REVIEW / SYNTHÈSE

On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession

Alejandro A. Royo and Walter P. Carson

Abstract: The mechanistic basis underpinning forest succession is the gap-phase paradigm in which overstory disturbance interacts with seedling and sapling shade tolerance to determine successional trajectories. The theory, and ensuing simulation models, typically assume that understory plants have little impact on the advance regeneration layer's composition. We challenge that assumption by reviewing over 125 papers on 38 species worldwide that form dense and persistent understory canopies. Once established, this layer strongly diminishes tree regeneration, thus altering the rate and direction of forest succession. We term these dense strata recalcitrant understory layers. Over half of the cases reviewed were linked to increases in canopy disturbance and either altered herbivory or fire regimes. Nearly 75% of the studies declared that competition and allelopathy were the likely interference mechanisms decreasing tree regeneration, yet only 25% of the studies used manipulative field experiments to test these putative mechanisms. We present a conceptual model that links the factors predisposing the formation of recalcitrant understory layers with their interference mechanisms and subsequent impacts on succession. We propose that their presence constricts floristic diversity and argue for their explicit inclusion in forest dynamics theory and models. Finally, we offer management suggestions to limit their establishment and mitigate their impacts.

Résumé : Le fondement mécaniste qui sous-tend la succession forestière est le paradigme de la phase de régénération par trouées durant laquelle la perturbation de l'étage dominant interagit avec la tolérance à l'ombre des semis et des jeunes tiges pour déterminer les trajectoires de la succession. La théorie, ainsi que les modèles de simulation qui en découlent, assument typiquement que les plantes en sous-étage ont peu d'impact sur la composition de la strate de régénération préétablie. Nous remettons en question cette hypothèse en passant en revue 125 articles portant sur 38 espèces qui forment des couverts denses et persistants en sous-étage partout à travers le monde. Une fois établie, cette strate diminue considérablement la régénération des arbres et modifie par conséquent le taux et la direction de la succession de la forêt. Nous qualifions ces strates denses de strates récalcitrantes de sous-étage. Plus de la moitié des cas que nous avons examinés étaient reliés à l'augmentation des perturbations de la canopée et ont modifié l'herbivorisme ou le régime des feux. Près de 75 % des études ont mentionné que la compétition et l'allopathie étaient vraisemblablement les mécanismes d'interférence qui diminuaient la régénération des arbres mais seulement 25% de ces études ont eu recours à des manipulations expérimentales sur le terrain pour tester ces mécanismes présumés. Nous présentons un modèle conceptuel mettant en relation les facteurs qui favorisent la formation des strates récalcitrantes en sous-étage avec leurs mécanismes d'interférence et leurs impacts subséquents sur la succession. Nous soumettons l'idée que leur présence limite la diversité floristique et plaidons pour qu'elles soient incluses de façon explicite dans les modèles et la théorie de la dynamique forestière. Finalement, nous offrons des suggestions d'aménagement pour limiter leur établissement et atténuer leurs impacts.

[Traduit par la Rédaction]

Introduction

Current forest successional theory focuses primarily on the processes that occur after major disturbances, particularly species recruitment, growth, survivorship, and turnover (Watt 1947; Bray 1956; Runkle 1981; 1982, Uhl et al. 1988; Houle 1990; Oliver and Larson 1996; Marks and Gardescu 1998; Greene et al. 1999; Antos et al. 2000; McCarthy 2001;

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see also *Ecology* Special Feature Vol. 70, 1989, and *Biotropica* Special Feature Vol. 28, 1996). This theory typically assumes that (1) the advance-regeneration layer is diverse and composed of a well-developed seedling and sapling layer, (2) tree species vary in shade tolerance, (3) overstory disturbances vary in size and frequency, and (4) variation in disturbances and the varying degrees of shade tolerance of the tree species interact to determine successional trajectories (e.g., SORTIE Forest Dynamics Model; Kobe et al. 1995; Pacala et al. 1996). In addition, this view of forest succession assumes that the rest of the understory community (herbs and shrubs) has little impact on postdisturbance tree species regeneration and subsequent canopy formation (Ehrenfeld 1980). In contrast, we present evidence the herb and shrub layer can act as a strong filter on tree species succession both after a major canopy disturbance and prior to any disturbance within closed-canopy forests (Runkle 1990).

On the development of recalcitrant understory layers worldwide

Recent changes in disturbance and browsing regimes have strongly impacted species composition in forest understories worldwide (de la Cretaz and Kelty 1999; Vandermast et al. 2002; Coomes et al. 2003; Mallik 2003). 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 (Fig. 1, Tables 1 and 2). We term these dense strata "recalcitrant understory layers". No matter where they occur worldwide, these layers 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). (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 the species that compose them have been termed "low canopies" (Schnitzer et al. 2000) and "native invasives", respectively (de la Cretaz and Kelty 1999). We prefer recalcitrant understory layer because this term emphasizes that this layer is resistant to displacement and that its effect occurs in the understory. Additionally, the term native invasive suggests these species, similar to exotic invasives, are invading novel habitat (e.g., exotic Japanese barberry, Amur honeysuckle; reviewed by Richburg et al. 2001), when, in fact, the species that formed these layers were present throughout the 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 forest-wide species diversity and patterns of succession.

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 present a conceptual model that synthesizes and identifies the most prominent causal mechanisms for the formation of these layers and outlines 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.

Processes causing the formation of recalcitrant understory layers.

Increased overstory disturbance

In the past century, direct and indirect human-induced disturbances, including logging, fires, insect outbreaks, and pathogens, have increased the extent and particularly the frequency of overstory disturbance (Sharitz et al. 1992; Youngblood and Titus 1996; Seymour et al. 2002; Carson et al. 2004). 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 (Hartshorn 1978; Runkle 1982, Denslow 1987; Canham 1989; Canham et al. 1994; Finzi and Canham 2000). 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 levels (Ehrenfeld 1980; Huenneke 1983; Schnitzer et al. 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 using sunflecks or clonal integration (e.g., Lipscomb and Nilsen 1990; Messier 1992; Brach et al. 1993; Moola and Mallik 1998).

There are numerous examples worldwide whereby canopy disturbances lead to the formation of recalcitrant understory layers (Table 1). Tappeiner et al. (1991) found that the abundance of salmonberry (*Rubus spectabilis*) tangles was nearly 300% greater in logged stands than in uncut stands. Throughout the tropics, large-scale disturbances can create bamboo and fern thickets that persist for decades (Guarigauta 1990; Walker 1994; Russell et al. 1998; Griscom and Ashton 2003). In temperate and boreal forests, both native and exotic insect outbreaks open up vast areas of forest canopies (e.g., Gypsy moth, *Lymantria dispar*, and spruce budworm, *Choristoneura fumiferana*), often leading to an increase in the density and dominance of a few shrub species (Ghent et al. 1957; Ehrenfeld 1980; Batzer and Popp 1985; Hix et al. 1991; Muzika and Twery 1995; Aubin et al. 2000). Fungal pathogens have opened up canopies in central New York (Dutch elm disease, *Ophiostoma ulmi*), thereby 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*

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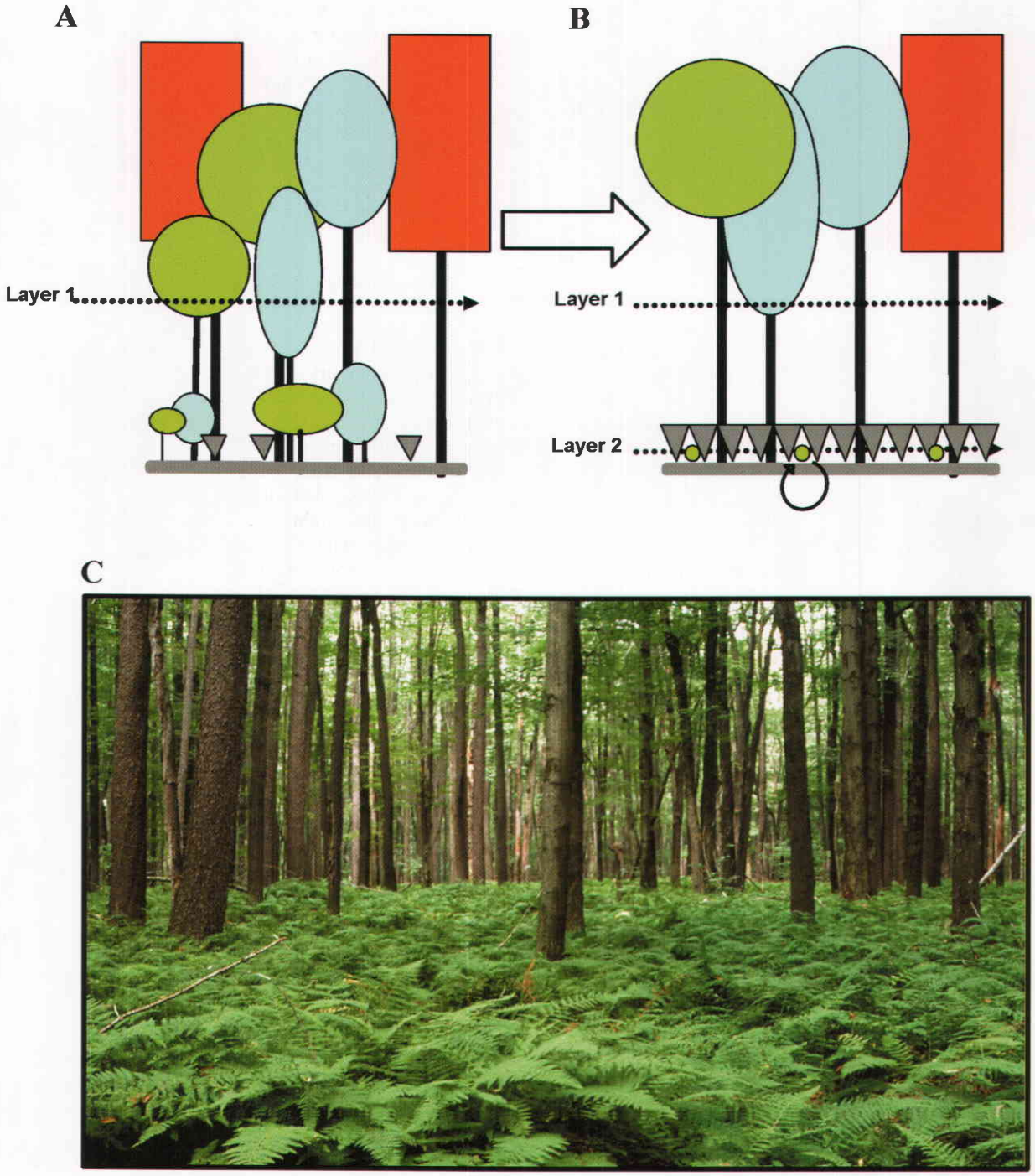
Fig. 1. Diagramatic representation of the conversion from (A) forests containing a diverse and structured advance-regeneration layer with sparse understory plant abundance (▼) to (B) forests where a native understory species expands and monopolizes the understory. The dense herbaceous or shrubby cover represents a new vegetation layer that exerts direct and indirect interference effects and prevents seedling (●) recruitment into the sapling class. (C) Example with hay-scented fern in northwestern Pennsylvania forests.



parasitica) apparently led to the aggressive expansion of *Rhododendron maximum* in the southern Appalachians (Vandermast et al. 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 (see below).

The interaction of elevated herbivory and canopy disturbance

In many parts of the world, large-scale canopy disturbances have coincided with extended periods of elevated browsing by either introduced or native mammalian herbivores (e.g., white-tailed deer in eastern United States; reviewed by McShea et al. 1997; Russell et al. 2001; Côte et al. 2004). Frelich (2002) has characterized this pattern of

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Table 1. Occurrence of dense, monodominant understory species around the world.

Species	Family	Areas affected	Rapid vegetative growth	Herbivory	Fire	Overstory disturbance	Mechanism	References
Dennstaedtia punctilobula	Dennstaedtiaceae	Northeastern USA	√	√ (T)	—	√	1, 2, 3, 5 (4)	Cody et al. 1977; Anderson and Egler 1988; Drew 1988, 1990; McWilliams et al. 1995; de la Cretaz and Kelty 1999, 2002; George and Bazazz 1999*a*, 1999*b*; Horsley and Marquis 1983; Horsley 1977, 1993*a*, 1993*b*; Horsley et al. 2003; Hill 1996; Hill and Silander 2001; Brach et al. 1993
Pteridium aquilinum	Dennstaedtiaceae	Worldwide	√	—	√ (T)	√	1, 2, 3, 5 (4)	Gliessman 1972, 1978; Gleissman and Muller 1978; Dolling 1996, 1999; Dolling et al. 1994; Ferguson and Adams 1994; den Ouden 2000
Thelypteris novaborensis	Thelypteridaceae	Northestern USA	√	√ (T)	—	√	(1)	Hill and Silander 2001
Blechnum spp.	Blechnaceae	New Zealand	√	√ (T)	—	√	—	Cunningham 1979; Coomes et al. 2003
Cyathea spp.	Cyatheaceae	New Zealand	√	√ (T)	—	√	—	Jane and Pracy 1974; Rogers and Leathwick 1997
Dicranopteris lineariz	Gleicheniaceae	Sri Lanka, Hawaii	√	—	√	√	—	Maheswaran and Gunatilleke 1988; Russell et al. 1998
Dicranopteris pectinata	Gleicheniaceae	Puerto Rico	√	—	√	√	(1)	Guariguata 1990; Walker 1994; Walker and Boneta 1995; Russell et al. 1998; May 2000
Gleichenia bifida	Gleicheniaceae	Puerto Rico	√	—	√	√	—	Guariguata 1990; Walker and Boneta 1995
Gleichenia lineariz	Gleicheniaceae	Malasia	√	—		√	—	Kochummen and Ng 1977
Calamagrostis canadense	Poaceae	N. America boreal forests	√	—	√ (T)	√	1, 5 (4)	Hogg and Lieffers 1991; Lieffers et al. 1993; Cater and Chapin 2000
Cortaderia spp.	Poaceae	New Zealand	√	√	—	√	—	Jane and Pracy 1974; Rogers and Leathwick 1997
Deschampsia flexuosa	Poaceae	European boreal forests	√	√ (T)	—	√	—	Berquist et al. 1999
Astrogyne martiana	Arecaceae	Costa Rica	—	—	—	—	1, 2, (6)	Denslow et al. 1991
Geonoma cuneata	Arecaceae	Costa Rica	—	—	—	—	1, 2, (6)	Denslow et al. 1991
Oenocarpus mapora	Arecaceae	Costa Rica	√	—	—	—	6, (1)	Farris-Lopez et al. 2004
Asplundia uncinata	Cyclanthaceae	Costa Rica		—	—	—	1, 2, (6)	Denslow et al. 1991
Aechmea magdalenae	Bromeliaceae	Panama	√	—	—	√	(1)	Brokaw 1983; Pfitsch and Smith 1988
Sinarundinaria gangiana	Poaceae	China	√	—	—	—	—	Taylor and Zisheng 1988
Chusquea spp.	Poaceae	Western S. America	√	—	—	√	(1, 4)	Veblen 1982; Lusk 2001; Gonzalez et al. 2002
Guadua sarcocarpa	Poaceae	S. America	√	—	√	√	(1, 6)	Griscom and Ashton 2003
Fargesia denudata	Poaceae	China	√	—	—	—	—	Taylor et al. 1995
Sasa spp.	Poaceae	Japan	√	—	—	√	(1, 4)	Wada 1993; Abe et al. 2002; Iida 2004

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Table 1 (*continued*).

Species	Family	Areas affected	Rapid vegetative growth	Herbivory	Fire	Overstory disturbance	Mechanism	References
Yushania microphylla	Poaceae	Bhutan	√	—	—	—	(1)	Gratzer et al. 1999
Calluna vulgans	Ericaceae	Western Europe	√	—	√ (T)	√	(3)	Mallik 1995
Kalmia angustifolia	Ericaceae	Eastern Canada and USA	√	—	√ (T)	√	(2, 3)	Hall et al. 1973; Meades 1983; Mallik 1995; Inderjit and Mallik 1996; Mallik and Inderjit 2002; Bradley 1997; Yamasaki et al. 1998
Kalmia latifolia	Ericaceae	Eastern USA	√	—	√ (T)	√	(1)	Woods and Shanks 1959; Monk et al. 1985; Lipscomb and Nilsen 1990; Mallik 1995
Rhododendron maximum	Ericaceae	Eastern USA	√	—	√ (T)	√	1, (2, 3, 4, 5)	Monk et al. 1985; Lipscomb and Nilsen 1990; Clinton et al. 1994; Clinton and Vose 1996; Walker et al. 1999; Nilsen et al. 1999, 2001; Beckage et al. 2000; Lei et al. 2002; Vandermast et al. 2002; Beckage and Clark 2003; Christy 1986; Hille Ris Lambers and Clark 2003; Vandermast and Van Lear 2002
Gaylussaccia baccata	Ericaceae	Eastern USA	√	—	—	√	1, 2	Beckage and Clark 2003
Gaultheria shallon	Ericaceae	Western Canada, Pacific Northwest	√	—	√ (T)	√	3	Price et al. 1986; Messier and Kimmins 1990, 1991; Klinka 1989; Messier 1992, 1993; Chang and Preston 2000; Chang et al. 1996*a*, 1996*b*; Bunnell 1990
Vaccinium myrtillus	Ericaceae	European boreal forests	√	—	√ (T)	√	1, 2, 3	Maubon et al. 1995; Jäderlund et al. 1997; Moola and Mallik 1998; Frak and Ponge 2002
Empetrum hermaphroditum	Ericaceae	European boreal forests	√	—	—	√	1, 2, 3	Michelsen et al. 1995; Mallik 2003; Nilsson 1994; Wardle and Nilsson 1997; Zackrisson et al. 1997; Nilsson et al. 2000
Pseudowintera colorata	Winteraceae	New Zealand	—	√ (T)	—	√	—	Godley and Smith 1981; Allen et al. 1984; Coomes et al. 2003; Husheer et al. 2003
Rubus spp.	Rosaceae	Pacific Northwest and Europe	√	—	—	√	(1, 4, 5)	Franklin and Pechanec 1967; Tappenier et al. 1991; Schreiner et al. 2000
Rhus glabra	Anacardiaceae	Eastern USA	√	—	—	√	1, 2	Putz and Canham 1992
Lianas (various genera)	—	Tropical forests and eastern USA	√	—	√	√	1, 2, (6)	Smith 1984; Dillenberg et al. 1993; Perez-Salicrup and Barker 2000; Schnitzer et al. 2000; Schnitzer and Bongers 2002; Gerwing 2001; Grauel and Putz 2004
Cornus spp.	Cornaceae	Northeastern USA	√	—	—	√	1, 2	Ehrenfeld 1980; Huenneke 1983; Putz and Canham 1992;

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Table 1 (*concluded*).

Species	Family	Areas affected	Rapid vegetative growth	Herbivory	Fire	Overstory disturbance	Mechanism	References
Corylus cornuta	Betulaceae	Lake States, USA	√	—	—	√	1, 2	Sabhasri and Ferrell 1960; Batzer and Popp 1985; Tappeiner 1971; Tappeiner and John 1973; Tappeiner et al. 1991, 2001; Kurmis and Sucoff 1989
Acer spicatum	Aceraceae	Southeastern Canada, northeastern USA	√	—	—	√	(1)	Aubin et al. 2000

Note: We summarize whether the species possess rapid vegetative growth, whether their increase in abundance is linked to alterations in the herbivory, fire, or overstory disturbance regimes, and whether they are fire or browse tolerant (T). "Mechanism" indicates the specific interference mechanisms exerted by a species (1, aboveground competition; 2, belowground competition; 3, allelopathy; 4, seed and (or) seedling predation; 5, litter accumulation; 6, mechanical damage). Mechanisms were tested using manipulative field experiments, unless they are in brackets, in which case they are speculative.

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

Species	Location	Forest type	Estimated area affected (ha)	Proportion of forested area affected	Reference
Dennstaedtia punctilobula	Pennsylvania	Temperate hardwoods	2.1×10^6	0.33	McWilliams et al. 1995
Dennstaedtia punctilobula	Allegheny National Forest, Pennsylvania	Temperate hardwoods	241 000 – 303 000	~0.47–0.59	A.A. Royo, unpubl. data
Rhododendron maximum	Southern Appalachian region, USA	Temperate hardwoods	2.5×10^6	—	Monk et al. 1985
Sasa spp.	Japan	Temperate hardwoods	6.9×10^6	0.25	N. Wada, pers. comm.
Lianas (various genera)	Barro, Colorado; Rep. of Panama	Tropical forests	—	~0.22 of all gaps	Schnitzer et al. 2000
Pteridium aquilinum	Fontainebleau Forest, France	Old growth beech forest	—	0.02–0.17	Koop and Hilgen 1987
Pteridium aquilinum	Netherlands	Temperate hardwood and conifer	288 500	~0.7 of entire country	den Ouden 2000
Kalmia angustifolia	Newfoundland	Black spruce	—	0.55	English and Hackett 1994 (cited in Mallik and Inderjit 2002)
Gaultheria shallon	British Columbia	Cedar–hemlock forest	100 000	—	Wheetman et al. 1990
Guadua sarcocarpa	Amazonia	Tropical forests	18×10^6	—	Nelson 1994
Calamagrostis canadensis	Western Canadian provinces	Boreal forests	—	0.25–0.5 of all cutover forest	V.J. Lieffers, pers. comm.

Note: 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.

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chronic overbrowsing as a low-intensity disturbance that over time can lead to depauperate understories composed almost entirely of highly browse-tolerant or unpalatable species (e.g., Frelich and Lorimer 1985; Waller and Alverson 1997; Rooney and Dress 1997; Horsley et al. 2003; Banta et al. 2005). 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 best examples of the interplay between long periods of overbrowsing and canopy disturbance can be seen with hay-scented fern (*Dennstaedtia punctilobula*). This species, which historically occupied <3% of the understory (Lutz 1930), currently forms a recalcitrant understory layer over more than a third of the forested area in Pennsylvania (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 into 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 (Fig. 1). Other examples can be found in Sweden, where clear-cutting and overbrowsing have converted forests to unpalatable grass-dominated communities (e.g., *Deschampsia flexuosa*; Bergquist et al. 1999), and in New Zealand, where arboreal herbivory by marsupials has opened up the canopy and, in combination with deer overbrowsing, has led to stands of unpalatable plant species (Jane and Pracy 1974; Allen et al. 1984; Rogers and Leathwick 1997; Wardle et al. 2001; Coomes et al. 2003). In parts of New Zealand, forest area cover by shrubs, ferns, and grasses has increased from <1% to nearly 30% in just 30 years (Batcheler 1984).

The interaction of altered fire regimes and canopy disturbance

Humans have either substantially decreased or increased the frequency or severity of fire in various ecosystems (Attiwill 1994; May 2000; Mallik 2003). Frequent understory fires thin the understory by reducing seedling and sapling densities, thereby increasing light availability; this process favors 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 relatively close together in time, 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 (Meades 1983; Mallik 1995). 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 (Gleissman 1978*a*; Finegan 1996; Dolling 1999; Nelson 1994; May 2000).

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 (*Rhododendron* spp.) and mountain laurel (*Kalmia latifolia*). These species now form recalcitrant understory layers that cover an estimated 2.5×10^6 ha in the southeastern United States alone (Table 2) (Monk et al. 1985; Vandermast and Van Lear 2002). Furthermore, studies from the Coweeta Basin in North Carolina confirm that the expansion continues with a doubling of rhododendron cover in only 17 years (Nilsen et al. 1999).

The separate and combined effects of disturbances and browsing act as strong filters on species richness, thereby 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 of the understory plant species (Roberts 2004). Overbrowsing selects for only those species that are well defended or tolerant to browsing (e.g., Horsley et al. 2003; Banta et al. 2005). Frequent fires select for only those species that can survive the fire or resprout thereafter (e.g., Gliessman 1978; Mallik 2003; Payette and Delwaide 2003). Finally, increased overstory disturbance selects for shade-intolerant species with rapid rates of vegetative spread as opposed to slower growing shade-tolerant herbs and shrubs (e.g., Ehrenfeld 1980; Moola and Mallik 1998; Schnitzer et al. 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.

Summary

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 similar conclusion with exotic invasives). Indeed, overbrowsing, altered fire regimes, and increased overstory disturbance were implicated in 18%, 34%, and 82% of the cases, respectively (Table 1). More importantly, our review suggests that the formation of a dense understory canopy layer often arises (53%) 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.

Recalcitrant understory layers arrest, delay, and alter forest succession

Arrested succession

In a small number of documented cases, recalcitrant understory layers appear to exclude tree regeneration for

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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 (Sutherland 1974; Connell and Sousa 1983; Peterson 1984; Sutherland 1990), there are compelling examples where shrubs and ferns have persisted for decades in stands formerly dominated by trees (Niering and Egler 1955; Horsley 1985; Koop and Hilgen 1987; Raich and Christensen 1989; Petraitis and Latham 1999; Den Ouden 2000; Latham 2003; Mallik 2003). It is unclear whether these layers are self- sustaining (e.g., via strong interference; Stromayer and Warren 1997) or whether 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 phenomenon delays stand development by 20–30 years until saplings eventually emerge through the *C. canadensis* canopy and the stands revert to forest (reviewed by Lieffers et al. 1993). Delayed successions also occur in other boreal forests; for example, a dense ericaceous shrub layer has been shown to suppress the growth and emergence of tree species, including western redcedar (*Thuja plicata*), Sitka spruce (*Picea sitchensis*), and Norway spruce (*Picea abies*) (Messier et al. 1989; Messier and Kimmins 1991; Mallik 1995; Maubon et al. 1995).

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

Altered gap-phase regeneration

A recalcitrant understory layer may differentially reduce establishment among cooccurring tree species, thereby controlling the composition of the advance-regeneration layer (George and Bazzaz 1999*a*, 1999*b*). 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 (George and Bazzaz 1999*a*; Farris-Lopez et al. 2004), while those that strongly preempt light can preclude the establishment of many shade-intolerant and intermediately tolerant species (Horsley 1993*a*; de la Cretaz and Kelty 2002; Gonzalez et al. 2002). 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 (Runkle 1990; Connell 1990). If so, then the species composition of the advance-regeneration layer and subsequent pattern of gap-phase dynamics will contrast sharply between a forest with a recalcitrant understory layer and those without.

Mechanisms of interference over tree establishment, survival, and growth

A dense understory canopy can suppress regeneration directly through resource competition, allelopathy, and physical impediment of seedling germination and growth, or indirectly through modifications of interspecific interactions (Fig. 2). 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. Below, we briefly review the literature to evaluate the evidence for six different mechanisms of interference between the understory layer and co-occurring tree species. 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 (see below)

Resource competition

In closed canopy forests, dense understories exacerbate the degree of light attenuation caused by the midstory and canopy (Messier et al. 1998; Beckage et al. 2000; Nilsen et al. 2001; de la Cretaz and Kelty 2002). Photosynthetically active radiation (PAR) levels can drop well below 5% of full sun beneath these layers (Nakashizuka 1987; Kelly and Canham 1992; Horsley 1993*a*; Wada 1993; Walker 1994; Clinton and Vose 1996; Hill 1996; George and Bazzaz 1999*a*; Aubin et al. 2000; Lusk 2001; Lei et al. 2002). Additionally, these dense low canopies can reduce light quality (e.g., red:far-red wavelengths), thereby preventing germination, altering internode elongation, and inhibiting flowering (Messier et al. 1989; Horsley 1993*a*; Mancinelli 1994). Furthermore, dense low canopies decrease the availability of sunflecks particularly for seedlings (Denslow et al. 1991; Nilsen et al. 2001; Lei et al. 2002). Finally, if canopy gaps do form, they may not operate as gaps at all if seedlings remain trapped beneath a dense understory layer (Beckage et al. 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 (Putz and Canham 1992; Messier 1993; Dillenburg et al. 1993). Some studies infer resource limitation by detecting increased growth or survival of target plants following fertilization or measuring lower nutrient

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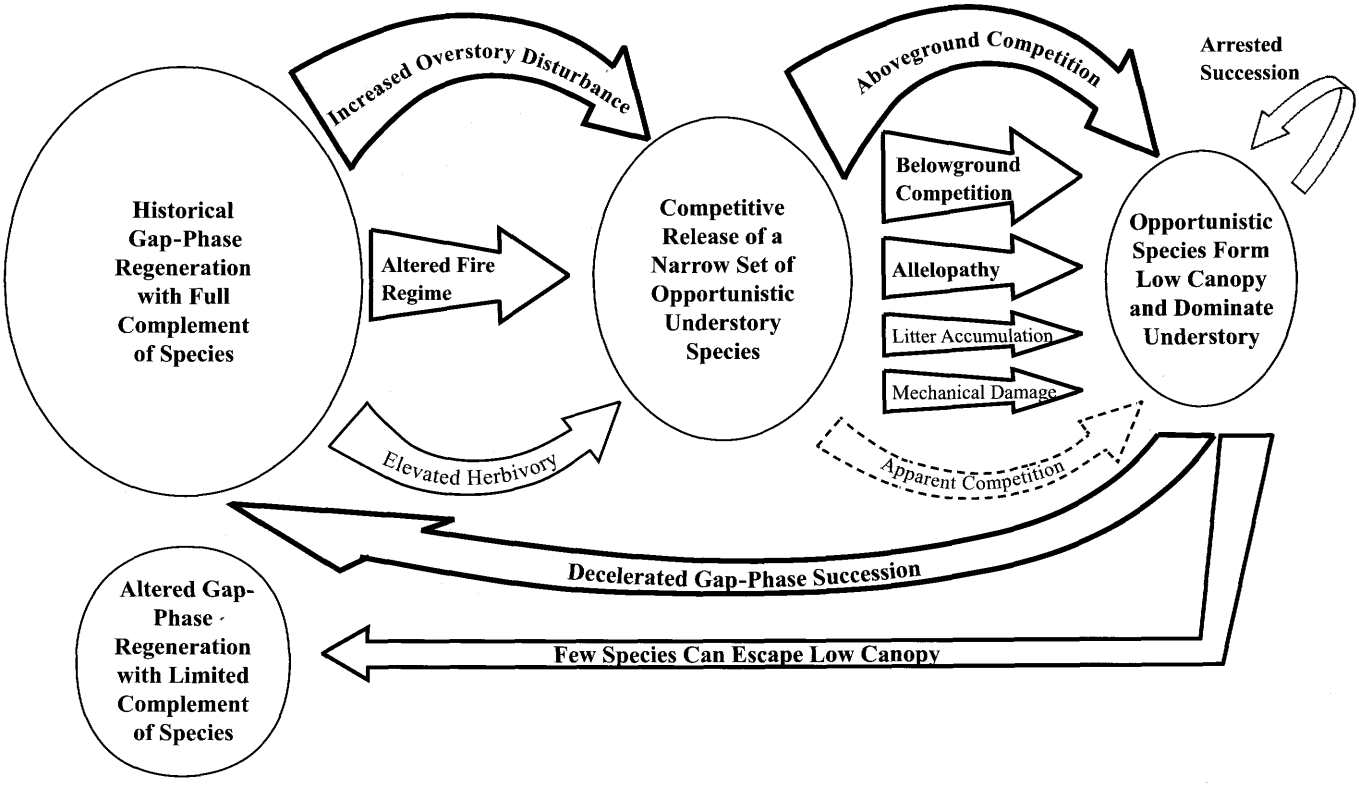
Fig. 2. Conceptual model illustrating factors precipitating change from historical gap-phase regeneration into low-canopy dominance. The model also reveals various interference mechanisms and illustrates the ensuing successional pathways. The size of the arrows denotes the relative importance of each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



and water concentrations in soil beneath dense understory cover than in soil in more open areas (e.g., Messier 1993; Yamasaki et al. 1998; Inderjit and Mallik 1996; Nilsen et al. 2001). Similarly, vine-covered saplings often have lower foliar nitrogen levels, reduced preleaf water potential, and decreased diameter growth when compared with vine-free saplings (Dillenburgh et al. 1993; Perez-Salicrup and Barker 2000). The above studies are suggestive of resource limitation, though they typically do not distinguish between competition for water and competition for soil nutrients. Because nutrient and water availability covary, decoupling these two factors is difficult (Nambiar and Sands 1993; Casper and Jackson 1997). Additionally, few experiments use factorial manipulations to disentangle a dense understory layer's aboveground versus belowground effects and their interactions (McPhee and Aarssen 2001).

Horsley (1993*a*) experimentally tested the influence of aboveground versus 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, and not belowground competition, was the mechanism of interference (Horsley 1977, 1993*a*, 1993*b*). 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 result 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 belowground and aboveground competition, although other processes may confound the results of these experiments (e.g., allelopathy, see below).

Allelopathy

Direct field evidence for allelopathy remains equivocal and elusive. In forests that have dense understories dominated by ericaceous shrubs, phenolics and other phytochemical compounds can disrupt nitrogen mineralization and inhibit ectomycorrhizal fungi, which can result in a significant reduction in conifer growth and survivorship (Walker et al. 1999; reviewed by Mallik 1995, 2003 and Wardle et al. 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 et al. (1997) found that *Vaccinium myrtillus* interfered with Norway spruce primarily through belowground competition. In forests where ferns form dense understories, bioassays and greenhouse studies have suggested that there is a potential for strong allelopathic effects on tree regeneration (Gliessman and Muller 1972; Horsley 1977; Gliessman and Muller 1978); however, further field experimentation failed to find strong allelopathic effects (Horsley 1993*b*; Dolling 1996; Nilsen et al. 1999; den Ouden 2000). Despite these results, too few studies have

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tried to experimentally disentangle resource competition from allelopathy via field experiments. Future research must move beyond merely documenting the mere existence of phytotoxic exudates in greenhouse and laboratory studies (Fuerst and Putnam 1983; Williamson 1990; Weidenhamer 1996; Inderjit and Callaway 2003).

Seed and (or) seedling predators

A dense understory layer can increase the activity of small mammals, thereby increasing the rate and impact of seed and seedling predation (Gliessman 1978; Wada 1993; George and Bazzaz 1999; Den Ouden 2000; Schreiner et al. 2000). 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 predation (Holt 1977, 1984; Connell 1990). Connell (1990) defined this as a type of apparent competition (sensu Holt 1977, 1984). Experiments that use canopy removals confound the direct competitive release of removing the understory layer with the indirect effects of removing this layer, particularly the decrease in small mammal predation (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 versus the role of 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; Ostfeld and Canham 1993; Howe and Brown 2001).

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 (1999*a*) found that a thick fern litter layer directly limited the establishment of small-seeded tree species (see also Veblen 1982; Beckage et al. 2000; Lei et al. 2002; Farris-Lopez et al. 2004). Alternatively, in boreal forests, the insulative properties of a dense grass litter layer result in decreased soil nitrogen mineralization, water uptake, and seedling photosynthetic rates, thus indirectly diminishing conifer growth and survival (Hogg and Lieffers 1991; Lieffers et al. 1993; Cater and Chapin 2000). 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 noncompetitive 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 (Putz 1991; Gerwing 2001; Schnitzer et al. 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., Guarigauta 1998; Gillman et al. 2003).

The relationship between mechanisms of interference and phenology

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., Nilsen et al. 2001; de la Cretaz and Kelty 2002). 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*), or species with early leaf expansion (e.g., *Betula lenta*) to overcome the understory stratum's deleterious effects on early establishment. This temporal advantage can provide sufficient photosynthetic and growth opportunities 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., *Acer saccharum*, *Fagus grandifolia*).

On the causes and consequences of a recalcitrant understory layer

We contend that the expansion and monopolization of the understory by a narrow set of plant species are 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 (Fig. 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 aboveground and belowground competition, allelopathy, microhabitat-mediated seed and (or) seedling predation, litter accumulation, 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., Veblen 1982; Clinton et al. 1994; Dolling 1996; Cater and Chapin 2000).

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The strength and selectivity of this filter can retard succession, alter the composition of tree species participating in the successional sere, or potentially arrest succession.

We found that only 25% of the published studies reviewed reported results of manipulative field experiments designed to identify the existence of one or more particular interference mechanism(s) (Table 1). Aboveground and belowground competition and allelopathy were the predominant mechanisms tested (37%, 32%, and 13%, respectively) (Table 1). Apart from competition and allelopathy, many papers speculated on various interference mechanisms but few, if any, were tested experimentally. Given the paucity of information, it is clear that for most systems, we lack the information to clearly establish by which mechanism a recalcitrant understory layer inhibits tree regeneration (see Levine et al. (2003) for 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 (Krause et al. 1978; Attiwill and Adams 1993; Kimmins 1996; Reich et al. 1997; reviewed by Coomes and Grubb 2000 and Ricard et al. 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; Nilsson 1994; Jäderlund et al. 1997). In contrast, temperate deciduous and tropical rain forests tend to be light limited (Pacala et al. 1994; Finzi and Canham 2000; Ricard et al. 2003). In these systems, we found that other mechanisms, including aboveground competition and seed predation, were generally more important than belowground competition (Table 1) (Denslow et al. 1991; Horsley 1993*a*; den Ouden 2000). Ideally, the best tests would link a series of carefully controlled laboratory or greenhouse studies with field experimentation 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 among these factors.

Implications for forest diversity, successional models, and management

Floristic diversity and forest succession

The increasingly common development of recalcitrant understory layers worldwide plays a strong, yet vastly underappreciated, role in determining future successional patterns and forest composition and diversity because these layers tend 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., Horsley and Marquis 1983; George and Bazzaz 1999*a*, 1999*b*; de la Cretaz and Kelty 2002; Hille Ris Lambers and Clark 2003). The presence of this additional filter on floristic diversity in forest understories, together with increased herbivory and altered fire regimes, undoubtedly restricts the number of species that can successfully regenerate. The potential consequences of these ecological filters (sensu George and Bazzaz 1999) on species composition remain poorly understood. Nevertheless, we suggest that floristic diversity in such areas is so severely constricted that succession may steadily march 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) as well as the 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 et al. 1996) remain the best tool for exploring 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 (15–750 cm in height) are applied to small seedlings as well (Pacala et al. 1994; Kobe et al. 1995). Additionally, the authors acknowledge that their recruitment parameter estimate is potentially unreliable, as the survival of individuals <5 years old is highly variable and mortality is often intense (Pacala et al. 1996). 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 et al. 2004). By constraining the model and its parameters to the ≥5-year-old age-class, SORTIE neglects part of the early dynamics that may occur close to the ground underneath a recalcitrant understory layer and help shape the composition sapling class.

As originally calibrated (Pacala et al. 1996), 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 et al. 2002) and the long-term development of shade-intolerant tree species following major disturbance (Tremblay et al. 2005). Both papers suggest that this may be due to the lack of an understory layer component in the model and stress that this goal is an ongoing research focus (see also Aubin et al. 2000; Beaudet et al. 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

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fern layer reflected the pattern of complete regeneration failure documented in the field (Hill 1996). We concur with Hill (1996) 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 (<5 years) seedling dynamics and (2) a failure to incorporate additional interference mechanisms causing seedling mortality (e.g., seed and seedling predation) beyond light competition.

Forest management

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 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 that 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, care should be taken when the control over overstory and understory factors fall under the purview of different agencies (e.g., wild game versus forestry management agencies). 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 et al. 1990). We further suggest the implementation of management practices that more closely resemble natural disturbance levels.

Understanding the interfering plant species' ecology could provide managers with alternative treatments to promote tree regeneration when conventional treatments like herbicide are not desired or permitted (Berkowitz et al. 1995). For example, mowing or cutting of ferns, grasses, and shrubby interfering vegetation may successfully limit their aboveground competitive effects and enhance regeneration (Davies 1985; Marrs et al. 1998; Biring et al. 2003). Alternatively, if belowground competition is the major interference mechanism, fertilizer application may mitigate the competitive effects of interfering plants and promote tree regeneration (Prescott et al. 1993; Haywood et al. 2003). 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 et al. 1998). 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 that are relatively unaffected by the interfering layer (e.g., shade-tolerant species) to attain a desirable and diverse mix regeneration outcome (Löf 2000).

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