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Temporal and Spatial Patterns of Herbaceous Layer Communities in the North Carolina Piedmont

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The questions ecologists, especially those who study plant communities, choose to ask are necessarily influenced by the character of landscapes immediately available for study. Thus, it is not surprising that researchers at mid-Atlantic universities in the first half of the twentieth century—individuals such as B. W. Wells, H. J. Oosting, W. D. Billings, and M. F. Buell, who established some of the first doctoral training programs in plant ecology—chose to focus much of their attention on the process of vegetation change that derives from the abandonment of farmland. Land degradation and a welter of economic factors resulted in abandonment of agricultural land across the mid-Atlantic region through the six decades after the Civil War, setting in motion a process of reforestation on an unprecedented regional scale. The region was awash in old fields and early successional forests. A unified theory of succession envisioned by many ecologists (e.g., Clements 1916, 1936) as a central element in our understanding of the distribution and structure of plant communities provided additional incentive to study these landscapes. The revegetation of old fields was destined to become the community ecologists' equivalent of the fruit fly or *E. coli*—in a sense, the “model organism” for the study of succession.

Although abandoned agricultural fields are now comparatively rare, and human actions associated with urban development have begun to reverse decades of forest spread, much of the landscape available to those of us who have succeeded those ecological pioneers retains the unmistakable imprint of old-field succession. Furthermore, we are the beneficiaries of research carried out over a period that begins to have real relevance to successional processes. Although ecologists no longer see succession as the integrated, unifying pro-

cess envisioned by Clements, disturbance and the processes that derive from it continue to shape our understanding of the distribution and abundance of organisms on landscapes. Ecologists today are no less opportunistic than were their predecessors. This body of work that has accumulated over nearly a century provides unique opportunities to explore the nature of change on a rapidly changing landscape.

Succession on many forested landscapes often is depicted as a process that progresses from plant assemblages dominated by herbaceous species, to even-aged forests, and finally to uneven-aged, late successional or old-growth forests, with an almost-implied decline in the ecological significance of herb species. Certainly, herbs in old fields have received more study than their counterparts at other stages of succession. The herbaceous component is important in each successional stage; indeed, its diversity generally increases at most spatial scales as succession proceeds. Although most would agree that the factors that structure herb communities change with time, there has been little systematic consideration of the nature and mechanisms of such changes.

Our primary goal in this chapter is to explore variations in and dynamics of herb layer assemblages across the Piedmont landscape. We are particularly interested two questions: what are the key environmental factors influencing herb distribution at various stages in the succession from land abandonment? What do these patterns tell us regarding the mechanisms that underlie the dynamics of herb populations? To address these questions, we draw on several strands of research carried out over the last 70 years to provide a more comprehensive picture of the successional patterns and mechanisms of change in herb layer communities of forested landscapes of the Piedmont region of North Carolina. The importance of these variations for management of herb diversity is also considered.

A Succession of Successional Ideas and Their Relevance to Herbs

Early studies of old-field succession were concerned more with describing the specific patterns of change in species composition over time they were with determining the processes (i.e., mechanisms) that caused such change. After nearly a century of study, debate continues regarding the nature of those processes. Because of this, we provide here a brief historical chronology of some of the more influential hypotheses regarding successional change. We then apply these to the specific case of old-field succession.

The pioneering work of Henry Chandler Cowles on dune succession (Cowles 1899, 1901, 1911) was described by Tansley (1935) as “the first thorough working out of a strikingly complete and beautiful successional series” (p. 284). It was Cowles who led the way in “chronosequence” or “space-for-time” approaches to the study of succession. Cowles also recognized that early-invading organisms modified their environment in ways that affected establishment of successors. Although Cowles reckoned that this led

to generally predictable patterns of change, he was also cognizant of the dynamic nature of plant communities in response to a variable abiotic environment. This awareness is captured in his characterization of succession as “a variable approaching a variable, not a constant” (Olson 1958).

Clements (1916, 1928) saw succession as much more predictable and directional, converging (regardless of starting conditions) inexorably to a stable climax community determined largely by climate. In Clements' view, the biotic reactions of dominant pioneer species determined the sequence of vegetational seres leading to that climax—a process later dubbed “relay floristics” (Egler 1954).

In his then-controversial paper, Gleason (1926) rejected virtually all of Clements' ideas on succession and, especially, on the nature of plant communities. Gleason reasoned that the principal mechanism driving succession was an interaction between migration of plant species (rates and modes of which varied greatly among species) and environmental selection (of a variable set of abiotic conditions, coupled with species-specific responses to those conditions). Acknowledging that successional change might be described as occurring in stages dominated by physiognomic types (e.g., herbs being replaced by shrubs and then trees), he argued that the sequence of invasion of species was highly individualistic and determined by their ability to disperse to a site and subsequently compete. This theme was reiterated by Drury and Nisbet (1973), who emphasized the importance of life-history traits of successional species. They suggested that most of what happens during succession is best understood as a consequence of differential growth, survival, and colonizing ability of species adapted to conditions along environmental gradients.

Egler (1954) argued in his initial floristic composition model of succession that, in many circumstances, succession was driven by patterns of early establishment and that subsequent change was largely a matter of differential longevity. Because early establishment would be variable owing to potentially random variations (e.g., in climate and seed rain), he posited that successional change is neither fixed nor predictable, as would be expected from Clements' relay floristics model. Mechanisms driving succession included stochastic migration of propagules to the disturbed site and differential longevity of plants. All pioneer species, many seral species, and some climax species are initially present after disturbance. Some of these germinate, becoming established quickly, whereas others germinate quickly but grow more slowly and for a longer period; still others become established later. Major changes in community dominance occur when larger, longer lived, and slower growing species outcompete smaller pioneer species.

In their often-cited review and syntheses of mechanisms of successional change, Connell and Slatyer (1977) concluded that succession is driven by one of three overriding mechanisms, proposed in their paper as alternative models. The facilitation model most closely fits the Clementsian vision of succession in which early invaders alter the environment in such a way as to make it more habitable for successors than themselves. The tolerance model

captured elements of both Gleason and Egler in proposing that succession was largely determined by patterns of dispersal and differences in life history. The inhibition model depicts succession as a process in which early invaders establish, usurp resources, and thereby competitively exclude would-be successors. In this model, succession only proceeds when the populations of the current occupants decline due to their inability to reestablish.

Peet and Christensen (1980) argued that population-based approaches were a prerequisite to distinguish among the Connell-Slatyer models, and much work over the past two decades has focused at that level. Grime (1977, 1979) proposed that spatial and temporal patterns could be understood in terms of three primary plant strategies: competitor, stress tolerant, and ruderal (ephemeral), reflecting basic trade-offs in life-history traits. Competitors are continuously abundant but depressed under low resource levels, as might exist early in some successional processes. Stress-tolerant species are continuously rare, being displaced spatially to resource-poor sites, they would be more characteristic of later stages of succession on unique sites. Ruderal species are generally easily dispersed but are not effective competitors. They are temporarily abundant and displaced in time by more competitive species. Grime argued that plants could be classified into one of these three categories and that the relative abundance of species among the categories would change through succession.

Tilman (1985) proposed that temporal and spatial variations in species composition through succession could be understood in terms of variations in relative growth (and reproductive) rates of species in response to varying proportions of resources. Succession results from a gradient through time in the relative availabilities of limiting resources. Tilman argued that succession should thus be repeatable or directional only to the extent that the resource supply trajectories are repeatable or directional. He proposed that succession often involves a gradient change from habitats with resource-poor soils but high available light at the soil surface to habitats with resource-rich soils but low light availability.

T. M. Smith and Huston (1989) drew on ideas from both Grime and Tilman and proposed that life-history strategies entail compromises that determine their competitive abilities under varying resource levels. Generally, plants can be competitive under high levels of resource availability or tolerant of low levels (i.e., stress tolerant), but cannot be both. For example, a plant that is competitive under high light conditions or high available soil resources cannot also be shade or drought tolerant. Focusing particularly on light and water availability, Smith and Huston (1989) then simulated species change based on whether species were competitive or stress tolerant for light and/or water. For their simulations, they assumed that successional responses were due largely to changing light levels and that spatial variation at any time was largely due to water availability (other resources might be substituted for this sort of simulation). Their results suggested that, with respect to light, species composition for herbs should shift from competitive to stress-tolerant during succession and that at any particular time in succession competitors should

be more prevalent on favorable sites with regard to soil resources. Correlations among species' abilities to compete for light and water might also explain observed differences in successional trajectories with respect to site. For example, some early successional species (e.g., pines) persist on dry sites because shade-intolerant (light competitors) species are often tolerant of drought stress.

Old-Field Herbs

In his 1932 description of the vegetation of North Carolina, Wells described the mosaic of old-fields as the “melting pot where foreigners and natives mingle” (p. 140). Wells described the general sequence of change, noting that the “foreigners” are relatively more important in the early years; indeed, many were weeds during cultivation, e.g., *Digitaria sanguinalis* (L.) Scop. (crabgrass) and *Cynodon dactylon* (L.) Pers. (Bermuda grass). Wells (1932; Crafton and Wells 1934) observed that the sequence of change in herbaceous dominance during the first 3–4 years was highly predictable, interpreting this as a facilitation process.

Oosting (1942) provided a much more quantitative sampling of abandoned fields of varying age (i.e., years after abandonment), paying particular attention to replicating each age with fields as similar as possible in physical features (e.g., soil type/texture, slope, aspect). Keever's (1950) classic study of the early stages of old-field development provided even more detail. One-year-old fields sampled early in the summer after abandonment had a total of 35 annual and perennial herbaceous species. Although these fields were not identical in species composition, they consistently had two species with highest density and frequency: *D. sanguinalis* and *Conyza canadensis* (L.) Cronq. (horseweed). Almost all first-year species, including *D. sanguinalis* and *C. canadensis*, were also found in 2-year-old fields. The Sorensen community coefficient of similarity for first- versus second-year fields was high (0.63), despite 26 new species appearing in the second year. At this time, however, there was a pronounced shift in dominance to *Aster ericoides* L., which was absent from first-year fields, and *Ambrosia artemisifolia* L., a minor component of first-year fields. Species richness dropped sharply in the third year after abandonment, corresponding to a rapid increase in dominance of the perennial grass, *Andropogon virginicus* L., which maintained dominance for several years.

Keever's (1950) experimental work showed little evidence for facilitation. Rather, she showed that the changes in species dominance could be understood in terms of modes of species dispersal and life histories (annuals replaced by biennials subsequently replaced by longer lived perennials). She rejected the hypothesis that such long-term dominance resulted from allelopathic compounds produced by *A. virginicus*, implicating competition for resources as a more likely mechanism—an implication more consistent with Connell and Slatyer's (1977) inhibition hypothesis. Keever (1983) later marveled at the

uniqueness of these changes compared to the process succession on abandoned land elsewhere: "the sequence of species and the timing of these changes in old-field succession in the Piedmont of the Southeast are not typical of such succession elsewhere. Nowhere else is there such a fast and distinct change in species dominance. In most places there is a gradual overlapping of species dominance often extended over a much longer time" (p. 402).

Much of the attention on old-field vegetation has been devoted to understanding general patterns of change, with little study of the variability in those patterns. Schafale and Christensen (1986) examined variations among herb communities among 3- to 7-year-old fields (fig. 9.1). They found that species richness varied widely among such fields (14 to >50 species/0.1 ha) and was positively correlated with soil pH and cation availability. These same factors were also highly correlated with trends in species composition indicated by first-axis DCA ordination scores. Standing crop and productivity, however, were more highly correlated with soil organic matter and may reflect other variables associated with the conditions of field abandonment or water availability. This suggests that, at least to some extent, factors influencing variations in species composition are independent of those that influence production.

It was during these early years that seedlings of wind-dispersed pine (*Pinus taeda* L. and *P. echinata* Miller) and hardwood species, such as *Fraxinus americana* L., *Ulmus alata* Michx., *Liquidambar styraciflua* L., *Liriodendron tulipifera* L., and *Acer rubrum* L., became established. Pines are generally favored in an environment of high light availability and nutrient and water stress, and typically form a closed canopy by year 10. On moister sites, *Liquidambar styraciflua* and *Liriodendron tulipifera* may share dominance with pine. The suite of herb species typical of old fields is virtually absent thereafter. There is ample evidence that the dominant old-field herbs significantly influence the patterns of early tree establishment. For example, most pine seedlings become established during the first 3 years after abandonment, before the development of an herbaceous thatch, which inhibits pine seedling growth (Oosting 1942). This explains the even-aged structure of most old-field pine stands.

De Steven (1991a, 1991b) experimentally evaluated the role of dominant old-field herbs (and the animals that associate with them) with regard to the invasion of loblolly pine and five early-successional hardwood species common in the North Carolina Piedmont: *Liriodendron tulipifera*, *F. americana*, *Liquidambar styraciflua*, *U. alata*, and *A. rubrum*. De Steven found that competition from herbs and rodent herbivory had significant effects on seedling emergence and the growth of many, though not all, of these species. Loblolly pine exhibited the highest levels of seedling emergence, seedling survival, and seedling height growth in all treatment combinations. Accordingly, her data help explain why, although all of these species produce wind-dispersed seeds (i.e., seed rain) that arrive at old-field sites in potentially large numbers, loblolly pine initiates the woody species stage of old-field succession. The success of hardwood species that become established initially with pines is

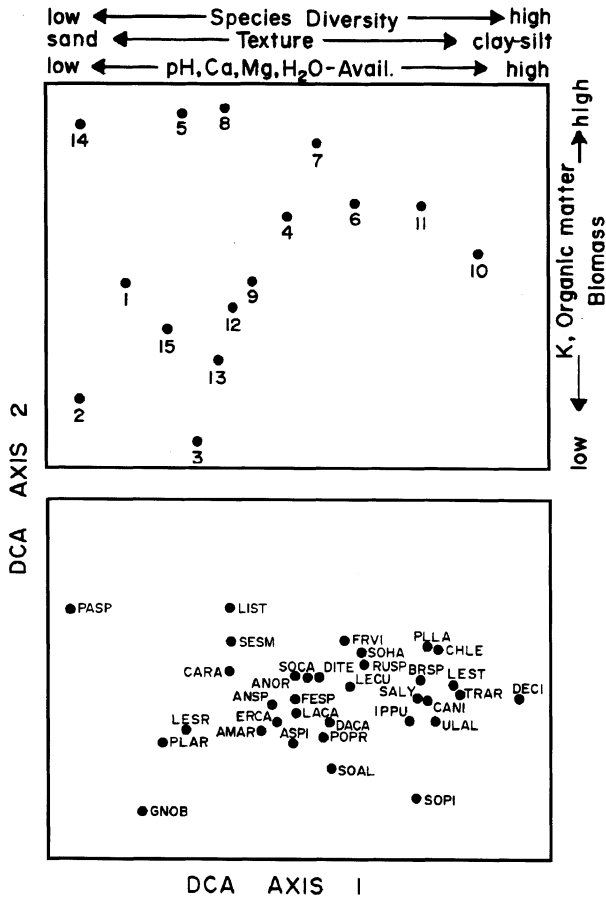


Figure 9.1. Detrended correspondence analysis (DCA) of herb community composition of 15 old fields 3–7 years after abandonment. Species codes are as follows: AMAR = *Ambrosia artemisiifolia* L.; ANOR = *Anthoxanthum odoratum* L.; ANSP = *Antenaria* spp., ASPI = *Aster pilosus* Willd.; BRSP = *Bromus* sp.; CANI = *Cassia nictitans* L.; CARA = *Campsis radicans* (L.) Seemann; CHLE = *Chrysanthemum leucanthemum* L; DACA = *Daucus carota* L.; DECI = *Desmodium ciliare* (Muhl. ex Willd. DC); DITE = *Diodia teres* Walter; ERCA = *Erigeron canadensis* L.; FESP = *Festuca* spp.; FRVI = *Fragaria virginiana* Duchesne; GNOB = *Gnaphalium obtusifolium* L.; IPPU = *Ipomoea purpurea* (L.) Roth; LACA = *Lactuca canadensis* L.; LECU = *Lespedeza cuneata* (Dumont) G. Don; LESR = *Lespedeza striata* (Thunberg) H. & A.; LEST = *Lespedeza stipulacea* Maxim.; LIST = *Liquidambar styraciflua*; PASP = *Panicum* spp.; PLAR = *Plantago aristata* Michaux; PLLA = *Plantago lanceolata* L.; POPR = *Polypreum procumbens* L.; RUSP = *Rubus* sp.; SALY = *Salvia lyrata* L.; SESM = *Senecio smallii* Britton; SOAL = *Solidago altissima* L.; SOCA = *Solanum carolinense* L.; SOPI = *Solidago pinetorum* Small; SOHA = *Sorghum halepense* (L.) Persoon; TRAR = *Trifolium arvense* L.; ULAL = *Ulmus alata*.

determined as much by their amount of seed rain as by factors affecting seedling performance (De Steven 1991a, 1991b). McDonnell (1986), studying similar fields in New Jersey, found that the structure and spatial distribution of herbaceous and shrubby species influenced the behavior of animals that disperse woody plant seeds, thereby affecting the future structure of forest communities.

The Herbaceous Layer in Successional Forests

Although we focus primarily on temporal patterns of change in the herbaceous layer following abandonment, we first provide an overview of successional change in woody species. The general pattern of change among woody species during succession is captured in the model proposed by Oliver (1982) and Peet and Christensen (1988). The variety of changes from old-field abandonment to the formation of an even-aged, closed-canopy forest constitutes the *establishment phase* of development. During this period species patterns and composition are heavily affected by dispersal and spatial patterns affecting seed availability. The duration of the establishment phase varies from less than 10 years to several decades in some cases. Peet and Christensen (1988) suggested that the actual length of time appears to be directly related to factors that influence the initial stocking of woody stems (e.g., seed rain and early seedling survivorship) and site productivity (i.e., tree growth is faster and canopy closure occurs earlier on productive sites).

Canopy closure marks the initiation of the *thinning phase*. During this period, vegetation patterns and composition are affected heavily by limited light and intense competition for soil resources. The duration of this phase is also inversely related to tree density and site productivity. Thinning progresses more rapidly on productive sites and where tree density is highest.

The *transition phase* begins as tree mortality begins to create obvious canopy gaps (i.e., surviving trees are no longer able to close the canopy after a mortality event). This phase is marked by considerable small-scale (1–50 m) spatial heterogeneity. It is during this period that shade-intolerant pioneer trees (e.g., pines) are replaced by more shade tolerant successors. This stage can begin as early as 30–40 years after field abandonment in very densely stocked stands, but 70–80 years is more typical of average densities.

The *equilibrium* (mature) *phase* is characterized by an uneven-aged stand structure. Vegetation patterns are determined by key environmental variables (e.g., gradients of moisture and soil properties) and gap-phase transients (Watt 1947a). It is presumed that the broad-leaved hardwood stands of the Piedmont are typical of this phase and the likely end point of the old-field successional process (Billings 1938; Oosting 1942). However, Peet and Christensen (1987, 1988) provide clear evidence that most of these forests are experiencing considerable thinning as a consequence of a variety of historic disturbances (e.g., timber high-grading and livestock grazing). Furthermore,

few of these stands were actually initiated as old fields (Christensen and Peet 1984).

Oosting (1942) compared the herb layer communities of forest stands representative of these various stages in upland and lowland areas. Generally, he found that herb species richness increased with stand successional age, and that, at any particular age, herb richness was highest in stands on moister sites. Like most ecologists of his time, Oosting paid little attention to variability among stands within broad age categories or within these broadly defined site types. However, the notion of successional convergence—that variations in initial conditions result in intersite variation in species composition that diminishes as communities mature—is all about the nature of changes in variance among sites through time.

Christensen and Peet (1984) sampled the herbaceous layer in 0.1-ha plots located in more than 200 forest stands representing a wide range of stand ages, site conditions and other landscape variables (e.g., tree density). They also measured a suite of more than 20 environmental features in each sample plot. They then divided the data set into 20–40, 40–60, 60–80, and 80+ year-old pine stands and hardwood stands for comparison. The range of environmental variation represented within each age class was very nearly equivalent.*

At the scale of 0.1 ha, herb layer diversity varied considerably among these stands, with some stands having only 20 species and other stands having well in excess of 100 species in the herb layer. On average, the number of species was remarkably constant among stand age classes at 50 species/ha. That said, only 203 species were sampled among all of the pine stands ($N = 111$), compared to 328 species among all hardwood stands ($N = 78$). As these results suggest, the range of variability in species composition among stands (Whittaker's β -diversity) was greater among hardwood than among pine stands.

Both species composition (indicated by first detrended correspondence analysis axis-ordination scores) and herb layer richness were highly correlated with a number of soil variables, most notably pH and soil cations (Fig. 9.2). Recall that Schafale and Christensen (1986) observed similar trends among old-fields. These relationships were strongest among the early and intermediate age pine stands and hardwoods and weakest (indeed, nonsignificant) in the 80+ year-old pines. These weak correlations in the older, transition phase pine stands suggest significant differences in the factors affecting diversity and species composition. Figure 9.3 shows that diversity varies most among stand ages (always greatest in oldest stands) at the lowest (least fertile) and highest (most fertile) soil cation sites.

These results suggest significant changes in the factors affecting the distribution of herb layer species during succession. Certainly, they indicate a

*Twenty deciduous forest stands on sites not represented among the pine stands (e.g., bottomlands and rocky outcrops) were excluded from this analysis.

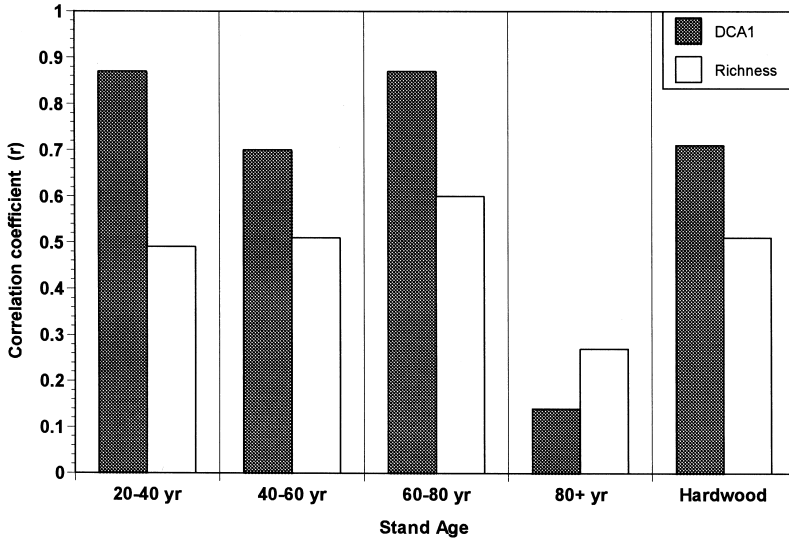


Figure 9.2. Spearman rank correlation comparisons of stand first-axis detrended correspondence analysis (DCA 1) ordination scores and species richness (number of species/0.1 ha) with soil pH.

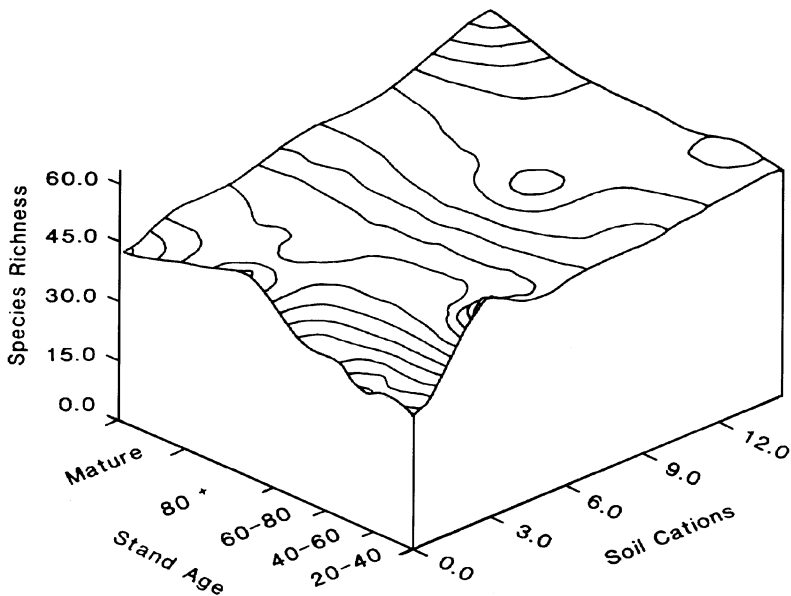


Figure 9.3. A three-dimensional representation of changes in species richness, stand age, and soil cations (highly correlated with pH) among Piedmont forests.

significant change in the relationship between species distributions and soil chemistry in transitional pine stands. High correlation between compositional variation and a factor such as pH implies that the range of conditions over which a typical species occurs is more constrained than where the correlation is lower. To test this, Christensen and Peet (1984) calculated the habitat breadth (abundance-weighted standard deviation of pH for stands within which a species occurs) for all species occurring in more than five stands with respect to soil pH. The results indicate that habitat breadth with regard to soil pH is greatest in the youngest pine stands, diminishes in intermediate-age stands, and increases slightly among transitional pine stands (fig. 9.4). It is lowest for species in hardwood stands.

If convergence in species composition were to occur as conceived by Clements (1936), one might predict that the variance in composition among stands (β -diversity) should diminish through time. Christensen and Peet (1984) found just the opposite, as β -diversity was highest in hardwood stands compared to pine stands of varying age. A more sophisticated approach to the convergence question is implied in Whittaker (1956) as the extent to which vegetation gradients (e.g., species composition—site relationships) in successional stands resemble those in hardwood stands. Christensen and Peet (1984) pursued this by comparing (using canonical correspondence analysis; CCA) the first three detrended correspondence analysis (DCA) axis scores of species in common between a particular pine age class and hardwood stands (fig. 9.5). The similarity generally increases with increasing pine stand age, but abruptly decreases in the transition-stage pines. This suggests that the distribution of species relative to one another becomes more like the distribution in hardwoods, but those relationships are altered considerably in transition-stage forests.

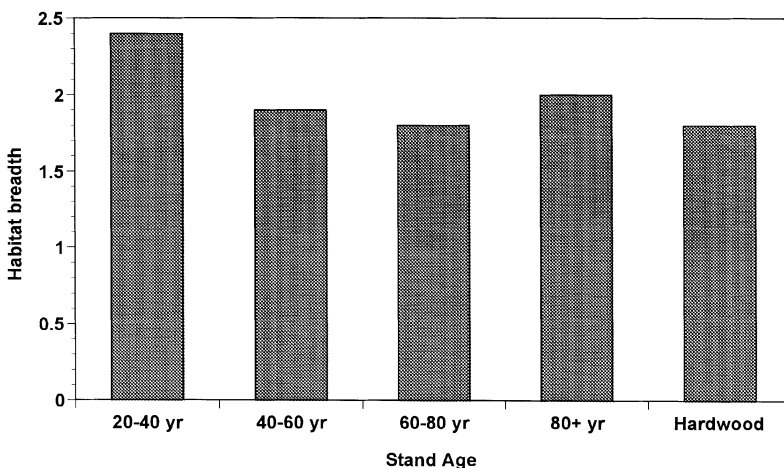


Figure 9.4. Habitat breadth (i.e., importance value weighted species distributions in relation to pH) among different-age forest stands.

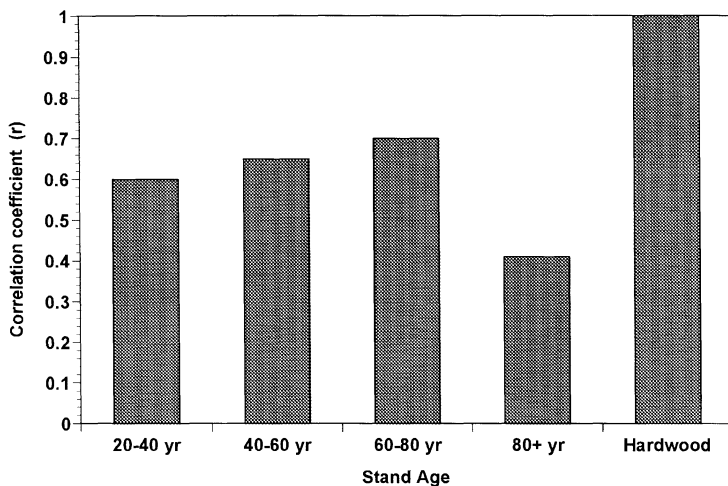


Figure 9.5. Canonical correlation analysis comparisons between axis 1, 2, and 3 detrended correspondence analysis species scores in pine stand age-classes and hardwoods. Hardwoods compared among themselves have a score of 1.0.

Conclusions

To conclude, we return to the questions posed in the introduction. First, what are the key environmental factors influencing herb distribution at various stages in the succession following land abandonment? Although there are major changes in species dominance and community composition during succession and across environmental gradients, these patterns are best understood as a consequence of individual responses of species related to their ability and opportunities to disperse to and compete at particular sites. A few of the individuals of woody plant species that will dominate late in succession may arrive early and simply outlive pioneers, supporting Egler's initial composition hypothesis; however, this is most certainly not the case for herbs. Virtually none of the herb species common in pine and hardwood stands is found in old fields.

At every stage of succession, a significant proportion of the variability in herbaceous species composition was correlated with soil site-variables. Across the entire landscape, soil moisture conditions (determined by topography and proximity to streams) accounted for much variation. However, when the very moist sites (e.g., riparian zones and swampy areas) were eliminated from consideration, soil chemical features such as pH and cation concentrations were most highly correlated with herb species distributions. Furthermore, these same variables were highly correlated with variations in overall species richness.

That soil resources explain variability throughout succession is certainly

consistent with the assumptions of T. M. Smith and Huston's (1989) simulation models. It is important to note, however, that the strength of the correlations described above varied considerably among successional ages, as does the relative importance of other factors. Whereas soil factors were correlated within variation vegetation among old fields, the strength of those correlations (e.g., r^2 , the proportion of total variance explained by a comparison) was not nearly as strong as among mid-aged pines or hardwoods. Although difficult to quantify, it was clear that old-field composition was heavily influenced by "landscape" effects such as the proximity of other fields and disturbed areas that provided important sources of seeds. Much of the variation among old-field soils was due to variations in farming practices (e.g., liming and fertilizer applications), whereas such variation among forest stands was tied to the chemical character of the parent rock. Thus, sites that might be considered to be rich in soil resources due to practices before land abandonment may become less so as those historical effects diminish through time.

The significant decline in correlation between soil site-variables and species composition among late-stage pine stands is noteworthy. Christensen and Peet (1984) suggested that this was a consequence of changes in the physical structure of these stands such as the creation of canopy gaps that produce considerable variance in the light environment. Put another way, understory light availability is uniformly low among pine stands at earlier stages and becomes highly variable at this stage. The change in the relative importance of explanatory variables in these transitional pine stands is certainly consistent with predictions from Tilman's (1985) resource ratio hypothesis and with T. M. Smith and Huston's (1989) simulations.

Variations in species richness through this successional process are considerably more complex than Odum's (1969) expectation that richness increases with increasing successional age. At the spatial scale of a 0.1-ha sample, the average number of herbaceous species encountered was remarkably similar (i.e., ~ 50 species) among successional ages. However, when comparing the total list of species encountered across the full range of environments among ages, Odum's prediction holds. Schafale and Christensen (1986) encountered fewer than 100 species among all their old fields, and Peet and Christensen (1988) encountered 203 and 328 in pine and hardwood stands, respectively. The key difference among these ages is in the numbers of species occurring in only a few stands at relatively low abundance. This coincides with Grime's (1979) prediction that low-abundance, stress-tolerant species should become more abundant in later stages of succession.

Our second question was, what do these patterns tell us regarding the mechanisms that underlie the dynamics of herb populations? Among the successional mechanisms proposed by Connell and Slatyer (1977), the tolerance and inhibition models seem to provide the most explanatory power for old-field succession in the North Carolina Piedmont. Keever's (1950) observations and experiments demonstrated clearly that variations in life history

account for much of the change observed early in the successional process (e.g., the succession from annuals to biennials to perennials). Longer-lived herbaceous dominants such as broomsedge severely limit light to the soil surface and thereby prevent the subsequent invasion of many other herb species (inhibition). Similarly, it appears that usurpation of resources by pines prevents invasion of later successional species until the pine canopy begins to deteriorate.

In its most simplistic form (i.e., a species directly prepares the way for another species) there is no evidence for facilitation. However, when one considers the full array of interspecies interactions (e.g., competition, dispersal, herbivory) occurring during succession, invasion of particular species is often facilitated by other species. Pines may limit light and soil nutrients (inhibition), but in doing so influence the outcome of competition among potential successors. Thus, the successful competitors depend on the pines (Connell and Slatyer's operational definition of facilitation). Similarly, that structural features in old fields influence the dispersal of later successional species could be viewed as a form of facilitation.

It is clear that changes in the relative availability of resources are important in explaining successional patterns and that they are probably responsible for shifts in the relative abundance of species fitting into Grime's three strategic categories. That said, it is also true that designations such as "competitive," "stress-tolerant," and "ruderal" are comparative and relativistic and cannot be defined operationally in a rigid fashion. Furthermore, as Tilman (1985) suggests, shifts in relative importance of resources need not be linear or directional; when they are not (as suggested in some of the data presented here), then species shifts may be complex as well.

Much effort (certainly much of this discussion) to explain variability in the distribution of herbs on successional landscapes is focused on the importance of competitive interactions in the context of changes in resource availability. If such interactions were the only factors shaping the distributions of herbs in time and space, we should expect to see very high correlations between compositional variations and patterns of environmental variation. Although such correlations do explain significant amounts of variation in composition, they leave large amounts (often the majority) of such variation unexplained. It is fitting in closing this chapter to note that other mechanisms are likely equally important and that they may defy our attempts to create a unified theory of change. Christensen (1989) described the array of historical effects that influence vegetation composition including pre- and postabandonment land use and landscape effects, such as context and patch spatial scale. Grubb (1977) presented compelling arguments that the distributions of many species are best understood in regard to the conditions required for their establishment. When this is the case, competition among mature plants may explain little in the way of distribution. Such problems provide ample opportunity for future research.