

## 6

# The Herbaceous Layer of Eastern Old-Growth Deciduous Forests

Brian C. McCarthy

The study of old-growth forests has long been a fascination of plant ecologists. In all likelihood this was an outgrowth of the Clementsian view of succession (Clements 1936; Weaver and Clements 1938) in which communities were perceived to change in an orderly and predictable way and culminate in a terminal climax community (chapter 10, this volume). Throughout much of eastern North America, old-growth forests were the epitome of the climax community (Braun 1950; Whitney 1987). Old-growth forests have been of continued interest in the study of plant ecology in large part because they are generally free of the myriad of disturbances caused by humans, thereby allowing the study of natural processes. This unique quality has generated an enormous research database on many aspects of eastern old-growth forests (Nowacki and Trianosky 1993). Due to the massive disturbances associated with European settlement, the landscape in eastern North America underwent enormous change (M. Williams 1989; Whitney 1994; Irland 1999). Lumbering, agriculture, grazing, and anthropogenic wildfires all altered the landscape such that now most deciduous old-growth forest exists only as small relicts. More recently, some have argued that no forest in eastern North America is free of anthropogenic disturbance (direct or indirect). There is certainly a need to better understand the ecology of human-dominated ecosystems (Vitousek et al. 1997; Grimm et al. 2000); however, natural systems will always be needed to serve as the controls or benchmarks in such studies.

The Clementsian concept of succession and the notion of a terminal old-growth climax have now been largely disputed, few ecologists currently accept this as a viable concept (McIntosh 1985), although the notion continued to be propagated in the biological literature throughout the early 1980s and

remains in some introductory ecology textbooks. Likewise, few, if any, communities exhibit an orderly and predictable pattern of development, and communities rarely if ever achieve a stable equilibrium due to natural disturbances (White 1979). Concomitant with changing ideas about community succession, ecosystem ecology began to flourish and generated a renewed interest in old-growth forest ecosystems (Franklin et al. 1972). These ecosystems provided considerable information about ecosystem development. Moreover, they provided permanent benchmarks in the landscape that could be used to evaluate management and conservation activities.

Faced with the recognition of an emerging biodiversity crisis in the 1980s, there was a large, albeit uncoordinated, effort instituted throughout the eastern United States to develop criteria for the identification of old-growth forests, to find these relicts in the landscape, and establish some form of preservation for their continued survival and study (e.g., T. L. Smith 1989). Forest managers were becoming increasingly aware of the need to manage forests for multiple reasons, including biological diversity. This period led to a focus on the characteristics of old-growth forest and what made them different from second-growth forests. Oddly, it was not until the early 1990s, with the controversial work of Duffy and Meier (1992), that we began to gain a heightened concern regarding the effects of forest management activities on the forest herb layer. In spite of its shortcomings (chapter 14, this volume), this landmark contribution spurred an interest in community-level understanding of the herb layer, which had before then been largely population based. The relative lack of attention to the herb layer relative to the overstory is curious given that it is the layer of greatest diversity in most hardwood forests throughout eastern North America (Braun 1950).

My focus in this chapter is fourfold: (1) to clarify the factors that constitute old-growth forests in most mesic eastern deciduous forests, (2) to describe what we know about composition, structure, and diversity of the herb layer in old-growth forests, (3) to evaluate the differences between old-growth and second-growth forests with respect to the herb layer, and (4) to assess the linkages among stability, diversity, and habitat invasibility. Although the herb layer contains both woody and herbaceous species (chapter 1, this volume), I restrict my focus to the herbaceous component only.

### The Nature of Eastern Mesic Old-Growth Forests

Before European settlement, forest vegetation of eastern North America could hardly be considered free from anthropogenic disturbance (Denevan 1992). Native Americans have been clearing hardwood forests since at least the last ice age (at least 10,000 years; Dickens 1976). However, Native American settlement appears to have been largely restricted to floodplain areas, and the long-term effects are questionable (M. Williams 1989). Evidence of the influence of Native Americans on the upland vegetation of the eastern de-

wise, few, if any, com-  
development, and com-  
due to natural distur-  
ances about community  
generated a renewed  
al. 1972). These eco-  
cosystem development.  
the landscape that could  
activities.

ity crisis in the 1980s,  
d throughout the east-  
n of old-growth forests,  
e form of preservation  
h 1989). Forest man-  
to manage forests for  
period led to a focus on  
them different from  
early 1990s, with the  
we began to gain a  
agement activities on  
pter 14, this volume),  
community-level under-  
en largely population  
ative to the overstory  
ity in most hardwood  
0).

factors that constitute  
rests, (2) to describe  
sity of the herb layer  
ween old-growth and  
and (4) to assess the  
y. Although the herb  
pter 1, this volume),

North America could  
ce (Denevan 1992).  
ince at least the last  
er, Native American  
oodplain areas, and  
89). Evidence of the  
n of the eastern de-

ciduous forest, particularly with respect to fire, is conflicting (Day 1953; Russell 1983; Patterson and Sassaman 1988). Observations suggest that Native Americans did clear some portion of the uplands for various purposes using a slash (girdle) and burn technique that the early European settlers subsequently adopted. Regardless, the influence of Native Americans in the uplands pales in comparison to the subsequent land clearing and land conversion associated with European settlement. Early descriptions of presettlement eastern hardwood forest from the late 1700s and early 1800s suggest a composition and structure very different from today's forests (Walker 1983). Many forests were cleared by Europeans for grazing pasture or crop agriculture. Catastrophic fire frequently followed logging activities. Today, large parts of the land base are being converted for development. As a result, there is a paucity of primary hardwood forest left in eastern North America. Those stands that continue to exist today were preserved by a family lineage, were not easily accessible to loggers, or were the result of surveying errors (Auten 1941; McCarthy 1995). Recent concerns regarding the biodiversity crisis have pointed to old-growth forests as potential reservoirs of genetic material and possible rare species reserves. Moreover, old-growth forests as an ecosystem are generally considered endangered in much of the eastern landscape.

Whitney (1987), Hunter (1989), Parker (1989), Martin (1992), and McCarthy (1995) all provide technical definitions and descriptions of old-growth hardwood forest in the eastern United States. A simple definition is difficult, if not impossible, to employ. Different authors have adopted different criteria for designation. Some use a functional definition associated with stand dynamics (e.g., Oliver and Larson 1996). Others use a historical criterion such as lack of evidence of direct human impact (i.e., logging; Duffy and Meier 1992). Martin (1992) and others have designated a suite of structural criteria for mesic forests. These criteria relate to species identity, structure, coarse woody debris, and forest floor characteristics, among other characteristics. Keddy and Drummond (1996) espouse this criteria-based approach and provide a summary of features that should be monitored, and potentially managed for, in eastern deciduous forests.

Although all approaches have their merits, I strongly endorse the use of specific, quantifiable criteria in old-growth designations to reduce unproductive semantic debates. For example, Martin (1992) argues that mesic forests should contain most of the following attributes in order to be considered old-growth: a moderate to high richness and diversity (*S* and *H*, respectively) of tree species ( $S > 20$ ;  $H' > 3.0$ ); uneven ages with a wide distribution of size and age classes (reverse J distribution); some large ( $> 75\text{cm dbh}$ ) canopy tree species; some large, high quality merchantable trees (i.e., of high economic importance suggesting no logging or high-grading); some trees older than 200 years; overstory density  $> 250$  trees/ha (for stems  $> 10\text{ cm dbh}$ ); overstory basal area  $> 25.0\text{ m}^2/\text{ha}$ ; strong presence of coarse woody debris (logs and snags) in multiple age and decay classes; tree-fall gaps from wind-thrown along with pit-and-mound topography; plants and animals that prefer

or reach their optimum in old-growth; undisturbed soils with a thick organic layer and presence of soil macropores; and little or no evidence of human disturbance (e.g., stumps, skid trails, wire fencing, cultivated plants, foundations).

Although an abundant and diverse spring herbaceous flora is one of the hallmarks of temperate deciduous forests, this feature has not been widely used in the old-growth designation debate. Keddy and Drummond (1996) make specific recommendations regarding spring ephemerals (*sensu* Givnish 1987) of mature deciduous forest (table 6.1). They note that, given the variability in herb communities associated with latitude and environment, it would be inappropriate to use the presence of specific indicator species for the designation of high-quality old-growth forests. But a number (richness) of indicator species from the local spring ephemeral guild may be useful in assessing stand quality (table 6.1):  $\geq 6$  for high quality (old-growth), 2–5 for intermediate, < 2 for poor (Keddy and Drummond 1996). Although this approach seems useful, additional studies are necessary to include a broader subset of vegetation types (beyond *Fagus-Acer*) and guilds (functional groups) in the herbaceous flora (i.e., summer species). Moreover, simple observation in the central Appalachians indicates that six of these ephemeral species are present in even the most degraded second-growth deciduous forests of the region (McCarthy pers. obs.).

Table 6.1. Spring ephemerals from seven old-growth forests, predominantly *Fagus-Acer*, located throughout the Kentucky, Ohio, Pennsylvania, and Michigan region

Species	Locale					
	KY	PA	OH	OH	OH	MI
<i>Allium tricoccum</i>			*	*	*	
<i>Caulophyllum thalictroides</i>	*	*		*		*
<i>Claytonia virginica</i>	*		*	*	*	*
<i>Dentaria diphylla</i>	*	*		*		
<i>Dentaria laciniata</i>	*		*		*	*
<i>Dicentra canadensis</i>			*	*	*	*
<i>Dicentra cucullaria</i>			*		*	
<i>Erythronium americanum</i>	*			*		*
<i>Maianthemum canadense</i>						*
<i>Podophyllum peltatum</i>	*		*	*	*	
<i>Polygonatum biflorum</i>	*	*	*	*	*	
<i>Sanguinaria canadensis</i>	*		*		*	
<i>Tiarella cordifolia</i>	*	*		*		
<i>Trillium grandiflorum</i>	*	*	*	*		*
Total number of species	10	5	9	11	8	7

Six species have been proposed as a minimum target number in this functional group to indicate the old-growth condition or quality. Presence or absence of an individual species is probably unimportant. From Keddy and Drummond (1996). Nomenclature follows Gleason and Cronquist (1991).

## Composition, Struc-

Beyond simple de- (Brewer 1980; Da- 1958), the compo- layer of mesic old- in the early 1980s torically ignored important oversto (as the ones prese and forest structu to understand the Historic views of understories shou succession would equilibrium. How (Brewer 1980; Da- ies of spatial pattoral and spatial attracting attention though these not Small and McCa in species-rich for magnitude, thus

Brewer (1980) herb community Woods) in southw (i.e., dense cover creased and some changes were not to changes in over than 150 years l being observed growth developm this time includ giniana L., Lapor Polygonatum pub slow-growing pe throw to be a m

Davison and F of forest herb co and shrub dyna HMF) in central understory layer They hypothesiz They found that 1969 and 26 in

### Composition, Structure, and Dynamics of the Herb Layer

Beyond simple descriptions of vegetation (e.g., Oosting 1942; Wistendahl 1958), the composition, structure, and dynamics of species in the herbaceous layer of mesic old-growth forests only began to receive significant attention in the early 1980s. Most foresters, land managers, and ecologists have historically ignored the understory layer in favor of the more economically important overstory. Indeed, most definitions and characteristics of old growth (as the ones presented here) are rooted primarily in tree species composition and forest structure or disturbance characteristics. There is an important need to understand the factors affecting herb layer dynamics in old-growth forests. Historic views of succession (i.e., climax concept) would suggest that forest understories should be largely stable over long periods. Modern views of succession would suggest that the understory is quite dynamic and not in equilibrium. However, long-term temporal studies of the herb layer are few (Brewer 1980; Davison and Forman 1982), as are geographically broad studies of spatial pattern (Rogers 1981, 1982). The relationships between temporal and spatial pattern (scale) in forest herb communities is only recently attracting attention (McCarthy et al. 2001; Small and McCarthy 2002), even though these notions have been around in ecology for some time. In fact, Small and McCarthy (2002) suggest that previous studies of the herb layer in species-rich forests may have been undersampled by at least an order of magnitude, thus making inference about pattern weak.

Brewer (1980) provided one of the first long-term (50 year) studies of herb community dynamics in an old-growth *Fagus-Acer* stand (Warren Woods) in southern Michigan. Warren Woods was found to have a luxuriant (i.e., dense cover) but a relatively species-poor herb layer. Some species decreased and some increased over the study period. Brewer concluded that changes were not related to exogenous factors (e.g., climate) but rather related to changes in overstory dynamics stemming from a major disturbance more than 150 years before (believed to be a catastrophic fire). Indeed, what was being observed were long-term successional changes associated with old-growth development. Species with the greatest increase (> 200%) during this time included *Asarum canadense* L., *Boehmeria cylindrical* L., *Epifagus virginiana* L., *Laportea Canadensis* L., *Osmorhiza claytoni* (Michx.) C. B. Clarke, *Polygonatum pubescens* (Willd.) Pursh., and *Viola* species, many of which are slow-growing perennials and tolerant of deep shade. He did not find wind-thrown to be a major influence with respect to diversity.

Davison and Forman (1982) also provided one of the few long-term studies of forest herb community dynamics. They conducted a 30-year study of herb and shrub dynamics in an old-growth oak forest (Hutcheson Memorial Forest; HMF) in central New Jersey. Their goal was to evaluate the stability of the understory layer over the 30 years and assess patterns of community change. They hypothesized that a stable climax forest should have a stable understory. They found that the herb layer declined from 33 species in 1950 to 24 in 1969 and 26 in 1979. Moreover, cover increased dramatically from 8% to

h a thick organic  
idence of human  
ted plants, foun-

ora is one of the  
not been widely  
ummond (1996)  
ls (sensu Givnish  
that, given the  
l environment, it  
cator species for  
umber (richness)  
ay be useful in  
old-growth), 2–5  
). Although this  
clude a broader  
nctional groups)  
le observation  
eral species are  
us forests of the

minantly *Fagus*-  
Michigan region

OH	MI
*	*
*	*
*	*
*	*
*	*
*	*
*	*
*	*
*	*
*	*
*	*
8	7

p to indicate the old-  
important. From Keddy

60%. *Podophyllum peltatum* L. increased in cover by 700%; *Circaeа quadrifolia* L. by 500%. The sharp increase in the former species was a partial explanation for the decrease in diversity. *Podophyllum* has a strong clonal nature and can displace other species. In addition, *Lonicera japonica* Thunb., an introduced vine, increased substantially and was believed to negatively influence the native species diversity. Davison and Forman also noted that a long period of fire suppression might have influenced the observed species composition. Increasing canopy gaps were believed to influence the understory by increasing light and moisture conditions.

McCarthy et al. (2001) established a long-term study of forest herb dynamics in an old-growth mesophytic forest dominated by white oak in southeastern Ohio (Dysart Woods; DW). Dysart Woods is comparable to HMF (Davison and Forman 1982) in many ways, including history, composition, structure, diversity, and natural disturbance regimes. Perhaps most important, DW is also experiencing a decline of white oak in the overstory. Many of the DW oaks are in excess of 85 cm dbh and 400 years of age (Rubino and McCarthy 2000) and are in a disease decline spiral (Manion 1991) associated with multiple predisposing and inciting agents (e.g., acidic deposition, drought stress, *Armillaria* root rot). This will likely result in dramatic long-term changes in the understory, but these patterns will only be revealed in the context of long-term permanent plot-type ecosystem data where both biological and environmental components are examined.

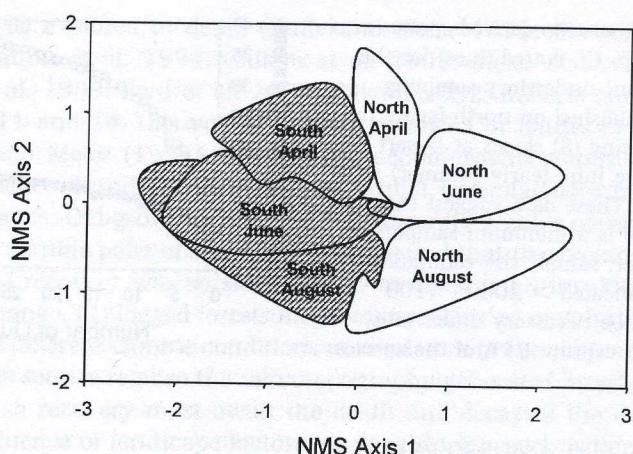
Within-year variability in the herb community is familiar to everyone who has worked in the eastern deciduous forest. McCarthy et al. (2001) provided a quantitative example of these short-term temporal (phenological) differences and local spatial differences. The vegetation varied dramatically among early spring, early summer, and late summer samples. Certainly, this would be expected between the vernal herbs and the summer species, but the differences between the two summer samplings were somewhat unexpected. Curiously, the phenological differences within seasons have only been rarely quantified in old-growth stands (Goebel et al. 1999). Most studies (e.g., McCarthy and Bailey 1996; Olivero and Hix 1998) use only a single sample period in midsummer and may not be representative. Further, McCarthy et al. (2001) also discovered a dramatic topographical aspect effect. Highly dissected topographies, like those found in much of the central Appalachians, may have dramatically different floras on north-and south-facing slopes (fig. 6.1). The interplay between spatial and temporal dynamics at various scales remains largely unexplored.

Rogers (1981, 1982) evaluated the understory layer of old-growth forests throughout Ohio, Indiana, Michigan, Wisconsin, and Minnesota. He noted that there had been few studies of the herb layer that were both quantitative and geographically extensive. He found that soil fertility, not climate, was the most important difference in explaining regional patterns of spring ephemerals. Within stands, soil drainage and microtopography had the most important influence on vernal herb diversity and abundance (higher on soil mounds than pits). Species with large perennial organs tended to be uncom-

Figure 6.1. A nonmetric multidimensional scaling (NMS) ordination plot used to sample the herbaceous layer in a 1-ha area of a mesophytic forest in southeastern Ohio. The plot shows the distribution of species in two sample plots (DW and HMF) for 33.0% and 24.0% of the area, respectively, on north- and south-facing slopes. The vertical axis is labeled "NMS Axis 2" and ranges from -2 to 2. The horizontal axis is unlabeled and ranges from 0 to 100. The plot shows distinct separation between the two sample plots along the NMS Axis 2.

mon in forests to rare in the summer herbaceous layer (present in  $\geq 33\%$  of the area unevenly, 15% to be both uncommon and generalizations made for future studies should be based on community data).

Interest in understanding the spatial patterns of diversity to certain environmental factors (Olivero and Hix 1998). However, the methods of assessing, interpreting, and generalizing these patterns of diversity and abundance are not well developed. An objective evaluation of the methods used to assess diversity and abundance requires the development of unbiased estimators of diversity and abundance, and the relationship between diversity and abundance (Small and McCarthy 1996). The relationship between diversity and abundance is often complex, involving factors such as species richness, evenness, and abundance (Hayek and Ballesteros 1998; van Belle and van der Valk 1998).

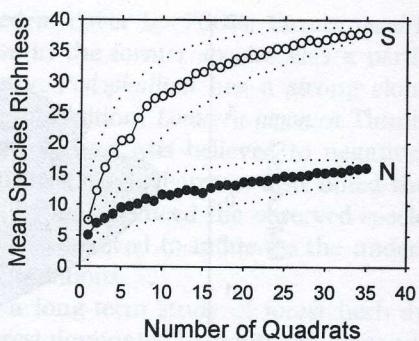


**Figure 6.1.** A nonmetric multidimensional scaling (NMS) ordination of 2-m<sup>2</sup> quadrats used to sample the herbaceous vegetation of Dysart Woods, an old-growth mesophytic forest in southeastern Ohio ( $n = 210$ ). The first two NMS ordination axes account for 33.0% and 24.1% of the variability, respectively. Axis I separates quadrats on the north-facing slope from those on the south-facing slope. Axis II is a temporal gradient separating spring, early summer, and late summer floras. Individual points are omitted for visual clarity; isopleths are drawn to encompass all sample points.

mon in forests that were relatively recently disturbed (Rogers 1982). Among the summer herbs, Rogers (1981) found 23% to be widespread and common (present in  $\geq 30\%$  of stands), another 23% to be common but distributed unevenly, 15% uncommon but widely distributed, and the remaining 40% to be both uncommon and highly restricted. This suggests that species-specific generalizations will be difficult or impossible to make and that current and future studies should focus on life-history types or guilds in analyzing community data.

Interest in spatial and temporal variation has returned the concept of diversity to center stage in understory ecological research (Wilson et al. 1998). However, few studies have explored the relationship of scale to patterns of understory diversity in eastern deciduous forests. In fact, the method of assessing, interpreting, and reporting understory diversity is less than clear. An objective evaluation of impending parameters is critical because many estimators of diversity are very sensitive to sample size, area measured, species rarity, grain of the environment, and so on. We recently explored the relationship between micro- (2 m<sup>2</sup>) and mesoscale (70 m<sup>2</sup>) herb diversity in DW (Small and McCarthy, 2002). We examined standard estimators of richness, evenness, and diversity, as well as species area curves, and more recent techniques such as SHE (richness [S], diversity [H], and evenness [E]) analysis (Hayek and Buzas 1997, 1998) and species richness estimators (E. P. Smith and van Belle 1984; Palmer 1990; Colwell and Coddington 1994; Chazdon

**Figure 6.2.** Bootstrap-derived species area curves ( $\pm 95\%$  CI, dotted lines) for the thirty-five 2-m $^2$  understory sampling quadrats established on north-facing (N) and south-facing (S) slopes at Dysart Woods for the June (early summer) sampling period. These data suggest that 70-m $^2$  (35 plots) is a minimum sampling area; however, sample size estimation equations indicated > 200-m $^2$  (100 plots) would be necessary under most conditions to capture 95% of the species.



et al. 1998). Although scale clearly had an effect on the reporting and interpretation of diversity, we found the species area curves and species richness estimators to be the most enlightening (fig. 6.2). We sampled thirty-five 2-m<sup>2</sup> plots on one northeast- and one southwest-facing slope—a relatively large sample compared to most studies. Each plot was sampled three times during the growing season to assess phenological variability (fig. 6.1). Based on the diversity patterns in this oak-dominated mesophytic old-growth forest and bootstrapped 95% confidence intervals around our estimators, we determined our sampling to be inadequate in this species rich stratum. In fact, sample size estimation equations suggest that 100–300 2-m<sup>2</sup> quadrats are necessary to describe and estimate species richness within any one stand. This sampling intensity is dramatically higher than anything published in the literature. This suggests that previous studies of the herb layer in temperate hardwood forests need to be reconsidered. The likelihood that representative samples were obtained is low, and the strength of inference is potentially quite weak.

## Old-Growth Versus Second-Growth Herb Layer Dynamics

In the absence of anthropogenic disturbance, the factors that affect herb distribution and abundance are numerous and include topographic and soil features such as elevation, aspect, soil quality (Bratton 1976; Elliott et al. 1997), overstory composition (Hicks 1980), stand structure attributes such as basal area and cover (Ford et al. 2000), herbivory (Alverson et al. 1988; van Deelen et al. 1996; Brown and Parker 1997; Rooney and Dress 1997a), and timing or size of gap disturbance (Collins and Pickett 1987; Clebsch and Busing 1989; Reader and Bricker 1992a). The relationship between disturbance, particularly anthropogenic disturbance in the form of logging, and herb community structure is still not well understood and has only recently

begun to be examined in 1993; Bratton & Goebel et al. 1994; see chapters 11 and 12).

Duffy and M  
90 years since  
growth stands.  
density in all m  
include (1) rec  
observe change  
because of differ  
herbaceous spe  
dynamics so re

The influence of an important environmental variable that examine the growth of eastern Ohio. However, and the other hypothesis, differences in basal area growth stands covered an intermediate range, interfered between them. The two did not differ on the same side of the exact opposite range. The diversity were measured on the northeast-facing slopes. Gholz et al. (1999) compared second-growth and old-growth stands up to two stands in each slope aspect in both spring and fall. Hix (1998), Gholz et al. (1999), and in old-growth woodlands.

From an experimental perspective, Olibe et al. (1999) found that the effect of Hix (1998) was significant in one way or another (Olibe 1984). Olibe et al. (1999) also found that only eight of the 10 studies they reviewed were replicated at least once. The remaining two studies were replicated at least twice. The results of the 10 studies were considered to be consistent with the hypothesis of primary vs. secondary effects within any one study. In addition, Olibe et al. (1999) found that the communities in the studies were not necessarily maintaining a modern

begun to be explored in detail (Duffy and Meier 1992; Gilliam and Turrill 1993; Bratton et al. 1994, Gilliam et al. 1995; Meier et al. 1995, 1996; Goebel et al. 1999; Ford et al. 2000; Gilliam 2002; Roberts and Zhu 2002; chapters 11 and 14, this volume; others reviewed in Battles et al. 2001).

Duffy and Meier (1992) argued that second-growth stands approaching 90 years since disturbance still did not exhibit a similar flora to paired old-growth stands. Old-growth stands had significantly greater cover and species density in all nine pairs of stands. They suggested that the explanations could include (1) recovery was so slow that 87 years was an insufficient time to observe change, (2) logged forests may never recover to match primary forest because of different climate conditions now relative to the past, and (3) many herbaceous species require the microtopography generated by pit-and-mound dynamics so recovery must await the death and decay of the overstory.

The influence of landscape factors, such as slope aspect, is known to have an important effect on vegetation (Wolfe et al. 1949), yet the few studies that examine this component are not in agreement. Olivero and Hix (1998) examined the ground flora in second-growth and old-growth stands in southeastern Ohio. Half the plots were located on mesic, northeast-facing slopes and the other half on dry, southwest-facing slopes. First, they found significant differences in both of the main effects (i.e., between old-growth and second-growth stands and between mesic and dry stands). However, they also discovered an interactive effect in that species richness and Hill's diversity differed between old-growth and second-growth on northeast-facing plots but did not differ on southwest-facing plots. McCarthy et al. (2001) found the exact opposite pattern within DW. In this old-growth forest, all measures of diversity were greater on the southwest-facing slope compared to the northeast-facing slope (but abundance was greater on the latter). Goebel et al. (1999) conducted another study comparing an old-growth forest and second-growth forest in southeastern Ohio; however, they restricted the study to two stands in each study area on southwest-facing slopes only, but sampled both spring and summer vegetation. In contrast to the study of Olivero and Hix (1998), Goebel et al. did find differences in southwest-facing slope floras in old-growth versus second-growth forests.

From an experimental design standpoint, all of the previous studies (Olivero and Hix 1998; Goebel et al. 1999; McCarthy et al. 2001) are problematic in one way or another, particularly in the context of pseudoreplication (Hurlbert 1984). Olivero and Hix (1998) sampled only once in midsummer and then only eight 2-m<sup>2</sup> plots were sampled in each of 32 study areas. Goebel et al. (1999) sampled both the spring and summer herb vegetation but pseudoreplicated at the forest level so they had only one replicate treatment (primary vs. secondary) and then only a relatively small sampling effort within any one time period. Based on data from Small and McCarthy (in press), considerably more sampling is required to describe within-stand herb communities in a species-rich forests. McCarthy et al. (2001), while maintaining a moderate within-stand sample size to explore phenological patterns,

pseudoreplicated at the stand level and thus had only one of each of the representative slope aspects in the one forest. In all likelihood, the limitations of time, money, and energy impinge on the scale of any one study. Investigators need to draw boundaries within the limits of their questions and available resources. The necessity to sample large numbers of plots multiple times within one season is very resource intensive, particularly when the flora is so phenologically dynamic that complete species turnover can occur within weeks. Clearly, many more studies are needed over a larger geographical area for longer periods of time before we can begin to draw conclusions or conduct informative meta-analyses.

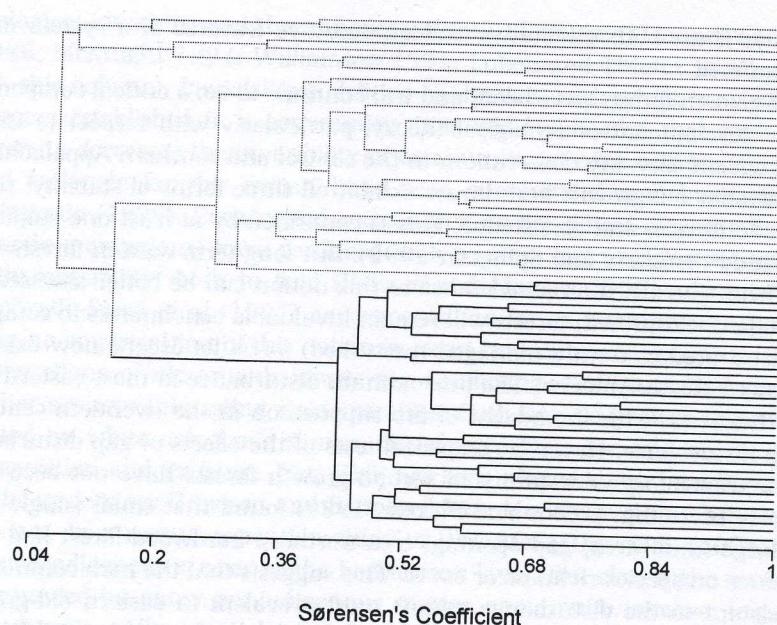
Several studies have now used successional chronosequences examining understory diversity recovery after major disturbances such as logging (Gilliam et al. 1995; Ford et al. 2000). Using this approach, neither Gilliam et al. (1995) nor Ford et al. (2000) was able to demonstrate any clear pattern in herb diversity with respect to stand age. These results could suggest that clearcutting mature second-growth stands does not significantly impact understory herb diversity. However, as Duffy and Meier (1992) and Meier et al. (1995) point out, several centuries may be required to develop the characteristics associated with old-growth outlined previously in this chapter. Thus, there may be a long time between stand maturity after clearcutting (75–100 years) and the old-growth condition (300–400 years) whereby herb community structure returns to its primary condition (chapters 11 and 14, this volume).

After disturbance, community composition and structure will be initially directed largely by propagule dispersal. Spatial properties such as patch isolation (landscape connectivity) and microenvironment (chapter 14, this volume) along with temporal factors such as seed banks, will be important determinants in the rates of recolonization. Unfortunately, most of the old-growth forest patches in the eastern deciduous forest exist in a nonforest matrix. For example, both DW in Ohio and HMF in New Jersey are surrounded by agriculture and/or suburban development. Without connectivity, disturbed forests will be slow to regenerate the previous community structure. Unfortunately, studies of temperate old-growth forest seed banks are uncommon. In contrast to general successional patterns found in the seedbank literature (e.g., Roberts and Vankat 1991), Leckie et al. (2000) found that weedy aliens of adjacent disturbed landscapes did not dominate the seedbank in an old-growth hardwood forest in Quebec. In fact, the seedbank was found to be fairly diverse and contained many shade-tolerant species. Leckie et al. also found that many of the species in the above-ground vegetation were also present in the seedbank. McCarthy et al. (unpublished data) found a similar pattern at DW. Many shade-tolerant forest species were found in the seed bank, and this could serve as an important propagule source after disturbance. However, unlike Leckie et al. (2000), McCarthy et al. (unpublished data) found little similarity (< 20% in most sample periods) between above-ground and below-ground species constituencies (fig. 6.3).

Figure 6.3. Unweighted pair-group average linkage clustering of species similarity, to compare the seedbank (solid lines) and above-ground (dotted lines) in the two sites (DW and HMF) shown at Dysart Woods.

### Stability, Diversity, and Disturbance

Concern over biodiversity has generated interest in the stability of communities (Levine and D'Antonio 1999) and ideas about the development of stable communities by his followers. According to Odum, a stable community achieves a homeostatic balance that continues today in many ecosystems. A stable community or ecosystem is one that remains relatively stable in species over time. It is important to distinguish between organisms versus the system. The concept of stability is quantitative, the measure of the resistance of a system to change when faced with perturbation. The issues focus on persistence, resilience, and



**Figure 6.3.** Unweighted pair group mean analysis, using Sørensen's coefficient of similarity, to compare the seedbank (solid lines) with the above-ground vegetation (dotted lines) in the 35 quadrats on the north-facing slope (June vegetation data shown) at Dysart Woods, Ohio.

### Stability, Diversity, and Habitat Invasibility

Concern over biodiversity loss with respect to ecosystem function has regenerated interest in the links among stability, diversity, and habitat invasibility (Levine and D'Antonio 1999). The notion of stability can be traced to early ideas about the development of the community as espoused by Clements and his followers. According to early thinking, at some point, all communities achieved a homeostatic equilibrium (the climax community). This idea continues today in many respects under the rubric "balance of nature." A community or ecosystem is often seen as stable when no change can be detected in species over time. However, as Connell and Sousa (1983) point out, it is important to distinguish between the degree of constancy of the numbers of organisms versus the constancy of species (presence or absence). The former is quantitative, the latter qualitative. Quantitative issues include both the *resistance* of a system to disturbance (the ability to remain at equilibrium when faced with potentially disturbing forces), as well as the *resilience* of a system (the ability to return to equilibrium after being disturbed). Qualitative issues focus on *persistence* (the ability of a species to not become locally

extinct). Thus, both qualitative and quantitative features of a system must be examined.

Old-growth forests have been, and will continue to be, a critical component to our development of ecological theory, particularly with respect to issues of system stability. My observations in the central and southern Appalachians suggest that old-growth herb layers exhibit all three forms of stability: resistance, resilience, and persistence. This is confirmed by at least one empirical field study (Brothers and Spingarn 1992). But long-term data in forests that have been perturbed are needed before this notion can be better assessed. In this regard, old-growth forests will remain invaluable benchmarks to compare against a predominantly managed (perturbed) forest landscape now existing in eastern North America. The predominant disturbance in most eastern old-growth forests, with the advent of fire suppression in the twentieth century, is gap disturbance. However, empirical tests of the effects of gap disturbance on the understory community in second-growth forests have not been particularly revealing. Collins and Pickett (1987) found that small (single-tree) and large (multi-tree) gap openings in a northern hardwood forest had little influence on species richness or cover. This suggests that the herb community is resistant to the disturbance regime most prevalent in eastern old-growth forests and therefore relatively stable. In a similar study, Reader and Bricker (1992a) were unable to show a positive relationship between gap size and perennial herb abundance over a 2-year period in hardwood forests of southern Ontario. They concluded that herbs might be under too much competition with advanced regeneration in larger gaps to allow increases in herb abundance.

For years, there has been the tacit assumption that there is a link between stability and diversity, probably first proposed by Elton (1958), who stated that "the balance of relatively simple communities of plants and animals is more easily upset than that of richer ones" (p. 145). However, the empirical evidence for this notion is less than apparent (McNaughton 1988), particularly in communities of vascular plants. Tilman (1996) recently examined this relationship using long-term plot data in grasslands and concluded that diversity did stabilize community and ecosystem processes (e.g., biomass), but not population processes (e.g., individual species abundance). However, the ultimate interpretation of these results is difficult due to confounding effects found in many ecological experiments (Huston 1997). Huston (1994) suggests that in a dynamic equilibrium context (assuming low levels of disturbance), high-diversity communities are likely to occur under conditions of low population growth rates, whereas low-diversity communities are likely to be found under conditions with high population growth rates. But the relationship between stability and complexity may simply be a consequence of the type of environment in which high-diversity communities exist, rather than an inherent property of diversity and complexity (Huston 1994). Many old-growth relicts are found on relatively high-quality sites. Empirical tests of the diversity-stability hypothesis are lacking for old-growth forests.

More recently, biologists have become concerned about the prevalence of

biological invasions (McKinney 1986; McKinney and Lewellen 1993). In 13, this volume, we will explore how these changes have become established, what diversity decreases have occurred, and what rational management practices D'Antonio (1994) has proposed directly manage these changes with invasive species. (McGrady-Steed et al. 1994) have been no empirical studies that observations made in the field earlier are typically terminated by winter. The composition of the understory layer has not. In a study of a nonindigenous species surrounded by *Fraxinus americana*, *Liquidambar styraciflua*, and *Populus tremuloides*, the effect of gypsy moth defoliation was observed, whereas disturbance by deer browsing in the community, disturbance resistance, and stable understory layer are needed in the field.

## Summary

I have reviewed the literature on eastern old-growth forests and found that the concept of stability is now coming into focus. Definitions with respect to the herbaceous layer have not been clearly defined, but it is clear that the most diverse vegetation in these forests is the herbaceous layer. To incorporate this diversity into the definition of stability, it is necessary to understand the factors that influence the diversity of the herbaceous layer. These factors include climate, soil, and disturbance. By understanding these factors, it is possible to predict the diversity of the herbaceous layer in different environments.

Because of the lack of empirical data, the sampling of the herbaceous layer remains a challenge. More work is needed to develop methods for accurately sampling the herbaceous layer in different environments.

of a system must be critical component with respect to issues of stability: resistance. At least one empirical test in forests that have been better assessed. In this paper, I will compare data from two sites in forests that have been gap disturbance regimes. These have not been parallel. The first site, a small (single-tree) gap in a forest, had little impact on the herb community. The second site, a larger old-growth forest, had a greater impact on the herb community. This paper will also examine the link between gap size and herb abundance.

In this paper, I will review the empirical literature (e.g., Bricker et al. 1988), particularly the work of Bricker and Bricker (1988), which has recently examined the impact of gap size on herb abundance. They concluded that gap size has a significant impact on herb abundance (e.g., biomass), but not on species richness. However, the results of their study are conflicting. Bricker and Bricker (1988) suggest that at low levels of disturbance, the impact of gaps on the herb layer is greater than at higher levels of disturbance. This suggests that under certain conditions of disturbance, the impact of gaps on the herb layer is likely to be greater than at higher levels of disturbance. But the results of their study are conflicting. Bricker and Bricker (1988) suggest that at low levels of disturbance, the impact of gaps on the herb layer is greater than at higher levels of disturbance. This suggests that under certain conditions of disturbance, the impact of gaps on the herb layer is likely to be greater than at higher levels of disturbance. Under normal disturbance regimes and climatic fluctuations, old-growth forests may contain stable understories. Considerably more observations and experimental work are needed in this area.

### Summary

I have reviewed and explored several features of the herbaceous layer in eastern old-growth deciduous forests. After many years of debate, we are now coming to consensus on how to define old-growth forest. Technical definitions with specific quantifiable criteria are now available, but the herb layer has not commonly been included in these definitions. It is important to incorporate the herb layer in these definitions because this is usually the most diverse vegetative layer in these ecosystems. More research is needed to understand the herbaceous layer diversity patterns along chronosequences that include old growth. The use of functional groups (in place of species) may be helpful in setting targets for preservation or conservation. This will permit better standards to emerge and ultimately assist with land management decisions.

Because of the temporal variability of forest understory communities, single samplings of the vegetation are inappropriate in most cases; yet many examples remain in the literature. There also appears to be a large emphasis

on the spring vernal herbs (perhaps because of their lower diversity), apparently at the expense of the rest of the summer flora. In fact, we know little of the complete herbaceous flora and its phenology in most forests. As I have described, given the high diversity in this layer, we need to better study the sampling methods and sample sizes required to capture at least 95% of the species. Furthermore, if we are to ever understand spatial and temporal patterns in the understory, we must expand our observations beyond the level of the stand and single-year study. As far as forest herb communities are concerned, I cannot overemphasize the need for long-term, permanent plot studies arranged in a stratified fashion throughout the landscape.

Finally, in recent years, biologists have become acutely aware of the threat of invasive, nonindigenous species to many natural ecosystems. However, our understanding of the relationships among diversity, stability, and invasibility are still weak and confined to specific types of microcosms or ecosystems. Forest systems have not been carefully examined in this light, especially old-growth forests. Despite a shifting emphasis toward a better understanding of the managed forest landscape, old-growth forests will remain an important component in our understanding of forest pattern and process. These systems serve as the benchmarks in our heavily disturbed eastern forest landscape.

What determines? To out possible Four explain in physical f dispersal, co impacts, and factors in deciduous f erogeneous

Disturbance of spe strategies (W 1973; Grubb 1978; Grime and Pickett 1999). Curr (1) richness frequent than communities disturbance i (Huston 19 that there is local processes Pastor and B