalist\*; Botanical Gazette; Butler University Botanical Studies\*; Canadian Journal of Botany; Castanea\*; Central Hardwood Forest Conferences\*; Ecology and Ecological Monographs\*; Journal of the Elisha Mitchell Scientific Society; Forest Ecology and Management; Forest Science; Bulletin of the Torrey Botanical Club\*; State Academy of Science Publications (Kentucky, Tennessee, Indiana\*, Illinois, Iowa, Pennsylvania); Master's theses and Doctoral dissertations with data from Kentucky and parts of adjacent states\*; reports of the Kentucky Nature Preserves Commission and Nature Conservancy; and other unpublished data from Kentucky. I have about 300 references and 1450 samples (300 from Kentucky). Due to taxonomic uncertainty, I used broad species concepts, combining Acer saccharum with nigrum, Tilia heterophylla with americana, Carya glabra with ovalis, Carya texana with buckleyi, Carya ovata with carolinae-septentrionalis, Quercus shumardii with schneckii, Q. falcata with pagoda, Fraxinus americana with biltmoreana, F. pennsylvanica with subintegerrima, Amelanchier arborea with laevis, and Nyssa sylvatica with biflora.

If different measures were presented in the same study, I selected that closest to density of stems over 10 cm in diameter (d.b.h.). Like most 'importance values', such density has emphasis intermediate between canopy trees (or basal area)

## RESULTS

### Ordination of Upland Forest Samples

and understory (or stems over 1 cm). But some studies have different size-limits, or provide only basal area or an IV measure for use here. In an initial trial, combined ordination of basal area and density data from the same samples showed shifts in scores exceeding 10% of axis length in about 10% of samples. Such differences increase 'noise', but they need not seriously distort the gradients. Understory gradients may still correspond to the canopy, though perhaps skewed in some successional or structural relationship. More detailed research would need to take such shifts into account. 'Samples' are individual plots or transects of various extent, or composites of samples scattered through a particular forested area or a locally defined forest type, mostly containing 50-200 trees over 10 cm. Such variety in scale should not generally distort an ordination (Goff and Mitchell 1975). More problematic is the lack of a rigorous sampling strategy, which may introduce biases towards certain species associations, e.g., rarer ones. But this still should not lead to spurious environmental relationships.

I ordinated these samples with DECORANA (Hill 1979), scaling species abundances as percentages of the total in each. Initial runs with 1000 samples emphasized separation of about 60 streamside samples, which I removed for separate analysis. For further clarity, I also removed about 20 outlying southern samples, mostly dominated by Quercus marilandica and Q. stellata. Thus, the main analysis presented here is based on 920 samples from sources searched up to 1980. Subsequently, I found another 450 samples, providing more data for environmental relationships. I positioned these, and replaced some of the southern samples, using species scores already generated. Each sample score is the mean of its contained species' scores, weighted by their abundances. To show environmental relationships with ordination axes, I used simple graphical methods. I fitted lines iteratively that maximized discrimination of environmental classes (or other external attributes of ordinated items). I measured each discrimination by the chi-squared value in a 2 x 2 contingency table. For testing significance, one extra degree of freedom must be used for each estimated parameter, i.e., two d.f. must be added for a fitted line. More detailed parametric statistics also provide significant results, but I only present such results for the non-linear pattern shown by species diversity (Simpson's Index), using multiple quadratic regression against two axes. The assumptions of such statistics may not be well met in these data, and they are not needed for the basic conclusions.

The first three axes of the ordination with 920 samples account for about 20% of the variance (sum of eigenvalues). Further axes are not readily interpreted. From species scores, the ordination is divisible into two taxonomic sectors, mostly along the first axis (fig. 1). On the right side are centered all Cupressaceae, Malviflorae and Salicaceae, most Rutiflorae, Rosaceae and Tubiflorous groups (following Thorne 1979). On the left side are centered all Pinaceae, most Theiflorae, Annoniflorae and Hamamelidiflorae. Species in more advanced families, with Sporne's (1980) Index over 45 (median here), are more frequent on the right ( $P < 0.001$  with chi-squared test). Roughly perpendicular to this primary separation, largely on the second axis, there are finer taxonomic divisions: Magnoliaceae, Tiliaceae-Moraceae, most Aceraceae-Hippocastanaceae (versus Fabales) and most Betulaceae (versus Hamamelidales) are centered in lower sectors; Pinus (versus Tsuga), Juniperus (versus Thuja), Quercus (versus Fagus) and Carya (versus Juglans) are centered in upper sectors. Further separations are of course evident at the species level, especially in Quercus and Carya. The third axis adds little higher taxonomic separation. But, with the second axis, it does emphasize a trend from species with diffuse-porous wood to those with ring-porous, especially some Quercus spp. (fig. 1;  $P < 0.001$  with chi-squared test).

Patterns of species dominance on the first and second axes enable broad zones to be outlined (fig. 2). From left to right, Pinus and Juniperus dominate at upper positions; Quercus prinus/coccinea, Q. alba/velutina and Q. muhlenbergii/shumardii (with associates), at central positions; Tsuga (with associated Betula), Fagus (with Liriodendron) and Acer saccharum (with Tilia), at lower positions. Old samples with Castanea dominant are concentrated between Q. prinus and Tsuga. Several local dominants are associated with Q. alba/velutina, suggesting subdivisions (Nyssa sylvatica, Acer rubrum and Carya spp.), and Q. rubra is concentrated in the transition to Fagus and A. saccharum. Fraxinus spp. and Ulmaceae (Ulmus/Celtis) replace Q. muhlenbergii and A. saccharum, respectively, as dominants at the right extreme.

Soil pH increases to the right of the primary gradient (fig. 3), suggesting some chemical control. However, this most frequently reported aspect of soil chemistry may have less direct importance than the various interacting mineral levels. It is reported for about 340 of the 1450 samples, including about 60 where only the soil series is stated, but where average pH for the series is given in Soil Conservation Service publications. The method of measurement is not always reported, but most cases probably

refer to the upper A horizon in a 1-to-1 mixture with water. I selected this method, if more than one was reported. Despite sampling error, which must be great, there is a strong relationship with the ordination ( $P < 0.0001$  in chi-squared test, dividing values above and below pH 5-5.9). There is almost no overlap in tree composition between samples with pH 3-4.9 and 6-7.9, while intermediate values of 5-5.9 occur more widely on the ordination. Actually, the trend in mean pH along the line of most variation shows no significant increase up to almost half way across, remaining about 4.6 (inset to fig. 3). But, beyond there, there is an approximately linear increase.

In Kentucky samples, this gradient is related to bedrock (fig. 3), from non-calcareous sandstones and shales of Pennsylvanian age (and some Devonian), through mixed non-calcareous and calcareous rocks of Mississippian age, to calcareous shales and limestones of Ordovician age (the 'Bluegrass'). On Pennsylvanian and Devonian rock, typical mature soils are hapludults and dystrochrepts (Bailey & Windsor 1964, U.S.D.A. 1975), with pH of 4.5-5, or 4-4.5 in some southeastern mountains (e.g., Braun 1935, Hinkle 1975), or 5-5.5 in the Western Coalfields (with alfisols). In the Mississippian region limestones predominate, but the typical paleudults, paleudalfs and eutrochrepts have pH of only 5.5-6. On Ordovician rocks, typical soils are hapludalfs and hapludolls, with pH of 6-6.5, or 5-6 on old terrace and glacial deposits, or 6.5-7.5 in thinner soils (e.g., Pittilo 1963, Bryant 1973, my unpublished data).

Basophilous forest increases from east to west (fig. 4). Although there is no shift along the gradient from Oak-Chestnut to Mixed Mesophytic samples, or from Western Mesophytic/Beech-Maple to Oak-Hickory/Maple-Basswood, there is a pronounced shift from Mixed to Western Mesophytic. Within each region, more hilly sections tend to have more acidophilous forest. The Bluegrass (with dissected areas of Illinoian Glaciation), and perhaps the less sampled Nashville Basin, have particularly distinct composition at the base-rich extreme. North-south trends, in contrast, mostly exist along the secondary gradient. Northern samples concentrate in lower ordination zones dominated by Tsuga, Fagus or Acer. However, the Oak-Chestnut region is exceptional, with northern samples concentrated towards the base-rich zone (fig. 4).

The secondary gradient, largely expressed by the second axis, is related to dry versus moist topographic sites. In each region, there is a shift in composition from ridges and S-SW slopes to bottoms and N-NE slopes (fig. 5;  $P < 0.0001$  with chi-squared tests). The discriminating line between these two site types, with all regions overlaid, is almost perpendicular to the trend in soil pH (fig. 3). There is no clear east-west shift along this dryness gradient. However, there are shifts in the discriminating lines

towards drier composition from Western Mesophytic to Oak-Hickory, and from Mixed Mesophytic to Oak-Chestnut. There is also a curious rotation in the lines from the two western regions to the two eastern regions, especially Mixed Mesophytic (fig. 5), where ridges and S-SW slopes have more acidophilous forest than N-NE slopes and bottoms, as well as more xerophytic.

Some successional relationships are also evident. Many studies have compared old-growth with nearby second-growth, and about 20 studies report real change over 10-60 years. Such compositional shifts in the mesic direction outnumber those in the xeric by 47 to 9 (fig. 6;  $P < 0.0001$  with chi-squared test against uniformity). There is no overall trend along the pH-related gradient, except for some convergence in the zone of Acer saccharum dominance. I treat studies of chestnut-blight separately, because this has not initiated a normal secondary succession towards former composition. Elimination of Castanea dentata has caused a general shift into a transitional zone typified by climax dominance of Quercus prinus, Q. alba, Fagus and Tsuga (fig. 6), though secondary species here have often assumed more importance, especially Acer rubrum, Robinia, Liriodendron and Betula lenta, while Carya spp. appear to be increasing more slowly (e.g., Karban 1978, McCormick and Platt 1980). This general shift is in the direction of increasing soil pH, but I know of no soil monitoring. Since Castanea occupied the acid extreme, loss would lead to less extreme forests even without soil changes. It is difficult to gauge just how much stronger the observed trend has really been. At the basic extreme, much Ulmus americana has also been killed by disease. There have been fewer studies of this, but they also indicate a potential for large transitions away from the extreme (fig. 6).

#### Ordination of Wetland Forest Samples

##### Swamp forests

I plotted about 60 samples of swamp forest separately due to their extreme third axis positions (fig. 7). Major trees are Liquidambar styraciflua with Quercus palustris, and Fraxinus pennsylvanica with Quercus bicolor. The shift to these dominants occurs about 2.85 on the third axis, which I used as the break. Acer rubrum and Ulmus americana are common, though widespread elsewhere. Most streamside and southern bottomland species are also centered here (fig. 1). There is a pH-trend parallel to the upland one, though values average lower (fig. 7;  $P < 0.01$  with chi squared). The Liquidambar-Q. palustris zone mostly has pH of 4-4.9, ranging up to 6.9; the Fraxinus-Q. bicolor zone mostly has 6-6.9. More work is needed to improve the overall pH relationship using the third axis as an extra variable. I have not compiled hydrological data, since it is well-known that the above species are typical of swampy sites.

Table 1.--Tree species with abbreviations for Figure 1 and higher taxonomic groups referred to in text<sup>1/</sup>.

Species	Abbrev.	Species	Abbrev.
<i>Acer negundo</i> (box-elder)	ACN (R)	<i>Magnolia acuminata</i> (cucumber tree)	MGA (A)
<i>A. pensylvanicum</i> (striped maple)	ACP (R)	<i>M. fraseri</i> (Fraser magnolia)	MGF (A)
<i>A. rubrum</i> s.l. (red maple)	ACR (R)	<i>M. macrophylla</i> (bigleaf magnolia)	MGM (A)
<i>A. saccharinum</i> (silver maple)	ACSN(R)	<i>M. tripetala</i> (umbrella magnolia)	MGT (A)
<i>A. saccharum</i> s.l. (sugar maple)	ACS (R)	<i>Morus rubra</i> (mulberry)	MR (M)
<i>A. spicatum</i> (mountain maple)	ACSP(R)	<i>Nyssa sylvatica</i> s.l. (black gum)	NS (X)
<i>Aesculus glabra</i> (Ohio buckeye)	ASG (R)	<i>Ostrya virginiana</i> (hop-hornbeam)	OS (H)
<i>A. octandra</i> (yellow buckeye)	ASO (R)	<i>Oxydendrum arboreum</i> (sourwood)	OX (T)
<i>Amelanchier arborea</i> s.l. (serviceberry)	AMA (R)	<i>Picea rubens</i> (red spruce)	PC (P)
<i>Asimina triloba</i> (pawpaw)	AN (A)	<i>Pinus echinata</i> (shortleaf pine)	PNE (P)
<i>Betula allegheniensis</i> (yellow birch)	BTA (H)	<i>P. pungens</i> (Table Mountain pine)	PNP (P)
<i>B. lenta</i> (sweet birch)	BTL (H)	<i>P. rigida</i> (pitch pine)	PNR (P)
<i>B. nigra</i> (river birch)	BTN (H)	<i>P. strobus</i> (white pine)	PNS (P)
<i>Bumelia lanuginosa</i> (woolly chittamwood)	BMLN(T)	<i>P. taeda</i> (loblolly pine)	PNT (P)
<i>B. lycioides</i> (smooth chittamwood)	BMLC(T)	<i>P. virginiana</i> (Virginia pine)	PNV (P)
<i>Carpinus caroliniana</i> (hornbeam)	CP (H)	<i>Platanus occidentalis</i> (sycamore)	PL (H)
<i>Carya cordiformis</i> (bitternut hickory)	CRC (R)	<i>Populus deltoides</i> (eastern cottonwood)	PPD (M)
<i>C. glabra</i> s.l. (pignut hickory)	CRG (R)	<i>P. grandidentata</i> (bigtooth aspen)	PPG (M)
<i>C. illinoensis</i> (pecan)	CRI (R)	<i>Prunus americana</i> (common plum)	PRAM(R)
<i>C. laciniosa</i> (shellbark hickory)	CRL (R)	<i>P. pensylvanica</i> (pin cherry)	PRP (R)
<i>C. ovata</i> s.l. (shagbark hickory)	CRO (R)	<i>P. serotina</i> (black cherry)	PRS (R)
<i>C. pallida</i> (sand hickory)	CRP (R)	<i>Quercus alba</i> (white oak)	QUA (H)
<i>C. texana</i> s.l. (black hickory)	CRTX(R)	<i>Q. bicolor</i> (swamp white oak)	QUB (H)
<i>C. tomentosa</i> (mockernut hickory)	CRT (R)	<i>Q. coccinea</i> (scarlet oak)	QUC (H)
<i>Castanea dentata</i> (American chestnut)	CSD (H)	<i>Q. ellipsoides</i> (Hill's oak)	QUE (H)
<i>C. ozarkensis</i> (Ozark chestnut)	CSO (H)	<i>Q. falcata</i> s.l. (southern red oak)	QUF (H)
<i>Catalpa speciosa</i> (northern catalpa)	CAS (X)	<i>Q. imbricaria</i> (shingle oak)	QUI (H)
<i>Celtis laevigata</i> (sugarberry)	CTL (M)	<i>Q. lyrata</i> (overcup oak)	QUL (H)
<i>C. occidentalis</i> (common hackberry)	CTO (M)	<i>Q. macrocarpa</i> (bur oak)	QUMC(H)
<i>C. tenuifolia</i> (dwarf hackberry)	CTT (M)	<i>Q. marilandica</i> (blackjack oak)	QUMR(H)
<i>Cercis canadensis</i> (redbud)	CC (R)	<i>Q. muehlenbergii</i> (yellow oak)	QUMU(H)
<i>Chionanthus virginica</i> (fringe-tree)	CH (X)	<i>Q. palustris</i> (pin oak)	QUPA(H)
<i>Cladrastis kentukea</i> (yellowwood)	CD (R)	<i>Q. prinus</i> (chestnut oak)	QUPR(H)
<i>Cornus florida</i> (flowering dogwood)	CNF (X)	<i>Q. rubra</i> s.l. (northern red oak)	QUR (H)
<i>Cotinus obovata</i> (smoke-tree)	CO (R)	<i>Q. shumardii</i> s.l. (shumard oak)	QUSH(H)
<i>Crataegus mollis</i> (downy hawthorn)	CGM (R)	<i>Q. stellata</i> (post oak)	QUST(H)
<i>Diospyros virginiana</i> (persimmon)	DS (T)	<i>Q. velutina</i> (black oak)	QUV (H)
<i>Fagus grandifolia</i> (beech)	FG (H)	<i>Rhamnus caroliniana</i> (buckthorn)	RM (M)
<i>Fraxinus americana</i> s.l. (white ash)	FXA (X)	<i>Rhododendron maximum</i> (common rosebay)	RD (T)
<i>F. nigra</i> (black ash)	FXN (X)	<i>Robinia pseudoacacia</i> (black locust)	RB (R)
<i>F. pennsylvanica</i> s.l. (green ash)	FXP (X)	<i>Salix amygdaloides</i> (peachleaf willow)	SXA (M)
<i>F. quadrangulata</i> (blue ash)	FXQ (X)	<i>S. nigra</i> (black willow)	SXN (M)
<i>F. tomentosa</i> (pumpkin ash)	FXT (X)	<i>Sapindus drummondii</i> (soapberry)	SP (R)
<i>Gleditsia triacanthos</i> (honey locust)	GL (R)	<i>Sassafras albidum</i> (sassafras)	SS (A)
<i>Gymnocladus dioica</i> (coffee-tree)	GM (R)	<i>Thuja occidentalis</i> (N. white-cedar)	TH (C)
<i>Halesia carolina</i> (silverbell)	HL (T)	<i>Tilia americana</i> s.l. (basswood)	TL (M)
<i>Hamamelis virginiana</i> (witch-hazel)	HM (H)	<i>Tsuga canadensis</i> (hemlock)	TS (P)
<i>Ilex montana</i> (mountain winterberry)	IXM (T)	<i>Ulmus alata</i> (winged elm)	ULAL(M)
<i>I. opaca</i> (holly)	IXO (T)	<i>U. americana</i> (American elm)	ULAM(M)
<i>Juglans cinerea</i> (white walnut)	JGC (R)	<i>U. rubra</i> (slippery elm)	ULR (M)
<i>J. nigra</i> (black walnut)	JGN (R)	<i>U. thomasii</i> (rock elm)	ULT (M)
<i>Juniperus virginiana</i> (red cedar)	JN (C)	<i>Viburnum prunifolium</i> (smooth black-haw)	VBP (X)
<i>Liquidambar styraciflua</i> (sweetgum)	LQ (H)	<i>V. rufidulum</i> (rusty black-haw)	VBR (X)
<i>Liriodendron tulipifera</i> (tulip poplar)	LR (A)		

<sup>1/</sup> Some species are defined sensu lato ("s.l."); see text. Thorne's (1979) groups are in parentheses:  
A = Annoniflorae; H = Hamamelidiflorae; T = Theiflorae; P = Pinaceae; C = Cupressaceae;  
R = Rutiflorae + Rosaceae; M = Malviflorae + Salicaceae; X = Tubiflorous groups and allies.



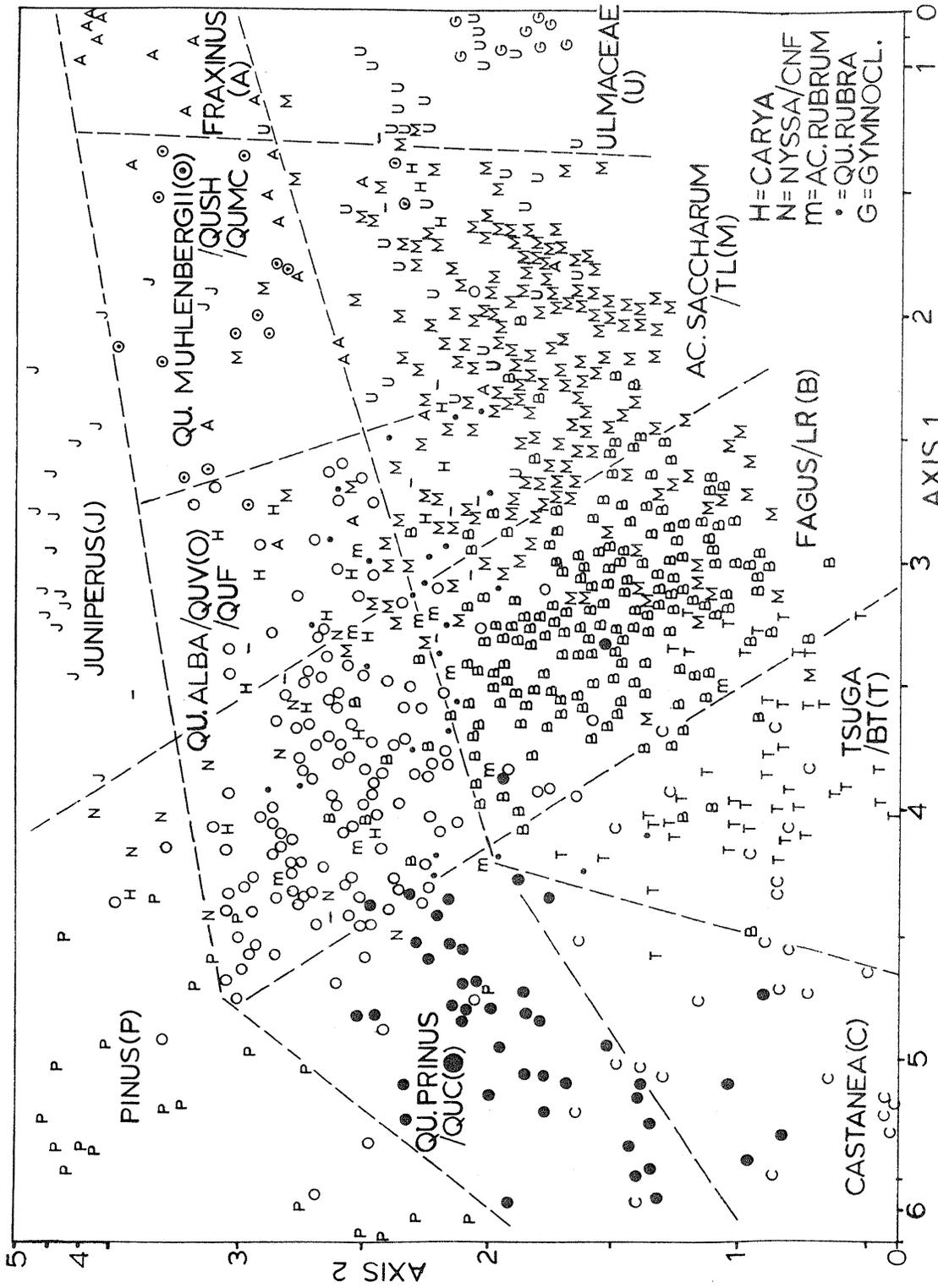


Figure 2a.—Pattern of dominant species in upland samples. The axes show sample scores, which are means of species scores in each sample; scale units are standard deviations of the 'average species' (Hill 1979). Each letter or other symbol indicates the most abundant species in the sample positioned there. Most symbols are used for two or more closely associated species, one of which must be dominant in the sample. Major zones of dominance are separated by dashed lines, with the commonest dominant species spelled out and their associates abbreviated (Table 1). Other miscellaneous species, mostly early successional, are indicated by "n.". Wetland samples and others excluded from this ordination are not shown.

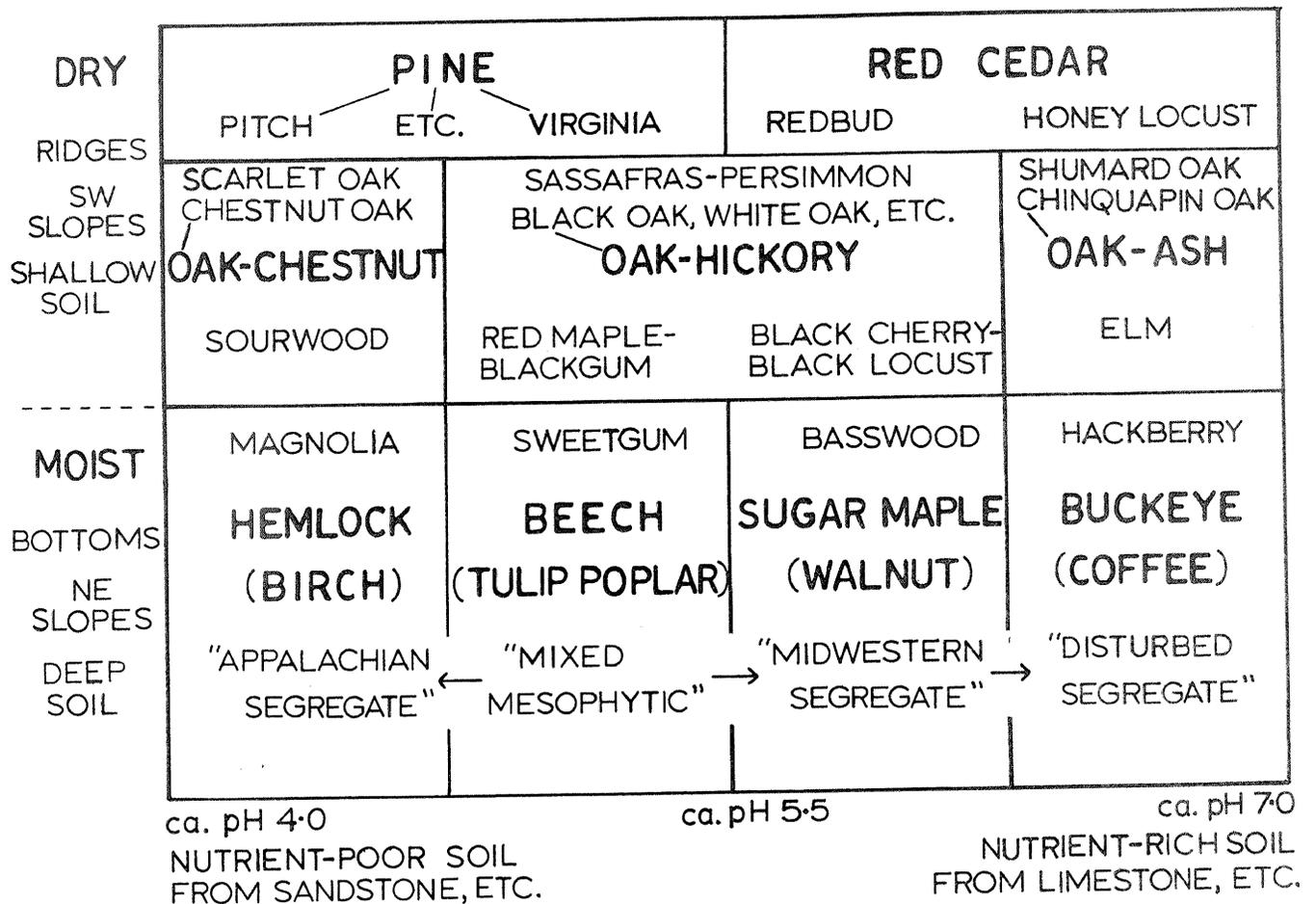


Figure 2b.—Conceptual summary of major upland forest types and environmental relationships. The arrangement is developed from the ordination of Figure 2a. Species shown in bold were climax dominants before settlement, with characteristic mesic successional associates in parentheses. Other trees shown are mostly successional, with broad moisture ranges. This diagram was initially designed for north-central Kentucky, but it can be applied, with minor changes, throughout most of the Central Hardwood Region. To the south, southern red oak, post oak and blackjack oak extend the oak-hickory sector into the pine-red cedar sector. The lower left sectors are particularly complex: northern red oak or bitternut hickory become major associates of sugar (or black) maple in later succession, while yellow buckeye can be locally codominant on rich slopes. Ohio buckeye and Kentucky coffee tree were characteristic of moist, rich plains that were moderately disturbed by animals before settlement (e.g., in the Bluegrass Region), but hackberry, black walnut and other early successional trees take over where disturbance has been more extreme. In the beech sector, sweetgum occurs mainly on wetter sites, and northern red oak may codominate on drier sites instead; also, silverbell is often dominant instead of beech in the Southern Appalachians.

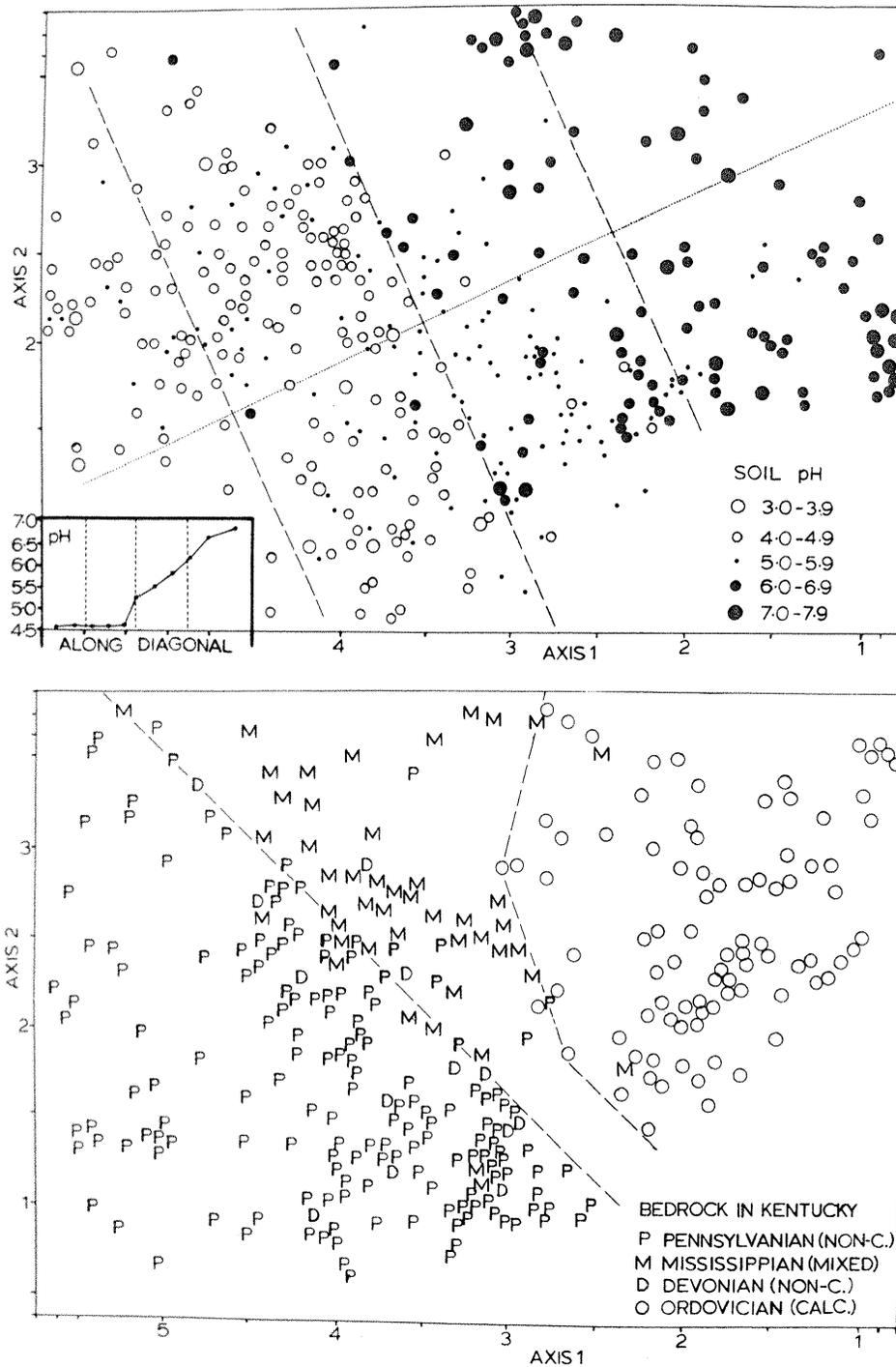


Figure 3.—Relationship of upland ordination to soil pH and bedrock. Upper: reported soil pH (1:1, upper A horizon:water, if possible) in upland samples; dashed lines show separation of values; the inset shows mean pH plotted along the dotted diagonal line; the dotted line is positioned to maximize separation of moist and dry sites (from fig. 5). Lower: age of rock beneath Kentucky samples, showing the separation of largely non-calcareous (P, etc.) versus calcareous (O, etc.) types.

However, these samples do not simply extend the upland dryness gradient, largely on the second axis. This indicates that wetness and dryness have independent influences on composition, perhaps through temporal fluctuations. Species centered in the corner with implied 'xerohydric' conditions include *Q. shumardii*, *Q. stellata*, *Q. falcata* and *Q. imbricaria* (fig. 1). There are not enough environmental data from swamp samples for correlation with the secondary gradient, but extrapolation from uplands suggests that the *Quercus* spp. of swampy sites may experience dryness more often than *Liquidambar* and *Fraxinus*.

#### Streamside forests

In initial runs with all data, the first axis separated streamside samples dominated by *Populus deltoides* (extreme), *Salix* spp., *Acer negundo* and *A. saccharinum* from the remainder, with swamp samples transitional. The second axis separated samples dominated by *Betula nigra*, with *Platanus occidentalis* transitional from *Betula* to *Acer* spp. More widespread species associated with the *Acer* spp. are *Ulmus* spp. and *Fraxinus pennsylvanica*. Separate ordination displays these dominance zones more clearly (fig. 7). Again, there is a pH-trend (fig. 7;  $P < 0.001$  with chi-squared). Samples with *Betula nigra* dominant have pH of 3.5-5.9; most others have 6-7.9. With almost no values below 5, there is an increase in average pH compared to swamp and upland samples. The second axis in this ordination separates *Populus* and *A. negundo* from *A. saccharinum*, which is typical of deeper soils along larger streams.

#### Species Diversity Patterns

To measure diversity within Kentucky samples, I used Simpson's Index - the reciprocal of the probability that any two trees randomly drawn from a population are the same species (Hill 1973). Differences in sample size contribute much noise, but some trends are clear. The index peaks at intermediate positions on both axes of the upland ordination (fig. 8,  $P < 0.001$  for each coefficient in multiple quadratic regression of the index against both axis scores). Values at extremes are typically 1-3, while central values are 4-13. At hydric extremes, swamp and streamside samples also have low diversity. In over 90% of hydric samples, from throughout the Central Hardwood Region, values are only 1-3.

#### DISCUSSION

##### The Gradient Related to Soil pH

The pH-related gradient has more species turnover than either moisture gradient. In addition to being largely projected by the first ordination axis (after streamside removal), it

has more shifts in dominant species (figs. 2 and 7). Several whole families or orders have most species centered on one side or the other, suggesting deep phylogenetic relationships (fig. 1). The concentration of more advanced families on the higher pH side might indicate more recent expansion of forests with higher pH soils (perhaps due to increasingly continental climates during the Tertiary), or more rapid evolution on such soils (perhaps due to faster growth).

This gradient was noted as early as 1805 by Francois Michaux (p. 229-230). However, most modern work is in small study areas on relatively uniform parent material, where moisture gradients and successions are more pronounced. Some early exceptions come from the Ozark region (Steiermark 1940, Read 1952). Even Braun's (1950) general treatment gave few indications of the gradient (p. 64, 66, 91, 106, 109, 119, 148). Only with the advent of more quantitative analysis, has its full description begun. The following studies document local aspects, but still mostly within areas lacking the full range of species: Elliott (1953), Whittaker (1956 - in the elevation gradient), Ward (1956), Crankshaw et al. (1965), Buell et al. (1966), Ohmann and Buell (1968), Safley (1970), McIntosh (1972), Rochow (1972), Keever (1973), Lewin (1974), Stout et al. (1975), Cribben and Scacchetti (1976), Martin and DeSelm (1976), Lodhi (1977), Vankat et al. (1977), Hinkle (1978), Martin (1978), Schmalzer et al. (1978), Sherman (1978), Jensen (1979), Nicholson et al. (1979), Runkle (1979), Thor et al. (1979), Brush et al. (1980), Golden (1981), Johnson and Ware (1982), Muller (1982), Parsons and Ware (1982), Stephenson (1982), Ware (1982), Whitney (1982), Balter and Loeb (1983), McCarthy et al. (1984), Johnson-Groh (1985), Nigh et al. (1985). Parallel gradients can be traced to the north (e.g., Bakuzis et al. 1960 - represented by Hansen 1980, Lemieux 1963, Coffman and Willis 1977) and the south (e.g., Monk 1968, Peet and Christensen 1980, Marks and Harcombe 1981).

Understanding the gradient's causes will require much more research. There have been some studies of selected responses, but little development of community or ecosystem models. Chemical influences of disturbances, successions and different species within abiotically homogeneous sites involve different processes from geological and climatic factors in landscape pattern. But interactions such as pH-dependent solubilities may force some similarity. The shift from pH 4 to 7 is often associated with higher Ca, Mo, K and Mg levels, lower Al, Fe, Mn and Zn solubility, higher nitrate and lower ammonium levels, and peak P solubility about 6.5 (e.g., Armson 1977, Barber 1984). Also, acidophilous species tend to form mor humus (e.g., Rackham 1980, p. 36), with much physicochemical change. Such factors probably have more direct importance than pH, especially in the low pH range of the gradient with no pH-relationship (fig. 3). Evidence suggests that basophilous species are more demanding of nutrients (e.g., Mitchell and

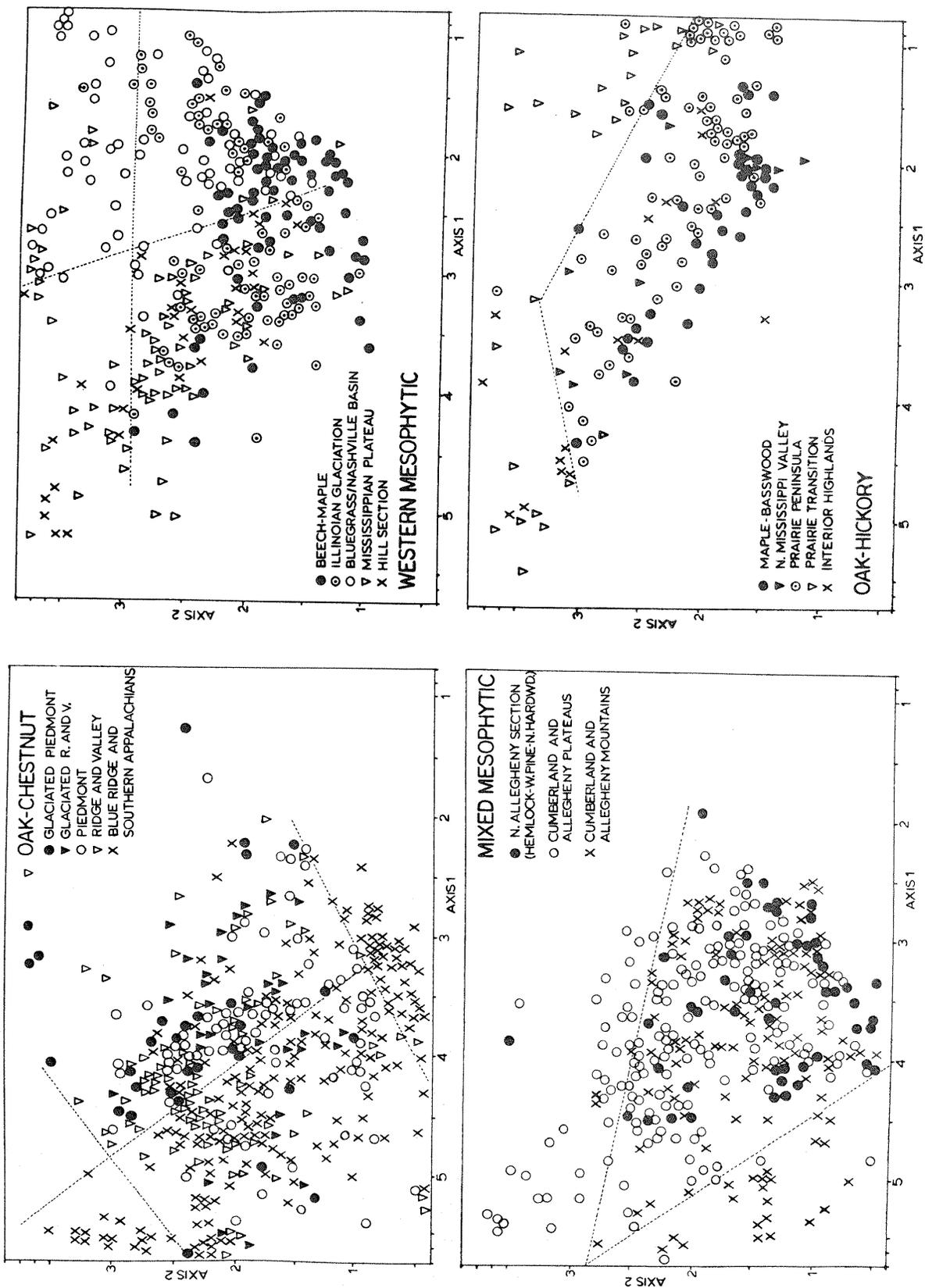


Figure 4.--Relationship of ordination to forest geography. Regional definitions are taken from Braun (1950), with the inclusion of more northern regions shown by solid symbols. Dashed lines indicate the partial separations of sections within the major regions.

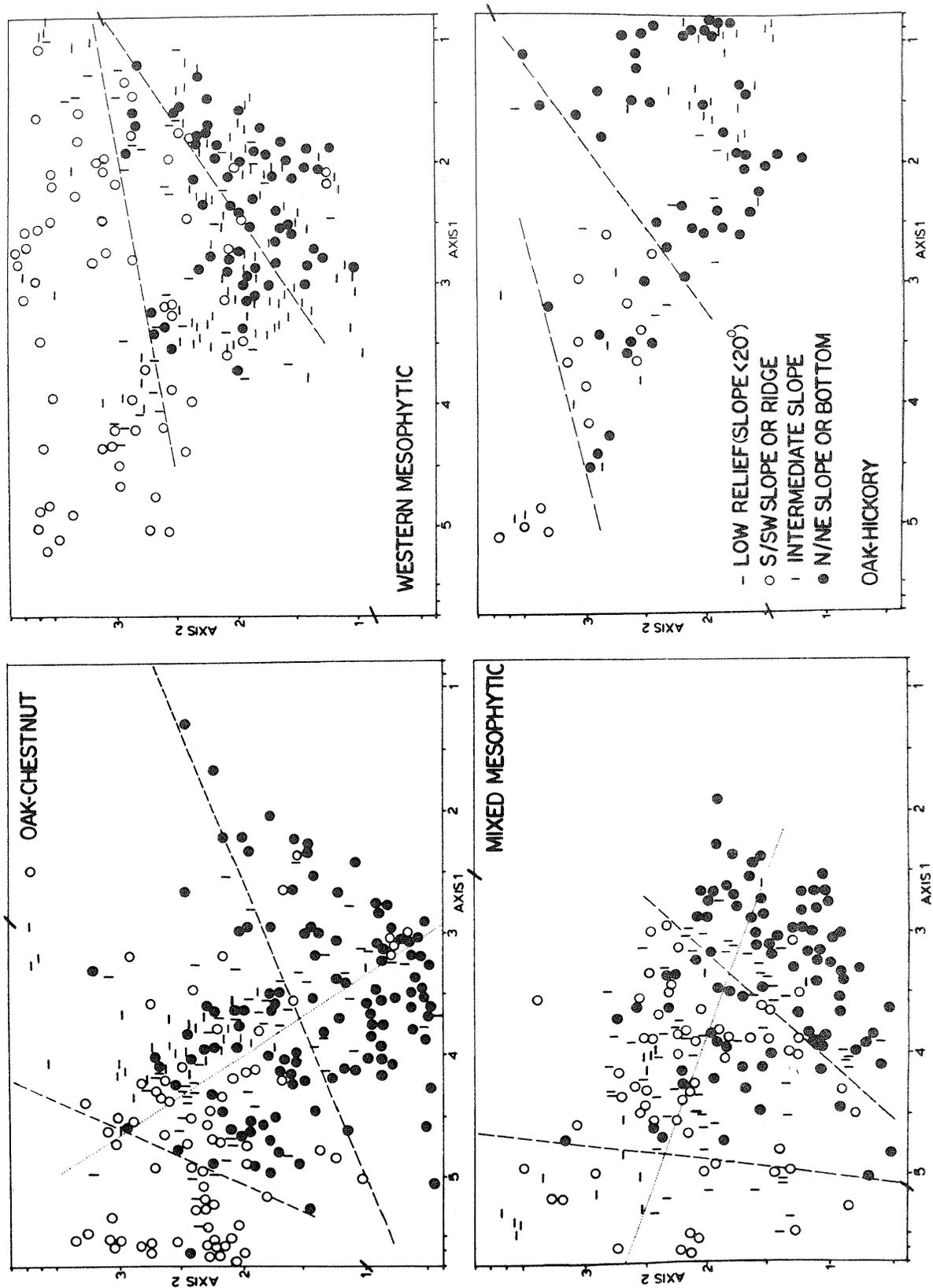


Figure 5.—Relationship of ordination to dry and moist sites, as indicated by rough topographic divisions. Dashed lines separate concentrations of dry or moist sites within each region. Bars crossing edges of diagrams mark diagonal lines that most discriminate between site types, using chi-squared (see text). Dotted lines show concentrations of low relief samples.

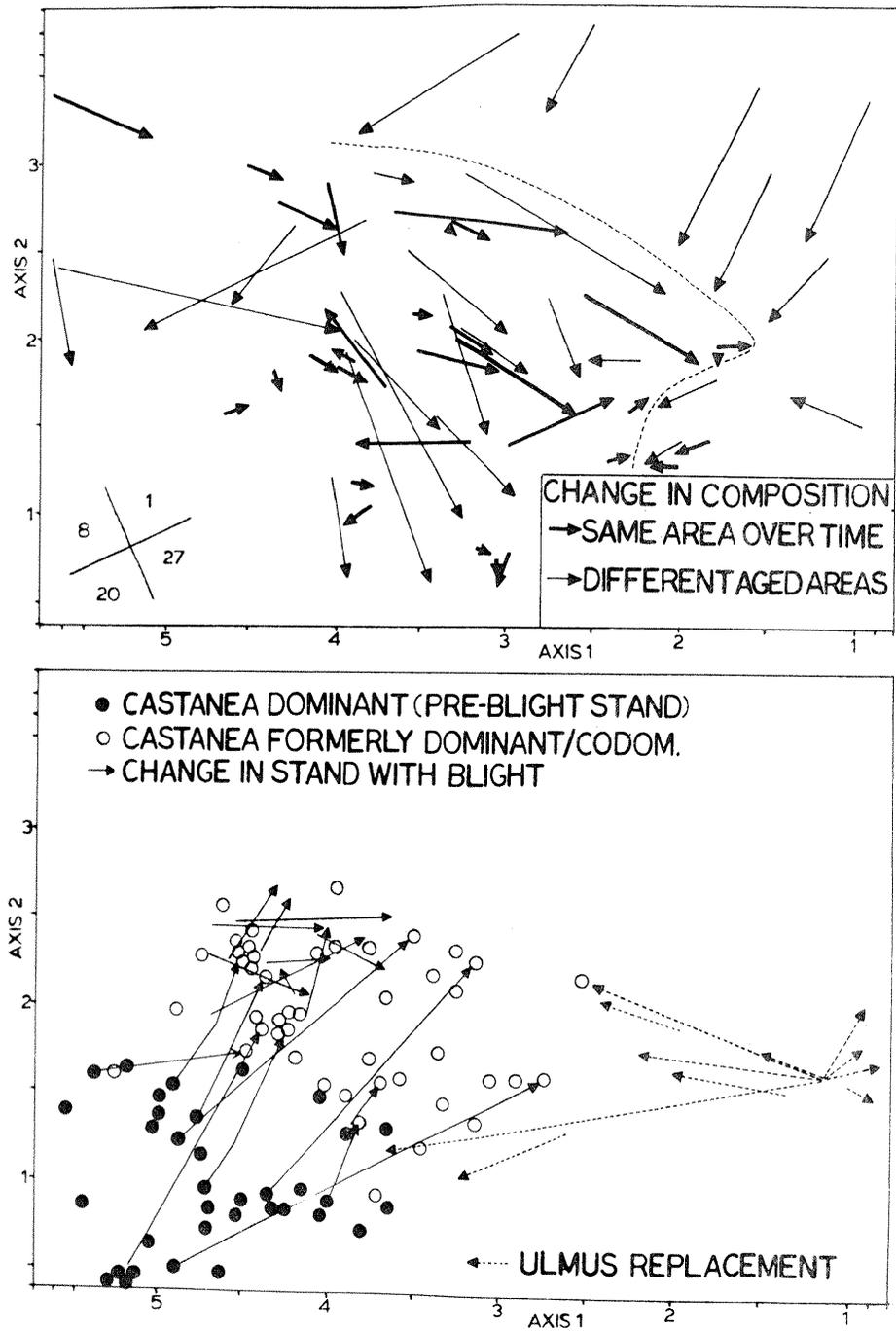


Figure 6.--Relationship of the ordination to temporal changes in composition. Upper: arrows join sample pairs with successional trend, either by direct resurveying of the same area, or by comparison of nearby areas differing in stand age; at lower left is shown the overall summation of directions within four quadrants defined by trends in soil pH (fig. 3) and moist versus dry topographic sites (fig. 5); the dashed line indicates possible convergence. Lower: separate display for changes after loss of Castanea dentata or Ulmus americana due to diseases.

Chandler (1939), Fowells 1965, Himelik et al. 1965, Neely et al. 1970, Safford 1973, Backner and Maki 1977, Safford and Czapowskyj 1979, Lamson 1980, Van Auken et al. 1985). But some fast-growing successional or gap-phase species of relatively acid soils (e.g., Liriodendron, Betula spp., Pinus spp., Cornus florida) appear to have greater nutrient demands than their associated climax dominants (see above refs.). The red oak group, in particular, may be relatively tolerant of low nutrient levels, and perhaps toxic Al (McCormick and Steiner 1978). There is undoubtedly much variation in chemical responses among associated species, which might be important for maintenance of local diversity, independent of the landscape patterns emphasized here.

Further complexity is suggested by the absence in some areas of an intermediate zone dominated by Fagus or Quercus alba (e.g., Whittaker 1956 - at mid-elevation, Hack and Goodlett 1960, Pearson 1962, Ohmann and Buell 1968, Anderson and Vankat 1978, DeSelm et al. 1978, Huennecke 1982, Kasmer et al. 1984, Woods 1984). Direct transition between extremes may be due to abrupt spatial shifts (e.g., Hack and Goodlett 1960), or perhaps due to rapid flushes of nutrients, as after mortality of Castanea, a former dominant in most of these areas. Alternatively, it is possible that different environmental controls of the gradient are sometimes dissociated, with independent relationships to different species. For example, the shift from the acid extreme to Fagus dominance might be particularly associated with increases in N or P, and the shift to Acer saccharum with higher base status (Hinkle 1978, Muller 1982, Kasmer et al. 1984, and my unpublished data).

Without experimental work, doubts about edaphic interpretation of the gradient may remain. Its east-west relationship might suggest that the trend from moist oceanic to more variable continental climate is involved. However, this relationship is weaker than that with soil pH (figs. 3, 4), and it is most unlikely that the many local expressions of the gradient, related to bedrock and pH (see above references), involve local climate as the major cause instead. Even the abrupt shift from Mixed to Western Mesophytic Regions along the gradient involves no increase in average climatic dryness (Lindsey and Sawyer 1971). Moreover, any climatic influence cannot be a simple trend from moist to dry as from ridges to bottoms, since that is perpendicular to the trend in pH. Climate may still be involved in the east-west shift along the gradient, but indirectly, since the general westward shift from ultisols to alfisols, with higher base status, may be attributed to reduced leaching by rain, as well as more base-rich parent material (U.S.G.S. 1969). The anomalous north-south relationship of the gradient within the Oak-Chestnut region (also Kasmer et al. 1984) accords with the richer

glacial soils there (U.S.G.S. 1969).

Rather than average moisture level, fluctuations in moisture may be confused with chemical factors. Concentration of low relief samples in higher pH zones of the gradient (fig. 5) could be attributed to the generally higher base-status of less resistant rocks, or to fluctuations in moisture stress promoted by lower relief itself, by associated fine-textured soil, and by associated variability in weather, especially to the west. However, such fluctuations may have more general expression in the second and third axes, as discussed below. Much more work is needed on this potentially important factor.

Historical interpretations can be largely dismissed. Braun (1950) suggested that the Appalachians have been a biological refuge, suffering less from climatic or other disturbances during the Cenozoic Era. With this view, concentration of some species in this acid region is attributable to greater sensitivity or slower recolonization. Although this hypothesis is tenable in a few cases (e.g., in explaining the virtual absence of heavy seeded species like Aesculus octandra and Castanea dentata on glaciated land), analysis of fossil pollen suggests that species have migrated during the Quaternary more than Braun assumed (e.g., Davis 1981). There is no evidence for a increase in disturbance-response or dispersal-ability along the pH-related gradient. Even in the very disturbed Bluegrass region, species of high pH are no more successional or intolerant of competition (based on Fowells 1965, etc.) than species of more acid regions nearby (Campbell 1980). However, the proportion of successional species in the Bluegrass was higher even before settlement, due to Indian fires, large herbivores or occasional droughts. Further study is needed to see how strong such association of biotic disturbance and richer soils has been (e.g., Delcourt et al. 1986). There may be some species of high pH especially suited to such disturbance, e.g., Gymnocladus has fruits dispersed by ungulates (and perhaps Indians), large seeds that may establish in dense ground vegetation, unpalatable foliage, and lateral root sprouts for frequent recovery and spread from forest edges (Campbell 1980). But high nutrient-status may still have maintained such species indirectly, if concentration of biotic disturbance was itself due to greater productivity.

The gradient has no clear relation to secondary succession, but there may be a tendency for convergence in the moderately high pH zone with Acer saccharum (fig. 6). Several studies indicate slow shifts among mesic climax dominants, from Tsuga to Fagus to Acer (Reed 1905, Hough and Forbes 1943, Stearns 1949, Ward 1956, Schneider 1966, McIntosh 1972, Zedler and Goff 1973, Henry and Swan 1974, Vankat et al. 1975, Abrell and Jackson 1977, Karban 1978, Sherman 1978, Runkle 1979, Barden 1980, Bryant

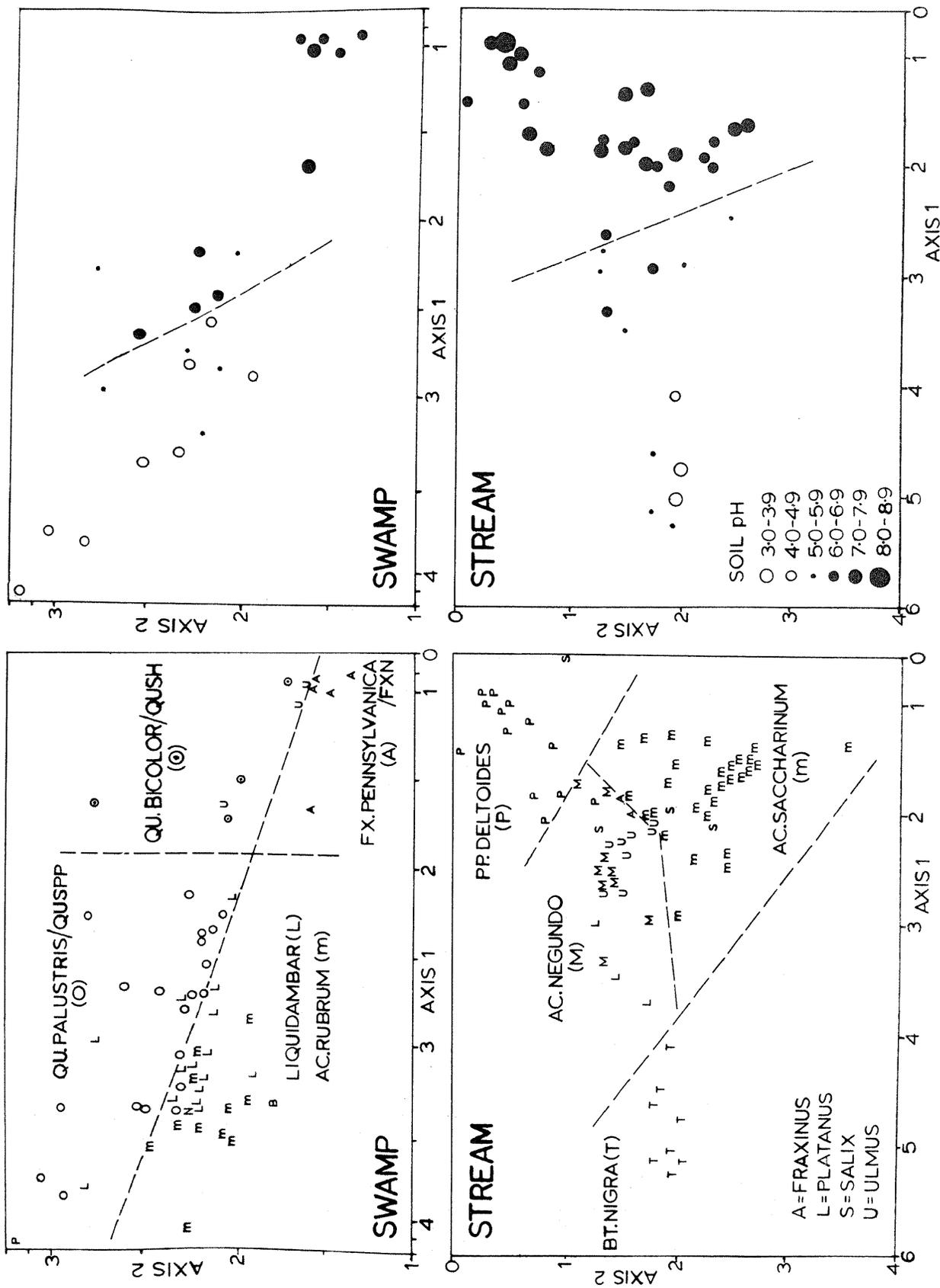


Figure 7.--Ordination patterns of distinct hydric samples. Left diagrams show patterns of dominant species (symbols as in fig. 2 if not indicated here). Right diagrams show patterns in soil pH (as in fig. 3). Upper: swampy samples, with score less than 2.85 on third axis of ordination with upland samples. Lower: separate ordination of streamside samples.

1985). However, other studies suggest cyclical trends among these species, especially in north-central Fagus-Acer forests (e.g., Woods 1984), and there is some evidence of the opposite trend, towards Tsuga, mostly in northeastern regions during the past 30-50 years (Leak 1970, Stephens and Waggoner 1970, Forcier 1975, Bjorkbom and Larson 1977, Zager and Pippen 1977, Nicholson et al. 1979, Runkle 1979, Charney 1980, Barden 1981, Hemond et al. 1983, Whitney 1984). The period 1850-1950 appears to have been unfavorable for establishment of Tsuga (Gates and Nichols 1930, Graham 1941, Hett and Loucks 1976, Lorimer 1980). Also at the acid extreme of the gradient, Castanea began to decline about 1850-75 as well (Zon 1904, Reed 1905, Hough and Forbes 1943, Woods 1953, Mackey and Sivec 1973, Lorimer 1980). Both declines may have been initiated by increasing temperatures, though in the case of Castanea diseases eventually became overwhelming. The interacting effects of climatic and edaphic change, disease, and perhaps pollution (Brand and Rhoades 1972, Cogbill 1976), on the balance of these species is a fascinating subject that deserves much more study, from physiology to paleo-ecology (e.g., Andersen 1969, Paillet 1982).

#### Moisture-Related Gradients

The dryness gradient in upland samples is also evident in many local studies (e.g., cited in previous section). Some of the best physiological evidence for the role of moisture concerns the major oak species (e.g., Bourdeau 1954, Wuenscher and Kozlowski 1971, Blackman and Ware 1982, Bahari et al. 1985). But there remains much need to integrate studies of individual species into ecosystem models. Moisture supply depends on much more than the topographic pattern shown here. It may need monitoring for many years to show frequencies of severe stress. Even within the same forest type, species may differ greatly in their ability to compete by extracting water from soil, versus their tolerance of low levels (e.g., Bunce et al. 1977). Further complexity comes from the general successional increase in mesic species (fig. 6), due to soil development, microclimatic change or fire suppression. This increase recalls the Clementsian view of succession (also Braun 1950), which cannot be totally dismissed.

Like the first axis here, many local topographic gradients combine pH-related and dryness gradients (e.g., Bray and Curtis 1957, Buell et al. 1966, Mowbray and Oosting 1968, Franzmeier et al. 1969, Gauch and Stone 1979, Adams and Anderson 1980, McCormick and Platt 1980, and refs. above). This combination appears most pronounced in the Mixed Mesophytic Region (fig. 5). It may be due to several factors: (a) tendency of coarser mineral matter to make drier and poorer soils; (b) exposure of more resistant base-poor bedrock on dry ridges, though glacial deposits are exceptional (e.g., Lewin

1974); (c) gravitation of minerals downslope, though leaching may still be great on lower slopes (Losche et al. 1970, Hutchins et al. 1976) and mid-slope nutrient peaks are also known (e.g., Muller 1982); (d) more weathering and leaching due to heat on drier slopes (Finney et al. 1962, Hicks and Frank 1984, and preceding refs.), though this may increase base-supply on more base-rich material (e.g., Cantlon 1953); (e) interference of nutrient uptake by moisture stress.

The lack of a clear east-west trend along the dryness gradient is surprising, given the westward decrease in rainfall. Drier western land was formerly covered by savannah or prairie, and is now mostly farmed, perhaps causing some bias towards moister forest in the literature. But there is at least some shift into the oak forest zone by the topographically discriminating lines, from Western Mesophytic to Oak-Hickory Regions (fig. 5). The similar shift from Mixed Mesophytic to the more eastern Oak-Chestnut Region is not related to total precipitation, but some dry warm seasons may be pronounced in the Ridge and Valley Province, and perhaps even in the Smokies (Whittaker 1956). The northern increase in mesic species like Tsuga, Fagus and Acer saccharum actually opposes the decline in total precipitation, which is compensated by lower temperatures and perhaps deep glacial soils.

The apparent independence of dryness and wetness gradients, suggesting that some species are associated with fluctuations in moisture supply, is a pattern that has received little attention. Braun (1950) noted the association of species like Q. falcata and Q. stellata with flatter ground in the Western Coalfields, Mississippian Plateaus and between the Knobs, and she alluded to the possible importance of moisture fluctuations (p. 189). Few studies have begun to quantify such trends (e.g., Bray and Curtis 1957, Huenneke 1982, Whitney 1982, Whitney and Steiger 1985). 'Xerohydric' conditions may be more pronounced to the south, typified by Quercus spp. like Q. phellos, or perhaps Pinus spp. on sandy flats (e.g., Peet and Christensen 1980, Marks and Harcombe 1981, Parsons and Ware 1982, Robertson et al. 1984). The concentration of species with ring-porous wood in the implied 'xerohydric' sector of the ordination suggests that the seasonal shift from large to small vessels in their wood may enable these species to maximize water conduction and growth during early wet seasons, then to be more conservative in later dry seasons. Ring-porous wood is generally more susceptible to embolism and pathogens, and on moister sites it presumably loses its advantages for water conduction (Hinckley et al. 1978, Zimmerman 1983). Some relatively mesic ring-porous species have declined greatly since the last century, largely due to vascular pathogens: Castanea dentata, Juglans cinerea, Ulmus americana, and perhaps Morus rubra and Fraxinus nigra in Kentucky (Campbell 1980).

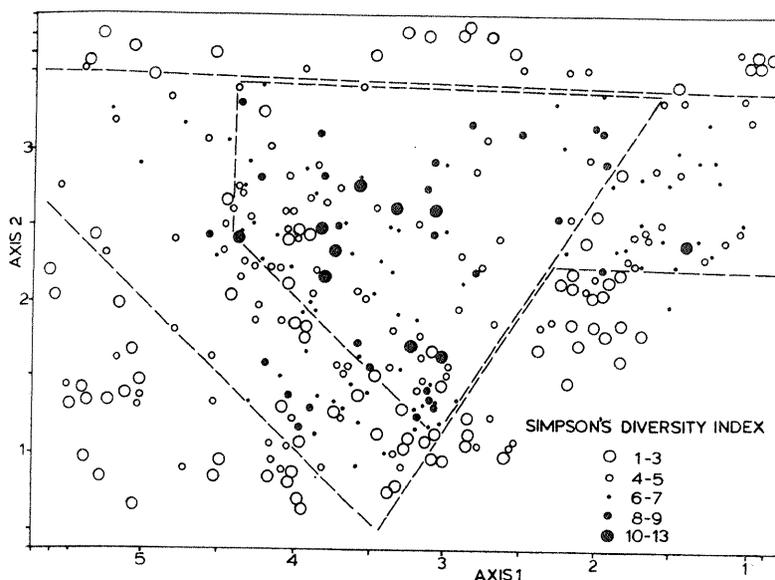


Figure 8.--Relationship of ordination to species diversity. Simpson's Diversity Index is the reciprocal of the sum of  $p_i^2$ , where  $p_i$  is the proportion of the  $i$ th species in the sample. Index values are shown only for upland samples from Kentucky.

Hydrological complexities must also be involved in the distinct composition of streamside samples. All of the typical streamside dominants, i.e., *Salicaceae*, *Acer* spp., *Platanus* and *Betula nigra*, have diffuse-porous wood, while only *Ulmus* spp., *Fraxinus* spp. and others in the transition to swampy or upland sites have ring-porous wood. Extending the hypothesis outlined above, this difference may be due to the more constant moisture near watercourses. Further distinctiveness may be caused by the disturbance from flooding. Most typical streamside species have relatively high ability to recover from physical damage (Fowells 1965), and all are wind-dispersed, allowing rapid local recolonization of fresh alluvium.

#### Species Diversity Patterns

Simpson's Index shows that dominance by one or two species is more frequent at extremes of major gradients. However, there is no corresponding clustering of species scores within central zones of the ordination (fig. 1), suggesting that extreme habitats do not have fewer characteristic species. This contrast may be due to several factors: (a) some samples with central composition may contain a wide range of habitats mixed together; (b) species of extreme habitats may often be absent due to fragmentation of their habitats, with frequent extinction and poor dispersal between 'islands'; (c) internal community organization in central zones may be conducive in some unknown way to a more equitable

mixture of species. Much has been written, but little concluded, about diversity trends and hypotheses like these. The problem should become clearer as the underlying gradients become better understood.

#### General Conclusions and Hypotheses

The major gradient of species composition in the Central Hardwood Forest is probably controlled by soil chemical factors associated with pH. Hydrological trends are more complex, with three gradients, related to dryness, wetness and streamside conditions, and upland successions generally involve increase in mesic species. Compositional patterns within limited areas can now be gauged against this general framework of gradients. For example, the major gradient in Oklahoma bottomland (Collins et al. 1981) has little correspondence here, but it involves a trend from species with nuts to fleshy fruit or small winged seeds, suggesting involvement of dispersal and disturbance history. It remains unclear whether there is a purely successional dimension in E. North America, related to disturbance, dispersal and competition, independent of the edaphic gradients shown here. Meanwhile, these major gradients provide hypotheses for other research. Higher taxonomic relationships may reflect phylogenetic divergence along ecological dimensions, for consideration in palaeobotany and biogeography. Physiological, soil chemical and topographic relationships suggest several lines of research with much relevance to whole forest communities.

## ACKNOWLEDGEMENTS

This work was initially supported through contract with the Kentucky Nature Preserves Commission in 1980. I thank the many people who have, over the years, contributed pieces of information and advice for this synthesis, especially Hal Bryan, Bill Bryant, Ray Cranfill, Hal DeSelm, Rich Hannan, Don Harker, Ron Houpp, Bill Martin, Bob Muller, Bob Peet and Paul Schmalzer. Also, I am particularly grateful to the two anonymous reviewers who provided useful criticism for the final draft.

## LITERATURE CITED<sup>1/</sup>

- Abrell, D.E., and M.T. Jackson.  
1977. A decade of change in an old-growth Beech-Maple forest in Indiana. *American Midland Naturalist*. 98:22-32.
- Adams, D.E., and R.C. Anderson.  
1980. Species response to a moisture gradient in central Illinois forests. *American Journal of Botany* 67:381-392.
- Andersen, S.T.  
1969. Interglacial vegetation and soil development. *Medd. Dansk. Geol. Foren.* 19:90-102.
- Anderson, D.S., and J.L. Vankat.  
1978. Ordination studies in Abner's Hollow, a small south central Ohio deciduous forest. *Botanical Gazette* 139:241-248.
- Armson, K.A.  
1977. *Forest Soils. Properties and Processes.* University of Toronto Press, 390 p.
- Backner, E., and T.E. Maki.  
1977. Seven-year growth of fertilized and irrigated yellow poplar, sweetgum, northern red oak, and loblolly pine. *Forest Science* 23:402-410.
- Bahari, Z.A., S.G. Pallardy and W.C. Parker.  
1985. Photosynthesis, water relations, and drought adaptation in six woody species of oak-hickory forests in central Missouri. *Forest Science* 31:557-569.
- Bailey, H.H., and J.H. Windsor.  
1964. *Kentucky Soils.* University of Kentucky Agricultural Experiment Station Miscellaneous Publication 308, 174 p.
- Balter, H., and R.E. Loeb.  
1983. Arboreal relationships on limestone and gneiss in northern New Jersey and south-eastern New York. *Bulletin of the Torrey Botanical Club* 110:370-379.
- Barber, S.A.  
1984. *Soil Nutrient Availability. A Mechanistic Approach.* J. Wiley and Sons, New York, 398 p.
- Barden, L.S.  
1980. Tree replacement in a cove forest of the Southern Appalachians. *Oikos* 35:16-19.
- Barden, L.S.  
1981. Forest development in canopy gaps of a diverse hardwood forest of the Southern Appalachian Mountains. *Oikos* 37:205-209.
- Bjorkbom, J.C., and R.G. Larson.  
1977. *The Tionesta Scenic and Research Natural Area.* U.S.D.A. Forest Service General Technical Report NE-31.
- Blackman, D., and S. Ware.  
1982. Soil moisture and the distribution of *Quercus prinus* and *Quercus rubra*. *Castanea* 47:360-367.
- Bourdeau, P.  
1954. Oak-seedling ecology determining segregation of species in Piedmont oak-hickory forests. *Ecological Monographs* 24:297-320.
- Brand, C.J., and R.W. Rhoades.  
1972. Effects of limestone dust accumulation on composition of a forest community. *Environmental Pollution* 3:217-225.
- Braun, E.L.  
1935. The vegetation of Pine Mountain, Kentucky. *Ecological Monographs* 10:193-241.
- Braun, E.L.  
1950. *Deciduous Forests of Eastern North America.* Blakiston, Philadelphia. 596 p.
- Bray, J.R., and J.T. Curtis.  
1957. An ordination of the upland forest communities of Southern Wisconsin. *Ecological Monographs* 27:325-349.
- Brush, G.S., C. Lenk and J. Smith.  
1980. The natural forests of Maryland: an explanation of the vegetation map of Maryland. *Ecological Monographs* 31:567-586.
- Bryant, W.S.  
1973. *An Ecological Investigation of Panther Rock, Anderson County, Kentucky.* Ph.D., Southern Illinois University, Carbondale.
- Bryant, W.S.  
1985. An analysis of the Lloyd Wildlife Preserve Forest, Grant County, Kentucky. *Transactions of the Kentucky Academy of Science* 46:116-120.
- Buell, M.F., A.N. Langford, D.W. Davidson and L.F. Ohmann. 1966. The upland forest continuum in northern New Jersey. *Bulletin of the Torrey Botanical Club* 82:463-472.

<sup>1/</sup> These are text references, not including all data sources (available from author).

- Bunce, J.A., L.N. Miller and B.F. Chabot.  
1977. Competitive exploitation of soil reserves by five eastern North American tree species. *Botanical Gazette* 138:168-173.
- Campbell, J.J.N.  
1980. Present and Presettlement Forest Conditions in the Inner Bluegrass of Kentucky. Ph.D., University of Kentucky, Lexington. 209 p.
- Cantlon, J.E.  
1953. Vegetation and microclimate on north and south slopes of Cushtunk Mountain, New Jersey. *Ecological Monographs* 23:127-148.
- Charney, J.D.  
1980. Hemlock-hardwood community relationships in the Highlands of southeastern New York. *Bulletin of the Torrey Botanical Club* 107:244-257.
- Coffman, M.S., and G.L. Willis.  
1977. The use of indicator species to classify climax sugar maple and eastern hemlock forest in Upper Michigan. *Forest Ecology and Management* 1:149-168.
- Cogbill, C.V.  
1976. The effect of acid precipitation on tree growth in Eastern North America. U.S.D.A. Forest Service General Technical Report NE-23, p. 363-370.
- Collins, S.L., P.G. Risser and E.L. Rice.  
1981. Ordination and classification of mature bottomland forests in North Central Oklahoma. *Bulletin of the Torrey Botanical Club* 108:152-165.
- Crankshaw, W.B., S.A. Qadir and A.A. Lindsey.  
1965. Edaphic controls of tree species in presettlement Indiana. *Ecology* 46:688-698.
- Cribben, L.D., and D.A. Scacchetti.  
1976. Diversity in tree species in southeastern Ohio *Betula nigra* communities. U.S.D.A. Forest Service General Technical Report NE-23, p. 979-990.
- Curtis, J.T.  
1959. The Vegetation of Wisconsin. University of Wisconsin Press, Madison, 657 p.
- Davis, M.A.  
1981. Quaternary history and the stability of forest communities. In D.C. West et al. (eds.) *Forest Succession: Concepts and Applications*, p. 132-153. Springer-Verlag, New York.
- Delcourt, P.A., H.R. Delcourt, P.A. Cridlebaugh and J. Chapman. 1986. Holocene ethnobotanical and paleoecological record of human impact on vegetation in the Little Tennessee River Valley, Tennessee. *Quaternary Research* 25:330-349.
- DeSelm, H.R., W.H. Martin and E. Thor.  
1978. The forest vegetation of Wilson Mountain, Tennessee. *Central Hardwood Forest Conference* 2:23-38.
- Elliott, J.C.  
1953. Composition of upland second growth hardwood stands in the tension zone of Michigan as affected by soils and man. *Ecological Monographs* 23:271-288.
- Finney, H.R., N. Holowaychuk and M.R. Heddleston.  
1962. The influence of microclimate on the morphology of certain soils of the Allegheny Plateau of Ohio. *Soil Science Society of America Proceedings* 26:287-292.
- Forcier, L.K.  
1975. Reproductive strategies and the co-occurrence of climax tree species. *Science* 189:808-810.
- Fowells, H.A. (ed.)  
1965. *Silvics of Forest Trees of the United States*. U.S.D.A. Agriculture Handbook 271, 762 p.
- Franzmeier, D.F., E.J. Pedersen, T.J. Longwell, J.G. Byrne and C.K. Losche. 1969. Properties of some soils in the Cumberland Plateau as related to slope aspect and position. *Soil Science Society of America Proceedings* 33:755-761.
- Gates, F.C., and G.E. Nichols.  
1931. Relation between age and diameter in trees of the primeval northern hardwoods. *Journal of Forestry* 28:395-398.
- Gauch, H.G., and E.L. Stone.  
1979. Vegetation and soil pattern in a mesophytic forest at Ithaca, New York. *American Midland Naturalist* 102:332-345.
- Goff, F.G., and R. Mitchell.  
1975. A comparison of species ordination results from plot and stand data. *Vegetatio* 31:15-22.
- Golden, M.S.  
1981. An integrated analysis of forest communities of the central Great Smoky Mountains. *American Midland Naturalist* 106:37-53.
- Graham, S.A.  
1941. The question of hemlock establishment. *Journal of Forestry* 39:567-569.
- Hack, J.T., and J.C. Goodlett.  
1960. Geomorphology and forest ecology of a mountain region in the central Appalachians. U.S.G.S. Professional Paper 347, 66 p.

- Hansen, H.L.  
1980. The Great Lakes Region. In J.W. Barrett (ed.). Regional Silviculture of the United States, p. 67-105. Wiley-Interscience, New York.
- Hett, J.M., and O.L. Loucks.  
1976. Age structure models of balsam fir and eastern hemlock. *Journal of Ecology* 64:1029-1044.
- Hemond, H.F., W.A. Niering and R.H. Goodwin.  
1983. Two decades of vegetation change in the Connecticut Natural Area. *Bulletin of the Torrey Botanical Club* 110:184-194.
- Henry, J.D., and J.M.A. Swan.  
1974. Reconstructing forest history from live and dead plant material - An approach to the study of forest succession in southwest New Hampshire. *Ecology* 55:772-783.
- Hicks, R.R., and P.S. Frank.  
1984. Relationship of aspect to soil nutrients, species importance and biomass in a forested watershed in West Virginia. *Forest Ecology and Management* 8:281-291.
- Hill, M.O.  
1973. Diversity and evenness: a unifying notion and its consequences. *Ecology* 54:427-432.
- Hill, M.O.  
1979. DECORANA. A FORTRAN program for Detrended Correspondence Analysis and Reciprocal Averaging. *Ecology and Systematics*, Cornell University.
- Himelik, E.B., D. Neely and W.R. Crowley.  
1965. Experimental field studies on shade tree fertilization. *Illinois Natural History Survey Biological Notes* 53, 12 p.
- Hinckley, T.M., S.W. Running and J.P. Lassoie.  
1978. Temporal and spatial variations in the water status of forest trees. *Forest Science Monographs* 20, 72 p.
- Hinkle, C.R.  
1975. A preliminary study of the flora and vegetation of Cumberland Gap National Historical Park, Middlesboro, Kentucky. M.Sc., University of Tennessee, Knoxville. 236 p.
- Hinkle, C.R.  
1978. The relationship of forest communities and selected species to edaphic and topographic factors on the Cumberland Plateau of Tennessee. Ph.D., University of Tennessee, Knoxville.
- Hough, A.F., and R.D. Forbes.  
1943. The ecology and silvics of Pennsylvania high-plateau forests. *Ecological Monographs* 13:299-320.
- Huennecke, L.F.  
1982. Wetland forests of Tompkins County, New York. *Bulletin of the Torrey Botanical Club* 109:51-63.
- Hutchins, R.B., R.L. Blevins, J.D. Hill and E.H. White.  
1976. The influence of soils and micro-climate on vegetation of forested slopes in Eastern Kentucky. *Soil Science* 121:234-241.
- Jensen, R.J.  
1979. Indirect ordination of forest stands of the Northwest Highland Rim. *Journal of the Tennessee Academy of Science* 54:10-14.
- Johnson, G., and S. Ware.  
1982. Post-chestnut forests in the central Blue Ridge of Virginia. *Castanea* 47:329-343.
- Johnson-Groh, C.  
1985. Vegetation communities of Ledges State Park, Boone County, Iowa. *Proceedings of the Iowa Academy of Science* 92:129-136.
- Karban, R.  
1978. Change in an oak-chestnut forest since the chestnut blight. *Castanea* 43:221-228.
- Kasmer, J., P. Kasmer and S. Ware.  
1984. Edaphic factors and vegetation in the Piedmont lowland of southeastern Pennsylvania. *Castanea* 49:147-157.
- Keever, C.  
1973. Distribution of major tree species in southeastern Pennsylvania. *Ecological Monographs* 43:303-327.
- Lamson, N.I.  
1980. Effect of fertilization on four species in mature Appalachian stands. *Central Hardwood Forest Conference* 3:449-457.
- Leak, W.B.  
1970. Successional change in northern hardwoods predicted by birth and death simulation. *Ecology* 51:794-801.
- Lemieux, G.J.  
1963. Soil vegetation relationships in the Northern Hardwoods of Quebec. In C.T. Youngberg (ed.). *Forest Soil Relationships in North America*, p. 163-176. Oregon State University Press, Corvallis.
- Lewin, D.C.  
1974. The vegetation of the Ravines of the southern Finger Lakes, New York, region. *American Midland Naturalist* 91:315-342.
- Lindsey, A.A., and J.O. Sawyer.  
1971. Vegetation-climate relationships in the eastern United States. *Proceedings of the Indiana Academy of Science* 80:210-214.

- Lodhi, M.A.K.  
1977. The influence and comparison of individual forest trees on soil properties and possible inhibition of nitrification due to intact vegetation. *American Journal of Botany* 64:260-264.
- Lorimer, C.G.  
1980. Age structure and disturbance history of a southern Appalachian virgin forest. *Ecology* 61:1169-1184.
- Losche, C.K., R.J. McCracken and C.B. Davey.  
1970. Soils of steeply sloping landscapes in southern Appalachian mountains. *Soil Science Society of America Proceedings* 34:473-478.
- Mackey, H.E., and N. Sivec.  
1973. The present composition of a former oak-chestnut forest in the Allegheny Mountains of western Pennsylvania. *Ecology* 54:915-919.
- Marks, P.L., and P.A. Harcombe.  
1981. Forest vegetation of the Big Thicket, Southeast Texas. *Ecological Monographs* 51:287-305.
- Martin, W.H.  
1978. White oak communities in the Great Valley of east Tennessee. *Central Hardwood Forest Conference* 2:39-61.
- Martin, W.H., and H.R. DeSelm.  
1976. Forest communities of dissected uplands in the Great Valley of east Tennessee. *Central Hardwood Conference* 1:11-29.
- McCarthy, B.C., T.I. Vierheller and W.A. Wistendahl. 1984. Species ordination of upper slope oak-hickory stands of southeastern Ohio. *Bulletin of the Torrey Botanical Club* 111:56-66.
- McCormick, J.F. and P.B. Platt.  
1980. Recovery of an Appalachian forest following the chestnut blight or Catherine Keever - you were right! *American Midland Naturalist* 104:264-273.
- McCormick, L.H., and K.C. Steiner.  
1978. Variation in aluminum tolerance among six genera of trees. *Forest Science* 24:565-568.
- McIntosh, R.P.  
1972. Forests of the Catskill Mountains, New York. *Ecological Monographs* 42:143-162.
- Michaux, F.A.  
1805. Travels to the West of the Allegheny Mountains. In R.G. Thwaites (ed.). 1904. *Early Western Travels*. Vol. III. Arthur C. Clark Co., Cleveland.
- Mitchell, H.L., and R.F. Chandler.  
1939. The nitrogen nutrition and growth of certain deciduous trees of northeastern United States. *Black Rock Forest Bulletin No.* 11, 94 p.
- Monk, C.D.  
1968. Successional and environmental relationships of the forest vegetation of north central Florida. *American Midland Naturalist* 79:441-457.
- Mowbray, T.E., and H. Oosting.  
1968. Vegetation gradients in relation to environment and phenology in a Blue Ridge Gorge. *Ecological Monographs* 38:309-344.
- Muller, R.N.  
1982. Vegetation patterns in the mixed mesophytic forest of Eastern Kentucky. *Ecology* 63:1901-1917.
- Neely, D., E.B. Himelick and W.R. Crowley.  
1970. Fertilization of established trees: a report of field studies. *Illinois Natural History Survey Bulletin* 30:235-266.
- Nicholson, S.A., H.T. Scott and A.R. Breisch.  
1979. Structure and succession in the tree stratum at Lake George, New York. *Ecology* 60:1240-1254.
- Nigh, T.A., S.G. Pallardy and H.E. Garrett.  
1985. Sugar maple - environment relationships in the River Hills and central Ozark Mountains of Missouri. *American Midland Naturalist* 114:235-251.
- Ohmann, L.F., and M.F. Buell.  
1968. Forest vegetation of the New Jersey Highlands. *Bulletin of the Torrey Botanical Club* 95:287-298.
- Paillet, F.L.  
1982. The ecological significance of American chestnut (*Castanea dentata* (Marsh) Borkh.) in the Holocene forests of Connecticut. *Bulletin of the Torrey Botanical Club* 109:457-473.
- Pearson, P.R.  
1962. Increasing importance of sugar maple on two calcareous formations in New Jersey. *Ecology* 43:711-718.
- Peet, R.K., and N.L. Christensen.  
1980. Hardwood forest vegetation of the North Carolina Piedmont. *Veroffentlichungen des Geobotanischen Institutes der ETH, Stiftung Rubel (Zurich)* 69:14-39.
- Pittillo, J.D.  
1963. Distribution and ecology of *Cladrastis lutea*. M.Sc., University of Kentucky, Lexington, 31 p.

- Rackham, O.  
1980. *Ancient Woodland: its History, Vegetation and Uses in England*. Arnold, London, 402 p.
- Reed, F.W.  
1905. Report on an examination of a forest tract in western North Carolina. U.S. Bureau of Forestry Bulletin 60, 32 p.
- Read, R.A.  
1952. Tree species occurrence as influenced by geology and soil on an Ozark north slope. *Ecology* 33:239-246.
- Rheinhardt, R.D., and S.A. Ware.  
1984. The vegetation of the Balsam Mountains of southwest Virginia: a phytosociological study. *Bulletin of the Torrey Botanical Club* 111:287-300.
- Robertson, P.A., M.D. Mackenzie and Lee F. Elliott. 1984. Gradient analysis and classification of the woody vegetation for four sites in southern Illinois and adjacent Missouri. *Vegetatio* 58:87-104.
- Rochow, J.J.  
1972. A vegetational description of a mid-Missouri forest using gradient analysis techniques. *American Midland Naturalist* 87:377-396.
- Rogers, R.S.  
1981. Mature mesophytic hardwood forest: community transition, by layer, from east-central Minnesota to southeastern Wisconsin. *Ecology* 62:1634-1647.
- Runkle, J.R.  
1979. Gap phase dynamics in climax mesic forest. Ph.D., Cornell University, 301 p.
- Safley, J.M.  
1970. Vegetation of the Big South Fork Cumberland River, Kentucky and Tennessee. M.Sc., University of Tennessee, Knoxville, 161 p.
- Safford, L.O.  
1973. Fertilization increases diameter growth of birch-beech-maple trees in New Hampshire. U.S.D.A. Forest Service Research Note NE-182, 4 p.
- Safford, L.O., and M.M. Czapowskyj.  
1979. Growth responses to fertilizer in a young aspen-birch stand. U.S.D.A. Forest Service Research Note NE-274, 6 p.
- Schmalzer, P.A., C.R. Hinkle and H.R. DeSelm.  
1978. Discriminant analysis of cove forests of the Cumberland Plateau of Tennessee. *Central Hardwood Forest Conference* 2:62-86.
- Schneider, G.  
1966. A 20-year investigation of a sugar maple-beech stand in southern Michigan. *Michigan Agricultural Experiment Station Bulletin* 15. 61 p.
- Sherman, M.D.  
1978. Community composition, species diversity, forest structure and dynamics as affected by soil and site factors in Savage Gulf, Tennessee. M.Sc., University of Tennessee, Knoxville, 146 p.
- Sporne, K.R.  
1980. A re-investigation of character correlations among dicotyledons. *New Phytologist* 85:419-449.
- Stearns, F.S.  
1949. Ninety years change in a northern hardwood forest in Wisconsin. *Ecology* 30:350-358.
- Stephens, G.R., and P.E. Waggoner.  
1970. The forests anticipated from 40 years of natural transitions in mixed hardwoods. *Bulletin of the Connecticut Agricultural Experiment Station* 707, 58 p.
- Stephenson, S.L.  
1982. A gradient analysis of slope forest communities of the Salt Pond Mountain area in southwestern Virginia. *Castanea* 47:201-215.
- Steyermark, J.A.  
1940. Studies on the vegetation of Missouri. I. Natural plant associations and succession in the Ozarks of Missouri. *Field Museum of Natural History, Botanical Series* 9:349-475.
- Stout, B.B., J.M. Deschenes and L.F. Ohmann.  
1975. Multispecies model of a deciduous forest. *Ecology* 56:226-231.
- Thor, E., H.R. DeSelm and W.H. Martin.  
1969. Natural reproduction on upland sites in the Cumberland Mountains of Tennessee. *Journal of the Tennessee Academy Science* 44:96-100.
- Thorne, R.F.  
1979. Phytochemistry and angiosperm phylogeny: a summary statement. In D.A. Young and D.S. Sieglar (eds.), p. 233-295. *Phytochemistry and Angiosperm Evolution*. Praeger, New York.
- U.S.D.A. Soil Conservation Service.  
1975. *General Soil Map of Kentucky*. Publication 4-R-34874.
- U.S.G.S.  
1969. *Soil Map, sheets 85-88 in National Atlas*. Washington, D.C.

- Van Auken, O.W., E.M. Gese and K. Connors.  
1985. Fertilization response of early and late successional species: Acacia smallii and Celtis laevigata. Botanical Gazette 146:421-430.
- Vankat, J.L., W.H. Blackwell and W.E. Hopkins.  
1975. The dynamics of Hueston Woods and a review of the question of the successional status of the southern Beech-Maple Forest. Castanea 40:290-308.
- Vankat, J.L., D.S. Anderson and J.A. Howell.  
1977. Plant communities and distribution factors in Abner's Hollow, a south-central Ohio watershed. Castanea 42:216-223.
- Voight, J.W., and R.H. Mohlenbrock.  
1964. Plant Communities of Southern Illinois. Southern Illinois University Press, Carbondale, 202 p.
- Ward, R.T.  
1956. The beech forests of Wisconsin - changes in forest composition and the nature of the beech border. Ecology 37:407-419.
- Ware, S.A.  
1982. Polar ordination of Braun's Mixed Mesophytic Forest. Castanea 47:403-407.
- Whitney, G.G.  
1982. Vegetation-site relationships in the presettlement forests of northeastern Ohio. Botanical Gazette 143:225-237.
- Whitney, G.G.  
1984. Fifty-years of change in the arboreal vegetation of Heart's Content, an old-growth hemlock-white pine northern hardwood stand. Ecology 65:403-408.
- Whitney, G.G., and J.R. Steiger.  
1985. Site factor determinants of the presettlement prairie-forest border of north-central Ohio. Botanical Gazette 146:421-430.
- Whittaker, R.H.  
1956. Vegetation of the Great Smoky Mountains National Park. Ecological Monographs 26:1-80.
- Woods, F.W.  
1953. Disease as a factor in the evolution of forest composition. Journal of Forestry 51:871-873.
- Woods, K.D.  
1984. Patterns of tree replacement: canopy effects on understory pattern in hemlock-northern hardwood forests. Vegetatio 56:87-107.
- Wuenschel, J.E., and T.T. Kozlowski.  
1971. Relationship of gas-exchange resistance to tree-seedling ecology. Ecology 52:1016-1023.
- Zager, P.E., and P.W. Pippen.  
1977. Fifteen years of change in a southwest Michigan hardwood forest. Michigan Botanist 16:201-211.
- Zedler, P.H., and P.G. Goff.  
1973. Size association analysis of forest successional trends in Wisconsin. Ecological Monographs 43:79-94.
- Zimmerman, M., and W.L. Wagner.  
1979. A description of the woody vegetation of oak-hickory forests in the northern Ozark Highland. Bulletin of the Torrey Botanical Club 106:117-122.
- Zimmerman, M.H.  
1983. Xylem Structure and the Ascent of Sap. Springer-Verlag, New York. 143 p.
- Zon, R.  
1904. Chestnut in Maryland. U.S.D.A. Bureau of Forestry Bulletin 53, 31 p.