

11-2007

# The Ecological Significance of the Herbaceous Layer in Temperate Forest Ecosystems

Frank S. Gilliam

*Marshall University*, [gilliam@marshall.edu](mailto:gilliam@marshall.edu)

Follow this and additional works at: [http://mds.marshall.edu/bio\\_sciences\\_faculty](http://mds.marshall.edu/bio_sciences_faculty)



Part of the [Forest Biology Commons](#), and the [Other Forestry and Forest Sciences Commons](#)

---

## Recommended Citation

Gilliam FS. 2007. The ecological significance of the herbaceous layer in forest ecosystems. *BioScience* 57:845-858.

This Article is brought to you for free and open access by the Biological Sciences at Marshall Digital Scholar. It has been accepted for inclusion in Biological Sciences Faculty Research by an authorized administrator of Marshall Digital Scholar. For more information, please contact [zhangj@marshall.edu](mailto:zhangj@marshall.edu), [martj@marshall.edu](mailto:martj@marshall.edu).

# The Ecological Significance of the Herbaceous Layer in Temperate Forest Ecosystems

FRANK S. GILLIAM

*Despite a growing awareness that the herbaceous layer serves a special role in maintaining the structure and function of forests, this stratum remains an underappreciated aspect of forest ecosystems. In this article I review and synthesize information concerning the herb layer's structure, composition, and dynamics to emphasize its role as an integral component of forest ecosystems. Because species diversity is highest in the herb layer among all forest strata, forest biodiversity is largely a function of the herb-layer community. Competitive interactions within the herb layer can determine the initial success of plants occupying higher strata, including the regeneration of dominant overstory tree species. Furthermore, the herb layer and the overstory can become linked through parallel responses to similar environmental gradients. These relationships between strata vary both spatially and temporally. Because the herb layer responds sensitively to disturbance across broad spatial and temporal scales, its dynamics can provide important information regarding the site characteristics of forests, including patterns of past land-use practices. Thus, the herb layer has a significance that belies its diminutive stature.*

*Keywords: forest ecology, vegetation science, herbaceous-layer dynamics, biodiversity*

**A** memorable moment in my graduate training occurred during my first course at Duke University in 1978. Our class was in the field, learning the ecology and taxonomy of tree species of the North Carolina Piedmont, when I had the temerity to inquire about the identification of a particular forest herb. “Oh, that’s just a step-over,” the professor replied, with a bit of humor, suggesting that herbaceous plants on the forest floor were of little importance to the forest and thus merited “stepping over” in the pursuit of studying trees.

I do not share this anecdote to suggest that most people with an interest in forests hold the herbaceous layer in low esteem. On the contrary, the ecology of the herbaceous layer has been the focus of numerous studies, including such recent syntheses as a book (Gilliam and Roberts 2003a) and extensive reviews (Whigham 2004, Roberts 2004, Gilliam 2006). Rather, this story shows how far vegetation scientists have come in the past few decades toward helping forest managers, conservation biologists, and other ecologists appreciate the importance of the herbaceous layer, and setting the stage for enhancing this appreciation among biologists in a wide variety of disciplines.

Studies of the ecology of the herbaceous layer of forests have been carried out over nearly half a century. Some of these earlier studies focused on the response of herb communities to environmental gradients within forests (Struik and

Curtis 1962, Anderson et al. 1969), whereas others emphasized structural aspects of the herbaceous layer, such as biomass (Zavitkovski 1976). Still other studies characterized ecosystem processes associated with the herbaceous layer, such as productivity (Siccama et al. 1970). In this article, I review the recent literature to highlight the ecological significance of the herbaceous layer to the structure and function of forest ecosystems. There is a natural tendency to overemphasize the dominant vegetation of forests—trees—which is understandable, considering that a forest is delineated from other vegetation types by the prevalence of trees. This overemphasis is unfortunate, however, because it ignores a component—the herbaceous layer—whose ecological importance to the forest ecosystem is quite disproportionate to its minimal biomass and limited visibility in the landscape.

## Terminology, definitions, and sampling methods

Among the challenges encountered in the study of herbaceous-layer ecology is a general lack of consistency in virtually any-

---

*Frank S. Gilliam (e-mail: gilliam@marshall.edu) is a professor in the Department of Biological Sciences at Marshall University in Huntington, West Virginia. His research includes the nitrogen biogeochemistry of forest ecosystems and the ecology of the herbaceous layer of deciduous forests. © 2007 American Institute of Biological Sciences.*

thing involving its study. This includes what terms are used for the herbaceous layer, how it is defined, and how it is sampled.

Vegetation scientists use numerous synonyms when referring to this forest stratum. Gilliam and Roberts (2003b) surveyed the ecological literature from 1980 to 1999 and found several synonyms for “herbaceous layer” (“herb layer” for short), the term I use herein. These included “herbaceous [or herb] stratum,” “herbaceous understory,” “ground layer,” “ground vegetation,” and “ground flora.” “Herbaceous layer” (or “herb layer”) and “ground vegetation” were the more commonly used terms, representing 34% and 31%, respectively, of occurrences during the 20-year period (table 1; Gilliam and Roberts 2003b). They also found that “herbaceous layer” or “herb layer” was more commonly used in North American studies, whereas “ground vegetation” was more typically used in non-North American (predominantly European) studies. Other terms include “ground cover,” commonly used for savanna-like forest ecosystems with open canopies, wherein the forest floor is often entirely covered by herbaceous species, low-growing shrubs, and juvenile trees (Gilliam et al. 2006a). Another synonym is “regeneration layer,” a term often used by foresters who are interested in the regenerative patterns of dominant overstory species, which can be determined largely by interactions among plant species in this stratum (Baker and Van Lear 1998). One should be aware of these terms and patterns of usage when conducting online searches for current and past literature.

Also problematic in the study of herb-layer ecology are the numerous ways in which vegetation scientists define the herbaceous layer in their studies. More common definitions emphasize the height, rather than the growth form (i.e., herbaceous versus woody), of forest vegetation. The herbaceous layer is most commonly defined as the forest stratum composed of all vascular species that are 1 meter (m) or less in height. This is an inclusive definition that combines true herbaceous species—often called “resident species” because they generally cannot grow taller than the maximum height of this stratum—and the seedlings, sprouts, and young saplings of woody species, called “transient species” because they occur in the herb layer only temporarily, having the ability to grow into higher forest strata. Variations in this

definition occur in the height distinction and in the inclusion or exclusion of nonvascular plant species (e.g., mosses) or woody species. For example, Siccama and colleagues (1970) used 0.5 m as an upper limit in their classic paper on the herb layer, part of the Hubbard Brook Ecosystem Study. Other studies have placed the cutoff as high as 2 m, and still others fail to state a specific height to delimit the herb layer. Figure 1 depicts herbaceous-layer communities for contrasting forest types.

The field of vegetation science, which seeks to understand the patterns and processes of plant communities, has developed a diverse methodology to study vegetation dynamics in the field. The numerous field methods employed by vegetation scientists typically vary with vegetation type. For example, methods used in grasslands generally contrast sharply with those used in forests because of the differences in the physiognomy (i.e., size and height) of the dominant vegetation. Similarly, in studying the highly stratified (i.e., layered) vegetation of forest communities, scientists typically use different methods in the same study, with plots of varying size and shape to accommodate, for example, the large oaks and hickories in the overstory and the violets covering the forest floor. Trees often are sampled by tallying species within relatively large plots (e.g., 400, 500, or even 1000 m<sup>2</sup>) of different shapes, including squares, rectangles, and circles; herbaceous-layer species are often sampled by estimating density or cover within much smaller plots (most commonly 1 m<sup>2</sup>) of equally varying shapes. Other methods for sampling avoid plots altogether, using line transects of varying lengths.

It is common, furthermore, to find field methods that sample both tree and herb strata simultaneously, with the herb-layer plots nested within tree plots. One such method, developed by the late Robert Whittaker (Shmida 1984), employs a series of nested subplots of decreasing size (usually from 100 m<sup>2</sup> down to 1 m<sup>2</sup>), recognizing that plant species richness can vary spatially and thus can be a function of the area sampled (Fridley et al. 2005). Variations of this approach using a square or rectangular shape—and with subplot size as small as 0.01 m<sup>2</sup> (Peet et al. 1998)—are frequently found in the literature (Peet et al. 1998, Keeley and Fotheringham 2005). By contrast, Gilliam and colleagues (1995) used circular 1-m<sup>2</sup> subplots nested within circular 400-m<sup>2</sup> plots to capture the tree and herb strata in a West Virginia hardwood forest, with the circular shape based on models of gap dynamics for forests.

Most of the plot-based approaches I have described are warranted when quantitative measures of herbaceous-layer plants (e.g., percentage cover, biomass, and density) are desired. When the aim is simply to record which species occur in the stratum, however, an inventory approach is preferable. For this, the researcher walks around a forest stand and records all the species encountered. The disadvantage of this approach is that it precludes quantitative measurements, but the advantage is that it captures a greater number of herbaceous species. For example, sampling within 208 plots throughout a 13.2-hectare watershed of the Hubbard Brook

**Table 1. Frequency of use of “herbaceous layer,” “herb layer,” and synonyms in the ecological literature from 1980 to 1999.**

Term	Frequency of use (%)
Herbaceous/herb layer	34.0
Ground vegetation	31.1
Ground layer	14.9
Ground flora	13.6
Herbaceous understory	3.4
Herbaceous/herb stratum	3.0

Source: Gilliam and Roberts (2003b).



Experimental Forest in New Hampshire yielded 37 species in the herbaceous layer, whereas inventory by searching yielded 71 species (Thomas G. Siccama, Yale School of Forestry and Environmental Studies, Yale University, New Haven, CT, personal communication, 17 July 2007).

I will frame my observations on the ecological significance of the herbaceous layer in forest ecosystems by highlighting five aspects of herb-layer ecology: (1) the contributions of the herb layer to forest biodiversity; (2) the importance of the herb layer as the site of initial competitive interactions for the regeneration phases of dominant canopy species; (3) the ability of the herb layer to form linkages with the overstory; (4) the influence of the herb layer on ecosystem functions, such as energy flow and nutrient cycling; and (5) the multifaceted responses of the herb layer to various disturbances of both natural and anthropogenic origin.

### Biodiversity

Loss of biodiversity is occurring on a global scale and at an ever-increasing rate. This is especially true for forest ecosystems, which often are near areas of high human population density. The resultant land use (including forest use, urban development, and conversion to agriculture) can exacerbate the loss of native species through habitat destruction or alteration and the introduction of invasive species. Although plant species richness is higher in the herbaceous layer than in any other forest stratum, discussions of threats to biodiversity often omit the herb layer. This is ironic, because herbaceous species have higher natural extinction rates than plant species in other strata. Levin and Wilson (1976) estimated that extinction rates in herbs are more than three times that of hardwood tree species and approximately five times that of gymnosperms. Thus, threats to forest biodiversity are most often a function of threats to herbaceous-layer species (Jolls 2003).

It is often stated, though less often in quantitative terms, that most plant biodiversity in forest ecosystems is found in the herbaceous layer (Gilliam and Roberts 2003b, Roberts 2004, Whigham 2004). To quantify this generalization, I have assembled data from studies in the literature in which the overstory and herb layer were sampled simultaneously and thus on the same spatial scale. I calculated the contribution of the herbaceous layer to forest plant biodiversity as a ratio between the species richness of the herb layer and that of the overstory for each unit represented in the summary (table 2). This ratio varied among the studies from 2.0 to 10.0, with a mean ratio of all data combined (except those for longleaf pine savanna) of 5.7, indicating that, on average, for every tree species in a forest, there are about six species in the herbaceous layer (table 2). The reciprocal of this ratio suggests that the herb layer averages more than 80% of the total plant species richness of a forest. These numbers represent conservative



**Figure 1.** Herbaceous-layer communities in contrasting forest ecosystems. (a) Mixed hardwood forest, north-central West Virginia. Photograph courtesy of Naomi S. Hicks. (b) Longleaf pine, south-central North Carolina. Photograph: Frank S. Gilliam. (c) Old-growth Pacific Northwest forest. Photograph courtesy of Scott McIntyre.

**Table 2. Species richness of tree and herbaceous layers, and ratio of herbaceous-layer to tree species, at several North American forest sites.**

Sample unit (area in hectares)	Number of species		Ratio	Site/ region	Forest type	Age (years)	Source
	Tree layer	Herb layer					
Watershed (34)	15	40	2.7	Fernow Experimental Forest, WV	Mixed hardwood	20	Gilliam et al. 1995
Watershed (39)	22	45	2.0	Fernow Experimental Forest, WV	Mixed hardwood	80	Gilliam et al. 1995
Watershed (24)	19	64	3.4	Fernow Experimental Forest, WV	Mixed hardwood	20	Gilliam et al. 1995
Watershed (14)	18	62	3.4	Fernow Experimental Forest, WV	Mixed hardwood	70	Gilliam et al. 1995
Stand (varying)	4	37	9.3	Cascade Range, WA	Mixed conifer	66 <sup>a</sup>	Halpern and Spies 1995
Stand (varying)	7	40	5.7	Cascade Range, OR	Mixed conifer	61 <sup>a</sup>	Halpern and Spies 1995
Stand (varying)	5	36	7.2	Coast Range, OR	Mixed conifer	57 <sup>a</sup>	Halpern and Spies 1995
Stand (varying)	6	38	6.3	Cascade Range, WA	Mixed conifer	133 <sup>a</sup>	Halpern and Spies 1995
Stand (varying)	5	47	9.4	Cascade Range, OR	Mixed conifer	114 <sup>a</sup>	Halpern and Spies 1995
Stand (varying)	4	40	10.0	Coast Range, OR	Mixed conifer	101 <sup>a</sup>	Halpern and Spies 1995
Stand (varying)	5	39	7.8	Cascade Range, WA	Mixed conifer	425 <sup>a</sup>	Halpern and Spies 1995
Stand (varying)	6	42	7.0	Cascade Range, OR	Mixed conifer	395 <sup>a</sup>	Halpern and Spies 1995
Stand (varying)	6	49	8.2	Coast Range, OR	Mixed conifer	316 <sup>a</sup>	Halpern and Spies 1995
Stand (1.75)	24	104	4.3	Waterloo Wildlife Research Station, OH	Mixed conifer	Mixed age	Small and McCarthy 2002
Stand (varying)	12	61	5.1	New Brunswick, Canada	Mixed conifer/ hardwood	–	Roberts and Zhu 2002
Watershed (59)	36	93	2.6	Coweeta Hydrologic Laboratory, GA	Mixed hardwood	20	Elliott et al. 1997
Watershed (40)	34	125	3.7	Coweeta Hydrologic Laboratory, GA	Mixed hardwood	Mixed age	Elliott and Knoepp 2005
Basin (2100)	53	476	9.0	Coweeta Hydrologic Laboratory, GA	Mixed forest types	Mixed age	Pittillo and Lee 1984
Plot (9)	13	65	5.0	Western North America	White spruce	–	Qian et al. 1998
Plot (9)	18	77	4.3	Central North America	White spruce	–	Qian et al. 1998
Plot (9)	13	65	5.0	Eastern North America	White spruce	–	Qian et al. 1998
Plot (9)	14	53	3.8	Western North America	Black spruce	–	Qian et al. 1998
Plot (9)	14	57	4.1	Central North America	Black spruce	–	Qian et al. 1998
Plot (9)	12	46	3.8	Eastern North America	Black spruce	–	Qian et al. 1998
Stand (3)	14	121	8.6	Gibbons Creek Barren, IL	Oak barren	–	Taft 2003
Stand (1.5)	13	69	5.3	Forest Service Barren, IL	Oak barren	–	Taft 2003
Stand (13.2)	14	71	5.1	Hubbard Brook Experimental Forest, NH	Northern hardwood	Mixed age	Siccama et al. 1970
Plot (8)	1	251	251.0	Camp Whispering Pines, LA	Longleaf pine	Old growth	Platt et al. 2006

a. Mean stand age.

estimates for herbaceous-layer richness, because most of the data in table 2 are derived from plot-based sampling, which generally underestimates richness relative to inventory sampling.

Linear correlation analysis comparing species richness of the herbaceous layer to that of the overstory (data not shown) revealed a highly significant, positive relationship, suggesting that species-rich herb layers generally occur in areas with species-rich overstories. However, this relationship clearly varies with forest type. Conifer forests (figure 1b, 1c), particularly those that are fire maintained (Platt et al. 2006), commonly comprise a species-poor overstory and a species-rich herb layer (Halpern and Spies 1995). De Grandpré and colleagues (2003) reported that the conifer forests of boreal Canada can contain 300 plant species, but that the total

vascular flora includes just over 20 tree species. Perhaps the most extreme example of this pattern is found in old-growth longleaf pine savannas, where a single tree species (longleaf pine) is underlain by an herbaceous-layer community of considerable species richness (table 2).

Even the occurrence of rare (often threatened or endangered) species in the herbaceous layer has practical relevance to the biodiversity of forest ecosystems. Spyreas and Matthews (2006) suggested that, because of their habitat and resource specificity, rare plants of the herbaceous layer can be used as indicators of biodiversity. Jolls (2003) identified several anthropogenic factors—including habitat loss and fragmentation, introductions of alien species, and overexploitation—that exacerbate the demise of such species. As Whigham (2004) pointed out, despite our understanding of the basic



ecology of herb-layer species, the paucity of detailed studies of individual species hampers our ability to conserve and restore those that are threatened with extinction.

### Competitive interactions

Following a stand-initiating disturbance, such as the 1988 Yellowstone fires—or even a small-scale disturbance, such as the death and toppling of a large canopy tree—the response of woody and herbaceous plant species usually is quite vigorous. Intense competition can result, as the seedlings and sprouts of regenerating overstory species compete with resident species (e.g., perennial herbs, such as *Trillium*) for aboveground and belowground resources before they pass through this layer to create a new overstory.

The outcome of these competitive interactions represents an important stage in the growth and development of the forest following a disturbance. Interspecific competition among resident and transient species can determine the type of forest that eventually becomes established. Because ferns represent a prominent component of the herb layer of hardwood forests in the northeastern United States (George and Bazzaz 2003), much research has focused on the nature of fern-tree seedling interactions. Horsley (1993) examined several mechanisms to explain the inhibitory effect of eastern hayscented fern (*Dennstaedtia punctilobula*) on establishment and growth of seedlings of black cherry (*Prunus serotina*). He concluded that aboveground competition for light was the primary influence on fern-mediated inhibition of black cherry. It is likely that other, nonfern species that also form tall, dense populations, such as wood nettle (*Laportea canadensis*), have the same effects on tree seedlings.

Other work has shown that some herbaceous species may be superior competitors for soil nutrients, compared with tree seedlings. Lyon and Sharpe (2003) found significantly lower concentrations of nitrogen (N), phosphorus (P), and potassium (K) in the leaves of northern red oak (*Quercus rubra*) seedlings grown with hayscented fern than in the leaves of seedlings grown without ferns. Conversely, fern fronds grown with oak seedlings were higher in N, P, and K than fronds grown with ferns alone (Lyon and Sharpe 2003).

George and Bazzaz (2003) summarized the results of extensive experimental work at the Harvard Forest, Massachusetts, evaluating the effects of ferns on the survival and growth of seedlings of several ecologically important tree species in New England. They combined experimental manipulations of naturally occurring ferns (removing the dominant ferns from some experimental plots by applying herbicide) with natural and experimental seeding of dominant tree species, including red maple (*Acer rubrum*), white ash (*Fraxinus americana*), red oak, white pine (*Pinus strobus*), and two species of birch (*Betula* spp.). They followed the early stages of recruitment of these species, from seedling emergence and survivorship to densities of established seedlings and relative growth rates of three-year-old seedlings. The salient results of George and Bazzaz (2003) are summarized in figure 2. Ferns inhibited the emergence of seedlings of red oak,

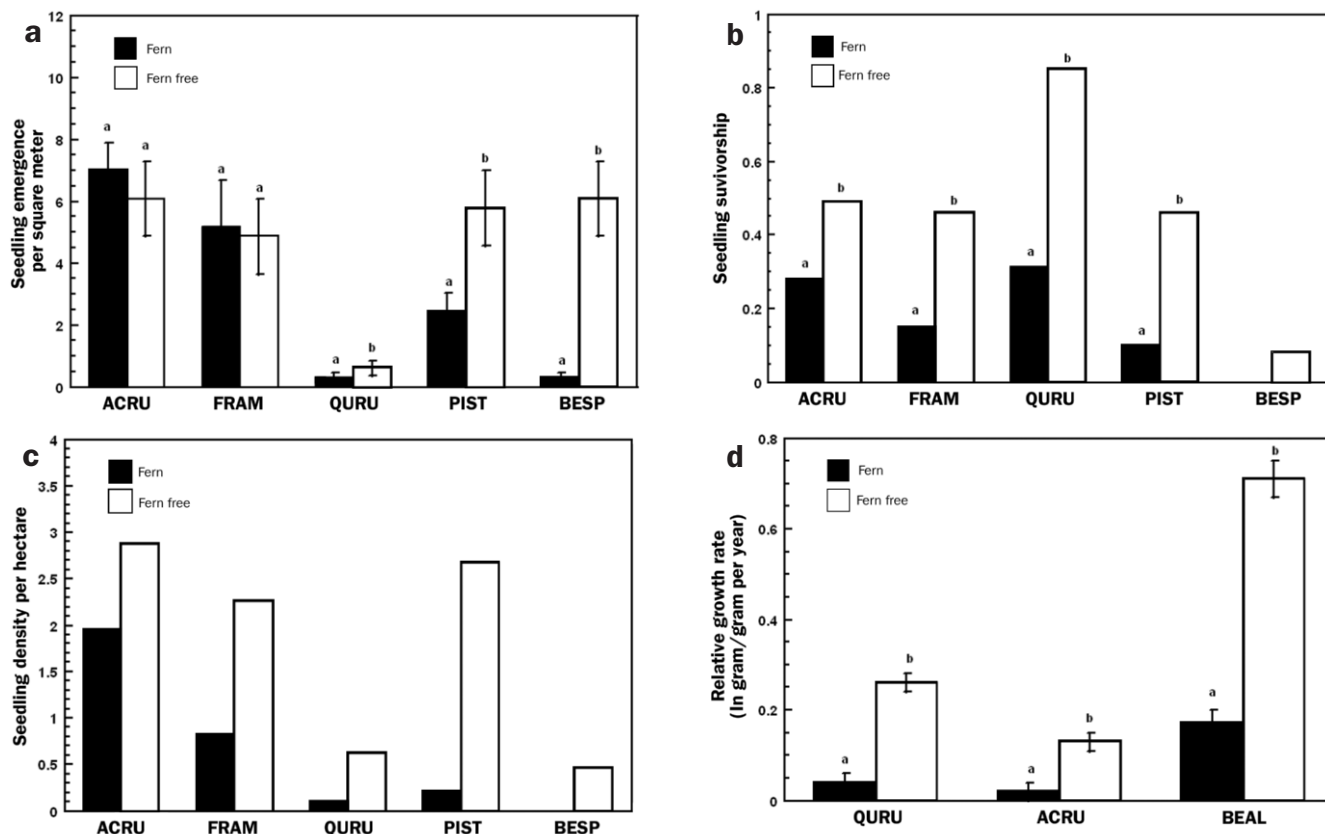
white pine, and birch (figure 2a), and decreased survivorship for seedlings of all species (figure 2b), resulting in lower tree seedling density in the presence of ferns (figure 2c). Finally, fern cover significantly decreased the growth of three-year-old seedlings of red oak, red maple, and yellow birch (*Betula allegheniensis*; figure 2d). In short, all stages of the early phase of reproduction of dominant overstory species were significantly influenced by ferns in the herbaceous layer. Moreover, that these effects were species specific indicates that the herb layer has the potential to determine, or at least influence, the composition of the regenerating forest.

### Linkage with overstory

The discussion above suggests that herb-layer composition can influence overstory seedling dynamics and overstory composition. Conversely, the composition of the overstory can influence the dynamics of herbaceous species on the forest floor by altering light availability and enhancing the spatial heterogeneity of soil fertility (Muller 2003, Neufeld and Young 2003). These reciprocal interactions can lead to the two strata attaining what is called *linkage*. Because overstory and herbaceous-layer species can be sampled in the same areas, it is possible to ask process-level questions regarding the distribution of species of one stratum as a function of the other. When the spatial pattern in species composition of one forest stratum is significantly correlated with that of another stratum, the strata are said to be linked. The phenomenon of linkage has been reported for several forest types (Gilliam and Roberts 2003c).

Gilliam and colleagues (1995) reported linkage between the herbaceous layer and the overstory for hardwood stands in West Virginia, but they concluded that, at least for that site, linkage was something that developed over stand age. That is, the two strata were not linked in young stands (in this case, approximately 20 years after clear-cut harvesting) but were linked in mature (80- to 100-year-old) stands. Gilliam and colleagues (1995) hypothesized that linkage is driven by the response of vegetation strata to environmental gradients (e.g., soil pH, elevation), that is, the herb layer and overstory respond to different gradients initially but respond to similar gradients in increasingly similar ways as the stand matures.

Gilliam and Roberts (2003c) tested this hypothesis using canonical correspondence analysis (CCA) of data from the West Virginia site. CCA is an analytical method that determines the importance of environmental gradients in explaining patterns of species composition as unit-less vectors; longer vectors represent more important, and shorter vectors represent less important, environmental gradients. In young stands, the herb-layer composition responded to soil cations calcium, magnesium, and potassium ( $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$ , and  $\text{K}^+$ , respectively) and cation exchange capacity (CEC, a measure of the cation-holding ability of the soil), but the overstory composition did not. Conversely, the overstory, but not the herb layer, responded to soil P (figure 3a). In mature stands, soil  $\text{Ca}^{2+}$ ,  $\text{K}^+$ , P, and clay content were important gradients for both



**Figure 2.** The effects of fern cover on (a) emergence, (b) survivorship, (c) density, and (d) relative growth rates of the seedlings of ecologically important tree species in the Harvard Forest, Massachusetts. Bars (means) labeled with the same letter are not significantly different from each other at  $p = .05$ . Abbreviations: ACRU, *Acer rubrum* (red maple); BEAL, *Betula allegheniensis* (yellow birch); BESP, *Betula* spp. (birch); FRAM, *Fraxinus americana* (white ash); PIST, *Pinus strobus* (white pine); QURU, *Quercus rubra* (northern red oak). Redrawn from George and Bazzaz (2003) with permission from Oxford University Press.

the herbaceous layer and the overstory, whereas  $Mg^{2+}$  and CEC were of lesser importance for both layers (figure 3b).

Gilliam and Roberts (2003c) further discussed the implications of linkage in forest communities, suggesting that it furthers ecologists' understanding of the complexities underlying the structure and function of forests, including responses to disturbance and mechanisms for secondary succession. The concept of linkage can also be applied to investigations of forest cover types and remote sensing.

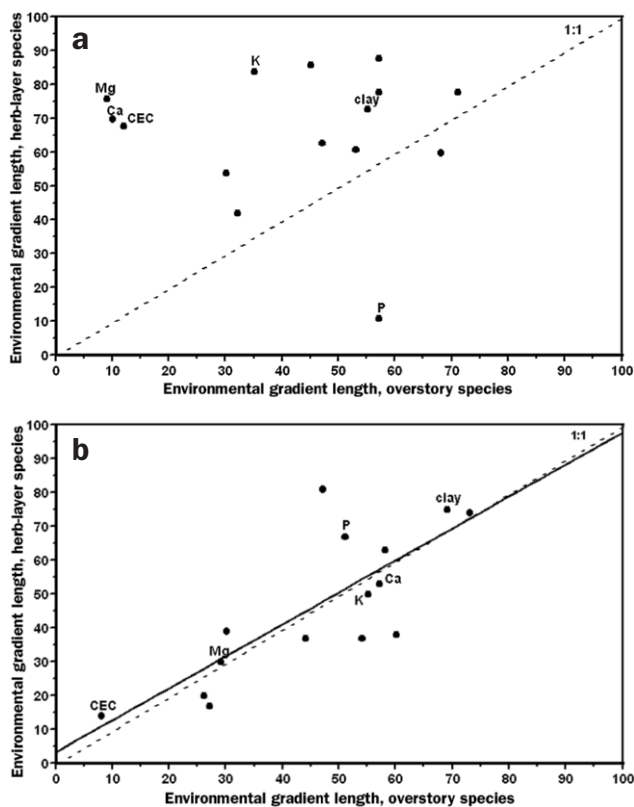
### Ecosystem functions

The study of forests as ecological communities stresses their species composition, with a focus on the number of species and their relative importance, two variables that determine species diversity. The study of forests as ecosystems takes a different perspective, emphasizing the intimate interlacing of the biotic community with its abiotic environment and focusing on (a) how energy moves through the forest and (b) how nutrients cycle within it.

Despite the small stature of the herbaceous layer—its aboveground biomass is less than 1% of the forest as a whole (figure 4)—it has a quantifiable significance at the ecosystem

level, mediating carbon dynamics and energy flow and influencing the cycling rates of essential nutrients, including N, P, K, and Mg. Relative to the canopy layer, the herbaceous layer contributes little to the overall biomass of a forest, making up an average of 0.2% of the aboveground biomass of typical forests in the Northern Hemisphere (figure 4). However, the herb layer provides approximately 4% of the net primary productivity (NPP, a measure of the rate of net conversion of light energy into biomass) in these same forests (figure 4), a 20-fold greater relative contribution to forest NPP than to biomass. Muller (1978) found a similar value of 3.7% of total ecosystem NPP for the herbaceous layer of hardwood forests of New England; Neufeld and Young (2003) reported contributions of up to 7% for the herb layer to total net ecosystem carbon gain. More notably, the herb layer can provide up to 16% of annual litter fall in forests (figure 4). Welch and colleagues (2007) found a similar proportion—herb litter as approximately 12% of total litter fall—for a deciduous forest in central Indiana.

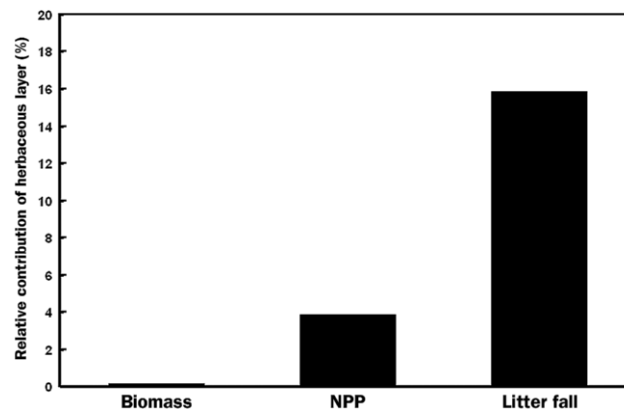
The herbaceous layer influences the cycling of essential plant nutrients (e.g., N, P, K) in a way that is disproportionate to its relative biomass in forest ecosystems. Muller (2003) sum-



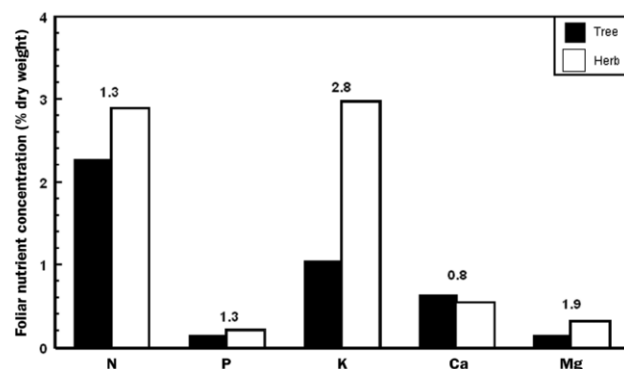
**Figure 3.** Environmental gradient lengths for herbaceous-layer and overstory species in (a) young and (b) mature hardwood stands in West Virginia. Each point in the graph represents a different environmental variable; six demonstrate the different herbaceous-layer/overstory relationships between stands of contrasting ages. Chemical symbols for magnesium (Mg), calcium (Ca), potassium (K), and phosphorus (P) represent available levels of these nutrients in the soil. CEC represents soil cation exchange capacity; clay represents soil clay content. Environmental gradient lengths were not correlated between herbaceous layer and overstory in young stands, but were significantly correlated in mature stands ( $p < .01$ ,  $r^2 = 0.62$ ,  $y = 3.01 + 0.94x$ , where  $y$  and  $x$  represent gradient lengths for herbaceous layer and overstory, respectively). Based on data from Gilliam and Roberts (2003b).

marized data from the Hubbard Brook Experimental Forest for concentrations of N, P, K, Ca, and Mg averaged across foliage from several tree species, compared with concentrations averaged across foliage from several herbaceous species. Concentrations of N and P were 30% higher in herb foliage than in trees; more notably, concentrations of Mg were nearly twofold and of K nearly threefold higher in herb foliage (figure 5). Welch and colleagues (2007) also concluded that the herb layer had a profound influence on the cycling of K in their Indiana forest.

These two roles of the herbaceous layer in the function of forest ecosystems—influencing energy flow and nutrient cycling—are connected by a common and important char-



**Figure 4.** Relative contribution of the herbaceous layer to aboveground biomass, net primary productivity (NPP), and litter fall in forests of the Northern Hemisphere. Drawn from data in Muller (2003).



**Figure 5.** Concentrations of plant macronutrients for tree and herb foliage. Numbers represent the ratio between nutrient concentrations in herb foliage and in tree foliage. Abbreviations: Ca, calcium; K, potassium; Mg, magnesium; N, nitrogen; P, phosphorus. Drawn from data in Muller (2003).

acteristic of most herbaceous plant species: the production of short-lived aboveground biomass, primarily in the form of foliage. Summarizing several studies in the literature, Muller (2003) found that, on average, herbaceous litter typically decomposes more than twice as rapidly as tree litter. Thus, herb-layer species can contribute greatly to the litter component of the forest ecosystem (litter fall in figure 4), even though there may be relatively little herb-layer vegetation at any point in time (biomass in figure 4). Because herb-layer species have high foliar concentrations of nutrients such as N, P, K, and Mg (figure 5), the rapid decomposition and high turnover rate of herb-layer foliage facilitates efficient recycling of nutrients in the forest.

Muller and Bormann (1976) documented that spring ephemeral species, such as dogtooth violet (*Erythronium americanum*), can decrease the potential loss of nutrients, especially N, through rapid uptake before the deciduous canopy develops, at a time when uptake by trees is minimal.



Rapid decomposition of spring ephemeral foliage makes these nutrients available to trees later in the spring, when they are more capable of taking up soil nutrients. This phenomenon has been called the vernal dam hypothesis (Muller 2003).

### Response to disturbance

Forest ecosystems experience a variety of natural and anthropogenic disturbances. Because of profound differences in growth form and mechanisms of reproduction, the plants of the herbaceous layer generally respond to such disturbances in ways distinct from trees. Here I distinguish herb-layer responses as a function of contrasting forms of disturbance. “Acute” responses follow discrete disturbance events, such as clear-cut harvesting or severe damage from wind (e.g., tornadoes), and are mostly short-lived. “Legacy” responses are those that follow the alteration of the environment on longer timescales, such as the conversion of forest to agricultural land and then back to forest. In addition, many anthropogenic changes in the environment represent chronic disturbances that may result in novel responses of herb-layer species. Of these, I will briefly examine four: increased concentrations of atmospheric carbon dioxide (CO<sub>2</sub>), increased incidence of ultraviolet (UV) radiation, invasions of forests by exotic species, and increased atmospheric deposition of N.

**Acute responses.** Natural disturbances to the forest canopy that can elicit acute responses in the herb layer include wind (e.g., tornado, hurricane), crown fire (i.e., fires that damage part of or the entire canopy of trees), ice storms, and outbreaks of insect defoliation. Roberts and Gilliam (2003) presented a disturbance model that defined disturbance type and severity as a function of two potentially independent variables—extent of canopy removal and degree of disturbance to the forest floor (figure 6). Thus, a disturbance to the canopy, such as a hurricane, may have indirect effects on the herb layer by altering the structure of the forest or by altering the physical environment of the forest floor. Other disturbances, such as a crown fire, also can have more direct influences by consuming preexisting plants and limiting the availability of seeds (figure 6). Roberts (2004) added a third dimension—the amount of herb-layer vegetation directly removed by the disturbance—to expand this model.

There has been a great deal of debate in the ecological literature regarding whether timber harvesting has a negative impact on the herbaceous layer. Some of the controversy arises from the large variability among studies that address this issue, including variation in forest types (e.g., conifer versus hardwood), stand ages (e.g., old-growth, mature, or young stands), sampling methods (e.g., size, shape, number, and location of plots), and variables measured (e.g., species composition, species diversity, herb-layer cover or biomass). The work of Duffy and Meier (1992) and Meier and colleagues (1995), which compared the herb layer of old-growth and second-growth stands in the southeastern United States, concluded that harvesting can cause long-lived decreases in herb-

layer cover and diversity. By contrast, other studies comparing mature second-growth stands with recently harvested stands of varying ages typically have found that the species composition, cover, and diversity of the herbaceous layer often return to preharvest levels within 10 to 20 years after timber harvesting (Gilliam et al. 1995, Halpern and Spies 1995, Roberts and Zhu 2002). Harvesting effects in a variety of forest types throughout North America are reviewed and summarized in Roberts and Gilliam (2003).

**Legacy responses.** The now forested landscape in much of the eastern United States is the outcome of conversion of primal forest to agriculture, followed by forest regrowth after the abandonment of farmlands (Bellemare et al. 2002, Christensen and Gilliam 2003, Flinn and Vellend 2005). Because of the responsiveness of herb-layer species to forest site conditions (Small and McCarthy 2005), these past events have created long-lived influences on the species composition and diversity (including genetic diversity; see Vellend 2004) of the herbaceous layer. Flinn and Vellend (2005) reported that in some regions up to 80% of current forested land was once under agricultural use. They further concluded that the herb-layer communities of forests that have recovered following agricultural abandonment are typically depleted in native species, compared with those of uncleared forests.

Many of the legacy effects created by past land use arise from disturbance-mediated limitations to dispersal for certain sensitive herbaceous species, most of which are slow to colonize space made available after conversion back to forest. Verheyen and colleagues (2003) carried out an extensive literature-based study that examined the responses of forest plant species to land-use changes in eight European countries and four states in the northeastern United States. They concluded that slow-colonizing species are typically those that have low fecundity, unassisted dispersal, large seeds that limit dispersibility, or combinations of these traits. Fraterrigo and colleagues (2006a) found that legacy effects of previous land use can include alterations in growth allocation of forest plants. For example, they found that herbaceous species in previously farmed southern Appalachian forests allocated more growth to leaves than to stems, whereas the opposite pattern occurred in reference stands that had not been farmed. Indeed, legacy effects can be extremely long-lived. Dambrine and colleagues (2007) demonstrated that the effects of Roman agriculture are still evident in the forests of central France. Millennia after agricultural abandonment, species richness and the prevalence of nitrophilous (high-N-requiring) species were higher around ancient Roman farm settlements.

One of the factors that contribute to the maintenance of species diversity in forests is the spatial heterogeneity of the forest environment, for example, from soil pits and tip-up mounds created when old trees die and fall over (Beatty 2003). Conversion of forest land to agricultural use decreases this naturally high spatial heterogeneity. Working in southern Appalachian forests, Fraterrigo and colleagues (2006b) evaluated the importance of land-use history on herb-layer

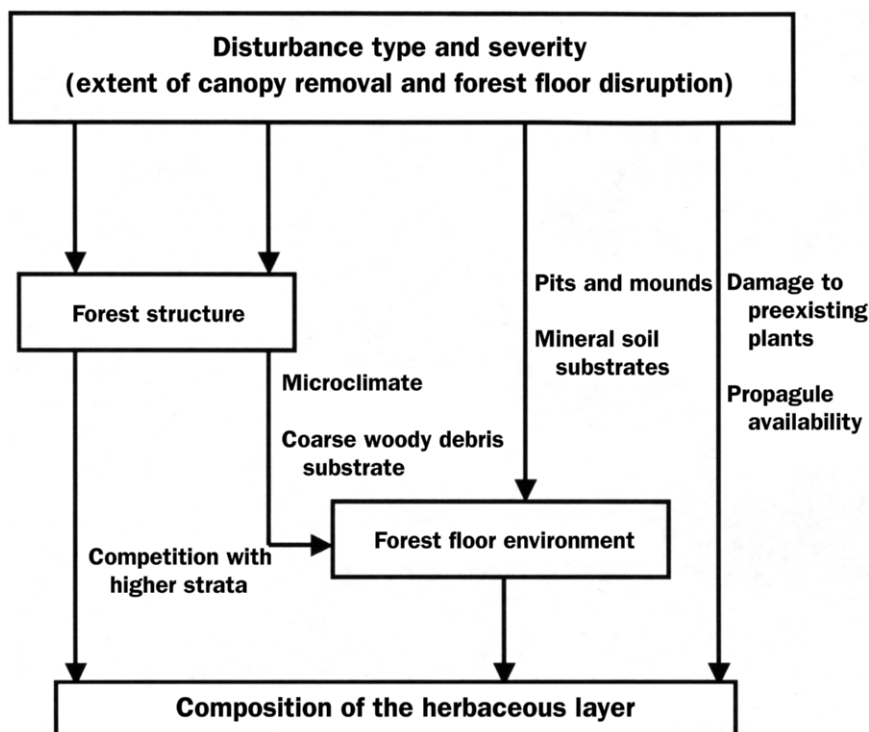


Figure 6. Conceptual model of processes that determine short- and long-term responses of the herbaceous layer to disturbances of varying severity. Modified from Roberts and Gilliam (2003) with permission from Oxford University Press.

communities. They concluded that past farming and logging practices in western North Carolina, followed by reforestation in the mid-1900s, have altered spatial heterogeneity of soil nutrient resources in ways that have, in turn, created long-term change in the herbaceous layer.

Most US forests are the result of recovery from some form of stand-destroying disturbance. As of 2002, approximately 85% of all forest stands in the United States as a whole were under 100 years old; only about 0.1% were over 200 years old (figure 7). This latter age is commonly used as part of a suite of characteristics used to delineate old-growth forests (Oliver and Larson 1996, McCarthy 2003). Thus, forest stands that have escaped any profound influences of human activity are by far the exception rather than the rule. Consequently, herb-layer characteristics that we currently observe often represent legacy responses to the land-use history of the forest. See Foster and colleagues (2003) for a recent review of the legacy effects of land use on a variety of ecological processes.

The kind of habitat fragmentation associated with land-use practices often drives species to local extinction, although there is often a lag time before the inevitable extinction occurs. Tilman and colleagues (1994) referred to the degree to which this time lag develops for a given habitat patch as “extinction debt.” Vellend and colleagues (2006) applied this concept to herbaceous species’ response to forest fragmentation in Europe, where temperate deciduous forests are particularly fragmented. They concluded that extinction debt in these stands can persist for more than 100 years.

Although, as the preceding discussion suggests, most of the legacy responses represent a negative impact of land use on forest biodiversity through the local extinction of sensitive forest herbaceous species, there has been a positive side to this interplay between agricultural practices and forest development. Christensen and Gilliam (2003) reviewed the rich historical ecological literature on studies of abandoned farmlands in the Piedmont region of North Carolina. They referred to this region as “the community ecologists’ equivalent of the fruit fly or *E. coli*—in a sense, the ‘model organism’” for the study of an ecological process, namely old-field succession, that has done much to shape ecologists’ understanding of the nature of vegetation dynamics. Land degradation coincided with bleak economic conditions in the North Carolina Piedmont to cause widespread agricultural abandonment for over a half-century after the Civil War. The landscape of that region became a patchwork of tracts of formerly agricultural land of varying ages following their abandonment and subsequent conversion back

to forest. This led to numerous space-for-time approaches to the study of succession, wherein plant ecologists would simultaneously sample plant communities in fields that differed in the time elapsed since their abandonment (Billings 1938, Oosting 1942). To this day, studies such as these help form the cornerstone for the foundations of vegetation science.

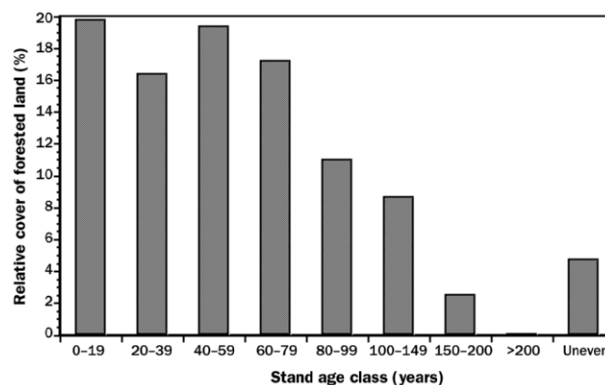


Figure 7. Relative cover of forest stands of varying age in the United States as of 2002. Values represent the percentage cover of all forested lands, calculated from data taken from the Forest Inventory and Analysis National Program, US Department of Agriculture Forest Service (<http://fia.fs.fed.us/program-features/rpa>).

**Chronic disturbances.** Several disturbances potentially affecting the herbaceous layer result in neither acute nor legacy responses. Although these disturbances vary considerably, they all share two common traits: (1) they are of anthropogenic origin, and (2) they occur in the form of chronically altered environmental conditions for species in the herbaceous layer. The responses of the herbaceous layer to these disturbances, owing to their chronic nature, are distinct from its responses to other types of disturbance.

**Increases in atmospheric carbon dioxide.** Although far more research on the effects of increased CO<sub>2</sub> has dealt with tree species and species in herb-dominated communities (e.g., grasslands) than with herb-layer species in forests, Neufeld and Young (2003) made a compelling argument that increases in atmospheric CO<sub>2</sub> can elicit novel responses among herb-layer species. Beerling and Kelly (1997) demonstrated a significant, positive relationship between the stomatal density of a prominent forest herb in England (*Mercurialis perennis*, or dog's mercury) and atmospheric CO<sub>2</sub> from 1927 to 1995, a time during which CO<sub>2</sub> increased by 18% (from 300 to 355 microliters [μL] per liter [L]). Using open-top chambers to vary CO<sub>2</sub> concentrations experimentally in intact spruce forests in Sweden, Hättenschwiler and Körner (1996, 2000) found that increased CO<sub>2</sub> had influences (e.g., changes in photosynthetic rates, growth rates, and plant-herbivore interactions) that exhibited great interspecific variation on both herbaceous species and seedlings of several tree species. This suggests that further increases in atmospheric CO<sub>2</sub> may alter the species composition of the herb layer of forests.

The changing herb layer may have implications for human health. Mohan and colleagues (2006) took advantage of free-air CO<sub>2</sub> enrichment (FACE), perhaps the most realistic field simulation of increased CO<sub>2</sub>, to study its effects on *Toxicodendron radicans* (poison ivy). FACE sites expose vegetation to experimentally controlled levels of CO<sub>2</sub> without enclosures, such as open-top chambers, that can alter the microenvironment of the plants (Schlesinger and Lichter 2001). The findings from Mohan and colleagues' six-year study at the loblolly pine FACE site at Duke University have disturbing implications for those who suffer from the allergy-mediated dermatitis caused by contact with *T. radicans*. Concentrations of CO<sub>2</sub> simulated at levels expected by the year 2050 (570 μL per L) increased net photosynthesis in *T. radicans* by nearly 80%, resulting in increases in biomass of 150%. Furthermore, greater concentrations of CO<sub>2</sub> stimulated production of urushiol, the hydrocarbon responsible for the allergic response, with an increase of more than 150% in its more potent unsaturated form. In short, there could be more, and more toxic, poison ivy in our CO<sub>2</sub>-enhanced future.

**Increases in the incidence of ultraviolet radiation.** The amount of UV radiation reaching the Earth's surface has grown dramatically over the past several decades, a result of reductions in the protective ozone layer in the stratosphere (Solomon 1999). It has long been known that UV radiation, and particularly UVB radiation (wavelengths 280 to 320 nm), can be harmful to plants (Caldwell 1971). Most early

work on the effects of UVB on plants involved species such as crops and alpine plants, which occupy environments with high solar radiation or a thin atmosphere, or both (Searles et al. 2001). Fewer studies have examined the effects of UVB radiation on forest herb-layer species—understandably, since far less UVB penetrates intact canopies to reach the forest floor (Brown et al. 1994).

In deciduous forests, the seasonal increase in solar radiation begins before leaf-out (the breaking of buds to produce new leaves), allowing an appreciable amount of direct solar radiation to reach the forest floor. Grant and colleagues (2005) demonstrated that the UVB radiation reaching the herbaceous layer of a deciduous forest was similar to that incident on the forest canopy during the period before spring leaf-out; this level continued to increase for nearly three weeks after the initiation of leaf-out. They predicted that herb-layer species would receive nearly 30% more UVB with a decrease of 20 Dobson units of stratospheric ozone. Rousseaux and colleagues (2001) concluded that increased UVB radiation associated with erosion of the ozone layer may inhibit the growth of some herbaceous species and alter their ecological relationships with insects (e.g., herbivory). Indeed, Ballaré and colleagues (1996) found that the intensity of herbivory was proportional to the dose of UVB exposure between near-zero and full ambient levels.

**Introductions of exotic species.** Introductions of exotic species to forests generally alter the often-delicate balance of factors that maintain the species composition of forest communities. Not surprisingly, the ecological impacts of invasive species have generated considerable interest among ecologists, particularly since the time of Sir Charles Elton in the 1950s. Invasions potentially include numerous species at all trophic levels. Here I focus on three types of invasions relevant to the composition and diversity of forest herb layers: invasive herbaceous species, exotic earthworms, and vertebrate herbivores. For a recent synthesis, see Sax and colleagues (2005).

Luken (2003) concluded that undisturbed forest communities with intact canopies are generally resistant to invasion by exotic plant species. Indeed, McCarthy (2003) found that an old-growth deciduous forest in Ohio contained no nonnative species in the herbaceous layer, despite being surrounded by relatively disturbed forests that were the potential source of numerous invasive species, such as *Alliaria petiolata* (garlic mustard). Thus, the degree of invasion by nonnative plant species can be a function of the degree of anthropogenic disturbance (e.g., harvesting [Roberts and Zhu 2002] or atmospheric deposition of pollutants [Gilliam 2006]).

Once exotic plants become established in the herb layer of a forest, they can rapidly become the dominant species, not only altering the species composition of the herb layer but also decreasing biodiversity. Mechanisms for this response include nonnative species' strong tendency to compete more successfully than native species; their ability to escape herbivory in their new environment; and their tendency to alter soil resources, which thus become less conducive to native species' success and more conducive to that of nonnative species.

For example, Ehrenfeld and colleagues (2001) found that invasive species in the forests of northern New Jersey caused significant increases in soil pH and in the availability of soil N. Other changes in soil conditions arise from differences between exotic and native species in terms of productivity, foliar chemistry, plant morphology, and phenology (Ehrenfeld 2003).

Many forests of eastern North America developed in the absence of native earthworms, yet introductions of exotic earthworm species began with the first European settlers and continue at an increasing rate as a result of human activities such as logging, road construction, relocation of used soil material (horticultural and fill), and release of unused bait by anglers (Bohlen et al. 2004). Of particular importance are European earthworms of the family Lumbricidae. Ecological problems associated with the further establishment of these species are related to their ability—indeed, proclivity—to alter soil characteristics by consuming soil organic matter, which influences both soil structure and nutrient availability for plants (Hale et al. 2006).

Such changes in soil physical structure and nutrient resources have potentially deleterious effects on the herbaceous layer of affected forests. Working in the hardwood forests of north-central Minnesota, Hale and colleagues (2006) found that increases in a single earthworm species—*Lumbricus rubellus*—brought about profound changes in the herb-layer community, which was notably diverse in the earthworm's absence. In areas with a maximum biomass of *L. rubellus*, however, the herb layer was dominated by only one or two species—or, at some sites, was totally absent. Bohlen and colleagues (2004) identified three direct effects of exotic earthworms on herb-layer species: (1) reduced reproduction and survival resulting from the consumption and deep burial of seeds, (2) alteration of germination microclimate, and (3) increased susceptibility to vertebrate herbivory.

An additional chronic disturbance to the herbaceous layer of forests is overbrowsing by vertebrate herbivores. In western North American forests, this is often the result of introduced herbivores (Vila et al. 2003). By contrast, in eastern North American forests, the problem is largely a function of overpopulation of native species, such as white-tailed deer, caused by the removal of top carnivores, such as wolves and mountain lions (Côté et al. 2004). Rooney and Waller (2003) reported that the diversity of herbaceous communities in forests throughout eastern North America has declined substantially in areas with high densities of white-tailed deer. Because of their sensitivity to overbrowsing, some species of herbaceous plants (e.g., *Trillium* spp.) have been used as indicators of browsing intensity (Côté et al. 2004).

**Atmospheric deposition of excess nitrogen.** Galloway and colleagues (2004) estimated that total atmospheric deposition of N to terrestrial ecosystems will have increased nearly 10-fold over the period 1860–2050 as a result of human activities, including high-energy combustion, fertilizer production, and agricultural practices. Characteristics of the herbaceous layer, such as biomass, composition, and

diversity, have been shown to respond sensitively to changes in available soil N (see Small and McCarthy 2005). Recent research has shown a direct relationship between excess N deposition and changes in forest species composition, accompanied by marked declines in species diversity of the herbaceous layer. This is not confined to vascular species; Mäkipää (1998) found that experimental N additions reduced by up to 80% the biomass of moss species that were the dominant plant forms in the understory of spruce stands in Finland. Other work in Europe has demonstrated that declines in herb-layer biodiversity caused by excess N can last up to 10 years or longer after N additions cease (Strengbom et al. 2001).

Comparisons among studies of hardwood forests in the eastern United States suggest that sensitivity varies widely among sites. For example, Hurd and colleagues (1998) found that the cover of three prominent herbaceous species, *Oxalis acetosella* (wood sorrel), *Maianthemum canadense* (Canada mayflower), and *Huperzia lucidula* (shining clubmoss), in the hardwood forests of the Adirondack Mountains, New York, declined significantly after only three years of experimental N additions. By contrast, Gilliam and colleagues (2006b) found no significant response of the herbaceous layer to six years of N applications (via helicopter) in a hardwood-dominated watershed of the Fernow Experimental Forest, West Virginia.

In a recent review, Gilliam (2006) concluded that herbaceous-layer response to increased N availability often includes the following stages: (a) initial increases in herb-layer cover; (b) decreases in species richness, caused by the loss of numerous species that are efficient under low-N conditions; (c) decreases in species evenness, caused by the increasing dominance of relatively few species that require high N availability; and (d) loss of forest biodiversity as a result of these decreases in species richness and evenness. Gilliam (2006) went on to propose the N homogeneity hypothesis, which predicts that as excess N inputs reduce the naturally high spatial heterogeneity in soil N availability (i.e., patchiness) that helps to maintain the species diversity of the herbaceous layer, the biodiversity of affected forests will decline.

## Conclusions

The herbaceous layer is significant to the structure and function of forest ecosystems in ways that belie its diminutive stature. It represents less than 1% of the biomass of the forest, yet can contain 90% or more of the plant species of the forest and contribute up to 20% of the foliar litter to the forest floor—litter that is generally of higher nutrient content than that of trees. As the site of intense competitive interactions, the herb layer can direct the development of forests after canopy-removing disturbances and can become intricately linked with species of the forest canopy. Herb-layer species with phenologies that dictate growth and development in the early spring (i.e., spring ephemerals) can mitigate the potential loss of nutrients, such as N, that are essential to all plants, including trees.



In many ways, herbaceous-layer communities are resilient to disturbance. A wealth of evidence suggests that the species composition and diversity of the herb layer can return rapidly, after a disturbance such as timber harvesting, to predisturbance conditions. However, species with narrow requirements for habitat conditions may be more sensitive to disturbances. Accordingly, the legacy effects of more intense disturbances, such as plowing as a part of agricultural practices, may exclude these species for a long period of time. This interspecific variability precludes broad generalizations regarding the response of the herb layer to disturbance.

Although discussed separately in this overview, the many chronic, anthropogenic alterations in the forest environment exert their influence on the herbaceous layer simultaneously. Indeed, determining the effects of these multiple stresses on species in the herbaceous layer presents current and future challenges to plant ecologists. In many ways, this form of disturbance represents an ecological “moving target” for sensitive species of the herb layer, given that current conditions are far different from those under which these species evolved, and they are continuing to change—often, as with CO<sub>2</sub>, unabatedly. Although it is difficult to predict the ultimate response of forest herbaceous layers under future scenarios of anthropogenic change, one thing seems likely: they will change, and will do so in unprecedented ways and at unprecedented rates.

### Acknowledgments

I thank Scott Collins and Dan Simberloff for their invitation and encouragement to write this manuscript, and Todd Ristau for his invitation to present an oral version of this article at the 2007 annual meeting of the Society of American Foresters. I am indebted to several valued colleagues for the exchange of ideas and herb-layer data, including Katherine Elliott, Charles Halpern, Brian McCarthy, and Christine Small. Tom Siccama was helpful following the review of the initial revision and shared useful information by e-mail, including data for table 2. I also thank Joan Ehrenfeld, Steve Horsley, Christine Small, and Nicole Welch for reading an earlier draft of the manuscript and making valuable critical comments. Beverly Surratt provided invaluable assistance with graphics preparation. Helpful suggestions from three anonymous reviewers further improved the manuscript. Finally, I express special appreciation for my good friend and colleague, Mark Roberts, for the use of data, for years of collaboration on herb-layer dynamics, and for an arid wit that makes this work fun. Funding for my work at the Fernow Experimental Forest was provided by grants from the US Department of Agriculture and the National Science Foundation.

### References cited

Anderson RC, Loucks OL, Swain AM. 1969. Herbaceous response to canopy cover, light intensity, and throughfall precipitation in coniferous forests. *Ecology* 50: 255–263.

- Baker TT, Van Lear DH. 1998. Relations between density of rhododendron thickets and diversity of riparian forests. *Forest Ecology and Management* 109: 21–32.
- Ballaré CL, Scopel AL, Stapleton AE, Yanovsky MJ. 1996. Solar ultraviolet-B radiation affects seedling emergence, DNA integrity, plant morphology, growth rate, and attractiveness to herbivore insect in *Datura ferox*. *Plant Physiology* 112: 161–170.
- Beatty SW. 2003. Habitat heterogeneity and maintenance of species in understory communities. Pages 177–197 in Gilliam FS, Roberts MR, eds. *The Herbaceous Layer in Forests of Eastern North America*. New York: Oxford University Press.
- Beerling DJ, Kelly CK. 1997. Stomatal density responses of temperate woodland plants over the past seven decades of CO<sub>2</sub> increase: A comparison of Salisbury (1927) with contemporary data. *American Journal of Botany* 84: 1572–1583.
- Bellemare J, Motzkin G, Foster DR. 2002. Legacies of the agricultural past in the forested present: An assessment of historical land-use effects on rich mesic forests. *Journal of Biogeography* 29: 1401–1420.
- Billings WD. 1938. The structure and development of old field short-leaf pine stands and certain associated physical properties of the soil. *Ecological Monographs* 8: 437–499.
- Bohlen PJ, Scheu S, Hale CM, McLean MA, Migge S, Groffman PM, Parkinson D. 2004. Nonnative invasive earthworms as agents of change in northern temperate forests. *Frontiers in Ecology and the Environment* 2: 427–435.
- Brown MJ, Parker GG, Posner NE. 1994. A survey of ultraviolet-B radiation in forests. *Journal of Ecology* 82: 843–854.
- Caldwell MM. 1971. Solar ultraviolet radiation and the growth and development of higher plants. *Phytophysiology* 6: 131–177.
- Christensen NL, Gilliam FS. 2003. Temporal and spatial patterns of herbaceous layer communities on the North Carolina Piedmont. Pages 224–237 in Gilliam FS, Roberts MR, eds. *The Herbaceous Layer in Forests of Eastern North America*. New York: Oxford University Press.
- Côté SD, Rooney TP, Tremblay J-P, Dussault C, Waller DM. 2004. Ecological impacts of deer overabundance. *Annual Review of Ecology, Evolution, and Systematics* 35: 113–147.
- Dambrine E, Dupouey J-L, Laüt L, Humbert L, Thion M, Beaufils T, Richard H. 2007. Present forest biodiversity patterns in France related to former Roman agriculture. *Ecology* 88: 1430–1439.
- De Grandpré L, Bergeron Y, Nguyen T, Boudreault C, Grondin P. 2003. Composition and dynamics of the understory vegetation in the boreal forests of Canada. Pages 238–261 in Gilliam FS, Roberts MR, eds. *The Herbaceous Layer in Forests of Eastern North America*. New York: Oxford University Press.
- Duffy DC, Meier AJ. 1992. Do Appalachian herbaceous understories ever recover from clearcutting? *Conservation Biology* 6: 196–201.
- Ehrenfeld JG. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* 6: 503–523.
- Ehrenfeld JG, Kourtev P, Huang W. 2001. Changes in soil functions following invasions of exotic understory plants in deciduous forests. *Ecological Applications* 11: 1287–1300.
- Elliott KJ, Knoepp JD. 2005. The effects of three regeneration harvest methods on plant diversity and soil characteristics in the southern Appalachians. *Forest Ecology and Management* 211: 296–317.
- Elliott KJ, Boring LR, Swank WT, Haines BL. 1997. Successional changes in plant species diversity and composition after clearcutting a Southern Appalachian watershed. *Forest Ecology and Management* 92: 67–85.
- Flinn KM, Vellend M. 2005. Recovery of forest plant communities in post-agricultural landscapes. *Frontiers in Ecology and the Environment* 3: 243–250.
- Foster D, Swanson F, Aber J, Burke I, Brokaw N, Tilman D, Knapp A. 2003. The importance of land-use legacies to ecology and conservation. *BioScience* 53: 77–88.
- Fraterrigo JM, Turner MG, Pearson SM. 2006a. Previous land use alters plant allocation and growth in forest herbs. *Journal of Ecology* 94: 548–557.
- . 2006b. Interactions between past land use, life-history traits and understory spatial heterogeneity. *Landscape Ecology* 21: 777–790.

- Fridley JD, Peet RK, Wentworth TR, White PS. 2005. Connecting fine- and broad-scale species-area relationships of southeastern U.S. flora. *Ecology* 86: 1172–1177.
- Galloway JN, et al. 2004. Nitrogen cycles: Past, present, and future. *Biogeochemistry* 70: 153–226.
- George LO, Bazzaz FA. 2003. The herbaceous layer as a filter determining spatial pattern in forest tree regeneration. Pages 265–282 in Gilliam FS, Roberts MR, eds. *The Herbaceous Layer in Forests of Eastern North America*. New York: Oxford University Press.
- Gilliam FS. 2006. Response of the herbaceous layer of forest ecosystems to excess nitrogen deposition. *Journal of Ecology* 94: 1176–1191.
- Gilliam FS, Roberts MR. 2003a. *The Herbaceous Layer in Forests of Eastern North America*. New York: Oxford University Press.
- . 2003b. Introduction: Conceptual framework for studies of the herbaceous layer. Pages 3–11 in Gilliam FS, Roberts MR, eds. *The Herbaceous Layer in Forests of Eastern North America*. New York: Oxford University Press.
- . 2003c. Interactions between the herbaceous layer and overstorey canopy of eastern forests: A mechanism for linkage. Pages 198–223 in Gilliam FS, Roberts MR, eds. *The Herbaceous Layer in Forests of Eastern North America*. New York: Oxford University Press.
- Gilliam FS, Turrill NL, Adams MB. 1995. Herbaceous-layer and overstorey species in clear-cut and mature central Appalachian hardwood forests. *Ecological Applications* 5: 947–955.
- Gilliam FS, Platt WJ, Peet RK. 2006a. Natural disturbances and the physiognomy of pine savannas: A phenomenological model. *Applied Vegetation Science* 9: 83–96.
- Gilliam FS, Hockenberry AW, Adams MB. 2006b. Effects of atmospheric nitrogen deposition on the herbaceous layer of a central Appalachian hardwood forest. *Journal of the Torrey Botanical Society* 133: 240–254.
- Grant RH, Apostol K, Gao W. 2005. Biologically effective UV-B exposures of an oak-hickory forest understorey during leaf-out. *Agricultural and Forest Meteorology* 132: 28–43.
- Hale CM, Frelich LE, Reich PB. 2006. Changes in cold-temperate hardwood forest understorey plant communities in response to invasion by European earthworms. *Ecology* 87: 1637–1649.
- Halpern CB, Spies TA. 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. *Ecological Applications* 5: 913–934.
- Hättenschwiler S, Körner C. 1996. Effects of elevated CO<sub>2</sub> and increased nitrogen deposition on photosynthesis and growth of understorey plants in spruce model ecosystems. *Oecologia* 106: 172–180.
- . 2000. Tree seedling responses to *in situ* CO<sub>2</sub>-enrichment differ among species and depend on understorey light availability. *Global Change Biology* 6: 213–226.
- Horsley SB. 1993. Mechanisms of interference between hayscented fern and black cherry. *Canadian Journal of Forest Research* 23: 2059–2069.
- Hurd TM, Brach AR, Raynal DJ. 1998. Response of understorey vegetation of Adirondack forests to nitrogen additions. *Canadian Journal of Forest Research* 28: 799–807.
- Jolls CL. 2003. Populations of and threats to rare plants of the herb layer: More challenges and opportunities for conservation biologists. Pages 105–162 in Gilliam FS, Roberts MR, eds. *The Herbaceous Layer in Forests of Eastern North America*. New York: Oxford University Press.
- Keeley JE, Fotheringham CJ. 2005. Plot shape effects on plant species diversity measurements. *Journal of Vegetation Science* 16: 249–256.
- Levin DA, Wilson AC. 1976. Rates of evolution in seed plants: Net increase in diversity of chromosome numbers and species numbers through time. *Proceedings of the National Academy of Sciences* 73: 2086–2090.
- Luken JO. 2003. Invasions of forests of the eastern United States. Pages 283–301 in Gilliam FS, Roberts MR, eds. *The Herbaceous Layer in Forests of Eastern North America*. New York: Oxford University Press.
- Lyon J, Sharpe WE. 2003. Impacts of hay-scented fern on nutrition of northern red oak seedlings. *Journal of Plant Nutrition* 26: 487–502.
- Mäkipää R. 1998. Sensitivity of understorey vegetation to nitrogen and sulphur deposition in a spruce stand. *Ecological Engineering* 10: 87–95.
- McCarthy BC. 2003. The herbaceous layer of eastern old-growth deciduous forests. Pages 163–176 in Gilliam FS, Roberts MR, eds. *The Herbaceous Layer in Forests of Eastern North America*. New York: Oxford University Press.
- Meier AJ, Bratton SP, Duffy DC. 1995. Possible ecological mechanisms for loss of vernal-herb diversity in logged eastern deciduous forests. *Ecological Applications* 5: 935–946.
- Mohan JE, Ziska LH, Schlesinger WH, Thomas RB, Sicher RC, George K, Clark JS. 2006. Biomass and toxicity responses of poison ivy (*Toxicodendron radicans*) to elevated atmospheric CO<sub>2</sub>. *Proceedings of the National Academy of Sciences* 103: 9086–9089.
- Muller RN. 1978. The phenology, growth and ecosystem dynamics of *Erythronium americanum* in the northern hardwood forest. *Ecological Monographs* 48: 1–20.
- . 2003. Nutrient relations of the herbaceous layer in deciduous forest ecosystems. Pages 15–37 in Gilliam FS, Roberts MR, eds. *The Herbaceous Layer in Forests of Eastern North America*. New York: Oxford University Press.
- Muller RN, Bormann FH. 1976. Role of *Erythronium americanum* Ker. in energy flow and nutrient dynamics of a northern hardwood forest ecosystem. *Science* 193: 1126–1128.
- Neufeld HS, Young DR. 2003. Ecophysiology of the herbaceous layer in temperate deciduous forests. Pages 38–90 in Gilliam FS, Roberts MR, eds. *The Herbaceous Layer in Forests of Eastern North America*. New York: Oxford University Press.
- Oliver CD, Larson BC. 1996. *Forest Stand Dynamics*. Update ed. New York: Wiley.
- Oosting HJ. 1942. An ecological analysis of the plant communities of Piedmont, North Carolina. *American Midland Naturalist* 28: 1–126.
- Peet RK, Wentworth TR, White PS. 1998. A flexible, multipurpose method for recording vegetation composition and structure. *Castanea* 63: 262–274.
- Pittillo JD, Lee M. 1984. Reference Plant Collection of the Coweeta Hydrologic Laboratory. Asheville (NC): US Department of Agriculture, Forest Service, Southeastern Forest Experiment Station. General Technical Report SE-29.
- Platt WJ, Carr SM, Reilly M, Fahr J. 2006. Pine savanna overstorey influences on ground-cover biodiversity. *Applied Vegetation Science* 9: 37–50.
- Qian H, Klinka K, Kayahara GJ. 1998. Longitudinal patterns of plant diversity in the North American boreal forest. *Plant Ecology* 138: 161–178.
- Roberts MR. 2004. Response of the herbaceous layer to disturbance in North American forests. *Canadian Journal of Botany* 82: 1273–1283.
- Roberts MR, Gilliam FS. 2003. Response of the herbaceous layer to disturbance in eastern forests. Pages 302–320 in Gilliam FS, Roberts MR, eds. *The Herbaceous Layer in Forests of Eastern North America*. New York: Oxford University Press.
- Roberts MR, Zhu L. 2002. Early response of the herbaceous layer to harvesting in a mixed coniferous-deciduous forest in New Brunswick, Canada. *Forest Ecology and Management* 155: 17–31.
- Rooney TP, Waller DM. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecology and Management* 181: 165–176.
- Rousseaux MC, Scopel AL, Searles PS, Caldwell MM, Sala OE, Ballaré CL. 2001. Responses to solar ultraviolet-B radiation in a shrub-dominated natural ecosystem of Tierra del Fuego (southern Argentina). *Global Change Biology* 7: 467–478.
- Sax D, Stachowicz JJ, Gaines SD. 2005. *Species Invasions: Insights into Ecology, Evolution, and Biogeography*. Sunderland (MA): Sinauer.
- Schlesinger WH, Lichter J. 2001. Limited carbon storage in soil and litter of experimental forest plots under elevated atmospheric CO<sub>2</sub>. *Nature* 411: 466–469.
- Searles PS, Flint SD, Caldwell MM. 2001. A meta-analysis of plant field studies simulating stratospheric ozone depletion. *Oecologia* 127: 1–10.
- Shmida A. 1984. Whittaker's plant diversity sampling method. *Israel Journal of Botany* 33: 41–46.
- Siccama TG, Bormann FH, Likens GE. 1970. The Hubbard Brook ecosystem study: Productivity, nutrients and phytosociology of the herbaceous layer. *Ecological Monographs* 40: 389–402.
- Small CJ, McCarthy BC. 2002. Spatial and temporal variation in the response of understorey vegetation to disturbance in a central Appalachian oak forest. *Journal of the Torrey Botanical Society* 129: 136–153.

- . 2005. Relationship of understory diversity to soil nitrogen, topographic variation, and stand age in an eastern oak forest, USA. *Forest Ecology and Management* 217: 229–243.
- Solomon S. 1999. Stratospheric ozone depletion: A review of concepts and history. *Review of Geophysics* 37: 275–316.
- Spyreas G, Matthews JW. 2006. Floristic conservation value, nested understory floras, and the development of second-growth forest. *Ecological Applications* 16: 1351–1366.
- Strengbom J, Nordin A, Näsholm T, Ericson L. 2001. Slow recovery of boreal forest ecosystem following decreased nitrogen input. *Functional Ecology* 15: 451–457.
- Struik GJ, Curtis JT. 1962. Herb distribution in an *Acer saccharum* forest. *American Midland Naturalist* 68: 285–296.
- Taft JB. 2003. Fire effects on community structure, composition, and diversity in a dry sandstone barrens. *Journal of the Torrey Botanical Society* 130: 170–192.
- Tilman D, May RM, Lehman CL, Nowak MA. 1994. Habitat destruction and the extinction debt. *Nature* 371: 65–66.
- Vellend M. 2004. Parallel effects of land-use history on species diversity and genetic diversity of forest herbs. *Ecology* 85: 3043–3055.
- Vellend M, Verheyen K, Jacquemyn H, Kolb A, Van Calster H, Peterken G, Hermy M. 2006. Extinction debt of forest plants persists for more than a century following habitat fragmentation. *Ecology* 87: 542–548.
- Verheyen K, Honnay O, Motzkin G, Hermy M, Foster DR. 2003. Response of forest plant species to land-use change: A life-history trait-based approach. *Journal of Ecology* 91: 563–577.
- Vila B, Torre F, Martin J-L, Guibal F. 2003. Response of young *Tsuga heterophylla* to deer browsing: Developing tools to assess deer impact on forest dynamics. *Trees* 17: 547–553.
- Welch NL, Belmont JM, Randolph JC. 2007. Summer ground layer biomass and nutrient contribution to aboveground litter in an Indiana temperate deciduous forest. *American Midland Naturalist* 157: 11–26.
- Whigham DF. 2004. Ecology of woodland herbs in temperate deciduous forests. *Annual Review of Ecology and Systematics* 35: 583–621.
- Zavitkovski J. 1976. Ground vegetation biomass, production, and efficiency of energy utilization in some northern Wisconsin forest ecosystems. *Ecology* 57: 694–706.

doi:10.1641/B571007

Include this information when citing this material.