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Interactions Between the Herbaceous Layer and Overstory Canopy of Eastern Forests

A Mechanism for Linkage

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A clear understanding of the nature of interactions between vegetation strata of forest ecosystems has implications for both basic and applied studies in forest ecology. For example, community mapping studies may rely on the dominant overstory strata as interpreted from aerial photographs or satellite imagery to represent the entire community. Conversely, site classification systems may use herbaceous layer vegetation to represent communities and their relationships to environmental factors (Cajander 1926; Rowe 1956; Pregitzer and Barnes 1992). In such studies, an understanding of relationships between vegetation strata is necessary if interpretations are to be made concerning the entire community.

This information is generally lacking in disturbed stands because site classification studies are usually carried out in mature stands. As increasing proportions of forested areas become disturbed, it is a critical to know whether the same overstory–understory relationships that occur in mature stands are also found in disturbed stands. Also, the need to manage for biodiversity, a need now recognized by national and global forestry organizations (Burton et al. 1992; Roberts and Gilliam 1995a), requires a shift in focus away from the small number of commercially important tree species toward all plant species, including noncommercial tree and herbaceous species. Thus, the nature of interactions among forest strata and their response to forestry practices need to be understood to maintain biodiversity (Gilliam and Roberts 1995).

In this chapter we have three primary objectives. First, we determine via literature review what is known of interaction among forest strata, with a specific focus on overstory–herbaceous layer interactions in eastern deciduous forests. We present contrasting views of the nature of these interactions, from

one that sees a quantifiable linkage among strata to one that sees little true interaction occurring. Second, we develop a mechanistic explanation for patterns of linkage in forest ecosystems, with emphasis on eastern deciduous forests. Finally, we examine data from two different forest types, a central Appalachian hardwood forest and a successional aspen forest of northern lower Michigan, for evidence supporting or refuting this explanation.

The Nature of Linkage Among Forest Strata

Studies of secondary succession often have emphasized changes in only dominant species in a single stratum of vegetation. For example, studies of old-field succession in the North Carolina Piedmont (e.g., Oosting 1942; Keever 1950; 1983; Christensen and Peet 1984; De Steven 1991b) have focused on the shift from herb-dominated communities early in succession to pine-dominated and then hardwood-dominated communities later and thus have not examined the herbaceous layer that develops beneath the woody overstory canopy during these later stages of old-field succession (but see chapter 9, this volume). Indeed, despite the increasing number of studies of the herbaceous layer in forest communities (see table 1.1), few consider interactions among strata in any forest type.

Influence of the Overstory on the Herbaceous Layer

There is little argument that the forest overstory and herbaceous layer exert reciprocating influences on each other. The forest overstory has a direct effect on the availability of resources to herb layer species, the most obvious being to decrease the quantity and alter the quality of light reaching the forest floor (chapter 3, this volume). Other effects would include decreasing nutrient and moisture availability by competitive uptake by fine roots of trees. Although he did not speculate about mechanisms, Rogers (1981) found nearly 20% higher species richness and around 70% higher cover for the herb layer of mature mesophytic stands (Minnesota to Michigan) with little or no *Fagus grandifolia* Ehrh. compared to that of stands with *F. grandifolia* codominance in the overstory. Crozier and Boerner (1984) reported tree species-specific differences in microhabitat conditions (e.g., different levels of soil nutrients caused by differences in stemflow chemistry) that resulted in spatial variation in cover of dominant herb species. Hill and Silander (2001) found that spatial dynamics of dominant ferns of mixed hardwoods-hemlock stands of Connecticut varied significantly among dominant tree canopy species (i.e., there was a species-specific effect of individual trees on distribution of ferns). They ascribed these differences in fern species dynamics to different light regimes among contrasting stand types.

Other studies have emphasized the importance of detrital inputs to the forest floor by overstory species. Whitney and Foster (1988) found substantial differences in percent occurrence of numerous herb layer species in conifer

and hardwood stands in New England, suggesting that, in addition to variation in soil moisture and light regimes, such differences resulted from contrasts in physical and chemical characteristics of litter of conifer versus hardwood species. Nemati and Goetz (1995) made similar conclusions for herb layer differences in stands of *Pinus ponderosa* Dougl. ex Laws. versus *Quercus gambelii* Nutt. Saetre et al. (1997) found that abundance of herb layer species was lower under pure *Picea abies* (L.) Karst. stands than under mixed *P. abies*/*Betula* stands. They proposed that foliar litter from *Betula* (and associated higher fertility) was the most important cause of such pronounced stand-related differences in the herb layer. McGee (2001) determined that decaying logs of dead overstory species provided sites for early establishment critical for some, but not all, herb layer species, suggesting an additional influence of the overstory on species composition of the herbaceous layer.

Influence of the Herbaceous Layer on the Overstory

Although the influence of the herbaceous layer on the overstory of forests may not be as obvious as that of the overstory on the herb layer, it is potentially as profound (Maguire and Forman 1983). In chapter 1 we discussed the temporal and spatial dynamics of resident and transient species of the herb layer, with resident species being the truly herbaceous (nonwoody) annual, biennial, and perennial component of the herb layer, and transient species being predominantly seedlings and sprouts of tree species. Although resident and transient species exhibit contrasting life histories, they share common resources when co-occurring in the herb layer. Maguire and Forman (1983) demonstrated that cover and composition of herbaceous species (residents) determined, in part, the density and distribution of seedlings of dominant tree species (transients) in an old-growth hemlock-hardwood forest.

Because of their typical growth characteristics that often include a dense spreading of fronds, fern species can have a particularly profound effect on survivorship and growth of juveniles of forest overstory species. Horsley (1993a) demonstrated a species-specific interference of *Dennstaedtia punctilobula* (Michx.) limiting growth of seedlings of *Prunus serotina* Ehrh. in hardwood forests of the Allegheny region of Pennsylvania. George and Bazzaz (1999a, 1999b) showed that high fern cover in a New England hardwood forest can function as a species-specific filter, affecting emergence and survival of tree species. This has particular ecological significance in the context of response of eastern hardwood forests to disturbance (chapter 11, this volume).

Linkage as Reported in the Literature

Several studies have reported significant relationships between species' patterns in overstory and herbaceous strata. Using canonical correlations between principal components axes, Gagnon and Bradfield (1986) concluded that tree and herb strata of coastal Vancouver Island forests were linked via their response to predominant site gradients. Roberts and Christensen (1988)

combined canonical correlation analysis with detrended correspondence analysis to examine vegetation strata of successional aspen stands of northern lower Michigan; they attributed significant correlations between strata to soil factors and disturbance regime. Hermy (1988) demonstrated correlations between strata in deciduous forests of Belgium, concluding that the degree of correspondence between compositional patterns was directly proportional to β diversity. Working in upland hardwood forests of northwestern lower Michigan, Host and Pregitzer (1992) determined that significant tree–herb linkages resulted from similar responses of strata to environmental and historical factors, citing moisture availability as especially predominant. Nematı and Goetz (1995) described a linkage between *Pinus ponderosa/Quercus gambelii* overstory and herbaceous understory by correlating canonical variable scores of the overstory to those for the herb layer. They concluded that linkage resulted from a variety of factors, but emphasized the importance of canopy-mediated changes in environmental conditions for herb layer species, such as light availability and soil acidity. Gilliam et al. (1995) studied interactions between the overstory and herb layer in second-growth hardwood forests of West Virginia. They found evidence of linkage for mature stands, but not for young (20-year old, even-aged) stands, and concluded that linkage changes through secondary succession, becoming tighter through time after disturbance.

Other studies, however, have concluded that forest strata do not form significant linkages. Looking at β diversity in undisturbed *Fagus grandifolia* communities of Great Smoky Mountains National Park, North Carolina, Bratton (1975) also found significant responses of species diversity to a moisture gradient. In contrast to Host and Pregitzer (1992), however, Bratton determined that overstory and herbaceous understory strata responded to this gradient in a manner that was neither linear nor parallel between strata.

Sagers and Lyon (1997) found that species associations in riparian forests of the Buffalo National River, Arkansas, were strongly influenced by gradients of pH and elevation. They concluded that forest strata largely responded to these gradients independently. They referred to this independent response as “incongruence” and suggested several possible reasons for its occurrence, including (1) environmental gradients appearing continuous at the landscape scale may be discontinuous at the local scale, and (2) each forest stratum may respond to a disturbance (in this case, largely flooding of riparian zones) in ways distinct from other strata (Lyon and Sagers 1998).

One of the more compelling arguments against the existence of linkage among forest strata was presented by McCune and Antos (1981). They reviewed earlier work in Europe (e.g., Lippmaa 1939) and North America (e.g., Cain 1936) that rejected the notion of linkage and instead urged a “synusial approach” to studying forest communities—taking a view that each stratum of a forest comprises a community (synusia) to be considered a distinct unit of vegetation (Oosting 1956). More important, McCune and Antos (1981) tested for linkage among five strata in forest stands of Swan Valley, Montana, using correlation of dissimilarity matrices, Bray-Curtis polar ordination, and cluster analysis. The different strata changed in composition across environ-

mental gradients neither at the same rate nor in the same pattern (McCune and Antos 1981). They further concluded that apparent linkages, when found, can be artifacts of diversity across large sample areas. By sampling over large areas, it might be possible to encounter, for example, a conifer stand with its associated herbaceous component and a hardwood stand with its contrasting associated herbaceous component. Ordination of such data would produce two discontinuous clusters of plots and might lead to a spurious conclusion that the herbaceous and overstory components are closely linked.

Thus, part of the debate over the existence of linkage among forest strata appears to have arisen from studies that have addressed the question at different spatial scales. Those working at the landscape scale (e.g., McCune and Antos 1981) have not found linkage to occur. We suggest that linkage is a phenomenon that does indeed occur in forest ecosystems but that linkage operates at spatial scales smaller than the landscape.

Linkage may arise in two ways: (1) from similarities among strata in response to the same environmental factors (e.g., Gagnon and Bradfield 1986; Hermy 1988; Roberts and Christensen 1988, Host and Pregitzer 1992) or (2) from direct and reciprocating influences of the overstory and the understory on each other. The second mechanism has been documented for many forest types at fine spatial scales (e.g., 1-m² plots) as the influence of individual canopy trees on herbaceous layer species (Everett et al. 1983; Turner and Franz 1986; Joyce and Baker 1987; Tyler 1989; Nemati and Goetz 1995; Berger and Puettmann 2000; Hill and Silander 2001) via various mechanisms including changes in soil acidity and fertility, light availability, or physical effects of litter under canopy trees.

A Mechanism for Linkage Between Forest Strata

It is notable that the reciprocating effects between overstory and herbaceous layer suggested in studies such as Maguire and Forman (1983) and Gilliam et al. (1995) occurred in mature forests. However, up through the thinning phase of secondary forest succession (chapter 9, this volume), the overstory and herb strata respond to different sets of environmental factors. Overstory composition at this time in succession is governed largely by competition for light (described by Bormann and Likens [1979] as the exploitive strategy), whereas herb layer growth and composition is determined largely by availability of moisture and nutrients (Gilliam and Turrill 1993, Morris et al. 1993; Wilson and Shure 1993). As the stand approaches steady state, the overstory becomes dominated by shade-tolerant species that were able to survive beneath the initial canopy of intolerant species. The new canopy is more closed and stratified and alters light conditions for herb layer species (chapter 3, this volume; Brown and Parker 1994). Seedlings and sprouts of woody species often increase (relative to herbaceous species) in the herb layer

because of more light-limited conditions (Wilson and Shure 1993; Gilliam et al. 1995; Walters and Reich 1997). Woody species also exhibit greater relative abundance at this time because of an increase in the number of juveniles from late successional overstory species that are typically prolific seed producers. The result of successional change, then, is that the two strata start responding to similar environmental gradients, establishing and intensifying the linkage between overstory and herbaceous layer (Gilliam et al. 1995). This leads us to pose the following hypothesis as a mechanism of linkage between forest strata: Linkage among forest strata arises from parallel responses of strata to similar environmental gradients.

One of the challenges of testing such a mechanism is establishing the appropriate environmental gradients to which species may be responding. Direct gradient techniques are possible by stratifying sampling along a known gradient, such as elevation in a forested watershed (Barbour et al. 1999). This, however, has the limitation of presuming that the chosen gradient (e.g., elevation) is indeed an overriding factor influencing both species composition and gradients of other important environmental factors (e.g., moisture and soil nutrients). Indirect gradient techniques are also possible, wherein a multivariate method, such as detrended correspondence analysis (DCA), is used to generate ordination axis scores for plots. Axis scores then are correlated to environmental variables measured at each plot (McCarthy et al. 1987; Roberts and Christensen 1988; Gilliam et al. 1993; Sagers and Lyon 1997). This has the obvious limitation of presuming that ordination axis scores and environmental variables are related in an inherently linear fashion.

Palmer (1993) assessed the advantages of yet another multivariate analytical approach, canonical correspondence analysis (CCA) (ter Braak 1986). In addition to pointing out the numerous improvements of CCA over DCA, Palmer (1993) showed that the output from CCA contains an important feature that is germane to testing our gradient-based hypothesis of linkage. Because CCA performs a least-squares regression of plot scores (species' weighted averages) as dependent variables onto environmental variables as independent variables, CCA is a form of direct gradient analysis (Palmer 1993). In addition to generating ordination diagrams with plot and species locations, CCA also generates environmental vectors originating from the center of the ordination space. The lengths of these vectors represent the gradient lengths of each measured environmental variable, such that vector length is proportional to the importance of an environmental gradient in explaining species' patterns. Thus, shorter lines represent gradients of lesser importance, longer lines represent gradients of more importance. Accordingly, whether the herbaceous layer and overstory are responding to environmental gradients in a similar fashion may be assessed by performing CCA on each stratum separately for a given stand age and then comparing vector lengths of herb layer versus overstory on a gradient-by-gradient basis.

Using such an approach, we examined two data sets for evidence of whether herbaceous and overstory layers respond to similar gradients. The data sets are each from a different site and study: the Fernow Experimental Forest in Tucker County, West Virginia, and the University of Michigan Biological Station in northern lower Michigan. Because these were carried out as unrelated studies, they were not done using identical sampling methods. Nonetheless, the important environmental gradients thought to control species distributions were quantified as appropriate in each study, including stand structural variables, as well as soil nutrient and moisture variables.

Study Sites

Fernow Experimental Forest

The Fernow Experimental Forest (FEF), an approximately 1900 ha area of largely montane hardwood forests in the Allegheny Mountain section of the unglaciated Allegheny Plateau, is located in Tucker County, north-central West Virginia. Mean annual precipitation is approximately 1430 mm, with most precipitation occurring during the growing season (Gilliam and Adams 1996a). Four contiguous watersheds were selected for this study: WS7 and WS3 were about 20 year-old, even-aged stands that developed following clearcutting (hereafter “young” stands); WS13 and WS4 were uneven-aged stands (>80 years old, hereafter “mature” stands).

Study watersheds at FEF support primarily mixed hardwood stands, with dominant trees varying with stand age. Early-successional species, such as *Betula lenta* L., *Prunus serotina*, and *Liriodendron tulipifera* L. are dominant in young stands, whereas late-successional species, such as *Acer saccharum* Marshall and *Quercus rubra* L., are dominant in mature stands (table 8.1). Dominant herbaceous layer species vary less with stand age and include *Laportea canadensis* (L.) Wedd., *Viola* spp., and several ferns, including *Dryopteris marginalis* L. Gray and *Polystichum acrostichoides* Michx. Schott. (table 8.2).

Soils are similar among study watersheds. These are relatively thin (<1 m in depth), acidic, sandy-loam Inceptisols of two series: Berks (loamy-skeletal, mixed, mesic Typic Dystrochrept) and Calvin (loamy-skeletal, mixed, mesic Typic Dystrochrept) (Gilliam et al. 1994). Soils of the study watersheds are generally acidic, but are high in organic matter, resulting in high cation exchange capacity (table 8.3).

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The study was conducted within a five-county (Cheboygan, Emmet, Charlevoix, Otsego, Montmorency) region of northern lower Michigan. Climatic conditions are relatively uniform throughout the area, with an average an-

Table 8.1. Important overstory (live woody stems ≥ 2.5 cm diameter at 1.3 m height) species of young versus mature stands of Fernow Experimental Forest, West Virginia

Species	Stand age class ^a	
	Young	Mature
<i>Acer pensylvanicum</i> L.	5	5
<i>A. saccharum</i>	33	90
<i>Betula lenta</i>	19	—
<i>Fagus grandifolia</i>	5	14
<i>Fraxinus americana</i>	10	2
<i>Liriodendron tulipifera</i>	16	5
<i>Prunus serotina</i>	76	20
<i>Quercus prinus</i> L.	—	12
<i>Q. rubra</i>	7	30
<i>Robinia pseudoacacia</i> L.	6	—
<i>Sassafras albidum</i> (Nutt.) Nees.	6	—

Data are mean importance values (sum of relative basal area and relative density) for two watersheds per age class. Nomenclature follows Gleason and Cronquist (1991).

^aYoung = 20 years; mature > 80 years.

Table 8.2. Important herbaceous layer (vascular plants ≤ 1 m tall) species of young versus mature stands of Fernow Experimental Forest, West Virginia

Species	Stand age class ^a	
	Young	Mature
<i>Acer pensylvanicum</i> L.	7	17
<i>Dryopteris marginalis</i>	30	6
<i>Laportea canadensis</i>	17	27
<i>Polygonatum biflorum</i> (Walter) Elliot	—	10
<i>Polystichum acrostichoides</i>	9	15
<i>Prunus serotina</i>	9	5
<i>Rubus</i> spp.	12	4
<i>Sassafras albidum</i> (Nutt.) Nees	8	—
<i>Smilax rotundifolia</i> L.	14	9
<i>Viola</i> spp.	20	20

Data are mean importance values (sum of relative cover and relative frequency) for two watersheds per age class. Nomenclature follows Gleason and Cronquist (1991).

^aYoung = 20 years; mature > 80 years.

nual precipitation of 770 mm and an average annual temperature of 6.2–6.7°C. Precipitation is distributed relatively evenly throughout the year (Albert et al. 1986).

Soils of the study area are Spodosols derived from parent materials of contrasting glacial origin. Study sites encompass a broader range of soil conditions than FEF, from dry-mesic sites with soils of the Rubicon series (sandy, mixed, frigid Entic Haplorthods), derived from glacial outwash deposits, to mesic soils of the Montcalm series (sandy, mixed, frigid Alfic Haplorthods), derived from glacial till (Roberts and Richardson 1985; Roberts and Christensen 1988). In general, these soils are acidic and low in organic matter, with extractable nutrients supplied largely from organic constituents (table 8.3).

The presettlement forests within the region were predominantly northern hardwoods such as *Fagus grandifolia* and *A. saccharum* on mesic sites and

Table 8.3. Means of environmental variables used in canonical correspondence analysis of young versus mature stands at Fernow Experimental Forest (FEF), West Virginia, and University of Michigan Biological Station (UMBS)

Variable	FEF ^a Stand age class		UMBS ^a Stand age class	
	Young	Mature	Young	Mature
Elevation (range in m)	725–860	735–870		
Tree basal area (m ² /ha)	22.5	42.8*	10.8	22.8*
Tree density (stems/ha)	2099	854*		
Texture (%)	67.3	65.7		
Sand				
Clay	10.8	9.0		
Silt	22.0	25.4		
Bulk density (g/cm ³) ^b			1.06	1.13*
WAI (%) ^c			2.62	2.93
Organic matter (%)	13.8	12.6	5.1	3.8*
Cation exchange capacity (μmol _c /g)	45.5	40.1		
pH	4.39	4.32	5.04	4.58*
Nutrients (μg/g)				
NO ₃	1.3	0.9		
NH ₄	2.1	1.9		
PO ₄	0.8	0.4	6.0	4.3
Ca	12.6	6.4	826	496
Mg	2.1	2.4	60.8	41.0
K	2.3	2.2	54.3	33.4*

Means of all measured variables, except for elevation, are compared between stand age classes with a *t*-test. Data summarized from previous studies at FEF (Gilliam 2002) and UMBS (Roberts and Gilliam 1995b).

^aYoung = 20 years (FEF), 1–20 years (UMBS); Mature >80 years (FEF), 55–167 years (UMBS).

^bDisturbed.

^cWater availability index (water content by weight between –0.033 MPa and –1.5 MPa moisture potential).

*Significant difference between age classes for a given variable at *p* < .05; others are nonsignificant at *p* < .05.

Table 8.4. Important overstory (live woody stems ≥ 2.5 cm diameter at 1.3 m height) species of young versus mature stands of University of Michigan Biological Station

Species	Stand age class ^a	
	Young	Mature
<i>Acer pensylvanicum</i>	—	4
<i>A. rubrum</i>	26	46
<i>A. saccharum</i>	10	33
<i>Amelanchier</i> spp.	6	—
<i>Fagus grandifolia</i>	—	10
<i>Fraxinus americana</i>	—	6
<i>Ostrya virginiana</i>	—	4
<i>Pinus resinosa</i>	—	6
<i>P. strobus</i>	—	5
<i>Populus grandidentata</i>	60	40
<i>P. tremuloides</i>	—	21
<i>Quercus rubra</i>	6	15

Data are mean importance values (sum of relative basal area and relative density) for 25 (young age class) and 36 (mature age class) stands. Nomenclature follows Gleason and Cronquist (1991).

^aYoung = 1–20 years; mature = 55–167 years.

coniferous species including *Pinus resinosa* Aiton, *P. strobus* L., and *Tsuga canadensis* (L.) Carriere on the dry-mesic sites (Kilburn 1957). From 1850 to 1920, extensive logging of the pine and hardwood forests occurred, followed by wildfires (Gates 1930; Kilburn 1957). Thus, the mature stands (55–167 years-old) in the present study are second-growth stands that originated from cutting and burning. The young stands (≤ 20 years old) originated from clearcutting (without burning) of these mature, second-growth stands.

In our sample, *Populus grandidentata* Michx. had the highest importance value for trees in young stands, in contrast to mature stands where *Acer rubrum* L. and *A. saccharum* shared dominance with *P. grandidentata*. Mature stands contained a greater variety of secondary species than young stands, including *Fagus grandifolia*, *Quercus rubra*, *Fraxinus americana* L., *Pinus strobus*, and *P. resinosa* (table 8.4).

Herbaceous layer dominants in young stands included several early successional species, such as *Pteridium aquilinum* (L.) Kuhn, *Rubus ideaus* L., *R. allegheniensis* T.C. Porter, and *Fragaria virginiana* Duchesne (table 8.5). Dominant species in the herb layer in mature stands included seedlings of shade-tolerant to mid-tolerant tree species, such as *A. saccharum*, *Fagus grandifolia*, *Ostrya virginiana* (Miller) K. Koch, *Fraxinus americana*, and shade-tolerant herbaceous species, such as *Maianthemum canadense* Desf.

Table 8.5. Important herbaceous layer (vascular plants ≤ 1 m tall) species of young versus mature stands of University of Michigan Biological Station

Species	Stand age class ^a	
	Young	Mature
<i>Pteridium aquilinum</i>	43	9
<i>Acer saccharum</i>	13	45
<i>Rubus ideaus</i>	10	—
<i>Fragaria virginiana</i>	9	—
<i>Rubus allegheniensis</i>	8	—
<i>Fraxinus americana</i>	7	12
<i>A. rubrum</i>	6	14
<i>Ostrya virginiana</i>	5	15
<i>Maianthemum canadense</i>	3	20
<i>Fagus grandifolia</i>	1	15

Data are mean importance values (sum of relative cover and relative frequency). Nomenclature follows Gleason and Cronquist (1991).

^aYoung = 1–20 years; mature = 55–167 years.

Field Sampling

Fernow Experimental Forest

Fifteen circular 0.04-ha sample plots were established in each watershed. In each plot, all woody stems ≥ 2.5 cm diameter at about 1.3 m in height (dbh) were tallied, identified, and measured for diameter at breast height to the nearest 0.1 cm. The herbaceous layer was sampled by identifying and estimating cover of all vascular plants ≤ 1 m in height within ten 1-m² circular subplots in each sample plot, using a visual estimation method as described in Gilliam and Turrill (1993). Subplots were located within sample plots using a stratified-random polar coordinates method (Gaiser 1951).

Methods for sampling mineral soil also have been described previously (Gilliam and Turrill 1993, Gilliam et al. 1994). Briefly, two 10-cm deep samples were taken from each plot and placed into separate bags; thus, values for each plot represent the average of two soil samples. Each sample was sieved (2-mm screen), air-dried, and analyzed for pH (1:1 weight:volume, soil:water), 1 N KCl-extractable calcium, potassium, magnesium, and phosphorous (with plasma emission), 1 N KCl-extractable NO₃ and NH₄ (with flow-injection colorimetry), and organic matter (loss-on-ignition method). Particle size (texture) was determined for each soil sample using the hydrometer method.

University of Michigan Biological Station

Data were taken from 0.1-ha (20×50 m) plots, one plot located in each of 61 stands. Stands were selected that were at least 0.5 ha and were relatively undisturbed since the last disturbance. A single plot was located near the center of each stand in an area that was representative of the stand composition and soil conditions. In each plot, trees (woody stems ≥ 1 m tall) were sampled as described in Roberts and Christensen (1988). Importance values for tree species (IVT) were calculated as relative density + relative basal area. Percent cover of species in the herbaceous layer (all vascular plants < 1 m in height) was visually estimated in twenty-five 0.5×2.0 m contiguous quadrats extending along the plot center line. Percent cover and frequency (proportion of quadrats in a plot in which a given species was found) were combined to generate importance values for herb layer species (IVH; relative cover + relative frequency). Species that occurred within the 0.1-ha plot but not sampled in the 0.5×2.0 m quadrats were assigned an IVH of 0.001.

Four replicate soil samples were taken from the A1 horizons, one sample from a soil pit adjacent to each plot and the other three at random points along the plot center line. Soil variables (see below) were calculated as mean values ($n = 4$) for each plot. Details of sample preparation and laboratory analysis can be found in Roberts and Christensen (1988). Briefly, after drying and sieving (2-mm screen), soil samples were analyzed for bulk density, water availability (% moisture content, by weight, between -0.033 and -1.5 MPa moisture potential), pH (1:1 soil: H_2O , glass electrode), and organic carbon. After extraction with a dilute acid solution (0.05 M HCl with 0.0125 M H_2SO_4), extractable PO_4 was determined by molybdenum blue colorimetry and extractable calcium, potassium, and magnesium were determined by atomic absorption spectrophotometry.

Data Analysis

Fernow Experimental Forest

Data for overstory and herbaceous layer species have been reported previously for each watershed separately (Gilliam et al. 1995). Because of minor differences between the two watersheds of each stand age and because of the focus of this paper on stand age-related comparisons, we combined data into two stand age classes: young (~ 20 years, even age) and mature (> 90 years, mixed age). Stand age means of environmental variables were subjected to t tests between the two age classes.

Gradient lengths of the environmental variables shown in table 8.3 were determined for the herbaceous and overstory strata separately in each age class using CCA. CCA was performed with the computer program CANOCO version 3.10 (ter Braak 1990), a version of the Cornell Ecology program

DECORANA (Hill 1979, ter Braak 1987); all program defaults were used. Unlike DCA, CCA focuses on the relationships between plant species and measured environmental variables; thus, it provides direct interpretation of axes in the ordination (ter Braak 1986). All data were ln-transformed before ordination, according to suggestions of Palmer (1993).

Of importance in this chapter is CCA output in the form of trajectories of environmental gradients. CCA yields one trajectory for each environmental factor, the length of which is indicative of the importance of that environmental gradient in explaining species' patterns. We determined gradient lengths for all environmental factors by measuring the length of the lines in the trajectory figure. The focus of this paper is on the relative importance, as measured by vector length, of environmental factors in influencing species' patterns in young and mature stands. Gradient lengths for herbaceous layer versus overstory ordinations were subjected to Spearman rank correlation for each stand age class (Zar 1996).

University of Michigan Biological Station

Site-dependent changes in soil nutrients and vegetation in these plots have been described elsewhere (Roberts and Gilliam 1995a, Roberts and Christensen 1988). The dry-mesic and mesic sites sampled in this study represent the typical variation in site conditions and vegetation composition found in upland forests of the region; thus, we combined stands from both site types for this analysis. Stands were then subdivided into two age classes: Young (1–20 years, 25 stands) or mature (55–167 years, 38 stands). These age classes correspond roughly to those used at FEF, although there is clearly a wider range of ages within each of the two age classes at UMBS than at FEF.

Data from UMBS were subjected to CCA, using the same defaults and ln-transformations as used at FEF. The *t* test (PROC TTEST; SAS Institute Inc. 1985) was used for comparisons of stand and soil variables between stand ages. Gradient lengths of the environmental variables from the herbaceous layer and overstory were measured in a manner identical to that used at FEF.

Stand Age Comparisons of Environmental Variables Used in CCA

Fernow Experimental Forest

The two stand structural variables measured at FEF (tree basal area and stem density) varied significantly ($p < .05$) with stand age (table 8.3). Basal area for the mature stands was nearly twice that of the basal area for the young stands. Conversely, stem density for the young stands was nearly 2.5 times that for the mature stands. Such differences are typical of young versus

mature forests: numerous, small stems early in succession followed by competitive thinning, which gives rise to fewer, but much larger, stems later in succession (Yoda et al. 1963; Christensen and Peet 1984). The other environmental data used in CCA for FEF were soil variables, including texture, organic matter, cation exchange capacity (CEC), pH, and extractable (exchangeable) nutrients, none of which varied significantly ($p < .05$) with stand age (table 8.3), confirming conclusions of earlier studies that general soil characteristics varied little across watersheds of sharply contrasting stand ages and histories (Gilliam 2002).

University of Michigan Biological Station

Although overstory basal area was lower at UMBS than at FEF, stand-age contrasts were similar among the two study sites. Basal area of the mature stands was just more than twice that of the young stands at UMBS (table 8.3), consistent with the successional thinning process that has been described for this forest type (Roberts and Richardson 1985). In contrast to the results of stand-age comparisons for FEF, several soil variables varied significantly with stand age at UMBS. In general, soils of mature stands were more acidic and less fertile than young stands, with soil fertility being largely a function of soil organic matter, which was significantly lower ($p < .05$) in mature stands than in young stands (table 8.3).

Canonical Correspondence Analysis of Vegetation Data

Individual CCA ordinations were run for both of the vegetation strata (herb layer and overstory) in both stand ages (young and mature) separately, resulting in four ordinations for each site. Original ordination figures (i.e., X-Y graphs of axis 1 by axis 2 scores for sample plots) for these analyses are not given; rather, the axis scores were used to make correlations between strata. In all cases, axis 1 explained the greatest amount of variability in species data; thus, axis 1 scores were used in comparisons between strata. The correlation diagrams produced give a measure of the similarities in the ordering of plots along the first axis in the herbaceous and overstory vegetation ordinations.

Fernow Experimental Forest

Correlations between overstory and herbaceous layer varied with stand age at FEF. The correlation for young stands was not significant at ($p < .05$), whereas that for mature stands was highly significant ($p < .001$; fig. 8.1). Accordingly, we conclude that, although the two strata are not linked in the young stands, they are linked in the mature stands.

Another way of viewing this conceptually is to consider the proximity of

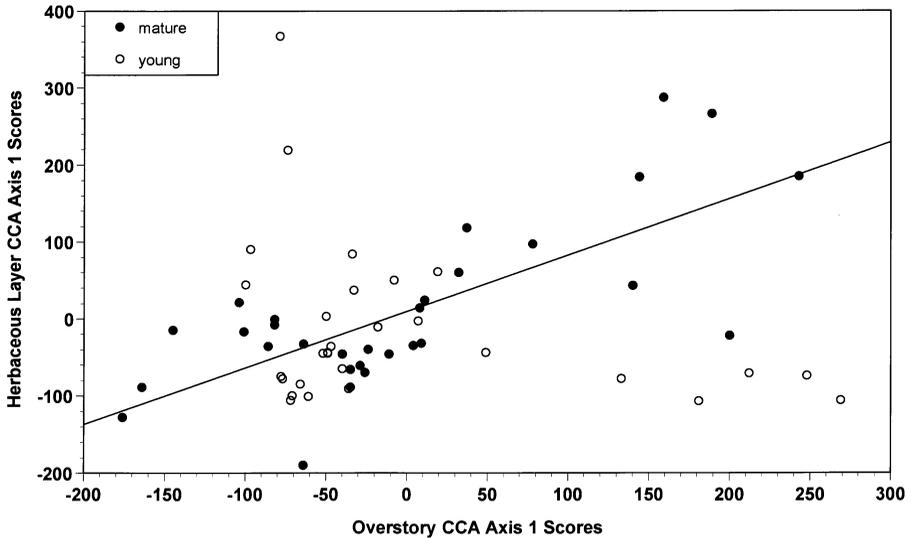


Figure 8.1. Correlation between overstory and herbaceous layer species composition of young stands (open symbols) and mature stands (filled symbols) for Fernow Experimental Forest, West Virginia. Overstory is represented on the X-axis as axis 1 scores from canonical correspondence analysis (CCA) of overstory species data. Herbaceous layer is represented on the Y-axis as axis 1 scores from CCA of herbaceous layer species data. Correlation for young stand plots was not significant ($p < .05$). The line shown is for mature stand plots only ($y = 9.51 + 0.73x$; $r^2 = .54$; $p < .001$).

points in the ordination diagrams. Points that are close to each other in ordination space represent sample plots that have similar species composition; conversely, points distant from each other represent plots that are dissimilar. Thus, a significant correlation between axis 1 scores from each stratum should indicate close similarity in the pattern and degree of spatial variation of species composition (sometimes referred to as *species turnover*) of the two strata. Once again, this degree of linkage appears to be related to stand age at FEF.

University of Michigan Biological Station

In contrast to results for FEF, overstory/herb layer correlations were highly significant ($p < .0001$) for both young and mature stands at UMBS (fig. 8.2). In fact, regression lines calculated to fit the data are nearly coincidental, with slopes of 0.85 and 0.88 for young and mature stands, respectively. Accordingly, we may conclude that the two strata are linked in these successional aspen forests, but that this occurs in a way that is independent of stand age (or certainly less dependent) than was found in stands at FEF.

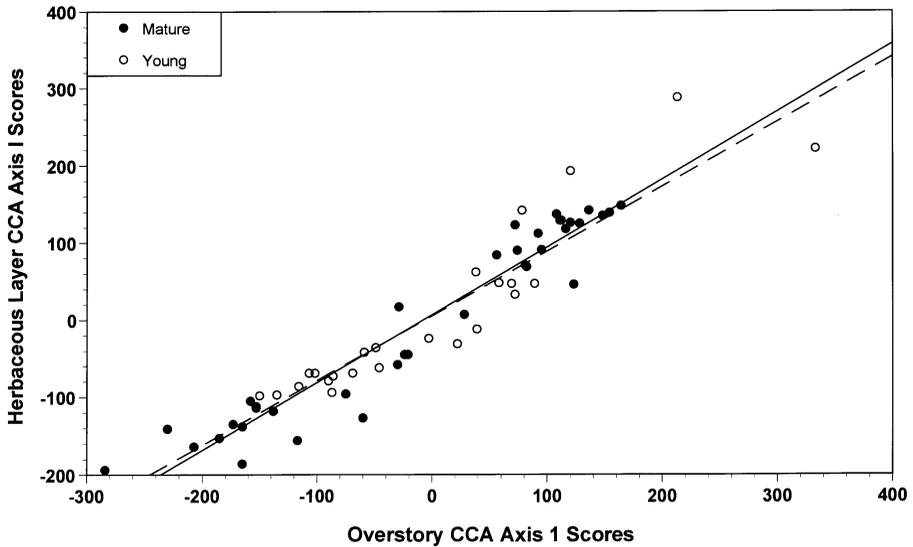


Figure 8.2. Correlation between overstory and herbaceous layer species composition of young stands (open symbols) and mature stands (filled symbols) for University of Michigan Biological Station. Overstory is represented on the X-axis as axis 1 scores from CCA of overstory species data. Herbaceous layer is represented on the y-axis as axis 1 scores from canonical correspondence analysis (CCA) of herbaceous layer species data. Solid line represents mature stands ($y = 7.02 + 0.88x$; $r^2 = .93$; $p < .001$). Dashed line represents young stands ($y = 5.21 + 0.85x$; $r^2 = .86$; $p < .001$).

Environmental Trajectories

As discussed previously, CCA output presents environmental data in the form of trajectories or vectors, one per environmental variable, the length of which is proportional to the importance of that factor (variable) in explaining species' patterns. Each line, along with the arrow, indicates the positive direction of the vector (i.e., increasing values).

CCA ordinations for this part of our discussion (e.g., figs. 8.3–8.10) are presented with vectors only (i.e., without the plot data discussed previously) because (1) the result is an ordination diagram with less clutter, and (2) the environmental trajectories are of primary importance in testing the mechanistic hypothesis for linkage of forest strata. Finally, because these are true vectors (ter Braak 1987, 1990; Palmer 1993), the direction of each line (originating from the center of ordination space) is also important in interpreting the meaning of CCA ordinations. Accordingly, vectors that point in similar directions represent environmental factors that are closely related to each other.

Fernow Experimental Forest

Some of the more important environmental factors for the overstory in young stands at FEF were elevation, stand density, and extractable NO_3 (which was of equal importance with sand content and extractable PO_4); some of the less important factors were cation exchange capacity and extractable calcium and magnesium (fig. 8.3). In addition, elevation and extractable NO_3 were closely related, along with soil organic matter (OM). This suggests that extractable NO_3 and soil OM increase with elevation in a way that is significant in influencing tree species' patterns in young stands. Furthermore, it links OM with the production of NO_3 in the soil, a relationship that has been demonstrated for this site using in situ incubations (Gilliam et al. 1996, 2001).

Environmental trajectories for the herb layer in young stands appeared to contrast sharply with those for the overstory in young stands, especially for extractable PO_4 (fig. 8.4). The most important environmental factors were, in descending order, extractable NO_3 , soil OM, and extractable potassium, whereas the least important were, in ascending order, extractable PO_4 , pH, and extractable NH_4 (fig. 8.4). The relative importance of both extractable NO_3 and potassium (and lack of importance of extractable NH_4) for the herb layer in young stands supports conclusions of Gilliam et al. (1996) that NO_3 is the predominant form of nitrogen taken up by plants of the herb layer at

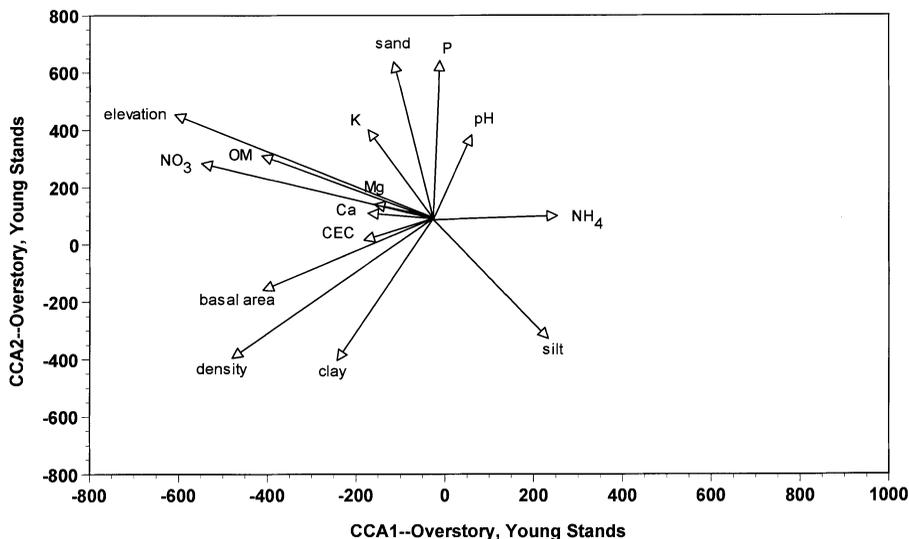


Figure 8.3. Environmental trajectories for the overstory of young stands for Fernow Experimental Forest, West Virginia, resulting from canonical correspondence analysis (CCA). The length of each line is proportional to the importance of the associated environmental factor in explaining species' patterns among sample plots within stands. CEC, cation exchange capacity; OM, organic matter.

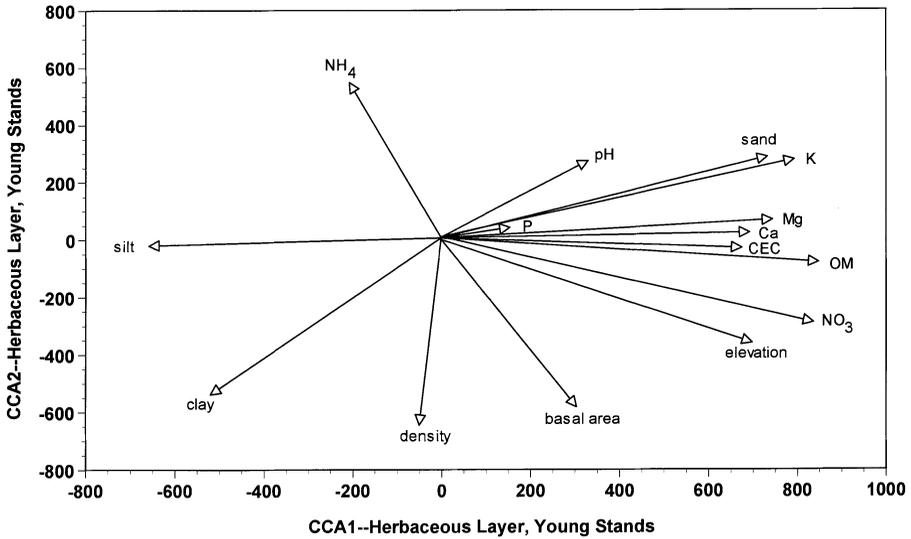


Figure 8.4. Environmental trajectories for the herbaceous layer of young stands for Fernow Experimental Forest, West Virginia, resulting from canonical correspondence analysis (CCA). The length of each line is proportional to the importance of the associated environmental factor in explaining species patterns among sample plots within stands. CEC, cation exchange capacity; OM, organic matter.

FEF and that NO_3 is taken up with potassium from these soils. This also confirms findings of numerous studies demonstrating the close correlation between nitrogen uptake and potassium availability (Barber 1995; Marschner 1995).

Environmental factors of importance for the overstory of mature stands differed somewhat from those for the overstory of young stands, suggesting a temporal (successional) shift in responses of tree species to variables such as soil resource availability. In descending order, the more important factors were stand density, soil clay content, soil OM, silt content, and extractable calcium, whereas the less important factors, in ascending order, were CEC, sand content, stand basal area, and extractable magnesium (fig. 8.5).

In contrast to comparisons of overstory versus herb layer for young stands, environmental vectors for the herb layer in mature stands appeared to be quite similar to those for the overstory in mature stands (fig. 8.6). The important factors were, in descending order, extractable NO_3 , clay, stand density, and the unimportant factors were, in ascending order, CEC, stand basal area, sand, and extractable magnesium. In short, the two strata in mature stands showed considerable overlap for environmental factors that were both important and unimportant in explaining species' patterns. Finally, patterns of correlation among environmental variables were similar between strata for mature stands, in contrast to those between strata for young stands. For

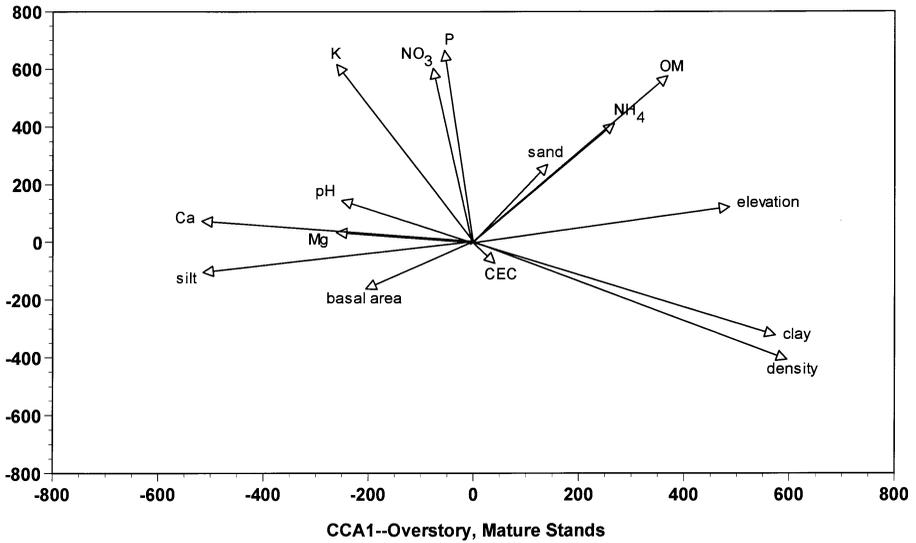


Figure 8.5. Environmental trajectories for the overstory of mature stands for Fernow Experimental Forest, West Virginia, resulting from canonical correspondence analysis (CCA). The length of each line is proportional to the importance of the associated environmental factor in explaining species patterns among sample plots within stands. CEC, cation exchange capacity; OM, organic matter.

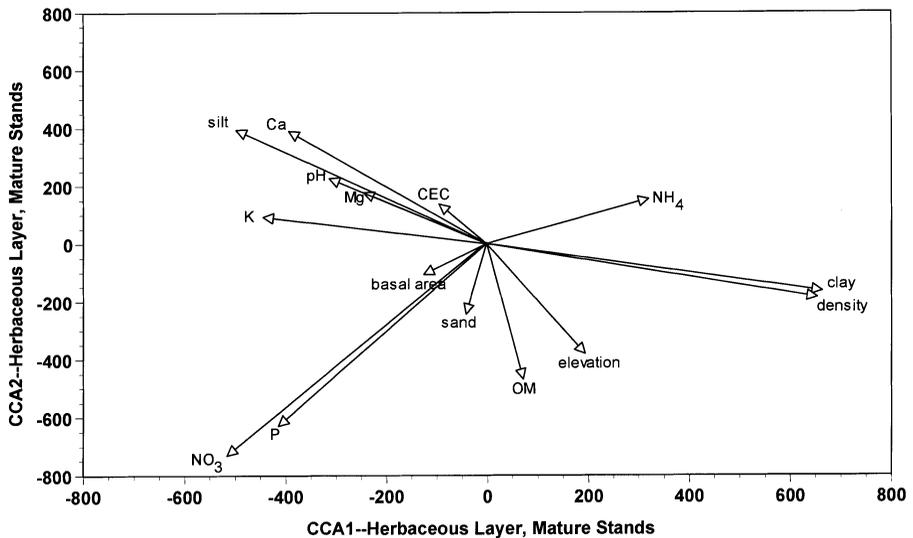


Figure 8.6. Environmental trajectories for the herbaceous layer of young stands for Fernow Experimental Forest, West Virginia, resulting from canonical correspondence analysis (CCA). The length of each line is proportional to the importance of the associated environmental factor in explaining species patterns among sample plots within stands. CEC, cation exchange capacity; OM, organic matter.

example, vectors for clay content and stand density showed close overlap, as did extractable NO_3 and phosphorus, for both strata in mature stands (figs. 8.5 and 8.6). Few such similarities were found in young stands (figs. 8.3 and 8.4).

University of Michigan Biological Station

The more important environmental factors for the overstory in young stands at UMBS were soil pH and extractable soil calcium, with less important factors being extractable soil potassium and tree basal area (fig. 8.7). In fact, pH and calcium were closely related, each with vectors essentially superimposed on one another, indicating that soil pH is determined in large part by levels of calcium in these soils. Also highly correlated were water availability index and OM, suggesting that OM is important in determining water availability in these coarse-textured, well-drained sandy soils.

Similar to the results for the overstory in young stands at UMBS, the more important environmental factors for the herb layer in young stands were pH and calcium, whereas soil potassium was of lesser importance; however, unlike the overstory, PO_4 was of equally high importance as calcium for the herb layer, and soil bulk density was the least important of all environmental variables (fig. 8.8). Thus, early in succession in these aspen stands, spatial

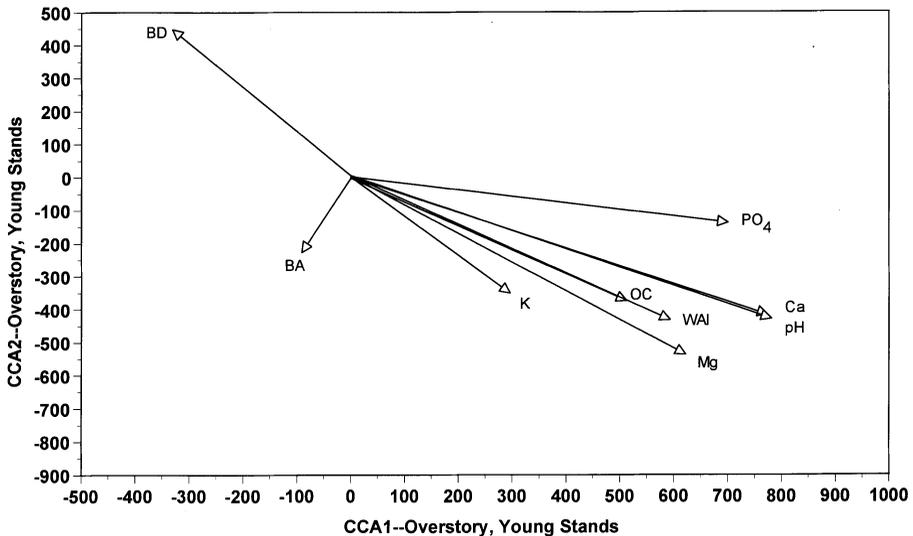


Figure 8.7. Environmental trajectories for the overstory of young stands for University of Michigan Biological Station, resulting from canonical correspondence analysis (CCA). The length of each line is proportional to the importance of the associated environmental factor in explaining species patterns among sample plots within stands. BA, basal area; BD, bulk density; OC, organic carbon; WAI, water availability index.

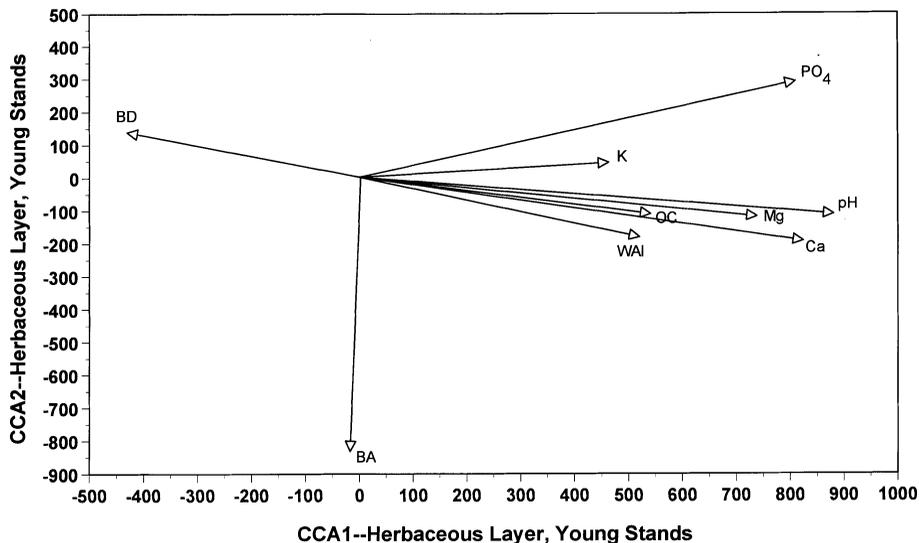


Figure 8.8. Environmental trajectories for the herbaceous layer of young stands for University of Michigan Biological Station, resulting from canonical correspondence analysis (CCA). The length of each line is proportional to the importance of the associated environmental factor in explaining species patterns among sample plots within stands. BA, basal area; BD, bulk density; OC, organic carbon; WAI, water availability index.

patterns of soil pH, as influenced by soil calcium, appears to exert a pronounced influence on the spatial patterns of composition of both overstory and herb layer species.

Soil calcium was by far the dominant environmental factor influencing species composition of the overstory in mature stands at UMBS, with extractable PO_4 and magnesium of secondary importance (fig. 8.9). Of minor importance were tree basal area and soil potassium, similar to results found for the overstory of young stands (fig. 8.7). As described previously (see "Study Sites"), these soils are generally acidic and low in fertility and OM, with available nutrients supplied largely from organic constituents, which is seen in the close coincidence of the OM vector with vectors of all extractable nutrients except potassium (fig. 8.9).

Finally, the more important environmental factors for the herb layer in mature stands at UMBS were soil calcium and magnesium, with extractable soil potassium and tree basal area being of minor importance (fig. 8.10), similar to the results found for the overstory of mature stands. In addition, the clustering of OM along with extractable nutrients (other than potassium) for the herb layer in mature stands was similar to that for the overstory in mature stands (fig. 8.9).

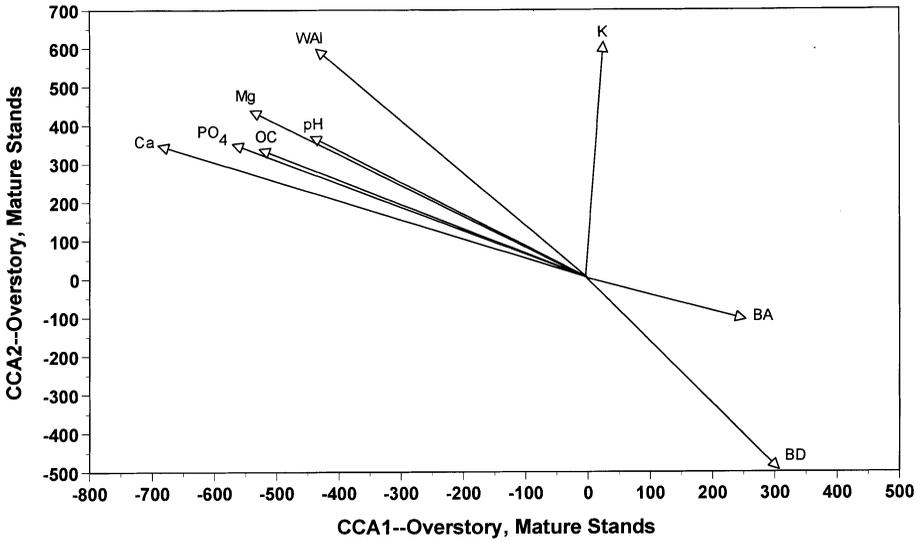


Figure 8.9. Environmental trajectories for the overstory of mature stands for University of Michigan Biological Station, resulting from canonical correspondence analysis (CCA). The length of each line is proportional to the importance of the associated environmental factor in explaining species patterns among sample plots within stands. BA, basal area; BD, bulk density; OC, organic carbon; WAI, water availability index.

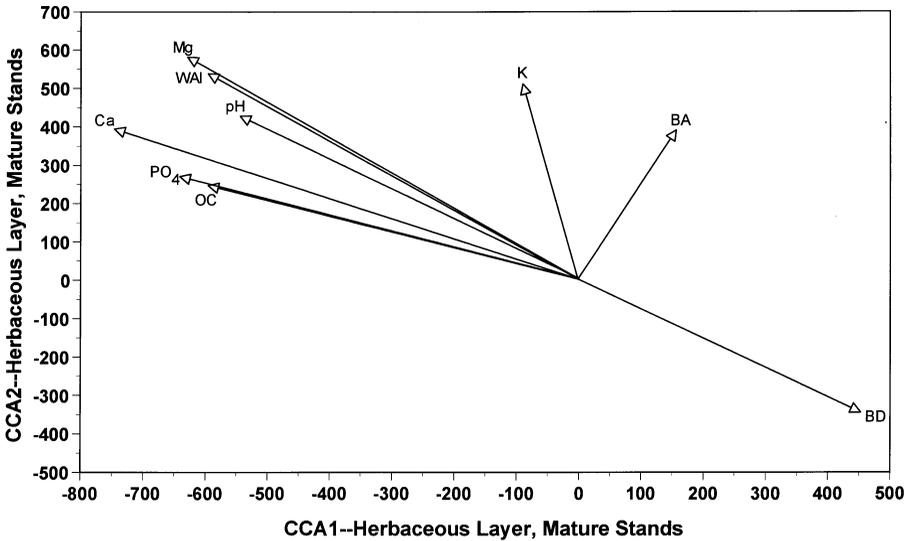


Figure 8.10. Environmental trajectories for the herbaceous layer of young stands for University of Michigan Biological Station, resulting from canonical correspondence analysis (CCA). The length of each line is proportional to the importance of the associated environmental factor in explaining species patterns among sample plots within stands. BA, basal area; BD, bulk density; OC, organic carbon; WAI, water availability index.

Correlations Between Strata

The preceding discussion essentially has been a visual inspection of environmental vector lengths to determine a gradient of importance of specific factors in explaining species patterns for each strata and stand-age combination. Quantitative evidence relevant to our mechanistic explanation of linkage can be provided by statistically determining whether the herbaceous layer and overstory are responding to environmental gradients in a parallel fashion. As described earlier in this chapter, because CCA performs a least-squares regression of species-based plot scores as dependent variables onto environmental factors as independent variables (Palmer 1993), it provides a direct quantitative assessment of these responses.

Accordingly, we can examine the evidence by comparing the rank order of environmental variables (from the most to the least important as determined by vector length) of herb layer versus overstory. Significant correlations in vector lengths between the herb layer and overstory would indicate that the two strata are responding to the same environmental factors to a similar degree. Consequently, considering our previous conclusions about stand-age-related linkage at FEF (i.e., strata are not linked early in succession, but become linked later in succession), our mechanistic explanation would be supported only if rank-order correlation is not significant for young stands at FEF but is significant for mature stands. Regarding UMBS, our explanation would be supported only if rank-order correlation is significant for both stand-age classes.

Fernow Experimental Forest

The herb layer–overstory correlation for young stands was not significant ($r = .02$, $p < .95$). In contrast, it was highly significant ($r = .92$, $p < .001$) for mature stands (table 8.6). Such stand-age-related contrasts in these comparisons support our hypothesis of linkage between forest strata. For FEF there appears to be a temporal (successional) shift in the degree of linkage. The lack of significant correlation between environmental vector lengths for herb layer and overstory in young stands indicates that the lack of linkage shown in figure 8.1 is the result of differences in response of these strata to environmental gradients at this point in successional time. The overstory appeared to respond to elevation and stand density, whereas the herb layer responded to factors related to soil fertility, such as soil OM and extractable NO_3 and potassium. Such results for the herb layer are consistent with conclusions of Gilliam and Turrill (1993) at FEF and those of other studies (e.g., Morris et al. 1993; Wilson and Shure 1993) that herb layer development early in forest succession is influenced strongly by competition for soil nutrients.

The significant correlation between environmental vector lengths for herb layer and overstory in mature stands indicates that the high degree of linkage shown in figure 8.1 is the result of the similar responses of these strata to

Table 8.6. Spearman rank correlation coefficients for importance of environmental factors for the herbaceous layer versus overstory of young and mature stands at Fernow Experimental Forest (FEF), West Virginia, and University of Michigan Biological Station (UMBS).

Site	Age class ^a	<i>r</i>	<i>p</i>
FEF	Young	0.02	.95
FEF	Mature	0.92	.001
UMBS	Young	0.90	.01
UMBS	Mature	0.97	.0001

Importance was measured as length of environmental vector for canonical correspondence analysis of each stratum and stand age for the two study sites.

^aYoung = 20 years (FEF), 1–20 years (UMBS); Mature >80 years (FEF), 55–167 years (UMBS).

environmental gradients, including factors related to stand characteristics, such as stand density, and to soil conditions, such as texture and nutrient availability. This supports conclusions of the herb layer study by Gilliam and Turrill (1993) at FEF that herb layer development may become more influenced by stand characteristics in later stages of forest succession.

University of Michigan Biological Station

In contrast to results for FEF, the correlation of herb layer versus overstory vector length for UMBS was highly significant for young stands ($r = .90$, $p < .01$); this correlation was even more significant ($r = .97$, $p < .0001$) for mature stands (table 8.6). As with results for FEF, these results for UMBS support our hypothesis that linkage arises from parallel responses of vegetation strata to environmental factors. Although it is not immediately clear why the two forest types contrasted with respect to stand-age-related changes in linkage, we suspect that it may be related to (1) the distinctness of the ecology of aspen-dominated successional stands of northern lower Michigan compared to the mixed-dominance of central Appalachian hardwood stands, and (2) a greater degree of soil heterogeneity at UMBS relative to FEF. That is, although soils of forest stands studied at UMBS are all Spodosols, they are derived from parent materials of widely varying glacial origin, including glacial outwash deposits (coarse-textured, sandy materials) and glacial till (mixtures of sand, silt, and clay). As we noted previously, there is a tendency to conclude that linkage occurs in studies that include a broader range of environments and β diversity. Thus, at UMBS, even the young stands showed linkage (although weaker than the mature stands). To adequately test the influence of diversity on linkage would require running ordinations of the

total data set, along with ordinations of each site class separately. Our data sets were not large enough to allow this type of analysis.

Soil calcium is clearly an overriding environmental variable determining spatial patterns of species composition of both the herbaceous layer and the overstory in both young and mature stands at UMBS. Although additional factors, such as pH or soil OM, vary in importance among strata and stand ages, calcium is consistently the factor of greatest importance. In this region, calcareous substrates (indicated by high calcium concentrations) are associated with clay lenses or clay till within or underlying the sandy outwash surface deposits (Spurr and Zumberge 1956; Roberts and Christensen 1988). Van Breemen et al. (1997) found significant correlation between soil calcium and overstory species composition in southern New England forests. Thus, soil calcium may serve as an indicator for a suite of co-related soil nutrient and moisture variables at UMBS.

Summary

We have provided evidence that supports our mechanistic explanation of linkage in forest communities. Linkage among forest strata appears to arise from similarities among strata of forest vegetation in the responses of their respective species to environmental gradients. In central Appalachian hardwood stands of West Virginia, these responses may change through secondary forest succession and thus may be a function of stand age. Early in succession, spatial variation in species composition of the overstory appears largely related to the density of the stand, whereas variation in herb composition is related more to soil fertility. This changes later in succession when variation in herb composition responds more to stand structure (i.e., tree density), a time when overstory variability is also related to density.

In successional aspen forests of northern lower Michigan, where correlations between strata were significant for both young and mature stands, these responses may be much less related to stand age. The degree to which linkage between strata is the result of higher β diversity in the Michigan sample is not clear. We believe, however, that it is not an artifact of simply sampling across two extremes of environmental conditions (see McCune and Antos 1981), given the continuum of points along axis 1 for both vegetation strata, as depicted in figure 8.2.

Although the concept of linkage among vegetation strata of forest communities likely will continue to be debated among vegetation scientists, we believe that it is a concept with a high degree of importance and application. It furthers our understanding of and appreciation for the complexities underlying the structure and function of forest ecosystems (e.g., responses to disturbance [chapters 11 and 13, this volume] and mechanisms of secondary succession [chapter 9, this volume]). It may also be applied toward landscape-level investigations of forest cover types and remote sensing.

The generality and utility of this explanation, however, will only be seen

after it is tested in a more formal and structured way. We invite further testing of this mechanism as a predictive hypothesis in other forest types and over a wider range of stand ages. Studies that examine linkage across different breadths of β diversity and spatial scales would be particularly useful. Given the widespread popularity and use of CCA among vegetation scientists (Barbour et al. 1999), this might be done with reasonable ease.