The Formation of Dense Understory Layers in Forests Worldwide: Consequences and Implications for Forest Dynamics, Biodiversity, and Succession

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Abstract

Alterations to natural herbivore and disturbance regimes often allow a select suite of forest understory plant species to dramatically spread and form persistent, mono-dominant thickets. Following their expansion, this newly established understory canopy can alter tree seedling recruitment rates and exert considerable control over the rate and direction of secondary forest succession. No matter where these native plant invasions occur, they are characterized by one or more of the following: (1) the understory layer typically has greater vegetation cover and lower diversity than was common in forest understories in the past; (2) this layer can delay stand renewal and alter species composition by inhibiting tree regeneration; and (3) once this layer is formed, it can resist displacement by other species and remain intact for decades. In this paper, we evaluate the processes that trigger the expansion of several plant species native to forests and review their ecological characteristics to provide general guidelines in assessing native invasion risk in forest stands.

We argue that major anthropogenic changes to disturbance and browsing regimes bring about the monopolization of the forest understory by native plants. In all cases reviewed, aggressive understory plant expansion followed alterations in overstory disturbance regimes. Although these disruptions included predictable and manageable impacts such as tree harvesting, other less predictable overstory disturbance agents including catastrophic fires, insect outbreaks, and pathogens were involved. Assessing and managing risk from these alternative threats is challenging as their occurrence is often erratic, hard to control, and not limited by land ownership and administrative boundaries. In many cases, the risk to forest understories was particularly acute if the effects of multiple stressors occurred in a stand, either in tandem or within a short period of time. Specifically, the synergy between overstory disturbance and uncharacteristic fire regimes or increased herbivore strongly controls species richness and leads to depauperate understories dominated by one or a few species.

We suggest that aggressive expansion by native understory plant species can be explained by considering their ecological requirements in addition to their environmental context. Some plant species are particularly invasive by virtue of having life-history attributes that match one or more of the opportunities afforded by multiple disturbances. Increased overstory disturbance selects for shade-intolerant species with rapid rates of vegetative spread over slower growing, shade-tolerant herbs and shrubs. Altered fire regimes select for only those species that can survive the fire or resprout thereafter. Finally, overbrowsing selects for only those species that are well defended or tolerant to browsing. Ultimately, these processes create novel conditions that favor only a small subset of species that possess some combination of the following life-history characteristics: rapid vegetative growth, relatively shade intolerant, fire tolerant, and herbivore tolerant. The result is a low diversity but dense understory that can persist for long periods of time even if the canopy closes.

The framework advanced by this review could aid land managers in implementing informed management policies and practices that both limit the spread of these plants and target control and remediation treatments directed at the precise mechanism of interference. We suggest vigilant monitoring of stand conditions to ensure that alterations to the overstory and understory disturbance regimes do not operate concurrently, particularly when control over these factors falls under the purview of different management agencies (e.g., wild game vs. forestry management agencies). Finally, we caution that decisions regarding partial or complete overstory removals should consider a site's understory conditions including inadequate advance regeneration, presence of clonal understory plants, fire history, and high herbivore impact.

Keywords: Competition, interference, invasive, recalcitrant understory layer, regeneration.

Introduction

Major anthropogenic changes in the frequency and severity of natural disturbance regimes can radically alter understory species composition and threaten the long-term sustainability and biodiversity of plant ecosystems (Alpert and others 2000, Roberts 2004, Rooney and others 2004). These changed disturbance regimes often trigger rapid expansion of native plant species that previously occupied a relatively minor portion of the understory flora (de la Cretaz and Kelty 1999, Mallik 2003, Vandermast and Van Lear 2002). Following their release, these herbs, shrubs, trees, and vines aggressively colonize and overtake disturbed patches forming persistent, nearly monospecific, and seemingly impenetrable thickets. This layer, identified in the literature as competing vegetation, interfering plants, low canopy, non-crop vegetation, native invasives, recalcitrant understory layer, or weeds, creates conditions below its canopy that reduce tree seedling establishment and survival, inhibit seedling growth into the sapling-size class, and alter species composition (Bashant and others 2005, Horsley 1993a, Messier and others 1989, Nilsen and others 2001, Tappeiner and others 1991). The impacts of this interfering layer alter the rate, direction, and composition of tree regeneration so profoundly that forest recovery following disturbance may contrast sharply with the predicted patterns of vegetation development for a particular forest type. Thus, these dominant understory layers often are the crucial factor determining success or failure of tree regeneration following harvest, thus threatening sustainable forest management (Ehrenfeld 1980, Gill and Marks 1991, Huenneke 1983).

In this paper, we first review the processes that cause the formation of recalcitrant understory layers. Second, we describe how these layers alter the rate and direction of forest succession. Third, we review published work to identify how these layers control tree recruitment, growth, and survivorship and, thus, patterns of tree regeneration and succession. Fourth, we identify the most prominent causal mechanisms for the formation of these layers and outline the consequences of their formation on successional dynamics and forest regeneration. Finally, we discuss how recalcitrant understory layers may reduce floristic diversity, we argue for their incorporation into forest successional models, and we explore management options for mitigation of their impacts.

On the Development of Recalcitrant Understory Layers Worldwide

Recent changes in disturbance and browsing regimes have strongly impacted species composition in forest understories worldwide (Coomes and others 2003, de la Cretaz and Kelty 1999, Mallik 2003, Vandermast and Van Lear 2002). Typically, these changes have led to large increases in the density and cover of a small number of native understory plant species (e.g., Mallik 2003). In many cases, these species expand to form persistent, monodominant layers that, in some cases, are nearly impenetrable (Figure 1, Tables 1 and 2). We term these dense strata recalcitrant understory layers. No matter where they occur worldwide, they are characterized by sharing one or more of the following attributes: (1) the understory layer is often more dense with greater vegetation cover and lower diversity than was common in forest understories in the past; (2) this layer can alter successional trajectories and slow the rate of succession by creating conditions in the understory near ground level that are inimical to seeds and seedlings of many tree species (e.g., very low light at the soil surface); or (3) once this layer is formed, it can resist displacement by other species and remain intact for decades, even beneath closed-canopy forests. These layers and species have been termed low canopies (Schnitzer and others 2000) and native invasives (de la Cretaz and Kelty 1999), respectively. We prefer recalcitrant understory layer because it emphasizes that the effect of this layer occurs in the understory and is resistant to displacement. Additionally, the term native invasive suggests these species, similar to exotic invasives (e.g., exotic Japanese barberry, Amur honeysuckle; reviewed by Richburg and others 2001), are invading novel habitat when in fact the species that formed these layers were present throughout the

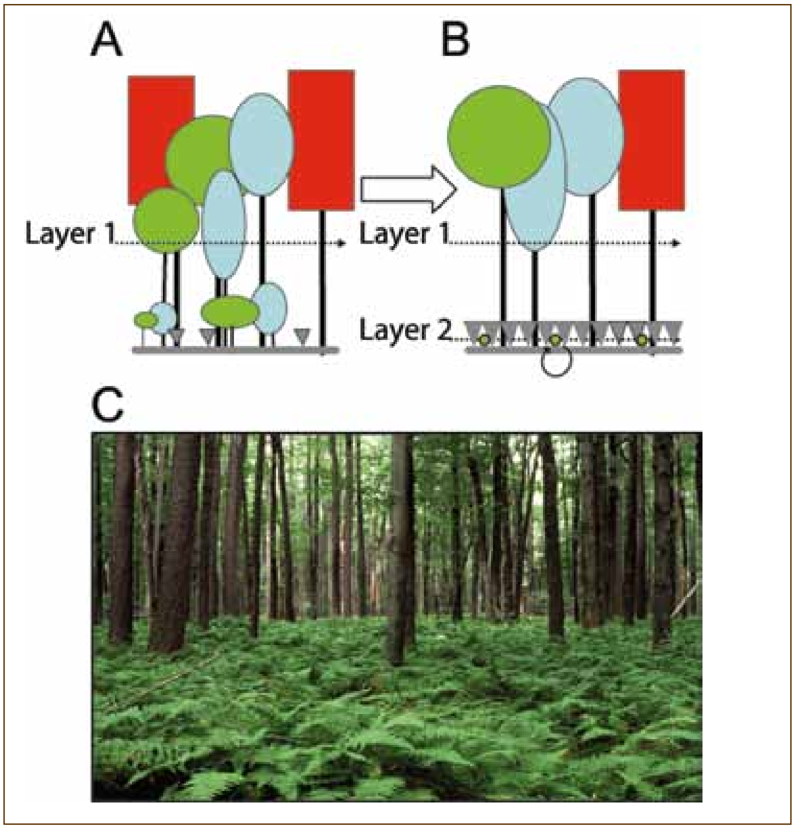

Figure 1—Diagrammatic representation of the conversion from (A) forests containing a diverse and structured advanced regeneration layer with sparse understory plant abundance (shown as grey inverted triangles), to (B) forests where a native understory species expands and monopolizes the understory. The dense herbaceous or shrubby cover represents a new vegetation layer that exerts direct and indirect interference effects and prevents seedling (shown as small green disks) recruitment into the sapling class. (C) Photographic example with hay-scented fern in northwestern Pennsylvania forests (Photograph by Alejandro Royo, USDA Forest Service)

habitat at varying degrees of abundance. Overall, we argue that models and theories of forest succession must now consider that many forests have a strong understory filter that determines which tree species are present to take advantage of a newly formed gap. In many cases, these recalcitrant understory layers are dramatically altering forestwide species diversity and patterns of succession.

Processes Causing the Formation of Recalcitrant Understory Layers

In this section, we discuss how natural processes, including such stressors as (1) overstory disturbance, (2) elevated herbivore regimes, and (3) altered fire regimes may be treated either as threats or benefits to forest communities. Overstory disturbances reinitiate stand development (Oliver and Larson 1996), and characteristic fire and herbivore regimes often promote species coexistence (reviewed in Bond and Keeley 2005, Huntly 1991). What constitutes a threat or a risk often is intrinsically linked (and, thus, often critiqued) to a subjective value of what constitutes a loss in biological or ecological diversity, function, or service (see Power and Adams 1997 for a vigorous debate). To be workable, we narrowly categorize an uncharacteristic disturbance regime as a threat or risk if its occurrence results in a persistent negative impact on the ability of the disturbed stand to regenerate its predisturbance tree species composition. Utilizing that definition, it is clear that alterations to disturbance regimes can constitute a threat to forest

Table 1—Interfering species examples[a]

Species	Family	Areas affected	Rapid vegetative growth	Herbivory	Fire	Overstory disturbance	Mechanism	References
Dennstaedtia punctilobula (Michx.) T. Moore	Dennstaedtiaceae	NE US	√	√ (T)	-	√	1,2,3,5 [4]	Cody and others 1977; Anderson and Egler 1988; Drew 1988; McWilliams and others 1995; de la Cretaz and Kelty 1999, 2002; George and Bazazz 1999 a,b; Horsley and Marquis 1983; Horsley 1977, 1993 a,b; Horsley and others 2003; Hill 1996; Hill and Silander 2001; Brach and others 1993
Pteridium aquilinum (L.) Kuhn	Dennstaedtiaceae	Worldwide	√	-	√	√ (T)	1,2,3,5 [4]	Gliessman 1978; Gleissman and Muller 1972, 1978; Dolling 1996, 1999; Dolling and others 1994; Ferguson and Adams 1994; Den Ouden 2000
Thelypteris noveboracensis (L.) Nieuwl.	Thelypteridaceae	NE US	√	√ (T)	-	√	[1]	Hill and Silander 2001
Blechnum spp.	Blechnaceae	New Zealand	√	√ (T)	-	√	-	Coomes and others 2003, Cunningham 1979
Cyathea spp.	Cyatheaceae	New Zealand	√	√ (T)	-	√	-	Jane and Pracy 1974, Rogers and Leathwick 1997
Dicranopteris linearis	Gleicheniaceae	Sri Lanka, Hawaii	√	-	√	√	-	Maheswaran and Gunatilleke 1988, Russell and others 1998
Dicranopteris pectinata (Burm.) Underw.	Gleicheniaceae	Puerto Rico	√	-	√	√	[1]	Guariguata 1990, Walker 1994, Walker and Boneta 1995, Russell and others 1998, May 2000
Gleichenia bifida (Willd.) Ching	Gleicheniaceae	Puerto Rico	√	-	√	√	-	Guariguata 1990, Walker and Boneta 1995
Gleichenia linearis (Burm. f.) C.B. Clarke	Gleicheniaceae	Malasia	√	-		√	-	Kochummen and Ng 1977
Calamagrostis canadense (Michx.) P. Beauv.	Poaceae Forests	N. America Boreal	√	-	√ (T)	√	1,5 [4]	Cater and Chapin 2000, Hogg and Lieffers 1991, Lieffers and others 993
Cortaderia spp.	Poaceae	New Zealand	√	√	-	√	-	Jane and Pracy 1974, Rogers and Leathwick 1997
Deschampsia flexuosa (L.) Trin. ex	Poaceae	European Boreal Forests	√	√ (T)	-	√	-	Berquist and others 1999

Species	Family	Areas affected	Rapid vegetative growth	Herbivory	Fire	Overstory disturbance	Mechanism	References
Astrogyne martiana (H. Wendl. ex Drude)	Arecaceae	Costa Rica	-	-	-	-	1,2,[6]	Denslow and others 1991
Geonoma cuneata H. Wendl. ex spruce	Arecaceae	Costa Rica	-	-	-	-	1,2,[6]	Denslow and others 1991
Oenocarpus mapora H. Karst.	Arecaceae	Costa Rica	√	-	-	-	6,[1]	Farris-Lopez and others 2004
Asplundia uncinata Harling	Cyclanthaceae	Costa Rica		-	-	-	1,2,[6]	Denslow and others 1991
Aechmea magdalenae (André) André ex Baker	Bromeliaceae	Panama	√	-	-	√	[1]	Brokaw 1983, Pfitsch and Smith 1988
Sinarundinaria gangiana	Poaceae	China	√	-	-	-	-	Taylor and Zisheng 1988
Chusquea spp.	Poaceae	W. South America	√	-	-	√	[1,4]	Lusk 2001, Veblen 1982, Gonzalez and others 2002
Guadua sarcocarpa Londono & Peterson, sp. nov.	Poaceae	S. America	√	-	√	√	[1,6]	Griscom and Ashton 2003
Fargesia denudata	Poaceae	China	√	-	-	-	-	Taylor and others 1995
Sasa spp.	Poaceae	Japan	√	-	-	√	[1,4]	Abe and others 2002, Iida 2004, Wada 1993;
Yushania microphylla Munro	Poaceae	Bhutan	√	-	-	-	[1]	Gratzer and others 1999
Calluna vulgans	Ericaceae	W. Europe	√	-	√ (T)	√	[3]	Mallik 1995
Kalmia angustifolia (L.)	Ericaceae	E. Canada & United States	√	-	√ (T)	√	[2,3]	Hall and others 1973, Meades 1983, Mallik 1995, Inderjit and Mallik 1996, Mallik and Inderjit 2001, Bradley and others 1997, Yamasaki and others 1998
Kalmia latifolia (L.)	Ericaceae	E. United States	√	-	√ (T)	√	[1]	Woods and Shanks 1959, Monk and others 1985, Lipscomb and Nilsen 1990, Mallik 1995

Species	Family	Areas affected	Rapid vegetative growth	Herbivory	Fire	Overstory disturbance	Mechanism	References
Rhododendron maximum	Ericaceae	E. United States	√	-	√	√ (T)	1,[2,3,4,5]	Monk and others 1985; Lipscomb and Nilsen 1990; Clinton and others 1994, Clinton and Vose 1996, Walker and others 1999; Nilsen and others 1999, 2001; Beckage and others 2000; Lei and others 2002; Beckage and Clark 2003, Christy 1986;, Hille Ris Lambers and Clark 2003; Vandermast and Van Lear 2002
aylussaccia baccata (Wang.) K. Koch	Ericaceae	E. United States	√	-	-	√	1,2	Beckage and Clark 2003
Gaultheria shallon Pursh	Ericaceae	W. Canada Pacific Northwest	√	-	√ (T)	√	3	Price and others 1986; Messier and Kimmins 1990, 1991; Messier 1992, 1993; Chang and Preston 2000, Chang and others 1996a,b; Bunnell 1990
Vaccinium myrtillus (L.)	Ericaceae	European boreal forests	√	-	√ (T)	√	1,2,3	Maubon and others 1995, Jäderlund and others 1997, Moola and Mallik 1998, Frak and Ponge 2002
Empetrum hermaphroditum (Lange ex Hagerup) Böcher	Ericaceae	European boreal forests	√	-	-	√	1,2,3	Michelsen and others 1995, Mallik 2003, Nilsson 1994, Wardle and Nilsson 1997, Zackrisson and others 1997, Nilsson and others 2000
Pseudowintera colorata	Winteraceae	New Zealand	-	√ (T)	-	√	-	Godley and Smith 1981, Allen and others 1984, Coomes and others 2003, Husheer and others 2003
Rubus spp.	Rosaceae	Pacific NW & Europe	√	-	-	√	[1,4,5]	Franklin and Pechanec 1967, Tappeiner and others 1991, Schreiner and others 2000
Rhus glabra	Anacardiaceae	E. United States	√	-	-	√	1,2	Putz and Canham 1992
Lianas (various genera)	-	Tropical Forests & E. United States	√	-	√	√	1,2,[6]	Smith 1984, Dillenberg and others 1993, Perez-Salicrup and Barker 2000, Schnitzer and others 2000, Schnitzer and Bongers 2002, Gerwing 2001, Grauel and Putz 2004
Cornus spp.	Cornaceae	NE United States	√	-	-	√	1,2	Ehrenfeld 1980, Huenneke 1983, Putz and Canham 1992
Corylus cornuta Marsh.	Betulaceae	Lake States United States	√	-	-	√	1,2	Sabhasri and Ferrell 1960; Batzer and Popp 1985, Tappeiner 1971, Tappeiner and John 1973, Tappeiner and others 1991, 2001; Kurmis and Sucoff 1989
Acer spicatum Lam.	Aceraceae	SE Canada, NE United States	√	-	-	√	[1]	Aubin and others 2000

[a] Occurrence of dense, monodominant understory species. Information in this table summarizes whether the species possess rapid vegetative growth; if their increase in abundance is linked to alterations in the herbivory, fire, or overstory disturbance regimes; and whether they are fire or browse tolerant (Ts). “Mechanism” indicates the specific interference mechanisms exerted by a species (1 = aboveground competition, 2 = belowground competition, 3 = allelopathy, 4 = seed/seedling predation, 5 = litter, and 6 = mechanical damage). Mechanisms were tested using manipulative field experiments, unless they are in brackets, in which case they are speculative.

regeneration if they result in a degraded understory plant community composition monopolized by a select species that interferes with tree regeneration.

We found that major anthropogenic changes to disturbance and browsing regimes underlie the development of most recalcitrant understory layers (see Hobbs and Huenneke 1992 for their similar conclusion regarding exotic invasives). Indeed, overbrowsing, altered fire regimes, and increased overstory disturbance were implicated in 18, 34, and 82 percent, respectively, of the cases in Table 1. More importantly, our review suggests that the formation of a dense understory canopy layer arises approximately 53 percent of the time in the cases when overstory disturbances and altered understory fire and browsing regimes occur in tandem (Table 1). Additionally, these understory layers are depauperate because repeated canopy disturbances combined with other processes (i.e., fire and browsing) strongly favor a small subset of species.

Increased Overstory Disturbance

Direct and indirect human-induced disturbances (including logging, fires, insect outbreaks, and pathogens) have increased the extent and particularly the frequency of overstory disturbance over the past century (Carson and others 2004, Seymour and others 2002, Sharitz and others 1992, Youngblood and Titus 1996). These disturbances typically increase resource availability (e.g., light) in the understory both in the short and long-term. There is little doubt that these disturbances increase the establishment and growth of seedlings and saplings of canopy trees at least in the short term (Canham 1989, Canham and others 1994, Denslow 1987, Finzi and Canham 2000, Hartshorn 1978, Runkle 1982). However, these extensive and repeated overstory disturbances may be most beneficial to a few understory species that possess high rates of growth and vegetative expansion when exposed to high light (Ehrenfeld 1980, Huenneke 1983, Schnitzer and others 2000) (Table 1). These species are typically shade intolerant, yet highly plastic, so that they can persist at low-light levels following canopy closure by utilizing sunflecks or clonal integration (e.g., Brach and others 1993, Lipscomb and Nilsen 1990, Messier 1992, Moola and Mallik 1998).

There are numerous examples worldwide whereby canopy disturbances lead to the formation of recalcitrant understory layers (Table 1). Tappeiner and others (1991) found that logging increased the formation of salmonberry (*Rubus spectabilis*) tangles by nearly 300 percent over uncut stands. Throughout the Tropics, large-scale disturbances can create bamboo and fern thickets that persist for decades (Griscom and Ashton 2003, Guariguata 1990, Russell and others 1998, Walker 1994). In temperate and boreal forests, both native and exotic insect outbreaks open up vast areas of forest canopies (e.g., Gypsy moth (*Lymantria dispar* L.) and Spruce budworm (*Choristoneura fumiferana* Clemens.) often leading to an increase in the density and dominance of a few shrub species (Aubin and others 2000, Batzer and Popp 1985, Ehrenfeld 1980, Ghent and others 1957, Hix and others 1991, Muzika and Twery 1995). Fungal pathogens have opened up canopies in central New York (Dutch elm disease, *Ophiostoma ulmi*) causing the formation of widespread and dense patches of *Alnus*, *Cornus*, and *Viburnum* spp. (Huenneke 1983). Both Huenneke (1983) and Ehrenfeld (1980) argued that these dense shrub layers would delay canopy formation and alter its composition. Likewise, Chestnut blight (*Cryphonectria parasitica*) apparently led to the aggressive expansion of *Rhododendron maximum* in the Southern Appalachians (Vandermast and Van Lear 2002). In general, any process (whether anthropogenic or not) that increases light availability in the understory has the potential to lead to the formation of recalcitrant understory layers. Nonetheless, it appears that several processes must be altered in combination before these recalcitrant layers can form.

The Interaction of Elevated Herbivore and Canopy Disturbance

This section describes how extended periods of elevated browsing by either introduced or native mammalian herbivores (e.g., white-tailed deer in the Eastern United States; reviewed by Côte and others 2004, McShea and others 1997, Russell and others 2001) often coincide with large-scale canopy disturbances leading to the development of dense interfering layers. Frelich (2002) characterized chronic overbrowsing as a low-intensity disturbance, which,

Table 2—Estimates of spatial coverage by understory native plant invasions in forested areas at both local and regional scales

Species	Location	Type	Estimated forest (ha)	Proportion of forested area affected	References
Dennstaedtia punctilobula	Pennsylvania	Temperate hardwoods	2.1 million	0.33	McWilliams and others 1995
Dennstaedtia punctilobula	Allegheny National Forest, Pennsylvania	Temperate hardwoods	241,000 - 303,000	Approx. 0.47 - 0.59	Royo, unpublished data
Rhododendron maximum	Southern Appalachian Region, U.S.	Temperate hardwoods	2.5 million	-	Monk and others 1985
Lianas (various genera)	Barro Colorado, Rep. of Panama	Tropical forests	-	Approx. 0.22 of all gaps	Schnitzer and others 2000
Pteridium aquilinum	Fontainebleau Forest, France	Old-growth Beech forest	-	0.02 - 0.17	Koop and Hilgen 1987
Pteridium aquilinum	The Netherlands	Temperate hardwood and conifer	288,500	Approx. 0.7 of entire country	den Ouden 2000
Kalmia angustifolia	Newfoundland, Canada	Black spruce	-	0.55	English and Hackett 1994
Gaultheria shallon	British Columbia	Cedar/hemlock forest	100,000	-	Weetman and others 1990
Guadua sarcocarpa	Amazonia	Tropical forests	18 million	-	Nelson 1994
Calamagrostis canadensis	Western Canadian Provinces	Boreal forests of all cutover forest	-	0.25 - 0.5	Lieffers, pers comm.

Note: dash (-) in “Estimated area affected” and “Proportion of forested area affected” means that no information was available for this entry.

[a] Coverage data convey either the total forested land area (in hectares) or the proportion of forested area dominated by a particular species within a region.

over time, can lead to depauperate understories composed almost entirely of highly browse tolerant or unpalatable species (Banta and others 2005, Frelich and Lorimer 1985, Horsley and others 2003, Rooney and Dress 1997, Waller and Alverson 1997). If these browse-tolerant or unpalatable species happen to be clonal shrubs or herbs, then any canopy disturbance that suddenly elevates understory light levels can cause the rapid expansion of these species. One of the best examples of the interplay between long periods of overbrowsing and canopy disturbance is hay-scented fern (*Dennstaedtia punctilobula*). This species historically occupied <3 percent of the understory in Pennsylvania (Lutz 1930) but currently forms a recalcitrant understory layer covering more than a third of the forested area in that State (Table 2) and is abundant throughout much of the Northeastern United States (de la Cretaz and Kelty 1999). Essentially, years of overbrowsing created a depauperate forest understory and suppressed woody establishment in the advance regeneration layer. When light levels increased, continued overbrowsing prevented successful seedling establishment and growth while the unpalatable hay-scented fern rapidly spread into this sparsely occupied habitat-forming dense monospecific stands (Figure 1). Other examples include Sweden, where clearcutting and overbrowsing convert forests to unpalatable grass-dominated communities (e.g., *Deschampsia flexuosa*; Bergquist and others 1999) and in New Zealand where arboreal herbivory by marsupials opens up the canopy, and, in combination with deer overbrowsing, leads to stands of unpalatable plant species (Allen and others 1984, Coomes and others 2003, Jane and Pracy 1974, Rogers and Leathwick 1997, Wardle and others 2001). In parts of New Zealand, forest area cover by shrubs, ferns, and grasses has increased from < 1 percent to nearly 30 percent in just 30 years (Batcheler 1983).

The Interaction of Altered Fire Regimes and Canopy Disturbance

This section discusses how human alterations to the frequency or severity of fire in various ecosystems (Attiwill 1994, Mallik 2003, May 2000) are often linked to the increase in interfering species. Frequent understory fires thin the understory by reducing seedling and sapling density, thereby increasing light availability, and favoring species that can survive the fire or resprout thereafter (Abrams 1992, Collins and Carson 2003, Donlan and Parker 2004). When canopy disturbances and surface fires occur in tandem or within a relatively short period, the increase in light can contribute to the development of a recalcitrant understory layer (Mallik 2003, Payette and Delwaide 2003). For example, in boreal forests, Payette and Delwaide (2003) found that a "synergy" existed between fires and overstory disturbance, which created shrub-dominated heathlands. These heathlands became dominated by shrub species, mainly *Calluna*, *Kalmia*, and *Vaccinium* spp., which can rapidly resprout and spread clonally following severe fires (Mallik 1995, Meades 1983). Similarly, in tropical forests, various shade-intolerant ferns (*Dicranopteris, Gleichenia*, or *Pteridium* spp.) or bamboo (*Guadua*) that also spread clonally can rapidly colonize and monopolize areas following catastrophic fires (Dolling 1999, Finegan 1996, Gliessman 1978, May 2000, Nelson 1994).

Alternatively, canopy disturbances that coincide with a decrease in fire frequency can lead to the development of recalcitrant understory layers. Mallik (2003) hypothesized that long-term fire suppression in logged or defoliated stands led to forest "conversion" to *Kalmia*, *Calluna*, and *Gaultheria* heathlands. In temperate forest systems, fire suppression and canopy disturbances contribute to the spread of rhododendron and mountain laurel (*Kalmia latifolia*). These species now form recalcitrant understory layers that cover an estimated 2.5 million hectares in the Southeastern United States alone (Table 2; Monk and others 1985, Vandermast and Van Lear 2002). Furthermore, studies from the Coweeta Basin in North Carolina confirm the expansion continues with a doubling of rhododendron cover in only 17 years (Nilsen and others 1999).

The separate and combined effects of disturbances and browsing act as strong filters on species richness creating depauperate understories dominated by one or a few species. The degree of control or release of specific species will depend on the degree to which disturbance and browsing regimes are altered as well as the life-history characteristics

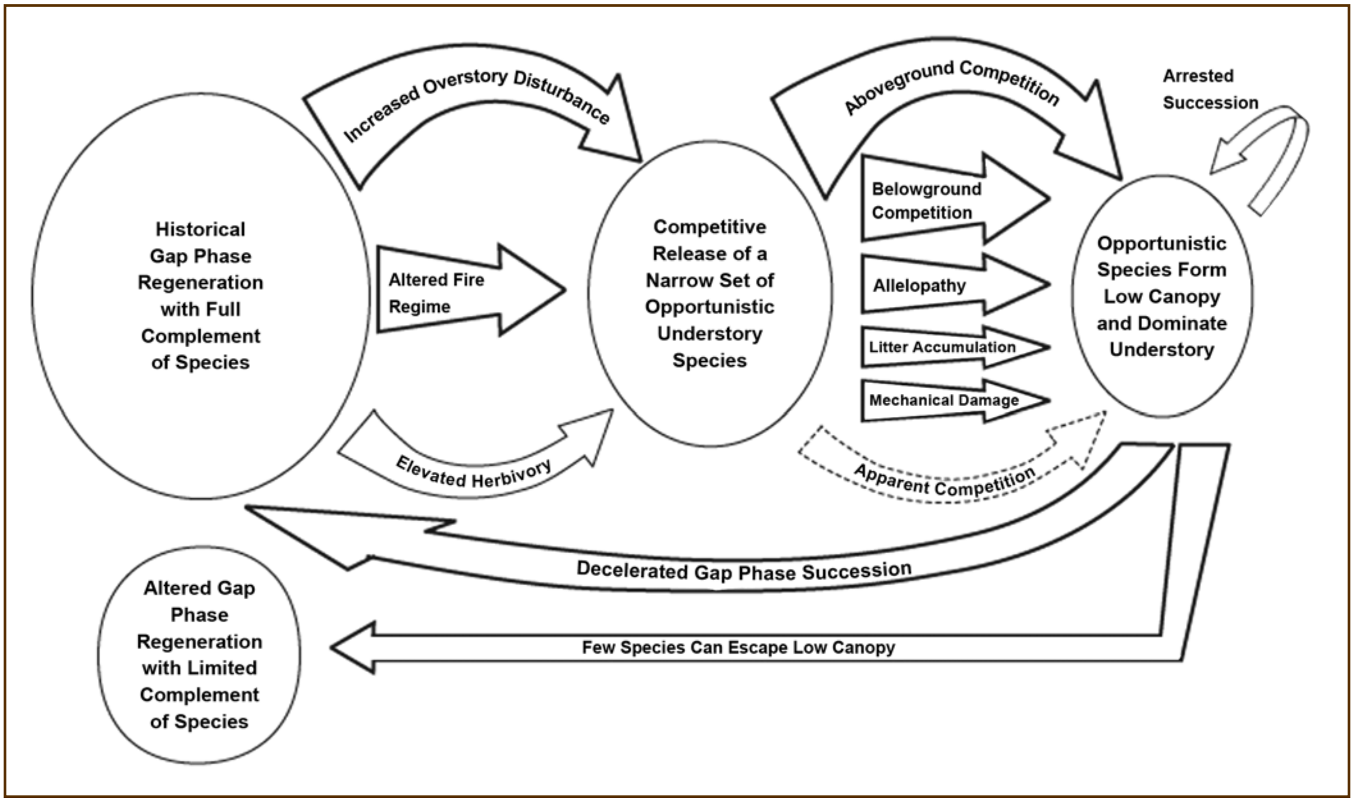

Figure 2—Conceptual model illustrating factors precipitating change from historical gap-phase regeneration into low-canopy dominance. The model also reveals various interference mechanisms and illustrates the ensuing successional pathways. The size and boldness of the arrows denote the relative importance of each transition as revealed by our review.

of the understory plant species (Roberts 2004). Overbrowsing selects for only those species that are well defended or tolerant to browsing (Banta and others 2005, Horsley and others 2003). Frequent fires select for only those species that can survive the fire or resprout thereafter (Gliessman 1978, Mallik 2003, Payette and Delwaide 2003). Finally, increased overstory disturbance selects for shade-intolerant species with rapid rates of vegetative spread vs. slower growing shade tolerant herbs and shrubs (Ehrenfeld 1980, Moola and Mallik 1998, Schnitzer and others 2000). Ultimately, these processes create novel conditions that favor only a small subset of species that possess some combination of the following life-history characteristics: rapid vegetative growth, relatively shade intolerant, and herbivore tolerant (Table 1; see also Roberts 2004). The result is a low diversity but dense understory that can persist for long periods of time even if the canopy closes.

Recalcitrant Understory Layers Arrest, Delay, and Alter Forest Succession

This section describes different ways that a recalcitrant understory layer can influence forest regeneration and stand development following a disturbance event. In the following sections we briefly review the literature to evaluate the evidence for three different successional pathways (Figure 2). These pathways include (1) indefinite suppression of subsequent tree regeneration (arrested succession), (2) a protracted period of stand establishment (delayed succession), and (3) a differential reduction of tree seedling recruitment that constricts species composition in the ensuing forest stand (altered succession).

Arrested Succession

In a small number of documented cases, recalcitrant understory layers appear to exclude tree regeneration for extended periods of time. This pathway is described by a variety of terms including self-perpetuating climax community (Horsley and Marquis 1983), alternate stable state (Schmitz and Sinclair 1997, Stromayer and Warren 1997), polyclimax (Tansley 1935), or arrested succession (Niering and Goodwin 1974). Although the long-term stability of these systems is difficult to confirm (Connell and Sousa 1983; Peterson 1984; Sutherland 1974, 1990), there are compelling examples where shrubs and ferns have persisted for decades in stands formerly dominated by trees (Den Ouden 2000, Horsley 1985, Koop and Hilgen 1987, Latham 2003, Mallik 2003, Niering and Egler 1955, Petraitis and Latham 1999, Raich and Christensen 1989). It is unclear whether these layers are self-sustaining (e.g., via strong interference; Stromayer and Warren 1997) or if continued browsing or frequent fire is required to perpetuate them and retard the reestablishment of trees (Hill 1996, Mallik 2003).

Delayed Succession

A recalcitrant understory layer can slow the growth rate of tree species, thereby slowing the rate of successional change without altering the eventual tree species composition. For example, in boreal forests, the grass *Calamagrostis canadensis* suppresses the regeneration of dominant tree species, including white spruce (*Picea glauca*). This delays stand development by 20 to 30 years until saplings eventually emerge through the *C. canadensis* canopy, and the stands revert to forest (reviewed by Lieffers and others 1993). Delayed successions also occur in other boreal forests where a dense ericaceous shrub layer suppresses the-growth and emergence of tree species including western redcedar (*Thuja plicata*), Sitka spruce (*Picea sitchensis*), and Norway spruce (*Picea abies*) (Mallik 1995, Maubon and others 1995, Messier and Kimmins 1991, Messier and others 1989).

Additionally, a recalcitrant understory layer may reduce tree species survivorship sufficiently to delay succession. For example, in tropical forests, gaps promote the expansion of resident understory lianas (Schnitzer and others 2000). These understory lianas can become so dense after gap creation that they inhibit the subsequent growth and survival of both pioneers and shade-tolerant trees, thus stalling succession for decades (Schnitzer and others 2000). This dynamic of delayed gap-phase regeneration occurs in tropical and temperate forests where lianas, fern, and bamboo thickets effectively clog gaps (Abe and others 2002, Guariguata 1990, Kochummen and Ng 1977, Schnitzer and others 2000, Taylor and Zisheng 1988, Walker 1994). In time, trees emerge from this layer and reach the canopy, apparently with little impact on species composition or the ensuing successional trajectories (Abe and others 2002).

Altered Forest Succession

A recalcitrant understory layer may differentially reduce establishment among co-occurring tree species, thereby controlling the composition of the advance regeneration layer (George and Bazzaz 1999a, 1999b). Dense understories create conditions near the soil surface that are inimical to tree germination and early growth and survivorship. For example, understory layers that generate a thick litter layer may inhibit germination of small-seeded species (Farris-Lopez and others 2004, George and Bazzaz 1999a), whereas those that strongly preempt light can preclude the establishment of many shade-intolerant and intermediately tolerant species (de la Cretaz and Kelty 2002, Gonzalez and others 2002, Horsley 1993a). These dense layers may substantially suppress tree recruitment by a combination of at least six different types of interference mechanisms (Table 1). Consequently, only a few tree species may possess the necessary traits to persist under, and eventually emerge through, this understory layer to constitute the advance regeneration layer (Connell 1990, Runkle 1990). If so, then the species composition of the advance regeneration layer and subsequent successional dynamics will contrast sharply in forests with a recalcitrant understory layer vs. one without.

Mechanisms of Interference Over Tree Establishment, Survival, and Growth

This section describes different ways that a dense understory canopy can suppress regeneration. Because most studies fail to distinguish among these mechanisms, Muller (1969) proposed the term interference to describe the suppression of one species or layer on another species. In the following sections, we briefly review the literature to evaluate the evidence for six different mechanisms of interference between the understory layer and co-occurring tree species. These mechanisms include (1) resource competition, (2) allelopathy, (3) physically impeding seedling germination and growth, (4) through modifications of interspecific interactions (Figure 2). We suggest that the most efficient and cost-effective remediation of the deleterious effects of these recalcitrant understory layers will require a greater understanding of how these layers alter patterns of forest regeneration and succession.

Resource Competition

In forested systems, perhaps the most prominent interference mechanism exerted by a recalcitrant understory layer would be direct competition for above- and belowground resources. In closed-canopy forests, dense understories exacerbate the degree of light attenuation caused by the midstory and canopy (Beckage and others 2000, de la Cretaz and Kelty 2002, Messier and others 1998, Nilsen and others 2001). Photosynthetically active radiation (PAR) levels can drop well below 5 percent of full sun beneath these layers (Aubin and others 2000, Clinton and Vose 1996, George and Bazzaz 1999a, Hill 1996, Horsley 1993a, Kelly and Canham 1992, Lei and others 2002, Lusk 2001, Nakashizuka 1987, Wada 1993, Walker 1994). Additionally, these dense, low canopies can reduce light quality (e.g., red: far-red wavelengths), thereby preventing germination, altering internode elongation, and inhibiting flowering (Horsley 1993a, Mancinelli 1994, Messier and others 1989). Furthermore, dense, low canopies decrease the availability of sunflecks particularly for seedlings (Denslow and others 1991, Lei and others 2002, Nilsen and others 2001). Finally, if canopy gaps do form, they may not operate as gaps at all if seedlings remain trapped beneath a dense understory layer (Beckage and others 2000, Lusk 2001, Webb and Scanga 2001). Under this scenario, regeneration may be limited to only a few individuals of those few species that are highly shade tolerant.

Dense understories may also exacerbate belowground competition (Dillenburgh and others 1993, Messier 1993, Putz and Canham 1992). Some studies infer resource limitation by detecting increased growth or survival of target plants following fertilization or measuring lower nutrient and water concentrations in soil beneath dense understory cover vs. more open areas (e.g., Inderjit and Mallik 1996, Messier 1993, Nilsen and others 2001, Yamasaki and others 1998). Similarly, vine-covered saplings often have lower foliar nitrogen levels, reduced preleaf water potential, and decreased diameter growth when compared to vine-free saplings (Dillenburgh and others 1993, Perez-Salicrup and Barker 2000). The above studies are suggestive of resource limitation though they typically do not distinguish between competition for water vs. soil nutrients. Because nutrient and water availability covary, decoupling these two factors is difficult (Casper and Jackson 1997, Nambiar and Sands 1993). Additionally, few experiments use factorial manipulations to disentangle a dense understory layer's aboveground vs. belowground effects and their interactions (McPhee and Aarssen 2001).

Horsley (1993a) experimentally tested the influence of aboveground vs. belowground competition. He tied back hay-scented fern fronds while leaving their roots and rhizomes intact, thereby reducing light competition and isolated seedlings within PVC tubes, thereby reducing root competition. He found that light attenuation, not belowground competition, was the mechanism of interference (Horsley 1977, 1993a, 1993b). Putz and Canham (1992) conducted similar aboveground and belowground manipulations. They found that a dense shrubby understory layer reduced tree regeneration primarily because of belowground competition (see also Christy 1986), although this varied with soil fertility. Belowground competition was more important in infertile sites, whereas aboveground competition was more important in fertile sites. Clearly well-replicated factorial experiments are required to ascertain the relative importance of aboveground vs. belowground competition, although other processes may confound the results of these experiments (e.g., allelopathy; see section on allelopathy).

Allelopathy

This section discusses the potential effects of the phenomenon called allelopathy: i.e., the inhibition of growth or survivorship of one plant species by chemicals produced by another species. Direct field evidence for allelopathy remains equivocal and elusive. In forests that have dense understories dominated by ericaceous shrubs, the phenolics and other phytochemical compounds produced by these shrubs can disrupt nitrogen mineralization and inhibit ectomycorrhizal fungi; this significantly reduces conifer growth and survivorship (Walker and others 1999; reviewed by Mallik 1995, 2003 and Wardle and others 1998). In these systems, Nilsson (1994) used factorial manipulations of aboveground and belowground competition and allelopathy to identify how the boreal shrub *Empetrum hermaphroditum* suppressed tree regeneration. She found that both belowground competition and allelopathy were important, but that belowground competition played the primary role. Similarly, Jäderlund and others (1997) found that *Vaccinium myrtillus* interfered with Norway Spruce (*Picea abies*) primarily through belowground competition. In forests where ferns form dense understories, bioassays and greenhouse studies have suggested the potential for strong allelopathic effects on tree regeneration (Gliessman and Muller 1972, 1978; Horsley 1977); however, further field experimentation failed to find strong allelopathic effects (Den Ouden 2000, Dolling 1996, Horsley 1993b, Nilsen and others 1999). Despite these results, too few studies have tried to experimentally disentangle resource competition from allelopathy via field experiments. Future research must move beyond merely documenting the existence of phytotoxic exudates in greenhouse and laboratory studies (Fuerst and Putnam 1983, Inderjit and Callaway 2003, Weidenhamer 1996, Williamson 1990).

Seed Predation

This section discusses how a dense understory layer can increase the activity of small mammals, thereby increasing the rate and impact of seed and seedling predation (Den Ouden 2000, George and Bazzaz 1999a, Gliessman 1978, Schreiner and others 2000, Wada 1993). This can create a situation where it appears that low seedling densities are caused by resource competition (e.g., light attenuation) when, in fact, they are caused by seed and seedling predation (Connell 1990; Holt 1977, 1984). Connell (1990) defined this as a type of apparent competition (sensu Holt 1977, 1984). Experiments that use canopy removals confound the direct competitive release caused by the removal of the understory layer with the indirect benefits of removing this layer, particularly the decrease in seed and seed predation by small mammals (Reader 1993). Even though small mammals are abundant, forage preferentially beneath dense vegetative cover, and consume copious quantities of seeds, few experiments have attempted to evaluate the role of seed or seedling predators vs. resource competition. Nonetheless, long-term studies in other plant systems have documented that selective seed and seedling predation can lead to rapid changes in plant community composition (e.g., Brown and Heske 1990, Gill and Marks 1991, Howe and Brown 2001, Ostfeld and Canham 1993).

Litter Accumulation

A thick litter layer typically reduces plant species diversity and density through a wide variety of direct and indirect mechanisms (see Facelli and Pickett 1991). For example, George and Bazzaz (1999a) found that a thick fern litter layer directly limited the establishment of small-seeded tree species (see also Beckage and others 2000, Farris-Lopez and others 2004, Lei and others 2002, Veblen 1982). Alternatively, in boreal forests, the insulative properties of a dense grass litter layer results in decreased soil nitrogen mineralization, water uptake, and seedling photosynthetic rates, thus indirectly diminishing conifer growth and survival (Cater and Chapin 2000, Hogg and Lieffers 1991, Lieffers and others 1993). Aside from these examples, there are few experimental tests that unravel the many facets of litter interference or evaluate its importance relative to other mechanisms (e.g., resource competition). However, in forests characterized by a recalcitrant understory litter layer, it is clear that this alternative remains a viable and potentially important mechanism.

Mechanical Interference

A dense understory layer can reduce tree seedling regeneration via non-competitive, physical interference. Clark and Clark (1991) demonstrated that the passive shedding of branches and leaves of subcanopy palms smothered seedlings present in the understory. Similarly, collapsing Guadua bamboo culms can reduce tree seedling growth and survival (Griscom and Ashton 2003). Additionally, the physical weight of a large liana load may suppress tree seedling and sapling growth (Gerwing 2001, Putz 1991, Schnitzer and others 2004). If tree species respond differentially to these physical stresses, then this mechanism alone can potentially alter understory tree species composition and modify future successional trajectories (e.g., Gillman and others 2003, Guariguata 1998).

The Relationship Between Mechanisms of Interference and Phenology

This section discusses how the intensity and duration of any particular interference mechanism can vary temporally as a result of the species' life history, whether evergreen, deciduous, or monocarpic. In fact, this trait may provide clues to understand both the strength and type of interference. For example, evergreen species may pose a greater impediment to tree regeneration as their effects are exerted throughout the year on all tree seedling life-history transitions (Givnish 2002). In contrast, herbaceous perennials that senesce in the fall or deciduous shrubby species only exert competitive effects during the growing season (e.g., de la Cretaz and Kelty 2002, Nilsen and others 2001). This delayed expansion of the recalcitrant understory layer provides a brief window of opportunity for evergreen tree species, species with early germination (e.g., *Acer rubrum* L.), or species with early leaf expansion (e.g., *Betula lenta* L.) to overcome the understory stratum's deleterious effects on early establishment. This temporal advantage can provide sufficient photosynthetic and growth opportunity to enable trees to survive and eventually grow through a fern layer (de la Cretaz and Kelty 2002). Additionally, if the intensity of seed and seedling predation decreases with senescence of the low canopy, then the impact of pervasive seed predation may decrease in the fall. This timing of senescence may generate increased predation on early seed dispersers (e.g., *Quercus* spp.) relative to later dispersers (e.g., *A. saccharum* Marsh., *Fagus grandifolia* Ehrh.).

Causes and Consequences of a Recalcitrant Understory Layer

In this section, we discuss our contention that the expansion and monopolization of the understory by a narrow set of plant species is often an inadvertent outcome of policies and management decisions that deviate from natural forest overstory disturbance, fire, and herbivory regimes. We propose a general conceptual model through which alterations in the dynamics of the overstory, understory, or both generate increases in a select few understory plant species (Figure 1). These alterations involve changes in the frequency and scale of overstory disturbance, increased or decreased fire frequency, or increased herbivory that release a restricted set of understory species from prior competitive constraints. Once released, these species increase dramatically in abundance and cover over large portions of the forested landscape (Table 1). Following its establishment, this recalcitrant understory layer interferes with tree regeneration through a variety of direct and indirect mechanisms including above- and belowground competition, allelopathy, microhabitat-mediated seed/seedling predation, litter, and mechanical damage. Consequently, this recalcitrant layer itself inhibits tree regeneration and strongly influences which tree species establish and survive beneath its canopy (e.g., Cater and Chapin 2000, Clinton and others 1994, Dolling 1996, Veblen 1982). The strength and selectivity of this filter can retard succession, alter the tree species participating in the successional sere, or potentially arrest succession.

We found only 25 percent of the published studies reviewed the reported results of manipulative field experiments designed to identify the existence of one or more particular interference mechanism(s) (Table 1). Above- and belowground competition and allelopathy were the predominant mechanisms tested (37, 32, and 13 percent, respectively; Table 1). Apart from competition and allelopathy, various interference mechanisms were speculated on in many papers, but few, if any, were tested experimentally. Given the paucity of information for most systems, we lack the information needed to clearly establish by which mechanism a recalcitrant understory layer inhibits tree regeneration (see Levine and others 2003 for a similar conclusion on exotic invasives).

We argue that a move towards a more mechanistic understanding of the "interference" phenomenon could begin by considering the most limiting resource(s) within a given system. For example, on a coarse scale, forested ecosystems differ in the identity of the most limiting resource(s) (e.g., light, soil nutrients, and water), and these differences could provide insight into the most plausible interference mechanism. Boreal and cool-temperate forests are typically nutrient poor (primarily N) and less light limited relative to their temperate and tropical counterparts (Attiwill and Adams 1993, Kimmins 1996, Krause and others 1978, Reich and others 1997) (reviewed by Coomes and Grubb 2000 and Ricard and others 2003). We found that dense low canopies in these forest types suppress regeneration directly via belowground competition and indirectly via allelopathic interactions that mediate resource availability and uptake (Table 1; Christy 1986, Jäderlund and others 1997, Nilsson 1994). In contrast, temperate deciduous and tropical rain forests tend to be more light limited (Finzi and Canham 2000, Pacala and others 1994, Ricard and others 2003). In these systems, we found that other mechanisms including aboveground competition and seed predation were generally more important than belowground competition (Table 1; Den Ouden 2000, Denslow and others 1991, Horsley 1993a). Ideally, the best tests would link a series of carefully controlled laboratory or greenhouse studies with field experimentation in order to identify which mechanisms merit further investigation. Furthermore, we strongly argue that manipulative field experiments remain among the best tools to test the relative importance of each factor independently as well as any interactions.

Floristic Diversity and Forest Succession

The increasingly common development of recalcitrant understory layers worldwide plays a strong, yet vastly under-appreciated role in determining future successional patterns, forest composition, and diversity because of their tendency to selectively suppress tree regeneration. Indeed, studies examining the regeneration success of a variety of tree species demonstrate that a majority of tree species suffer decreased seedling densities and limited height growth underneath recalcitrant understory canopies (e.g., de la Cretaz and Kelty 2002; George and Bazzaz 1999a, 1999b; Hille Ris Lambers and Clark 2003; Horsley and Marquis 1983). The presence of this additional filter on floristic diversity in forest understories together with increased herbivory and altered fire regimes strongly restricts the number of species that can successfully regenerate. The potential consequences of these ecological filters (sensu George and Bazzaz 1999a, 1999b) on species composition remains poorly understood. Nevertheless, we suggest that floristic diversity in such areas is so severely constricted that succession may move steadily toward monodominance or complete regeneration failure. These extreme cases include the fern-and grass-covered orchard stands in Pennsylvania where 50- to 80-year-old failed clearcuts remain devoid of tree regeneration (Horsley 1985) or bracken-covered tropical regions of Central America that have persisted for centuries following forest removal (Den Ouden 2000).

Forest Dynamics Models

Computer-based forest successional models (e.g., JABOWA-FORET [Shugart and West 1977, Smith and Urban 1988] and SORTIE [Pacala and others 1994]) remain the best tool to explore long-term successional outcomes; however, forest dynamics models typically fail to include a dense understory layer's impact on early seedling survival and growth. For example, in the original SORTIE calibrations, the growth and mortality parameters derived from saplings (15 to 750 cm in height) are applied to small seedlings as well (Kobe and others 1995, Pacala and others 1994). Additionally, the authors acknowledge their recruitment parameter estimate is potentially unreliable as the survival of individuals < 5 years old is highly variable, and mortality is often intense (Pacala and others 1994. Indeed, researchers have documented that density dependent (e.g., Packer and Clay 2000) and density independent mortality can dramatically alter initial seedling distribution patterns, particularly under a dense understory layer (Hille Ris Lambers and Clark 2003, Schnurr and others 2004). By constraining the model and its parameters to the 5-or more-year-old age class, SORTIE assumes away part of the early dynamics that may occur low to the ground underneath a recalcitrant understory layer and help shape the composition sapling class.

As originally calibrated (Pacala and others 1994), SORTIE did not include the effects of a recalcitrant understory layer into its resource (light) submodel. More recent developments note that SORTIE can underestimate light attenuation (Beaudet and others 2002) and the long-term development of shade-intolerant tree species following major disturbance (Tremblay and others 2005). It is suggested in both papers that this may be due to the lack of an understory layer component in the model, and it is stressed that this goal is an ongoing research focus (see also Aubin and others 2000 and Beaudet and others 2004). We know of only one effort that has integrated a recalcitrant understory layer into SORTIE. Hill (1996) incorporated hay-scented fern abundance as a function of light as well as hay-scented fern's impact on light availability as a function of frond density. With the increased light limitation imposed by fern cover, successional projections indicated faster reductions in shade-intolerant species abundance and an accelerated shift towards dominance by shade-tolerant species (Hill 1996). Nevertheless, none of the simulations containing a dense fern layer reflected the pattern of complete regeneration failure documented in the field (Hill 1996). We concur with Hill that the inconsistencies between model projections and observable field patterns likely result from overestimates in seedling growth and underestimates in seedling mortality inherent in SORTIE. We argue these inconsistencies are due to (1) ignoring the early (fewer than 5 years) seedling dynamics, and (2) failure to incorporate additional interference mechanisms causing seedling mortality (e.g., seed and seedling predation) beyond light competition.

Forest Management

Understanding the autoecological characteristics of interfering plant species may allow land managers to preemptively limit the aggressive spread of these species as well as provide alternative options for their control. We found that alterations in forest canopy disturbance, fire, and herbivory regimes may lead to the establishment of recalcitrant understory layers, particularly when alterations to the overstory and understory disturbance regimes occur in tandem (e.g., Payette and Delwaide 2003). We suggest managers monitor overstory and understory conditions to ensure that modifications to either of these strata do not operate concurrently in an effort to mitigate invasion risk. Furthermore, if control over overstory and understory factors falls under the purview of different agencies (e.g., wild game vs. forestry management agencies), then communication and coordination between them is essential in order to minimize the chance of concurrent or overlapping disturbance events. We caution that decisions regarding partial or complete overstory removals should consider the site's understory conditions including inadequate advance regeneration, presence of clonal understory plants, and high herbivore impact (e.g., Marquis and others 1990). We further suggest the implementation of management practices that more closely resemble natural disturbance levels.

Knowledge of a species life-history traits and interference mechanisms may also provide managers with alternative treatments to promote tree regeneration when conventional treatments like herbicides are not desired or permitted (Berkowitz and others 1995). For example, mowing or cutting of ferns, grasses, and shrubby interfering vegetation may successfully ameliorate their aboveground competitive effects and enhance regeneration (Biring and others 2003, Davies 1985, Marrs and others 1998). Alternatively, if belowground competition is the major interference mechanism, fertilizer application may mitigate the competitive effects of interfering plants and promote tree regeneration (Haywood and others 2003, Prescott and others 1993). Additional remediation techniques tailored to other interference mechanisms could include direct seeding of propagules coated with small mammal repellent (Campbell 1981, Nolte and Barnett 2000), soil scarification or controlled burning to reduce litter interference (Nyland 2002), and activated carbon as a treatment to mitigate allelopathic interference (Jäderlund and others 1997). A basic understanding of possible successional outcomes following the establishment of a low canopy may further aid land managers. In areas where the low canopy simply stalls succession, successful regeneration will ultimately occur without any silvicultural techniques. Finally, where the recalcitrant understory layer filters tree species composition or arrests succession, managers could manipulate the rate and direction of regeneration by underplanting tree species relatively unaffected by the interfering layer (e.g., shade-tolerant species) in order to attain a desirable and diverse mixture of regeneration species (Löf 2000).

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