

11 Temporal Patterns in Herbaceous Layer Communities of 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 20th century—individuals such as B. W. Wells, H. J. Oosting, W. D. Billings, and M. F. Buell, who established some of the first American 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 massive abandonment of agricultural land across the mid-Atlantic region for the century that started with the Civil War, and set 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 of the North Carolina Piedmont region was destined to become the community ecologists' equivalent of the fruit fly or *E. coli*—the “model system” 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 (chapter 19, this volume). 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 process 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. This body of work, which has accumulated over nearly a century, provides unique opportunities to explore the nature of change in a rapidly changing landscape.

Succession on forested landscapes is often 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, our understanding of the nature and mechanisms of such changes remains limited.

Over the past few decades, it has become obvious that successional trends associated with old-field abandonment are occurring against a backdrop of chronic and directional change of other sorts. The dominant oak and hickory species of the mature hardwood forests of the region are not reproducing sufficiently to maintain their current role (Abrams 2003; Nowacki and Abrams 2008). Open field and forested landscapes are becoming ever more dissected and fragmented by urban development (Tilman et al. 1994; Murcia 1995; Ries et al. 2004). These changes, as well as other factors, have resulted in explosive growth in populations of white-tailed deer, which thrive on herbs and seedlings of woody plants (Cote et al 2008; Rooney 2009; chapter 16, this volume). Exotic insect pests and pathogens are changing the character and understory environment of many forests through their impact on the canopy species (Lovett et al. 2006). Nonnative herbaceous species appear to be inexorably increasing in abundance at the expense of their native counterparts (chapter 15, the volume). Changes in climate, most notably increases in temperature and the length of growing seasons, are well documented for the mid-Atlantic Piedmont, although their specific effect on the herbaceous layer is not yet understood (chapters 3 and 21, this volume).

Our primary goal in this chapter is to explore variations in and dynamics of herb layer assemblages across the North Carolina Piedmont landscape. We are particularly interested in three questions: (1) What are the key environmental factors influencing herb distributions at various stages in the succession following land abandonment? (2) What do these patterns tell us with respect to the mechanisms that underlie the dynamics of herb populations? (3) Are Piedmont forest herbaceous communities changing in ways not related to old-field plant succession? To address these questions, we draw on several strands of research carried out over the last 80 years to provide a more comprehensive picture of the successional patterns and mechanisms of change in herb-layer communities of the forested landscapes of the Piedmont region of North Carolina.

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 than with determining the processes (i.e., mechanisms) that caused those changes. After nearly a century of study, debate continues regarding the nature of the underlying 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 Piedmont old-field succession.

The pioneering work of 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.” 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 typically modify their environments in ways that affect establishment of successors. Although Cowles reckoned that this leads to generally predictable patterns of change, he was also aware 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” (see Olson 1958).

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

In his then-controversial paper, Gleason (1926) rejected virtually all of Clements’s ideas on succession and, especially, 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 vary greatly among species) and environmental selection. 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 is 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.

In contrast to Drury and Nisbet (1973), Egler (1954) argued in his initial floristic composition model of succession that, in many circumstances, succession is driven by patterns of early establishment and that subsequent change is 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, in contrast to what would be expected from Clements’s relay floristics model. Mechanisms driving succession include 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 quickly established, 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 out-compete smaller pioneer species.

A common failing of early studies of succession was lack of consideration of mechanisms that might be responsible for the observed changes. The work of Egler (1954) and Drury and Nisbet (1973) represented progress in that they suggested mechanisms for observed patterns, but they fell short of providing a conceptual framework for thinking about the multiple patterns observed in nature. The lack of scientific rigor in earlier studies of succession caught the attention of Connell and Slatyer (1977), who recognized that successional mechanisms need to be “stated in the form of hypotheses testable by controlled field experiments.” To facilitate this approach, they proposed three models of succession, which they called facilitation, tolerance, and inhibition. While these do not really represent distinct mechanisms (i.e., various combinations could apply at any one time), they did help ecologists organize their thinking about the processes that drive succession and how they vary with environmental and disturbance context. 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 for themselves. The tolerance model captures the key elements of Gleason’s framework in proposing that succession is largely determined by patterns of dispersal and differences in life history and physiology. The inhibition model depicts succession as a process in which early invaders establish, usurp resources, and thereby competitively exclude would-be successors, ideas similar to those introduced by Egler. In this final model, succession only proceeds when the populations of the current occupants decline due to their inability to reestablish.

An alternative approach to understanding succession is to examine traits of individual species and the progression of those traits through the successional sequence. For example, Grime (1977, 1979) proposed that spatial and temporal patterns could be understood in terms of three primary plant strategies: ruderal (ephemeral), competitor, and stress-tolerant, reflecting basic tradeoffs in life history traits. Ruderal species are generally easily dispersed and reproduce quickly, but they are not effective competitors, with the consequence being that they are most important early in the successional sequence. Competitors increase during the initial succession sequence owing to their greater ability to grow quickly and out-compete other species for light, but because they are depressed under low soil resource levels, they tend to be less important in climax communities. Stress-tolerant species are generally poor competitors in a context of rapid community development, but do well in the resource-limited later stages of succession. In a similar conceptual framework, Tilman (1985) proposed that temporal and spatial variation in species composition through succession could be understood in terms of variation 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 from habitats with resource-poor soils but high available light at the soil surface to habitats with resource-rich soils but low light availability.

Peet (1992) explained that most examples of secondary succession can be viewed as driven by a combination of two models or sets of linked processes: a gradient-in-time model where biological characteristics of species can be used to explain their

distributions along temporal gradients (Whittaker 1953; Pickett 1976), and a competitive sorting model where population interactions, particularly competition, cause a temporal gradient in the level of community organization and predictability (Margalef 1963, 1968). These models are neither mutually exclusive nor all encompassing, but it is possible to view autochthonous community change as variously representing the contributions of these two sets of mechanisms. In much the same fashion as different adaptations of species result in their being arrayed as an overlapping series along a resource or physical environment gradient, so too might they be expected to form a successional sequence representing a sequence of physiological or life history adaptations. This model captures the core ideas of Grime (1979), Tilman (1985), and Smith and Huston (1989). The competitive sorting model applies to the case where all species can readily disperse to a site, but they sort out over time through competition to ultimately match the specifics of the site, with composition becoming more predictable from site variables over time, and beta diversity increasing.

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.” 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, such as *Digitaria sanguinalis* (L.) Scop. [Botanical nomenclature follows Weakley et al. 2012] (crabgrass) and *Cynodon dactylon* (L.) Pers. (Bermuda grass). Wells (1932) and Crafton and Wells (1934) observed that the sequence of change in herbaceous dominance during the first three to four years was highly predictable, interpreting this as a process consistent with facilitation as subsequently described by Connell and Slatyer (1977).

Oosting (1942) provided a synthesis based on 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 and 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 roughly 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 two-year-old fields. The Sørensen community coefficient of similarity for first- as compared to 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 *Symphyotrichum pilosum* (Willd.) G. L. Nesom (hairy aster), which was absent from first-year fields, and *Ambrosia artemisiifolia* L. (ragweed), a minor component of first-year fields (except those abandoned in the spring, a time when horseweed is not dispersing). Species richness dropped sharply in the third year after abandonment, corresponding to a rapid increase in dominance of the perennial grass *Andropogon virginicus* L. *s.l.* (broomsedge), 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 suggested that the shift to dominance by broomsedge resulted from superior ability to compete for resources, a mechanism consistent with the gradient-in-time model. Keever (1983) later marveled, after a few decades on the faculty of the more northern Millersville College in Pennsylvania, at the uniqueness of these changes compared to the process of 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."

Keever's observation foreshadowed the subsequent work of Wright and Fridley (2010; Fridley and Wright 2012) where they document an eastern North American latitudinal gradient in the speed of woody plant invasion during old-field succession.

Much of the attention toward 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 variation among herb communities in three-to-seven-year-old fields. They found that species richness varied widely among such fields (14 to > 50 species/1,000 m²) and was positively correlated with soil pH and cation availability. These same factors were also highly correlated with trends in species composition, suggesting that by year three, significant competitive sorting had already occurred. Standing crop and productivity, however, were more highly correlated with soil organic matter and may reflect other variables associated with the conditions of the field at abandonment or water availability. This suggests that there are multiple, independent factors influencing variation in old-field species composition that are independent of those that influence production.

During the early years of succession, seedlings of wind-dispersed *Pinus echinata* Miller (shortleaf pine) and *P. taeda* L. (loblolly pine) (in the 1930s and earlier, largely *P. echinata*, but by the 1950s, almost exclusively *P. taeda*) and hardwood species, such as *Fraxinus americana* L. (white ash), *Ulmus alata* Michx. (slippery elm), *Liquidambar styraciflua* L. (sweetgum), *Liriodendron tulipifera* L. (yellow poplar), and *Acer rubrum* L. (red maple), 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 the 10th year. On moister sites, sweetgum and tulip popular may share dominance with pine. The suite of herb species typical of old fields is virtually absent thereafter, because of the reduced light and soil resources under the closed forest canopy. In addition, 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 three years after abandonment, before the development of an herbaceous thatch, which inhibits pine seedling growth (Oosting 1942). This accentuates the even-aged structure of the old-field pine stands.

De Steven (1991a,b) 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 the five previously mentioned early successional hardwood species common in the North Carolina Piedmont. De Steven found that competition from

herbs, along with 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 that arrive at old-field sites in potentially large numbers, loblolly pine usually initiates the woody species stage of old-field succession.

Although the North Carolina Piedmont provides the primary model system for old-field succession in eastern North America, a number of other areas have received intensive study, such as the Buell plots in New Jersey (e.g., Myster and Pickett 1992). Wright and Fridley (2010) conducted a meta-analysis of these various old-field systems and found a strong inverse latitudinal gradient in the speed of woody plant invasion. These results beg the question of what drives this gradient and how typical the North Carolina Piedmont old fields might be when placed in a broader context. Fridley and Wright (2012) subsequently examined three hypotheses for the cause of the gradient: climate, species pool, and soil fertility. Their experimental study provided convincing evidence that soil fertility was the primary driver. Thus, whereas the North Carolina Piedmont retains its place as the primary model system, one should keep in mind that it represents the low-fertility end of a gradient of old-field study systems ranging geographically from Florida to New England.

SUCCESSIONAL CHANGE IN THE FOREST HERB LAYER

Although we focus primarily on temporal patterns of change in the herbaceous layer following old-field abandonment, it is important that we first provide an overview of successional change in woody species, as these plants greatly influence the environment in which the herbaceous layer occurs. The general pattern of change among woody species during succession is captured in the models proposed by Bormann and Likens (1979), Peet (1981), and Oliver (1982). The changes from old-field abandonment to the formation of an even-aged, closed-canopy forest constitute the establishment phase of development. During this period, species composition is heavily affected by dispersal and spatial processes influencing seed availability. The duration of the establishment phase varies from less than 10 years to several decades in some cases, and outside the Piedmont region, it can be significantly longer (Peet 1992; Wright and Fridley 2010). Peet and Christensen (1988) (fig. 11.1) 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), competition from herbaceous species, and site productivity (i.e., tree growth is faster and canopy closure often occurs earlier on productive sites, provided fertility is not sufficient for a dense herbaceous layer to develop and preclude tree establishment).

Canopy closure marks the initiation of the thinning phase. During this period, vegetation pattern and composition are affected heavily by limited light and intense competition for soil resources. Little tree establishment occurs during this period; rather, trees get larger and decline significantly in density (Peet and Christensen 1980a; Knox et al. 1989; Peet 1992). The duration of this phase is also inversely related to tree density and site productivity. Thinning progresses more rapidly on productive sites and where growth rates are high.

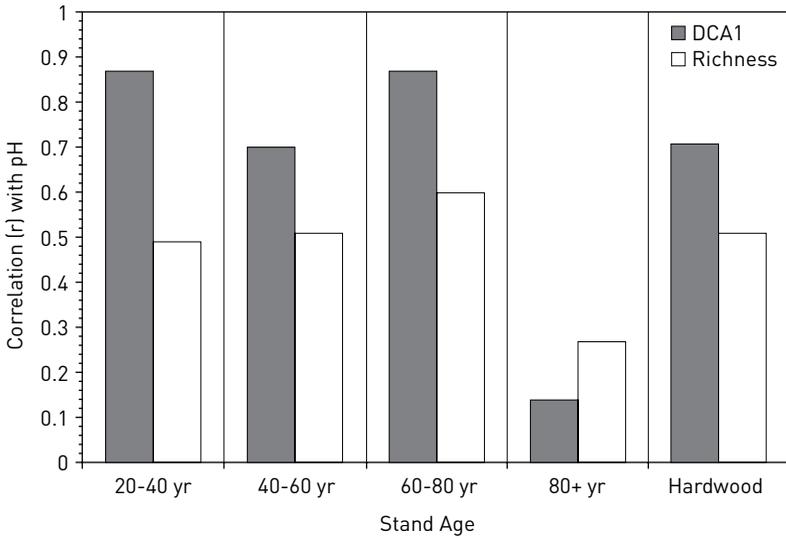


FIGURE 11.1 Spearman rank correlation comparisons of stand first-axis detrended correspondence analysis (DCA 1) ordination scores and species richness (number of species/0.1 ha) with soil pH. Data from Christensen and Peet 1984, Peet and Christensen 1988.

The transition phase begins as tree mortality becomes less driven by natural thinning and 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 in the understory by more shade-tolerant successors. In the Piedmont region, initiation of this stage can begin as early as 50 years after field abandonment in densely stocked stands, but 70–80 years is more typical. Of course, disturbance events such as hurricanes and tornadoes can dramatically alter the timing (see Xi et al. 2008).

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 has generally been presumed that the broadleaved hardwood stands of the Piedmont are typical of this phase and represent the endpoint of the old-field successional process (Billings 1938; Oosting 1942; Braun 1950). 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, livestock grazing, and elimination of chronic, low-intensity fire). Furthermore, few of these stands actually originated as old fields (Christensen and Peet 1984).

During the growing seasons of 1977 and 1978, Peet and Christensen sampled the herbaceous layer (cover below 1 m height) with 252 1,000-m² plots in Piedmont forest stands representing a wide range of stand ages, site conditions, and other landscape variables (Peet and Christensen 1980a,b; Christensen and Peet 1981, 1984). They also measured a suite of more than 20 environmental features in each sample plot. They then divided the dataset into 20–40, 40–60, 60–80, and 80+ year-old pine stands and all-aged hardwood stands for comparison. After exclusion of 20 hardwood forest stands located in bottomlands and on rock outcrops, the range of environmental

variation represented within each age class was very nearly equivalent (Christensen and Peet 1984).

At the scale of 1,000 m², herb layer diversity varied considerably among these stands, with some stands having fewer than 20 and others having well in excess of 100 species in the herb layer. However, the average number of species was remarkably constant among stand age classes at ~ 50 species/1,000 m². That said, only 203 species were sampled among all of the pine stands, compared to 328 species among a smaller number of hardwood stands. As these results suggest, the range of variability in species composition among stands (Whittaker's β -diversity; 1960) was greater among hardwoods than among pine stands.

Both species composition (represented by the first axis of a detrended correspondence analysis; see Peet and Christensen 1980b, 1988; also see chapter 10, this volume) and herb layer richness were highly correlated with a number of soil variables, most notably pH and soil cations (fig. 11.2). Recall that Schafale and Christensen (1986) observed similar trends among much younger old-field herb communities. These relationships were strong among the early and intermediate-age pine stands, as well as in the mature hardwoods, but weaker (indeed, non-significant) 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, and potentially relaxation of competition due to fewer trees competing for resources. Fig. 11.2 shows that diversity increases with stand age at sites with the lowest and highest soil cation levels. It also shows less change with change in cations for the old pine stands than for any other age class.

These results suggest significant temporal changes in the factors affecting the distribution of herb-layer species during succession. In particular, they indicate a significant change in the relationship between species distributions and soil chemistry in transitional pine stands. High correlation between compositional variation and a factor such

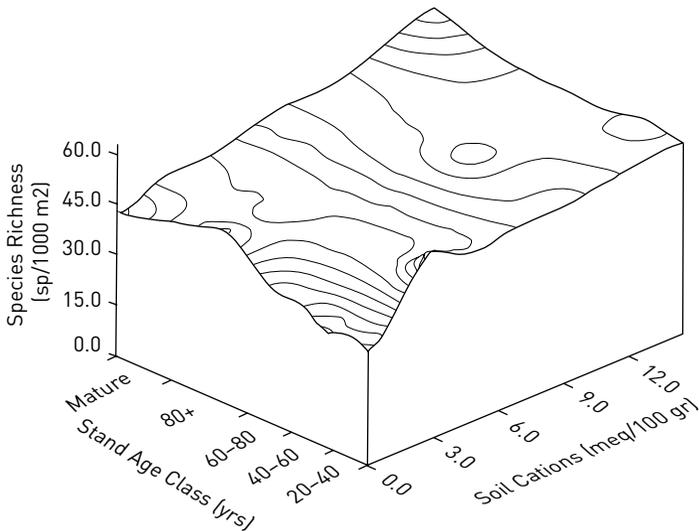


FIGURE 11.2 A three-dimensional representation of changes in species richness (species/0.1 ha with contours of three species) with stand age, and soil cation availability (sum of Ca, Mg, and K meq; highly correlated with pH) among Piedmont forests. Reproduced from Peet and Christensen 1988.

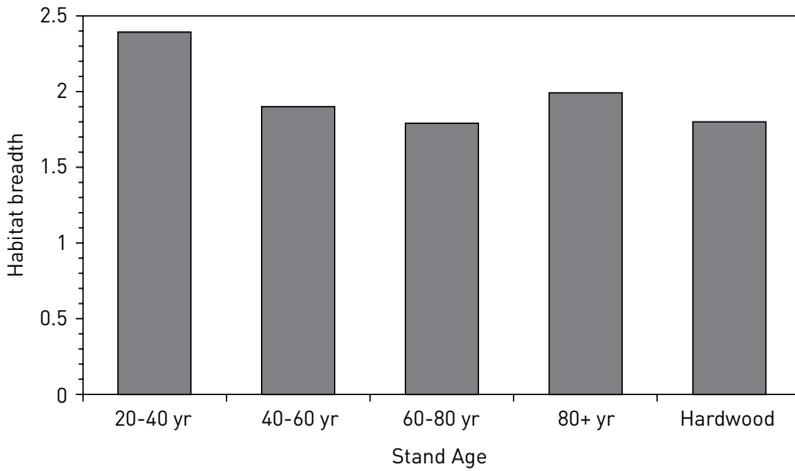


FIGURE 11.3 Habitat breadth (i.e., importance value-weighted species distributions in relation to pH) among different-age forest stands, showing a decline during the thinning phase, followed by an increase in the breakup phase and a decline again into the mature hardwoods. Data from Christensen and Peet 1984.

as pH implies that the range of conditions over which a typical species occurs is more constrained than when 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 indicated that habitat breadth with regard to soil pH is greatest in the youngest pine stands, diminishes in intermediate- age stands (where competition is intense and there has been time for competitive sorting), and increases slightly among transitional pine stands (with relaxation of competition for soil resources because of canopy breakup; fig. 11.3). It is lowest for species in mature hardwood stands.

If convergence in species composition were to occur as conceived by Clements (1936), we would predict that the variance in composition among stands (β -diversity) should diminish through time. Christensen and Peet (1984) found just the opposite; β -diversity was higher in hardwood stands as compared to pine stands of various age classes. A more sophisticated approach to the convergence question implied in Whittaker (1956) is the extent to which vegetation gradients 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. 11.4). This 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 when canopy breakup relaxes competition for soil resources.

NON-SUCCESSIONAL CHANGE IN FOREST HERBS

Chronosequence studies, observations of different-age forests at a single point in time, assume that the environmental context (e.g., climate, landscape features) remains

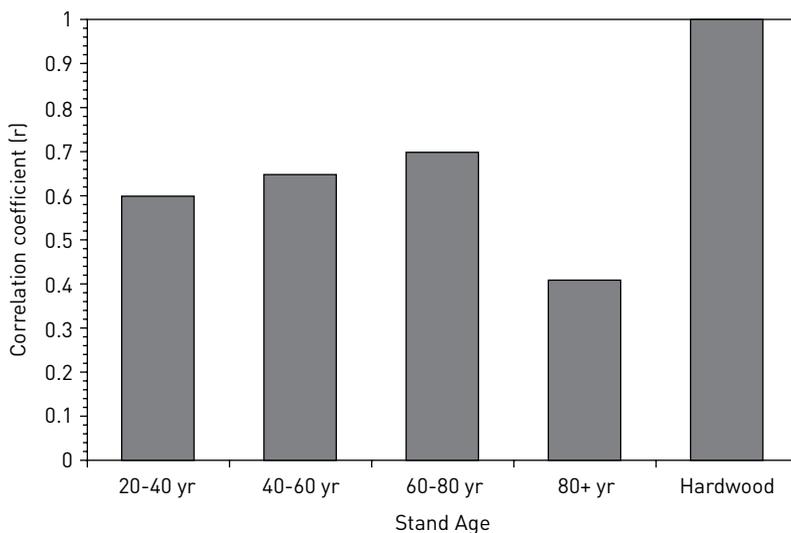


FIGURE 11.4 Comparison of species detrended correspondence analysis ordination scores on the first three axes, with scores in the mature hardwood stands using canonical correlation analysis. Species sorting gradually approaches that of the hardwood stands through competitive sorting, but then declines with breakup of the canopy in the old pine stands. Data from Christensen and Peet 1984.

constant across successional time and differences among different-age plots are due to succession alone (Pickett 1989; Foster and Tilman 2000). Given the extent of directional, non-successional environmental changes like fragmentation, mesophication (Nowacki and Abrams 2008), invasion of nonnative species (chapter 15, this volume), increased deer browse (chapters 16 and 17, this volume), increased deposition of nitrogen (chapter 20, this volume), and climatic change on the Piedmont landscape over the past century (chapters 3 and 21, this volume), this is almost certainly not the case.

A large number (83) of the 1977 Peet and Christensen permanent plots were resampled in 2000 (± 1 ; Taverna et al. 2005) and again (72) in 2010 (± 1 ; Israel 2012). The wide range of successional ages represented in this dataset provided an opportunity to assess the impacts of non-successional change as separate from changes directly associated with succession over a 33-year timespan.

Taverna et al. (2005) presented the 2000 resampling results for 36 hardwood-dominated stands distributed across a wide range of site conditions. As expected, soil variables such as pH and cation concentration appear responsible for a considerable portion of the variation in herb composition in these stands as represented by first-axis ordination scores (Nonmetric multidimensional scaling; fig. 11.5). However, the vectors of compositional change over the 1977–2000 period in individual stands were consistently aligned and pointed in the same direction along the second ordination axis. This was even true for several stands that had been significantly damaged by Hurricane Fran in 1996. Nearly all of these stands were changing in composition in a consistent manner away from their 1977 composition. Israel (2012) examined change in these plots again in 2010 and found the trends continuing, but with the rate of change having more than doubled from the previous resample.

Schwartz (2007) observed a similar pattern of herb layer compositional change in 47 pine-dominated stands (fig. 11.6). Ages of pines in 1977 ranged from < 20 to $>$

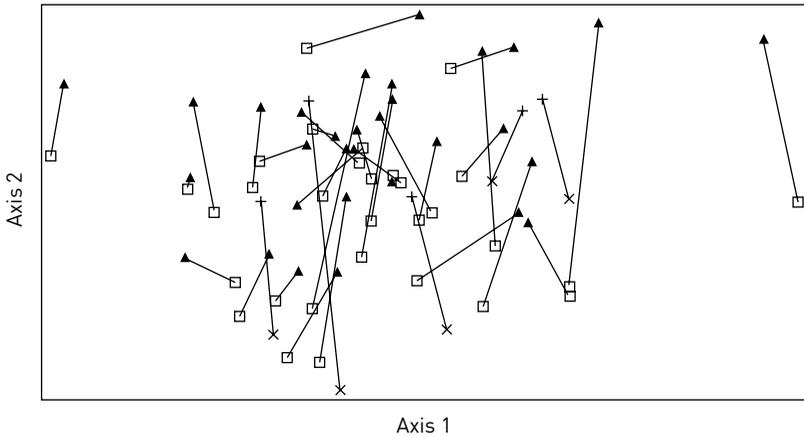


FIGURE 11.5 Nonmetric multidimensional scaling ordination of 36 hardwood plots in species space with paired-plot vectors from the 1977–2000 plot observation. Symbols are plots coded for year: closed diamond = 1977, open square = 2000, + = 1977 hurricane plot, × = 2000 hurricane plot. Reproduced from Taverna et al. 2005.

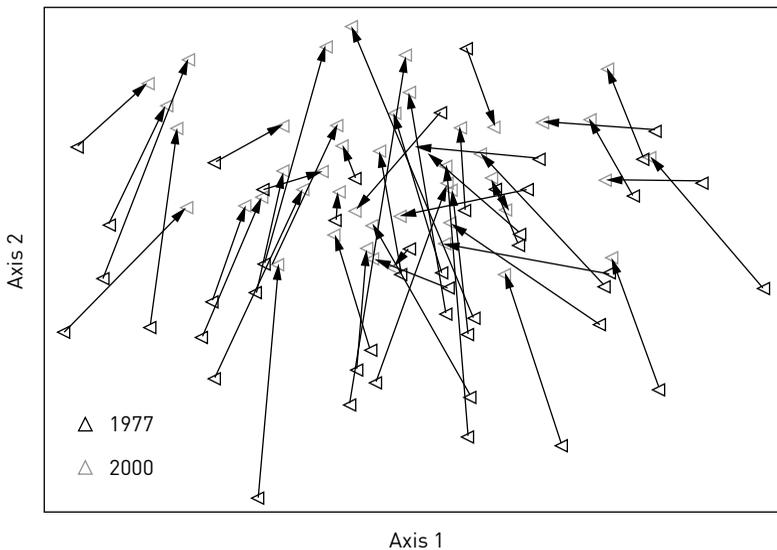


FIGURE 11.6 Nonmetric multidimensional scaling ordination of 47 pine-dominated plots in species space with paired-plot vectors from the 1977–2000 plot observation. Symbols are plots coded for year: black diamond = 1977, gray diamond = 2000. Reproduced from Schwartz 2007.

100 years. The first ordination axis was again correlated with soil pH and cation concentration, and the second axis was correlated with compositional change between 1977 and 2000. This was true regardless of successional age, indicating that much of the directional change in herb layer composition was not related to forest succession, but instead to non-successional changes. Israel (2012) followed up on this analysis by again resampling the plots in 2010. The trend away from the range of 1977 composition continued, but the changes were much greater between 2000 and 2010 than during the much longer period of 1977–2000. She then projected the 2010 composition

of the 1977 stands based on the differences in plot composition associated with age in 1977 (the classic space-for-time approach advocated by Pickett 1989) and compared this projected composition with the observed composition. She observed that all of the plots had changed dramatically away from the projected change and in a consistent direction within ordination space. These studies make it clear that Piedmont forests are changing dramatically in ways unrelated to old-field succession.

The herb-layer censuses described above included species of true herbs, as well as low (< 1 m tall) shrubs and tree seedlings. At the scales of 1,000, 25, and 1 m², Schwartz (2007) found that species richness of herbs alone significantly decreased between sample dates, whereas richness of herb layer woody species increased in both pines and hardwoods. The net effect of these changes was that herb-layer species richness at all three scales remained relatively constant between sampling intervals in both hardwood and pine stands. However, when Israel (1912) resampled these same plots in 2010, she found that species richness had declined significantly in both pine and hardwood plots, and across the pH gradient.

Schwartz (2007) reported that total species richness across all plots showed a net decline between 1977 and 2000 of 7.3 percent in the hardwood plots and 1.8 percent in the pine plots. Furthermore, there was considerable turnover in species composition. For example, among the hardwoods, 70 herb-layer species disappeared between 1977 and 2000, and all of these were natives. A total of 49 new species appeared in 2000, and of these, 42 were natives and seven were exotic. Species that were less common in 1977 were more likely to disappear. Sixty-one percent (89 out of 145) of herb species that occurred in 10 or fewer plots in 1977 declined in plot frequency, and more than half of those that declined (52 species) were not recorded at all in 2000. Schwartz (2007) observed similar patterns of species turnover and net increase in nonnative herb species in successional pine stands. This overall loss of herb-layer species richness is consistent with other studies showing regional losses of species (e.g., Tilman et al. 1994; Pimm et al. 1995).

Although it is not possible to pinpoint the precise cause of these non-successional changes, closer examination of compositional change during the 1977–2000 period suggests that three factors were especially important: hurricane disturbance, grazing by white-tailed deer, and increased abundance of exotic species. Two native weedy herbs, *Phytolacca americana* L. and *Erechtites hieracifolia* (L.) Raf. ex de Candolle, increased dramatically in hurricane-damaged pine and hardwood stands for a period of two years, suggesting a temporary relaxation in the competitive environment of the herbaceous layer that would facilitate establishment of other species. Browsing by white-tailed deer likely accounts for a significant amount of the observed changes in herb-layer composition and species richness. Exact numbers are not available for the 1970s, but deer populations in the North Carolina Piedmont were quite sparse at that time (fewer than 1/km²) and in our study area remained so until after 1990. Today, deer populations exceed 16/km² in many places, including the vicinity of the Peet and Christensen study plots. In both pines and hardwoods, significant declines in the frequency and abundance of preferentially browsed species, including all legumes, *Chimophila maculata* (L.) Pursh., *Goodyera pubescens* (Willd.) R. Brown, and *Euonymus americana* L., are almost certainly due to deer. Legume cover declined by 40 percent during 1977–2000, and by 2010, had declined by over 70 percent in all plots compared to 1977, and in hardwood plots in 2010, it was at less than 20 percent the level of cover exhibited in 1977. By 2010, orchids had nearly disappeared. Vine cover, largely composed of such charismatic

species as *Lonicera japonica* Thunberg (Japanese honeysuckle), *Toxicodendron radicans* (L.) Kuntze (poison ivy), *Smilax* spp. L. (greenbriar), *Muscadinia rotundifolia* (Michaux) Small (muscadine), and *Vitis* spp. L. (grape), had declined by 70 percent in 2000 and by over 90 percent in 2010. The only family that showed a large increase was the Poaceae, due to the spread of the exotic *Microstigeum vimineum* (Trinius) A. Camus, which increased across all plots by a factor of eight between 1977 and 2000, but by a factor of 24 between 1977 and 2010. Despite the increase in deer browse, other exotic species continued to invade and increase in this landscape with their total cover having increased by a factor of 10 over the 33-year period.

Increased abundance of woody species in the herb layer between 1977 and 2000 was contrary to the expected effects of deer browsing, but likely a response to the canopy being opened in many stands by the occurrence of Hurricane Fran in 1996. However, between 2000 and 2010, this pattern reversed, perhaps because of canopy closure and the large-scale elimination of herbaceous food for deer, which then fed more intensively on woody species.

One pattern widely observed in Piedmont hardwood stands (e.g., McDonald et al. 2002; Taverna et al. 2005) has been the steady increase in *Acer rubrum* L. (red maple) and *Fagus grandifolia* Ehrh. (American beech) at the expense of the canopy oaks (*Quercus* spp.) and hickories (*Carya* spp.), species traditionally viewed as the climax species of the region (Oosting 1942; Braun 1950). The steady decline in the importance of oaks and hickories relative to maples and beech over the 33 years of observation suggests a long-term trend in canopy composition consistent with the hypothesis of mesophication of eastern forests (Nowacki and Abrams 2008). Abrams (1998) describes *Acer rubrum* as a “supertree,” able to compete under varied conditions, the only conspicuous exception being in the presence of recurrent fire. The consistent decline of oaks and hickories, particularly evident in plots dating back to the early 1930s and now spanning 80 years (McDonald et al. 2002), is consistent with the loss of low-intensity fire early in the 20th century, though deer herbivory, which has become a factor only since the early 1990s, may now be accelerating the process due to preferential feeding on oak (Waller and Alverson 1997; Wakeland and Swihart 2009). Regardless of the mechanism, this mesophication is resulting in much denser canopies and consequent lower light levels to support the herbaceous layer.

Other changes in this landscape during the period 1977–2010 have likely influenced change in forest herb layer composition and diversity, but their effects are more difficult to diagnose from these data. The human population of this region increased by over 70 percent during the interval 1977–2010 (U.S. Census Bureau), and this growth was accompanied by similar increases in urban development and land fragmentation. McDonald and Urban (2006) examined the herbaceous layer near urban and suburban edges in Piedmont forests and found large increases in exotics and significant increases in temperature associated with these edges. Subsequent unpublished work by Sexton and Urban has documented increases of up to 10°C in temperature within Piedmont forests near urban heat islands (see White et al. 2002; Carreiro and Tripler 2005; Imhoff et al. 2010).

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 abandonment of agricultural land on the North Carolina Piedmont?

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 responses of individual species related to their opportunities to disperse and their competitive abilities at particular sites. A few 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 tracks soil variation. Across the entire landscape, soil chemistry and moisture conditions (determined by parent material, topography, and proximity to streams) account for much of the variation. Furthermore, these same variables are highly correlated with variation in overall species richness. It is important to note, however, that the strength of the correlations vary considerably with successional stage, as does the relative importance of other factors. Whereas soil factors are correlated with variation in vegetation among old fields, and the correlation increases in the competitive environment of the thinning phase of forest development, the strength of those correlations is not nearly as strong among old, transitional pine stands. Although difficult to quantify, it is clear that old-field composition is heavily influenced by landscape effects, such as proximity to other fields and disturbed areas that provide important sources of seeds. Much of the variation among old-field soils is due to variation in farming practices (e.g., liming and fertilizer applications), whereas such variation among forest stands is generally 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 (see Satterson 1985; chapter 19, this volume).

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 is a consequence of changes in the physical structure of these stands (such as the existence of canopy gaps) that produce considerable heterogeneity in the light environment and reduce competition for soil resources. Put another way, understory light availability is uniformly low among pine stands at earlier stages and becomes highly variable at this stage, whereas soil resources are extremely limiting in successional stands, but likely become more available with reduced competition from canopy trees.

Variation in species richness through this successional sequence is considerably more complex than Odum's (1969) expectation that richness increases with increasing successional age and more in keeping with the competition-driven hypotheses of Peet and Christensen (1988). At the spatial scale of a 1,000 m² sample, the average number of herbaceous species encountered is remarkably similar (i.e., about 50 species) among successional ages. However, when comparing the total list of species encountered across the full range of environments among ages, species number consistently increases, suggesting increased beta diversity and increased competitive sorting with time.

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 variation 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 at 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.

There is no evidence for facilitation in its most simplistic form (i.e., a species directly prepares the way for another species). 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 so doing, 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, structural features in old fields influence the dispersal of later successional species, which could be viewed as a form of facilitation.

It is clear that changes in the relative availability of resources are important for explaining successional patterns, and that they are probably responsible for shifts in the relative abundance of species. That said, it is also true that designations like "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, then species shifts may be complex as well.

Finally, we asked whether Piedmont forest herbaceous communities are changing in ways not related to old-field plant succession. It is clear that dramatic changes are taking place and the speed of these changes is accelerating. Piedmont forests indeed are moving toward some unknown future composition, something Gilliam (2007) referred to as an "ecological moving target." This is driven by multiple factors including increased deer populations, increasing abundance of exotic species, landscape fragmentation, proximity to urban areas, climate change, and replacement of the original canopy species of the mature hardwood forest with more shade-tolerant species like red maple and beech. Other factors may be responsible as well, and this will likely be an active area of future research.

Much effort to explain variability in the distribution of herbs in successional landscapes has been 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 would expect to see very high correlations between compositional variation and patterns of environmental variation. Although such correlations do explain significant amounts of variation in composition, they leave large amounts unexplained. It is fitting in closing this chapter to note that other mechanisms are likely to be 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 post-abandonment 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 be limited in its explanatory power, and the extant pattern may be in large part a consequence of history. Such problems provide ample opportunity for future research.

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