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Floristic Diversity in Managed Forests: Demography and Physiology of Understory Plants Following Disturbance in Southern New England Forests

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Current interest in the conservation of biodiversity is generating a need for forest management and silvicultural techniques designed to maintain the integrity of ecosystems while satisfying society's need for timber resources. The conservation of forest understory plant communities should be a major emphasis of this effort as they contain the majority of plant diversity in most U.S. forests and play a significant role in many ecosystem functions. This article reviews the literature regarding plant responses to disturbance—most importantly changes in light environments—and applies that information to forest management. A comparison of developmental plasticity and rapid acclimation as response pathways is used to discuss plant level responses. At the landscape level, diversity models, silviculture treatments, and site characteristics are used to discuss changes in understory community composition following disturbance. Results of ongoing research on the effects of forest management on floristic patterns for southern New England forests are summarized.

KEYWORDS canopy, diversity, herbaceous, nonequilibrium models, oak-hickory, photosynthesis, plant conservation, richness, stand dynamics

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INTRODUCTION

Current interest in sustainable forestry based on managing entire forest ecosystems is generating a need for an increased understanding of the effects of forest management on floristic diversity patterns at the landscape-, stand-, and plant-levels (Reader & Bricker, 1992; Gilliam, Turrill, & Adams, 1995; Meier, Bratton, & Duffy, 1995; Roberts & Gilliam, 1995; Maschinski, Kolb, Smith, & Philips, 1997; Bunnell & Huggard, 1999; Jenkins & Parker, 1999; Lindenmayer, 1999; Rubio, Gavilan, & Escudero, 1999; Battles, Shlisky, Barrett, Heald, & Allen-Diaz, 2001; Brosofske, Chen, & Crow, 2001; Johnson, Shifley, & Rogers, 2002; Small & McCarthy, 2002; Lindenmayer, Franklin, & Fischer, 2006). Maintenance of biological diversity has become a paramount concern along with the successful regeneration of forest tree species of economic value.

These objectives were first mandated by the U.S. National Forest Management Act of 1976, and continue as major management priorities explicit in the goals of The Forest Stewardship Council (1993), The Montreal Process (1998), The Sustainable Forestry Initiative (1995), The Forest Guild, and The Society of American Foresters. Given this trend, it is imperative that forest managers refine current silvicultural methods to give greater attention to the autecology of noncommodity forest species.

THE IMPORTANCE OF CONSIDERING UNDERSTORY FLORISTICS IN FOREST MANAGEMENT PRACTICES

For U.S. forests, it is the herbaceous understory plants as a group that must be better understood physiologically and demographically if forest managers are to successfully maintain or increase biological diversity within vegetative communities. The herbaceous layer is typically the most diverse stratum in eastern deciduous (Braun, 1950; Bratton, 1976; Huebner, Randolph, & Parker, 1995; Ford, Odom, Hale, & Chapman, 2000; Small & McCarthy, 2002) and western coniferous (Thomas, Halpern, Flak, Ligouri, & Austin, 1999; Battles et al., 2001) forests of North America. The herbaceous layer also accounts for a major percentage of total groundcover in New Hampshire forests (36%) (Siccama, Bormann, & Likens, 1970) and in West Virginia forests (36.8%) (Maguire & Forman, 1983). In Connecticut, 40% of the plant species listed as endangered, threatened, or special concern, including virtually all listed orchid (Orchidaceae) species, occur in forested ecosystems (Connecticut Department of Environmental Protection, 2004).

In addition to its significant contribution to forest biodiversity, the herbaceous forest component has been identified as an important indicator of (a) land use history (Foster, 1992), (b) microclimatic and microsite conditions (Beatty, 1984), (c) soil moisture conditions (Davidson & Forman, 1982), (d)

nutrient cycling pathways (Siccama et al., 1970; Bormann & Likens, 1994; Muller, 2003; Chastain, Currie, & Townsend, 2006), (e) ecosystem resilience postdisturbance (Halpern, 1988; Gilliam et al., 1995; Meier et al., 1995; Roberts & Gilliam, 1995), (f) a determinant of spatial distribution and relative densities of seedlings (Maguire & Forman, 1983), (g) as a potential tool for indicating site index for timber production (Cajander, 1926; Fountain, 1980; Jones & Churchill, 1987; Strong, Pluth, La Roi, & Corns, 1991), and (h) as an important factor in the early stages of stand development (Oliver & Larson, 1996; Smith, Larson, Kelty, & Ashton, 1997).

Research efforts have begun to focus on the long-term effects of forest management on the spatial and temporal distributions of forest herbs. Some of the earlier studies that attempted to draw a direct link between timber management and floristic diversity point to clearcutting, logging damage, disruption of competitive dynamics, rapid micro- and macro-environmental changes and short harvest rotations as negative influences on herb populations (Duffy & Meier, 1992; Meier et al., 1995). Vernal herbs, rare and late-seral species, and species with low dispersal capabilities are usually reported to be the most adversely affected. However, some of this work has come under criticism due to methods that may not accurately test floristic changes across comparable temporal and physiographic gradients (Elliot & Loftis, 1993; Johnson, Ford, & Hale, 1993; Lindenmayer, 1999). Others contend that the importance of the early work, methods, and results aside, is that the appropriate questions regarding biological diversity in managed forests were beginning to be addressed (Bratton, 1994; Matlack, 1994; Roberts & Gilliam, 1995).

Although forest management certainly affects floristic diversity patterns, the magnitude and trajectory of those effects are not well known for the variety of silvicultural techniques that managers have at their disposal, or across the multitude of forest types currently under management. The majority of studies that exist use observational methods to make snapshot assessments of current floristic patterns and compare them to past management records and unmanaged stand conditions (Metzger & Schultz, 1981; Jenkins & Parker, 1999; Peltzer, Bast, Wilson, & Gerry, 2000; Small & McCarthy, 2005). What little work has been conducted on the physiological, anatomical, and morphological plasticity of understory plants in response to the environmental changes brought about by forest management has mostly been conducted in the tropics (Clearwater, Susilawaty, Effendi, & van Gardingen, 1999). Currently there is very little information on the effects of timber management on the understory flora of the mixed-hardwood forests of southern New England. The purpose of this review is to discuss what is known about understory plant responses to disturbance in an effort to inform silviculture practices aimed at conserving floristic diversity in managed forests.

FLORISTIC DIVERSITY AND MANAGED FORESTS

During and immediately after timber harvest, understory plants are exposed to major changes in their physical environment. These changes can include increased nutrient levels, greater diurnal temperature fluctuations, and fluctuations in soil moisture content and relative humidity (Minckler, Woerheide, & Schlesinger, 1973; Denslow, 1985; Phillips & Shure, 1990). The most dramatic change is in the form of increased levels of direct Photosynthetically Active Radiation (PAR) on the previously shaded groundstory strata (Chazdon & Fletcher, 1984; Collins, Dunne, & Pickett, 1985; Canham, 1988; Canham et al., 1990). The PAR levels in eastern hardwood forests can range from 1% to 5% incident radiation under the intact canopy, to full sun after canopy removal (Anderson, 1964; Hicks & Chabot, 1985). These changes are not uniform across a forest gap, and can vary significantly depending on the position of a microsite in relation to the edge or center of the zone of disturbance and the spatial orientation of noncircular gaps (Runkle, 1982; Canham et al., 1990).

The temporal component of changes in understory light environments is less emphasized, and depends on the direction in which light levels are changing. Typically, increases in light levels to the groundstory are instantaneous through natural treefall or canopy tree removal as a result of timber harvest. In contrast, understory vegetation undergoes a much slower transition to decreased light levels through the shading caused by lateral canopy closure or the development of a tree seedling and/or sapling strata (Oliver, 1981; Brokaw, 1985; Runkle, 1985; Whitmore, 1989; Naidu & DeLucia, 1998).

The ability of species to establish and persist in changing light environments has been a topic of considerable study, and in many habitats is a major factor in determining floristic patterns inherent on a landscape. Grime (1977) developed a general theory for describing plant survival strategies under various levels of resource stress and disturbance conditions. He designated three groups of strategists: plants that persist in zones of low stress and high disturbance (ruderals), plants that persist in zones of high stress and low disturbance (stress-tolerants), and those that persist under conditions of low stress and low disturbance (competitive plants). Grime's work applies as a general model for many types of resource stress and disturbance types, and has been applied to studies conducted on light stress and forest herbs (Meier et al., 1995; Clearwater et al., 1999; Rothstein & Zak, 2001).

Early work by Sparling (1967) placed herbaceous forest species into three groups based on light physiology in relation to PAR levels (converted from ft-c): shade intolerants (light saturation points between $200 \mu\text{mol m}^2 \text{s}^{-1}$ and $600 \mu\text{mol m}^2 \text{s}^{-1}$; compensation points $> 10 \mu\text{mol m}^2 \text{s}^{-1}$), semi-shade tolerants (light saturation points between $70 \mu\text{mol m}^2 \text{s}^{-1}$ and $200 \mu\text{mol m}^2 \text{s}^{-1}$; compensation points $<$ intolerants), and shade-tolerants (light saturation

points $< 50 \mu\text{mol m}^2 \text{s}^{-1}$ and compensation points $< 5 \mu\text{mol m}^2 \text{s}^{-1}$). Phenological responses to seasonal light conditions have also been used to group herbaceous forest vegetation into identifiable categories such as vernal photosynthesis, summer green, late-summer green, and semi-evergreen (Mahall & Bormann, 1978). Collins et al. (1985) combined physiological and phenological traits into a ranking system that designates: (a) sun herbs (high metabolism plants that persist in open habitats or vernal herbs that complete their lifecycle before canopy closure); (b) light-flexible herbs (plants that are photosynthetically plastic and are widely dispersed across both sunny and shaded patches), and (c) shade herbs (low metabolism plants that photoinhibit at low light levels and mature and senesce under closed canopies). More recently, a shade tolerance index has been developed for 185 herbaceous species and 91 bryophyte and lichen species of the northeastern United States (Hubert, Gagnon, Kneeshaw, & Messier, 2007). The ability to predict how these guilds of forest understory plants will respond to canopy removing disturbances should be a major goal of silviculture practices that consider the integrity of whole forest systems.

RESPONSES OF FOREST UNDERSTORY PLANTS TO CHANGING LIGHT ENVIRONMENTS

The components of natural and anthropogenic disturbance that are most often referred to are the frequency, intensity, and size of the event (White, 1979; White & Pickett, 1985). Far less attention has been given to the timing of disturbance events and its effect on the distribution and successional dynamics of plants (Oliver, 1981; Runkle, 1985; Berger & Puettman, 2004). In southern New England forests, the majority of timber operations are conducted from early summer through winter, with few operations being conducted during the wet spring months. This has special significance in the life-history of many forest interior plants which spend winters below ground as geophytes or have already fully developed their anatomical, physiological and morphological leaf traits by summer and autumn.

The above disturbance regime presents three distinctly different options: (a) plants that are in areas where the canopy is removed during winter are able to develop in the new light environment and adjust their ontogeny accordingly, (b) fully developed plants that are in areas of summer canopy removal must adjust their anatomy, physiology, or morphology to the new environment through acclimation of leaves that are already present, or (c) the latter must discard the current leaves and produce new ones that are able to respond more efficiently to increased light levels. This is especially true of the shade-adapted groundstory flora of closed-canopy eastern hardwood forests which is typically composed of long-lived, perennial, or clonal plants that allocate more resources to vegetative growth than reproductive structures

and therefore demonstrate low fecundity rates and dispersal capabilities (Bierzychudek, 1982; Meier et al., 1995; Collins et al., 1985). Without the capacity to quickly colonize new sites when exposed to unfavorable conditions, these species must be able to demonstrate a level of response that would allow them to adjust to the new environment if they are to take advantage of, and remain in, a recently harvested stand.

Exposure to sudden increases in light levels resulting from canopy removal has been shown to be detrimental to some understory species of temperate (Meier et al., 1995) and tropical forests (Clearwater et al., 1999). Understory plants usually show physiological, anatomical, and morphological characteristics that differ significantly from species of more open environments (Bazzaz, 1979). These shade adapted traits include low light compensation points, low light saturation points, high quantum yield, low dark respiration rates, large specific leaf areas (surface area/dry weight), low mesophyll thickness, greater susceptibility to photoinhibition, low stomatal densities, and lower stomatal conductivity rates when compared to sun grown plants. (Taylor & Pearcy, 1976; Boardman, 1977; Bazzaz, 1979; Mulkey & Pearcy, 1992; Larcher, 1995). While these traits provide understory plants with the adaptive ability to persist in low-light environments, they can also put these species at a serious competitive disadvantage when light levels are increased dramatically (Clearwater et al., 1999). This situation can be somewhat mediated if the species in question is able to express some degree of adaptive capability, whether through acclimation or plasticity, allowing it to take advantage of the new light environment (Givnish, 1988; Pearcy & Sims, 1994; Kusar & Coley, 1999).

While acclimation is sometimes considered a special type of phenotypic plasticity, for the purposes of this study the two are considered different processes that facilitate responses at different stages of plant development (Strauss-Debenedetti & Bazzaz, 1991; Sims & Pearcy, 1992; Chazdon & Kaufman, 1993; Strauss-Debenedetti and Berlyn, 1994). Acclimation in the context of this study refers to a plant's ability to make changes to the physiology, anatomy, or morphology of mature leaves in response to changing light environments. Plasticity on the other hand, refers to a plant's ability to adjust the ontogeny of developing leaves in response to a new light environment. It should be noted here that a species' ability to respond to changes, either through acclimation or plasticity, is usually dependent on a combination of environmental stressors such as desiccation or heat stress that often accompany increased light levels (Mulkey & Pearcy, 1992; Muraoka, Tang, Koizumi, & Washitani, 2002). In general, it has been shown that shade-intolerant, early-seral species display a greater range of response capabilities, than shade-tolerant late-seral species (Bazzaz, 1979; Ashton & Berlyn, 1994; Strauss-Debenedetti & Berlyn, 1994; Bazzaz, 1996).

Studies by Sparling (1967), Taylor and Pearcy (1976), and Rothstein and Zak (2001) have all shown that shade adapted understory plants have the

ability to seasonally adjust their photosynthetic processes in relation to diminishing light levels coincidental with canopy closure. Photosynthetic capacity, light compensation point, and dark respiration rates for the summer green *Viola pubescens* all decreased from spring to summer, while the same trend for the semievergreen *Tiarella cordifolia* was followed by an increase in the same parameters when light levels increased again during the fall (Rothstein & Zak, 2001). Sparling (1967) reports the same trends in net assimilation rates and compensation and saturation points for the shade tolerant *Maianthemum canadense* monitored from May through July, while Landhauser, Stadt, and Lieffers (1997) also showed seasonal shifts in photosynthetic capacity for *Aralia nudicaulis* and *Rubus pubescens*. Interestingly enough, both Sparling (1967) and Taylor and Percy (1976) found that *Erythronium americanum* was unable to adapt its photosynthetic apparatus to decreasing light levels beneath developing canopies. As both consider *E. americanum* a sun adapted species that takes advantage of full sun conditions, this finding somewhat contradicts the previously stated proposition that shade intolerant species should demonstrate greater photosynthetic plasticity than shade tolerant species.

Studies on the ability of plants to show physiological, anatomical, and morphological responses to transfers from low light to high light situations are numerous (see reviews in Caldwell & Percy, 1994). One of the classic studies in this area was conducted on *Alocasia macrorrhiza*, a tropical understory herb that can grow in deep shade but requires treefall gaps for reproduction (Sims & Percy, 1992). Sims and Percy found that plants grown in high light had significantly higher photosynthetic capacity (66%) as well as thicker mesophyll layers (52%) and overall leaf thickness (41%) than plants grown in shade. However, when plants were transferred from low light to high light only leaves that were in the early stages of development were able to show increases in these parameters, while leaves that were already fully developed showed no increase. They concluded that *Alocasia*'s primary strategy for responding to high light environments is to replace mature shade adapted leaves with new sun leaves that are thicker and able to sustain higher photosynthetic rates.

Kusar and Coley (1999) conducted a similar study on *Hybanthus* and *Ouratea*, two shade tolerant tropical shrubs that have short (1 year) and long (5 years) leaf lifespans, respectively. In the study, both species exhibited photoinhibition, lowered F_v/F_m ratios, reduced light use efficiency, and depressed photosynthetic capacities, for about 2 weeks after transfer. After the initial stress, the two species demonstrated very different strategies for responding to the new light environment, either through quickly replacing shade leaves with sun leaves that had two times greater photosynthetic capacity (*Hybanthus*) or retaining most of the sun leaves with an increased photosynthetic capacity of 50% (*Ouratea*). These results show that plants with short lived leaves may respond quicker to changes in the light environment

with compensation being made at the whole-plant level, where as plants with longer-lived leaves may be less responsive, with changes more a function of leaf level plasticity (Kusar & Coley, 1999).

Further insights into the anatomical and biochemical aspects of light response can be found in Chazdon and Kaufman's (1993) study on the tropical shrubs *Piper sancti-felis* and *P. arieianum* across gap light regimes. *P. arieianum*, an understory shrub, showed lower photosynthetic acclimation potential under varying light conditions than *P. sancti-felis*, a gap shrub, even though the former showed greater variation in palisade and mesophyll thickness and overall leaf thickness. *P. sancti-felis* had demonstrated greater chloroplast density, higher chlorophyll and nitrogen use efficiency, and increased carboxylation efficiency. The increased acclimation shown by *P. sancti-felis* was therefore contributed to greater plasticity at the cellular and biochemical levels, while *P. arieianum* was not limited by anatomy, but rather its inability to adjust its metabolism at the cellular level. Morphological acclimation, as defined by Chazdon and Kaufman (1993), is less commonly demonstrated at the leaf level, although Rothstein and Zak (2001) report that *Viola pubescens* is able to seasonally adjust the leaf mass area (LMA) of individual leaves in response to changes in canopy cover.

DISTURBANCE AND FLORISTIC DIVERSITY

The role of disturbance in mediating species diversity at the landscape level has been given much attention (White, 1979; Denslow, 1985; Petraitis, Latham, & Neisenbaum, 1989) and is quite appropriately applied in the context of managed forests (Roberts & Gilliam, 1995). Equilibrium and nonequilibrium models have been proposed to define the role of disturbance in determining species diversity within various ecosystems (Connell, 1978). Equilibrium models propose that after a disturbance, species composition develops to some maximum threshold and remains at that point until the next event restarts the process. According to nonequilibrium models, repeated random and catastrophic disturbance events prevent species composition from ever reaching equilibrium.

While these two schools, and their many subhypotheses, have merit and overlapping usefulness in explaining species diversity as a result of disturbance, the equilibrium based hypothesis of compensatory-mortality is especially fitting for forests that are actively managed for timber. The compensatory-mortality theory (Connell, 1978, Petraitis et al., 1989) states that the mortality of a superior competitor maintains diversity at equilibrium. As Roberts and Gilliam (1995) point out, this is a hypothesis that explicitly requires a disturbance event to maintain diversity. In managed forests it is the overstory trees that are the superior competitors through their ability to intercept light and moisture and subsequently influence understory

conditions. It is by way of their removal that understory species composition is re-shuffled. In fact, Gilliam et al. (1995) found a temporal shift in the processes that influence species composition of central Appalachian hardwood forests from allogenic factors to autogenic factors over the course of succession, with overstory composition becoming a more important determinant in later-seral stages. Whitney and Foster (1988) also make note of the dependency of understory vegetation to overstory composition in central New England forests, but consider it a more dynamic (nonequilibrium) relationship in which relatively frequent disturbance of the canopy keeps understory floristic patterns in "flux."

Species diversity goes through transitions during the process of stand development, which begins immediately after an initial stand replacing disturbance event and can continue for many decades (Oliver & Larson, 1996). In general, it has been shown that species richness oscillates through several peaks and lows over the course of succession or stand development (Peet & Christensen, 1980; Halpern & Spies, 1995; also see review in Roberts & Gilliam, 1995). These studies show that species richness tends to increase through the course of stand initiation as resources are plentiful and new species invade the disturbed site. Richness would then decrease to a minimum during stem exclusion when competition for light is at a maximum. With stand reinitiation, species richness would again increase due to increased light levels from canopy gaps, and follow a somewhat stable or slightly decreasing trend into the old growth stage. If these propositions hold true, it would stand to reason that a forest management plan that creates a mixture of stand stages would promote the greatest levels of floristic diversity by providing a variety of niches and site conditions, facilitating the shifting mosaic steady state (Bormann & Likens, 1994).

One of the most basic and often applied measurements of diversity at the entity or species scale is species richness (S), which calculates diversity as the number of species present per unit land area, regardless of specific type (Peet, 1974; Gotelli & Colwell, 2001). When combined with data on individual abundances of species, richness can be used to calculate such informational theory indices as Shannon Index (H') or Evenness Index (E) (Magurran, 1988). While Shannon's Index and Richness have value in understanding the heterogeneous nature of diversity at different locations, care must be taken in their interpretations as they lack the ability to provide information on which species are present at any temporal point or spatial extent. This problem is exemplified in numerous studies on the effects of forest management on understory vegetation patterns. In oak-hickory forests of Pennsylvania, neither S or H' changed with standing timber volume, but early-seral species dominated low volume stands and late-seral species dominated high volume stands (Fredericksen et al., 1999). In Japanese *Cryptomeria* and *Chamaecyparis* plantations, S and H' were found to be similar for both 20-year-old strip cut stands and 30-year-old clearcut stands, although the

strip cuts were dominated by understory species typical of seminatural stands, while the understory at clearcuts was dominated by disturbance related species (Ito, Ishigami, Mizoue, & Buckley, 2006). The same was found for mixed hardwood-white pine forests in Wisconsin where changes in species composition between mature hardwood stands and clearcuts were significantly greater than changes in either S or H' (Brofoske et al., 2001). Battles et al. (2001) also found that species richness in a Sierran conifer forest was greatest in plantations and shelterwoods, but these stands also had the greatest number of introduced exotic species in comparison to other treatment types.

The majority of studies investigating the influence of forest management on species diversity compare clearcut stands to primary or secondary stands (Duffy & Meier, 1992; Johnson et al., 1993; Meier et al., 1995), although other harvest practices have also been assessed (Metzger & Schultz, 1981; Reader & Bricker, 1992; Fredericksen et al., 1999; Quinby, 2000; Kern, Palik, & Strong, 2006). These studies exist for a multitude of forest types and regions in the United States including southern pine (Blair & Brunett, 1976), Sierran conifer (Battles et al., 2001), northwestern Douglas fir (Halpern & Spies, 1995; North, Chen, Smith, Krakowiak, & Franklin, 1996), as well as beech forests of Europe (Graae & Heskjaer, 1997; Aubert, Alard, & Bureau, 2003). Results of studies linking forest management to understory diversity patterns for forests of the eastern and central United States are summarized in Table 1.

It is apparent that changes in understory floristics following disturbance vary by management intensity and forest type. Some trends do exist such as a negative correlation between groundstory cover and stand age (Metzger & Schultz, 1981; Yorks & Dabydeen, 1999). This most likely is the product of competition in the low-light environment and the previously mentioned tendency for S and H' to remain constant while compositional diversity changes (Fredericksen et al., 1999; Ruben, Bolger, Peart, & Ayres, 1999; Brofoske et al., 2001). However, the conflicting results regarding changes in S and H' demonstrate some of the problems inherent in using numerical indices to compare ecological processes between forest types (Roberts & Gilliam, 1995). Also, numerous studies have shown that differences in topographic position or aspect are of significant importance and must be incorporated into successful interpretations of the effects of disturbance on floristic patterns (Jenkins & Parker, 1999; Ford et al., 2000; Small & McCarthy, 2002, 2005). However, this was not found to be the case for the mid-Atlantic hardwoods studied by Yorks and Dabydeen (1999).

Other important site factors that have been shown to influence the relationship between disturbance, stand development, and understory diversity patterns include soil moisture, standing dead trees, soil rooting depth (Huebner et al., 1995), microtopography including tip-up mounds (Bratton, 1976), and forest floor characteristics such as litter cover, duff depth, and

TABLE 1 A Review Of Studies Investigating the Relationship Between Timber Management and Understory Diversity Patterns for Forests of the Eastern and Central United States

Forest type	Treatment	Time since treatment	Reference stand	Results
Mixed-Hardwood, N. Michigan ⁴	cc ¹ (>12cm, >30 cm) group selection w/3 entries	50 years	None	groundcover denser but less diverse on cc; woody seedlings and shrubs more abundant on group selection
Central Hardwood, Indiana ⁵	cc (n/a), group selection, single tree selection	7 to 26 years	80–100 year 2nd growth stand	size of openings more important than age in determining ground cover; cc and group greater cover of ecological groups than reference or single tree; topography important
Northern Hardwood, New Hampshire ⁶	cc	(n/a) years	25 and 60 2nd growth stand	>90-year mean S ² did not differ between treatments; sensitive species less common in cc and decreased in density w/distance into cc
Oak, SE Ohio ⁷	cc (n/a)	7 years	125 year 2nd growth stand	S greater in cc; S and abundance greater NE and SW aspects and lower slopes; summer herbs more affected by cc than spring herbs; exotics increased at cc
Oak-Hickory, N. Hardwoods, NE Pennsylvania ⁸	cc (< .06 m ² /ha ⁻¹ standing), selection	1 to 9 years	70 year 2nd stand	neither S or H ³ varied w/ volume for either forest; ground cover increased w/ harvest intensity; early seral species w/ low volume, late seral sp. w/high volume

Mixed Hardwood-Hemlock-W.Pine, W. Maryland ⁹	cc (> 5cm)	1 to 26 years	75–80 year 2nd growth stand	no difference in <i>S</i> or <i>H</i> w/stand age or aspect; % cover negatively correlated to stand age
Mixed Hardwood-Pine, N. Wisconsin ¹⁰	mature and young hw (10–15 years), mature red and jack pine, young mixed pine (7–15 years), cc (n/a)	None		<i>S</i> differed only between mature hw and cc; overstory composition important in determining understory diversity; <i>S</i> and <i>H</i> changed less than compositional diversity
Mixed Hardwood, West Virginia ¹¹	cc (n/a)	20 years	> 70 year 2nd growth stand	neither <i>S</i> or <i>H</i> differed between cc or 2nd stand; understory correlated to overstory at 2nd stands but not at cc
Oak-Pine, Maine ¹²	patch cuts (58% of basal area residual: gaps ranging in size from 36 to 3393 m ²)	10 years	Uncut control	<i>S</i> higher in gaps than controls mostly due to novel species; gap dependent species declined over time; <i>H</i> not affected by treatment
Mixed Hardwood-W. North Carolina ¹³	irregular shelterwood 5 m ² /ha ⁻¹ ; shelterwood 9 m ² /ha ⁻¹ ; group selection .01–.02 ha openings, 75% BA residual	1 and 3 years	Uncut control	<i>H</i> higher for both shelterwood treatments in comparison to group selection and control; <i>S</i> greatest immediately after harvest

¹cc = clearcut (indicates prescription detail if available, cm is diameter limit, m²/ha⁻¹ is standing volume after harvest); ²*S* = species richness; ³*H* = Shannon's Index;
⁴(Metzger & Schultz, 1981); ⁵(Jenkins & Parker, 1999); ⁶(Ruben et al., 1999); ⁷(Small & McCarthy, 2002); ⁸(Fredericksen et al., 1999); ⁹(Yorkes & Dabydeen, 1999);
¹⁰(Profoske et al., 2001); ¹¹(Gilliam et al., 1995); ¹²(Schumann, White, & Whitman, 2003); ¹³(Elliot & Knoepp, 2005).

coarse woody debris (Brofoske et al., 2001). Gap position and disturbance intensity have also been shown to have a significant impact on the colonization and extirpation of herbaceous vegetation following canopy removal (Aikens, Ellum, McKenna, Kelty, & Ashton, 2007). Recent emphasis has also been given to the long lasting and significant influence that past land-use can have on current forest structure, sometimes to the point of overriding the effects of current management (Donohue, Foster, & Motzkin, 2000; Gerhardt & Foster, 2002; Thompson et al., 2002; Foster et al., 2003).

CONCLUSION

Understanding the ability of forest understory plants to respond, at multiple levels, to disturbances caused by timber harvest is essential if silviculture practices are to incorporate techniques for plant conservation as well as crop tree regeneration. My ongoing research in southern New England indicates that the seasonal timing of canopy removing disturbances may play a major role in the growth and survival of some forest understory plants. Dormant season disturbances allow these plants to adjust their anatomy, morphology, and physiology through developmental plasticity, resulting in positive responses to increased light levels (Ellum, 2007). However, rapid acclimation—the response necessary for adjusting to increased light levels that occur during the growing season—does not provide for survival in the postdisturbance environment. This research also indicates that forest cover type and topographic position greatly influence floristic diversity patterns, and that the long-term effects of past land use practices may mask the short-term response of understory vegetation to current silviculture treatments (Ellum, 2007).

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