Population patterns through twenty years of oldfield succession*

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Abstract

Using 48 permanent, 0.5 × 2.0 m quadrats, changes in species composition and cover were followed in an oldfield abandoned after plowing in the spring of 1960. Twenty years of data collected since then show the succession to be individualistic, that is, composed of broadly overlapping population curves through time. In general, the population curves exhibit long, persistent tails, indicating that, through this time span, succession is a process in which species that are present for much of the time become dominant at different times. Invasion and extinction are not the major mechanisms of community change. Bi- or multi-modal peaks were discovered in some species, but there is no clear explanation of such patterns yet. Many species which are important later in the sequence invade early. Information on the biologies of representative species from early, middle, and late portions of the sequence are correlated with the population patterns. In particular, the mode of dispersal, life cycle, germination behavior, and assimilation requirements are related to species positions. However, there is need for coordinated, comparative study of species strategies as well as experimental study of species interactions in order to more fully understand the mechanisms of this succession. The patterns discovered in this oldfield are compatible with contemporary concepts of succession as an organism-based phenomenon, in which probabilistic gap creation and filling are critical.

Introduction

Both the idea of vegetation change and the body of expectation about such change have been central to plant ecology, yet few studies have examined the changes on a given site through time. Rather, the theory has grown up around studies which substitute examination of stands of varying ages at the same time for temporal study of given sites. There are a few long term studies of forest dynamics (e.g. Miceli *et al.,* 1977; Falinski, 1978; Peet & Christensen, 1980; Davison & Forman, 1982), but the vegetation change in oldfields has been subject to only short-term analysis. Long-term analyses of vegetation change have been more common in Europe (vanden Bergh, 1979). For example, Beeftink (1979a) and ter Borg (1979) reported on changes in

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* Nomenclature follows Fernald (1958).

** The late Dr. Murray F. Buell, Dr. Helen F. Buell, and the late Dr. John A. Small deserve special mention because, in 1958, they began the long-term, permanent quadrat study partly reported here. Such unselfish, prospective behavior merits notice and I am happy to acknowledge my debt to them. I thank Helen Buell for her patient teaching and helpful discussion and criticism. Dr. Thomas G. Siccama encoded the pre-1971 data. I thank Ms. Angela Salvemini for patient and trustworthy entry of the more recent data. The Research Council of Rutgers University partially defrayed the cost of a computer terminal, and Dr. R. T. T. Forman, Director of HMF, provided computing funds. I have benefitted from discussions with Dr. R. J. Frye, and from criticism by Dr. F. A. Bazzaz and Dr. T. D. Lee. The figures were prepared by Lisa Bandazian.

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species composition and vegetation structure resulting from unusual weather, or changes in tidal influence in Netherlands salt marshes over 15 yr, and van der Maarel (1978, 1981) reported fluctuation in dune grassland resulting from different rabbit grazing intensities and rainfall fluctuation. Particularly notable are the studies by Watt (1960, 1971) showing changes since 1935 in English Breckland grass-heath communities and the important role of grazers.

Here I present data for 20 yr of change in permanent plots in a field abandoned after plowing. Portions of this data set have been reported on previously (Buell *et al.*, 1971; Small *et al.*, 1971; Monte, 1973). This paper will both serve as an introduction to further analyses of this system and permit a discussion of aspects of successional theory. I will present the trends in species population dynamics through time, raise questions that will guide future analysis, and relate the study to concepts of vegetation dynamics. Some of the central ideas in current successional theory will provide a background against which the patterns will be presented and discussed. This brief discussion can only focus on some major conclusions of recent theoretical arguments rather than their development.

Recovery from exploitation, such as agriculture, has provided many examples of vegetation change and stimulated development of much of successional theory. Currently, such change is thought to follow multiple mechanisms (Drury & Nisbet, 1973; Connell & Slatyer, 1977; Miles, 1978; Horn, 1981) including mostly inhibition or tolerance or a combination of the two. Early invasion and persistence of species are additional features now though to be common in vegetation dynamics (Egler, 1954). Furthermore, vegetation change is considered to be composed of individualistic patterns of species population response through time (Gleason, 1917; Whittaker, 1975; Horn, 1974) and to be driven by the different strategies of resource use that the individualistic patterns imply (Pickett, 1976; Beeftink, 1979b; Nobel & Slatyer, 1980). Only a few long term studies exist to illustrate these features of vegetation change (Beeftink, 1979a; van den Bergh, 1979; ter Borg, 1979).

Successional theory motivates the following questions about the population basis of 20 yr of post-agricultural vegetation change. 1) What are the population patterns through time? 2) Do population patterns reflect species strategies? 3) Are the species patterns individualistic in the sense of Gleason (1917)? 4) What interactions among populations are suggested by the patterns? This is certainly only some of the possible questions, but they will serve to introduce subsequent analyses of the Hutcheson Memorial Forest Succession Study, and help to evaluate theory of the plant community and succession.

Study site and methods

The results are a small portion of a study begun in 1958 by Drs. Murray F. and Helen F. Buell, and Dr. John A. Small. Two comparable fields were abandoned every two years for 10 years at the Hutcheson Memorial Forest (HMF). HMF is located in Somerset Co., at 40°30′N, 74°34′W, 11 km from New Brunswick, NJ, USA and experiences a subcontinental, temperate climate with 112 cm of precipitation distributed fairly evenly throughout the year. Mean annual temperature is 11.7 °C; mean January temperature is 0 °C, while mean July temperature is 24 °C (Robichaud & Buell, 1978; Biel, 1958; U.S. Weather Bureau, 1959). Forest in the region is described as mixed oak (Buell, 1957; Monk, 1961; Robichaud & Buell, 1975; Forman & Elfstrom, 1975). Braun (1950) includes this area in her oak-chestnut region. The forest is located on the Triassic red shales of the Piedmont (Wolfe, 1977), thus the soils of this gently rolling topography are formed from a soft, highly weathered, high clay content bedrock. The soils underlying the successional fields are classified as Penn Shaly Silt Loam and Penn Silt Loam (Kirkham, 1976). These are shallow, poorly horizonated, endodynamomorphic soils (Ugolini, 1964). General post-agricultural vegetation trends in the Piedmont of New Jersey have been elucidated by Bard (1952).

Field D-3, the subject of this study, was plowed and disked in the spring of 1960 after a crop of soybeans *(Glycine max)* and sorghum (*Sorghum vulgare).* Forty-eight permanent plots, each 2 × 0.5 m (a size used successfully in prior studies of succession in the area (Bard, 1952)), were established on a grid. The plots were examined each late July or early August. The cover of each species was estimated visually with the aid of a sampling frame,

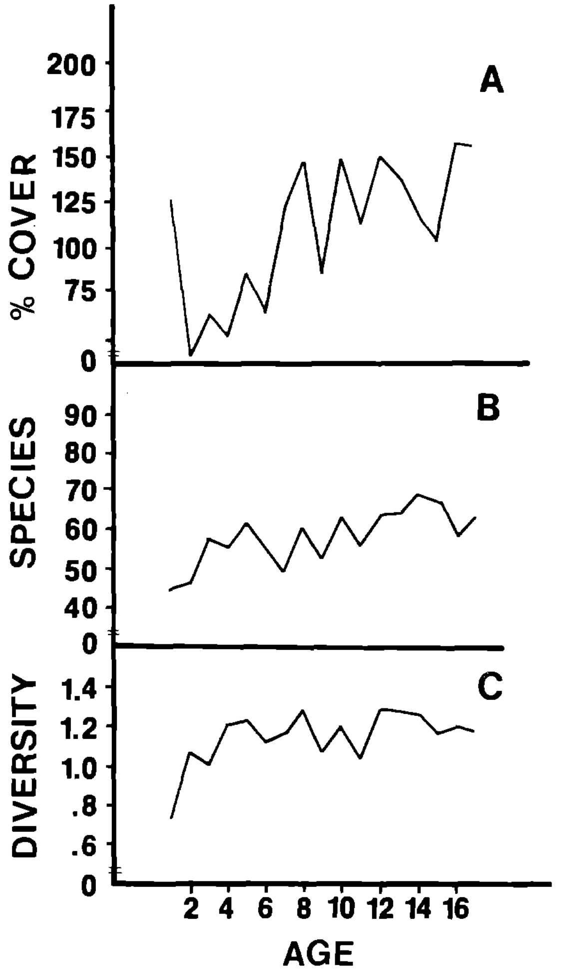

Fig. 1. Community characteristics through 17 years of vegetation change. A) Percent cover of all species summed over all plots. B) Species richness. C) Shannon-Wiener diversity. After Frye (1978).

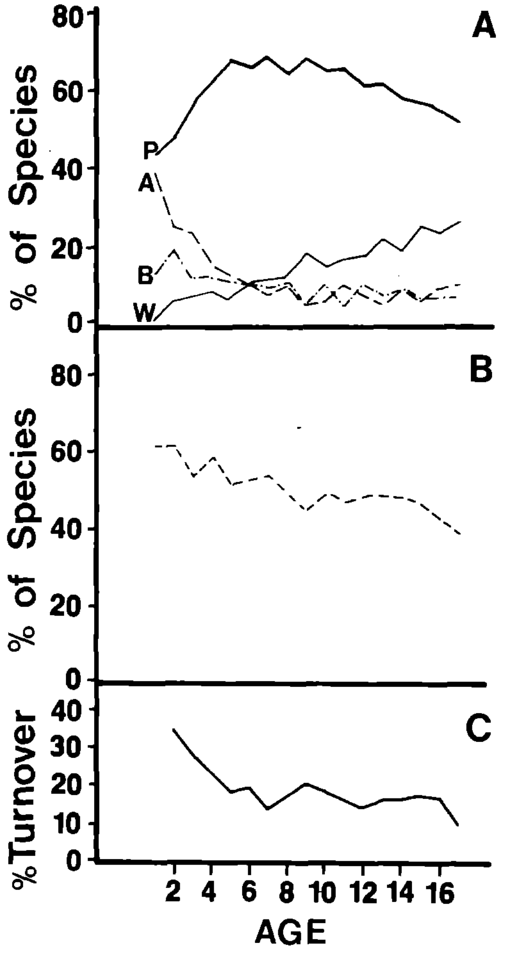

Fig. 2. Characterization of species groups through 17 years of vegetation change. A) Percentage of species represented by perennials (P), annuals (A), biennials (B), and woody (W) growth forms. B) Percentage of introduced species. C) Species turnover between years. After Frye (1978).

and the numbers of stems of tree species were recorded in each plot. The study continues, but only data for 1960–1979 are included here. Data were accessed, analyzed and plotted using the Statistical Analysis System (Helwig & Council, 1979). For each species mean cover per plot ± S.E. and number of plots occupied were calculated.

Results and discussion

Community patterns

As background to the population trends, I review the community trends that were extracted by Frye (1978) for 17 yr in field D-3. Richness of species fluctuates greatly during this early phase of succession (Fig. 1). Between year 17, the last shown in Frye's data, and year 20, the richness remained near 60. Rough congruence exists between Shannon-Wiener diversity and species richness (Fig. 1). Total vegetation cover also fluctuates greatly, but the same upper bound appears between years 8 and 16 (Fig. 1). There is a major decline in cover between years 2 and 7. As expected (Bard, 1952), percentage of annuals peaks first, followed by biennials, herbaceous perennials, and woody species (Fig. 2). The proportion of introduced species declines somewhat in the latter portion of the study period

(Fig. 2). Percent turnover, calculated after the method of Diamond (1969, in Frye, 1978), declined rapidly at first and maintained a relatively low level later in the study (Fig. 2).

Population trends

Phases

The patterns of individual species can be examined for their shape and level of performance in particular ranges of the sequence. For convenience, the 20 year span was arbitrarily divided into phase I (1–4 yr), II (5–15 yr), and III (16–20 yr). These phases were established before examining the data, but on the basis of other succession studies (e.g. Odum, 1969; Bazzaz, 1975; Bard, 1952), they may broadly represent functionally different situations. These phases are not equivalent to the traditional 'stages' of succession. The patterns will be discussed below in terms of these three temporal phases.

Table 1. Dominant species and year of peak cover during 20 yr of vegetation change at Hutcheson Memorial Forest.

Phase	Species	Year
I	*Ambrosia artemisiifolia*	1
	Mollugo verticillata	1
	Digitaria sanguinalis	1
	Barbarea vulgaris	2
	Erigeron canadensis	2
	E. annuus	3
	Plantago lanceolata	3
	P. rugellii	2–3
	Oxalis stricta	3
II	*Rumex acetosella*	5
	Daucus carota	5
	Aster spp*	7
	Chrysanthemum leucanthemum	8
	Hieracium pratense	10
	Hieracium florentinum	12
	Lepidium campestre	10
	Trifolium pratense	11
	Convolvulus sepium	13
	Poa pratensis	15
	Agrostis alba	12
III	*Rhus glabra*	19–20
	Lonicera japonica	17
	Juniperus virginiana	19
	Acer rubrum	20
	Poa compressa	17
	Acer negundo	18
	Solidago graminifolia	19
	Rhus radicans	20
	Rosa multiflora	20
	Solidago juncea	19

* *Aster pilosus*, *A. ericoides*, and *A. vimineus* cannot be reliably distinguished in the field in central New Jersey in early August

The population patterns may be further discriminated by dividing the species into those with high and low importance in the community. An arbitrary classification of expected patterns and levels of dominance is used here. For the purpose of this discussion, I define dominant species as those which attain 5% or greater cover at any time during the study. This level of mean cover separates out the species which are often thought of as predominant in oldfields, but functional dominance is not implied by this term. The remaining species are classed as subdominants. Within these two arbitrary classes of dominance, species may be expected to show peak cover in at least one phase. On the basis of topographic gradient analysis (Whittaker, 1975), no species is expected to have >5% cover over the whole or a large part of the sequence, a situation which I would call 'constant dominance'. In contrast, within the subdominant group, species may be present for a long period in the succession. Species represented in 18 of the 20 yr are here defined as constant. Other subdominant species may be only sporadically present, having gaps of two or more yr in their occurrences. One or two dominant species will be used to illustrate the behaviors and characteristics of species in each phase.

Population patterns and characteristics

Dominance in Phase 1 is exhibited by 10 species (Table 1). *Mollugo verticillata* is present only in the first year. *Ambrosia artemisiifolia* exemplifies the remainder of the group and provides an excellent basis for assessing the role of the life history strategy in producing the population response curve. Cover of *Ambrosia** in year 1 exceeds cover of any other species in the entire sequence (Fig. 3). Cover crashes to near 0 in years 2 and 3. This decline in cover is followed by a decline in frequency from 48 plots (100%) in year 1, 44 in year 2, to 24 in year 3. Cover and frequency rebound together in year 4 (Figs. 3, 4). Thereafter, frequency declines with drastic fluctuations. *Ambrosia* is absent only in year 11.

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* Species are identified by generic names when ambiguity will not result.

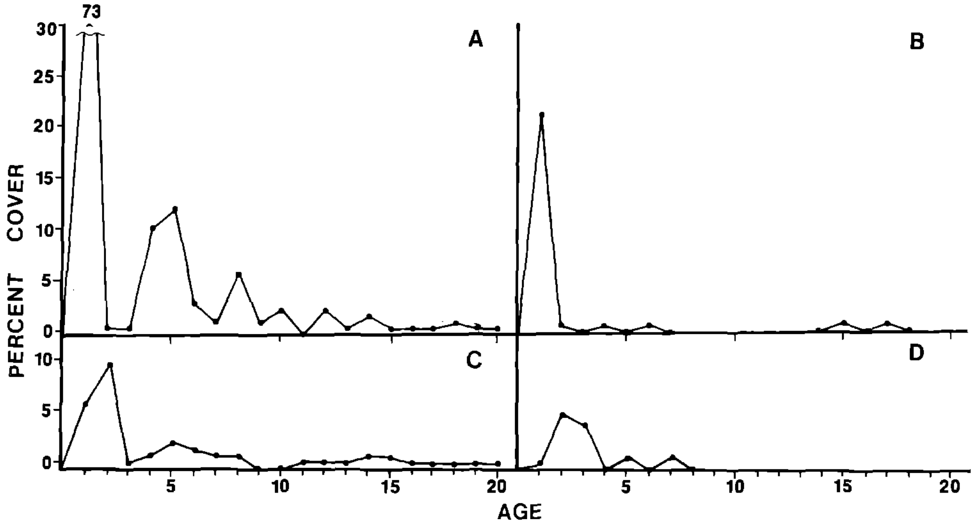

Fig. 3. Mean percent ground covered by A) *Ambrosia artemisiifolia,* B) *Digitaria sanguinalis,* C) *Barbarea vulgaris,* and D) *Erigeron canadensis* in each of 20 years since abandonment.

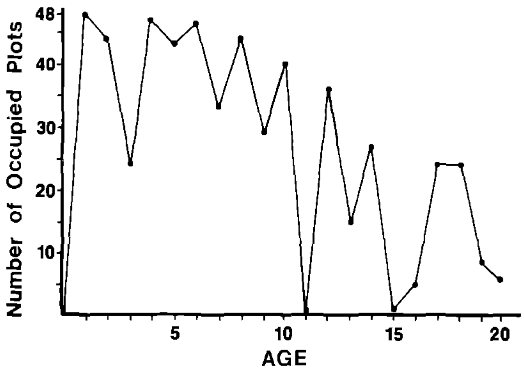

Fig. 4. Frequency of *Ambrosia artemisiifolia* through 20 years since abandonment.

The position of *Ambrosia* as first dominant is explained well by its life history strategy and ecophysiology. Seeds form a large and persistent bank in the soil and germination is stimulated by light, high and fluctuating temperature, and decreased CO_2 (Bazzaz, 1970; Pickett & Baskin, 1973; Baskin & Baskin, 1980). Established plants have a broad tolerance to nutrient supply (Parrish & Bazzaz, 1982) and water supply (Pickett & Bazzaz, 1982). Thus, *Ambrosia* seeds are present in the soil, keyed to conditions attending soil disturbance, and the established plants have a broad niche, enabling them to take advantage of uncontested resources.

The decline of *Ambrosia* the second year can be attributed to its poor ability to tolerate interference. *Ambrosia* is a poor competitor in closed communities (Raynal & Bazzaz, 1975) and allelopathy may be involved in its decline on the New Jersey Piedmont (Jackson & Willemsen, 1976) although such inhibition does not occur in some other systems (Raynal & Bazzaz, 1975).

Species which dominate in year 2 are winter annuals which require the intervening winter to mature (Table 1). It is these species, primarily, which preempt the resources which are available to *Ambrosia* in the first year after plowing. Thus, much of the change in vegetation in phase I is due to the fitting together of life cycle types, as was found by Keever (1950) in the Piedmont of North Carolina. Many of the species in this phase are summer annuals, winter annuals, biennials, or short-lived perennials. Dispersal is largely by wind, or in time by complex germination behaviors and seed longevity. Species of this phase typically have high rates of assimilation and growth, and low structural allocation (Bazzaz, 1979), although data are not available on the species of this particular site. The cover peaks are sharp and distinct for most of the group (Figs. 3, 4, and 5) except *Plantago lanceolata* and *Rumex acetosella.*

The decline in total plant cover to less than 75% in year 2 and its slow recovery is not typical of other fields in the HMF study (Frye, 1978). Frye (1978) discovered a significant correlation between total

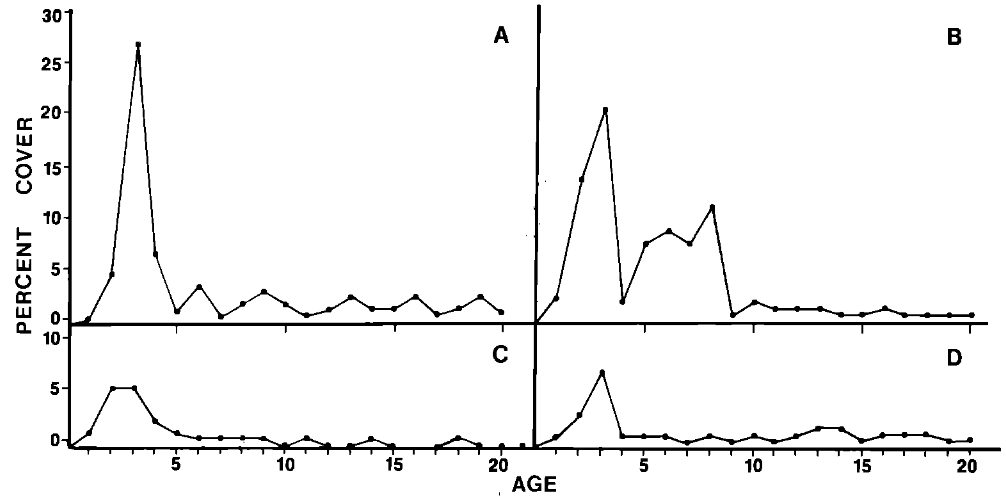

Fig. 5. Mean percent ground covered by A) *Erigeron annuus,* B) *Plantago lanceolata,* C) *Plantago rugelii,* and D) *Oxalis stricta* in each of 20 years since abandonment.

plant cover and annual rainfall in a series of HMF fields including D-3. Year 2 of this field is a wetter than normal one, while years 3 and 4 are much drier than normal. Hence, the maintenance of low cover until year 6 may be partially attributable to drought. Certainly, however, the initial decline must result from other causes. The dominance of some early colonists appears to be delayed relative to other successions on richer, deeper soils in the Midwest (Bazzaz, 1968; unpub.). Huston's (1978) hypothesis that high resource availability speeds competitive exclusion may apply here (cf. also van den Bergh, 1979).

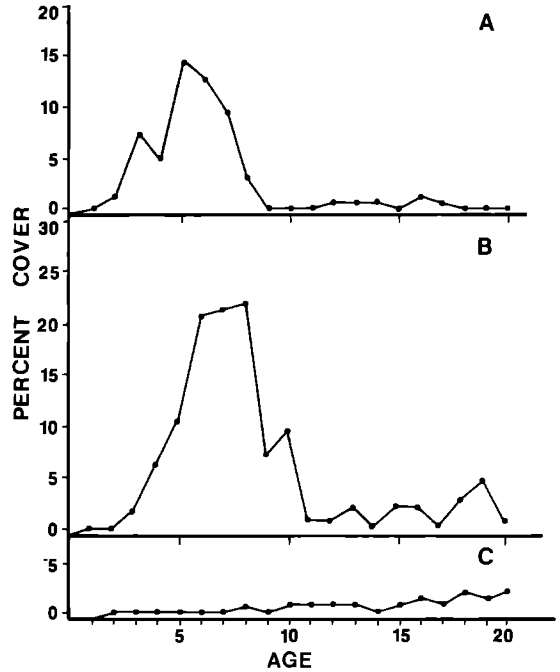

Fig. 6. Mean percent ground covered by A) *Rumex acetosella,* B) *Chrysanthemum leucanthemum,* and C) *Ailanthus altissima* in each of 20 years since abandonment.

Eleven taxa attain peak dominance between years 5 and 15 (Table 1). The *Aster* complex, including *A. pilosus, A. ericoides* and *A. vimineus* is treated as a single taxon. This complex may be taken as the paradigm of species behavior in phase II. *Aster pilosus* is one of the few species of this range to have had its adaptive life cycle attributes studied systematically (Keever, 1950; Peterson & Bazzaz, 1978). The timing of *Aster* dominance is partially regulated by its life cycle characteristics. *Aster* plants, germinating in the spring (as it would largely be expected to do in this spring-plowed field), normally do not flower until their second year if resources, particularly nutrients, are limited or strongly contested (Peterson & Bazzaz, 1978). Perhaps the highly weathered soils, which have been eroded in some HMF fields, slow the growth and maturation of *Aster.* Peak dominance is not attained until the 7th year (Fig. 7). Peterson & Bazzaz (1978) report that *Aster* germination in Illinois is enhanced by high red light intensity, and moderate levels of NO_3, conditions which might be associated with disturbance or persist for a short time thereafter. They further emphasize the general flexibility of the life

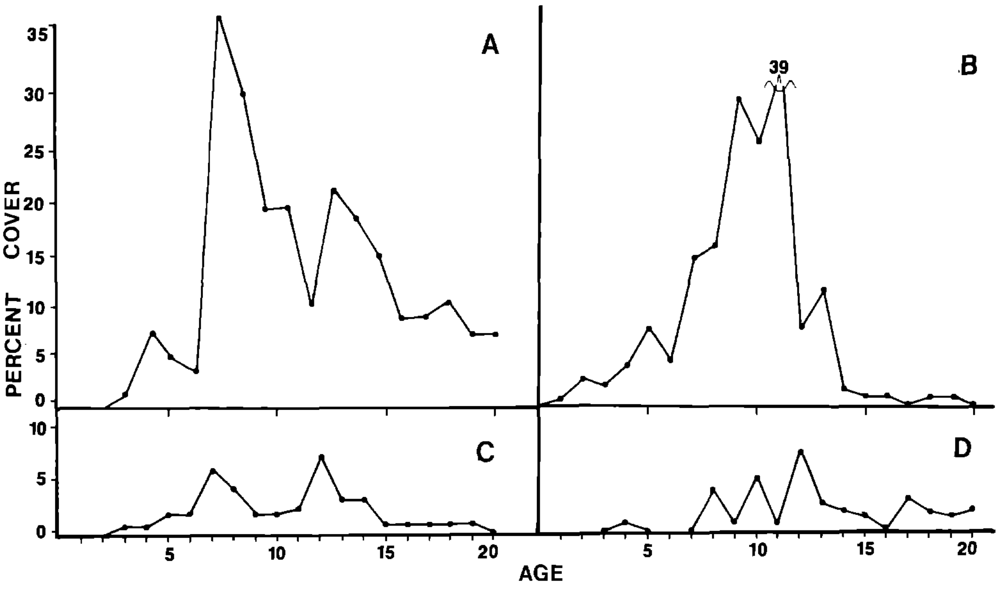

Fig. 7. Mean percent ground covered by A) *Aster* spp., B) *Trifolium pratense,* C) *Agropyron repens,* and D) *Hieracium florentinum* in each of 20 years since abandonment.

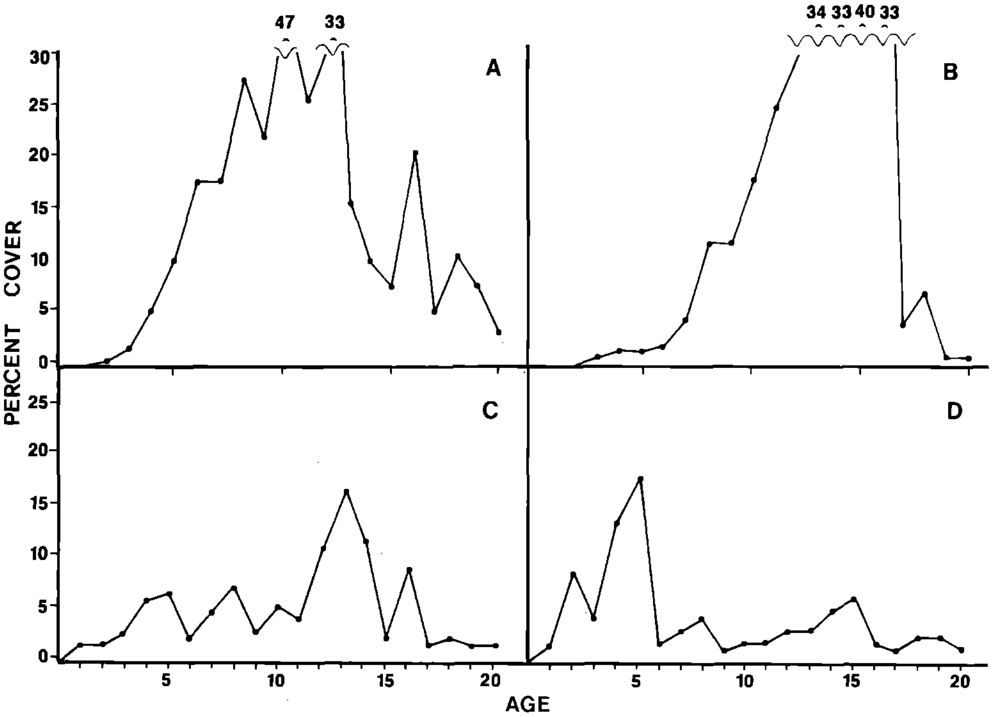

Fig. 8. Mean percent ground covered by A) *Hieracium pratense,* B) *Poa pratensis,* C) *Convolvulus sepium,* and D) *Daucus carota* in each of 20 years since abandonment.

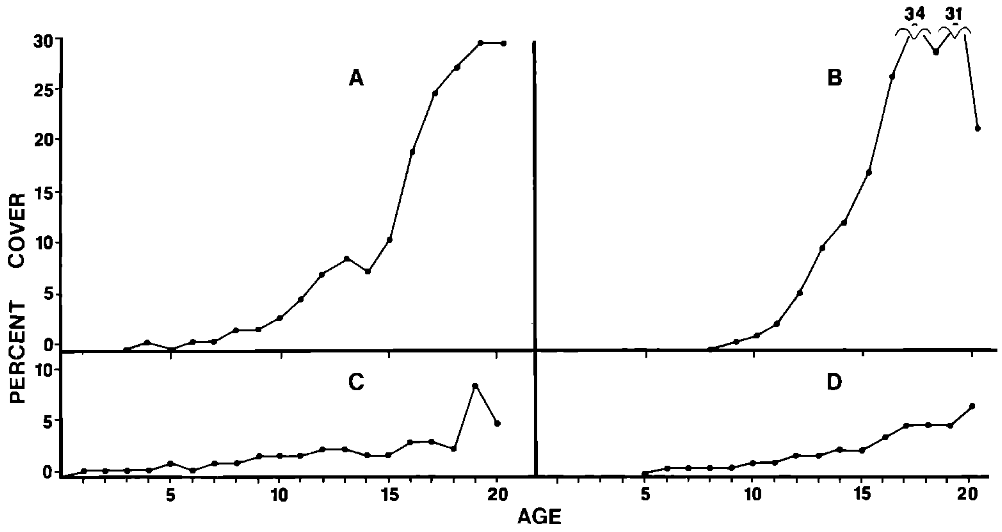

Fig. 9. Mean percent ground covered by A) *Rhus glabra,* B) *Lonicera japonica,* C) *Juniperus virginica,* and D) *Acer rubrum* in each of 20 years since abandonment.

cycle and physiological functions. Photosynthesis of non-bolted juveniles is shade-tolerant, while that of bolts is highest in bright light. The perennial, interoparous behavior is another facet of flexibility. While the other species of phase II have not been investigated, it may be that similar flexibility in the face of changing resource levels characterizes them as well. For example, *Lepidium* may behave as an annual or a biennial. Further evidence of flexibility is found in the existence of thresholds for flowering which would increase the probability of success of the first reproductive bout as well as enhance the survival of the parent plant. Such behavior has been found in other species playing similar successional roles (Werner, 1975).

Another characteristic of many of the dominant species in phase II is their usually low or turf growth form. These species may initially invade in the shade of earlier dominant canopies (as apparently do *Erigeron annuus* and *Plantago* spp. of phase I). The structure of oldfield vegetation may thus be important in its dynamics. This is a considerably different viewpoint from the common idea that old-field communities are single lavered and simple. Furthermore, this suggests that ecophysiological flexibility may characterize many of the species.

The peaks of many of the phase II dominants are differentially dispersed through time (Figs. 5–8). Differentiation in germination, photosynthetic, and allocation strategies may account for some of the difference; however, this cannot now be assessed.

There are 11 species attaining dominance in phase III between years 16 and 20 (Table 1, Figs. 9 and 10). Vegetation change, of course, continues past the 20th year. Two woody species of strikingly different growth from, *Rhus glabra* and *Lonicera japonica,* illustrate the characteristics and response of species dominant in this phase. *Rhus glabra* dominates the upper layer of the community. It exhibited an essentially smooth, sigmoid increase (Fig. 9). The steepest rise in cover occurred between years 14–17. Early establishment of *Rhus* up to year 13, tended to be closer to the forest or to the older field to the south. This undoubtedly is because *Rhus glabra* is bird dispersed. Stiles (1980; pers. comm.) reports that the fruit of *Rhus* are taken only after higher quality fruit are exhausted or during periods of unusual food shortage in late winter. The importance of invasion patterns on distance from source and the mode of dispersal, including dispersal agent and attractiveness of the fruit, has been shown by Debussche *et al.* (1980).

After year 15, the increase of *Rhus* cover parallels an increase in its frequency. Furthermore, many of the plots which *Rhus* invades are adjacent, indicating the effectiveness of clonal spread in this species. Little else is known about the strategy and behavior of *Rhus glabra.* It has a sparse and presumably economical branching pattern, and compound leaves may further reduce cost of leaf display (Giv-

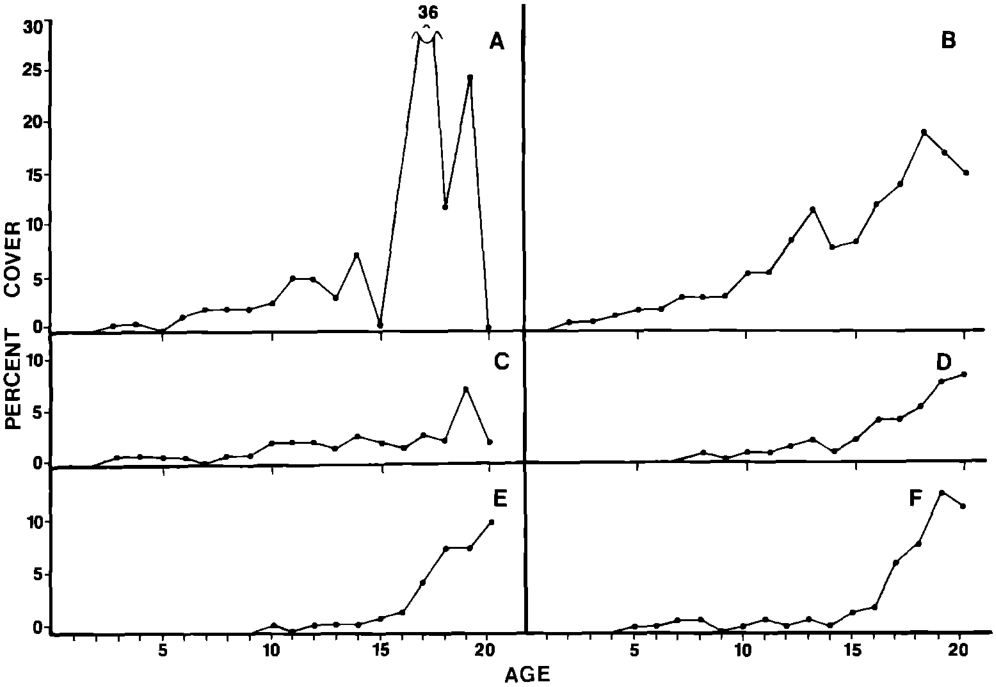

Fig. 10. Mean percent ground covered by A) *Poa compressa, B) Acer negundo,* C) *Solidago graminifolia,* D) *Rhus radicans,* E) *Rosa multiflora,* and F) *Solidago juncea* in each of 20 years since abandonment.

nish, 1979). Rates of assimilation and tolerance of competitive stress are not known.

Lonicera japonica is an introduced, scrambling or climbing vine. Its cover rises sharply in year 12 (Fig. 8). The steep increase continues through year 17. Unlike *Rhus,* the curve of *Lonicera* is not sigmoid. *Lonicera* dominance coincides with the general increase in cover of woody species in the field, and the plants do depend to some extent on those species for support. The presence of vines per se is not restricted to this phase, however. The annual vine *Ipomoea hederacea* occurs, and the herbaceous perennial *Convolvulus sepium* dominates earlier. The lianes in HMF can climb over the herbaceous layer or over woody plants.

The two major woody dominants of phase III clearly occupy different layers of the aboveground community. A third major dominant, *Poa compressa,* is a turf plant and occupies yet a third layer. *Poa compressa* is the only turf plant to be a major dominant in this phase. The other turf plants (e.g. *Poa pratensis, Agrostis alba,* inter alia) peak earlier.

The data collected in this study are in terms of cover. Much of the impact of woody species in oldfield vegetation change is undoubtedly due to cover or its correlates, such as shading or root spread. However, much of their impact may reside in their acting as dispersal foci for bird dispersed seed (McDonnell & Stiles, pers. comm.). Because projection above the adjacent herbaceous canopy and clumping may be important factors in this function, the question of when various woody species begin to be functionally dominant remains open. Presumably, increase in structural impact of woody species would preceed cover dominance in phase III.

Both the exemplars of phase III, *Lonicera* and *Rhus glabra,* are animal dispersed. *Juniperus, Parthenocissus, Rhus radicans,* and *Rosa* also are dispersed by birds. These species were present earlier than phase III (Figs. 9, 10), but in general became established later than wind dispersed woody species. Major or notable wind dispersed species include *Acer negundo, A. rubrum* and *Ailanthus* (Figs. 6, 9). Bard (1952) noted the increasing importance of animal dispersal with increasing time since abandonment. The different cover curves of wind and animal dispersed species (Figs. 6, 9, 10) indicate the importance of the difference between the two dispersal modes (see Debussche *et al.*, 1980). *Viburnum dentatum, Quercus* spp. and *Vitis,* among other animal dispersed species, first establish late in phase III. Mammals may be more important dispersers of this group than birds.

Multimodal dominance

A third dominance pattern which was not predicted at the outset of the analysis, also exists. Eight species show various degrees of multimodal dominance (*Ambrosia, Lepidium, Convolvulus, Daucus, Agropyron, Plantago lanceolata, Hieracium pratense* and *Aster* spp.). In all but one case *(Plantago lanceolata),* they have distinct peaks separated by 2 or more years and low (<3% cover), non-overlapping standard errors in peaks and troughs. Additional analysis of this pattern is forthcoming; however the veracity of several of these bimodal curves is reinforced by the correspondence of cover and frequency troughs. For example, *Agropyron* was absent from 9 of the 16 plots it occupied during the first peak; *Convolvulus* lost 21 of 38 plots held during the first peak at year 5. Between peak frequency in year 4 at 47 plots, and minimum frequency and cover in year 9, *Daucus* lost 30 plots. Not only do perennial species exhibit bimodal dominance, but one annual, *Ambrosia,* also shows a clearly multimodal pattern of cover that is reflected in frequency declines and recoveries (Fig. 4). *Ambrosia* can exhibit this pattern because of its long-lived seeds.

The reasons for bimodality are not evident in most cases. Association analyses among the species and examination of plot-by-plot trends may generate hypotheses. In the case of *Ambrosia,* initial decline is likely due to interference as noted earlier. While this rapid and early decline is expected for this species, the subsequent rise in cover in year 4 is not usual for *Ambrosia* in other successions, although it has been noted in Indiana (P. M. Vitousek, pers. comm.). Perhaps the lowered rainfall from March through July in 1962 and 1963 accounts for the first recovery of *Ambrosia* by affecting other species, thus thinning the canopy and releasing *Ambrosia* from competition. Subsequent *Ambrosia* peaks are often associated with relatively higher rainfall. Ongoing study and comparison of different HMF fields will indicate whether this is a likely mechanism.

An additional hypothesis for bimodal dominance is that different parts of the field may be in different successional stages (cf. Watt, 1947). Localized disturbance may open small, discrete patches or gaps within an oldfield community. Competitively inferior species or gap specialists may then succeed in those gaps. Even without disturbance, succession may proceed at different rates over a field (e.g. Watt, 1960). Similar fluctuations occur elsewhere (van den Bergh, 1979).

Population invasion, turnover, and persistence

In contrast to the behavior of individuals, a notable characteristic of many of the populations is persistence. The species which participate in the first 20 years of change in this field are present largely through that time span. Bard (1952) discovered this in her spatial survey as well. Thus, species do not simply come and go in the dynamics, rather, dominance is differentially expressed through time. Egler's (1954) idea of initial floristic composition is clearly supported here.

There is a large group of species in this field that are present but at no time dominant. Of these 106 species, 10 are present for at least 18 of the 20 years. *Acalypha rhomboidea* serves as an example of this group, which includes species of all strata and life forms. *Acalypha* very rarely reaches its potentially large size, and, as a suppressed member of the understory, usually stands only a few cm tall. These small plants often flower and fruit. Frequency of *Acalypha,* as with others in this group, rarely reflects mean cover.

Species which are present sporadically also occur. In the case of some of these, such as *Chenopodium album,* which is an annual, dependence on fine scale disturbed patches like animal burrows may explain the pattern. In most cases however, there are no observations to suggest hypotheses.

Some characteristic forest species become established in phase III. *Quercus* spp., *Viburnum dentatum, Berberis thunbergii, Circaea lutetiana, Botrychium* spp., and *Geum canadense* all appear in years 18–20. These species are apparently shade tolerant, and many require animals for dispersal. They are, for the most part, also slowly growing canopy species or species of the understory of more closed forests. They would not be expected to have much immediate impact on the community. Indeed it is not known whether these early-established individuals will play a role in the old forest. Certainly many woody individuals will succumb to intense competition as the oldfield woodland develops and closes. If some do survive they will encounter vastly different environments than they now do. Population differentiation or individual plasticity may be common features of persistent species. *Cornus florida* and *Acer rubrum,* for example, establish within the first 20 years, yet also occur in the old growth forest at HMF. Open field and closed forest individuals of both species possess significantly different branching structures (Pickett & Kempf, 1980) and patterns of allocation to wood vs. leaves (Nicola & Pickett, unpubl.). In both cases, forest grown individuals exhibit more complex branching to reduce mutual shading, planar leaf displays to intercept zenith light, and higher proportions of biomass devoted to wood. Roos & Quinn (1977) found that populations of *Andropogon scoparium* from older fields devoted less biomass to sexual reproduction than plants from younger fields. Since the differences persisted in the greenhouse they apparently have a genetic component. Differences in *Acer* and *Cornus* populations are not known to be genetic, but because of the high potential for turnover through time, the possibility exists.

Conclusion

In answering the basic questions of what are the population patterns through time in early oldfield succession, the problem of their relation to species strategies has also been addressed. It is clear that, for those instances where the ecophysiology, life history characteristics, and population properties are known, they do indeed correlate with the population pattern in oldfield succession. However, very few species have been studied from this perspective and much remains to be learned before this question can be satisfactorily answered.

Population process and community pattern

Another important question concerns the nature of the composite pattern of populations through time. Just as the broadly applicable individualistic concept has appropriately been used to explain the spatial nature of the plant community, so it appears to relate to vegetation dynamics or community change through time (Gleason, 1917; Loucks, 1970; Drury & Nisbet, 1973; Pickett, 1976). A contemporary view of this idea, which appears in the works of Whittaker (1975) and Gomez-Pompa & Vazquez-Yanes (1974), is expressed as a series of bell-shaped curves of increasing breadths, ending with a few species showing sigmoid rises to a stable K. The combined cover curves for the dominant species (Figs. 3–10) yields a clearly individualistic pattern. Future analyses will attempt to discern species clusters along this continuum, but the community pattern is clearly a temporal continuum as has been long expected (Gleason, 1917). Examining only the *peaks* of the 10 or 12 leading species, i.e. ignoring the lower portions and tails of the species distributions, would allow the description of groups that correspond to the aspect dominant stages of succession often referred to. Clearly, however, examining the whole suite of species and their complete responses shows that the mechanism of community change is not one of sudden shifts between discrete compositional communities.

An individualistic distribution of populations in time suggests differential adaptation and response as the causal mechanisms for the population patterns. Species-packing in time is one way to view the trends (Loucks, 1970). Some of the processes possibly involved are 1) differential tolerance to the changing physical environment, 2) competitive displacement, 3) relations with predators, and 4) relations with dispersers. Clearly, all of these may play a role (Connell & Slatyer, 1977). It appears that competitive displacement may be a major factor since so many of the species are present for much longer periods than they are dominant. If environmental tolerance were the principal mechanism, fewer persistent tails of species distributions would be expected (cf. Egler, 1954). Some general examples of displacement include the decline in herbaceous species, except *Solidago* spp. and turf-forming *Poa compressa,* as woody species increase in the third phase (Figs. 8, 9). Displacements are also suggested by the staggering of species peaks throughout the sequence, though the mechanisms are not known for most these. However, displacement of population patterns in time is conspicuously lacking within most genera having at least two species at HMF. Genera having complete or major overlap between species are *Hieracium, Plantago, Trifolium, Solidago, Rhus, Erigeron, Rumex, Acer* and *Quercus.* Only *Poa pratensis* and *P. compressa* show clear differentiation. It is not known whether niche division or competition caused the temporal differentiation in *Poa* spp. In many genera, the time niche of one species is entirely included in that of the major dominant in that genus. Some spatial differentiation may lessen competition as it does in *Hieracium* elsewhere (Thomas & Dale, 1976). Spatial association analysis coupled with controlled competition experiments may determine the role of spatial differentiation or competitive refuges for the included-niche species (Colwell & Fuentes, 1975).

Relations of the plants to animals is important in this succession. Predation and herbivory, although they have not been examined, may be important due to differential defensiveness and mode of consumer deterrence by plants having different roles in vegetation dynamics (Feeny, 1975). *Viburnum dentatum* appears to be more susceptible to herbivore damage than the later invading *V. acerifolium* at HMF (Pickett & Stiles, unpubl.). The role of dispersers has been seen to be a major component in affecting the entry of animal-dispersed species. In the case of the wind dispersed *Andropogon scoparium*, low importance in HMF fields may be due to the blocking of wind currents by the forest itself which lies to the south and west of the fields (G. E. Bard, pers. comm.). Perhaps *Andropogon* is a poor competitor in the face of the relatively recently introduced *Rosa multiflora* or *Lonicera japonica*, as well (H. F. Buell, pers. comm.). The plumed seeds of *Andropogon* are, surprisingly, not easily dispersed (Keever, 1950).

General conclusions

One proposition of recent theory of vegetation dynamics is that the patterns or trends in community change through time can be substantially understood in terms of processes that occur on the level of the population. Any biological phenomenon involves two components. At the level of organization of immediate interest, patterns are observed, which may be compared with other situations at the same level, or used to infer the mechanisms that actually drive the pattern. The second component involves the next lower level of organization, the level on which the immediate mechanisms or controlling processes occur. Thus, understanding the mechanisms of community change through time requires a knowledge of the nature and interaction of its populations, and the factors which influence those interactions (Horn, 1974; 1975; Pickett, 1976, 1980; Connell & Slatyer, 1977; Beeftink, 1979b; Nobel & Slatyer, 1980).

This study has attempted to illustrate the population patterns in one post-agricultural field through 20 years. Some aspects of the strategic basis of these patterns have been discussed where data are available. However at the level of the population, much of the information presented here necessarily remains in the realm of pattern since few of the relevant population interactions and species strategies have been studied. Mechanistically, only very early succession on the North Carolina Piedmont (Keever, 1950) and in Central Illinois (cf. Bazzaz, 1979) are well known. In the HMF study, which is the longest study of herbaceous vegetation change after field abandonment in North America, many questions remain at the community level, and many others have been generated at the population level by this initial analysis.

There are of course limitations of this study in addressing some mechanistic questions. It is inappropriate as a vehicle for true demographic analysis since individuals were not marked. However, study of species persistence or behavior in the individual plots, which will be pursued in the future, may allow inference about the demography of the species at HMF. An additional problem is that vegetation performance rather than potential reproductive output, itself only a rough approximation of fitness, was measured. Further, environmental conditions and resource levels which might explain some of the population patterns were not studied. Standard weather data do exist at HMF and an aspect of their utility was shown earlier. Spatial variation within the fields, most likely an important phenomenon, will receive attention in future research. The remaining shortcomings of the study can be remedied as studies of species and populations accumulate in this and other laboratories. Specifically, competitive ability, dispersal, resource demand, allocation and phenology need to be determined for the participating species. Such an approach has greatly enhanced the understanding of community level patterns in other systems (Bazzaz, 1979).

The trends presented here may be summarized by referring to the four major questions posed initially. What population patterns occur in the first 20 yr of oldfield vegetation change? The expected range of population patterns was found. Long term persistence is a common feature of the behavior of both dominant and subordinate species. Sudden invasions and extinctions in the field as a whole are rare. Significantly, constant high levels of cover >5% are lacking, consistent with the idea that differential growth, resource demand and allocation are the strategic bases of community trends. It suggests, furthermore, that the same group of species is exposed to a constantly changing environmental and competitive array through time. Much of the reason for change must therefore reside in the community itself and much of this is the result of interaction with animals or other plants in the context of spatial heterogeneity and year-to-year variation.

In addition to the expected population patterns, a bimodal dominance was found in several species. Detection and verification of this pattern in other fields remain to be done, but the biology of at least one species *(Ambrosia artemisiifolia),* the concommitant changes in frequency in it and many of the others, and non-overlapping standard errors in adjacent peaks and throughs attest to its biological reality. The causes of bimodal dominance require investigation (also van den Bergh, 1979).

Are species poulations distributed individualistically through time? Figures 4–8 clearly indicate an individualistic pattern. The curves are, of course, not smooth as are the hypothetical examples often encountered. The demonstration of broadly overlapping, staggered population response curves is an important contribution to knowledge of community structure in space and time. Individualistic behavior has now been shown in space (Whittaker, 1977), geological time (Davis, 1976), and, as long predicted (Gleason, 1917), in successional time by this study and other recent work (Beeftink, 1979a; van den Bergh, 1979; ter Borg, 1979).

Do the population distributions have a basis in species biology and interactions? Where the strategies of the species are known, they are consistent with the population patterns observed. Competitive ability, life cycle timing and maturation, and dispersal characteristics, for example, are reflected in the population patterns. Ultimately, the differences in species and the variety of patterns are due to differential resource demand. Early invaders presumably require a pool of uncontested resources while later dominants tolerate smaller fluxes of resource (cf. Parrish & Bazzaz, 1982). Clearly, however, more information is required on the tactics of the species involved in this community.

What interactions among the populations underlie the species patterns of cover through time? Individualistic distributions in space have generated many useful hypotheses about the spatial interaction of species (Whittaker, 1969): competitive divergence, differential tolerance, herbivory, and differential dispersal capacities are conspicuous factors which may contribute to the community trends, and which have been often documented. Additionally, for some species (e.g. *Ambrosia* and *Chenopodium*) and at some times during the 20 year span, the effects of diffuse or point disturbance appear to be important. Detailed examination of the shapes of response curves may generate testable hypotheses. For example, many curves appear smooth on one side but jagged on the other (e.g. *Chrysanthemum,* Fig. 6). A smooth rise or fall may imply largely a gradual change in environment or simply population expansion without severe limit, whereas jagged change in species cover may imply competitive or catastrophic biotic causes. Examination of other fields and individual plots will indicate whether these trends are consistent, and if so, are they a response to the same mix of associated species.

The dynamics of a field after agricultural abandonment lies at one end of a continuum of dynamics at various scales. The opposite end of the spectrum involves the fine scale dynamics of closed communities. All scales of vegetation dynamics may be included in the concept of patch dynamics (Thompson, 1978; Pickett & Thompson, 1978), which has as components, sizes of patches, frequency of patch or gap creation, and duration of patches. The processes acting on all scales are based on changes in resource availability within patches relative to the matrix (Pickett, 1980). Species have evolved differences in resource use, and can therefore exploit different sizes or types of patches (Grubb, 1977). The different resource utilization spectra are then filtered by historical and spatial phenomena peculiar to a particular site. Dispersal accidents, predation, the intensity, size and timing of disturbance, all of which are unpredictable in an ecological sense and may be modified by the status of the community, affect the organization of the community (Pickett & Bazzaz, 1978). Thus, there is a combination of deterministic factors, the species strategies, and a stochastic element, variance in disturbance regime and environment, which can be used to understand the organization of any plant community. This same array of phenomena applies to oldfields and to closed communities. This paper has served to introduce the questions and hypotheses that will guide future analyses of succession at HMF, and to present population patterns that bear directly on the theory of the plant community.

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