

**PART FOUR
COMMUNITY
DYNAMICS
OF THE
HERBACEOUS
LAYER AND
THE ROLE OF
DISTURBANCE**

13 Response of the Herbaceous Layer to Disturbance in Eastern Forests

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Forests are exposed to a wide variety of both natural and anthropogenic disturbances, variously defined (see below). The herbaceous layer is not only potentially quite sensitive to these events, but such effects also vary considerably among forests and types of disturbance. The dynamic response of the herb layer to disturbance has been of increasing interest to plant ecologists in recent decades (fig. 13.1), which is likely responsible for the increased attention paid to the herb layer in the ecological literature.

Several definitions of disturbance have been proposed, some restricted to discrete events (White and Pickett 1985) and others with long-term environmental fluctuations (Ryan 1991). We restrict our discussion to relatively discrete events because these are more readily tractable, and most types of direct management interventions (e.g., forest harvesting) are discrete in time and space. Accordingly, we adopt the definition of White and Pickett (1985) as our working definition of disturbance: “any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment” (7). We recognize the admonition of Pickett et al. (1989) that disturbance affects all levels of organization differently, from individuals to ecosystems and landscapes, and that most empirical work focuses on effects of disturbance on community structure rather than on ecological processes.

Although ecologists generally recognize that disturbances of various kinds strongly influence the structure and function of plant communities (e.g., White 1979; Pickett and White 1985), most attention has focused on disturbance size and frequency, with little explicit consideration of severity (Malanson 1984; Peterson and Pickett 1991; Peterson 2000). If more attention were given to the severity aspect of the disturbance

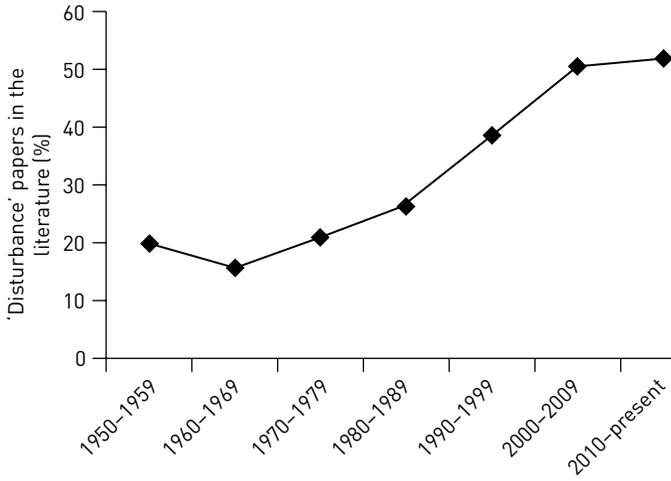


FIGURE 13.1 Relative (%) number of herb layer papers with focus on effects of disturbance by decade, from 1950 to present. Based on a literature search by Google Scholar™.

regime, our understanding of ecosystem dynamics and our ability to predict consequences of management actions would be greatly refined. Thus, we emphasize disturbance severity and give due consideration to size and frequency when appropriate. We modify Oliver and Larson's (1996) definition of *disturbance severity* as the amount of forest overstory removed and the amount of understory vegetation, forest floor, and soil destroyed. With disturbance severity quantified in this manner, we are able to evaluate disturbances that vary in degree of overstory and understory destruction. Quantifying overstory and understory disturbance independently is particularly important with respect to forest harvesting because different degrees of overstory removal and different harvesting systems can be combined with a variety of understory treatments, creating numerous combinations of overstory and understory disturbance conditions.

The herbaceous layer is simultaneously exposed to and responds to many forest disturbances, ranging from microscale disturbances such as frost heaving and trampling by large vertebrates (McCarthy and Facelli 1990) to more extensive and intensive disturbances resulting from herbivory (Rooney and Dress 1997a,b), tree mortality (Beatty 1984; Collins et al. 1985; Moore and Vankat 1986; Stone and Wolfe 1996; Goldblum 1997), inundation (Lyon and Sagers 1998; C. E. Williams et al. 1999b), periodic fire (Gilliam and Christensen 1986; De Granpre' and Bergeron 1997), catastrophic wind damage (Peterson et al. 1990; Castelli et al. 1999; Peterson 2000), and forest management practices, including timber harvesting and use of herbicides (Duffy and Meier 1992; Roberts and Dong 1993; Gilliam et al. 1995; Halpern and Spies 1995; Hammond et al. 1998; Falk et al. 2008).

This chapter provides a conceptual overview of many of these disturbances. In addition, subsequent chapters address specific disturbances in more detail, including invasive species (chapter 15, this volume), deer herbivory (chapters 16 and 17, this volume), timber harvesting/agricultural practices (chapters 18 and 19, this volume), nitrogen pollution (chapter 20, this volume), and global warming (chapter 21, this volume).

PRINCIPAL TYPES OF DISTURBANCES IN EASTERN FORESTS

Natural Disturbances that Primarily Affect the Forest Canopy

Using the above definition of disturbance severity, the principal types of relatively discrete natural disturbances in eastern forests can be generally categorized into those that primarily affect the overstory and those that primarily affect the understory. Insect defoliation, wind, and ice storms are the most common types of disturbances affecting the forest canopy. Outbreaks of the defoliating insect spruce budworm (*Choristoneura fumiferana* [Clem.]) are common throughout the range of balsam fir (*Abies balsamea* (L.) Mill.) in eastern forests (Blais 1983). Balsam fir is the most susceptible species to damage by spruce budworm defoliation, although the spruces (*Picea* spp.) are the preferred host for the insect. Severity of defoliation can range from light (partial removal of current foliage) to severe (complete shoot destruction with widespread tree mortality). The spruce budworm prefers large, mature overstory trees, but at extremely high larval densities, the insect may also defoliate understory saplings and seedlings (Pardy 1997). Numerous studies have addressed growth responses of defoliated trees and stands (e.g., Peine 1989), tree regeneration (e.g., Osawa 1994) and succession of woody species (e.g., Ghent et al. 1957; Batzer and Popp 1985) after insect attack. Overstory mortality typically results in growth release or advance regeneration of balsam fir and spruces and establishment of shade-intolerant and mid-tolerant deciduous species such as *Betula papyrifera* Marsh., *B. allegheniensis* Britt., *Populus* spp., and *Acer rubrum* L. (Ghent et al. 1957; Batzer and Popp 1985). Studies of herbaceous layer response to spruce budworm defoliation are lacking.

The gypsy moth (*Lymantria dispar* L.) is another important canopy-defoliating insect in eastern forests, affecting hardwood forests throughout the northeastern and mid-Atlantic states of the United States (USDA Forest Service 1993). Like the spruce budworm, the gypsy moth preferentially selects certain tree species over others, such as *Quercus* spp., *Betula* spp., *Tilia* spp., and *Populus* spp. (Muzika and Liebhold 1999), and larger size classes of trees, principally those in the forest canopy (Campbell and Sloan 1977). The overall effect of moderate to severe defoliation by insect larvae is to release understory individuals, thereby altering species composition and initiating a new cohort of woody seedlings and saplings (Collins 1961; Fajvan and Wood 1996).

Mattson and Addy (1975) pointed out that plant-eating insects help maintain high primary productivity in forest communities by consuming less vigorous plants and opening the canopy for more vigorous plants. In addition to increased light in the understory, nutrient and moisture levels in the understory also increase because of removal of transpiring foliage in the overstory and additions of frass and debris to the forest floor (Eshleman et al. 1998). Several studies have documented increases in the abundance and growth of shrub species after insect attack (Ghent et al. 1957; Batzer and Popp 1985), but few have addressed changes in the herbaceous layer. Ehrenfeld (1980) found no significant differences in herb cover and no obvious changes in species composition between gap and control sites in a gypsy moth-defoliated forest. She concluded, however, that the spatial pattern and relative densities of plants in the forest understory, in combination with the size and pattern of gaps, are the critical factors determining the pattern of forest understory response to canopy gaps created by insect defoliation.

Wind damage in forests has been the subject of considerable study (see review by Everham and Brokaw 1996). As with insect defoliation, the severity of wind disturbance can vary from small gaps created by broken branches or the fall of individual canopy trees (Moore and Vankat 1986) to catastrophic removal of the majority of the canopy (Dunn et al. 1983; Foster 1988a; Merrens and Peart 1992; Peterson and Pickett 1995; others cited in Everham and Brokaw 1996). The severity of damage is related to wind intensity in combination with a number of biotic and abiotic factors, including tree species, stem size, canopy evenness, previous weakening by pathogens, and topographic exposure (Everham and Brokaw 1996). Wind influences conditions for understory herbaceous vegetation by increasing light, altering substrate (snapped trees versus uprooted), and depositing litter (Everham and Brokaw 1996). It is likely that the frequency of uprooted trees, and likewise the frequency of pits and mounds, is generally higher after wind disturbance than after insect defoliation.

Several studies (e.g., Beatty 1984; Peterson et al. 1990) have documented differences in species composition in pits and on mounds and have demonstrated the importance of pit and mound microsites in maintaining the species diversity of understory vegetation (chapter 8, this volume). Others have found subtle changes in understory composition after creation of individual tree windthrow gaps in mature forests (Brewer 1980; Moore and Vankat 1986). Moore and Vankat (1986) studied the portions of the gaps where soil had not been disturbed by uprooting and found significantly higher solar radiation and soil moisture within one-to-two-year-old gaps compared to older gaps and intact forest. They concluded that higher total herbaceous cover in the young gaps was related to increases in species that were present under the intact canopy before gap creation as opposed to invasion of new species. It is likely that invasion increases in importance with increasing soil disturbance and canopy removal.

Ice or glaze storms are common recurring disturbances in forests throughout eastern North America, with the exception of Florida (Oliver and Larson 1996; Rebertus et al. 1997; Lautenschlager and Nielsen 1999). Lemon (1961) showed that major ice storms occur more frequently in northeastern forests than do large wind storms or fires. Most studies of forest recovery after ice storm damage have focused on the canopy layer (e.g., Lemon 1961; Siccama et al. 1976; Bruederle and Stearns 1985; De Steven 1991b) and have concluded that the effects depend on storm intensity, landscape position, wind, and forest type and structure. Succession of forest tree species may be accelerated or retarded depending on the degree of damage and current successional stage; removal of early successional canopy dominants may allow late successional understory trees to fill canopy gaps, whereas extensive canopy damage might allow reproduction of early successional species (Whitney and Johnson 1984).

Little information is available on the response of the herbaceous layer to ice storms. Given that storm damage typically occurs from breakage of limbs or whole trees (Runkle 1985; Oliver and Larson 1996), we would predict that (1) canopy gaps would be created, favoring shade-tolerant shrubs and herbs in smaller gaps and shade-intolerant species in larger gaps; (2) there would be relatively little uprooting and disruption of the forest floor with little mineral soil exposure, resulting in (3) growth stimulation of preexisting plants with relatively little invasion of new individuals (as compared to wind disturbance, for example); and (4) the input of coarse, woody debris to the forest floor can be substantial (Bruederle and Stearns 1985), eventually providing substrate for herbaceous plants.

The ice storm of 1998, which affected Ontario, Quebec, and the Maritime Provinces of Canada, as well as portions of New England in the United States (Irland 1998), was widespread. This storm was unprecedented in terms of the total area affected (603,654 ha in Ontario alone), as well as the duration and the amount of freezing rain that was deposited (Lautenschlager and Nielsen 1999; Van Dyke 1999). More than 80 hours of freezing rain and drizzle occurred between January 5 and January 10 in Ontario, producing 73–108 mm of precipitation. This was twice the duration and amount of previous ice storms. The amount of woody litter (19.9 metric tons/ha) produced by the 1998 ice storm in an old-growth forest at Mont St. Hilaire, Quebec, was the greatest of any ice storm on record and approached amounts produced by the most powerful hurricanes (Hooper et al. 2001). Such damage was found by Jones et al. (2001) to be predominantly a function of tree size for a mature, deciduous forest in eastern Ontario; that is, large stems in the canopy experienced much greater damage than did smaller stems in the subcanopy. Whether there are significant effects on the herbaceous layer after this and other ice storms will likely depend on stand structure and species composition, in addition to storm intensity (Van Dyke 1999). The magnitude of the response of herbs is likely to be greater where canopy openings are large and shade-tolerant tree seedlings, saplings, or shrubs are sparse.

Natural Disturbances that Affect Only the Forest Floor or Both Floor and Canopy

The natural fire return interval (before European settlement) in eastern forests varies from two to 1,000 years, depending on climate, site, species, stand growth patterns, and influences of other disturbances (Oliver and Larson 1996 and studies reviewed therein). The forest types exhibiting the shortest return intervals are the longleaf and loblolly pine forests of the southeastern U.S. coastal plain and the jack pine forests in the Lake States. Upper-elevation conifer forests and mixed forests of northeastern Maine show the longest return intervals (Lorimer 1977; Wein and Moore 1977), whereas the eastern boreal forest, northern hardwoods of central New England, spruce/hemlock/pine types of eastern Canada, and the aspen/birch and birch/maple/hemlock types of the Lake States have intermediate return intervals of 50–350 years (Oliver and Larson 1996).

Various authors have emphasized the autecological characteristics of plant species in examining the response of plants to fire. We would expect plant species to have developed a wide range of adaptations, given the historical role of fire in eastern forests. Rowe (1983) cautioned, however, that there is considerable variability in the selection process, resulting in only very broad, overlapping strategies among species for coping with fire. Correlations between the historical occurrence of fire and specific life history adaptations are likely to be weakest within broad regions containing mostly wide-ranging species, such as the boreal forest (Rowe 1983).

The effects of fires on vegetation are generally correlated with fire intensity and duration (Rowe 1983; Oliver and Larson 1996; Hutchinson et al. 2005). The heat from fires remains principally above the soil surface, except where soils are extremely dry, fuel is very concentrated, or fires burn in underground roots (Oliver and Larson 1996). Depth of heat penetration can be expected to affect regeneration from buried propagules (Moore and Wein 1977). Martin (1955) found that all of the herbaceous and

shrub species two years after a severe burn survived the fire either as underground stems or dormant seeds. The resprouting plants originated from underground stems buried 2.5 cm in the humus and occurred only in parts of the burn where the humus was not completely consumed. In response to the temporal and spatial variability of the fire regime, species have evolved a variety of strategies for survival or regeneration after fire. Skutch (1929) noted that *Pteridium aquilinum* (L.) Kuhn resprouted from deep-seated rhizomes even where the humus had been burned away on a severely burned site in Maine. He also observed sprouting of *Epilobium angustifolium* L. from the primary and secondary roots within the first year, a phenomenon that has also been documented for *Rubus ideaus* L. (Roberts and Dong 1993). The cryptogams *Marchantia polymorpha* L., *Polytrichum commune* Hedw., and *P. juniperinum* Hedw. were in high abundance on burned sites in Maine (Skutch 1929) and Nova Scotia (Martin 1955). The early establishment of these species on burned sites has been attributed to their widely dispersed spores and preference for high light environments (Skutch 1929).

Ahlgren (1960) classified plants into three types regarding fire: (1) species found only on unburned sites, consisting of shade-loving perennials reproducing mostly by shallow or surface rhizomes or bulbs; (2) species found only on burned-over sites (mostly those that reproduce by seed); and (3) species occurring on both burned and unburned sites, including both seed and vegetatively reproduced species. Based on Noble and Slatyer's (1980) modes of persistence, Rowe (1983) proposed a classification of plant strategies in the context of fire. The first division in the classification is based on method of regeneration and reproduction, being either disseminule-based or vegetative-based. Disseminule-based species were subdivided into *invaders* (highly dispersive, pioneering fugitives with short-lived propagules), *evaders* (species with long-lived propagules stored in the soil or canopy), and *avoiders* (shade-tolerant, late successional species, often with symbiotic requirements). Vegetative-based species were subdivided into *resisters* (shade-intolerant species that can survive low-severity fires in the adult stage) and *endurers* (resprouting species with buried perennating buds). Lyon and Stickney (1976) also provided a classification of plants based on their autecological characteristics. They found that most plant species on a site before intense fires in the northern Rocky Mountains survived or reestablished by virtue of on-site surviving parts and seeds or the transport of seeds from adjacent, unburned communities. McLean (1969) found that fire resistance was related to rooting depth.

Another line of research has focused on changes in the physical environment caused by burning in explaining herbaceous layer response. Ahlgren (1960) attributed differences in species composition on lightly and severely burned sites to seedbed characteristics. He also noted that some species requiring open conditions might be limited by competition with resprouting species on light burns. Martin (1955) noted higher species richness and more luxuriant growth in plots under shade cloth than in open plots two years after burning. He attributed the difference to higher moisture in the shaded plots. Gilliam and Christensen (1986) found higher species richness and total cover of the herbaceous layer after burning on infertile sites in the southeastern coastal plain of the United States. This effect was found only after winter burns and disappeared after two years. They attributed the result to decreased shading and increased nutrient availability immediately after burning. Indeed, the fertilization effect of burning has been well documented (e.g., Ahlgren 1960; Wilbur and Christensen 1983; Skre et al. 1998), although the possible counterbalancing losses of nutrients to volatilization, leaching,

and overland flow must also be considered (MacLean et al. 1983). Gilliam (1991) suggested that some fire-prone ecosystems may depend on fire to maintain the availability of essential resources that would otherwise be growth-limiting.

Although consumption of herb layer plants can occur via invertebrate herbivores (Hahn et al. 2010), herbivory by mammals is a common understory disturbance that has been frequently documented in the forests of eastern North America (chapters 4, 16, and 17, this volume). Because of dramatic increases in populations of white-tailed deer (*Odocoileus virginianus* Zimmermann) and moose (*Alces alces* L.) in specific regions throughout the 1900s, damage from these two animals is often cited. Crawley (1983) stresses that herbivores have both direct and indirect effects on plant species richness and community dynamics. Plants may be affected directly by being eaten to extinction or by being favored if they are unpalatable. Indirect effects operate by altering the relative competitive abilities of plants. Both categories of effects are clearly evident in studies that have documented browsing in eastern forests. As with other types of disturbances, most browsing studies have focused on the tree layer or tree regeneration; effects on the herbaceous layer have been seldom described.

Studies of moose browsing suggest that the effects on the herbaceous layer are mostly indirect. On Isle Royale, Michigan, moose browsing reduced the cover of canopy trees, particularly *Abies balsamea* and *Populus tremuloides* Michx., and promoted a well-developed understory of shrubs and herbaceous species (McInnes et al. 1992). The herbs, in general, were not browsed and became a greater proportion of total community biomass. Thompson et al. (1992) documented reduced densities of *Abies balsamea*, *Prunus pensylvanica* L.f., *Viburnum trilobum* Marsh., and *Amelanchier* spp., and increased densities of *Kalmia angustifolia* L. in response to moose browsing in Newfoundland. Although the herbaceous layer was not assessed in this study, one would expect the number and cover of herbaceous species to be low in areas where *Kalmia angustifolia* is dominant. Snyder and Janke (1976) found twice as much herbaceous layer cover on moose-browsed sites as on unbrowsed sites, which they attributed to increased light.

Populations of white-tailed deer began to increase throughout much of eastern North America in the early 20th century after enactment of numerous game laws (Marquis and Brenneman 1981). Heavy browsing of preferred species by deer has resulted in regeneration failures of many commercially important forest tree species, as well as noticeable changes in understory composition (Marquis and Brenneman 1981; Horsley and Marquis 1983). Preferred species of browse in northwestern Pennsylvania included *Prunus serotina* (Ehrh.), *P. pensylvanica*, *Acer rubrum*, *A. saccharum* (Marsh.), *Fraxinus americana* (L.), *Betula* spp., and *Rubus* spp. (Horsley and Marquis 1983). Species favored in areas that are heavily browsed included *Fagus grandifolia* (Ehrh.), *Acer pensylvanicum* (L.), ferns, grasses, *Solidago* spp., and *Aster* spp. (Marquis and Brenneman 1981). Horsley and Marquis (1983) documented an interaction between browsing and interference from ferns and grasses that caused regeneration failures of commercially important tree species in Pennsylvania. Deer browsing on *Rubus* spp. and tree seedlings promoted increases in cover of *Dennstaedtia punctilobula* (Michx.), *Thelypteris novaboracensis* (L.), and *Brachyelytrum erectum* (Schreb.), thereby reducing densities of preferred tree species. Any surviving tree seedlings that grew above the herb layer were browsed by deer. It is likely that richness and cover of other herbaceous species are low in areas with high abundance of the interfering ferns and grasses.

Heinen and Currey (2000) documented changes in tree species composition after browsing by introduced Rocky Mountain elk (*Cervus elaphus nelsonii* L.) and deer in Michigan. *Populus grandidentata* Michx. and *Acer rubrum* decreased in abundance, and *Populus tremuloides* increased in browsed areas. Approximately half of the browsed area was dominated by non-tree vegetation, predominantly *Pteridium aquilinum* and *Rubus* spp.

Unlike moose, deer browse directly on herbaceous species. Deer forage on herbs during the spring and summer, and then switch to woody browse in the winter months (Balgooyen and Waller 1995). Skinner and Telfer (1974) found that species of the lily family (Liliaceae), principally *Clintonia borealis* (Aiton) Raf. and *Maianthemum canadense* Desf., supplied 29 percent of the spring diet for white-tailed deer in New Brunswick, Canada. Other commonly browsed herbaceous species included *Gaultheriaprocumbens* L., *Erythronium americanum* Ker Gawler, grasses (Poaceae) in the spring, and *Cornus canadensis* L. in the fall (Skinner and Telfer 1974). Among woody species, *Acer spicatum* Lam., *Betula allegheniensis*, *Sorbus decora* (Sarg.) C. K. Schneider, and *Taxus canadensis* Marshall were reduced in abundance in areas with high deer densities in northern Wisconsin (Balgooyen and Waller 1995). Several herbaceous species, including *Aralia nudicaulis* L., *Maianthemum canadense*, and *Clintonia borealis*, also had decreased frequency and cover in areas with high densities of deer relative to areas with low densities. Other commonly grazed herbaceous species included *Aster macrophyllus* L., *Habenaria orbiculata* (Pursh) Torr., *Sanguinaria canadensis* L., *Smilacina racemosa* L. (Desf.), *Streptopus roseus* Michx., *Trillium cernuum* L., *T. grandiflorum* (Michx.) Salisb., and *Uvularia sessilifolia* L. (Balgooyen and Waller 1995). R. C. Anderson (1994) found that *Trillium grandiflorum*, *Erythronium americanum*, and *Claytonia virginica* L. were preferentially browsed in Illinois.

In some cases, herbaceous species have been used as indicators of deer browsing intensity. For example, percent cover, number of leaves/plant, scape height, and number of pedicels/umbel of *Clintonia borealis* were negatively correlated with deer densities in the study by Balgooyen and Waller (1995). R. C. Anderson (1994) found the height of *Trillium grandiflorum* to be a useful indicator of deer browsing intensity.

Deer browsing may also produce indirect effects on the herbaceous layer if the shrub, seedling, or sapling layers are heavily browsed. One example of the indirect effects of browsing is provided by Balgooyen and Waller (1995), who found greater herb diversity and cover in areas where *Taxus canadensis* was more heavily browsed.

Anthropogenic Disturbances: Agriculture and Forestry

The combined forces of clearing for agriculture and lumbering transformed eastern North America from a forested to a predominantly agricultural landscape in the two centuries following European settlement (Flinn and Vellend 2005; Baeten et al. 2011; chapter 19, this volume). Agriculture is the most severe form of these disturbances and has the greatest effect on the herbaceous layer because of the removal of vegetative propagules and seed banks associated with annual cultivation and the dramatic change in microenvironment (Runkle 1985; Vellend 2004; Fraterrigo et al. 2006). Grazing by pigs, sheep, and cattle can also dramatically affect woody and herbaceous vegetation composition in woodlands (Whitney 1994). The effects of forest harvesting depend on

a number of factors, including type of harvesting system, equipment used, season of year, site conditions, soil type, subsequent treatments, and others.

Forest management approaches common in the eastern deciduous forest can be viewed as a gradient of disturbance intensity, varying from the least intense with single tree selection to the most intense with clearcutting (Gilliam and Roberts 1995; Hammond et al. 1998; Moola and Vasseur 2008; von Oheimb and Härdtle 2009). Recent research has looked at the direct effects of harvesting alone, as well as in combination with other management techniques, on herb layer composition and diversity (Reader and Bricker 1992a,b; Halpern and Spies 1995; Roberts and Gilliam 1995b; Elliott et al. 1997; Hammond et al. 1998; Thomas et al. 1999; He and Barclay 2000; Elliott and Knoepp 2005). Other work has examined herb layer recovery after more extreme treatments not associated with forest management, such as deforestation and regrowth suppression with repeated herbicide applications (Kochenderfer and Wendel 1983; Reiners 1992). Still others have provided valuable information on species dynamics of the herb layer by comparing patterns in second-growth forest stands to those in old-growth stands (Qian et al. 1997; Goebel et al. 1999; chapter 7, this volume). The lack of consistency in findings of these studies demonstrates the site-specific nature of herb layer responses to anthropogenic disturbances to forests (Roberts and Gilliam 1995b), precluding broad generalizations and underlining the importance of in-depth study of these responses for different forest types and harvest techniques.

Several studies have looked at post-harvest responses of herb layer vegetation to clearcutting either alone or in combination with other silvicultural treatments. Halpern and Spies (1995) found that changes in herb layer diversity were short-lived after clearcutting and slash-burning of Douglas fir forests of western Oregon and Washington and that herb diversity returned to pre-harvest conditions before canopy closure (10–20 years). Roberts and Gilliam (1995b) found that responses of the herb layer to clearcutting were highly site-dependent in mesic and dry mesic aspen stands. Harvested stands approximately 15 years old had higher diversity and richness than mature stands on mesic sites, whereas there were no significant differences on dry mesic sites. De Grandpre' and Bergeron (1997) found that site dependence of herb response to disturbance might be related to the age of the stand at the time of disturbance in southern boreal forests of Quebec (i.e., younger communities changed less after clearcutting than did more mature communities). Fredericksen et al. (1999) concluded that only the most intense levels of harvesting measurably affected herb layer richness, diversity, composition, and cover in northern hardwood and oak-hickory forests of Pennsylvania.

Several lines of evidence suggest that forest harvesting may have long-term detrimental effects on the composition and diversity of herbaceous plants (Wyatt and Silman 2010; chapter 18, this volume). Based on direct comparisons of harvested and old-growth stands in southern Appalachian forests, Duffy and Meier (1992) argued that the harvested stands are impoverished even after 150 years. Because of methodological problems, the accuracy of the results of this study has been questioned (Elliott and Loftis 1993; Johnson et al. 1993). Replies to these criticisms (Duffy 1993a,b) and further work (Meier et al. 1995) by these authors failed to resolve the problems (see chapter 7, this volume, for further discussion). Although similar findings have been reported for a variety of European and North American forest communities (e.g., Hill 1979b, Scanlan 1981, Peterken and Game 1984, Whitney and Foster 1988, Dzwonko and Loster 1989, and others reviewed in Matlack 1994a), all have compared second-growth

Table 13.1 Effects of clearcut harvesting on herbaceous layer species diversity in selected forests of eastern North America.

Study and forest type or site type	Type of comparison		Treated		Control		Effect on herbaceous species diversity
			H'	S	H'	S	
Yorks and Dabydeen (1999)	Clearcuts and mature second-growth reference stands						No effect on H'
Frostburg Watershed	3.14 ^a	2	3.42	90			
	3.91	13-14					
	3.93	19					
Savage R. (NW aspect)	2.25	2	4.23	75			
	3.63	13					
	3.79	17					
	2.80	26					
Savage R. (SE aspect)	4.49	2	3.26	80			
	3.96	13					
	3.16	26					
Jenkins and Parker (1999)	Clearcuts and mature second-growth reference stands						S and H' significantly greater on mesic slopes
Dry mesic slopes	2.20	28	9-15	2.40	27	> 80	No differences in S or H' with clearcut age; S and H' not different from control
	2.10	30	16-24				
Mesic slopes	2.50	38	9-15	2.40	27	> 80	No differences
	2.20	39	16-24				

Gilliam (2002)	Clearcuts and mature second growth reference stands	1.64	14 ^b	20	1.53	13 ^b	> 70	No differences in S or H'; variations in H' related more to changes in evenness than richness
Goebel et al. (1999)	Second growth compared to old growth	2.12 ^c	14	70-79	2.54	19	> 150	No significant differences in S or H'
Elliott et al. (1997)	Clearcut harvest vs. mature forest before harvest	2.19	22	2	2.52 ^d	27	> 70 ^e	Sustained decreases in S and H' after harvest compared to precut forest
Cove hardwoods		0.82	20	16				
Mixed-oak hardwoods		2.04	18		3.14	49	> 70 ^e	
Hardwood-pines		1.32	16	16				
		2.28	25	2	2.40	45	> 70 ^e	
Roberts and Zhu (2002)	Clearcut harvest vs. mature forest before harvest	1.90	27	16				Significantly greater S and H' after harvest compared to precut forest
Clearcut only		0.80 ^f	13 ^b	2	0.60 ^f	12 ^b	> 80	
Clearcut and planted		0.88 ^f	19 ^b	2	0.79 ^f	16 ^b	> 80	
Roberts and Gilliam (1995b)	Clearcuts and mature second- growth reference stands							
Mesic sites		3.76	35	3-14	3.34	26	57-82	S and H' significantly greater in young clearcuts
Dry mesic sites		3.04	24	3-12	2.76	23	55-80	No significant differences in S or H'

(Continued)

Table 13.1 (Continued)

Study and forest type or site type	Type of comparison	Treated			Control			Effect on herbaceous species diversity
		H'	S	Age (years)	H'	S	Age (years)	
Meier et al. (1995)	Clearcut and old-growth reference stand	10 ^b		5	14 ^b		?	S significantly greater in control
Roberts (2002)	Plantations and mature reference stands	1.73	27	5–16	1.75	24	> 90	No significant differences in S or H'

^a Average of June and August sampling periods.

^b Mean no. species/plot.

^c Average of late spring and summer sampling periods.

^d Pre-harvest inventory.

^e Originated from cutting and burning, followed by selective logging.

^f Mean H'/plot.

stands or plantations on abandoned agricultural fields to natural forests. It is not clear from these studies what the effects of harvesting on the herbaceous layer would have been independent from the effects of agriculture. Thus, further research is needed to determine the influence of harvesting on herbaceous layer composition and diversity. Long-term studies along gradients of disturbance type and severity would be of particular value.

Evidence from early botanical descriptions and herbarium records suggests that many species have declined in abundance or have become extinct in North America as a result of the combined effects of European settlement. Indeed, the impact of historical land use on forest floras has been frequently documented (Matlack 1994a); however, the extent to which these changes can be attributed to forest management activities, as distinct from other land uses, remains unknown.

Other studies have also found that the forest understory remains impoverished for long periods (perhaps centuries) after natural disturbances such as wildfires (Spies 1991; MacLean and Wein 1977). Thus, the effects of harvesting must be balanced against the natural patterns of succession (Roberts and Gilliam 1995a). It is not clear whether harvesting would cause more severe effects than natural disturbances, but any differences would likely be related to the intensity of the disturbance. Without doubt, more research is needed to identify patterns and mechanisms of herbaceous layer response to harvesting.

Published results of harvesting effects on herbaceous layer diversity of forest types throughout North America were reviewed by Battles et al. (2001). We have taken a similar approach with a narrower focus on studies in northeastern forests. We present the actual values as calculated in the various studies for species richness (S ; usually the average number of species per plot) and the Shannon-Wiener index (H' ; table 13.1). It was not possible to compare results among studies because of differences in methods; rather, we compared the treated condition to the reference condition within each study and noted the direction of change in S and H' for each case. Only treatments that involved clearcutting (with or without plantation management) were included because clearcutting constitutes the most severe management disturbance (Roberts and Zhu, 2002). Thus, if clearcutting shows no significant effect on species richness or diversity, it is unlikely that a less severe management treatment, such as selection harvest, would show a significant effect in that forest type.

The studies in eastern forests that we reviewed showed diverse patterns, including no differences in S or H' between clearcuts and controls (Goebel et al. 1999; Yorks and Dabydeen 1999; Gilliam 2002; Roberts, 2002), greater S or H' in clearcuts than in controls (Jenkins and Parker 1999; Roberts and Zhu 2002), and lower S or H' in clearcuts than in controls (Meier et al. 1995; Elliott et al. 1997; table 13.1). Roberts and Gilliam (1995b) found that the patterns depended on site type, with no difference on dry mesic sites and greater S and H' in clearcuts compared to controls on mesic sites in northern lower Michigan (table 13.1). Neither type of control (second growth versus old growth) nor age of treated stand appeared to explain any trends in S or H' . For example, Goebel et al. (1999) compared mature clearcuts (70–79 years) to old-growth reference stands, whereas Yorks and Dabydeen (1999), Gilliam (2002), and Roberts (2002) studied young clearcuts (2–26 years) in relation to mature second-growth reference stands, yet all found no significant differences between treatments and controls.

In the studies that included a chronosequence of treated stands, conflicting patterns were reported. Yorks and Dabydeen (1999) found no statistically significant differences

with stand age but noted that S and H' peaked in recent clearcuts (3–4 years) and controls (90 years) on the moister northwestern aspects but tended to decrease over time on drier southwestern aspects. Jenkins and Parker (1999) also found no significant differences with stand age, although there was a slight tendency for H' to decrease and S to increase with age (9–15 year age class versus 16–24 year age class; table 13.1). In Elliott et al. (1997), two community types on moister sites (cove hardwoods and mixed-oak hardwoods) showed significantly lower H' in 1993 than in 1979, but the drier hardwood-pines site did not have significant differences with stand age (table 13.1). Certainly, changes in diversity over time are influenced by site conditions, as noted elsewhere (e.g., Roberts and Gilliam 1995b), along with a complex of additional factors, making generalizations difficult.

Without doubt, more research is needed to identify patterns and mechanisms of herbaceous layer response to harvesting. In the next section, we present a summary of theories that can be applied to this problem.

COMMUNITY PATTERNS AND MECHANISMS OF SUCCESSIONAL CHANGE IN UNDERSTORY COMMUNITIES

Hypothesized Changes in Species Diversity with Succession

Peet and Christensen (1988) hypothesized that diversity would wax and wane during stand development according to the changing intensity of competition (chapter 11, this volume). For example, species richness is initially high after disturbance, then decreases to a minimum during the stem exclusion stage (*sensu* Oliver and Larson 1996), when competition among the overstory trees is at a maximum. Subsequently, richness should increase again during the transition to the old-growth stage. During the old-growth stage, richness should either decline slightly due to the loss of early successional species or reach a new peak as slowly dispersed climax-specialist species invade. Beta (between-habitat) diversity should increase during the periods of most intense competition because of a decrease in niche breadth induced by competition (Peet and Christensen 1988). Gilliam et al. (1995) suggested that the link between forest strata becomes tighter as competition increases after the establishment phase. We hypothesize that different strata show increasingly similar responses to environmental gradients with successional time (chapter 9, this volume). Certainly, patterns of change in herbaceous layer diversity are related to the intensity of the disturbance as determined by the management regime.

Mechanisms of Change in Understory Communities during Succession: Initial Effects

Halpern and Spies (1995) have suggested that we separate disturbance effects into two broad classes: initial effects on existing plant populations and long-term effects on recovering plant populations. We follow this convention because different mechanisms are involved in each case (Roberts and Gilliam 1995a). The *initial effects* influence plant community response through destruction of vegetative stems and propagules, effects on propagule availability and species invasion, and modification of habitats, including seedbed conditions, light, temperature, and moisture. Initial effects could vary widely depending on the type and severity of disturbance. For example, management treatments such as clearcutting with mechanized site preparation influence early vegetation response quite

differently from clearcutting alone (Roberts and Zhu, 2002). The type of disturbance in terms of its effects on the vegetation and environment is the important consideration here.

The *long-term effects* are manifested as changes in species composition, rate of stand development, and competitive interactions. Control of competing vegetation with herbicides is a typical example of a management treatment that has all of these long-term effects (e.g., Horsley 1994). Other long-term effects include composition and density of planting, timing and intensity of thinning, and length of harvest rotation (Halpern and Spies 1995). The analogues in natural disturbances are variations in initial stand density and stand structure, as well as the occurrence of minor disturbances during stand development.

One of the most important factors controlling the initial effects of disturbance on the herbaceous understory is the nature of the disturbance. As discussed above, characterizing the disturbance in terms of amount of forest canopy removed, amount of forest floor vegetation, forest floor, and soil removed (severity), and the frequency, size, and shape (Oliver and Larson 1996) captures the processes involved in understory recovery. Classifying disturbances in this fashion eliminates the need to exhaustively assess each individual disturbance event. This approach allows us to accurately categorize each disturbance in terms of its effects on the physical environment and the forest community and to examine understory response to these factors. Many studies have documented the changes in light (e.g., Jackson 1959; Berry 1964), soil temperature, moisture (e.g., Minckler et al. 1973; Fowler 1974; Hungerford and Babbitt 1987; McInnis and Roberts 1995), and nutrient availability (Johnson and Schultz 1999) that occur after disturbances of varying severities. Others have related disturbance severity to differences in vegetation response (Halpern 1988; Roberts and Dong 1993).

Taken in conjunction with disturbance characteristics, the life history characteristics (principally reproductive and survival strategies) provide the means for predicting initial vegetation response (Roberts and Gilliam 1995a). Various plant classifications based on functional (life history) characteristics have been proposed, including life forms (Raunkiaer 1934), competitor/stress tolerator/ruderal strategies (Grime 1977, 1979), assembly/response rules (Keddy 1992), vital attributes (Noble and Slatyer 1980; Rowe 1983), functional types (reviewed in T. M. Smith et al. 1997), or subsets of specific life history traits (Matlack 1994b; McIntyre et al. 1995). Numerous studies have demonstrated the importance of species' life histories in long-term successional community dynamics (e.g., Drury and Nisbet 1973; Sousa 1980; Roberts and Richardson 1985; Peet and Christensen 1988; Halpern 1989; others reviewed in McCook 1994). Different life history traits have been found to be relevant depending on the nature of the disturbance (Kirchner et al. 2011). Malanson (1984) pointed out the fundamental difference in regeneration mechanisms between light (survival in situ or vegetative regeneration) and severe disturbance (invasion). In the case of harvesting disturbance, we would expect to find correlations between species composition and a suite of life history traits including rooting habit, shade tolerance, ability to reproduce vegetatively, seed storability, seed production, seed size, and dispersal mechanism.

Species in the herbaceous layer may reappear following disturbance via one or more of four basic mechanisms:

1. Survival in situ. Depending on the disturbance severity, plants may survive in the vegetative form. Given the patchy nature of many types of disturbance and the low severity of others, considerable numbers of individual plants may survive the disturbance.

2. Vegetative regeneration. In situations where aboveground vegetation is damaged or killed, new individuals may reappear by vegetative means (Zobel and Antos 2009). Vegetative regeneration is the primary means of reproduction for many deciduous forest herbs (chapters 5 and 6, this volume). Rhizome growth rates may approach 1 m/year in some species (Sobey and Barkhouse 1977). Through a combination of these first two mechanisms, early vegetation composition often closely resembles the pre-disturbance composition (Lyon and Stickney 1976).
3. Regeneration from the seed bank. There is a potential for some species of the herbaceous layer to regenerate from the seed bank. Typically, however, buried seed reserves are modest in coniferous forests and are dominated by early successional species (Archibold 1989). Seed bank composition tends to greatly differ from the aboveground vegetation in most forest types (Pickett and McDonnell 1989).
4. Regeneration by dispersed propagules. Most temperate forest herbs flower and produce seeds regularly, and regeneration from seed may be the most important reproductive mechanism for many of these species (Bierzychudek 1982a; Cain et al. 1998; chapters 5 and 6, this volume). Seeds may be dispersed from individuals surviving in adjacent patches within the disturbed area or from nearby undisturbed communities.

Mechanisms of Change in Understory Communities during Succession: Long-Term Effects

After the initial effects of disturbance and the immediate response of the herbaceous layer, we must consider the long-term influences of the disturbance on the successional recovery of the herbaceous layer. Spies (1991) notes four factors that contribute to successional change:

1. The microclimate becomes more cool and humid during the dry season in old forests, and soil moisture may be higher because of litter accumulation.
2. There is an increase in horizontal spatial heterogeneity of resources and environments, relating to the development of canopy gaps in a matrix of closed forest. Some species survive in deep shade but require gaps for long-term survival.
3. An increase in vertical environmental diversity occurs (e.g., increase in height and number of canopy layers). This may be more important in habitat for foliose lichens and epiphytes than for forest herbs.
4. Sensitivity to disturbance (e.g., fire) and slow rates of reestablishment and growth after the disturbance are important. In addition to affecting initial vegetation response, the type and intensity of the disturbance also have long-term consequences by influencing the initial mix of species, propagule availability, environmental conditions, competitive relationships, and individual growth rates.

These factors help explain the changes in species richness with stand development hypothesized by Peet and Christensen (1988), Oliver and Larson (1996), and others.

These patterns correspond to an invasion of shade-intolerant herbs and shrubs into the surviving community of shade-tolerant forest species soon after disturbance, followed by a decrease in diversity during the stem-exclusion stage of stand development, and then higher diversity in the old-growth stage in which the increases in horizontal and vertical heterogeneity and changes in microclimate are expressed.

A number of factors may modify this idealized pattern of successional change. Site conditions, such as soil moisture and fertility, may exert an overriding control on successional patterns of species diversity as noted by Auclair and Goff (1971), Roberts and Christensen (1988), and Roberts and Gilliam (1995b). Auclair and Goff (1971) hypothesized that a more nearly linear increase in species diversity with increasing stand age would occur on xeric, hydric, or infertile sites as compared to mesic, fertile sites. Disturbance-related influences on resource availability may affect the rate and direction of succession, depending on the type and severity of disturbance. Indeed, several resource-mediated models of succession are based on the assumption that resource availability changes as a result of disturbance and continues to change with time (Grime 1977; Tilman 1985; Vitousek 1985). The competitive balance among species can vary as a consequence of differences in disturbance type and severity or chance factors (e.g., seed production, weather) controlling initial plant densities, resulting in different successional trajectories (Oliver and Larson 1996).

Conceptual Models of Herbaceous Layer Response to Disturbance

The factors discussed in the previous section have been incorporated into general conceptual models that attempt to capture the essential processes controlling response of the herbaceous layer to variations in disturbance severity in both the short term and long term (figs. 13.2 and 13.3). Disturbance affects forest structure in terms of overstory and understory density and cover, presence and relative densities of different vegetation layers (vertical stratification), and abundance of standing snags and coarse, woody debris. These effects depend on disturbance severity (overstory and understory). In turn, forest structure affects the environment and substrate for the herbaceous layer through modifications in microclimate (light intensity, relative humidity, temperature, surface moisture) and substrate (abundance of coarse, woody-debris and stages of decay). Forest structure, of course, changes over successional time, with resulting changes in levels of competition between the herbaceous layer and overtopping vertical strata. Disturbance also affects the forest floor directly by creating or destroying pits and mounds, creating mineral soil substrates, and modifying abundance and condition of coarse, woody debris substrates. Finally, disturbance affects the preexisting plant community by damaging or killing individual plants and changing propagule availability by modifying seed banks and seed rain. Using this framework, we are able to make improved predictions of the effects of disturbance on the herbaceous layer in eastern forests.

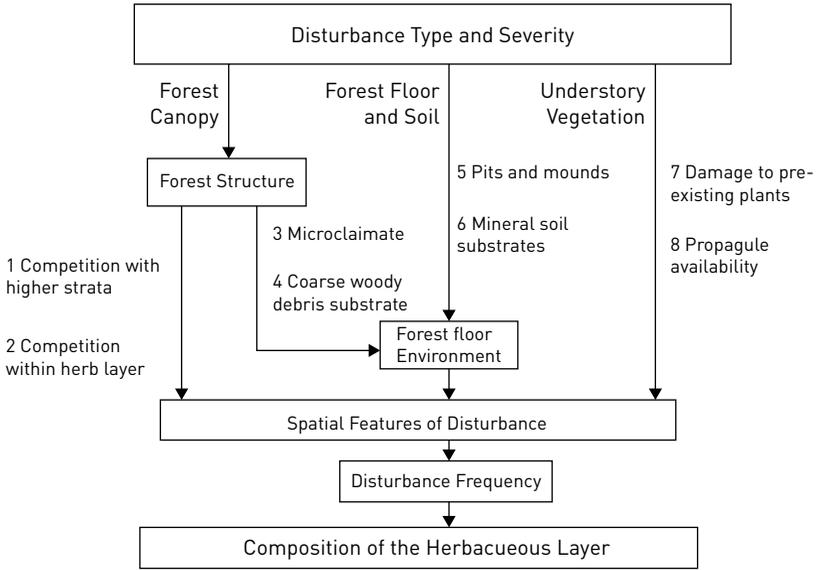


FIGURE 13.2 Mechanisms proposed for the effects of disturbance on structure and composition of the herbaceous layer in forests. Taken from Roberts (2004).

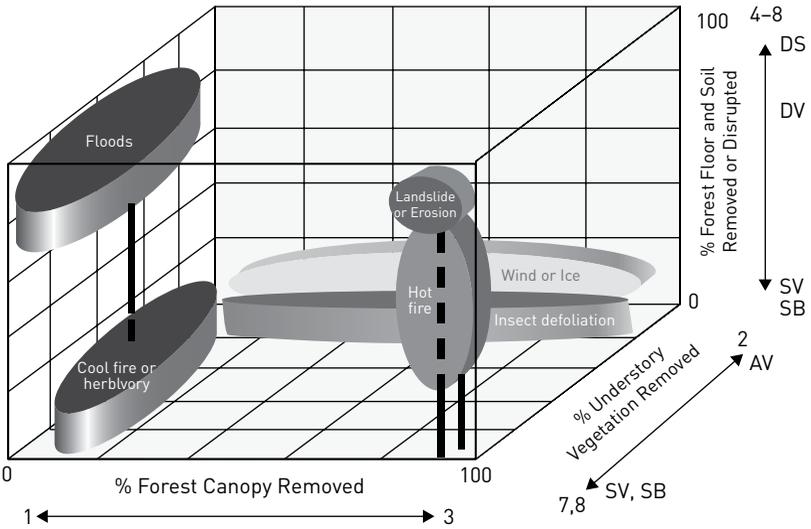


FIGURE 13.3 A three-dimensional model of disturbance severity, with each of three forest vegetation strata (forest canopy, understory vegetation, forest floor and soil) on separate axes. Labeled shapes represent the ranges in conditions on these axes created by the common natural disturbances in North American forests. Numbered arrows adjacent to axes represent the eight key factors controlling herbaceous layer response (see fig. 13.2). Letter codes adjacent to the arrows represent species' regeneration mechanisms: DV, deep-seated vegetative (deep rhizomes, root sprouts, bulbs); SV, surficial vegetative (shallow rhizomes, stolons); AV, aboveground vegetative (lateral extension, runners); SB, seed bank; DS, widely dispersed seed. Increasing importance of the particular factors and regeneration mechanisms is indicated by direction of arrow. Taken from Roberts (2004).

CONCLUSIONS AND RECOMMENDATIONS

Many studies have documented effects of disturbance on eastern forests, but surprisingly few have looked at the herbaceous layer. In assessing the nature of disturbance and its effects on the herbaceous layer, it is useful to characterize disturbance severity in terms of the amount of destruction of both the overstory and understory. Insect defoliation, wind, and ice storms are typical natural disturbances in eastern forests that primarily affect the forest canopy. Their effects on the herbaceous layer and forest floor are expressed largely through changes in environment (increased light) and substrate (additions of litter, frass, and coarse, woody debris to the forest floor and creation of pits and mounds). In contrast to canopy disturbances, fire and herbivory by mammals exert their greatest effects on the understory layers. The herbaceous layer is affected by these disturbances by direct mortality and damage of plants, alteration of propagule availability (reduction or destruction of the seed bank and changes in composition of the seed rain), and changes in competitive relationships among plant species. Forest harvesting and other anthropogenic disturbances can vary greatly in disturbance severity and in their relative effects on canopy and understory, depending on the types of treatment and how they are applied.

Characterizing disturbance in terms of severity at both the canopy and understory levels allows us to examine the effects of disturbance based on its impact on the ecosystem independent of the causal agent. Thus, we are able to focus more clearly on processes that control ecosystem response. This is particularly useful in characterizing the nature of anthropogenic disturbances and evaluating their effects on the ecosystem. With our current emphasis on ecosystem management and the need to pattern forest management after natural disturbance regimes, it is important to be able to compare disturbances on a common basis.

In characterizing the effects of disturbance on the herbaceous layer, it is useful to recognize two general types of effects: direct effects, which include direct damage to preexisting plants and alterations in propagule availability, and indirect effects, comprising changes in microclimate and forest floor substrates, as well as modification of competitive relationships with other plants in all forest strata. In addition, there are initial effects and long-term effects, the former including direct and indirect effects of the disturbance on preexisting plants, propagule availability, microclimate and substrates, and the latter including the development of competitive relationships, propagule availability, microclimate, and substrates over succession time. The interaction of species' life history characteristics with these disturbance factors determines the direction and outcome of forest succession.