CONVERGENCE DURING SECONDARY FOREST SUCCESSION

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SUMMARY

(1) Successional convergence in community composition was examined in terms of three questions: (i) for a given site is there a continuous shift in composition toward that characteristic of climax? (ii) does variation in community composition along an environmental gradient increase or decrease with succession? (iii) to what extent is the species composition along a successional gradient determined by site characteristics rather than by chance factors? Hypotheses regarding the nature of successional convergence are reviewed in terms of these questions.

(2) These hypotheses were tested using data for tree (>0·5 cm dbh) and herb (all foliage <1 m tall) abundance from 191 upland forest stands on the North Carolina piedmont which were grouped in five successional age classes (20–40-, 40–60-, 60–80-, and >80-yr-old pines, and uneven-aged hardwoods). For each age-group first axis ordination scores (detrended correspondence analysis) were highly correlated most consistently with soil pH as compared with other soil and site variables. This correlation was greatest in the intermediate-age (40–60- and 60–80-yr-old) pines and in the hardwood stands, and lowest in old pine stands. The distribution of species in the ordination space was most similar between the intermediate-age pine stands and the hardwoods; in contrast, young and old pine age classes were dissimilar to hardwoods. Species distributions in relation to the soil pH gradient were also most similar between intermediate-age pines and hardwoods. Thus, there is a shift in species composition toward that characteristic of climax, but it is probably not monotonic.

(3) Beta-diversity was highest in the hardwoods and lowest among the pines. Community differentiation along gradients increased in this chronosequence.

(4) Predictability of soil pH, based on stand species composition, was highest in the intermediate-age pines and in the hardwoods. Habitat breadth in relation to soil pH decreased steadily with successional age. These results are consistent with the hypothesis that the role of chance factors (e.g. site history and seed rain) decreases with successional age.

INTRODUCTION

Convergence toward a stable, predictable species composition was a central theme in Clements's (1916, 1928) classical model of plant succession, and remains a notion implicit in many more recent schemes (e.g. Drury & Nisbet 1971; Horn 1974; Pickett 1976; Connell & Slatyer 1977). In this paper, tests are presented of various concepts of convergence of species composition using data from the North Carolina piedmont forests.

Generally, successional convergence in terrestrial plant communities has been defined only vaguely. Cowles (1901) and Clements (1916) described it as a trend toward increased uniformity in species composition which results from interactions among dominant species

and their alteration of the physical environment. The large site-to-site variation in composition of immature communities was thought to be a result of variation in initial conditions and to decrease with community maturation. Early successional composition was, nonetheless, considered to be highly deterministic, allowing the definition of a multitude of seres (eusere, hydrosere, mesosere, psammosere, pyrosere, xerosere, etc.), each with a unique and predictable series of species assemblages. In this model there was little allowance for chance effects such as spatial and temporal variation in seed rain or between-year climatic variation.

In contrast to the highly deterministic composition of pioneer communities imagined by Clements (1916, 1928), Margalef (1963, 1968) suggested that the composition of pioneer communities is determined by chance arrival during the initial period of colonization when competition is low. Variability in community composition along environmental gradients might increase or decrease during succession, but increasing competition should result in decreasing niche breadth and increasing species fidelity to site conditions. Thus, for any given site community composition should become more predictable as succession proceeds. In contrast, Egler's (1954, 1975) view that initial conditions have lasting impact on community composition implies that both early and late stages of succession are mainly determined by chance.

In this paper gradient analysis techniques are used to test several hypotheses regarding successional convergence in vegetational composition which are implicit in the theories of Clements and Margalef. Toward this end three related questions are posed.

(i) For a given site, is there a continuous shift in composition toward that characteristic of climax? Convergence in this sense is implicit in most models of succession and can be measured by the extent to which vegetational composition at various stages of succession correlates with that composition characteristic of mature communities.

(ii) Does change in community composition along environmental gradients increase or decrease with succession? Convergence in this sense can be measured in terms of beta-diversity or species turnover along gradients (Whittaker 1972). Clements's (1916) theory in its extreme form predicts convergence to a monoclimax. A more temperate view consistent with Clements's reasoning is that the dominant species should ameliorate the natural environment sufficiently to reduce the species turnover encountered on a given range of sites. Other studies suggest that compositional differentiation increases with succession (e.g. Matthews 1979; Pineda *et al.* 1981a). This would occur, for example, if early successional communities consisted of species with broad ecological amplitudes, while near-climax communities were characterized either by specialist species or by the same species but with much narrower realized niches (*sensu* Hutchinson 1958). Examples of decreasing niche breadth during succession can be seen in the work of Werner & Platt (1976) on *Solidago*, Auclair & Goff (1971) on Wisconsin forests, and Pineda *et al.* (1981b) on Iberian pastures. It is also possible that variability among communities is independent of successional change, resulting in no systematic change in beta-diversity. This might be expected if the initial conditions fix the course of succession, as suggested by Egler (1954, 1975) and others, and documented for marine fouling communities by Sutherland (1974).

(iii) To what extent is species composition along a successional gradient determined by site characteristics rather than by chance factors, such as seed rain? Margalef hypothesized convergence from an initial, highly random composition toward a largely deterministic climax. If this is correct, site conditions should account for a larger portion of compositional variation in more mature communities.

STUDY AREA

Our data are from forests of the North Carolina piedmont, many of which have developed on old agricultural fields after they were abandoned. The general pattern of succession on such fields is well known (Billings 1938; Oosting 1942). For 10–15 yr following abandonment the fields are dominated by herbs, together with seedlings of a range of coniferous and broadleaved tree species. Subsequently, pines (*Pinus echinata** and *P. taeda*) overtop the other woody species and form an even-aged (<5 yr age spread) canopy with an understory of herb and hardwood tree species. Although the density of pine trees decreases continuously during this period (Peet & Christensen 1980a), ordinarily the recruitment of hardwood trees into the canopy does not occur until the pines are 70–100 yr old. Eventually the pine community is replaced by an uneven-aged, hardwood deciduous forest, which typically is dominated by various species of *Carya* and *Quercus*. Extensive abandonment of agricultural land since the mid-nineteenth century has resulted in stands of all successional ages on a wide variety of sites.

METHODS

A total of 238 forest stands in Durham, Orange, and Wake countries (36°N, 79°W; altitude 75–230 m), representing various time intervals since field abandonment, were sampled. Stands-were selected to include the range of soil and topographic conditions over which typical old field succession occurs. Alluvial, swamp, and rocky bluff hardwood stands (see Peet & Christensen 1980b) were subsequently deleted because few old field pine stands occur in these habitats. A few stands which occurred on very acid soils (pH < 4·0) were also deleted because such sites were not available for all age-classes. The Duke Forest archives provided records of disturbance and management which enabled stands which had been heavily thinned or disturbed during the past 50 years to be avoided.

The vegetation in each stand was sampled using a centrally located 0·1 ha plot in which all trees (woody plants >1 m tall) were recorded. The frequency and cover of herbs (all vascular plants with leaf area below 1 m) were sampled using twenty-five 1-m² quadrats spaced regularly along a central 50 m transect. The presence of other species in the plot was also recorded.

Five samples of the 0–10 cm soil layer were collected from each plot, dried, sifted to remove particles greater than 2 mm, and analysed for pH, organic matter content, texture, water retention at −0·1 MPa and −1·5 MPa, and exchangeable calcium, magnesium, potassium, manganese, aluminum, and phosphate-phosphorus. Details of the techniques used in vegetation sampling and soil analysis are described in Peet & Christensen (1980b).

Stands were grouped into five age-classes based on growth ring counts of the largest trees and records in the Duke Forest archives: (i) 20–40-yr-old pines; (ii) 40–60-yr-old pines; (iii) 60–80-yr-old pines; (iv) over 80-yr-old pines; and (v) uneven-aged hardwoods. The average stand composition for each age-class is summarized in Fig. 1. Although the total stand basal area is highest in the over 80-yr age-class, basal area is greatest for pines in the 40–60 yr age-class. Pines are present in 35% of all hardwood stands, but they account for a relatively small proportion of the basal area in hardwood stands. Wind-dispersed hardwood canopy trees are common in young pine stands. Although their

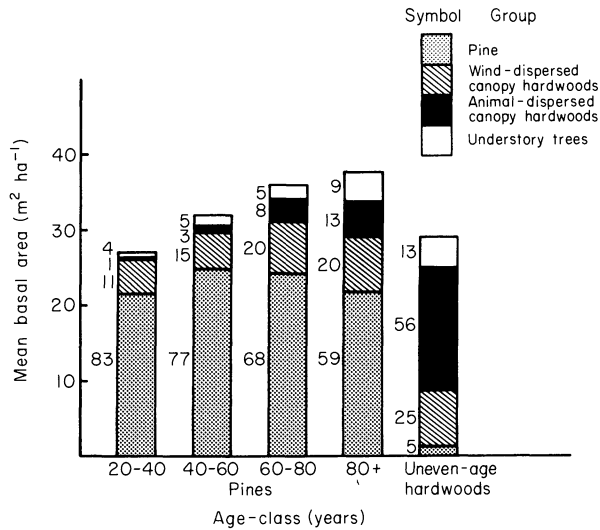* Nomenclature follows Radford, Ahles & Bell (1968).

FIG. 1. Mean basal area of four tree groups for each of five forest age-classes. The mean numbers to the left of each bar indicate the basal area (as a percentage of the total) for each group.

basal area increases with successional age, most of these species are actually less widespread among older pine and hardwood stands. For example, *Liquidambar styraciflua* occurs in 93% of all pine stands and has the greatest basal area of all hardwood species in these forests. However, it is found in only 51% of the hardwood stands. Animal-dispersed hardwoods increase gradually with increasing stand age and are dominant in the climax hardwood stands.

Both tree and herb data for each age class were ordinated using detrended correspondence analysis (Hill 1979; Hill & Gauch 1980; Gauch 1982). This is a refined version of reciprocal averaging (Hill 1973), a technique which has the virtue of being relatively tolerant of nonmonotonic species responses along gradients (Gauch, Whittaker & Wentworth 1977; Gauch, Whittaker & Singer 1981). It is well suited for our purposes. Axis scores are scaled with respect to species turnover such that their length provides a direct measure of beta-diversity (Hill 1979; Hill & Gauch 1980). Like several other ordination techniques, detrended correspondence analysis also provides simultaneous species and stand coordinates.

RESULTS

Indirect gradient analysis

For these analyses the range of samples from uneven-aged hardwood forests is assumed to be representative of the range of climax forests in the region. Indirect gradient techniques, such as detrended correspondence analysis, provide geometric representations of stands and species wherein stands of similar composition, or species of similar distribution are found near each other. Presumably the primary dimensions of such a geometric space are correlated with those factors which most greatly influence stand composition (Gauch 1982). The first test of convergence was to compare, using Spearman's rank correlation analysis (Sokal & Rohlf 1969), the order of species scores

along the first detrended correspondence analysis axis for each seral age-class with the order for species along the first axis of hardwood stands, the presumed endpoint of the successional sequence. Correlations were compared between age-classes in pairs using the test for homogeneity suggested by Sokal & Rohlf (1969, p. 520).

For tree data, rank correlation indicated that the order of species converged on the climax configuration through the first three age-classes, but diverged in the oldest pine stage (Table 1). The herb data show a similar initial convergence. Divergence in the old age stands was sufficiently pronounced that there was virtually no correspondence between the order of species in those stands and the mature hardwoods.

Examination of the first axis only from each ordination could conceivably lead to errors in interpretation if different environmental or historical factors were of primary importance in the various age groups. Simultaneous examination of species positions on the first three ordination axes using canonical correlation analysis allowed for this possibility. In effect, canonical correlation analysis rotates the ordination space of the successional class relative to that of the hardwoods, seeking the best possible match of the two spaces (Morrison 1967). Canonical correlation coefficients, which indicate the degree of matching between the two spaces, are highest between hardwoods and the intermediate age classes. For both the herb and tree data sets there are increases in relative convergence in the over 80-yr-old pines which suggests the possibility that much of the apparent divergence in this age-class, observed using only first axes, is due to a change in the relative importance of environmental factors. Light, for example, might take on added importance with death of the pines in the older stands.

Direct gradient analysis

Stand scores for each axis generated by the ordination were compared with values of the soil variables using Spearman's rank correlation coefficient (Table 2). Within each successional stage except the over 80-yr-old pines, the soil factors most strongly correlated with first axis stand ordination scores for both trees and herbs were pH and exchangeable soil cations (calcium, magnesium, and manganese). As would be expected, there was

TABLE 1. Comparison of species detrended correspondence analysis scores for four age groups of successional pine stands with those of near-climax hardwood forests of the North Carolina piedmont using rank and canonical correlation analyses. Indices within a row with the same superscript are not statistically different at $P = 0.01$, based on pairs of comparisons. Significance symbols: *, $P < 0.05$; **, $P < 0.001$.

Forest type	Pine	Pine	Pine	Pine	Hardwood
Age-class (years)	20–40	40–60	60–80	>80	uneven–aged
Number of stands	20	35	34	30	72
Number of tree species	27	33	34	32	36
Number of herb species	158	175	170	158	328
Rank correlation coefficient: first axis species scores for pine compared with hardwood classes					
Trees	0.16[a]	0.43[b]*	0.65[b]**	0.40[b]*	(1.00)
Herbs	0.37[a]**	0.49[a]**	0.33[a]**	0.02[b]	(1.00)
Canonical correlation coefficient: first three axes for pine compared with hardwood classes					
Trees	0.64	0.80	0.86	0.79	(1.00)
Herbs	0.60	0.65	0.70	0.41	(1.00)

TABLE 2. Mean values for soil factors and their rank correlation with tree and herb first detrended correspondence analysis axis stand scores in four age groups of successional pine stands and near-climax hardwood forests of the North Carolina piedmont. Correlation coefficients within a row with the same superscript are not statistically different at $P = 0.01$ based on comparisons of pairs. Significance symbols: *, $P < 0.05$; **, $P < 0.01$.

Forest type Age-class (years)	Soil factor Mean ± 1 S.D.					Spearman rank correlation coefficient (r) with: First axis trees					First axis herbs				
	Pine 20–40	Pine 40–60	Pine 60–80	Pine >80	Hardwood uneven	Pine 20–40	Pine 40–60	Pine 60–80	Pine >80	Hardwood uneven	Pine 20–40	Pine 40–60	Pine 60–80	Pine >80	Hardwood uneven
pH	4.80 ±0.52	4.86 ±0.53	4.75 ±0.45	4.71 ±0.44	4.74 ±0.48	0.36[a]	0.65[b]**	0.70[b]***	0.44[a]**	0.65[b]***	0.87[a]***	0.70[a]***	0.87[a]***	0.14[b]	0.71[a]***
Calcium (μg g^{-1})	362.1 ±335.8	362.7 ±265.8	347.9 ±276.1	315.8 ±259.1	384.5 ±408.3	0.40[a]	0.65[b]**	0.53[a]*	0.47[a]*	0.65[b]***	0.69[a]***	0.56[b]**	0.69[a]***	0.14[c]	0.66[a]***
Magnesium (μg g^{-1})	195.3 ±134.9	110.4 ±116.3	96.1 ±103.9	92.9 ±77.3	88.5 ±80.0	0.36[a]	0.59[b]*	0.49[a]*	0.59[b]**	0.73[b]***	0.76[a]***	0.43[b]*	0.56[a]***	0.11[c]	0.74[a]***
Potassium (μg g^{-1})	52.8 ±32.1	54.0 ±21.0	51.8 ±27.7	63.1 ±41.2	63.0 ±22.5	0.31[a]	0.07[a]	0.23[a]	0.13[a]	0.49[b]***	0.45[b]	0.22[b]	0.42[b]	0.23[b]	0.45[a]***
Aluminum (μg g^{-1})	76.2 ±83.4	94.2 ±158.1	144.1 ±193.5	101.8 ±85.2	134.4 ±162.5	0.08[a]	0.17[a]	0.08[a]	0.51[b]*	0.39[b]*	0.40[a]*	0.47[a]*	0.19[b]	0.10[b]	0.39[a]**
Manganese (μg g^{-1})	403.2 ±350.9	480.0 ±315.0	404.6 ±213.5	366.9 ±171.4	438.9 ±312.2	0.49[a]**	0.61[b]***	0.63[b]***	0.59[b]**	0.67[b]***	0.59[a]**	0.75[a]***	0.82[a]***	0.02[c]	0.61[a]***
Phosphate-P (μg g^{-1})	2.08 ±0.92	2.41 ±1.53	2.61 ±2.18	1.95 ±0.76	3.36 ±2.09	0.22[a]	0.10[a]	0.14[a]	0.26[a]	0.41[b]**	0.01[a]	0.03[a]	0.33[a]	0.24[a]	0.37[a]*
Organic matter (%)	4.93 ±2.56	5.85 ±1.99	5.52 ±2.26	5.20 ±2.71	6.95 ±2.24	0.06[a]	0.10[a]	0.01[a]	0.26[a]	0.17[a]	0.56[a]**	0.39[a]*	0.20[b]	0.15[b]	0.14[b]
H$_2$O at 0.1 MPa (%)	13.9 ±4.9	17.0 ±5.3	16.3 ±5.5	15.2 ±6.2	19.0 ±4.6	0.02[a]	0.09[a]	0.03[a]	0.12[a]	0.04[a]	0.43[a]	0.28[b]	0.16[b]	0.11[b]	0.05[b]
H$_2$O at 1.5 MPa (%)	8.7 ±4.0	8.9 ±4.0	8.2 ±3.1	8.1 ±3.4	9.4 ±4.2	0.17[a]	0.30[a]	0.18[a]	0.28[a]	0.41[b]*	0.49[a]**	0.29[b]	0.31[b]	0.15[b]	0.40[a]**
Clay (%)	12.1 ±5.0	12.8 ±6.0	11.6 ±5.5	11.1 ±5.0	11.2 ±4.5	0.55[a]**	0.45[a]**	0.49[a]**	0.17[b]	0.51[a]***	0.46[a]**	0.26[b]	0.51[a]***	0.27[b]	0.57[a]***

considerable covariance among pH and cation availability ($r = 0.60$–0.93). Peet & Christensen (1980b) have previously demonstrated this relationship between pH or cation availability, and vegetation variation in mature hardwood stands. There were only weak correlations between later axes (which accounted for considerably less variation among stands within an age-class) and other environmental variables. Because soil pH was correlated consistently highly with vegetation composition, the soil pH gradient was used to test for convergence. It is of little consequence here that the pH gradient represents a complex soil chemical gradient and that pH *per se* is probably neither the proximate nor ultimate factor controlling vegetation composition.

Rank correlations between pH and first axis stand scores for tree data (Table 2) were low and not significant in the 20–40-yr-old pine stands but were highly significant in intermediate-age (40–60- and 60–80-yr-old) stands; in older pine stands the correlation was weaker but it was high in the hardwood stands. The pattern of change in the relationship of pH and first axis herb scores was similar to that for trees except that the correlation in the 20–40-yr-old pines was high. For both tree and herb data the relationship between pH and first axis stand scores was weaker in old than in intermediate-age pine stands. This suggests that the composition of old pine stands is less predictable in terms of those factors most important in predicting climax composition. This result is consistent with the divergence suggested by comparison of species detrended correspondence analysis scores for old pine stands with those for hardwoods (Table 1).

For both the tree and herb data sets, species distributions were examined with respect to the pH gradient for each seral age-class compared with the hardwoods. The importance weighted mean pH (H_i) was calculated for each species (i) occurring in at least five stands in an age-class as follows:

$$H_i = \frac{\sum\limits_{j=1}^{n} s_j \cdot V_{ij}}{\sum\limits_{j=1}^{n} V_{ij}}$$

where n is the number of stands in an age-class, s_j is the soil pH of the jth stand, and V_{ij} is the importance of species i in stand j (V = basal area for trees and percentage cover for herbs). The result is a direct ordination of species along the pH gradient.

The mean pH score of each species in each successional age-class was compared with those from the hardwood stands using rank correlation (Table 3); note that only species shared between a particular age-class and the hardwoods were considered in this analysis. In general, these correlations were stronger than those for similar comparisons using the ranks of species along ordination axes (cf. Table 1). However, it was again the intermediate age-classes which were most similar to mature hardwoods.

Using the mean pH scores for the same species, it is possible to predict stand pH based on species composition as follows:

$$\text{Predicted pH stand}_j = \frac{\sum\limits_{i=1}^{s} H_i V_{ij}}{\sum\limits_{i=1}^{s} V_{ij}}$$

where H_i is the mean pH of species i, s is the number of species in stand j, and V_{ij} is the importance of species i in stand j. Species pH means derived from analysis of hardwood

TABLE 3. Comparison of locations of species on soil pH gradient for four age groups of successional pine stands with near-climax hardwoods of the North Carolina piedmont, and comparison of the predicted and observed soil pH values for each age group (see text). Only species occurring in at least five stands in an age-class were included in these analyses. Indices within a row with the same superscript are not statistically different at $P = 0.01$, based on comparisons of pairs. Significance symbols: *, $P < 0.05$; **, $P < 0.001$.

Forest type	Pine	Pine	Pine	Pine	Hardwood
Age-class (years)	20–40	40–60	60–80	>80	uneven-aged
Number of tree species	20	35	34	32	36
Number of herb species	93	97	106	93	146
Rank correlation coefficient: species mean pH, pines compared with hardwoods					
Trees	0.60^{a*}	0.70^{a**}	0.56^{a**}	0.45^{a*}	(1.00)
Herbs	0.65^{a*}	0.71^{a**}	0.76^{a**}	0.56^{b*}	(1.00)
Product-moment correlation coefficient: predicted compared with observed soil pH					
Trees	0.48^{a*}	0.64^{b*}	0.55^{a*}	0.48^{a*}	0.70^{b**}
Herbs	0.81^{a**}	0.84^{a**}	0.86^{a**}	0.62^{b*}	0.75^{a**}

TABLE 4. Changes in beta-diversity among age-classes based on the first detrended correspondence analysis axis (S.D. units) in four age groups of successional pine stands and near-climax hardwood forests of the North Carolina piedmont.

Forest type	Pine	Pine	Pine	Pine	Hardwood
Age-class (years)	20–40	40–60	60–80	>80	uneven-aged
S.D. units along first axis					
Trees	1.78	2.32	2.25	1.57	2.50
Herbs	2.32	2.35	2.13	2.52	2.73

stands were used for each age class. Predicted stand soil pH values were compared to actual soil pH values using rank correlation analysis (Table 3). The results were consistent with those of the other analyses; correlations were highest in intermediate-age pine and hardwood stands.

Beta-diversity

Beta-diversity or species change along a gradient is calculated directly by the program DECORANA used for detrended correspondence analysis (Hill & Gauch 1980) in units of standard deviations of species abundance. These units are roughly equivalent to half-changes of species composition (half-change ≈ 1.19 S.D.; see Hill 1979). The results for the first detrended correspondence analysis axes are shown in Table 4. The prediction of maximum beta-diversity at climax is supported. Convergence, in the Clementsian sense of decreased community differentiation along gradients, does not occur in these forests.

Compositional predictability

For a particular age-class, the more randomly species are distributed relative to the pH gradient, the greater should be species habitat breadth along that gradient. Thus, habitat breadth can be viewed as a measure of the randomness of species distributions. We estimated the habitat breadth (B_i) of each species which occurred in at least five stands as the importance-weighted standard deviation of the mean location of the species on the pH gradient (H_i) using the index proposed by McNaughton & Wolf (1970):

$$B_i = \left[\left\{ \sum_{j=1}^{n} (V_{ij} \cdot S_j)^2 - \sum_{j=1}^{n} (V_{ij} \cdot S_i)^2 \middle/ \sum_{j=1}^{n} V_{ij} \right\} \middle/ \sum_{j=1}^{n} V_{ij} \right]^{\frac{1}{2}}$$

Table 5. Habitat breadth along the soil pH gradient and stand heterogeneity for four age groups of successional pines and near-climax hardwood forests of the North Carolina piedmont. Values within a row with the same superscript are not statistically different at $P = 0.01$ based on t-tests of pairs.

Forest type	Pine	Pine	Pine	Pine	Hardwood
Age-class (years)	20–40	40–60	60–80	>80	uneven-aged
Habitat breadth					
Trees	2.10[a]	1.55[b]	1.51[b]	1.61[b]	1.47[b]
Herbs	2.40[a]	1.93[b]	1.86[b]	1.98[b]	1.81[b]
Stand heterogeneity					
Trees	0.91[a]	0.86[b]	0.84[b]	0.82[b]	0.74[c]
Herbs	0.68[a]	0.57[b]	0.54[b]	0.54[b]	0.49[c]

where V_{ij} is the importance of the ith species in the jth stand, s_j is the position of the jth stand on the pH gradient, and $\sum V_{ij}$ is the sum of all the importances of that species. The results (Table 5) show that habitat breadth is highest in the youngest stands, drops steadily through the intermediate-aged stands, shows a statistically insignificant increase in the oldest pine stands, and then reaches a minimum in the near climax hardwood stands. This result is consistent with Margalef's hypothesis that species–site relations become more predictable as communities mature.

High values of habitat breadth could result either from stands being composed of species of highly variable H_i or from stands with high deviation from predicted pH, but composed of species having similar values of H_i. As an alternative comparison independent of stand order along the pH gradient, for each stand the standard deviation of H_i values (mean pH for species i in hardwood stands) over all species in that stand was calculated. This is a measure of within-stand compositional heterogeneity relative to the pH gradient. This index differs from the previous one in that it looks at within-stand variation rather than species distribution along the gradient. Thus, it is sensitive, not just to habitat breadth, but to the predictability of a species occurring at any point along the gradient. The results (Table 5) show a steady decline in average stand heterogeneity with increasing stand age, a result consistent with Margalef's hypothesis of increasing predictability. No increase in compositional heterogeneity was observed in the oldest pine stands.

DISCUSSION

The three questions posed (p. 26) about secondary forest succession following cropland abandonment on the North Carolina piedmont, can now be addressed.

(i) There is not a continuous shift in compositional variation toward the characteristic climax. In most comparisons of the characters of hardwood stands with those of successional stands, the hardwood stands were most similar to the intermediate-age pine stands. Thus, pine stand development involves convergence followed by divergence before the eventual final convergence to climax. Climax composition is more predictable from a knowledge of intermediate-age stand composition than from composition of stands immediately preceding hardwoods in this chronosequence.

(ii) In general, compositional differentiation along environmental gradients (beta-diversity) increases during succession and beta-diversity was highest in mature forests. This trend is consistent with the results of Matthews (1979) and Pineda et al. (1981a) for herb-dominated ecosystems.

(iii) The extent to which species composition along a successional gradient is determined by site characteristics or chance factors cannot be answered definitively, because it is not

possible to examine all possible environmental factors and their combinations as potential determinants of community composition. However, the related question, 'Are species distributions in early successional stands less closely correlated with the environmental factors examined than the species in near climax stands?' can be addressed. In early successional stands the species have broader habitat widths along the soil pH gradient than in intermediate age and hardwood stands. Similarly, variation in the mean pH values of species (H_i from hardwoods) within individual stands decreases with increasing stand age. These results are consistent with Margalef's (1968) contention that community composition becomes increasingly predictable as succession proceeds. The greater habitat breadths and lower correlations with soil variables early in succession suggest that chance variables, such as site history and seed rain, play important but transient roles in determining stand composition at this age.

The significant role that pines play in determining plant community composition in successional stands is amply demonstrated by the response of both herbaceous and woody species in the trenching experiments of Korstian & Coile (1938). These studies, as well as those of Kramer & Decker (1944) and Oosting & Kramer (1946), indicate that soil resources, as well as light are important in determining community composition. The intensity of competition in pine stands appears to be maximal in the intermediate ages (40–80 yr old). Graphs of log mean tree biomass in relation to log density show slopes close to $-3/2$ for stands in which the total biomass is increasing but in which the rate of increase is resource limited (Yoda *et al.* 1963; Westoby 1983). The time at which this occurs varies with site conditions and the initial pine density, but for an average tree density, a $-3/2$ slope is characteristic of stands in the 40–60 yr age-class (Peet & Christensen 1980a). Stands in the 60–80 yr age-class usually have slopes approaching -1, indicating that the biomass remains constant (R. K. Peet & N. L. Christensen, unpublished). The observed changes in the average habitat breadth of species are likely to be a consequence of changes in the intensity of competition as indicated by the slope of the thinning curve. Under conditions of intense competition, species are limited to sites on which they can compete most effectively, and species fidelity to site conditions will be high. As thinning and stand growth continue, total biomass and resources are divided among a few, large individuals such that the mortality of canopy trees results in a decrease in total stand biomass, and the increased production by survivors is insufficient to compensate for this loss (Peet & Christensen 1980a; Peet 1981a). Such stands are characterized by a comparatively broken canopy structure with more light reaching the forest floor. Competition for available resources may be reduced until a new cohort of trees becomes established and fills the gaps in the canopy. These changes may be responsible for the apparent divergence observed in older stands.

It would be premature to conclude that the patterns of convergence documented here are characteristic of forest succession in general. If, however, the extent of convergence is related to variation in intensity of competition for limited resources, then changes in species fidelity and habitat breadth should parallel that variation. Results similar to those reported here are likely to occur in chronosequences where one or two species clearly dominate the successional for a long initial period, and in which resource availability is likely to be tied to the rise and decline of those species. In North America, such situations might include *Populus* stands in the upper Midwest or the Rocky Mountains (Gates 1930), conifer stands in the Rocky Mountains (Peet 1981b) and certain *Pseudotsuga menziesii* forests in the Pacific Northwest (Franklin & Hemstrom 1981). In regions where the early and intermediate stages are dominated by a more diverse assemblage of tree species as, for

example, the post-felling hardwood stands of the north-eastern United States (Bormann & Likens 1979), the demise of these early dominant populations may be a more gradual process and convergence, in the various ways it is described it here, is likely to be more continuous.

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