

Title of Thesis: Linking community dynamics and ecosystem function in mixed conifer broad-leaved forests

Summary of thesis presented by

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Human activities are effecting profound changes in the structure and function of natural ecosystems. A comprehensive understanding of current ecosystem dynamics and future ecosystem responses to global environmental change requires an integrated investigation of ecological processes at many levels of organization. My thesis research addressed this goal by examining interactions between community- and ecosystem-level dynamics in mixed conifer broad-leaved forests in eastern North America. I specifically investigated: (1) the mechanisms underlying community-level processes in mixed forests, (2) the impact of a novel environmental perturbation (nitrogen deposition) on these processes, and (3) the influence of changes in forest composition on future ecosystem productivity.

Hypothesis 1: Coniferous and broad-leaved stand types persist within mixed temperate forests, because canopy trees influence understory environmental conditions to favor regeneration of conspecifics (a positive feedback). I addressed the nature of canopy-seedling feedbacks in mixed forests by relating patterns of seedling regeneration in contrasting stand types to understory conditions, and by directly manipulating resource availability to separate the individual effects of particular resources. The experiments demonstrated that canopy-seedling feedbacks played a major role in regeneration dynamics in both coniferous (hemlock) and broad-leaved (red oak) stands. Hemlock seedlings were favored in hemlock stands (a true positive feedback), as a result of high seed inputs, and relatively high seedling emergence and survival, while a suite of mid-successional species were favored in red oak stands through high overall seedling survival. These dynamics may act to slow successional trajectories in the future. Lower light availability and more acidic soils in hemlock stands compared with red oak stands emerged as the primary causes of stand-level differences in seedling dynamics.

Hypothesis 2: Nitrogen deposition differentially influences regeneration of coniferous and broad-leaved tree species under both gap and closed canopy conditions. To investigate how nitrogen deposition will influence future forest composition, I examined the impact of increased nitrogen availability on regeneration of both coniferous and broad-leaved tree species. In the understory experiment, only survival of the most late successional species (hemlock) was increased by nitrogen addition, while in the simulated gap experiment, there was a significant positive correlation between a species' growth rate and its nitrogen-induced growth enhancement. As a result, successional position emerged as a more important determinant of species' responses to increased nitrogen than did leaf habit. With increased nitrogen loading in the future, successional dynamics in mixed temperate forests are likely to become more exaggerated, as earlier successional species are further favored following canopy disturbance events, while later successional species (particularly hemlock) are able to maintain a more persistent seedling bank, and thus remain a dominant component of old-growth forests. On balance, however, nitrogen deposition will interact with other human-induced physical and chemical disturbances to increase the early successional character of forests by promoting faster growing species, such as yellow birch, at the expense of later successional species, such as hemlock.

Hypothesis 3: Coniferous and broad-leaved tree species differ in their contributions to ecosystem-level carbon gain. Future changes in forest composition might also influence ecosystem productivity. Using two separate scaling approaches (leaf-level aggregation, whole-tree sap flow), I examined how the dominant coniferous (hemlock) and broad-leaved (red oak; red maple) species in mixed temperate forests differed in their contributions to canopy-level photosynthesis. A lower than average leaf area index (compared to most conifers) and cold winter temperatures meant that hemlock only gained limited benefits from maintaining an evergreen canopy, and overall the broad-leaved species (particularly red oak) finished with higher rates of gross and net annual carbon gain. If earlier successional species do increase in abundance at the expense of hemlock, as predicted, this change will increase forest productivity two- to four-fold, although consequences for long-term carbon storage are still uncertain.

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CHAPTER 1

INTRODUCTION: TEMPERATE FORESTS IN A CHANGING ENVIRONMENT

An integrated approach to ecosystem dynamics

At its most basic, ecology is the study of the interactions between organisms and their abiotic and biotic environment, and how these interactions scale up to influence the dynamics of populations, communities, and ecosystems. In recent years, there has been particular interest in understanding ecological processes at these higher levels of organization (Ehleringer & Field 1993), as we increasingly recognize both the importance of natural ecosystems in regulating many global biogeochemical processes, and also the profound impact of human activities on ecosystem structure and function (Walker *et al.* 1999, Canadell *et al.* 2000). Most ecological research has focused on processes at one level of organization, but a comprehensive understanding of current ecosystem dynamics and future ecosystem responses to global environmental change requires investigation of both individual processes and their interactions (O'Neill *et al.* 1986, Bazzaz & Sipe 1987). My dissertation research investigates how we might achieve such an understanding by examining interactions between community- and ecosystem-level dynamics for mixed temperate forests in eastern North America.

The important role that community structure plays in regulating many ecosystem processes has only been emphasized in the last few years (e.g., Naeem *et al.* 1999). It is now clear that the number and identity of species within a community can influence the processing of energy and matter within ecosystems (Grime 1998, Tilman 1999). Identifying links between community composition and ecosystem function is now particularly critical as humans have an ever increasing impact on all natural ecological systems (Chapin *et al.* 2000). Global environmental changes may influence ecosystem processes directly by altering species functioning (e.g., Magill *et al.* 1997, DeLucia *et al.* 1999), but also indirectly through modification of community species composition (Wedin & Tilman 1996, Saleska *et al.* 1999, Dukes & Field 2000). In my thesis research, I examine both how a novel environmental perturbation influences current community dynamics, but also how such changes might scale up to affect future ecosystem function (Figure 1.1).

Mixed temperate forests as a study system

My research questions focus on community and ecosystem processes in mixed conifer broad-leaved forests in eastern North America. Forests in this region are commonly placed in the northern hardwoods-hemlock-white pine vegetation zone (Braun 1974), and are often considered intermediate between the conifer-dominated boreal forests further north and the cool temperate deciduous forests to the south (Pastor & Mladenoff 1992). Such mixed forests also occur in the northern temperate regions of other continents, such as Europe (Fulton & Prentice 1997) and east Asia (Hiura & Fujiwara 1999). These forests offer an ideal system for process-based studies of community and ecosystem dynamics, because they contain a mixture of two distinct kinds of tree species (evergreen coniferous and deciduous broad-leaved) that differ from one another in their basic biology (Reich *et al.* 1995, Smith & Hinckley 1995). As a result of this functional diversity, characterizing broad-scale community dynamics in mixed forests is made possible by examining responses of the dominant coniferous and broad-leaved tree species to the major environmental gradients within the community (Collins 1990, Cornett *et al.* 1997). In addition, community patterns in mixed forests might be particularly sensitive to future environmental changes (Melillo *et al.* 1996), as the two major groups of species are likely to respond in contrasting ways to novel perturbations. Furthermore, shifts in the abundance of coniferous and broad-leaved tree species could have profound influences on ecosystem-level processes in mixed temperate forests. These two groups of tree species often differ in their contributions to ecosystem properties due to the contrasting ways that they process energy and matter (Swank & Douglass 1974, Gower *et al.* 1993, Baldocchi & Vogel 1996, Reich *et al.* 1997).

Understanding controls on temperate forest ecosystem processes is now a particularly critical ecological priority, because these forests currently act as a significant terrestrial sink for atmospheric CO₂ (Tans *et al.* 1990, Houghton *et al.* 1998), and thus their continued functioning could serve to slow current human-induced CO₂ increases and mitigate future climate change (Woodwell *et al.* 1998). Global measurements of the spatial and temporal patterns of atmospheric CO₂ (Ciais *et al.* 1995, Keeling *et al.* 1996), along with direct empirical measurements of forest productivity

(Wofsy *et al.* 1993, Dixon *et al.* 1994, Valentini *et al.* 2000), have demonstrated that forests in northern temperate regions are now accumulating carbon (Schimel 1995). The strength and exact location of the sink in temperate forests is still equivocal (Fan *et al.* 1998, Houghton *et al.* 1999), however, as are the mechanisms that have led to this increased productivity, e.g., land-use change (Houghton 1995), elevated CO₂ (Saxe *et al.* 1998, Ceulemans *et al.* 1999), increased nitrogen deposition (Holland *et al.* 1997, Nadelhoffer *et al.* 1999). In addition, it is currently difficult to assess the prospects for the continued existence of a northern temperate carbon sink, as forests in this region are threatened by a suite of novel environmental perturbations that will affect their future structure and function (Bazzaz *et al.* 1996, Foster *et al.* 1997), and we do not have a complete mechanistic understanding of the impact of such perturbations on these forests. In order to further develop this understanding, my thesis research examines (1) the mechanisms underlying community-level processes in mixed conifer broad-leaved forests, (2) the impact of a novel environmental perturbation (increased nitrogen deposition) on these processes, and (3) the influence of changes in forest community composition on future ecosystem productivity.

Community dynamics in mixed temperate forests

Before we can examine the impact of novel environmental perturbations on temperate forest community structure, we need to determine the major processes currently controlling community species composition in these forests. Chapters 2 and 3 of my thesis address factors influencing community-level dynamics in conifer broad-leaved forests in eastern North America. The landscape-scale distribution of tree species within these mixed forests has emerged as a characteristic feature of such communities. Rather than forming mixed species stands, coniferous and broad-leaved tree species typically form a mosaic of distinct stand types across the landscape (Pastor & Mladenoff 1992). In eastern North America, the dominant conifer (eastern hemlock, *Tsuga canadensis*) can form almost monospecific stands within a matrix of broad-leaved trees (typically sugar maple in the mid-west, and red oak/red maple further east) (Pastor & Broschart 1990).

The occurrence of this distinct community attribute has intrigued ecologists for many years (Daubenmire 1930). Paleo-ecological studies have demonstrated that many

of these stands have persisted for thousands of years with little change in composition, and that the distribution of these stands cannot be associated with any clear site characteristic or disturbance regime (Davis *et al.* 1994, but see Foster & Zebryk 1993). It has been hypothesized that distinct coniferous and broad-leaved stand types develop within mixed temperate forests as a result of positive feedbacks between stand composition and seedling regeneration dynamics (Frelich *et al.* 1993). According to this view, hemlock-dominated stands favor regeneration of hemlock seedlings over broad-leaved seedlings, while the reverse occurs in stands dominated by broad-leaved tree species, and thus stand composition remains relatively stable over multiple regeneration cycles (Wilson & Agnew 1992, Petraitis & Latham 1999). Chapters 2 and 3 of my thesis test this positive feedback hypothesis in mixed temperate forests in eastern North America, and additionally examine the population-level mechanisms underlying such feedbacks. A complete understanding of community dynamics in these forests cannot be achieved unless we determine what biological processes lead to the development of positive feedbacks in each stand type.

Positive feedback dynamics are part of a larger set of ecological processes concerned with species' effects on their environment (van Breemen & Finzi 1998). Ever since Frederic Clements (1916) proposed his theory of plant succession, ecologists have recognized that the dynamics of plant communities are driven both by species' responses to local environmental conditions and by species' effects on these conditions (Horn 1971, Connell & Slatyer 1977, Bazzaz 1983). However, in contrast to the many studies addressing species' responses to their resource environment, very few studies have directly considered the role played by species' effects on their surroundings in the structure and dynamics of plant communities. By examining in detail how temperate forest trees influence the understory environment beneath them and how seedlings respond to this resource heterogeneity, my community-level research in mixed conifer broad-leaved forests further highlights the importance of species' effects on the environment in controlling plant community patterns, in addition to providing a clear process-based picture of the dynamics of these mixed forests. I directly relate canopy tree-mediated changes in understory resource environment to the dynamics of multiple

stages of seedling regeneration, and thus provide a much needed mechanistic link between current community patterns and future forest dynamics. Seedling regeneration patterns have only been directly related to the effect of particular canopy species on their local environment in a few cases (Collins 1990, Pacala *et al.* 1996).

In chapter 2, I investigate the nature of canopy-seedling feedbacks in mixed temperate forests by examining natural patterns of seedling regeneration in contrasting stand types (hemlock vs. red oak, *Quercus rubra*, the dominant broad-leaved species in the region). I then relate these seedling dynamics to variation in understory resource conditions in these contrasting stand types to develop a mechanistic understanding of such feedback effects. In chapter 3, to complement this demographic approach to temperate forest community dynamics, I directly manipulate resource conditions (light, nitrogen availability, soil pH) for seedlings emerging from the soil seed bank in hemlock stands. By experimentally varying understory resource environment, I can separate the individual effects of particular resources on regeneration patterns, as well as monitoring seedling dynamics in a more controlled setting.

Influence of nitrogen deposition on forest community structure

Human activities now affect all ecosystems on Earth to some degree, either directly through use and appropriation of ecosystem products and services, or indirectly through modification of the major global biogeochemical cycles (Vitousek *et al.* 1997b). A central goal of ecological research involves examining the impacts of such human-induced global changes on future ecosystem structure and function, so that we can understand the full consequences of human activities on the biosphere, and also so that we can make recommendations for mitigation of such changes (Houghton *et al.* 1996, Watson *et al.* 1996). In temperate regions, a major threat to ecosystem integrity arises from human modification of the nitrogen cycle. More nitrogen is now fixed through human activities (fossil fuel burning, fertilizer production, development of legume crops) than through natural processes (lightning strikes, symbiotic and free-living nitrogen-fixing bacteria) (Galloway *et al.* 1995, Vitousek *et al.* 1997a). The products of nitrogen fixation (NH_3 , NO_x) have short residence times in the atmosphere, and thus tend to be deposited close to their point of release (Lovett 1994). As a result, nitrogen

deposition is concentrated in industrialized northern temperate regions (Europe, North America, and now parts of east Asia) where human population demands for food and energy are high (Holland *et al.* 1999). Natural ecosystems in all these temperate regions are commonly nitrogen limited (Vitousek & Howarth 1991), and thus nitrogen deposition is likely to exert profound effects on the structure and function of these ecosystems (Bobbink *et al.* 1998, Lee 1998).

As already discussed, forests in northern temperate regions are currently of particular ecological concern because of their role as a terrestrial sink in the contemporary global carbon cycle (Houghton *et al.* 1998). Increased nitrogen loading in this region clearly threatens the future integrity of such ecosystems, and there is now interest in examining how nitrogen deposition will affect future forest structure and function. Some studies suggest that forest productivity will increase with increased nitrogen loading, and thus enhance the current temperate sink (Townsend *et al.* 1996, Holland *et al.* 1997), while other research points to a decline in productivity as forests reach nitrogen saturation (Magill *et al.* 1997, Emmett *et al.* 1998, Nadelhoffer *et al.* 1999). The situation becomes further complicated when we recognize that effects of nitrogen deposition will interact with other novel environmental perturbations (e.g. elevated atmospheric CO₂), and thus impacts will be sensitive to the rate and degree of change of other factors (Bazzaz *et al.* 1996).

Rather than directly focusing on the ecosystem-level effects of nitrogen deposition, my thesis research investigates how increased nitrogen loading will influence temperate forest community structure. Few studies to date have specifically considered how nitrogen deposition will alter future canopy tree species composition (but see Crabtree & Bazzaz 1993). Nitrogen deposition may further influence ecosystem function through its effects on community species composition (Wedin & Tilman 1996). These indirect effects through changes in community structure could potentially be more substantial than direct effects on plant and soil function (Pastor & Post 1988, Bolker *et al.* 1995), especially in forests that contain a mixture of two functionally distinct groups of tree species (evergreen coniferous vs. deciduous broad-leaved). In this section of my thesis (chapters 4 and 5), I examine how increased nitrogen

deposition will influence the relative abundance of the major coniferous and broad-leaved tree species in mixed temperate forests. Scaling from these nitrogen-induced changes in forest community composition to ecosystem properties is addressed in the subsequent section.

My research on effects of nitrogen deposition on temperate forest community structure builds on the demographic studies of patterns of seedling regeneration described in chapters 2 and 3. I examine the impact of increased nitrogen availability on regeneration patterns of both coniferous and broad-leaved tree species. Seedlings of these species may respond differently to nitrogen deposition because of their contrasting patterns of nutrient use (Aerts 1995, Aerts & Chapin 2000). I focus on early stages of species' life-cycles, as alteration of seedling regeneration patterns may drive changes in future species composition (Bolker *et al.* 1995, Pacala *et al.* 1996). In addition, I compare seedling responses to nitrogen deposition in hemlock stands with responses in broad-leaved tree stands (red oak dominated), as chapters 2 and 3 demonstrate how seedling dynamics in these contrasting stand types are strikingly different. I describe separate experiments that address nitrogen effects on (a) understory seedling bank dynamics (chapter 4), and (b) seedling responses to canopy gap formation (chapter 5). Both of these life-cycle stages may be critical components of an individual's regeneration strategy (Figure 1.2) (Canham 1989). Tree seedlings may respond in complex ways to combinations of light and soil conditions (Latham 1992, Canham *et al.* 1996, Grubb *et al.* 1996, Walters & Reich 2000). As my experiments incorporate varying combinations of above- and below-ground resources (gap vs. understory, contrasting stand types), I am able to decouple components of seedling responses to these resources (Figure 1.3), and thus further develop our mechanistic understanding of effects of novel environmental perturbations on forest community dynamics.

Influence of forest canopy composition on ecosystem properties

The last part of my thesis (chapters 6 and 7) examines how shifts in forest community composition brought about by novel environmental perturbations might influence whole-ecosystem fluxes of water and carbon. The central role played by the terrestrial biosphere in the major global biogeochemical processes has increased interest in

understanding what factors control the functioning of natural ecosystems (Polis 1999, Canadell *et al.* 2000). Until recently, ecosystems were viewed as 'black boxes', where changes in fluxes were predominantly controlled by large-scale, extrinsic factors (e.g. climate, disturbance regimes). There is now a growing realization that processes within ecosystems themselves (intrinsic factors) could exert strong controls on these dynamics (Pace & Groffman 1998). In this section of my thesis, I examine one major characteristic of natural ecosystems that may dramatically influence ecosystem-level processes. Specifically, I consider how mixed forest species composition may control water and carbon flux through such ecosystems.

Two distinct components of community structure may influence ecosystem processes: (1) species identity, and (2) species richness and diversity (Tilman 1999). Physiological differences between species could scale up to influence ecosystem-level processes (Ehleringer & Field 1993), and thus the identity of species present in a particular community may determine ecosystem function (Chapin *et al.* 1997). However, not all species' differences are significant at the ecosystem scale. There has been a recent move to use functional traits of species for classification in ecosystem-level analyses (Smith *et al.* 1997), with individual functional groups referring to sets of species that have similar effects on specific ecosystem-level processes (Vitousek & Hooper 1993, Catovsky 1998). In this way, changes in the relative abundance of different functional groups of species will likely have more significant impacts on ecosystem processes than would changes in the abundance of individual species within a functional group. This idea, however, still needs to be tested further (Bazzaz 1996).

Higher-level properties of ecological communities (e.g., species richness and diversity) may also have important effects on whole ecosystem function (Naeem *et al.* 1999). The relationship between biodiversity and ecosystem function is now of particular interest because of the rapid rate of species loss we are now experiencing (Sala *et al.* 2000). A number of recent, high-profile experiments have addressed how many species must be present for a given ecosystem to function appropriately, e.g., the Ecotron experiment (Naeem *et al.* 1994), field studies on California serpentine grassland communities (Hooper & Vitousek 1997) and on mid-western tall-grass prairie

communities (Tilman *et al.* 1997), and the BIODDEPTH experiment carried out at eight grassland sites across Europe (Hector *et al.* 1999). The limited experimental evidence that we now have suggests that the flux of material and energy through ecosystems is a saturating function of biodiversity (Tilman 2000). Unfortunately, there is still considerable uncertainty about the validity of such experiments (Huston 1997), and what mechanisms might be driving these diversity-productivity patterns (Grime 1998, Wardle *et al.* 2000).

Given the lack of a mechanistic understanding of the relationship between species diversity and ecosystem function, and the lack of empirical data for many ecosystem types, we cannot yet know whether species richness can be regarded as a functional community characteristic or not. As a result, this component of my thesis research focuses exclusively on changes in community species composition as a means for alteration of ecosystem properties (Hooper & Vitousek 1997, Tilman *et al.* 1997). Both natural and anthropogenic disturbance processes may alter temperate forest community composition (Bazzaz 1996, Foster *et al.* 1997) (Sections 1 and 2). These changes may have substantial impacts on future ecosystem function (Pastor & Post 1988, Bolker *et al.* 1995), as tree species may have different functional roles in forest ecosystems (Canham & Pacala 1995, Bassow & Bazzaz 1998). As discussed, we expect particularly close coupling between community- and ecosystem-level processes in mixed conifer broad-leaved forests, as the two major groups of trees may influence ecosystem properties in different ways (Reich *et al.* 1995, 1997). Given the current importance of temperate forest ecosystems in the global carbon cycle (see 'Mixed temperate forests as a study system' section), I specifically consider species' contributions to forest carbon flux. I investigate how the dominant coniferous (hemlock) and broad-leaved (red oak; red maple, *Acer rubrum*) species in New England temperate forests differ in canopy carbon uptake rates, on seasonal, annual, and decadal time scales.

As the size of forest trees makes it difficult to measure directly the contribution of individual species to total ecosystem carbon flux, I explore different methods of scaling up from physiological measurements to total canopy photosynthesis (Jarvis 1995). In chapter 6, total canopy carbon uptake rates during the main growing season

are calculated for each study species using a bottom-up approach where individual weighted measurements of *in situ* leaf-level photosynthesis are summed together through the canopy (Norman 1993). This approach contributes useful information on within-canopy heterogeneity in photosynthetic rates, but only provides an instantaneous picture of canopy processes that cannot be extrapolated to longer time-scales without further mechanistic details.

As my research compares evergreen and deciduous species, which have different patterns of carbon gain through the year (Chabot & Hicks 1982), I take a second scaling approach in chapter 7 that extends these instantaneous measurements to a comparison of annual carbon gain between the species. To consider carbon flux on a longer time scale, I modify an existing scaling technique to calculate total canopy photosynthesis from continuous measurements of whole-tree transpiration rates. Using whole-tree measures of plant function avoids many of the limitations with 'bottom-up' approaches to scaling (Jarvis 1993, 1995). We can now accurately measure whole-tree transpiration by monitoring sap flow through tree trunks (Granier 1987, Granier *et al.* 1996). As photosynthesis and transpiration are connected through the activity of stomata (Farquhar & Sharkey 1982), there is potential to use whole-plant sap flow to estimate total canopy carbon uptake. By combining continuous measurements of sap flow with leaf-level of gas exchange, I study intra-annual variability in whole-plant carbon gain for both dominant coniferous and broad-leaved tree species. These measurements are then validated on a decadal scale using tree growth rings to examine inter-annual variation in net biomass gain.

Details of study sites

My research experiments were based at the Harvard Forest Long-Term Ecological Research Site (Petersham, MA; 42° 32' N, 72° 11' W, elevation 340 m a.s.l.). For all seedling experiments, I set up study sites in three hemlock- and three red oak-dominated forest stands in the Tom Swamp tract of Harvard Forest (Figure 1.4). The forest is located in the transition hemlock-white pine-northern hardwoods vegetation zone (Spurr 1956, Westveld 1956), and is representative of forest types in the New England region (Foster *et al.* 1998). Red oak and red maple dominate the broad-leaved

component of the forest (~ 70 % by basal area), interspersed with stands dominated by eastern hemlock. Further west, sugar maple (*Acer saccharum*) and American beech (*Fagus grandifolia*) become a more significant component of broad-leaved tree stands (Woods 1984, Davis *et al.* 1994, Woods 2000).

The Tom Swamp tract of Harvard Forest is one of the least disturbed parts of Harvard Forest, but nonetheless has undergone a series of both natural and human disturbances through time (Oliver & Stephens 1977), most recently the 1938 hurricane (Foster 1988). Hemlock and red oak contributed over 50 % of the basal area in each of three stands at my sites (Figure 1.5). The other major species at the sites were similar between stands, with only four species other than the dominant ever making a significant contribution to stand composition (*Acer rubrum*, *Betula alleghaniensis*, *Betula lenta*, *Pinus strobus*). The sites were all located on well-drained loams, and shared many similar physical and biological characteristics (Table 1.1). There was some variation in past natural and human disturbance (Raup & Carlson 1941), but the patterns were not consistent across stand type, so effects of history were not confounded with the influence of stand composition.

The ecosystem-level experiments (chapters 6 and 7) were not carried out in the Tom Swamp tract of Harvard Forest. Instead, the sites for these experiments were located 150 – 500 m west and north-west of the Environmental Monitoring Station (EMS) tower in the Prospect Hill tract of Harvard Forest (42° 32' N, 72° 10' W) (Wofsy *et al.* 1993, Goulden *et al.* 1996). In this way, carbon uptake rates for individual study trees would be part of the ecosystem carbon flux signal measured from the tower, and thus tree- and ecosystem-level fluxes could be directly related (e.g., Bassow & Bazzaz 1998).

Relevance to current and future forest dynamics: a starting point for research

The ability to compare results from experiments on different spatial and temporal scales represents one of greatest advantages of working at a long-term ecological research site. Harvard Forest supports a broad array of research projects, many of them with the general aim of 'comparing the effects on ecosystem structure and function of both historically important natural disturbances and recent and projected chemical and

climatic stress' (quote from Foster *et al.* 1997). Historical research at Harvard Forest has demonstrated that temperate forest structure and function have undergone dynamic changes in the past as a result of various natural disturbance processes, e.g., hurricanes, fire, ice storms, exotic pests (Foster *et al.* 1996), but have remained remarkably resilient to such perturbations on longer time-scales (Foster & Zebryk 1993, McLachlan *et al.* 2000). Subsequent to European arrival in North America, however, forests began to experience a suite of perturbations that had larger, more long-lasting impacts on structure and function (Foster *et al.* 1998). Widespread land clearance for agriculture uncoupled species' relationships to broad-scale climate factors and landscape features, even after forest cover returned (Fuller *et al.* 1998). Since then, as human impacts on the global environment have intensified, forests are becoming further influenced by recent climatic and chemical perturbations, e.g., elevated atmospheric CO₂ (Bazzaz *et al.* 1996), increased nitrogen deposition (Magill *et al.* 1997), tropospheric warming (Peterjohn *et al.* 1995), and novel exotic pests (Orwig & Foster 1998). There is concern that these changes are pushing the resiliency of such forests to their ecological limit and may have dramatic future impacts (Bazzaz 1996, Foster *et al.* 1997).

My thesis research on community and ecosystem processes in mixed temperate forests begins in the context of this dynamic history and recent human domination of the landscape (Foster & Motzkin 1998). A comprehensive understanding of temperate forest dynamics must account for both historical impacts of natural/human disturbances and novel chemical/climatic stresses. However, the complexity of natural ecosystems and the uncertainty of novel changes makes it challenging to make predictions about future forest dynamics. A process-based mechanistic approach may allow us to achieve a more complete understanding of forest structure and function, and additionally develop predictions for a range of future scenarios. By identifying the critical resources controlling seedling behavior in these forests, we can determine how a variety of perturbations to the system (e.g., increasing nitrogen deposition interacting with increasing frequency of disturbance, Figure 1.3) will influence forest community patterns. All perturbations ultimately involve alteration of an individual's resource environment, and thus a resource-based approach provides a way to examine forest

dynamics under different future conditions (Bazzaz & Sipe 1987, Bazzaz 1996). Then, by examining the role that individual species play in ecosystem-level processes, we can determine how a range of changes in forest community structure will influence whole-ecosystem properties, such as canopy carbon gain. Focusing on particular processes within ecosystems allows us the flexibility to make predictions about mixed temperate forests under a range of future scenarios, and it is from this view-point that I launch into my thesis research.

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TABLE 1.1. Characteristics of study sites (three hemlock and three red oak dominated), obtained from field measurements and from the Tom Swamp map series (Harvard Forest Archives). Current canopy composition for each site is shown in Figure 1.5.

| Stand Characteristics | Hemlock | | | Red oak | | |
|---|--------------------|--------------------|--------------------|--------------------|-------------------------------|--------------------|
| | 1 | 2 | 3 | 1 | 2 | 3 |
| Soil Type | Brookfield loam | Brookfield loam | Brookfield loam | Brookfield loam | Montauk fine sandy loam | Brookfield loam |
| Drainage | Well drained | Well drained | Well drained | Well drained | Well drained | Well drained |
| Slope / Aspect | 5 ° NE | 7 ° NW | 4 ° N | 4 ° W | 4 ° S | 7 ° N |
| Elevation (m) | 820 | 790 | 820 | 870 | 870 | 780 |
| Density ^a (ha ⁻¹) | 1190 | 600 | 840 | 980 | 750 | 1450 |
| Total Basal Area ^a (m ² ha ⁻¹) | 42.4 | 39.8 | 47.2 | 38.4 | 37.2 | 42.8 |
| 1938 Hurricane damage (%) | 15 - 25 | 0 - 10 | 80 - 90 | 90 - 100 | 0 - 10 | 60 - 70 |
| Land use in 1850 ^b | Farm | Farm | Woodlot | Woodlot | Farm | Meadow |

^a For all trees greater than 10 cm DBH.

^b From Raup & Carlson (1941).

Figure 1.1 Conceptual model showing how links between community and ecosystem-level processes provide an integrated approach for assessing the influence of global environmental change on natural ecosystems. Numbers refer to the three parts of my thesis research.

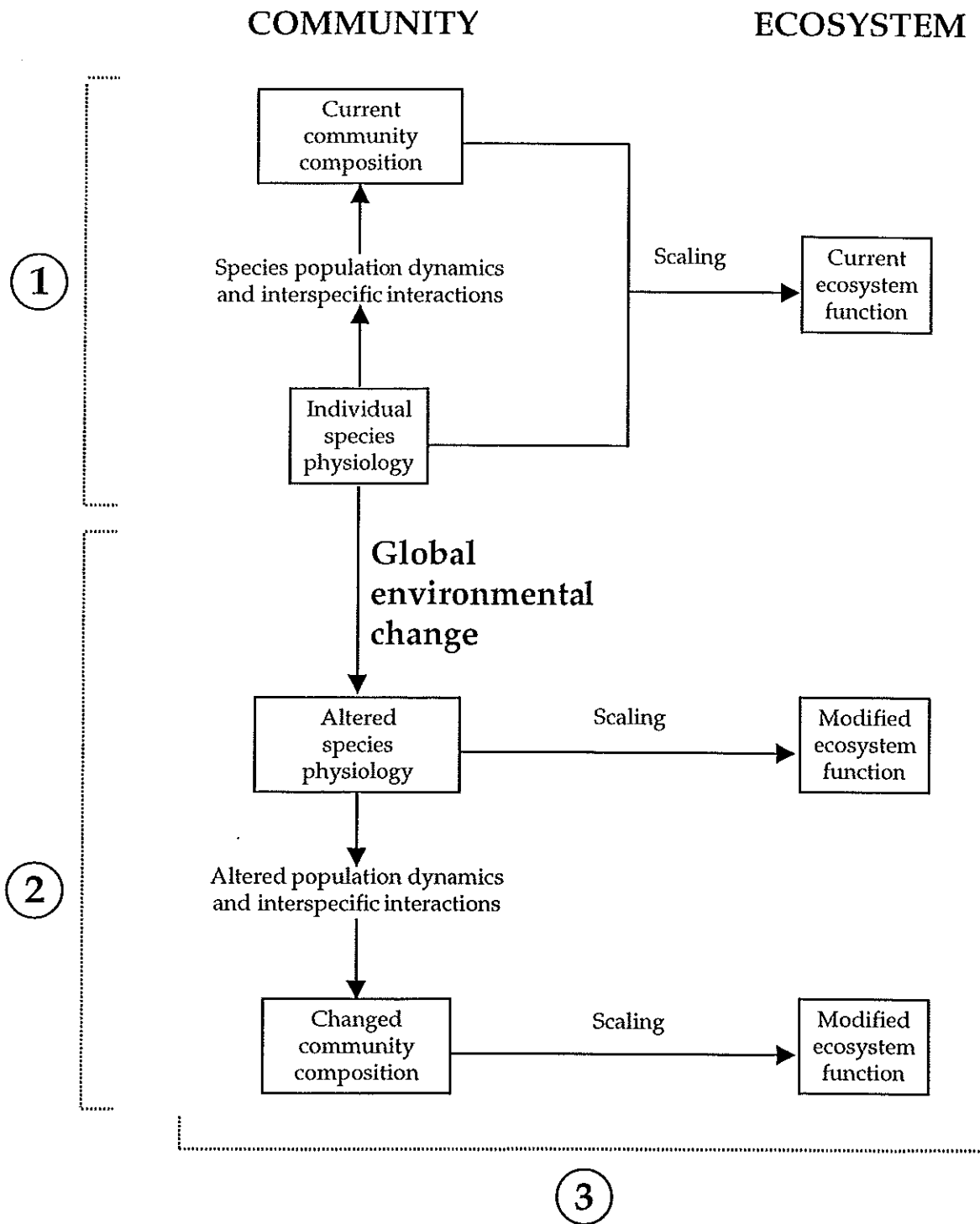
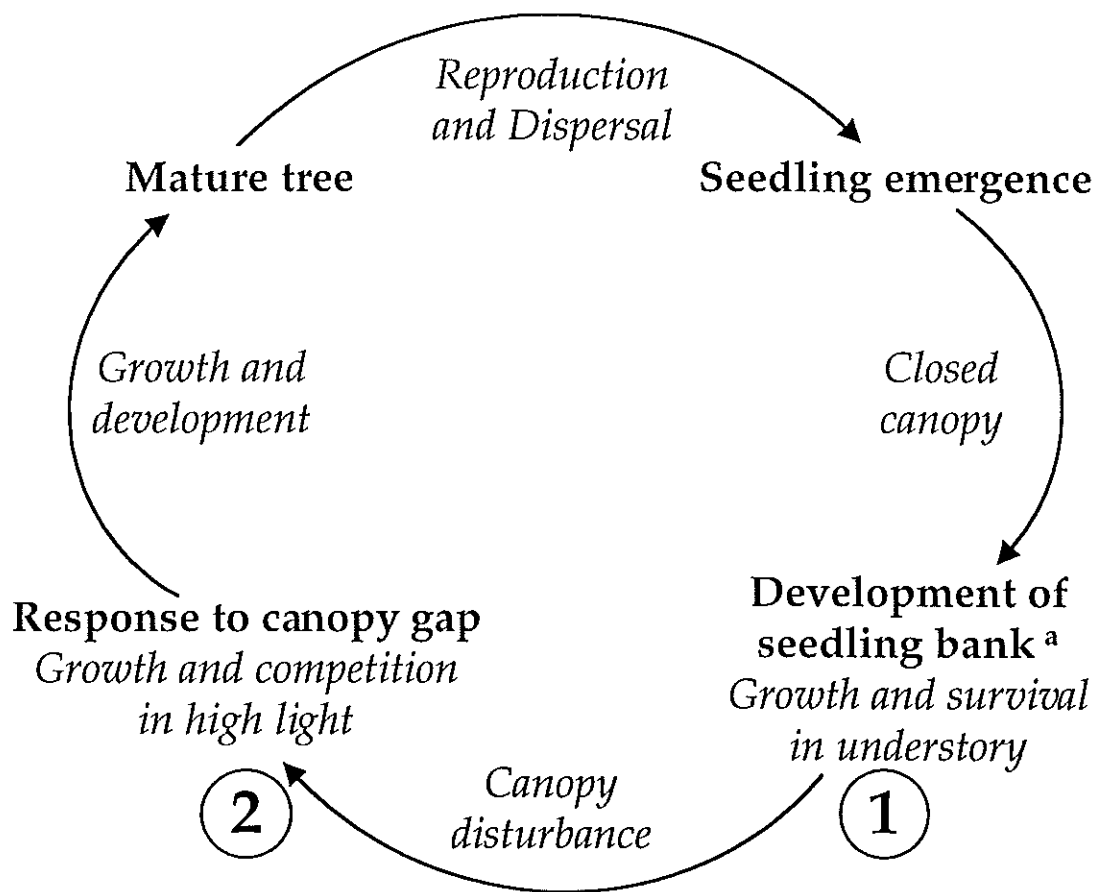


Figure 1.2 Outline of life-cycle of tree populations. Numbers represent the components of the life-cycle addressed in my thesis.



^a Earlier successional species rely less on a seedling bank as part of their regeneration strategy.

Figure 1.3 Resource-based framework for investigating how nitrogen deposition may influence seedling regeneration under different environmental conditions.

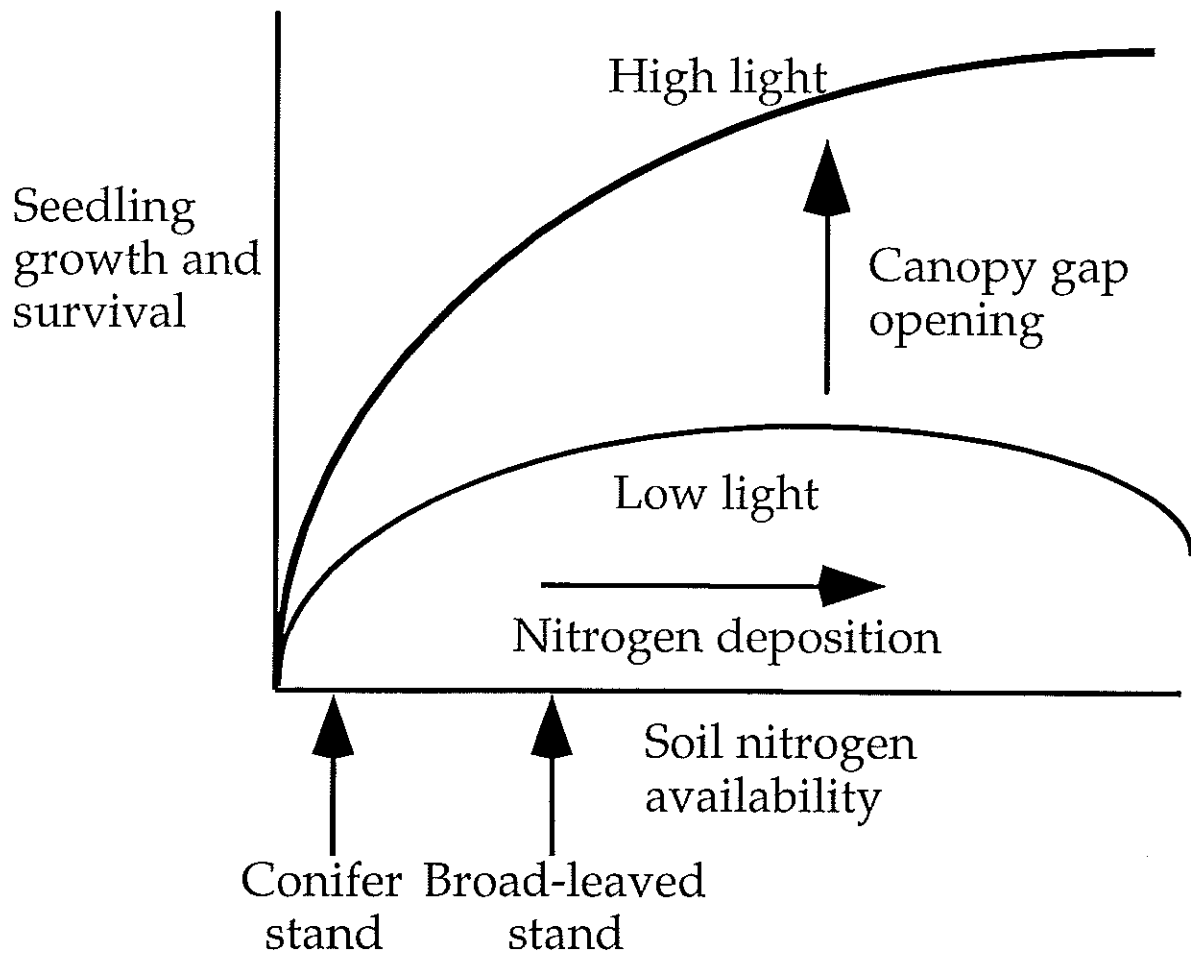


Figure 1.4 Map of study sites in Tom Swamp tract at Harvard Forest. Plots were mapped using a hand-held GPS system and displayed using ArcView GIS software.

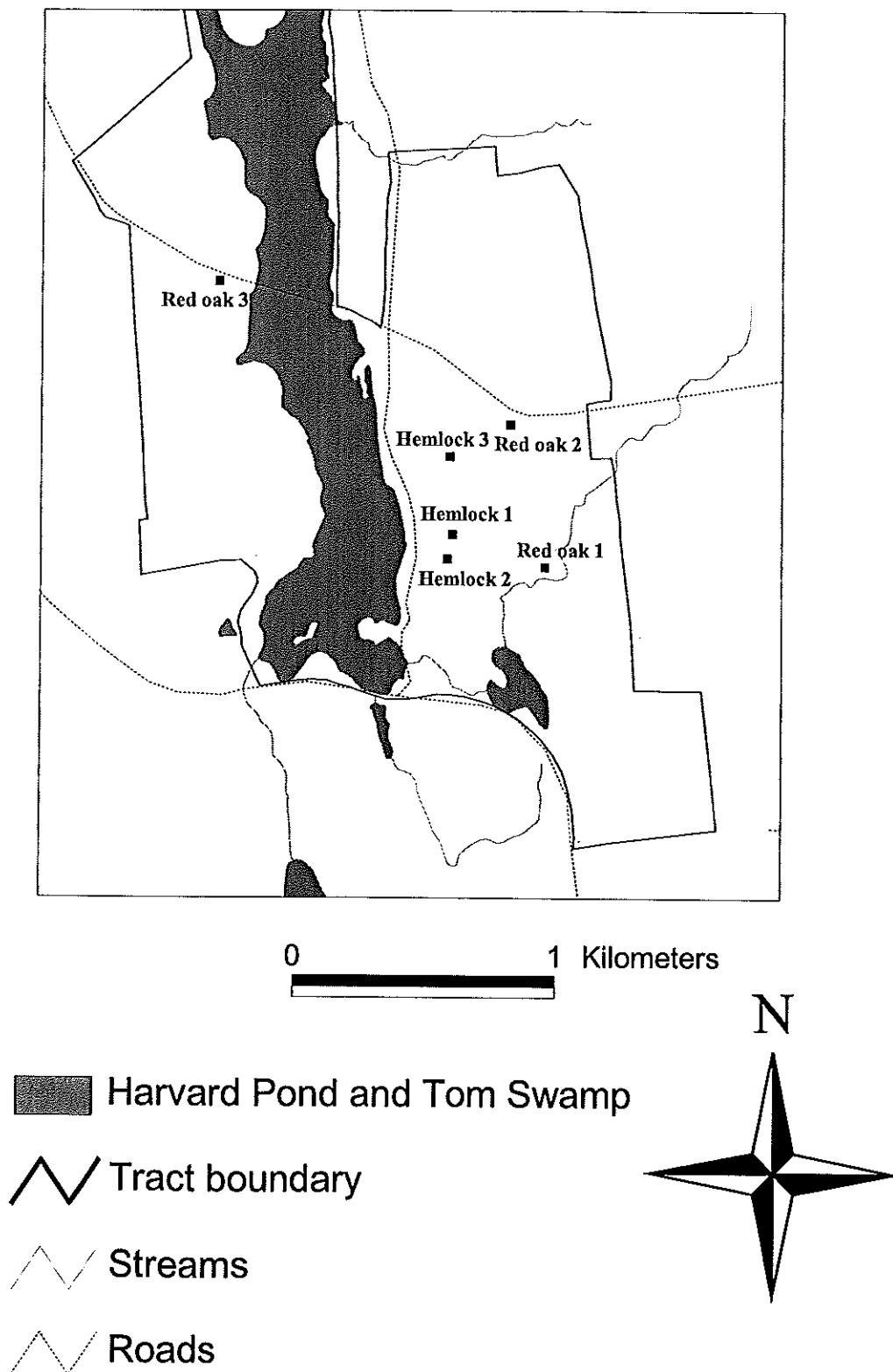
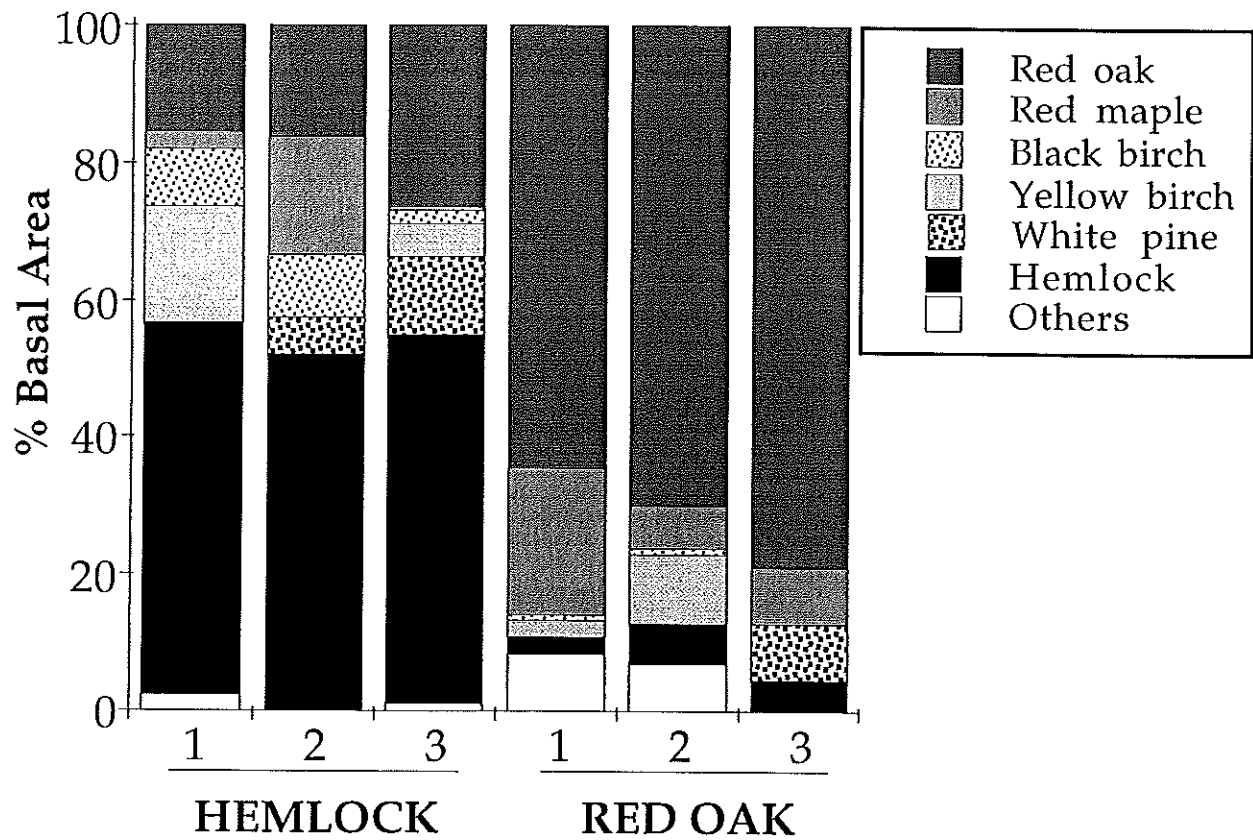


Figure 1.5 Canopy tree composition at study sites, expressed as species' contributions to total stand basal area. All trees above 10 cm DBH were included, and all species that made more than a 5 % contribution to stand basal area at any one site are shown individually.



CHAPTER 2

FEEDBACKS BETWEEN CANOPY COMPOSITION AND SEEDLING REGENERATION IN MIXED CONIFER BROAD-LEAVED FORESTS

Abstract. Individual species can exert a large influence on their local environment. Very few studies, however, have directly considered the role played by species' effects on their environment in the structure and dynamics of plant communities. These species' effects may be a particularly important control on seedling regeneration patterns in forests composed of distinct stand types. To address the role of canopy-seedling feedbacks in the structure and dynamics of mixed conifer broad-leaved forests in the eastern US, I monitored characteristics of the seedling bank (demography, age structure, long-term persistence) for three years in three stands dominated by a eastern hemlock and in three stands dominated by red oak. I then related these seedling patterns to differences in understory conditions (light, nitrogen, water, pH, litter depth) in the two contrasting stand types to develop a mechanistic understanding of the feedback effects. Seedling regeneration dynamics in the understory of hemlock and red oak stands showed very distinct patterns, with hemlock stands characterized by high seedling emergence and low survival, leading to high seedling turnover, while seedlings in the understory of red oak stands were more persistent and exhibited a more even-aged structure. Hemlock seedlings were favored in hemlock stands (a true positive feedback), as a result of high seed inputs, high seedling emergence and relatively high seedling survival, while a suite of mid-successional species (including red oak itself, red maple, and birch) were favored in red oak stands, through adequate seedling emergence and high overall seedling survival. These dynamics in red oak stands may act to slow successional trajectories in these forests in the future. Hemlock stands were characterized by very low light availability ($\sim 1.5\%$) and acidic soils (pH 3.9), in contrast to red oak stands, which had higher understory light levels ($3 - 4\%$) and higher soil pH (4.4). These canopy-mediated variations in both light availability and soil pH were found to be the primary causes of stand-level differences in understory seedling bank dynamics. In the present study, I have demonstrated that canopy-seedling feedbacks (mostly positive) operate in both coniferous and broad-leaved stands in mixed temperate forests, and I was able to determine both dispersal and resource-based mechanisms underlying such feedbacks.

INTRODUCTION

It has long been acknowledged that the dynamics of plant communities are driven both by species' responses to their habitat and by species' effects on local environmental conditions (Clements 1916, Horn 1971, Connell & Slatyer 1977). It is only recently, however, that both these components of species-environment interactions have been incorporated into our understanding of vegetation dynamics (Pacala *et al.* 1996). In contrast to the many studies addressing species' responses to local environmental condition, very few studies have directly considered the role played by species' effects on their environment in the structure and dynamics of plant communities (van Breemen & Finzi 1998). In forest systems, these species' effects may be a particularly important control on community patterns. As canopy trees are large and long-lived, they can substantially influence environmental conditions in the understory (Boettcher & Kalisz 1990, Vesterdal & Raulund-Rasmussen 1998), and thus determine patterns of seedling regeneration beneath them (Forcier 1975, Pacala *et al.* 1996). The influence of canopy trees on understory conditions varies between species, with the result that canopy composition determines many stand characteristics, including future recruitment patterns (Woods 1984, Cornett *et al.* 1997). These canopy-seedling interactions should be particularly important in forest communities composed of distinct stand types (Woods 1979, Hiura & Fujiwara 1999) where species' legacies may be additive and long-lasting (Bazzaz 1983). For example, in many transition northern hardwood forests in eastern North America, persistent stands dominated by eastern hemlock (*Tsuga canadensis* (L.) Carr.) occur in a matrix of predominantly deciduous, broad-leaved trees (Pastor & Broschart 1990, Foster 1992). In the present study, I examined seedling dynamics in these contrasting stand types to investigate the importance of stand composition in controlling regeneration in the forest understory.

In these mixed temperate forests, the distribution of hemlock and broad-leaved stands across the landscape remains relatively stable in the long term, and does not appear to be related to any distinct site or disturbance features (Davis *et al.* 1994). It has been suggested that the landscape structure in mixed temperate forests in North

America arises from feedbacks between stand composition and seedling regeneration (Frelich *et al.* 1993). The distinctiveness of hemlock stands in forests in the eastern US has long been recognized (Daubenmire 1930, Oosting & Hess 1956). Compared with most stands dominated by broad-leaved trees, hemlock canopies cast a particularly deep shade (Canham *et al.* 1994), and produce soils of low pH and low nutrient availability (Finzi *et al.* 1998a,b). As species have differing abilities to grow and survive in the forest understory (Kobe *et al.* 1995, Walters & Reich 1996), the altered forest floor conditions created by hemlock's presence could significantly influence seedling dynamics in the understory, and ultimately drive changes in future stand composition. Hemlock seedlings are commonly favored over broad-leaved tree seedlings in the low resource conditions characteristic of hemlock stands, while the reverse is the case in stands dominated by broad-leaved species. These interactions set up stand-level positive feedbacks where the presence of a species at a site promotes its continued dominance (Wilson & Agnew 1992, Petraitis & Latham 1999). This notion is similar to Clements' (1916) self-perpetuating climax community.

The mechanisms leading to such feedbacks have not yet been well established. Recruitment patterns are determined by complex interactions between species' regeneration traits and environmental conditions (Houle 1994, Schupp & Fuentes 1995). In mixed conifer broad-leaved forests, we currently do not know what stages of seedling regeneration are affected by canopy feedbacks, and what particular environmental conditions lead to differential species' responses in the contrasting stand types. Determining the mechanisms underlying regeneration dynamics in these forests would allow us to establish the importance of feedback processes for forest structure and dynamics, and we might be able to predict community changes if environmental conditions or forest structure were to change in the future. For example, there is now renewed interest in the future status of hemlock stands in mixed conifer broad-leaved forests, as hemlock is currently threatened by an invasive insect pest (the hemlock woolly adelgid, *Adelges tsugae* Annand) (McManus *et al.* 2000). A basic understanding of the distinct structure and dynamics of hemlock stands compared with the surrounding broad-leaved matrix should help us better predict the consequences of any change in hemlock's importance across the landscape.

To address the role of canopy-seedling feedbacks in the structure and dynamics of mixed conifer broad-leaved forests in the eastern US, I monitored components of the understory seedling regeneration dynamics (seed rain, seedling emergence and survival, age structure, long-term seedling persistence) in stands dominated by either hemlock or red oak (*Quercus rubra* L.), the dominant broad-leaved species in the region (Foster *et al.* 1998). I then related these seedling patterns to differences in understory conditions (light, nitrogen availability, soil moisture, pH, litter depth) in these contrasting stand types. I hypothesized that, as a result of influences on resource conditions in the understory, canopy composition differentially affects patterns of seedling regeneration to favor seedlings of the dominant species (a positive feedback). I predicted that, due to higher resource availability in broad-leaved tree stands than in hemlock stands (especially light, Pacala *et al.* 1996), seedling emergence, survival, and growth would be higher in oak stands, and the seedling bank would be more even-aged, with a higher proportion of older seedlings. As hemlock is particularly tolerant of understory conditions (Godman & Lancaster 1990, Kobe *et al.* 1995), I predicted that these effects would be more marked for broad-leaved tree species than for hemlock, thus creating stand-level positive feedbacks.

MATERIALS AND METHODS

Seedling bank dynamics

I set up study sites in three hemlock- and three oak-dominated forest stands at Harvard Forest (see Chapter 1 for details). At each site, I set up thirty 4 m² plots (2 x 2 m) in a stratified random design. The plots were laid out along three 50 m transects (each separated by 10 m), with one plot positioned randomly within every 5 m segment of the transect. From June 1997 until September 1999, I took monthly censuses of seedling emergence and survival in all study plots during the growing season. Seedlings were individually tagged once they emerged from the seed bank, and their survival was monitored in subsequent months (including once after each winter). In addition, in the first growing season, I tagged all seedlings up to 50 cm tall and monitored their survival over the three years of the experiment. Seedlings up to five years old were also aged, based on stem scars formed at the initiation of annual shoot growth.

Seed rain into the plots for the 1998 and 1999 field seasons was measured from seed traps placed beside each seedling plot (30 per site). Seed traps were constructed as inverted muslin cones (opening 0.2 m²) suspended 50 cm above the forest floor with a PVC frame (modified from Hughes *et al.* 1987). In 1997 and 1998, seed traps were emptied in July (for red maple seeds) and then monthly from September to December. For some species (oak, maples), I was able to distinguish filled vs. empty seeds, and I only recorded filled seeds. For hemlock and the birch species, I counted all seeds and then sub-sampled to look at the percentage of seeds filled (65 % for hemlock, 85 % for mid-successional birch species, 75 % for early-successional birch species). Seed rain in 1997 and 1998 was then used in combination with seedling emergence in 1998 and 1999 to calculate proportional seedling emergence, based on the assumption of no seed bank for any of these species. This assumption should be reasonable as only a very small fraction of seeds of my study species will remain viable past their first growing season (Burns & Honkala 1990).

Environmental measurements

Above- and below-ground resource availability in each plot was determined using methods and sampling protocols that would provide a good indication of integrated plant-available resources. Light availability was measured using two independent techniques: (1) stacked light-sensitive diazo paper (described in George & Bazzaz 1999), and (2) quantum sensors placed above and below the canopy on a uniformly overcast day to give a good estimate of mean daily % photon flux density (PFD) (Parent & Messier 1996). In July 1997, stacks of diazo paper (1 x 2 cm, ten sheets thick) were placed horizontally on stakes at 5 cm and 1 m above the ground in each plot. After five days of exposure, the stacks were developed in ammonia vapor. Simultaneously, I set up a calibration with identical diazo paper stacks exposed for different lengths of time under another forest canopy, using a leveled Li-Cor LI-190SA quantum sensor attached to LI-1000 data-logger (Li-Cor, Lincoln, NE) to measure moles of light received for each time interval. This calibration ($r^2 = 0.98$) was then used to calculate moles of light received by each stack of diazo paper in the demography plots.

On a uniformly overcast day in July 1999, the same quantum sensor and data-logger combination was placed on the top of one of the canopy access towers at Harvard Forest and set to record instantaneous PFD (measured every second and averaged over one minute intervals). I used a second quantum sensor (leveled each time) and data-logger combination to record PFD beneath the canopy at each of my 2 x 2 m demography plots (at 5 cm and 1 m). Data-loggers were synchronized and the data were used to calculate percent PFD transmitted through the canopy above each plot.

Nitrogen availability in each plot was also measured using two techniques: (1) *in situ* buried bags to calculate mineralization rates (Pastor *et al.* 1984), and (2) ion exchange resin bags to determine season-long integrated availability of ammonium and nitrate (Gibson 1986). In July 1997, two organic horizon soil cores (10 cm diameter, 5 – 15 cm deep) were collected from the edge of each 2 x 2 m plot. One core of each pair was brought back to the lab soon after extraction, while the second was placed in a polyethylene bag surrounded by mesh and buried in the organic horizon at each plot until the end of August that year. For each core (initial and incubated) 10 g of sifted soil

(5.6 mm mesh) was extracted with 100 ml of 2 N potassium chloride solution (25 °C, 48 hours), and then frozen immediately following suction-filtration. Extracts were analyzed for ammonium and nitrate ion concentrations on a Technicon TRAACS 800 analyzer (Braun and Luebbe, Buffalo Grove, IL). Ammonium was measured using the Berthelot Reaction chemistry (Method No. 780-86T) and nitrate was measured using hydrazine sulphate reduction (Method No. 782-86C). Detection limit for both these methods was 0.2 mg L⁻¹. Water content of each soil sample was determined by weighing 2 - 3 g of soil before and after oven drying (105 °C, 72 hours), so that nutrient availability could be expressed per g dry soil.

In 1999, ion exchange resin bags were placed in the field from early June until late October. The bags were constructed with 1.5 tablespoons (22 ml) of mixed bed strong acid (cation) and strong base (anion) gel resins (Sybron Chemicals, Birmingham, NJ) sealed in nylon mesh, and placed at a depth of 5 cm in the soil. After removal from the soil, 4 g of dried resin (70 °C, overnight) was extracted with 100 ml of 2 N potassium chloride solution (25 °C, 24 hours), and then frozen immediately following suction-filtration. Ammonium and nitrate in all resin extracts were measured using a LaChat continuous flow ion analyzer using methods 12-107-06-1-A and 12-407-04-1-B (LaChat Instruments, Milwaukee, WI). Blanks were created from resin bags that had been sealed in polyethylene bags for the length of the growing season. These resins were used to determine the lower threshold of detection.

Water availability was determined at three times during the 1997 and 1999 growing seasons and averaged to give full season integrated estimates. At each time, soil cores from both organic (10 cm diameter, 5 – 10 cm deep) and mineral (2 cm diameter, 20 cm deep) horizons were taken from the edge of each plot. Sieved soil (5.6 mm mesh for organic, 2 mm mesh for mineral) was dried (105 °C, 48 hours) to determine gravimetric water content. These values were expressed on a volumetric basis using bulk density measurements (0.12 g cm⁻³ for organic, 0.70 g cm⁻³ for mineral) taken at each study site, but then pooled across sites as there were no significant differences between sites ($F_{4,30} = 1.88$ for organic and 0.16 for mineral, both $p > 0.05$).

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In 1998, soil pH for the organic horizon was measured from 10 cm diameter soil cores (depth 4 – 12 cm). pH of sieved soil (5.6 mm mesh) was measured on a mixture of 2 g of air-dried soil in 20 ml distilled water (pH 5.5) using an Orion 250A pH meter (Orion Instruments, Boston, MA). In the same year, depth of the litter layer and the organic horizon were measured in each plot using a trowel to gently expose the upper layers of the soil profile. At the end of the year, litter collected in seed traps (described in previous section) was dried (70 °C, 100 hours), and coniferous and broad-leaved litter types were sorted and weighed.

Statistical analysis

Multi-factor analyses of variance (Anova) were used to investigate seedling regeneration dynamics in the forest understory. I constructed full interaction linear models with a variety of fixed, discrete factors (stand type, species, year, month) and occasional continuous factors (e.g., seedling age). Models also included a nested series of random factors (site nested within stand, and plot nested within site). Since I was most interested in comparing species' regeneration patterns in different stand types, any significant interactions involving species x stand interactions were investigated further using sequential Bonferroni corrected planned contrasts to test for differences in species' responses between hemlock and red oak stands (Sokal & Rohlf 1995).

Seedling bank community composition was investigated with multivariate analysis of variance on plot scores from the first two axes of detrended correspondence analysis (DCA, ter Braak 1995). When necessary, data were transformed to ensure that the assumptions of analysis of variance were met (normality of residuals, homoscedascity). Common transformations included natural logarithm (seed rain, emergence, abundance, age, biomass) and the logit function (proportional survival). Presence/absence of older seedlings (> 5 years old) in study plots was examined using the non-parametric Mantel-Haenszel test (Sokal & Rohlf 1995), as logistic models did not converge. I initially tested for homogeneity between sites (no significant difference between sites for any species) and then combined data from all the sites within one stand type to make pairwise treatment comparisons.

Relationships between seedling dynamics and environmental variables were investigated with stepwise multiple regression models (Sokal & Rohlf 1995), including year and species as fixed discrete factors, and site as a random discrete factor. Stand type was replaced in the model with a suite of environmental variables (continuous factors). Each model began with the same set of environmental factors – % photon flux density (PFD) at ground level, availability of soil ammonium and nitrate from ion exchange resin bags, O horizon volumetric water content averaged over 1997 and 1999 (consistency between years, see Table 2.4), soil pH, and litter depth. These measurements were chosen to give a good indication of a seedling's eye-view of local environmental conditions. Variables that explained little of the variance in the model were removed in a stepwise manner. Significant species x environment interactions in the models were further investigated by examining significance of standardized partial regression coefficients for individual species. Certain species were excluded from some analyses due to lack of data – white pine from proportional emergence analysis, red oak from survival analysis, and hemlock from age structure analysis.

RESULTS

First-year seed and seedling regeneration dynamics

Only five species made any significant contribution to the understory seedling bank at my study sites: birch (*Betula* spp., could not be identified to species at these early growth stages), red maple (*Acer rubrum*), red oak (*Quercus rubra*), white pine (*Pinus strobus*), and eastern hemlock (*Tsuga canadensis*). Seed rain inputs of all species except white pine were recorded during both of the seed rain measurement years (1997, 1998) (Figure 2.1). White pine had a large seed production year in 1996 (Chapter 3), but not during either of the measurement years. Hemlock, red maple, red oak and grey/white birch (seeds could not be distinguished) all had larger seed production years in 1997, while seed production of black/yellow birch was larger in 1998. Patterns of species' seed inputs differed between both stand types and years of study (significant species \times stand \times year interaction in Anova, $F_{4,1602} = 13.32$, $p < 0.001$). Red maple seed inputs did not differ between stand types, while both hemlock and black/yellow birch had between 30 and 150 times greater seed inputs in hemlock stands than in red oak stands (Figure 2.1). In contrast, grey/white birch and red oak (only 1997) had significantly higher seed inputs in red oak stands than in hemlock stands.

Species exhibited differential seedling emergence from the soil seed bank in contrasting stand types, and these effects varied between years of study (significant species \times stand \times year interaction in Anova, $F_{3,1009} = 12.36$, $p < 0.001$). For birch and hemlock, not only were seed inputs greater in hemlock stands than in red oak stands, but proportional emergence of the seeds that arrived was also greater (Figure 2.2), with birch having 0.5 % emergence in hemlock stands compared with 0.0075 % in red oak stands, and hemlock having 1.2 % and 0.0005 % (respectively). The larger seeded species, red maple and red oak, did not differ in proportional emergence between hemlock and oak stands (Figure 2.2).

This variation in seed input and proportional emergence from seed led to overall species' differences in total seedling emergence from the soil seed bank in contrasting stand types, and again these effects varied between years of study (significant species \times

stand x year interaction in Anova, $F_{8,2496} = 28.35$, $p < 0.001$). Both birch and hemlock consistently showed greater total emergence in hemlock stands than in red oak stands (Figure 2.3), with a 30- to 70-fold increase for birch, and a 2- to 2000-fold increase for hemlock. Emergence of white pine seedlings was also significantly greater in hemlock stands than in red oak stands, but only in 1997, which was the only seed production year for white pine during the course of the study (S. Catovsky, *personal observation*). Given the lack of variation in seed inputs and proportional emergence, red oak and red maple seedlings showed no difference in total emergence between the two stand types in any year (Figure 2.3).

Species' first-year survival during the growing season was also contingent on stand composition and year of study (significant species x stand x year interaction in Anova, $F_{6,817} = 5.13$, $p < 0.001$). Red maple consistently had significantly higher seedling survival in red oak stands (25 - 85%) than in hemlock stands (1 - 2.5%) (Figure 2.4). In 1997 and 1998, birch also had significantly higher survival in red oak stands (6-8%) than in hemlock stands (0.25 - 0.75 %). Red oak had the highest first year survival (close to 100 % each year) of all the species, and only underwent a significant reduction in survival in hemlock stands in 1999 (Figure 2.4). Neither hemlock nor white pine showed any significant differences in survival between hemlock and red oak stands, although there was a tendency for survival to increase for white pine in red oak stands and decrease for hemlock.

Patterns of seedling emergence and survival were reflected in species-specific seasonal changes in seedling abundance that differed between stand types, and to some extent, between years of study (Table 2.1, significant species x stand x year x month interaction). Birch and red maple both showed distinct regeneration dynamics in contrasting stand types that were relatively consistent across years of study (Figure 2.5a,b). For birch, high seedling emergence in hemlock stands combined with low seedling survival created a spike in seedling abundance in hemlock stands in July ($0.2 - 2.0 \text{ m}^{-2}$), which soon disappeared (abundance down to $3 - 8 \times 10^{-4} \text{ m}^{-2}$ by end of season), such that birch abundance did not differ between hemlock and red oak stands by the end of the growing season. In contrast, for red maple seedlings, there was no clear

emergence peak, but significantly lower survival in hemlock stands led to lower overall seedling abundance in hemlock stands ($3 - 30 \times 10^{-4} \text{ m}^{-2}$) than in red oak stands ($1 - 15 \times 10^{-3} \text{ m}^{-2}$) later in the growing season.

Hemlock and white pine also exhibited contrasting seasonal changes in seedling abundance between hemlock and red oak stands, but these effects differed between years of study (Figure 2.5c,d). In a similar way to birch, in 1997, high white pine and hemlock seedling emergence in hemlock stands led to greater seedling abundance in hemlock stands early in the season. For hemlock and white pine, however, survival in hemlock stands was greater than for birch, so they were able to maintain this higher seedling abundance in hemlock stands vs. red oak stands throughout the growing season (40 vs. $3 \times 10^{-4} \text{ m}^{-2}$ for hemlock, 70 vs. $3 \times 10^{-3} \text{ m}^{-2}$ for white pine). In 1999, although hemlock seedling survival was lower in hemlock stands than in 1997, hemlock seedlings in the understory underwent similar seasonal changes in abundance, still managing to maintain a higher seedling abundance in hemlock stands than in red oak stands by the end of the growing season. In poor seed years for both white pine (1998, 1999) and hemlock (1998), differences in seedling abundance between stand types were insignificant. Red oak seedlings generally had low emergence and high survival, and did not show different regeneration patterns between hemlock and red oak stands during the first growing season (data not shown).

Distinct species' regeneration dynamics in contrasting stand types led to differences in species' contributions to the understory seedling bank in the two stand types, as assessed from a DCA seedling community ordinate (Figure 2.6). Seedling bank composition underwent pronounced seasonal trends, which differed between stand types and years of study (Table 2.2, significant stand \times year \times month interaction). In years with substantial hemlock seedling emergence (1997, 1999), seedling community composition in hemlock stands differed significantly from red oak stands. Plots from hemlock stands had consistently lower scores on the first DCA axis than plots from red oak stands, as a result of hemlock (and white pine in 1997) seedling dominance in hemlock plots, compared with red maple dominance in red oak plots. In 1998, differences in species composition between seedling plots in hemlock and red oak

stands were only apparent during July, when the high emergence peak of birch seedlings in hemlock stands significantly shifted plot scores down the first two axes.

Over-winter survival and later stages of seedling regeneration

Species' responses to understory conditions in both stand types continued to shape regeneration patterns of seedlings beyond their first growing season. Canopy composition was a strong determinant of species' over-winter survival (significant species x stand interaction in Anova, $F_{4,201} = 5.68$, $p < 0.001$), and this effect was not dependent on year of study (no significant species x stand x year interaction, $F_{1,201} = 0.90$, $p > 0.05$). All species but hemlock had significantly higher over-winter survival in red oak stands than in hemlock stands (Figure 2.7). These effects were particularly noticeable for red oak and red maple, which both had less than 1 % over-winter survival in hemlock stands, and 90 % and 50 % survival, respectively, in red oak stands. Hemlock had very few seedlings surviving over the winter in any stand.

The cumulative effect of seedling survival responses during the first five years of life was assessed by examining age structure of the understory seedling bank at the end of each growing season. As a result of differences in over-winter survival, species' differed in their average seedling age in contrasting stand types (significant species x stand interaction in Anova, $F_{4,380} = 4.24$, $p < 0.01$) and again this effect was consistent across study years (no significant species x stand x year interaction, $F_{7,380} = 1.33$, $p > 0.05$). All species but hemlock had higher average seedling age in red oak stands (1.2 – 2.0 years) than in hemlock stands (1.0 – 1.3 years). As expected from hemlock's extremely low over-winter survival, I found very few hemlock seedlings that were older than one year. Older seedlings (> 5 years old, < 50 cm height) also showed differential responses to stand type. Red oak, red maple and birch all had significantly greater seedling abundance in red oak stands than in hemlock stands (Figure 2.9, $\chi^2_1 = 7.6 - 22.3$, $p < 0.01$), while hemlock had greater seedling abundance in hemlock stands than in red oak stands ($\chi^2_1 = 8.1$, $p < 0.01$). White pine had few older seedlings in either stand type.

All seedlings up to five years old were harvested at the end of the 1999 growing season. Species showed contrasting growth responses to differences in understory

conditions between hemlock and red oak stands (significant species \times stand interaction $F_{4,166} = 2.67$, $p < 0.05$), and this effect persisted when the effects of seedling age were removed (significant age \times species interaction, $F_{3,166} = 6.49$, $p < 0.001$; but no significant age \times species \times stand interaction, $F_{1,166} = 1.05$, $p > 0.05$). Both red maple and hemlock seedlings were significantly larger in general in red oak stands than in hemlock stands (2- and 5-fold increases in biomass, respectively). Other species showed a tendency for increased biomass in red oak vs. hemlock stands, but these changes were not significant (Figure 2.10).

Stand environmental characteristics

Hemlock and red oak stands differed significantly in light availability at the forest floor and at 1 m above the floor ($F_{1,4} = 10.42 - 57.48$, $p < 0.05$), with hemlock stands commonly experiencing light levels that were two to three times lower than their red oak counterparts (Table 2.3). Understory herbs and shrubs had a larger effect on light availability in red oak stands than in hemlock stands. Light at the forest floor was on average 25 % lower than at 1 m in red oak stands, while there was little difference in hemlock stands. In contrast to stand effects on light availability, many soil characteristics showed greater variability among sites than between stand types. Water availability barely differed between stand types ($F_{1,4} = 0.01$ and 1.73 , $p > 0.05$). Hemlock stands showed a trend for lower nitrogen availability (as assessed by both *in situ* buried bag mineralization rates and by resin bag ammonium and nitrate availability), but no differences were significant ($F_{1,4} = 0.01 - 0.66$, $p > 0.05$). pH emerged as one soil characteristic that did differ significantly between stand types ($F_{1,4} = 8.18$, $p < 0.05$), with soils in hemlock stands having a lower pH than those in red oak stands (by 0.4 pH units on average). Hemlock stands also had deeper organic soil horizons than did red oak stands ($F_{1,4} = 8.27$, $p < 0.05$), but litter depth itself did not differ between stand types ($F_{1,4} = 2.22$, $p > 0.05$). Hemlock and red oak stands had similar annual quantities of litter fall (close to 300 g m^{-2}), although litter composition showed clear differences between stand types ($F_{1,4} = 13.38$ for % broad-leaved litter and 82.59 for % coniferous litter, $p < 0.05$ and 0.001 , respectively). More than one-third of the litter fall in hemlock stands was

composed of coniferous litter, while broad-leaved litter dominated litter fall in red oak stands (Table 2.3).

A number of environmental variables were correlated with one another across stand types (Table 2.4). Both coniferous and broad-leaved litter fall were strongly correlated with light and pH, as expected by the consistent differences observed for these variables between stand types, and showed weaker, but still significant, correlations with water availability and litter depth. Light and pH were also positively correlated with each other, and negatively correlated with water availability. Soil nitrogen availability (as measured with resin bags and buried bags) did not correlate with most other environmental variables, although there was a positive correlation between water availability and nitrogen mineralization rates.

Relationships between seedling regeneration and environmental variables

Overall, variation in both pH and light correlated best with seedling regeneration patterns in the understory of hemlock and red oak stands (Table 2.5). Water availability correlated well with proportional seedling emergence from seed (Table 2.5), but rarely correlated with seedling patterns at later stages. For all species, there was a significant positive relationship between water availability and seedling emergence (Table 2.5a), although the strength of the effect varied between years. Proportional seedling emergence was also negatively related to light availability for all species. Light availability, however, only explained a substantial proportion (~ 20 %) of the variation in seedling emergence for the smaller seeded species. Due to the correlations between light and coniferous/broad-leaved litter fall (Table 2.4), this negative regression between light and emergence may be driven by a positive relationship between conifer litter fall and emergence.

Early seedling survival and growth were both related almost exclusively to light availability and soil pH (Table 2.5b). The broad-leaved species, birch and red maple, showed a clear increase in survival during the growing season with both increasing light availability and increasing pH (less acid), and these effects were consistent across years. White pine survival similarly showed a positive relationship with light, but not

pH, although this light effect was only observed in the study year with high white pine seedling abundance (1997). Hemlock survival was not related to pH and was only mildly related to light availability ($r^2 < 2\%$), and this effect was only significant in one of the study years (1999). Over-winter survival of all species except hemlock was also positively related to pH, with particularly strong effects for red oak and white pine (Table 2.5c). In contrast, light (rather than pH) was the only environmental factor measured that related to early seedling growth, with the conifers (white pine and hemlock) and red maple showing increased growth with increased light availability (Table 2.5d).

These effects of light and pH on early seedling performance carried through to later stages of regeneration. Ages of white pine, red oak, and red maple seedlings in the understory were all positively related to both light availability and pH (not red maple), so that microsites with higher light availability and less acid soils had higher seedling age on average (Table 2.5e). Age was also negatively related to water availability, but this effect may have been driven by the negative correlation between light/pH and water (Table 2.4). Older seedling age classes showed similar distribution patterns to those less than five years old (Table 2.5f). Red maple seedling abundance was positively related to both light and pH, while abundance of white pine was related predominantly to light and that of red oak to pH. I found a significant negative coefficient for the regression between hemlock older seedling abundance and light availability, such that plots with higher light availability were less likely to contain hemlock seedlings.

Individual species' responses to environmental conditions in the understory combined together to influence community-level responses of the understory seedling bank. Again, in this case, light and pH were the major environmental factors correlated community composition (as assessed by DCA ordination). Both factors were positively related to plot scores on the first DCA axis (Table 2.5g), which separated species that were dominant in the understory of hemlock stands (hemlock; low axis 1 score) vs. red oak stands (red maple, red oak; high axis 1 scores). Increasing light and/or pH was correlated with increased dominance of the understory seedling bank by red maple and red oak, and decreased dominance by hemlock. These effects were strongest in years

with high hemlock seedling abundance (1997, 1999). At these times, pH explained more of the variation in community composition than did light (15 – 30 % for pH, 2 – 15 % for light). Light had some effect on the plot scores on the second DCA axis, but, once again, pH effects were the predominant controlling factor (Table 2.5h). The second DCA axis separated species that were dominant early in the growing season (birch, low axis 2 score) vs. later in the season (white pine, high axis 2 score). pH was often negatively related to axis 2 scores, as those species with lower axis 2 scores (red maple, birch) became more abundant as soil pH increased (Table 2.5b,h).

DISCUSSION

General nature of canopy-seedling feedbacks

Results of the present experiment have clearly demonstrated that, in mixed conifer broad-leaved forests, feedbacks between canopy composition and seedling dynamics may act at many stages of regeneration, and thus that current landscape structure can influence future forest community dynamics. In particular, I found good evidence for a strong positive feedback operating in hemlock stands. Under a hemlock canopy, hemlock seedlings were favored over other species' seedlings. I found a persistent bank of older hemlock seedlings in the understory of hemlock stands that did not occur in red oak stands. This positive feedback in hemlock stands has been demonstrated in a previous study (Chapter 3), and may allow hemlock to dominate particular stands for many generations (Frelich *et al.* 1993). Hemlock is a quintessential late successional species, which has been shown to be able to persist in the low light conditions of its own canopy for many generations (Godman & Lancaster 1990, Kobe *et al.* 1995), and may fit into Clements' (1916) definition of a classic 'climax' species. Apart from hemlock, the only other species that showed some evidence of being favored under hemlock stands was white pine. These effects were only apparent during the first growing season and disappeared soon after.

In red oak stands, there was also evidence for strong feedbacks between canopy composition and patterns of seedling regeneration. In this case, however, the understory conditions in red oak stands favored persistence of a number of broad-leaved tree species, rather than just red oak (the canopy dominant). A true positive feedback would only arise if red oak was clearly favored at the expense of all other species under its own canopy (Wilson & Agnew 1992). In the present experiment, however, red maple and red oak, and even birch to some degree, were all favored over hemlock in red oak stands compared with hemlock stands (Figure 2.9). Thus, the presence of red oak in temperate forests may act to slow successional dynamics by preventing early establishment of hemlock in the understory of such stands. Stand-level canopy-seedling interactions have been documented in other mixed temperate forests

(Bartlett *et al.* 1991, Cornett *et al.* 1997). These feedbacks, however, are not always positive. Some studies have found that regeneration of other species may be favored over that of canopy dominants, leading to reciprocal replacement effects on the landscape level (Woods 1979, Hiura & Fujiwara 1999).

Demographic processes underlying canopy-seedling feedbacks

Seed rain, emergence from the soil seed bank, and seedling survival in the understory all made significant contributions to canopy-seedling feedbacks in both hemlock and red oak stands. Species differed in the way that each component of their life-history strategy contributed to their relative regeneration success in each stand type. A number of species showed a patchy distribution of seed rain across stands, and these patterns initiated positive feedbacks for the dominant species in each stand type (hemlock, red oak). The particularly low dispersal distances of hemlock and the moderate distances for red oak (Ribbens *et al.* 1994) likely enhanced the high degree of spatial structure in seed rain brought about the heterogeneous distribution of canopy trees. Conifer broad-leaved mosaics in other mixed temperate forests have similarly been shown to be maintained by spatial patterns of seed rain in some cases (Cornett *et al.* 1997), but not always (Bartlett *et al.* 1991). Dispersal is often thought to enhance the importance of chance events in community patterns (Hurt & Pacala 1995, Hubbell *et al.* 1999), but in the present study, I have shown that dispersal patterns, by contributing to canopy-seedling feedback effects, can play a role in deterministic community dynamics as well.

High inputs of both hemlock and birch seeds in hemlock stands were reinforced by higher proportional seedling emergence for both species in hemlock stands than in red oak stands. The higher amount of conifer litter in hemlock stands may lead to a greater proportion of mineral soil being exposed, providing an ideal substrate for emergence of small seeded species such as birch and hemlock (Collins 1990, Bartlett *et al.* 1991, Yoshida & Ohsawa 1999). The negative relationship between hemlock/birch emergence and light, which itself was positively correlated with proportion of litter fall contributed by broad-leaved species, supports this notion to some extent, but must now be examined experimentally (S. Catovsky, *unpublished data*). For hemlock, relatively high seed input and high proportional seedling emergence in hemlock stands led to

early dominance of the understory seedling bank in these stands, which persisted over the course of the growing season. Hemlock's large contribution to these early stages of the seedling community was necessary for the development of a positive feedback in hemlock stands. In the one study year with poorer hemlock seed production and seedling emergence (1998), I found that seedling bank community composition did not differ markedly between hemlock and red oak stands. In contrast, low hemlock seed input and very low proportional emergence in oak stands meant that hemlock rarely made any significant contribution to the understory seedling bank in these stands.

Most species except hemlock showed substantially lower survival (first and subsequent growing seasons, over-winter) in hemlock stands compared with red oak stands, and thus rarely made a significant contribution to the understory seedling bank in hemlock stands. Even birch, which showed remarkably high seed rain and high seedling emergence in hemlock stands (also found in Yorks *et al.* 2000), was a minor component of the seedling bank in hemlock stands as its seedlings suffered such high mortality under the low light conditions characteristic of hemlock stands. This temporary pulse of birch seedlings under hemlock stands was also found in my previous study on seedling regeneration from hemlock seed banks (Chapter 3), and represents a good example of a seed-seedling conflict (Schupp 1995), as conditions in hemlock stands favor birch seedling emergence but not survival. High seed rain into hemlock stands might allow birch to colonize canopy gaps rapidly in such stands and thus explain the association of yellow birch trees with old-growth hemlock stands (Stearns 1951, Woods 2000).

In contrast with most species' low survival responses in hemlock stands, hemlock commonly showed no difference in response between hemlock and red oak stands. Hemlock's extreme shade tolerance (Kobe *et al.* 1995) allowed it to persist under its own canopy despite very low light availability, and thus maintain its early dominance in the understory of hemlock stands (produced by high seed rain and high seedling emergence). It was unexpected, then, that hemlock exhibited very low over-winter survival, and that remarkably few hemlock seedlings were between two and five years old in either stand type. The high abundance of older hemlock seedlings in

hemlock stands suggests that hemlock seedlings are able to establish in the understory of hemlock stands, but that these events might be relatively infrequent and that establishment might only coincide with very good seed years. Seedling growth was the only measure of hemlock performance that was favored in red oak stands over hemlock stands. It is now clear, however, that survival rates under a closed canopy arise as a more important determinant of understory seedling dynamics than do growth rates (Pacala *et al.* 1996, Walters & Reich 1999), and thus growth responses will have little long-term impact on canopy-seedling feedbacks.

Canopy-seedling feedbacks in red oak stands also operated at many stages of regeneration – from survival both during the growing season and over-winter, to age structure of the understory seedling bank, and persistence of older understory seedlings. Red oak stands favored a suite of mid-successional broad-leaved species over hemlock and, to some extent, white pine. The conifers were both partially excluded from red oak stands by virtue of their low seed input and low seedling emergence in such stands. Hemlock rarely made any significant contribution to the seedling bank in these stands. Red maple was able to dominate many understory seedling plots in red oak stands by virtue of adequate seed rain, high seedling survival over many growing seasons (evidence from a more even age structure) and good seedling growth. Although red maple seed inputs and seedling emergence were similar between hemlock and red oak stands, high seedling survival led to persistence of seedlings in the understory in red oak stands. Red oak was also favored in red oak stands (especially over-winter survival), but the relatively low seed inputs during all three years of study prevented oak from developing an adequate seed bank. Birch suffered higher mortality than either red maple or red oak, but still maintained a small seedling bank in red oak stands. These early dynamics led to these species having a number of persistent older seedlings in red oak stands and very few in hemlock stands.

Mechanisms underlying canopy-seedling feedbacks

Differences in seedling regeneration dynamics in hemlock and red oak stands can be attributed in large part to canopy tree influences on understory environmental conditions and species specific seedling responses to these conditions. Light availability

and soil pH differed substantially between stand types, and both of these factors were clear determinants of seedling survival and growth in the present experiment. The relative effects of each individual factor differed between species and between different components of seedling regeneration (see Collins 1990). Light availability and pH were closely correlated to one another in my experiment, and so individual effects may be difficult to separate without any experimental manipulation (see Chapter 3 for results of experimental manipulation). Of the major broad-leaved species in mixed temperate forests, red oak produces litter with the highest carbon to nitrogen ratio (closest to hemlock) (Finzi *et al.* 1998b), and so it is perhaps not surprising that I did not see any significant differences in soil nitrogen availability between stand types. In addition, because soil processes may operate over longer time scales than light (Caldwell & Pearcy 1994), changes in soil characteristics following alteration of community composition will tend to lag changes in above-ground microclimate (Willis *et al.* 1997).

Numerous studies have recorded canopy effects on understory resource environment in temperate forests, both on an individual tree basis (Zinke 1962, Boettcher & Kalisz 1990) and at the stand level (Beatty 1984, Vesterdal & Raulund-Rasmussen 1998). Canopy trees may influence many of the major environmental variables that are important determinants of seedling performance, e.g., light (Canham *et al.* 1994, Messier *et al.* 1998), soil nutrient availability (Turner & Franz 1985, Finzi *et al.* 1998b), and soil pH (France *et al.* 1989, Finzi *et al.* 1998a). In addition, studies have examined how seedling regeneration dynamics may differ between contrasting stand types (Forcier 1975, Woods 1984, Cornett *et al.* 1997), but these patterns have been directly related to the effect of particular canopy species on their local environment only in a few cases (Collins 1990, Pacala *et al.* 1996). Making the connection between tree influences on understory conditions and seedling responses to these conditions is essential for developing a mechanistic understanding of forest community dynamics.

I established that species' responses to canopy-mediated variation in both light and soil pH underpin stand-level positive feedback dynamics. Species-specific responses to these major environmental axes explained much of the variation in seedling regeneration dynamics between hemlock and red oak stands. For most species

in the understory seedling bank (birch, red maple, red oak, white pine), many components of seedling regeneration were positively associated with light availability and/or pH, with the result that performance of these species was favored in red oak stands (higher light and pH) over hemlock stands. In contrast, regeneration of hemlock seedlings was never significantly related to soil pH and only rarely related to light availability. Hemlock seedling growth was positively related to light availability, while seedling emergence and presence of older hemlock seedlings in the understory showed a significant negative association with light, such that they were favored in hemlock stands (lower light and pH) over red oak stands.

Light availability is highly heterogeneous at many spatial and temporal scales in forests (Bazzaz & Wayne 1994), and has previously been found to be an important determinant of seedling regeneration dynamics in temperate forests (Pacala *et al.* 1996, Finzi & Canham 2000). Species show varying responses to changes in light availability, and these differences in response may drive the spatial and temporal course of succession (Pacala *et al.* 1994, Kobe *et al.* 1995, Bazzaz 1996). In the present experiment, I found that, for survival at least, species' responses to light availability could be predicted to some extent from their successional position. The most late successional species in the system (hemlock) was the only species whose survival did not respond positively in general to light availability. As light is a critical resource for all plants, the mechanistic basis for these light responses is relatively well established. In contrast, the physiological processes underlying seedling responses to changes in pH are less clear [Gough, 2000 #109]. It has long been hypothesized that soil pH plays a critical role in the development of landscape mosaics in mixed temperate forests (Daubenmire 1930), and more recently, soil pH has been shown to alter species' responses to light availability (Kobe 1996). The mechanisms driving these responses, however, have not yet been experimentally established. Soil pH is not a resource *sensu stricto* (Bazzaz 1996), but rather controls the availability of a number of critical soil nutrients, such as phosphorus and many of the major cations (Marschner 1995). Its precise role in determining the structure and dynamics of temperate forests needs to be investigated further. Other environmental factors showed less variation between hemlock and red

oak stands, but may still be important under different circumstances, e.g., nutrient availability [Ferrari, 1999 #108], water availability (Parshall 1995), and litter depth (Collins 1990).

Importance of canopy-seedling feedbacks for forest structure and dynamics

Feedbacks between stand composition and seedling regeneration are likely to play a critical role in the structure and dynamics of many forests containing a distinct landscape mosaic of stand types, in both temperate (Frelich *et al.* 1993, Cornett *et al.* 1997) and tropical regions (Connell & Lowman 1989, Hart *et al.* 1989). Canopy-seedling feedbacks emphasize the importance of species' effects on their environment in controlling vegetation structure and dynamics, as first proposed by Clements (1916). As conifer broad-leaved forests in eastern North America are composed of a mosaic of contrasting stand types (Pastor & Broschart 1990), determining the mechanisms underlying feedbacks between stand composition and seedling regeneration is critical for a full understanding of the processes controlling the structure and dynamics of these forests. While the present study focused on feedbacks between canopy trees and the understory seedling bank, these dynamics may influence later stages of regeneration as well, e.g., seedling responses to canopy disturbance [Frelich, 1999 #107].

A mechanistic understanding of the dynamics of temperate forests is also necessary if we wish to predict how natural and human-related disturbance processes will shape future forest structure. Temperate forests are currently threatened by a wide variety of environmental perturbations, from hurricane damage (Cooper-Ellis *et al.* 1999), to invasion of exotic pests (McManus *et al.* 2000), and changes in atmospheric chemistry (Bazzaz *et al.* 1996). Many novel perturbations involve changes in resource environment (Bazzaz & Catovsky 2000), which will ultimately affect seedling regeneration patterns and the composition of these forests in the future (Bazzaz 1996). Investigation of seedling responses to changes in multiple resource availability provides the framework for predicting forest composition under a range of future scenarios.

In the present study, I have demonstrated that canopy-seedling feedbacks operate in both coniferous (hemlock dominated) and broad-leaved (red oak dominated)

stands in mixed temperate forests, and I was able to determine both dispersal and resource-based mechanisms underlying such feedbacks. Seedling regeneration dynamics in the understory seedling banks of hemlock and red oak stands showed very distinct characteristics, with hemlock stands characterized by high seedling emergence and low survival, leading to high seedling turnover, while seedlings in the understory of red oak stands were more persistent and exhibited a more even aged structure. Hemlock seedlings were favored in hemlock stands (a true positive feedback), as a result of high seed inputs, high seedling emergence and relatively high seedling survival, while a suite of mid-successional species (including red oak, red maple, and birch) were favored in red oak stands, through adequate seedling emergence and high overall seedling survival. These dynamics may act to slow future successional trajectories in these forests. Extensive monitoring of resource availability and environmental conditions at the plot level revealed that variations in both light availability and soil pH were the primary causes of stand-level differences in seedling regeneration patterns. By elucidating the dynamics of canopy-seedling feedbacks and their underlying processes, we should better understand the major factors controlling the structure and dynamics of mixed conifer broad-leaved forests, and thus be better able to predict their responses to novel perturbations in the future.

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TABLE 2.1. Analysis of variance results (degrees of freedom, F ratios, p values) for first-year seedling abundance (natural logarithm transformed; m⁻²).

| Factor | d.f. | F ^a | p ^b |
|--------------------------------|------|----------------|----------------|
| Year | 2 | 65.28 | *** |
| Month | 3 | 217.52 | *** |
| Year x Month | 6 | 36.61 | *** |
| Stand | 1 | 2.87 | NS |
| Site (Stand) | 4 | 18.00 | *** |
| Plot (Site) | 158 | 4.73 | *** |
| Stand x Year | 2 | 37.28 | *** |
| Stand x Month | 3 | 83.83 | *** |
| Stand x Year x Month | 6 | 6.59 | *** |
| Species | 4 | 422.51 | *** |
| Species x Year | 8 | 235.92 | *** |
| Species x Month | 12 | 61.05 | *** |
| Species x Month x Year | 24 | 15.57 | *** |
| Species x Stand | 4 | 151.93 | *** |
| Species x Stand x Year | 8 | 49.71 | *** |
| Species x Stand x Month | 12 | 25.16 | *** |
| Species x Stand x Year x Month | 24 | 6.45 | *** |

^a Error mean square: 6.18, degrees of freedom: 10518.

^b NS p>0.05, * p<0.05, ** p<0.01, *** p<0.001.

TABLE 2.2. Multivariate analysis of variance results (degrees of freedom, F ratios, p values) for scores on the first two axes of detrended correspondence analysis (DCA) of first-year understory community composition.

| Factor | d.f. | Overall Effect ^a | | DCA Axis 1 | | DCA Axis 2 | |
|----------------------|------|-----------------------------|----------------|----------------|-----|------------|-----|
| | | F | p ^b | F ^c | p | F | p |
| Year | 2 | 328.00 | *** | 237.49 | *** | 388.98 | *** |
| Month | 3 | 46.00 | *** | 52.93 | *** | 46.33 | *** |
| Year x Month | 6 | 18.50 | *** | 9.86 | *** | 24.03 | *** |
| Stand | 1 | 3.53 | NS | 9.33 | * | 0.01 | NS |
| Site (stand) | 4 | 26.90 | *** | 11.62 | *** | 27.64 | *** |
| Plot (site) | 173 | 3.67 | *** | 4.15 | *** | 4.00 | *** |
| Stand x Year | 2 | 95.50 | *** | 127.96 | *** | 45.52 | *** |
| Stand x Month | 3 | 17.70 | *** | 22.58 | *** | 12.49 | *** |
| Stand x Year x Month | 6 | 10.50 | *** | 5.58 | *** | 15.95 | *** |

^a Based on Wilks' Lambda criterion.

^b NS p>0.05, * p<0.05, ** p<0.01, *** p<0.001.

^c Error mean square: 2520 (axis 1), 1708 (axis 2), d.f. 1297.

TABLE 2.3. Summary of environmental measurements in hemlock and red oak stands, showing means for each stand type and significance of difference.

| Factor | Position/Type | Year of measurement | Units | Hemlock ^a | Red oak ^a | p ^b |
|--------------|------------------------------------|---------------------|----------------------------------|----------------------|----------------------|----------------|
| Light | 1 m | 1997 | mol day ⁻¹ | 0.40 | 1.22 | ** |
| | | 1999 | % PFD | 1.65 | 3.98 | * |
| | 5 cm | 1997 | mol day ⁻¹ | 0.37 | 0.91 | ** |
| | | 1999 | % PFD | 1.54 | 2.98 | ** |
| Nitrogen | Mineralization | 1997 | mg Kg ⁻¹ | 65.6 | 68.6 | NS |
| | Resin NH ₄ ⁺ | 1999 | mg Kg ⁻¹ | 4.63 | 4.80 | NS |
| | Resin NO ₃ ⁻ | 1999 | mg Kg ⁻¹ | 0.13 | 0.84 | NS |
| Water | O horizon | 1997 | cm ³ cm ⁻³ | 0.12 | 0.08 | NS |
| | | 1999 | cm ³ cm ⁻³ | 0.07 | 0.05 | NS |
| | A horizon | 1997 | cm ³ cm ⁻³ | 0.31 | 0.31 | NS |
| | | 1999 | cm ³ cm ⁻³ | 0.27 | 0.26 | NS |
| pH | - | 1998 | - | 3.92 | 4.39 | * |
| Soil profile | Litter depth | 1998 | cm | 1.34 | 1.52 | NS |
| | O horizon depth | 1998 | cm | 3.54 | 2.93 | * |
| Litter fall | Conifer | 1998 | g m ⁻² | 114.0 | 15.8 | *** |
| | Broad-leaved | 1998 | g m ⁻² | 179.9 | 280.9 | *** |

^a Means of three sites per stand type, with 30 plots nested within each site.

^b Significance of stand effect (tested over site mean square) in multivariate analyses of variance: NS p>0.05, * p<0.05, ** p<0.01, *** p<0.001.

TABLE 2.4. Correlations between major environmental measurements taken in both hemlock and red oak stands (see Table 2.3 for details of measurements).

| % PFD | Resin NH ₄ | Resin NO ₃ | Mineral- ization rate | Water (1997) | Water (1999) | pH | Litter depth | Conifer litter | Broad- leaved litter | |
|-------|--------------------------|--------------------------|-----------------------------|-----------------|-----------------|-------|-----------------|-------------------|----------------------------|-----------------------------|
| 1.00 | 0.10 | -0.05 | 0.04 | -0.41 | -0.33 | 0.30 | 0.03 | -0.48 | 0.31 | % PFD |
| | 1.00 | 0.25 | -0.02 | 0.01 | 0.00 | 0.15 | -0.01 | -0.06 | 0.19 | Resin NH ₄ |
| | | 1.00 | -0.03 | -0.01 | -0.01 | -0.02 | 0.04 | 0.05 | 0.02 | Resin NO ₃ |
| | | | 1.00 | 0.21 | 0.23 | -0.19 | 0.15 | -0.08 | 0.03 | Mineral- ization rate |
| | | | | 1.00 | 0.85 | -0.35 | 0.03 | 0.33 | -0.12 | Water (1997) |
| | | | | | 1.00 | -0.46 | -0.07 | 0.38 | -0.22 | Water (1999) |
| | | | | | | 1.00 | 0.13 | -0.63 | 0.60 | pH |
| | | | | | | | 1.00 | -0.37 | 0.41 | Litter depth |
| | | | | | | | | 1.00 | -0.73 | Conifer litter |
| | | | | | | | | | 1.00 | Broad- leaved litter |

NOTE: Results of correlations presented as Pearson product-moment coefficients, with significant correlations shown in bold ($p < 0.05$, based on sequential Bonferroni corrected significance tests).

TABLE 2.5. Results of multiple regression models examining dependence of seedling regeneration variables on environmental factors. For each variable, r^2 values, regression coefficients, and their significance, are shown for individual species/year/month combinations, depending on the degree of interaction in the main model.

| a) Emergence ^a | | | | | | | |
|---------------------------|-----------|------|-------|--------------------|-----|-------|----------------|
| Factor ^b | Species | Year | r^2 | Slope ^c | n | F | p ^d |
| Light | Birch | 1998 | 18.14 | -0.366 | 180 | 39.22 | *** |
| | | 1999 | 7.24 | -0.215 | 180 | 13.82 | *** |
| | Red oak | 1998 | 2.92 | -0.124 | 141 | 4.16 | * |
| | | 1999 | 3.84 | -0.148 | 97 | 3.75 | * |
| | Red maple | 1998 | 3.70 | -0.167 | 173 | 6.54 | * |
| | | 1999 | 2.33 | -0.172 | 161 | 3.77 | * |
| | Hemlock | 1998 | 0.77 | -0.053 | 92 | 0.69 | NS |
| | | 1999 | 19.35 | -0.449 | 179 | 42.22 | *** |
| Water | Birch | 1998 | 1.63 | 0.113 | 180 | 2.93 | * |
| | | 1999 | 10.30 | 0.265 | 180 | 20.33 | *** |
| | Red oak | 1998 | 9.54 | 0.239 | 141 | 14.56 | *** |
| | | 1999 | 1.55 | 0.078 | 97 | 1.48 | NS |
| | Red maple | 1998 | 11.95 | 0.310 | 173 | 23.07 | *** |
| | | 1999 | 1.84 | 0.143 | 161 | 2.96 | * |
| | Hemlock | 1998 | 0.82 | 0.053 | 92 | 0.74 | NS |
| | | 1999 | 13.36 | 0.382 | 179 | 27.15 | *** |

TABLE 2.5 cont. (i).

| b) Survival (growing season) ^a | | | | | | | |
|---|------------|------|----------------|--------------------|-----|-------|----------------|
| Factor ^b | Species | Year | r ² | Slope ^c | n | F | p ^d |
| Light | Birch | 1997 | 6.82 | 0.342 | 167 | 12.00 | *** |
| | | 1998 | 16.03 | 0.460 | 259 | 48.88 | *** |
| | | 1999 | 2.33 | 0.154 | 161 | 3.78 | * |
| | White pine | 1997 | 3.87 | 0.105 | 254 | 10.12 | ** |
| | | 1998 | 20.54 | 0.426 | 13 | 2.64 | NS |
| | | 1999 | 0.00 | 0.000 | 4 | 0.00 | NS |
| | Red maple | 1997 | 11.74 | 0.344 | 249 | 32.72 | *** |
| | | 1998 | 4.86 | 0.196 | 324 | 16.40 | *** |
| | | 1999 | 16.20 | 0.406 | 191 | 36.34 | *** |
| | Hemlock | 1997 | 0.22 | 0.048 | 109 | 0.23 | NS |
| | | 1998 | 8.04 | 0.501 | 16 | 1.15 | NS |
| | | 1999 | 1.64 | 0.139 | 226 | 3.71 | * |
| pH | Birch | 1997 | 1.23 | 0.102 | 167 | 2.05 | NS |
| | | 1998 | 7.69 | 0.226 | 259 | 21.31 | *** |
| | | 1999 | 3.27 | 0.135 | 161 | 5.35 | * |
| | White pine | 1997 | 0.16 | 0.041 | 254 | 0.40 | NS |
| | | 1998 | 22.87 | 0.720 | 13 | 3.03 | NS |
| | | 1999 | 0.00 | 0.000 | 4 | 0.00 | NS |
| | Red maple | 1997 | 13.37 | 0.371 | 249 | 37.95 | *** |
| | | 1998 | 5.39 | 0.243 | 324 | 18.27 | *** |
| | | 1999 | 9.61 | 0.294 | 191 | 19.99 | *** |
| | Hemlock | 1997 | 1.65 | -0.143 | 109 | 1.78 | NS |
| | | 1998 | 10.82 | 0.834 | 16 | 1.60 | NS |
| | | 1999 | 0.97 | 0.089 | 226 | 2.19 | NS |

TABLE 2.5 cont. (ii).

| c) Survival (over winter) ^a | | | | | | |
|--|------------|----------------|--------------------|-----|--------|----------------|
| Factor ^b | Species | r ² | Slope ^c | n | F | p ^d |
| pH | Birch | 7.16 | 0.132 | 62 | 4.55 | * |
| | White pine | 32.40 | 0.558 | 95 | 44.13 | *** |
| | Red oak | 22.46 | 0.726 | 36 | 9.58 | ** |
| | Red maple | 4.03 | 0.229 | 135 | 5.54 | * |
| | Hemlock | 1.36 | 0.023 | 37 | 0.47 | NS |
| d) Growth ^a | | | | | | |
| Factor ^b | Species | r ² | Slope ^c | n | F | p ^d |
| Light | Birch | 2.33 | 0.061 | 7 | 0.104 | NS |
| | White pine | 46.18 | 0.267 | 11 | 7.079 | * |
| | Red oak | 7.93 | 0.077 | 29 | 2.248 | NS |
| | Red maple | 4.20 | 0.073 | 164 | 7.054 | ** |
| | Hemlock | 24.95 | 0.206 | 54 | 16.974 | *** |

TABLE 2.5 cont. (iii).

| e) Seedling age ^a | | | | | | |
|------------------------------|------------|----------------|--------------------|-----|-------|----------------|
| Factor ^b | Species | r ² | Slope ^c | n | F | p ^d |
| Light | Birch | 2.33 | 0.119 | 81 | 1.87 | NS |
| | White pine | 10.19 | 0.264 | 123 | 13.62 | *** |
| | Red oak | 36.29 | 0.821 | 71 | 38.75 | *** |
| | Red maple | 6.38 | 0.249 | 227 | 15.28 | *** |
| Water | Birch | 0.16 | 0.023 | 81 | 0.13 | NS |
| | White pine | 14.50 | -0.463 | 123 | 20.36 | *** |
| | Red oak | 23.30 | -0.571 | 71 | 20.67 | *** |
| | Red maple | 2.12 | -0.132 | 227 | 4.85 | * |
| pH | Birch | 2.30 | 0.069 | 81 | 1.84 | NS |
| | White pine | 13.26 | 0.416 | 123 | 18.35 | *** |
| | Red oak | 13.97 | 0.554 | 71 | 11.05 | ** |
| | Red maple | 0.44 | 0.069 | 227 | 1.00 | NS |

| f) Older seedling presence/absence ^a | | | | | | |
|---|------------|----------------|--------------------|-----|-------|----------------|
| Factor ^b | Species | r ² | Slope ^c | n | F | p ^d |
| Light | Birch | - | -0.010 | 180 | 0.03 | NS |
| | White pine | - | 0.216 | 180 | 14.85 | *** |
| | Red oak | - | 0.065 | 180 | 2.27 | NS |
| | Red maple | - | 0.105 | 180 | 5.95 | * |
| | Hemlock | - | -0.119 | 180 | 4.56 | * |
| pH | Birch | - | 0.194 | 180 | 7.62 | ** |
| | White pine | - | 0.083 | 180 | 0.45 | NS |
| | Red oak | - | 0.178 | 180 | 7.42 | ** |
| | Red maple | - | 0.133 | 180 | 3.92 | * |
| | Hemlock | - | -0.073 | 180 | 1.08 | NS |

TABLE 2.5 cont. (iv).

| g) DCA - Axis 1 | | | | | | | |
|---------------------|------|-------|----------------|--------------------|-----|-------|----------------|
| Factor ^b | Year | Month | r ² | Slope ^c | n | F | p ^d |
| Light | 1997 | June | 2.24 | 0.117 | 124 | 2.78 | NS |
| | | July | 1.65 | 0.069 | 161 | 2.65 | NS |
| | | Aug | 2.11 | 0.090 | 151 | 4.20 | * * |
| | | Sept | 2.40 | 0.100 | 132 | 4.17 | * * |
| | 1998 | June | 0.19 | -0.032 | 128 | 0.24 | NS |
| | | July | 13.59 | 0.242 | 165 | 25.48 | *** |
| | | Aug | 0.87 | -0.088 | 136 | 1.16 | NS |
| | | Sept | 11.15 | -0.287 | 100 | 12.18 | *** |
| | 1999 | June | 2.20 | 0.188 | 127 | 3.79 | * |
| | | July | 15.27 | 0.456 | 142 | 25.06 | *** |
| | | Aug | 8.98 | 0.451 | 78 | 7.39 | ** |
| | | Sept | 4.37 | 0.315 | 54 | 3.33 | * |
| pH | 1997 | June | 2.17 | 0.109 | 124 | 2.68 | NS |
| | | July | 17.83 | 0.289 | 161 | 34.28 | *** |
| | | Aug | 19.40 | 0.353 | 151 | 35.61 | *** |
| | | Sept | 18.45 | 0.357 | 132 | 29.20 | *** |
| | 1998 | June | 14.64 | -0.248 | 128 | 21.43 | *** |
| | | July | 1.14 | 0.068 | 165 | 1.86 | NS |
| | | Aug | 3.35 | -0.168 | 136 | 4.61 | * |
| | | Sept | 12.14 | -0.286 | 100 | 13.40 | *** |
| | 1999 | June | 4.33 | 0.213 | 127 | 5.61 | * |
| | | July | 30.04 | 0.497 | 142 | 59.70 | *** |
| | | Aug | 27.19 | 0.632 | 78 | 28.02 | *** |
| | | Sept | 22.19 | 0.538 | 54 | 14.56 | *** |

TABLE 2.5 cont. (v).

| h) DCA - Axis 2 | | | | | | | |
|---------------------|------|-------|----------------|--------------------|-----|-------|----------------|
| Factor ^b | Year | Month | r ² | Slope ^c | n | F | p ^d |
| Light | 1997 | June | 0.21 | 0.048 | 124 | 0.25 | NS |
| | | July | 11.47 | 0.284 | 161 | 20.48 | *** |
| | | Aug | 0.55 | 0.057 | 151 | 0.81 | NS |
| | | Sept | 0.30 | 0.040 | 132 | 0.39 | NS |
| | 1998 | June | 0.50 | -0.059 | 128 | 0.62 | NS |
| | | July | 15.37 | 0.293 | 165 | 29.44 | *** |
| | | Aug | 0.00 | 0.005 | 136 | 0.00 | NS |
| | | Sept | 4.39 | -0.151 | 100 | 4.45 | * |
| | 1999 | June | 2.11 | -0.112 | 127 | 2.67 | NS |
| | | July | 4.65 | -0.181 | 142 | 6.79 | * |
| | | Aug | 3.80 | -0.127 | 78 | 3.29 | * |
| | | Sept | 1.47 | -0.073 | 54 | 0.76 | NS |
| pH | 1997 | June | 2.14 | -0.144 | 124 | 2.65 | NS |
| | | July | 4.10 | -0.216 | 161 | 6.86 | ** |
| | | Aug | 20.67 | -0.453 | 151 | 38.54 | *** |
| | | Sept | 28.92 | -0.505 | 132 | 52.50 | *** |
| | 1998 | June | 9.52 | -0.228 | 128 | 13.16 | *** |
| | | July | 1.08 | 0.076 | 165 | 1.77 | NS |
| | | Aug | 3.41 | -0.147 | 136 | 4.69 | * |
| | | Sept | 10.94 | -0.227 | 100 | 11.91 | *** |
| | 1999 | June | 18.26 | -0.266 | 127 | 27.71 | *** |
| | | July | 11.71 | -0.224 | 142 | 18.44 | *** |
| | | Aug | 13.62 | -0.192 | 78 | 11.83 | *** |
| | | Sept | 13.15 | -0.165 | 54 | 7.74 | ** |

TABLE 2.5 cont. (vi) Footnotes.

^a Y variables were transformed to meet assumptions of linear regression models: natural logarithm for emergence, growth, and age, and logit transformation for survival. Older seedling presence/absence was investigated with a purely logistic regression model, and thus r^2 values are not shown in this case.

^b Only factors that produced significant terms in the multiple regression are shown.

^c Regression slopes are shown as standardized partial regression coefficients, which are scaled to the standard deviations of the x and y variables, and thus range from -1 to +1. Significant slopes ($p < 0.05$) are shown in bold.

^d ^{NS} $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Figure 2.1. Annual seed rain inputs (mean \pm 1 SEM, $n = 90$) in hemlock and red oak stands, shown for the two seed rain measurement years separately (a,b). Note logarithmic scale of y-axis. Means that were significantly different between stand types are marked with asterisks (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, based on sequential Bonferroni corrected comparisons).

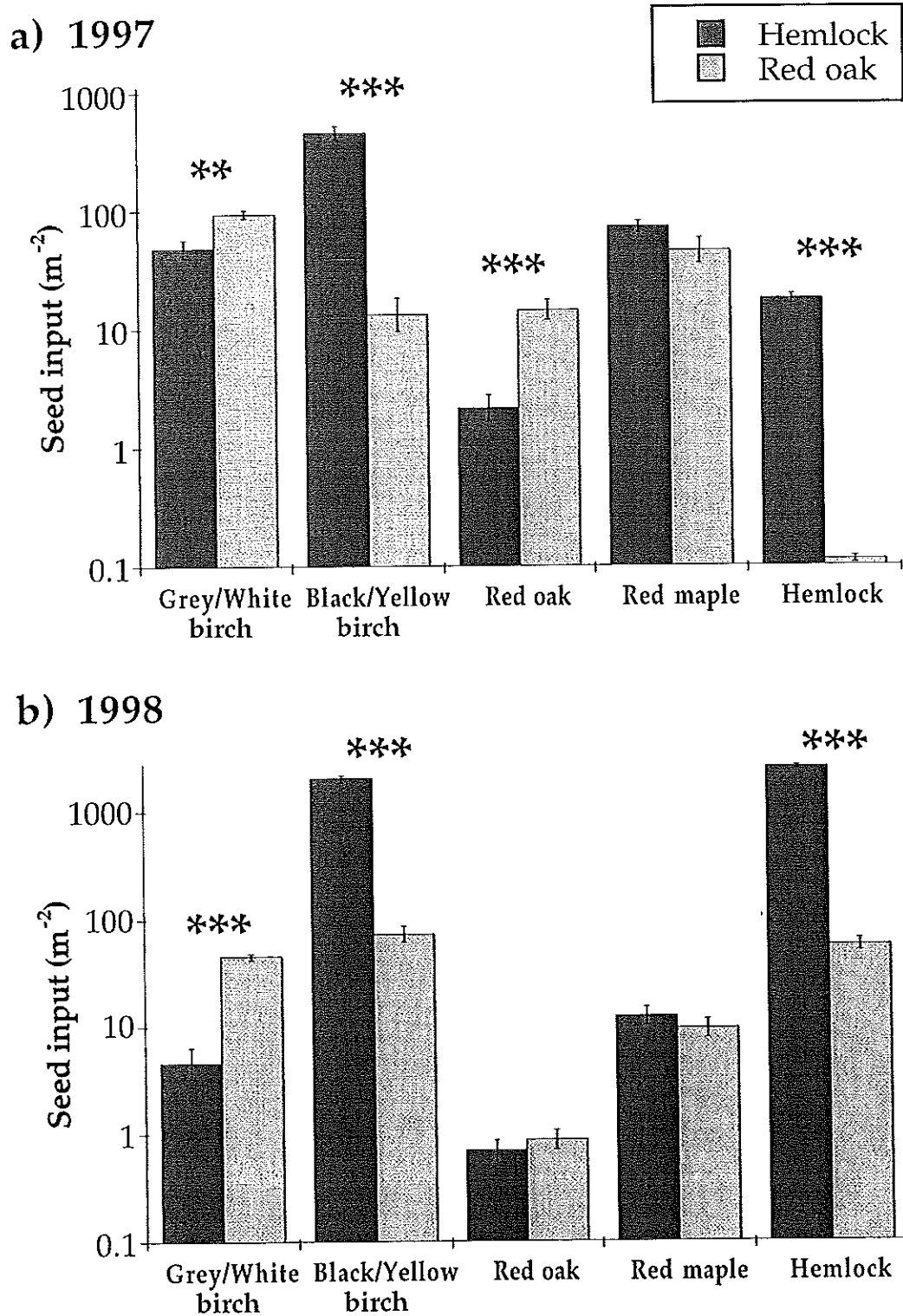


Figure 2.2. Proportional seedling emergence (mean \pm 1 SEM, $n = 37 - 90$) in hemlock and red oak stands, shown separately for each year for which the previous year's seed rain data were available (a,b). Note logarithmic scale of y-axis. Means that were significantly different between stand types are marked with asterisks (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, based on sequential Bonferroni corrected comparisons).

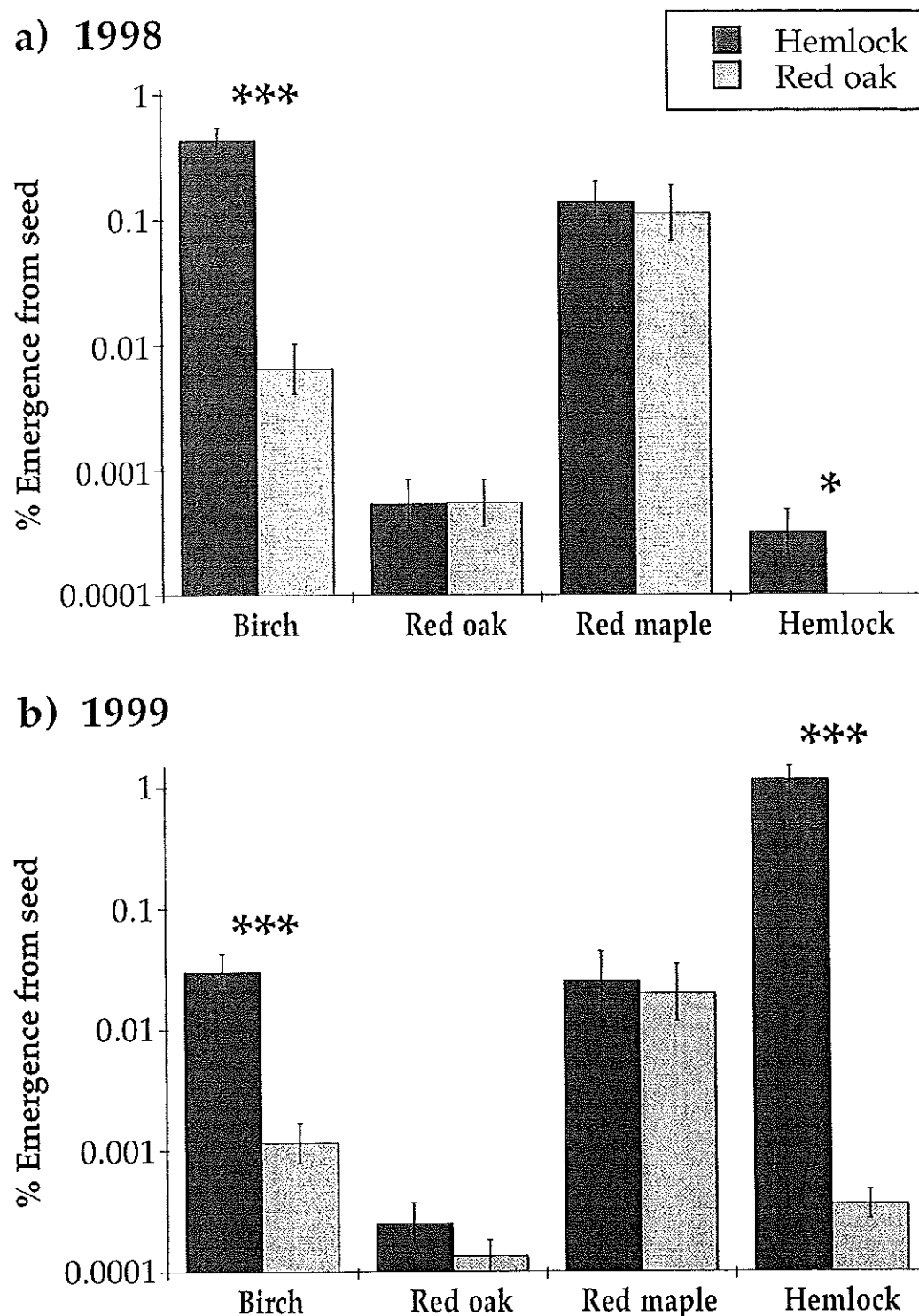


Figure 2.3. Total seedling emergence (mean \pm 1 SEM, $n = 90$) from the soil seed bank in hemlock and red oak stands, shown for each year of study separately (a - c). Note logarithmic scale of y-axis. Means that were significantly different between stand types are marked with asterisks (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, based on sequential Bonferroni corrected comparisons).

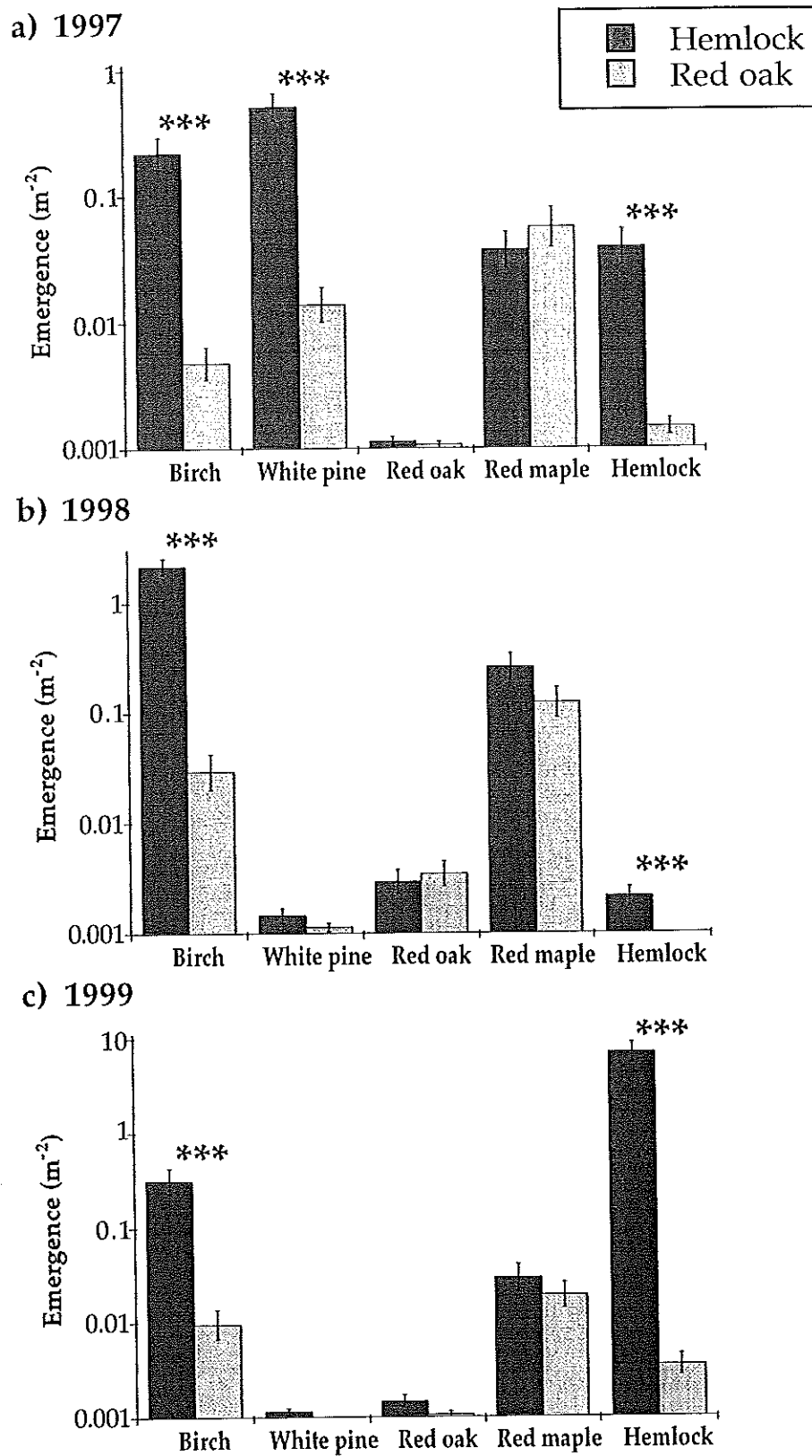


Figure 2.4. Survival of first-year seedlings during the growing season (mean \pm 1 SEM, $n = 1 - 66$) in hemlock and red oak stands, shown for each year of study separately (a - c). Missing values (no seedling emergence) are marked with a dot (•), while means that were significantly different between stand types are marked with asterisks (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, based on sequential Bonferroni corrected comparisons).

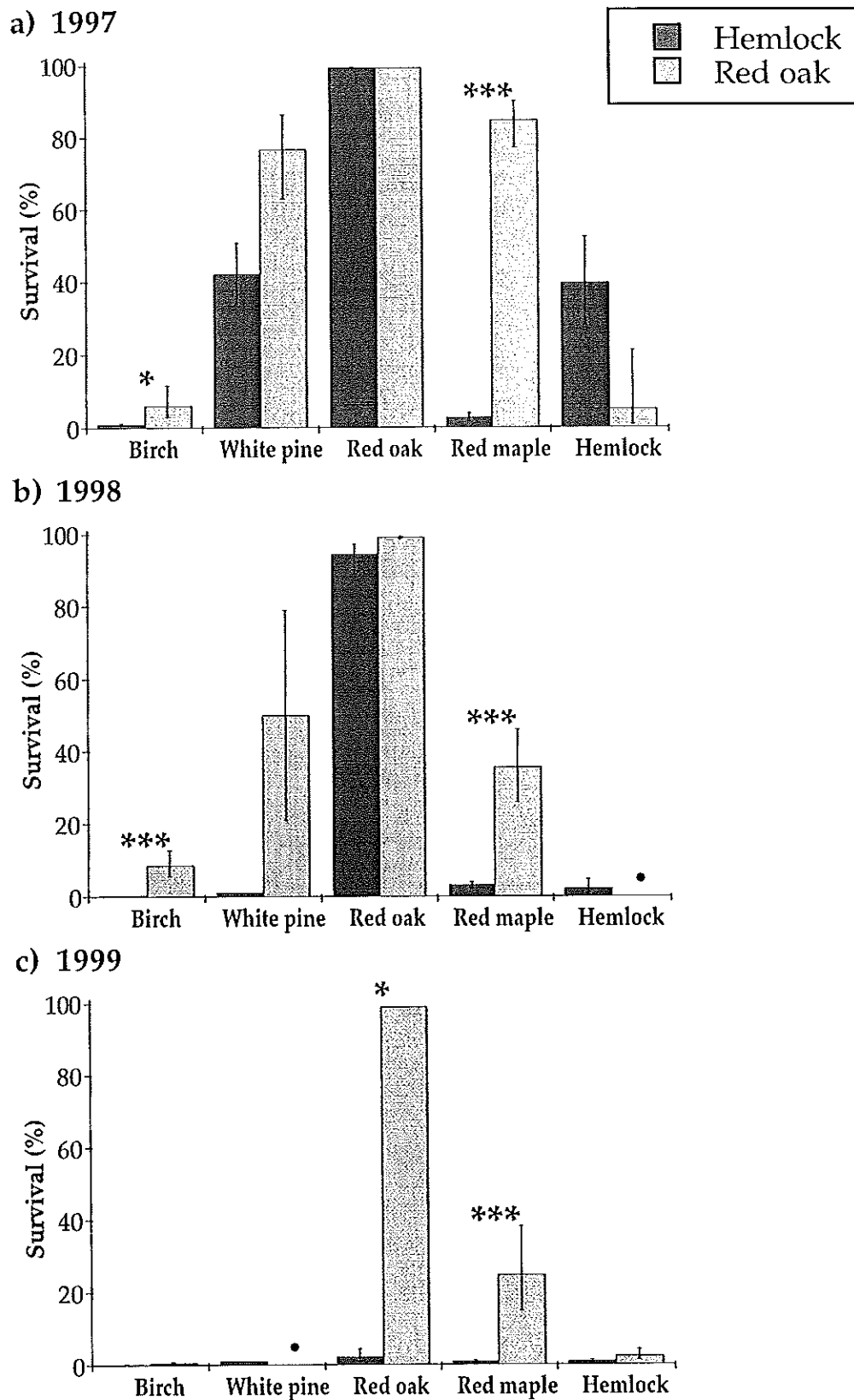
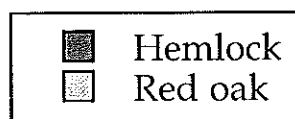
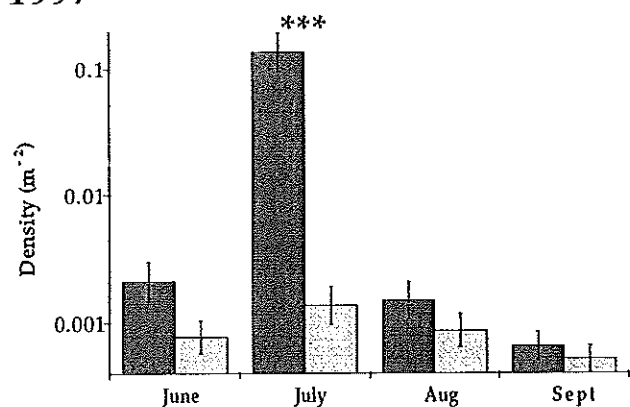


Figure 2.5. Changes in first-year seedling abundance during the growing season (mean \pm 1 SEM, $n = 90$) in hemlock and red oak stands, shown for each study species and year separately. Note logarithmic scale of y-axis. Means that were significantly different between stand types are marked with asterisks (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, based on sequential Bonferroni corrected comparisons).

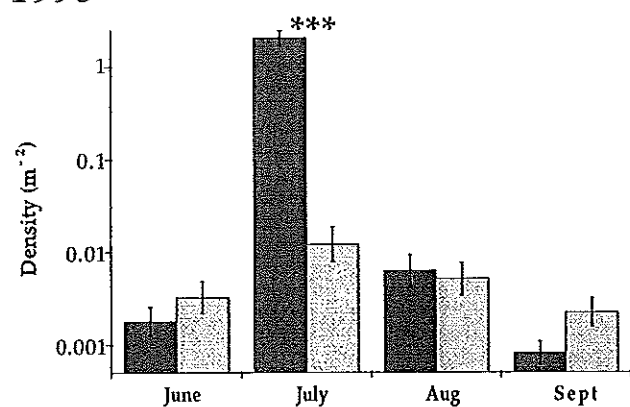
a) Birch



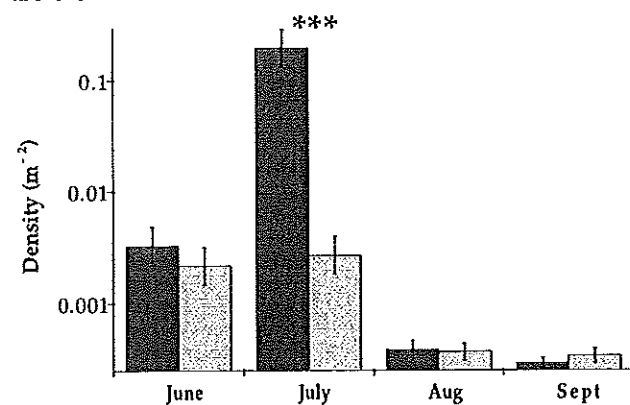
1997



1998

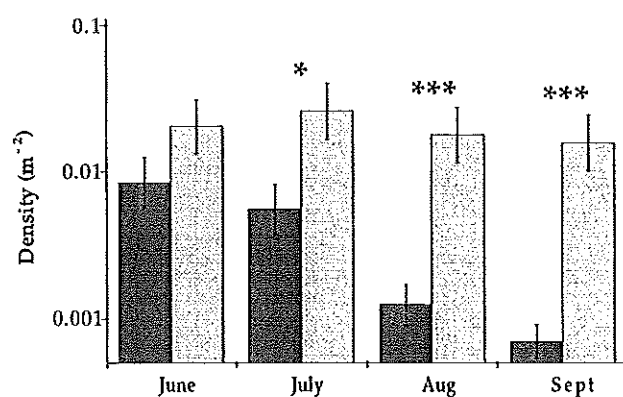


1999

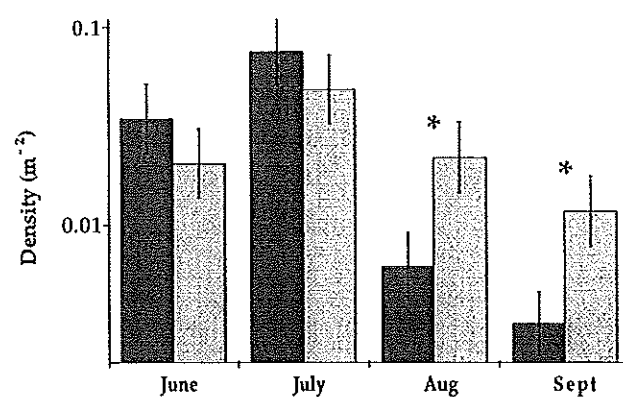


b) Red maple

1997



1998



1999

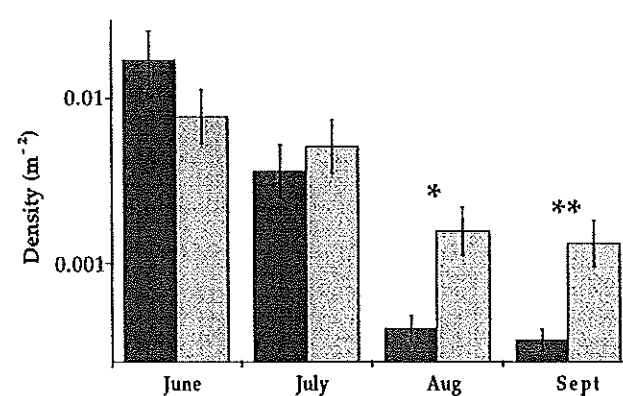
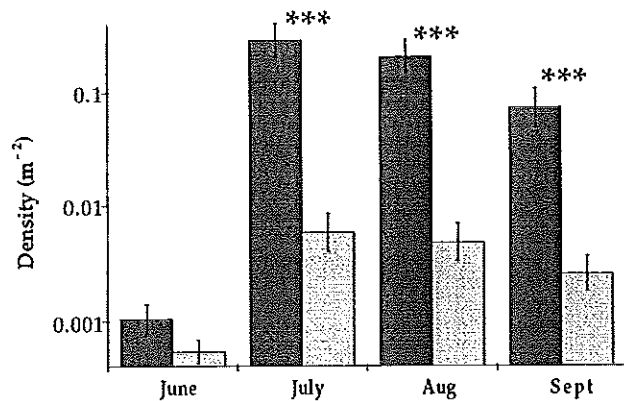


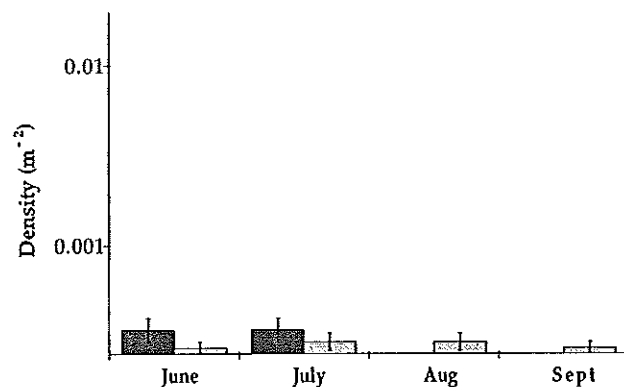
Figure 2.5. cont.

c) White pine

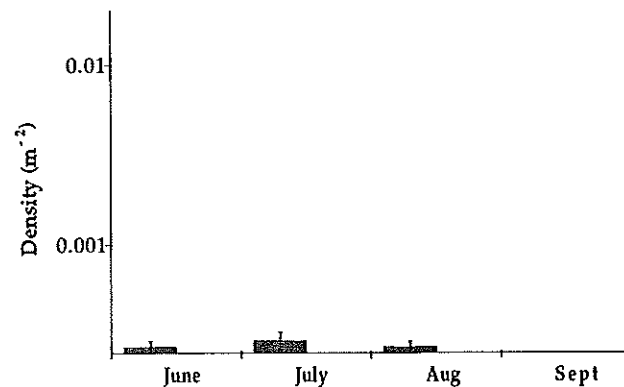
1997



1998

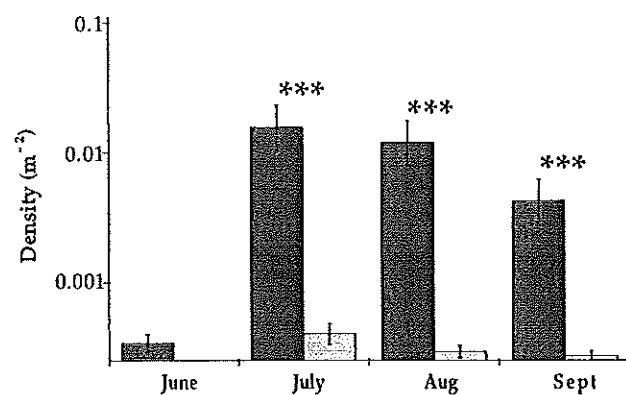


1999

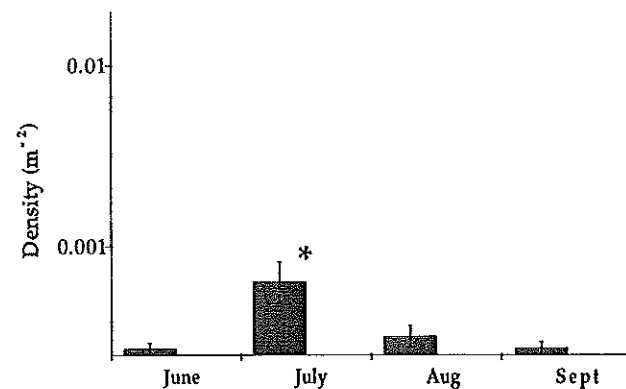


d) Hemlock

1997



1998



1999

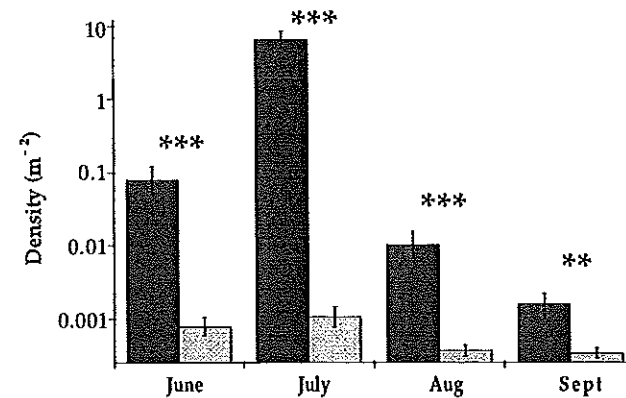
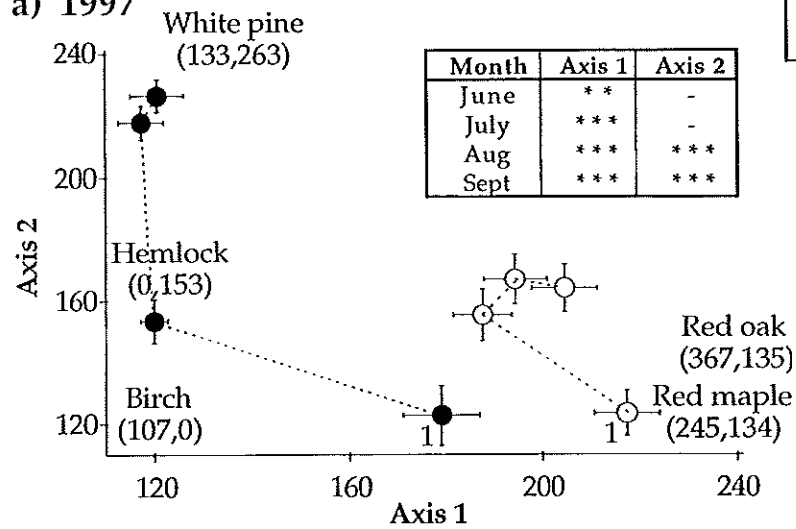
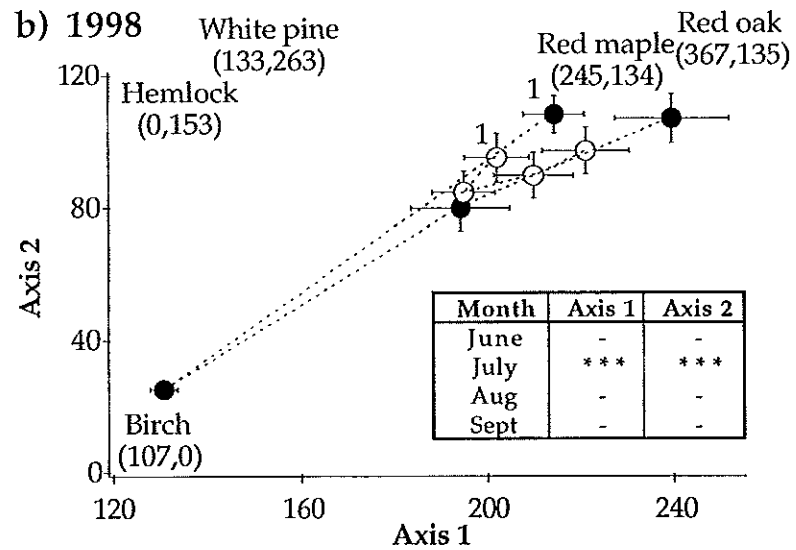


Figure 2.6. Seasonal changes in seedling community composition in hemlock and red oak stands over three growing seasons (a - c), represented by mean monthly plot scores (± 1 SEM) on first two axes of detrended correspondence analysis (DCA), with axis 1 explaining 41 % of variation and axis 2 explaining 31 % of variation. Plot scores for each month ($n = 26 - 90$) are connected in chronological order, beginning with June (marked with a '1'). Relative positions of species' scores are shown, with species' names and their actual coordinates (x,y). Significance of planned comparisons between monthly plot scores in hemlock and red oak stands are shown for each axis separately in the inset table (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, based on sequential Bonferroni corrected comparisons).

a) 1997



b) 1998



c) 1999

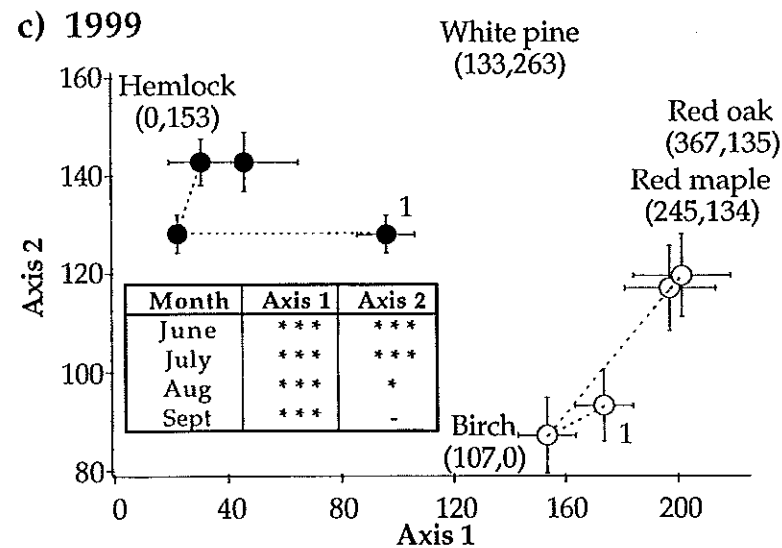


Figure 2.7. Over-winter survival of seedlings after their growing season (mean \pm 1 SEM, n = 1 - 91) in hemlock and red oak stands, shown pooled across both winters of study. Means that were significantly different between stand types are marked with asterisks (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, based on sequential Bonferroni corrected comparisons).

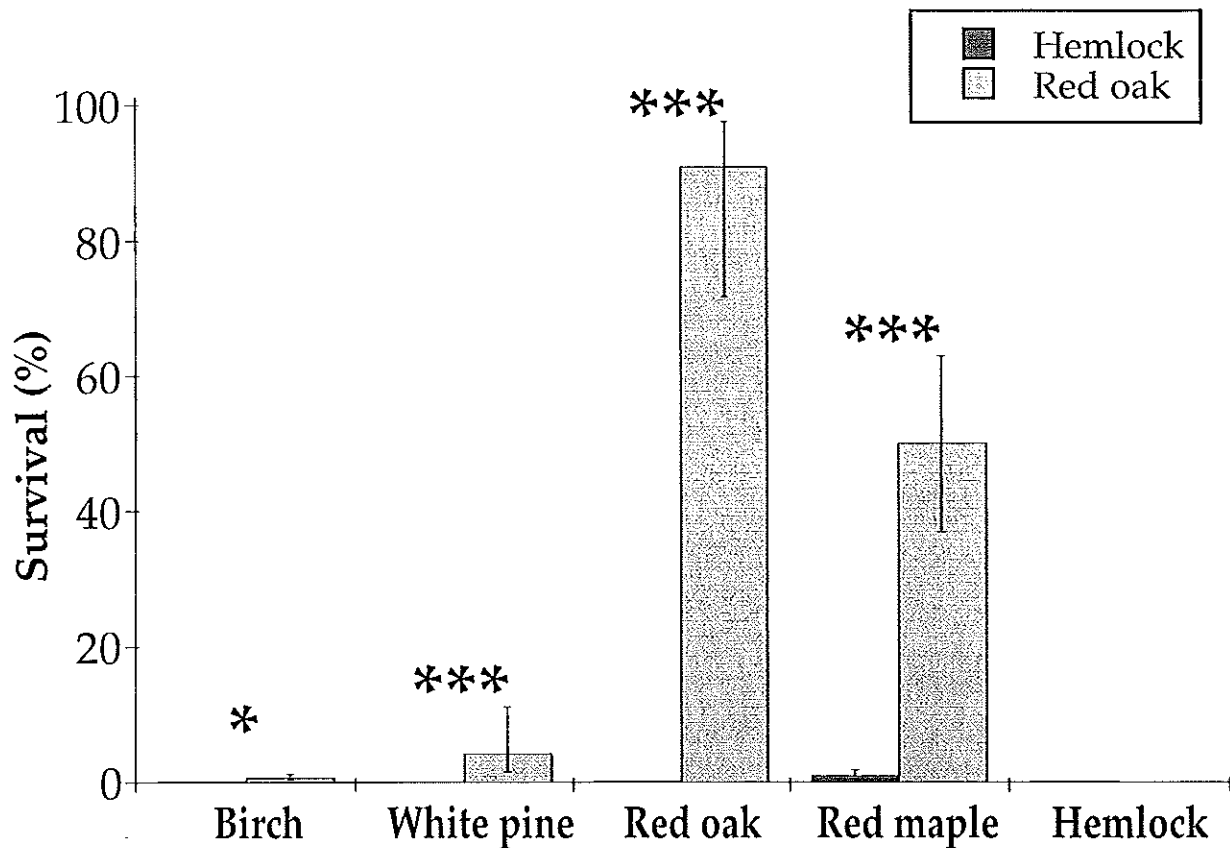


Figure 2.8. Average age of seedlings (mean \pm 1 SEM, $n = 5 - 165$) at the end of each growing season in hemlock and red oak stands, shown pooled across all study years. Means that were significantly different between stand types are marked with asterisks (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, based on sequential Bonferroni corrected comparisons).

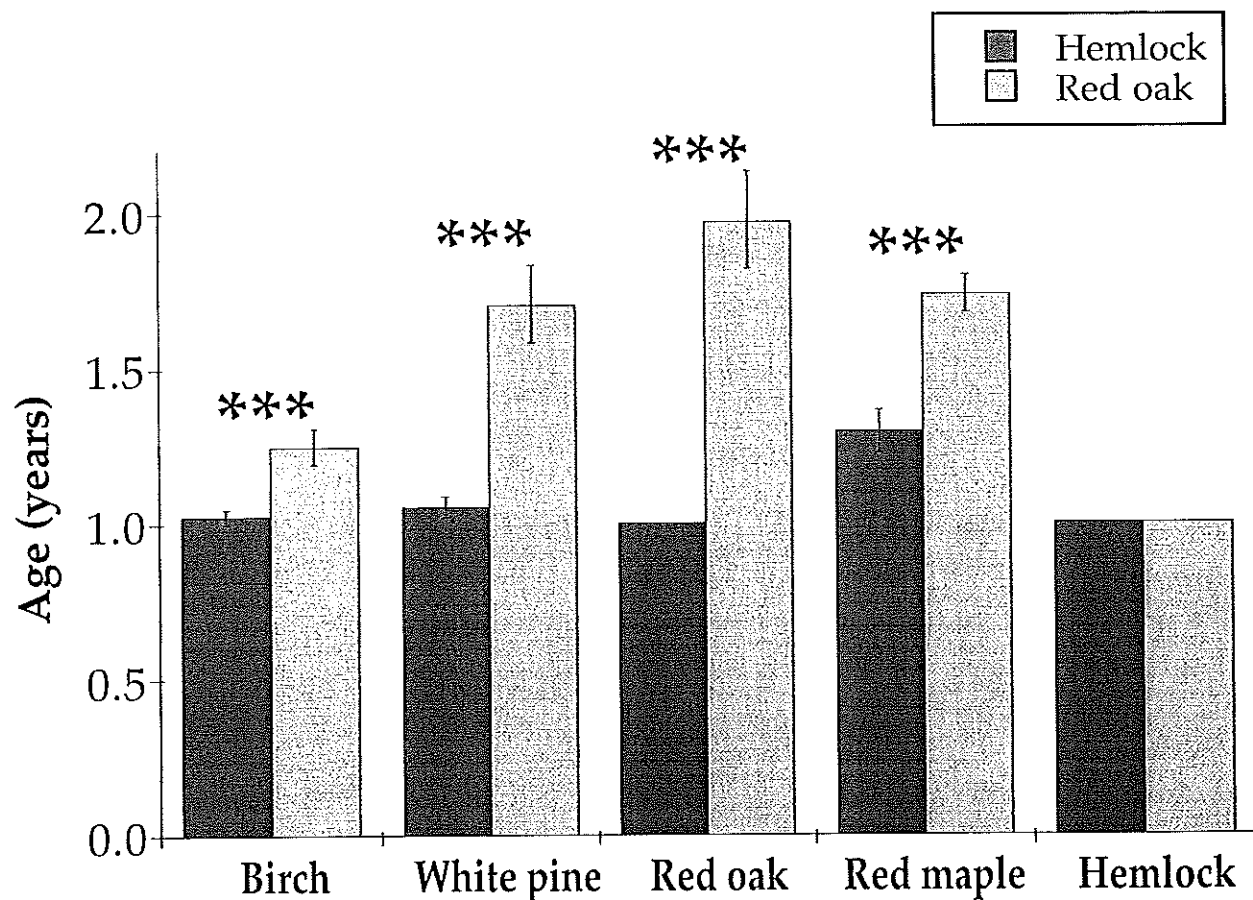


Figure 2.9. Proportion of plots (mean \pm 1 SEM, n = 3 sites) within hemlock and red oak stands containing seedlings greater than 5 years old and less than 50 cm in height. Means that were significantly different between stand types are marked with asterisks (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, based on Bonferroni corrected comparisons).

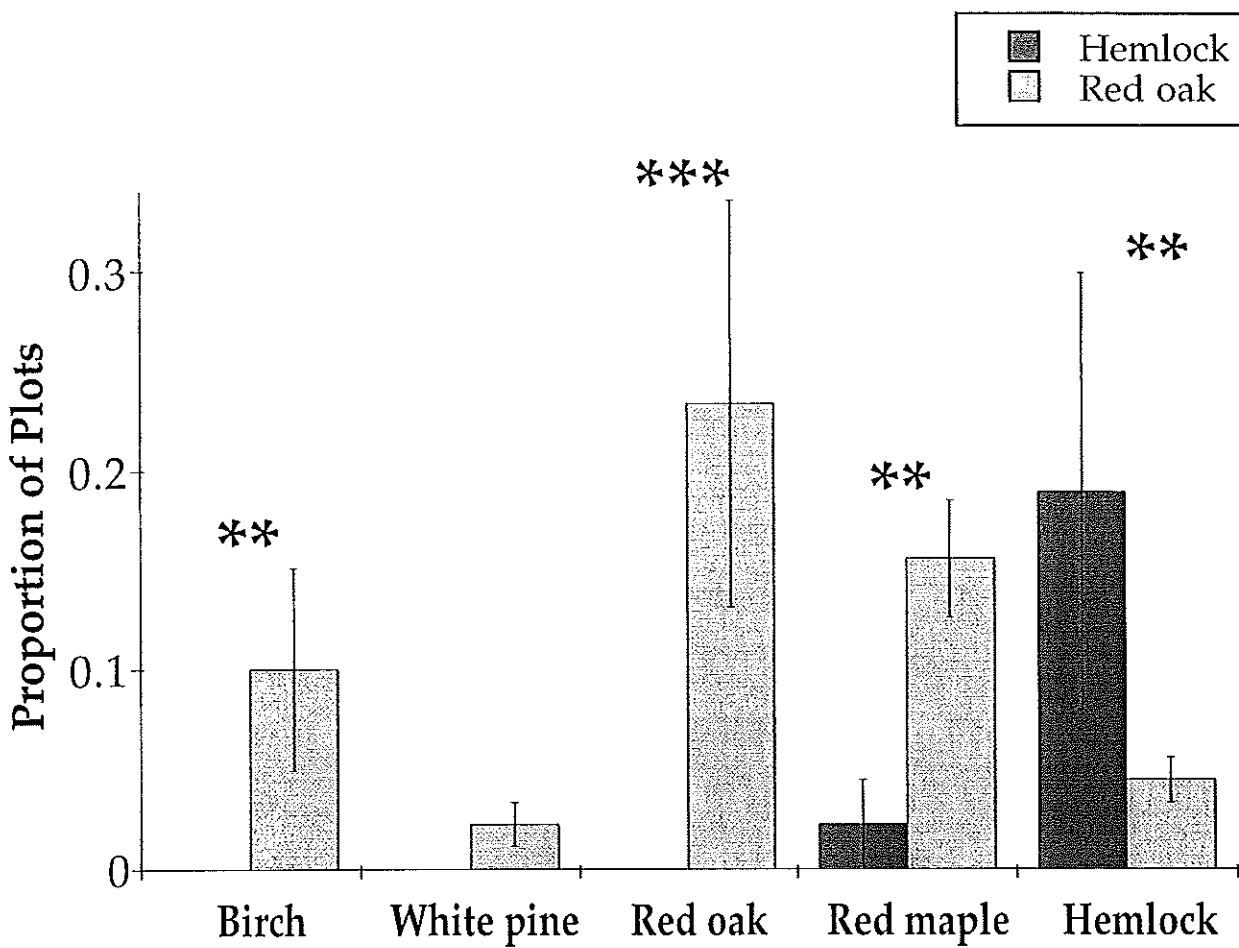
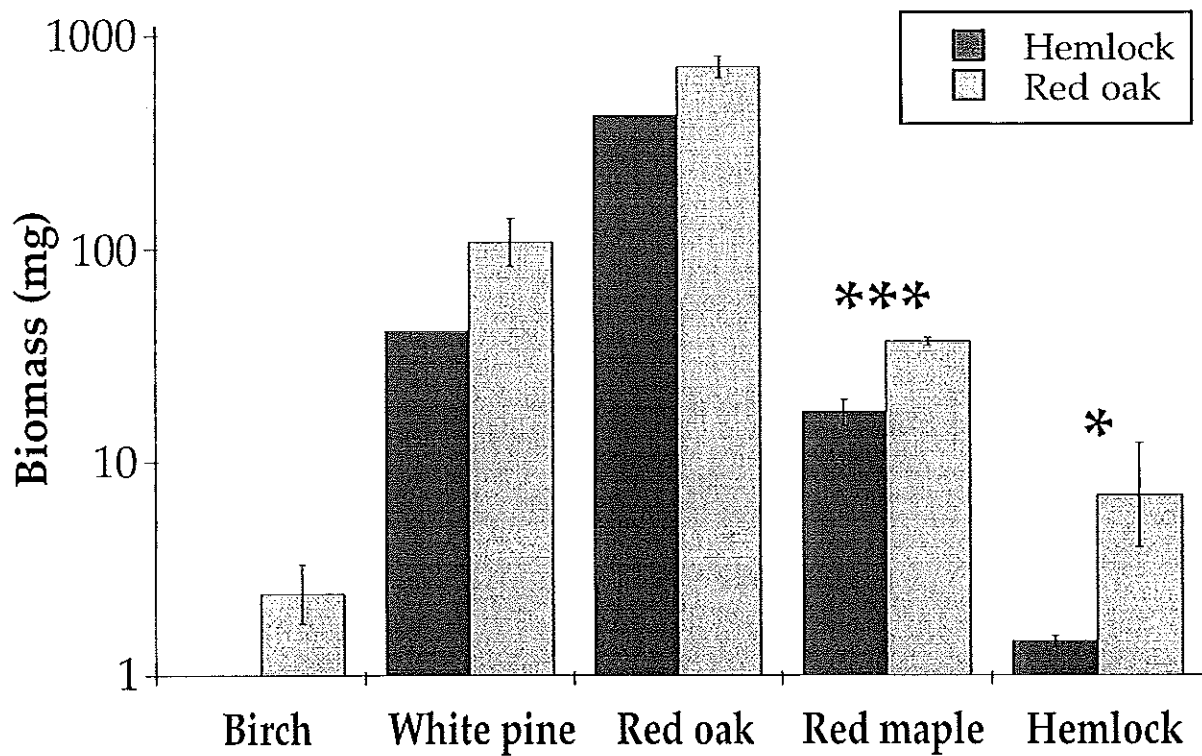


Figure 2.10. Seedling biomass (mean \pm 1 SEM, $n = 1 - 150$) in hemlock and red oak stands at the end of the study, shown pooled across all seedling ages (1 - 5 years). Note logarithmic scale of y-axis. Means that were significantly different between stand types are marked with asterisks (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, based on sequential Bonferroni corrected comparisons).



CHAPTER 3

THE ROLE OF RESOURCE INTERACTIONS AND SEEDLING REGENERATION IN
MAINTAINING A POSITIVE FEEDBACK IN HEMLOCK STANDS

Abstract. When a species influences conditions at a site to promote recruitment of conspecifics, the community may remain dominated by this species until the next major disturbance. I examine the occurrence of possible mechanisms for such a positive feedback in one community where it may be important: forests dominated by eastern hemlock (*Tsuga canadensis*). Intact soil divots were collected from a hemlock stand in central Massachusetts, USA, and placed in shade-houses at either 1.5 % or 60 % full sun. Soil was amended with nitrogen ($5 \text{ g m}^{-2} \text{ yr}^{-1}$), lime ($1 \text{ Kg m}^{-2} \text{ yr}^{-1}$ to increase soil pH), or left untreated. Emergence, survival and growth of seedlings arising from the soil seed bank were subsequently monitored. Light availability had a very large influence on seedling regeneration dynamics. Birch (*Betula* spp.) seedlings were most sensitive of all species to light availability, with low light reducing emergence by 43 %, and substantially decreasing seedling growth (by 99 %) and survival (by 94 %). In contrast, light treatments had smaller effects on performance of other species (hemlock and white pine, *Pinus strobus*). Birch survival was also increased by nitrogen addition, but only in low light. Liming had only marginal effects on seedling performance. Differential seedling responses to resource availability led to dominance of final seedling communities by hemlock in low light, unamended soils (i.e., under conditions naturally found in hemlock stands), but by birch in high light, as well as in low light, nitrogen amended soils. Positive feedbacks in hemlock stands are mediated both by availability of light and nitrogen, and by species' life-history strategies.

INTRODUCTION

Ever since Frederic Clements (1916) proposed his theory of plant succession, species' effects on their environment have been recognized as an important component of plant community dynamics. Whether species-mediated changes favor individuals of the same or different species often determines the subsequent structure and dynamics of the community (Horn 1975, Connell & Slatyer 1977, Bazzaz 1983). If the presence of a species at a site changes environmental conditions to promote recruitment of conspecifics, this species may come to dominate and persist in a community until the next major disturbance event. This situation was originally known as a 'climax' by Clements (1916), but more recently has been termed a 'positive feedback switch' (Wilson & Agnew 1992). Despite the potential importance of these feedbacks in controlling plant community structure, mechanisms underlying such patterns have rarely been established experimentally (van Breemen & Finzi 1998, Petraitis & Latham 1999). In this paper, I examine mechanisms responsible for a positive feedback in temperate forests.

Northern hardwood forests in North America are often composed of distinct stands dominated by either eastern hemlock (*Tsuga canadensis* (L.) Carr.) or sugar maple (*Acer saccharum* Marsh.) (Pastor & Broschart 1990). Many of these stands have persisted for thousands of years with little change in composition (Davis *et al.* 1994, 1998), perhaps as a result of a positive feedback between current stand composition and future seedling regeneration (Frelich *et al.* 1993). Hemlock-dominated stands are similarly present in New England forests, although the surrounding matrix is composed of a number of broad-leaved, deciduous tree species (including red oak, *Quercus rubra* L., and red maple, *Acer rubrum* L.), rather than predominantly sugar maple.

Stands of hemlock and broad-leaved species present seedlings with quite different conditions for regeneration. Differences in understory conditions between these contrasting stand types have long been acknowledged (Moore *et al.* 1924, Oosting & Hess 1956), and recently have been quantified—under hemlock, light availability is lower (Canham *et al.* 1994), and soils are more acidic, with lower nutrient availability

than under broad-leaved tree species (Finzi *et al.* 1998a,b). Such variation may influence the distribution and abundance of herb species (Beatty 1984, Turner & Franz 1986), as well as tree regeneration dynamics (Woods 1984, Collins 1990, Cornett *et al.* 1997).

The ultimate factors leading to patch development and persistence in northern hardwood forests remain unclear. It has been proposed that the low light and nitrogen conditions under hemlock trees favor regeneration of hemlock over other species, while the deep litter layer and low soil moisture content under sugar maple trees favors sugar maple (Frelich *et al.* 1993, Davis *et al.* 1994). However, SORTIE, a spatially explicit forest dynamics model, predicts that it is light availability patterns that predominantly drive development of stands dominated by either hemlock or sugar maple/beech (*Fagus grandifolia* Ehrh.) (Pacala *et al.* 1996). Furthermore, it has long been thought that the low soil pH in hemlock stands inhibits development of understory vegetation and seedling regeneration (e.g., Daubenmire 1930). All of these hypotheses must now be directly tested.

In the present study, I consider how interactions between resource availability and seedling regeneration dynamics may contribute to positive feedbacks in hemlock stands. I hypothesize that low light levels, low nitrogen availability, and low soil pH in such stands limit seedling regeneration, but that, of the various species, the performance of hemlock seedlings will be least affected, due to their high tolerance of understory conditions (Godman & Lancaster 1990, Kobe *et al.* 1995). I test these hypotheses by examining patterns of emergence, survival and growth of seedlings that arise naturally from the seed bank in hemlock stands when soil samples are exposed to different experimental conditions (varying light, nitrogen, and pH).

MATERIALS AND METHODS

Soil collection

In December 1996, soil divots were collected from a hemlock-dominated stand at Harvard Forest (Petersham, MA; 42° 32' N, 72° 11' W, elevation 340 m). The study area was comprised principally of eastern hemlock (*Tsuga canadensis*; over 75% basal area), with scattered individuals of white pine (*Pinus strobus* L.), red oak (*Quercus rubra*), red maple (*Acer rubrum*), black birch (*Betula lenta* L.), yellow birch (*Betula alleghaniensis* Britt.), paper birch (*Betula papyrifera* Marsh.) and American beech (*Fagus grandifolia*), in approximately decreasing order of importance (Foster & Zebryk 1993). The surrounding broad-leaved matrix is dominated by red oak and red maple, with occasional birch trees.

Within the stand, four sampling points were established along each of three parallel 100 m transects, each separated by 50 m. At each sampling point, six intact soil divots were collected. Each divot measured 35 x 30 cm and included both O and A horizons (10 - 15 cm deep). Divots were placed over coarse silica sand in plastic containers (20 cm deep), and then transported to the experimental garden at Harvard University (Cambridge, Massachusetts). The sand provided suitable drainage but no additional nutrients. Divots were left in the garden over winter and subjected to experimental treatments in early spring.

In the forest, seed rain at each sampling point was measured throughout the following year (1997) using conical muslin litter traps (opening 0.2 m²) suspended 50 cm above the forest floor with a PVC frame (modified from Hughes *et al.* 1987). Seed traps were emptied once during the summer of 1997 (for red maple seeds), and then monthly from September to December. For most species (hemlock, maples), I was able to distinguish filled vs. empty seeds, and I only recorded filled seeds. For the birch species, I counted all seeds and then sub-sampled to look at the percentage of seeds filled (~ 80 % for most samples).

Experimental treatments and analysis

Each set of six intact soil divots collected from each sampling point in the field was exposed to a factorial combination of two light and three soil treatments. Thus, each experimental combination was applied to four replicate soil divots within each transect, and this pattern was then replicated across three transects.

To control light availability, the soil divots were placed in shade-houses (each 2 x 2 x 2 m), set up in a split-block design. One half of each shade-house was exposed to low light (1.5 % full sun and a red:far red ratio of 0.28), mimicking conditions within a typical hemlock stand (Kozlowski *et al.* 1991, Canham *et al.* 1994), and the other half was exposed to high light (60 % full sun and a red:far red ratio of 1.1), simulating conditions in a multiple tree-fall forest gap (Bazzaz & Wayne 1994). Light quantity was manipulated using different grades of neutral shade-cloth, while light quality was simultaneously altered with colored filter plastic placed beneath the shade-cloth (Lee *et al.* 1997). I placed vertical slits in sections of the shade-cloth not receiving direct sunlight to ensure adequate ventilation within the shade-houses and prevent temperatures from climbing much above ambient air temperature. I constructed one shade-house for each sampling transect (three in total), and placed all soil divots from one transect in the same shade-house, dividing divots equally between light treatments.

The plastic covering over the shade-houses did not permit rain water to reach soil divots, and so all divots were watered thoroughly every 2 - 3 days. I measured moisture content once during the growing season (in August) and found no significant differences between shade-houses or between experimental treatments. At this time, average soil moisture across the soil divots was 0.556 g g^{-1} ($\pm 0.008 \text{ g g}^{-1}$, standard error), which is well within the range of soil moisture values observed in hemlock stands in the field (Chapter 2).

Each soil divot was exposed to one of three soil manipulations: unamended (control), increased nitrogen availability, and increased soil pH. Nitrogen was added as a solution of ammonium nitrate (NH_4NO_3) over 10 applications through the growing season, equivalent to $5 \text{ g m}^{-2} \text{ yr}^{-1}$. This rate was chosen to match background net nitrogen mineralization rates in conifer stands in this region (Aber *et al.* 1989), and thus

approximately to double nitrogen availability. Soil pH was increased by surface application of coarse powdered lime (96% calcium carbonate, CaCO_3) at the beginning of the experiment. Such pH-manipulated soil divots received the equivalent of 1 Kg lime m^{-2} , based on the lime requirement of the soil (Carter 1993), which had been determined in an earlier analysis (University of Massachusetts Soil and Plant Tissue Testing Lab, Amherst, MA).

In addition to direct manipulation of light and soil resources for each soil divot, I examined the effects of experimental treatments on the actual conditions produced under each resource combination. Light availability in each half of the shade-houses was assessed at hourly intervals through the course of one day in mid-July using a Li-Cor LI-190SA quantum sensor attached to LI-1000 data-logger (Lincoln, NB). Effects of soil treatments were determined by taking 2 cm diameter soil cores from each divot at the end of the experiment. The soil was then sifted and homogenized through a 3.5 gauge sieve (mesh size 5.6 mm). 2 g of air-dried soil from each sample was mixed with 20 ml of distilled water, and its pH determined (Orion 250A pH meter, Boston, MAA). 10 g of sifted soil was mixed with 100 ml of 2 N potassium chloride (KCl) solution, and incubated at 25 °C for 48 hours. The mixture was then filtered and frozen. Extracts were analyzed for NO_3^- and NH_4^+ ion concentrations on a Technicon TRAACS 800 analyzer (Braun and Luebbe, Buffalo Grove, IL). NH_4^+ was measured using the Berthelot Reaction chemistry (Method No. 780-86T) and NO_3^- was measured using hydrazine sulphate reduction (Method No. 782-86C). Detection limit for both these methods was 0.2 mg L^{-1} . Water content of each soil sample was determined by weighing 2 - 3 g of soil before and after drying in an oven at 105 °C for 48 hours, so that nutrient availability could be expressed per g dry soil.

Seedling measurements

At approximately two-weekly intervals from 5 May until 25 September 1997, I monitored seedling emergence from the soil seed bank and subsequent survival. On emergence, plants were tagged and identified to species when possible. Many *Betula* individuals died before they had developed true leaves, particularly under low light conditions, and thus could not be distinguished from one another. Therefore, I present

Betula emergence and survival only on a genus level. The inability to identify beyond genus prevented observation of individual *Betula* species' responses to experimental treatment combinations, because any species-specific responses could have been swamped by those of the other species within the genus. In high light treatments, however, where survival and growth were higher, all species but *Betula alleghaniensis* and *Betula lenta* could be identified and distinguished. To record individual seedling growth through the season, surviving plants were harvested after the last census. Individual root systems were obtained by washing away the soil and separating individual root systems by hand. Plant material was dried at 70 °C for seven days and then weighed.

Data analysis

Only species that emerged in more than ten soil divots were included in the analyses (i.e., birch species, hemlock and white pine). Other species were excluded because of low statistical replication. Seedling emergence, growth and survival were examined using multi-factor analyses of variance, with light, soil, and species effects included as main fixed factors in the models. A random block term was included to incorporate variation due to both transect and shade-house, while a plot-level term, grouping soil units taken from the same sampling point, was included as a random factor nested within block. The mean squares of most terms were tested over the residual error mean square. Light effects were tested over the light x block interaction, following the split-block design (Sokal & Rohlf 1995), while block effects were tested over plot mean square from nesting. Community composition was examined with multivariate analysis of variance on plot scores from the first two axes of detrended correspondence analysis. In addition, I used Fisher's Exact Test to examine community-wide seedling survival in low light.

Treatment effects on experimental conditions were examined in a similar way, but with some modifications. Light effects were examined with diurnal photon flux density (PFD) measurements taken on the level of a shade-house. Thus, individual divots were not included in the analysis, while time was added as another fixed factor. Soil analyses were examined with the basic design described above, but with no species

term. In addition, as nitrogen analyses were performed for both NH_4^+ and NO_3^- , both components were incorporated into a mixed model multivariate analysis of variance.

When necessary, the data were transformed to ensure that the assumptions of Anova were met (normality of residuals, homoscedascity). For each significant main effect with more than two levels and for each significant interaction, I examined the significance of individual treatment mean comparisons using Scheffé *post hoc* tests (Day & Quinn 1989).

RESULTS

Treatment effects

Photon flux density (PFD) in the two light treatments differed significantly from one another ($F_{1,2} = 8640$, $p < 0.0001$; Figure 3.1a), with the high light treatment averaging 54.4 % of PFD in the open, and low light averaging 1.2 %. Light environment did vary across blocks ($F_{2,36} = 4.22$, $p < 0.05$), but there was no significant light \times block interaction ($F_{2,36} = 1.29$, $p > 0.05$).

Both light and soil treatments significantly affected overall soil nitrogen availability (Manova light \times soil interaction, $\lambda_{\text{Wilks}} = 0.416$, $p < 0.0001$; Figure 3.1b), as well as the individual nitrogen forms (light \times soil, $F_{2,48} = 25.28$ for NH_4^+ and 4.00 for NO_3^- , $p < 0.0001$ and 0.05, respectively). Soil cores were taken one week after the final fertilization event, by which time much of the added nitrogen had been taken up in the high light treatments by the dense seedling growth that had developed through the course of the experiment (see later). As a result, nitrogen availability was consistently low in all high light treatments (25 mg N Kg^{-1} soil in high light vs. 400 mg N Kg^{-1} in low light). In low light, soil treatment effects were clear (Figure 3.1b). Nitrogen additions caused significant increases in both the availability of NH_4^+ and NO_3^- (*post hoc*s, $p < 0.01$ and 0.05, respectively), enlarging the NH_4^+ pool by 58 % and the NO_3^- pool by 170 %. In low light, liming altered the composition of nitrogen species present in the soil by increasing the proportion of NO_3^- from 8 % to 67 %. This change in composition meant that NO_3^- availability did not differ between nitrogen and lime treatments (*post hoc*s, $p > 0.05$), but that NH_4^+ was significantly lower in the lime treatment than in either of the other two treatments ($p < 0.0001$). Liming probably increased the activity/abundance of nitrifying bacteria, which are commonly inhibited in acid soils (Paul & Clark 1996).

Both soil and light treatments influenced final soil pH. Liming significantly increased soil pH by 0.8 pH units on average ($F_{2,48} = 14.6$, $p < 0.0001$; Figure 3.1c). In addition, soils from high light treatments had a significantly lower pH values than

those from low light ($F_{1,2} = 98.7$, $p < 0.01$). This light effect may again have been caused by the presence of high seedling density in high light soil divots.

Seedling demography

Most of the seedlings emerging from the soil seed bank were birch (94 %, Table 3.1), with smaller amounts of hemlock (4 %) and white pine (1 %). There were scattered individuals of other herb, shrub and tree species, each represented by less than five individuals across all soil divots.

There was substantial heterogeneity in seedling emergence between transects/shade-houses (significant block effect, Table 3.2). In addition, seedling emergence differed significantly between species (Tables 3.1 and 3.2), with higher birch emergence than that of all other species (*post hocs*, $p < 0.0001$), and higher hemlock emergence than all species except birch ($p < 0.05$). Soil treatments had no effects on seedling emergence, while light treatments differentially influenced emergence depending on species (significant light x species interaction, Table 3.2). Only emergence of birch was affected by light, decreasing by 43 % from high to low light (Figure 3.2).

Similarly, light effects on seedling survival were species-dependent (significant light x species interaction), while soil conditions did not affect survival (Table 3.2). Birch seedling survival increased most with increasing light availability (an almost 20-fold increase), compared with a 2.5-fold increase for hemlock and no significant increase for white pine (Figure 3.3; *post hocs*, $p < 0.001$ for birch and hemlock, $p > 0.05$ for pine). Relationships between survival of different species changed with light treatment. In low light, birch had significantly lower survival than either hemlock or white pine (*post hocs*, $p < 0.01$), while in high light, hemlock had lower survival than birch ($p < 0.05$). Lack of an overall light effect on survival was primarily the result of a strong light x block effect ($MS = 13.68$), which was likely to have been caused by substantial heterogeneity in white pine emergence.

Examination of survival data at the level of individual soil divots provided evidence for interactions between light and soil treatments. In low light, nitrogen significantly increased the proportion of soil divots that had at least one surviving birch

seedling compared with control soils, while liming caused a marginally significant decrease in the number of divots with surviving hemlock (Table 3.3).

Seedling growth

Average seedling growth of different species responded in different ways to changing light availability (Table 3.4; significant light x species interaction), but not altered soil conditions. All tree seedlings increased growth with higher light levels, but the magnitude of change was species-specific (Figure 3.4). Birch seedlings showed the greatest increases in growth with increasing light (300 times larger), while hemlock and white pine showed more modest, but significant increases (5 and 15 times larger, respectively). There were no differences in growth between any species at low light (*post hoc*s, $p > 0.05$). In contrast, at high light, birch seedlings grew the most, followed by white pine, and then hemlock (*post hoc*s, $p < 0.0001$). Birch seedlings also showed the greatest variation in individual seedling size parameters, especially at high light (Table 3.5). High seedling density and asynchrony in emergence date created a strong size hierarchy within high light stands by the end of the experiment.

Experimental treatments influenced individual seedling biomass, along with patterns of emergence and survival, and thus affected each species' contributions to final seedling community biomass. Light and soil both differentially influenced species' total biomass responses, although light effects were not contingent on soil conditions and vice versa (Table 3.4; significant light x species and soil x species interactions, but non-significant three-way interaction). High emergence, survival and growth of birch under high light conditions meant that birch dominated high light seedling communities, often by two orders of magnitude (Figure 3.5a). In low light, in contrast, all species made similar contributions to seedling community biomass (no significant species differences; *post hoc*s, $p > 0.05$). The large variability in white pine emergence from the soil seed bank meant that its contribution to final seedling composition did not differ between light treatments ($p > 0.05$). Soil treatments did not have dramatic effects on species' total biomass within each soil divot, except that hemlock seedlings had significantly lower biomass in treated soils (nitrogen, lime) than in control soils (Figure 3.5b; *post hoc*s, $p < 0.05$).

In high light treatments, I was able to identify birch seedlings to species. I performed a second analysis on growth of individual birch species and their contribution to final seedling community biomass for all high light treatments. There were no significant interactions between soil and species effects for either analysis ($F_{4,63} = 0.64$ and $F_{4,88} = 0.29$, $p > 0.05$ for both individual and total biomass), although there was a trend (non-significant) for increasing paper birch total seedling biomass and decreasing black/yellow birch total biomass in soils with nitrogen added. Individual black/yellow birch seedlings were significantly smaller than either paper birch or gray birch (1.32 g vs. 2.40 g and 3.65 g; *post hocs*, $p < 0.001$), while black/yellow birch and paper birch made significantly greater contributions to final seedling community biomass than did gray birch in general (11.71 and 15.11 vs. 1.80; *post hocs*, $p < 0.0001$).

Seedling community composition

Final seedling composition of each soil divot was investigated using plot scores from detrended correspondence analysis on both species abundance and species biomass data. In both cases, there was a significant light x soil interaction on final seedling community composition (Figure 3.6; $\lambda_{\text{Wilks}} = 0.651$, $p < 0.01$ for abundance; $\lambda_{\text{Wilks}} = 0.617$, $p < 0.01$ for biomass), and these interactions were evident on both DCA axes in each case (Table 3.6). In both analyses, low light, unamended soils had significantly different final seedling composition (hemlock dominated) from any of the high light treatments, as well as the low light, nitrogen amended soils, which, like the high light treatments, was birch dominated. This difference was evident on both axes for abundance data, but only on axis 1 for biomass data.

Seed rain

Patterns of seed rain across the experimental transects differed between species (significant species x transect interaction, $F_{8,36} = 5.04$, $p < 0.01$; Figure 3.7). Larger seeded species (red maple and sugar maple) had heterogeneous seed rain distributions across the transects (*post hocs*, $p < 0.05$), while smaller seeded species (birch, hemlock) had more even distributions ($p > 0.05$).

DISCUSSION

My results demonstrate that low resource conditions in hemlock stands do set up a positive feedback at early stages of regeneration by favoring hemlock over other species. Hemlock dominated the seedling community under conditions naturally found in hemlock stands (low light, low nitrogen), while resource supplementation by increasing either light or nitrogen availability led to dominance by birch species (Figure 3.6). Light had a particularly large effect on early regeneration dynamics following seedling emergence from the soil seed bank, and played an important part in the positive feedback effect. The two most common genera to emerge from the soil seed bank (birch, hemlock) exhibited contrasting responses to light treatments. Birch seedlings were particularly responsive to increased light availability (with survival and growth increasing more than emergence; Figs 3 - 5), leading to a large increase in birch contribution to total seedling community biomass in high vs. low light (99.5 % vs. 20.1 %). In contrast, hemlock seedlings exhibited much smaller changes in survival and growth in response to light availability, and so their relative contribution to final seedling community composition declined in high light treatments.

Species-specific responses to light availability have been observed in many previous studies (e.g., Pacala *et al.* 1996, Kobe 1999). The behavior of birch and hemlock seedlings in different light environments might have been predicted to some extent from their respective successional positions (Bazzaz 1979, 1996). The birch species that emerged from the soil seed bank ranged from quite early successional (gray birch, paper birch) to mid-successional (yellow birch and black birch) (see Burns & Honkala 1990). In contrast, hemlock is a quintessential late successional species, characterized by slow growth rates (Hibbs 1982, Kelty 1986) and extreme shade tolerance (Godman & Lancaster 1990, Kobe *et al.* 1995). In keeping with this dichotomy of successional position, previous studies have found that birch species respond favorably to increases in resource availability, especially high light and nitrogen conditions (Crabtree & Bazzaz 1993, Wayne & Bazzaz 1993, Carlton & Bazzaz 1998b), while hemlock seedlings show more moderate responses to such increases (Pacala *et al.* 1994).

Although light availability was the predominant factor underlying the positive feedback acting at early stages of seedling regeneration, there were some significant interactions between light and soil treatments, especially nitrogen addition. Beatty (1984) similarly showed that soil properties in hemlock stands can exert a strong influence on the understory community. In my study, the composition of low light, nitrogen amended seedling communities converged during the growing season towards that of high light communities (i.e., birch dominance). In low light, high seedling mortality created communities of very low density (~ 10 seedlings m^{-2}), so that small differences in seedling dynamics between treatments led to some large changes in eventual seedling community composition. My original analysis of variance did not detect these small differences between relatively high mortality values. However, by using a community-wide analysis, I found that, in low light, nitrogen addition significantly increased the proportion of seedling communities with at least one surviving birch (from 8 % to 50 %), while tending to decrease the proportion with at least one surviving hemlock (from 63 % to 17 %, but not significant). These changes following nitrogen addition led to a shift from hemlock to birch dominance of the seedling community. Mechanisms for these changes, however, still require further investigation. Nitrogen addition could improve seedling growth and survival in low light by allowing seedlings to increase their photosynthetic capacity, perhaps due to a shift in allocation from root growth to leaf area production (e.g., Peace & Grubb 1982), and/or due to increased foliar chlorophyll concentrations leading to increased quantum efficiency (Evans 1989).

Contrary to my expectations, liming had only marginal effects on seedling performance or overall seedling community composition. Soil pH has been shown substantially to influence light growth functions of two of the primary species that emerged from the soil seed bank in the present experiment (hemlock and white pine) (Kobe 1996). In addition, many investigators have suggested that the highly acidic soils within hemlock stands inhibit performance of understory vegetation and seedling regeneration (e.g., Daubenmire 1930). In the present experiment, the only detectable pH effect was the marginally reduced survival of hemlock seedlings on limed soils in low

light, which shifted the final composition of limed seedling communities away from hemlock dominance. This change, however, was not statistically robust because of the small number of soil divots with any surviving seedlings following liming.

Seedling regeneration dynamics in hemlock stands are not only a function of species-specific responses to resource availability, but are also dependent on patterns of seed rain into stands. I found, in particular, that very large numbers of birch seeds reached almost all of my experimental plots, and that these translated into high birch seedling emergence in most divots (average 320 m⁻²). Seed rain and seedling emergence of birch exceeded that of hemlock (the most abundant canopy species and the second highest seed producing species) by 8-fold and 50-fold, respectively. Although mature birch trees were not particularly abundant in the hemlock stand sampled, the high numbers of seeds produced and their extensive dispersal distances (Houle 1994, Ribbens *et al.* 1994, Clark *et al.* 1998) ensured that many birch seeds fell in each plot within the stand. In contrast, a number of the larger-seeded tree species (e.g., red maple, red oak, and sugar maple) made a much smaller contribution to seed rain and the seedling community.

As seed production in temperate forests could be quite variable from year to year (e.g., Houle 1994, Koenig & Knops 1998), it is important to examine to what extent the results of my experiment are contingent on seed rain conditions in the particular year of the study. The considerable similarity between the quantity and identity of seedlings emerging from the seed bank in the experiment and seed rain into the plots in the subsequent year suggest that dominance of seed availability by birch, followed by hemlock, with little contribution from larger-seeded hardwood species is likely to be a relatively robust pattern. Other measurements in other hemlock stands at Harvard Forest confirm that birch and hemlock consistently dominate seed rain (Chapter 2), while seeds of other common canopy species (maple, oak, pine) have more heterogeneous distributions in space and time (Carlton & Bazzaz 1998a). Seedling regeneration dynamics in these hemlock stands also match closely with those found in the present experiment: high birch and hemlock emergence, followed by low birch survival, and therefore dominance of the seedling bank by hemlock. In addition, dense

regeneration of black birch following hemlock tree mortality in stands infested with an exotic insect pathogen (*Adelges tsugae* Annand, the hemlock woolly adelgid) (Orwig & Foster 1998) further confirms that the considerable potential for recruitment of birch within hemlock stands is likely to be a common feature in the New England landscape.

Results from the present experiment illustrate the importance of both resource availability and species' life-history strategies in determining patterns of regeneration in hemlock stands. As I only examined seedling dynamics for one season, it is important to be cautious about extrapolating my results much beyond these early stages of seedling regeneration. Nevertheless, within the first year of seedling growth, I observed occurrence of a clear positive feedback in hemlock stands through preferential regeneration of hemlock over other species. Birch species had abundant seed dispersal into hemlock stands (while many species did not), but they could not establish under the low resource conditions (light and nitrogen) characteristic of hemlock stands, primarily due to low survival. Birch seedling survival was reduced by 95 % from high to low light, causing the disappearance of the brief pulse of high birch seedling density observed early in the season, even in low light. Birch seedling growth was also severely affected by low light availability, but these effects did not appear to drive changes in seedling community composition (see also Kobe *et al.* 1995). Hemlock regeneration in such stands was favored both through abundant seed rain from canopy dominants and through seedling tolerance of low resource availability. The present experiment highlights the different kinds of recruitment patterns that may be responsible for the development of positive feedbacks in plant communities.

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Table 3.1. Identity and average density of species that emerged from the soil seed bank.

| Species | Common name | Growth habit | Density (m ⁻²) |
|------------------------------------|---------------|------------------|----------------------------|
| <i>Betula</i> spp. ^a | Birch | Canopy tree | 320 |
| <i>Tsuga canadensis</i> (L.) Carr. | Hemlock | Canopy tree | 12 |
| <i>Pinus strobus</i> L. | White pine | Canopy tree | 4 |
| <i>Rubus flagellaris</i> Willd. | Blackberry | Understory herb | 1.5 |
| <i>Gaultheria procumbens</i> L. | Wintergreen | Understory herb | 1 |
| <i>Vaccinium</i> spp. ^b | Blueberry | Understory shrub | 1 |
| <i>Acer rubrum</i> L. | Red maple | Canopy tree | 0.3 |
| <i>Prunus serotina</i> Ehrh. | Black cherry | Canopy tree | 0.3 |
| <i>Populus tremuloides</i> Michx. | Quaking aspen | Canopy tree | 0.1 |
| <i>Prunus pensylvanica</i> L.f. | Pin cherry | Canopy tree | 0.1 |

^a Includes *Betula lenta* L. (black birch), *Betula alleghaniensis* Britt. (yellow birch), *Betula papyrifera* Marsh. (paper birch), and *Betula populifolia* Marsh. (gray birch).

^b Includes *Vaccinium corymbosum* Ait. (highbush blueberry) and *Vaccinium angustifolium* L. (lowbush blueberry).

Table 3.2. Anova F ratios for seedling demographic parameters: emergence (per soil divot), and % seedling survival through the growing season. Significance shown as follows: ^{NS} $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

| Factor ^a | Degrees of freedom | Emergence ^b | %Survival ^c |
|------------------------|--------------------|------------------------|------------------------|
| Block | 2 | 13.92 ** | 0.49 NS |
| Plot | 9 | 1.24 NS | 2.95 ** |
| Light | 1 | 74.39 * | 7.12 NS |
| Light x Block | 2 | 0.06 NS | 10.82 *** |
| Soil | 2 | 0.18 NS | 0.88 NS |
| Light x Soil | 2 | 0.42 NS | 1.65 NS |
| Species | 3 | 273.29 *** | 2.77 NS |
| Light x Species | 3 | 6.69 ** | 26.02 *** |
| Soil x Species | 6 | 0.44 NS | 0.77 NS |
| Light x Soil x Species | 6 | 0.09 NS | 0.35 NS |

^a Mean squares of most factors were tested over error mean square (degrees of freedom 185 for emergence, 95 for survival). Plot was nested within Block, and its mean square was used to test for a Block effect, while Light effects were tested over Light x Block mean square.

^b Mean squares for Emergence F ratios: Error = 1.71, Plot = 2.13, Light x Block = 0.11.

^c Mean squares for % Survival F ratios: Error = 1.27, Plot = 3.73, Light x Block = 13.68.

Table 3.3. Number of soil divots in low light treatment (1.5 % PAR) that contained no survivors or at least one surviving seedling of a particular species at the end of the growing season.

| Species | Treatment | Number of divots | | Fisher's p ^a |
|------------|-----------|------------------|----|-------------------------|
| | | None | ≥1 | |
| Birch | Control | 11 | 1 | • |
| | Nitrogen | 6 | 6 | 0.054 |
| | Lime | 10 | 2 | 0.842 |
| Hemlock | Control | 3 | 5 | • |
| | Nitrogen | 5 | 1 | 0.138 |
| | Lime | 6 | 1 | 0.093 |
| White pine | Control | 2 | 1 | • |
| | Nitrogen | 3 | 1 | 0.857 |
| | Lime | 1 | 0 | 0.956 |

^a Probability of observing differences between treatment frequencies (Nitrogen, Lime) and Control frequencies by chance (based on two-tailed Fisher's Exact Test).

Table 3.4. Anova F ratios for seedling growth parameters: individual seedling biomass and total seedling biomass per soil divot (individual biomass x number of seedlings). Significance shown as follows: ^{NS} $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

| Factor ^a | Degrees of freedom | Individual Biomass ^b | Total Biomass ^c |
|------------------------|--------------------|---------------------------------|----------------------------|
| Block | 2 | 2.47 NS | 2.31 NS |
| Plot | 9 | 1.82 NS | 1.59 NS |
| Light | 1 | 55.75 * | 143.92 ** |
| Light x Block | 2 | 2.68 NS | 1.49 NS |
| Soil | 2 | 0.35 NS | 1.99 NS |
| Light x Soil | 2 | 0.25 NS | 2.56 NS |
| Species | 3 | 44.52 *** | 141.02 *** |
| Light x Species | 3 | 46.71 *** | 106.28 *** |
| Soil x Species | 6 | 0.99 NS | 4.34 ** |
| Light x Soil x Species | 6 | 0.28 NS | 0.36 NS |

^a Mean squares of most factors were tested over error mean square (degrees of freedom 47 for individual biomass, 185 for total biomass). Plot was nested within Block, and its mean square was used to test for a Block effect, while Light effects were tested over Light x Block mean square.

^b Mean squares for Individual Biomass F ratios: Error = 0.34, Plot = 0.61, Light x Block = 0.90.

^c Mean squares for Total Biomass F ratios: Error = 7.52, Plot = 11.97, Light x Block = 11.18.

Table 3.5. Range of individual seedling size parameters, separated by light treatment, but pooled across soil treatments and blocks.

| Light | 1.5% PAR | | | 60% PAR | | |
|--------------------|---------------|-----------------|---------------|------------------|-------------|-----------------|
| Species | Birch | Pine | Hemlock | Birch | Pine | Hemlock |
| Dry weight | 3 - 7 μ g | 15 - 40 μ g | 3 - 8 μ g | 2 μ g - 18 g | 0.1 - 0.5 g | 8 - 100 μ g |
| Height (cm) | < 1 | < 3 | < 1 | 1 - 50 | 4 - 8 | 1 - 4 |
| No. of true leaves | 1 - 2 | 5 - 8 | 3 - 6 | 2 - 60 | 10 - 40 | 3 - 25 |

Table 3.6. F ratios from separate Anovas (within Manova) on plot scores from detrended correspondence analysis using species abundance and species community biomass at the end of the growing season. Significance shown as follows: ^{NS} $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

| Factor ^a | Degrees of freedom | Species abundance ^b | | | | Species biomass ^c | | | |
|---------------------|--------------------|--------------------------------|---------------|--------|---------------|------------------------------|---------------|--------|---------------|
| | | Axis 1 | | Axis 2 | | Axis 1 | | Axis 2 | |
| Block | 2 | 3.12 | ^{NS} | 0.91 | ^{NS} | 3.79 | ^{NS} | 2.46 | ^{NS} |
| Plot | 9 | 2.88 | * | 1.04 | ^{NS} | 2.10 | ^{NS} | 1.63 | ^{NS} |
| Light | 1 | 7.59 | ^{NS} | 6.75 | ^{NS} | 2.26 | ^{NS} | 1.17 | ^{NS} |
| Light x Block | 2 | 0.94 | ^{NS} | 1.42 | ^{NS} | 4.56 | * | 3.26 | ^{NS} |
| Soil | 2 | 6.53 | ** | 7.45 | ** | 2.84 | ^{NS} | 3.55 | * |
| Light x Soil | 2 | 3.54 | * | 5.50 | ** | 3.41 | * | 3.83 | * |

^a Mean squares of most factors were tested over error mean square (degrees of freedom 35). Plot was nested within Block, and its mean square was used to test for a Block effect, while Light effects were tested over Light x Block mean square.

^b Mean squares for Species Abundance F ratios. Axis 1: Error = 8.78, Plot = 25.33, Light x Block = 8.27. Axis 2: Error = 16.71, Plot = 17.46, Light x Block = 23.70.

^c Mean squares for Species Biomass F ratios. Axis 1: Error = 5.98, Plot = 12.57, Light x Block = 27.30. Axis 2: Error = 4.39, Plot = 7.16, Light x Block = 14.29.

Figure 3.1. Effects of treatments on experimental conditions (means \pm 1 SEM): (a) PFD levels across shade-houses (n=3) for both low (1.5 % PAR) and high (60 % PAR) light treatments, along with open sky PFD, (b) availability of NO_3^- and NH_4^+ in soil divots, and (c) soil pH. For soil treatments, columns without any shared letters (lower case for NO_3^- and pH, upper case for NH_4^+) are significantly different from one another (Scheffé *post-hoc* comparisons, $p < 0.05$).

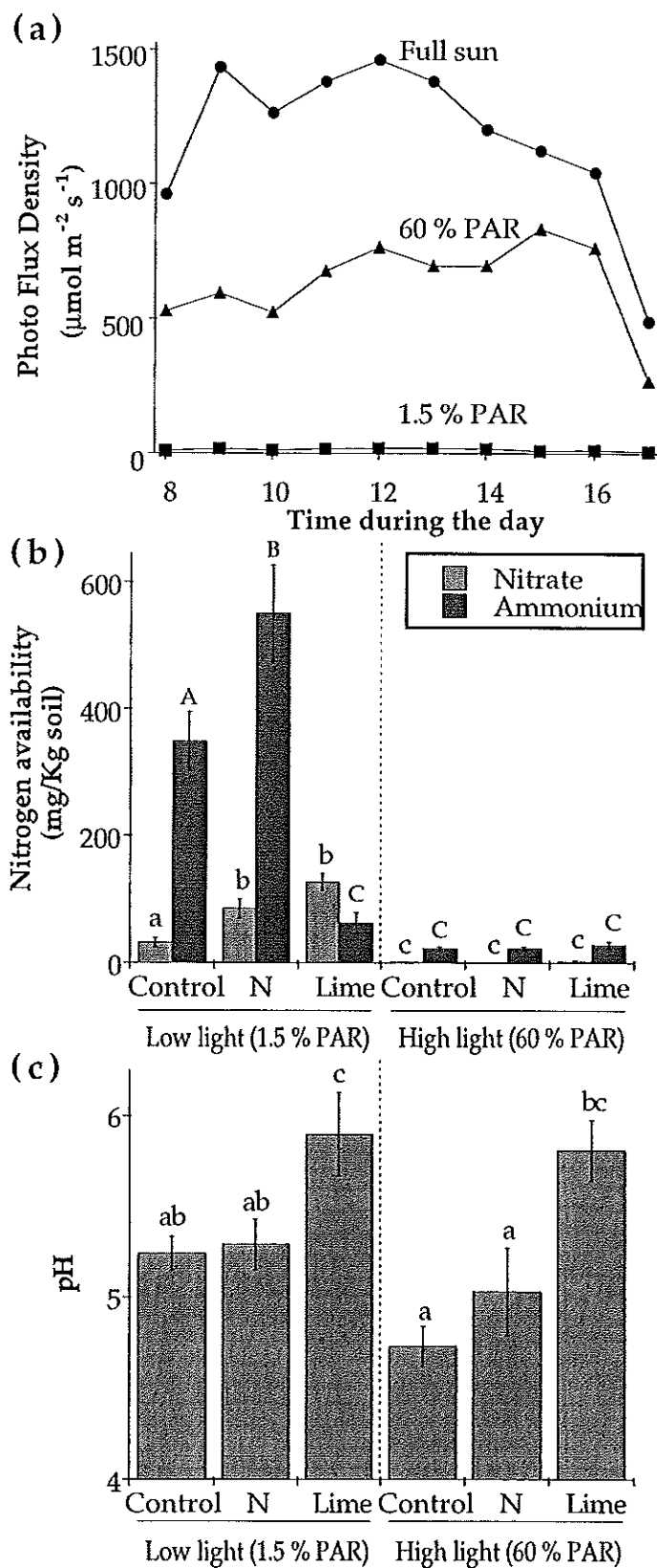


Figure 3.2. Seedling emergence per soil divot (mean \pm SEM, n = 36) under low (1.5 % PAR) and high (60 % PAR) light treatments. Note the difference in scales for birch vs. other species. Columns without any shared letters are significantly different from one another (Scheffé *post-hoc* comparisons, $p < 0.05$).

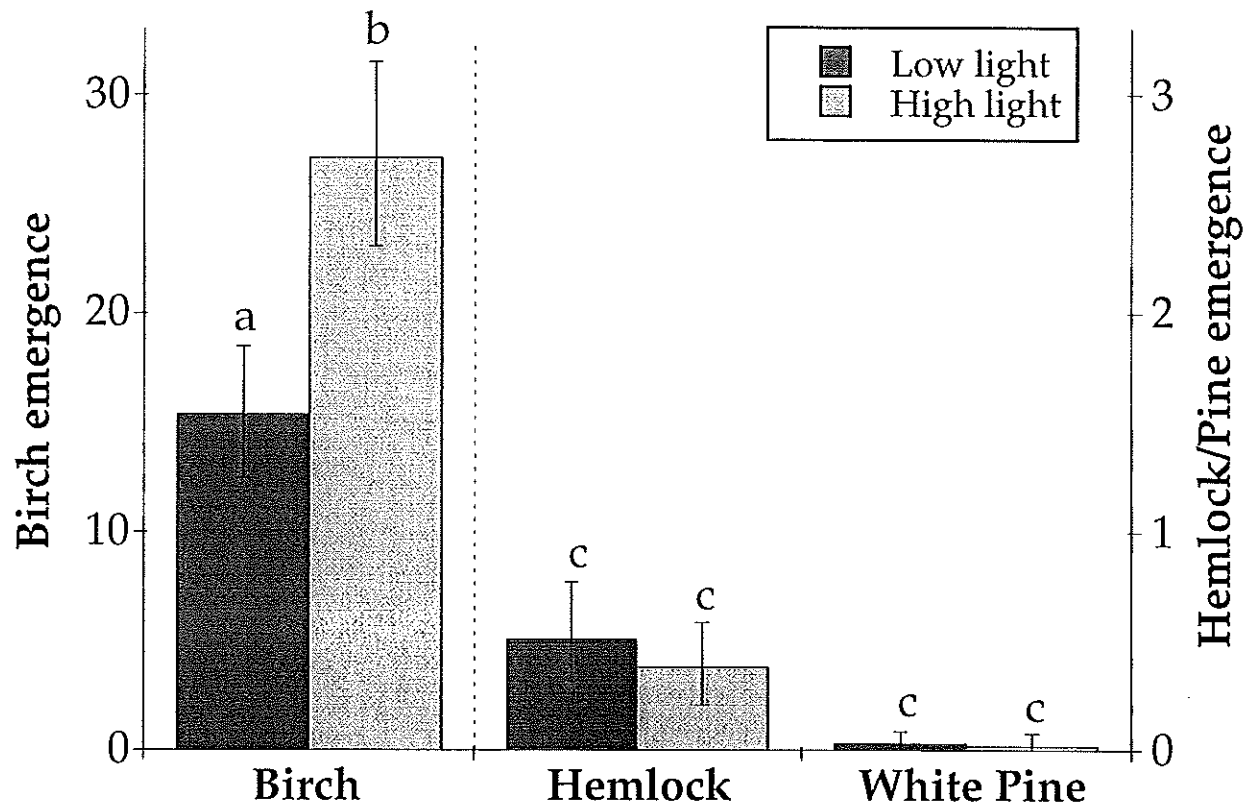


Figure 3.3. Seedling survival through the growing season (mean \pm SEM, n = 6 - 36) under low (1.5 % PAR) and high (60 % PAR) light treatments. Columns without any shared letters are significantly different from one another (Scheffé *post-hoc* comparisons, $p < 0.05$).

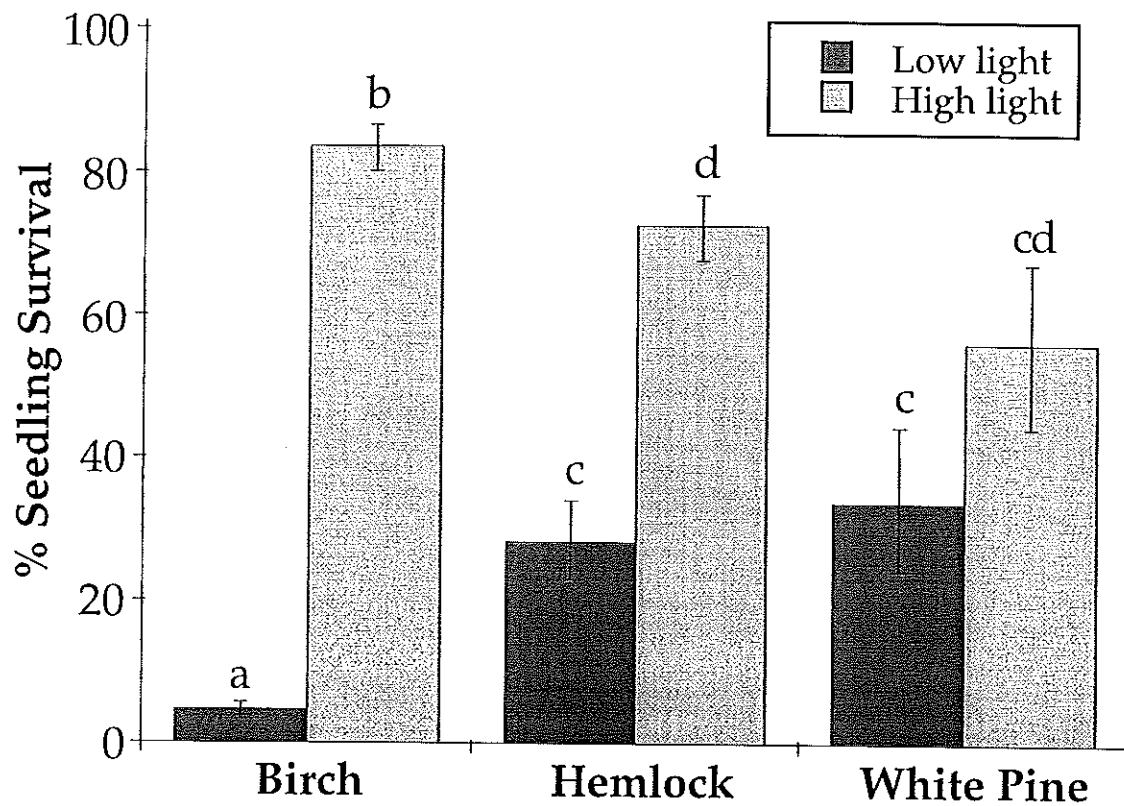


Figure 3.4. Average biomass of seedlings surviving through the growing season (mean \pm SEM, $n = 3 - 36$) under low (1.5 % PAR) and high (60 % PAR) light treatments. Columns without any shared letters are significantly different from one another (Scheffé *post-hoc* comparisons, $p < 0.05$).

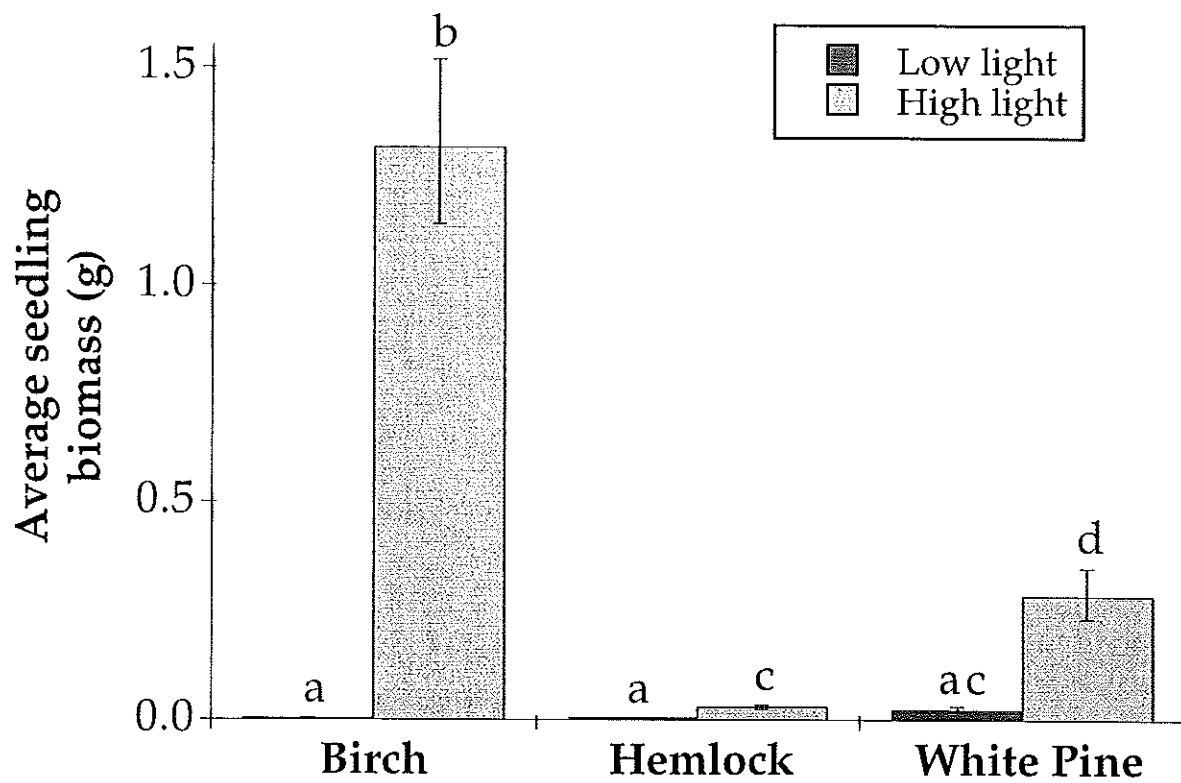
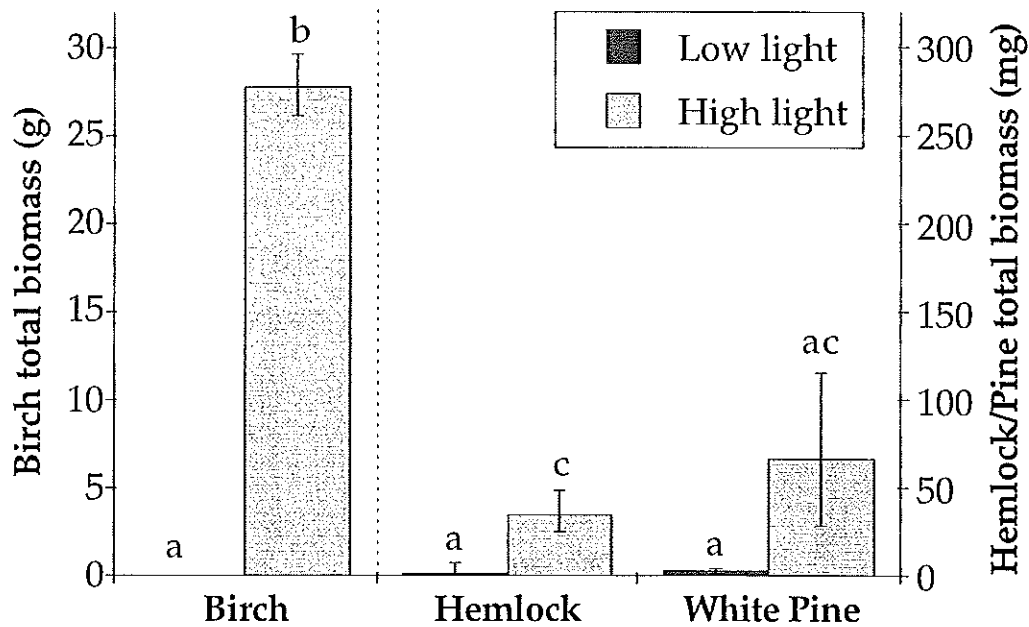


Figure 3.5. Total biomass of seedlings surviving through the growing season (mean \pm 1 SEM, $n = 24 - 36$) under light (a) and soil (b) experimental treatments. Note the difference in scale for birch vs. other species. Columns without any shared letters are significantly different from one another (Scheffé *post-hoc* comparisons, $p < 0.05$).

(a) Light Treatments



(b) Soil treatments

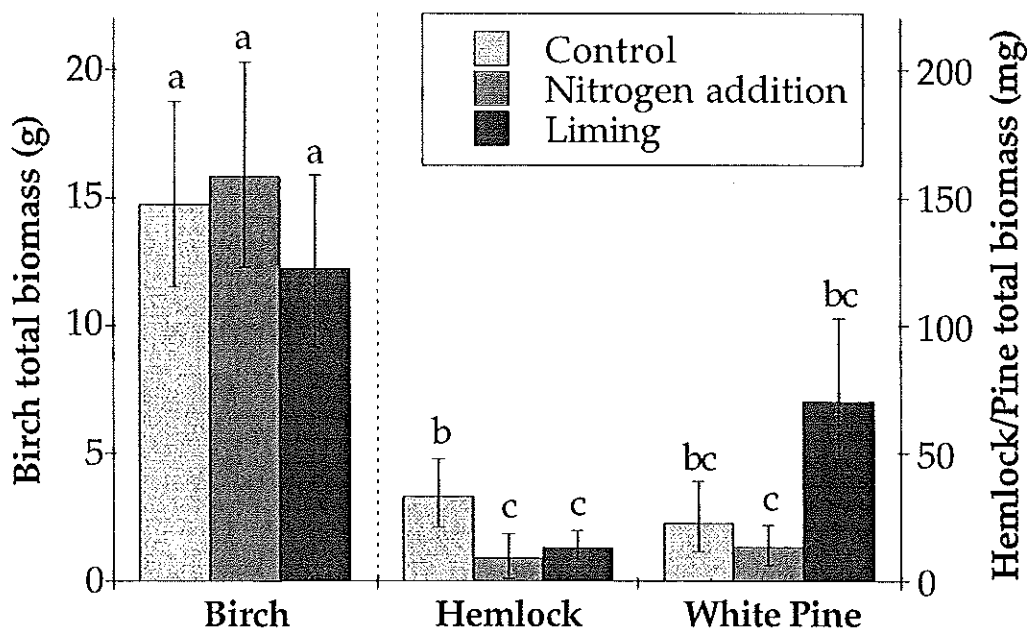
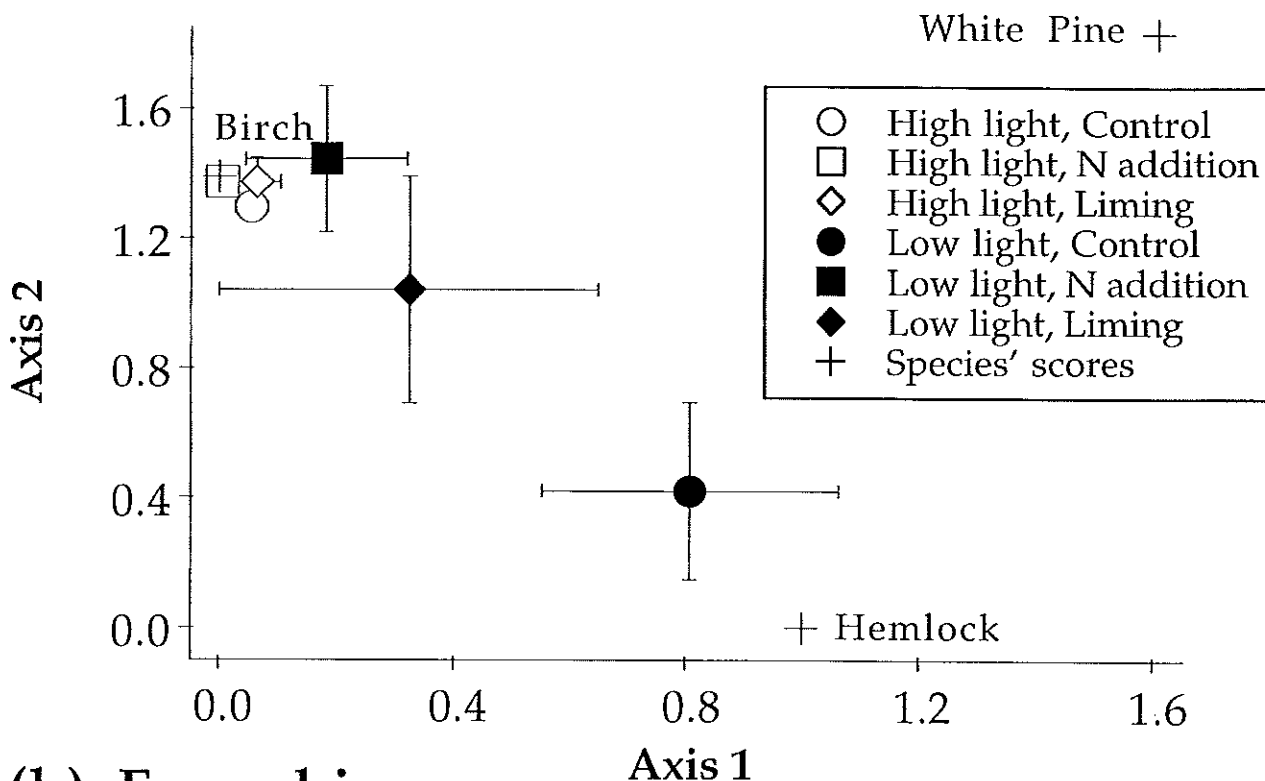


Figure 3.6. Scores (mean \pm SEM, $n = 2 - 12$) of the first two axes from detrended correspondence analysis (DCA) on final species community composition, based on (a) species abundance, and (b) species biomass data. Axes explained 56 % and 33 % of variation (for a) and 63 % and 25 % of variation (for b).

(a) From abundance



(b) From biomass

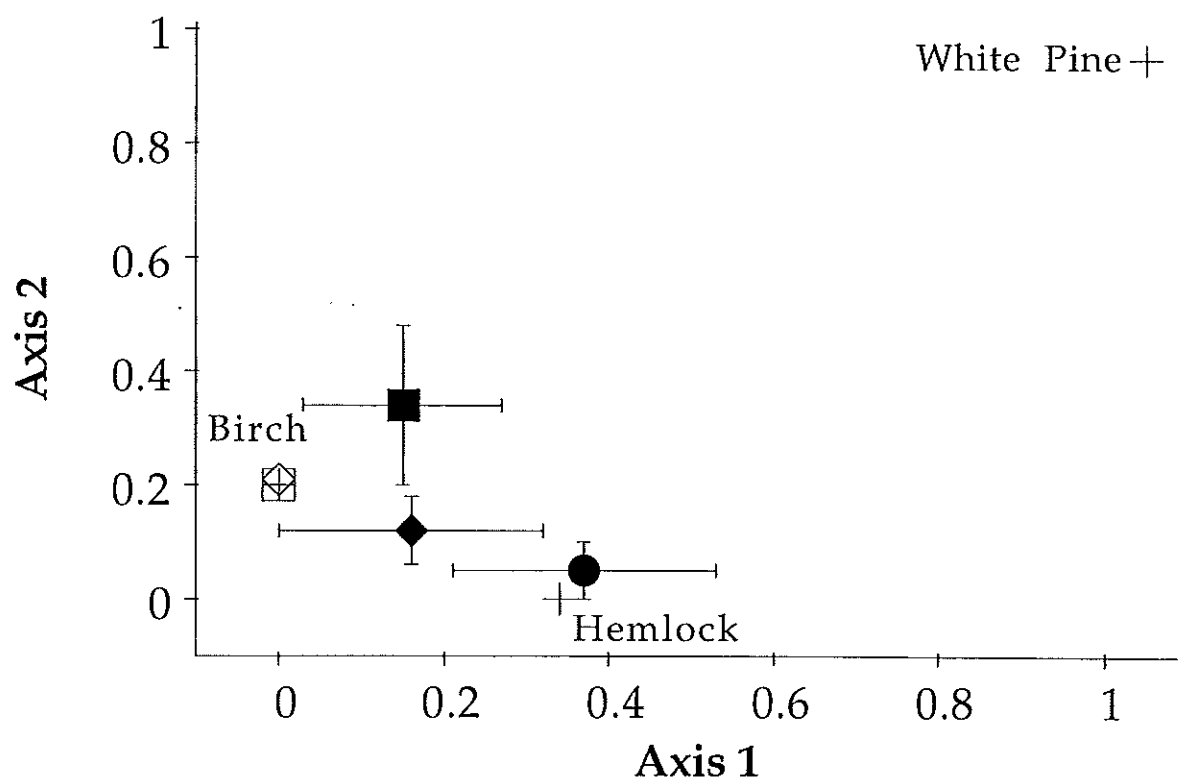
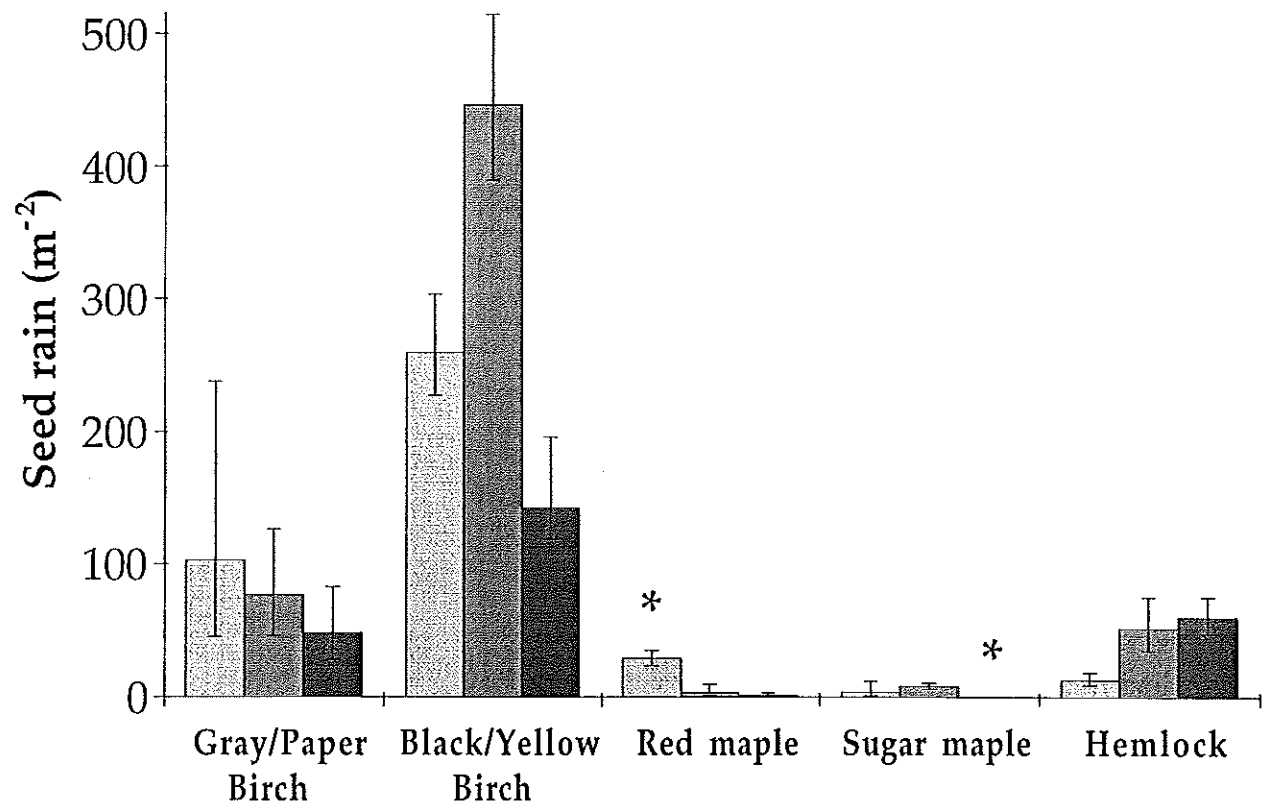


Figure 3.7. Seed rain (mean \pm SEM, $n = 5$) across three experimental transects (different shades of grey). Asterisks (*) mark transects that are significantly different from other transects within that species (Scheffé *post-hoc* comparisons, $p < 0.05$).



CHAPTER 4

NITROGEN DEPOSITION INFLUENCES REGENERATION OF CONIFEROUS AND BROAD-LEAVED TREE SPECIES. I. DYNAMICS IN THE UNDERSTORY SEEDLING BANK

Abstract. Despite increasing levels of nitrogen deposition at temperate latitudes, no studies to date have considered how this perturbation will alter temperate forest species composition. Nitrogen deposition may have a particularly large effect on mixed temperate forests due to differences in nutrient use patterns between evergreen coniferous and deciduous broad-leaved species. To examine how nitrogen deposition may alter the composition of mixed conifer broad-leaved forests, I investigated nitrogen impacts on the dynamics of both coniferous and broad-leaved trees species in the understory seedling bank. In addition, I compared these regeneration responses across coniferous (eastern hemlock) and broad-leaved (red oak) stand types. I applied nitrogen ($0, 2.5, 7.5 \text{ g m}^{-2} \text{ yr}^{-1}$) to replicated understory plots in three hemlock and three red oak dominated stands, and examined seedling survival and growth for three coniferous and three broad-leaved species over two years. Changes in seedling bank structure were driven primarily by differential seedling survival, with secondary effects of emergence. Successional position emerged as a more important determinant of species' responses to increased nitrogen deposition in the understory than did leaf habit (coniferous vs. broad-leaved). Hemlock was the only species whose survival was increased by nitrogen additions in the forest understory, while red maple, white pine, and red spruce all showed nitrogen-induced declines in survival. In addition, birch emergence from the soil seed bank was enhanced in nitrogen addition plots. Effects were particularly marked in hemlock stands (characterized by very low light availability), suggesting nitrogen-induced declines in seedling abundance were likely due to an imbalance between above- and below-ground resources, with seedlings of earlier successional species allocating biomass to growth at the expense of survival. Increasing nitrogen deposition will certainly alter the composition of the understory seedling bank in mixed temperate forests, although the exact nature of the change will depend on future forest landscape composition. Nitrogen-induced changes in seedling bank structure will be more marked if hemlock remains a significant component of these forests. As hemlock seedlings were favored in hemlock stands over other common seedling bank species, nitrogen deposition might accentuate current positive feedback effects acting in these stands, and thus encourage the persistence of hemlock stands across the landscape in the absence of any other major disturbances.

INTRODUCTION

Human activities are leading to substantial perturbations in the major biogeochemical cycles on Earth (Vitousek *et al.* 1997b). Alteration of the nitrogen cycle has emerged as one of the most dramatic human-induced changes since industrialization (Vitousek *et al.* 1997a). Burning of fossil fuels and intensification of agricultural practices have increased atmospheric concentrations of reactive nitrogen species (NO_x and NH_4^+) (Galloway *et al.* 1995), which are ultimately deposited via rain or dust into natural ecosystems (Lovett 1994). As these forms of nitrogen have relatively short residence times in the atmosphere, nitrogen deposition is most pronounced close to points of emission and is concentrated in highly populated areas of the world – Europe, North America, and now parts of east Asia (Holland *et al.* 1999). Natural ecosystems in all these temperate regions are commonly nitrogen limited (Vitousek & Howarth 1991), and nitrogen deposition might exert profound effects on the structure and function of these ecosystems (Wilson *et al.* 1995, Wedin & Tilman 1996).

Most research on the influence of nitrogen deposition on forest ecosystems in these temperate regions has addressed effects either on ecosystem-level processes (Magill *et al.* 1997, Emmett *et al.* 1998) or on composition of forest understory communities (Rainey *et al.* 1999, van Dobben *et al.* 1999). Few studies to date, however, have considered how this perturbation will alter future canopy tree species composition (Crabtree & Bazzaz 1993). Many forests in these temperate regions are likely to be particularly sensitive to changes in nitrogen availability, as they often contain a mixture of evergreen coniferous and deciduous broad-leaved species (Walter 1984), which differ greatly in their basic biology (Reich *et al.* 1995, Smith & Hinckley 1995). As evergreen species tend to exhibit more conservative patterns of nutrient use than deciduous species (Chapin 1980, Aerts 1995), and as coniferous species are typically more slow-growing initially than broad-leaved species (Bond 1989, Reich *et al.* 1998), we might expect that the two major groups of tree species in mixed temperate forests would respond differently to increased nitrogen deposition.

In the present study, I examine how nitrogen deposition will alter the composition of mixed conifer broad-leaved forests in eastern North America. I focus on

the influence of nitrogen deposition on patterns of seedling regeneration, as dynamics at these early stages of a tree's life-cycle are critical determinants of future forest composition (Grubb 1977, Pacala *et al.* 1996). For many species, an important component of their regeneration strategy involves developing a seedling bank under closed canopy forest (Marks & Gardescu 1998). Seedlings emerge from the soil seed bank and persist in the forest understory until they either die or grow up to the canopy after a disturbance event. This strategy is particularly important for later successional species that have difficulty competing with faster growing, early successional species following gap formation unless they have an early lead in the form of already established seedlings (Bazzaz 1996). These later successional species typically show alternating periods of suppression and release events through time as they make their way to the canopy (Kelty 1986, Abrams & Orwig 1996). In the current study, I investigate how increased nitrogen deposition will influence the structure and dynamics of the early stages of an understory seedling bank in temperate forests.

Furthermore, my experimental approach recognizes the importance of landscape structure in controlling the dynamics of temperate forests. Mixed conifer broad-leaved forests in eastern North America are commonly composed of a mosaic of either coniferous or broad-leaved dominated stands (Pastor & Mladenoff 1992). The prevalent conifer in these forests (eastern hemlock, *Tsuga canadensis* (L.) Carr.) frequently forms single-species stands within a matrix of broad-leaved tree species (Pastor & Broschart 1990), including sugar maple (*Acer saccharum* Marsh.) in the mid-west, and red oak (*Quercus rubra* L.) and red maple (*Acer rubrum* L.) in areas of New England. These hemlock and broad-leaved dominated stands have been shown to have persisted stably within these forests for thousands of years (Davis *et al.* 1994), likely as a result of a positive feedback between canopy trees and seedlings (Frelich *et al.* 1993, see also Chapters 2 and 3). The understory resource environment created by canopy trees often favors regeneration of current stand dominants over other species, allowing a species or group of species to dominate a stand for multiple generations (Frelich *et al.* 1998). As seedling regeneration dynamics differ markedly between hemlock and broad-leaved dominated stands in these mixed temperate forests (see Chapter 2 of this thesis), a complete understanding of the impacts of nitrogen deposition of future forest

composition cannot be attained without considering nitrogen effects on seedling regeneration in both stand types. In the present experiment, I examine how nitrogen deposition alters the structure and dynamics of the understory seedling bank in both hemlock and broad-leaved dominated stands.

Understory resource environment differs substantially between these contrasting stand types. Light availability and soil pH were both found to be significantly lower in hemlock stands than in red oak stands (dominant broad-leaved species in southern New England) (see Chapter 2), as might be expected from the effects of individual canopy trees on their surrounding environment (Canham *et al.* 1994, Finzi *et al.* 1998). Thus, in addition to providing critical information on the influence of novel perturbations on natural ecological systems, my experimental approach allows examination of the importance of the prevailing resource environment in determining seedling responses to global environmental change. Resources are heterogeneously distributed on many temporal and spatial scales within plant communities (Caldwell & Pearcy 1994), and investigations on the influence of global change on natural ecosystems must take account of this environmental heterogeneity to make accurate predictions about future impacts.

The current study tests the hypothesis that coniferous and broad-leaved tree seedlings show contrasting responses to increased nitrogen deposition in the understory of mixed temperate forests, and that these responses are contingent on canopy tree composition. I used three coniferous and three broad-leaved tree species whose natural distributions overlap in southern New England (my study location). As I did not wish to confound effects of leaf habit with those related to successional position, I chose species within each group that ranged from mid- to late successional (Table 4.1). Because broad-leaved and early successional species are faster growing and exhibit more flexible patterns of nutrient use than coniferous and late successional species (Bond 1989, Bazzaz 1996), I predicted that, in the forest understory, these species would show greater increases in growth and survival in response to nitrogen. I also predicted that seedling responses would be greater in the understory of broad-leaved tree stands than in hemlock stands, as the higher resource availability in broad-leaved stands (especially light; see Chapter 2) should allow seedlings to take advantage of additional

nitrogen to a greater extent (Latham 1992, Canham *et al.* 1996, Walters & Reich 2000). I tested my hypothesis on different stages of seedling regeneration, so that I could consider a broader range of responses. I used (1) planted seedling plots to examine effects of nitrogen deposition on growth and survival of already established seedlings of my study species, (2) seed addition plots to address nitrogen effects on emergence and establishment of my study species from the soil seed bank, and (3) natural regeneration plots to determine impacts of nitrogen deposition on a naturally created understory seedling bank.

MATERIALS AND METHODS

Nitrogen deposition treatments

I set up experimental plots in three hemlock- and three red oak-dominated forest stands at Harvard Forest in central Massachusetts, USA (42° 32' N, 72° 11' W, elevation 340 m). The sites were established in the Tom Swamp tract and were chosen so that hemlock and red oak contributed over 50 % of the basal area in each of three stands. Details of the stands are clearly described in Chapter 1. At each site, I set up nine 12 m² plots (2 x 6 m) within a 20 x 20 m square. Each experimental plot received one of three nitrogen addition treatments (0, 2.5, 7.5 g N m⁻² yr.⁻¹), with the result that each treatment was replicated three times per site. Plots were arranged in a 3 x 3 grid and nitrogen treatments were applied in a latin square design (each row and column received one of each treatment level). In both 1998 and 1999, plots were given nitrogen eight times per year at approximately three-weekly intervals, beginning mid-April and ending mid-September. At each addition, nitrogen was applied as prilled ammonium nitrate pellets (J. T. Baker, Phillipsburg, NJ) using a hand-held seed spreader to ensure adequate and even broadcast. After addition, each plot was given 5 L of water to dissolve the pellets partially. I chose to apply nitrogen as pellets, as preliminary observations suggested that this method substantially reduced leaf burn (pellets were too heavy to settle on leaves) and allowed for a more gradual release of nitrogen into the soil between additions. Nitrogen addition treatments were chosen to reflect current and future levels of deposition. 2.5 g N m⁻² yr.⁻¹ represents current high levels of deposition in parts of eastern North America (Ollinger *et al.* 1993), and 7.5 g N m⁻² yr.⁻¹ reflects predicted increases in rates of deposition in the future (Galloway *et al.* 1995). Nitrogen was added as ammonium nitrate as both ammonium and nitrate each compose close to half of the deposition in New England (Ollinger *et al.* 1993).

Assessment of seedling regeneration patterns

Each plot was divided into three 4 m² sub-plots (2 x 2 m). In one of the sub-plots, a cohort of seedlings was planted each year (planted seedling plots). Seeds of each study

species were collected from multiple trees at Harvard Forest in the autumn of 1996, 1997 and 1998 (Table 4.1). Any seeds that were not to be used the following year were air-dried and stored at 4 °C. In late autumn 1997 and 1998, seeds were placed in cloth bags and buried in trays of wet, coarse sand. These trays were placed outside through the winter to stratify the seeds and were collected the following spring. In 10 cm deep germination flats, seeds were spread out evenly over a peat-based potting mix with added perlite, and then covered with a thin layer of vermiculite. These flats were then placed in shade-houses (neutral shade-cloth filtering 95 % incoming PAR) in an experimental garden at Harvard University (Cambridge, MA) in mid-April and the seeds were left to germinate. The flats were monitored bi-weekly and watered when necessary. Seedlings began to germinate in early to mid-May. In mid-June, the seedling flats were transported to Harvard Forest. At this point, most seedlings had between two and four true leaves. In both 1998 and 1999, five seedlings of each species were transplanted into each 'seedling' plot. Plots were watered immediately afterwards to prevent early transplant-related mortality. Two weeks later, any dead seedlings were replaced with new transplants. Typically, 1 - 2 seedlings of each species died per plot.

In the second of each sub-plot, seeds of each study species were added (seed addition plots). These seeds were collected in the same way as those used for the planted seedling plots. At the end of the autumn in 1997 and 1998, seeds were broadcast over each sub-plot using a hand-held seed spreader to ensure even spread. The number of seeds added per plot varied according to species (Table 4.2), and depended on seed quantity collected, probable seed rain inputs, and seed viability estimated from germination trials. In the third of each sub-plots, no seeds or seedlings were added. Instead, the natural dynamics of seedlings emerging from the soil seed bank were monitored (natural regeneration plots).

From June 1998 until September 1999, I took monthly censuses of seedling emergence and survival in all study plots during the growing season. Seedlings were individually tagged once they were planted or once they emerged from the seed bank, and their survival was subsequently monitored monthly during the main growing seasons of 1998 and 1999, and once after the 1998-99 winter.

Seedling biomass and foliar nitrogen measurements

In August 1999, in every planted seedling plot, leaf samples were taken from one surviving seedling of each species belonging to each seedling cohort (1998, 1999). For maple seedlings with relatively large leaves, three leaf discs (6 mm diameter) were punched. For all other seedlings, 3 – 6 leaves were removed, depending on seedling size. In these cases of unknown leaf area, samples were photocopied and leaf area subsequently calculated using NIH Image software v1.6 (NIH, Bethesda, MD). To determine leaf chlorophyll concentrations, two to four of these leaf discs/samples were placed in 3 ml dimethyl-formamide and left for 72 hours at 4 °C in complete darkness (García & Nicolás 1998). Absorbance of the resulting solution at 664 and 647 nm was measured using a Spectronics 20D spectrophotometer (Spectronic Unicam, Rochester, NY), and chlorophyll concentrations calculated from standard equations (Wellburn 1994). The remainder of each set of leaf samples was weighed after drying in an oven for 48 hours at 70 °C, and specific leaf weight calculated (SLW, g m^{-2}). In this way, chlorophyll concentration could be expressed on both an area and dry weight basis.

At the end of the second growing season (late September 1999), all remaining seedlings were harvested. All seedlings were gently extracted from the soil and washed to remove any soil. Seedlings from seed addition and natural regeneration plots were weighed whole after one week drying in an oven at 70 °C. Planted seedling cohorts were additionally separated into leaves, stems and roots.

Environmental measurements

To determine how nitrogen additions affected seedling resource environment, above- and below-ground resource availability were measured for each plot during the 1999 growing season. I used methods and sampling protocols that would provide a good indication of 'plant available' resources. Season-long integrated nitrogen availability was determined using ion exchange resin bags placed in each nitrogen plot from June until October 1999 (Binkley & Vitousek 1989). The bags were constructed with 1.5 tablespoons (22 ml) of mixed bed strong acid (cation) and strong base (anion) gel resins (Sybron Chemicals, Birmingham, NJ) sealed in nylon mesh, and placed at a depth of 5 cm in the soil. After removal from the soil, 4 g of dried resin (70 °C, overnight) was

extracted with 100 ml of 2 N potassium chloride solution (25 °C, 24 hours), and then frozen immediately following suction-filtration. Ammonium and nitrate in all soil and resin extracts were measured using a LaChat continuous flow ion analyzer using methods 12-107-06-1-A and 12-407-04-1-B (LaChat Instruments, Milwaukee, WI). Blanks were created from resin bags that had been sealed in polyethylene bags for the length of the growing season. These resins were extracted in the same way as the resins placed in the field and were used to determine the lower threshold of detection.

Light availability was measured using canopy hemispherical photographs (Canham 1988). On a uniformly overcast day, photos were taken at 5 cm and 1 m above the ground in the center of each plot using a fish-eye lens (180 °) attached to Canon camera body (with self-timer). The camera was leveled and oriented towards north before each photo. 200 speed color slide film was used to capture the photos. The resulting images were scanned into the computer with a slide-scanner (500 dpi resolution) and analyzed using GLI/C software (courtesy of C. D. Canham, Institute of Ecosystem Studies, Millbrook, NY). Thresholds were set manually in both blue and green spectra on each image separately, and the software used to calculate % open sky, % direct beam radiation, % diffuse beam radiation, and % global radiation (direct plus diffuse).

Water availability was determined by taking a soil core (2 cm diameter, 20 cm depth) from the edge of each plot. Sieved soil (2 mm mesh) was dried (105 °C, 48 hours) and weighed to give gravimetric soil moisture. Further soil cores (10 cm diameter, 4 - 12 cm deep) were taken to determine soil pH in the organic horizon. pH of sieved soil (5.6 mm mesh) was measured on a mixture of 2 g of air-dried soil in 20 ml distilled water (pH 5.5) using an Orion 250A pH meter (Orion Instruments, Boston, MA).

Statistical analysis

Multi-factor analyses of variance were used to investigate influence of nitrogen addition on understory seedling bank development. Linear models included nitrogen addition as a continuous factor, and different combinations (plus interactions) of a variety of fixed, discrete factors (stand type, species, year, month, seedling age). Models also included a nested series of random factors. Site was nested within stand, and plot was nested

within site (stand), with the result that stand mean square was tested over site, and site was tested over plot mean square (Sokal & Rohlf 1995). Significant multi-factor interactions involving nitrogen were investigated by examining the magnitude and significance of regression slopes (dependent variable vs. nitrogen addition) using standard errors. *Post-hoc* comparisons of means were carried out using Scheffé multiple comparisons (Day & Quinn 1989), and comparisons between slope coefficients were carried out using T', GT2 and Tukey-Kramer methods (Sokal & Rohlf 1995).

Community composition was investigated with multivariate analysis of variance on plot scores from the first two axes of detrended correspondence analysis (ter Braak 1995), and by using the Shannon-Weaver diversity index on a plot-level ($-\sum p_i \ln(p_i)$ where p_i is proportional abundance of species i in plot). Changes in allocation between roots and shoots under different nitrogen treatments were studied by examining changes in Model II linear regression slopes (geometric mean regression) for the natural logarithm of root or shoot biomass against natural logarithm of total biomass, according to the method described by McConnaughay & Coleman (1999) for distinguishing ontogenetic and true allocation responses. Allometric analyses were carried out for individual species, nitrogen treatments, and stand types.

When necessary, data were transformed to ensure that the assumptions of analysis of variance were met (normality of residuals, homoscedascity). Common transformations included natural logarithm (biomass), natural logarithm of square root (emergence, abundance), and the logit function (proportional survival) (Sokal & Rohlf 1995). For figures, the level to which data were pooled across treatments was determined by the highest order significant interaction in the analysis of variance.

RESULTS

Environmental conditions

Nitrogen additions significantly increased availability of both ammonium and nitrate (Table 4.3a). In unamended plots, ammonium resin concentrations averaged 0.03 mg/g, while that of nitrate averaged 0.15 mg/g. Based on the regression slopes (Table 4.3b), every gram of nitrogen added (per m² per year) increased ammonium availability by 0.04 mg/g and nitrate availability by 0.14 mg/g. Nitrogen additions did not significantly affect availability of other resources (Table 4.3a). Resources were, however, significantly different between stand types. Both light transmitted through the canopy and soil pH were significantly higher in red oak stands compared with hemlock stands (Table 4.3a; light: 6.0 vs. 1.4 %, pH: 4.6 vs. 4.2). Chapter 2 of this thesis discusses these stand-level differences in more detail.

Emergence

In seed addition plots, all study species emerged from added seed except sugar maple, which suffered high seed predation (Table 4.2; Figure 4.1). In natural regeneration plots, the major species to emerge from the soil seed bank were birch, hemlock, and red maple (Table 4.2). At these early stages of the life-cycle, birch species could not be distinguished beyond genus. In both seed addition and natural regeneration plots, emergence varied with species identity, stand type, and year (Table 4.4; significant species x stand x year interaction). Many of these basic patterns are described in more detail in Chapter 2 of this thesis. Most species showed higher emergence in hemlock stands than in red oak stands (Table 4.2), with birch exhibiting the largest and most consistent differences between stand types (30- to 100-fold increase in hemlock vs. red oak stands). Differences in emergence for red maple and hemlock were strongest in years with good seed crops (1998 and 1999, respectively).

Nitrogen addition altered some of these natural emergence patterns, but mainly in plots where seeds were added (Table 4.4, significant N x species x stand interaction in seed addition plots only). In these plots, effects of nitrogen on seedling emergence were

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only significant in hemlock stands (Figure 4.1), where nitrogen addition enhanced birch emergence by almost three-fold (from 16 to 46 seedlings m⁻²), but decreased white pine emergence.

Survival

Seedlings exhibited strong seasonal dynamics in monthly survival rates in all sub-plots (Table 4.5; significant month, species x month, and species x month x year interactions). In seed addition and natural regeneration plots, these dynamics were particularly marked for birch seedlings, which suffered highest mortality in August (99 % vs. 40 % in other months, *post hocs*, $p < 0.05$). Other small-seeded species, such as hemlock and red spruce, similarly suffered high mortality in August, but not to the same degree. In planted seedling plots, monthly survival tended to increase through the season, with significant increases in survival for red maple, yellow birch, sugar maple (only 1998) and red spruce (only 1999) (*post hocs*, $p < 0.05$).

Increasing nitrogen deposition led to overall changes in first-year seedling survival in both seed addition and natural regeneration plots, but did not affect survival in planted seedling plots (Table 4.5, no significant N x species interactions). In seed addition plots, the differential responses of species to increased nitrogen were contingent on both stand type and year (significant N x species x stand and N x species x year interactions). Nitrogen addition decreased first-year survival for red maple, white pine, and red spruce seedlings, but only in hemlock stands (Figure 4.2a) and not in red oak stands (Figure 4.2b). For both red maple and white pine, increasing nitrogen exacerbated the lower overall seedling survival in hemlock stands vs. red oak stands (accounting for the significant species x stand interaction, Table 4.5). Nitrogen effects were stronger for red maple and red spruce in 1998 (Figure 4.2c), and for white pine in 1999 (Figure 4.2d). I also found significant declines in red maple survival with increasing nitrogen in natural regeneration plots (Figure 4.2e), but the effects were not contingent on stand type or year (Table 4.5; significant N x species interaction, but no higher order interactions).

Although I was unable to detect nitrogen effects on planted seedlings in the first year, influences of increasing nitrogen appeared after the first growing season. Nitrogen

significantly increased hemlock survival over the seedlings' first winter, and led to non-significant declines in red maple and sugar maple survival (Figure 4.3a; significant N x species interaction in Anova, $F_{5,171} = 3.06$, $p < 0.05$). Hemlock survival in the second growing season was also enhanced by increasing nitrogen, but only in stands dominated by hemlock trees (Figure 4.3b; significant N x species x stand interaction in Anova, $F_{3,100} = 2.72$, $p < 0.05$). Nitrogen additions also decreased red maple seedling survival in the second growing season, but in contrast to seed addition plots, this effect was only significant in red oak stands (Figure 4.3c). In hemlock stands, there was a tendency for nitrogen to decrease survival in second-year planted seedling plots for the same species that showed nitrogen-induced declines in survival in seed addition plots in the first year, i.e., red maple, white pine, and red spruce (Figure 4.3b). High overall seedling mortality in hemlock stands, however, reduced sizes of seedling populations at the start of the second growing season. Low sample sizes increased variability in nitrogen effects and reduced significance of these nitrogen-induced declines for these species. In seed addition and natural regeneration plots, mortality both within the growing season and over winter was so high that sample sizes were inadequate to examine regeneration dynamics of any second-year seedlings.

Abundance

Emergence and survival combined to influence seedling abundance in the understory. First-year seedling abundance was highly dynamic through the growing season (Table 4.6, significant species x month and species x month x year interactions). In seed addition and natural regeneration plots, most species showed a peak in abundance in July corresponding to high seedling emergence and low mortality. Patterns differed between species as a result of differences in timing of demographic events. Similar dynamics were observed in natural demography plots in the same stands (see Chapter 2 for full details). Differential species emergence and survival in contrasting stand types (see earlier sections) created differences in species' first-year seedling abundance in hemlock vs. red oak stands (Table 4.6, significant species x stand and species x stand x month interactions). In seed addition and natural regeneration plots, most species had significantly higher abundance in hemlock stands earlier in the season compared to red

oak stands (*post hoc*s, $p < 0.05$) due to greater emergence from the seed bank. For red maple and birch, increased mortality in hemlock stands resulted in significantly lower seedling abundance in hemlock stands than in red oak stands by the end of the season (*post hoc*s, $p < 0.05$). In contrast, hemlock and white pine maintained higher understory seedling abundance throughout the season in hemlock stands than in red oak stands (*post hoc*s, $p < 0.05$). In planted seedling plots where differential emergence did not determine abundance, all species had higher understory abundance in red oak stands compared to hemlock stands.

Through its effects on different components of seedling demography, nitrogen additions altered variation in understory seedling abundance patterns. First-year seedling abundance was differentially affected by increasing nitrogen (Table 4.6, significant N \times species interaction), but in all cases, these effects depended on stand type or year of study (Table 4.6, significant N \times species \times stand \times year interactions). During the 1998 growing season, first-year red maple seedling abundance decreased with increasing nitrogen in both seed addition ($F_{1,413} = 6.21$, $p < 0.05$) and natural regeneration plots ($F_{1,388} = 4.18$, $p < 0.05$). These effects were only significant in hemlock stands in the former case (Figure 4.4a-d) and in red oak stands in the latter (Figure 4.4e-h). Nitrogen additions similarly led to declines in red spruce seedling abundance in both planted seedling ($F_{1,430} = 7.77$, $p < 0.01$) and seed addition plots ($F_{1,393} = 5.06$, $p < 0.05$). Changes in red spruce abundance only occurred during the 1998 growing season in seed addition plots (Figure 4.4a-d), and only in red oak stands in 1999 in planted seedling plots (Figure 4.5a-d). Birch and sugar maple first-year seedling abundance both increased in response to nitrogen, but only under certain conditions. Nitrogen increased birch abundance in natural regeneration plots in hemlock stands in 1999 (Figure 4.4g), while birch actually declined in red oak stands in 1998 (Figure 4.5f). Sugar maple abundance increased with increasing nitrogen in planted seedling plots during the 1999 growing season only (Figure 4.5d).

Second-year seedling abundance in planted seedling plots exhibited an even stronger influence of nitrogen deposition (significant N \times species \times stand interaction in Anova, $F_{5,1450} = 7.03$, $p < 0.001$). After two years of nitrogen additions, red spruce, red maple, birch, and sugar maple all showed significantly lower seedling abundance in

both hemlock and red oak stands (Figure 4.5e,f). Hemlock abundance was unaffected by nitrogen, while white pine abundance increased in red oak stands (Figure 4.5f) and decreased in hemlock stands (Figure 4.5e) with increasing nitrogen.

Seedling bank community composition and species diversity

Nitrogen effects on understory seedling abundance led to overall changes in seedling bank composition. Species' differences in seasonal patterns of emergence and survival (see above) created temporal variation in the composition of the first-year seedling bank (Table 4.7; significant month and month x year terms). In seed addition and natural regeneration plots, birch and red maple dominated early (emergence peak in June/July), but as the season progressed, increased conifer emergence from the soil seed bank combined with high birch mortality led to greater conifer dominance towards the end of the summer (*post hoc*s, $p < 0.05$). This dynamic was particularly marked in hemlock stands (Table 4.7; significant stand x month interaction). In planted seedling plots where all species began with the same number of individuals per plot, maple species and white pine made a larger contribution to the seedling bank later in the growing season (*post hoc*s, $p < 0.05$). For second-year old seedlings, however, there were no significant changes in composition through the growing season (all Manova terms with month, $0.33 < F_{8,340} < 1.09$, $p > 0.1$).

Nitrogen addition significantly altered the overall composition of the understory seedling bank. In seed addition and natural regeneration plots, the direction of change depended on stand type (Table 4.7, significant N x stand interactions), and in first-year planted seedling plots, changes varied with stand type and year of study (significant N x stand x year interaction). In both seed addition and natural regeneration plots, nitrogen-induced community changes were reflected in movement of plots down DCA axis 2. In seed addition plots, nitrogen significantly lowered axis 2 scores in both hemlock and red oak stands (Figure 4.6a). In hemlock stands, this decline was caused predominantly by decreased abundance of red maple, white pine and red spruce (Figure 4.4a,c), while in red oak stands, significant increases in the relative abundance of birch led to movement of plots down axis 2 (Fig 6b,d). In natural regeneration plots, nitrogen-induced changes in seedling bank composition were only significant in

hemlock stands and were caused by increased birch abundance relative to red maple (Figure 4.4e,g). In the first-year of planted seedling plots, nitrogen additions similarly led to alteration of community composition, but these effects were only significant in hemlock stands in 1998 (Figure 4.6c) and in red oak stands in 1999 (Figure 4.6d). There was no clear change driving these effects in hemlock stands (Figure 4.5a,c), while in red oak stands, the changes were likely related to declines in red spruce abundance and increases in sugar maple in 1999. By the second-year in planted seedling plots, nitrogen effects on seedling bank community composition were substantial and again contingent on stand type (stand \times N interaction, $F_{2,170} = 3.15$, $p < 0.05$). Nitrogen additions moved plots down axis 1 in hemlock stands and down axis 2 in red oak stands. Decreasing abundance of white pine seedlings in hemlock stands (Figure 4.5e) and increasing abundance in red oak stands (Figure 4.5f) were driving these changes.

Nitrogen addition also reduced seedling bank species diversity in first-year seed addition and natural regeneration plots (Table 4.7). In seed addition plots, nitrogen effects were contingent on both stand type and year of study. Nitrogen-induced declines in Shannon-Weaver diversity index were particularly significant in hemlock stands (from 0.70 to 0.52, $F_{1,219} = 5.0$, $p < 0.05$) and during the 1998 growing season (from 0.76 to 0.55, $F_{1,229} = 8.1$, $p < 0.01$). Similarly, natural regeneration plots only exhibited declines in species diversity in response to nitrogen-deposition in 1998 (from 0.33 to 0.13, $F_{1,181} = 16.0$, $p < 0.001$). In both kinds of sub-plot, effects became more significant as the growing season progressed and differential mortality patterns in relation to nitrogen addition altered community diversity (Table 4.7, significant N \times month \times year interaction).

Biomass, allocation patterns and tissue chlorophyll

By the end of 1999, only planted seedling plots contained enough seedlings to harvest. For all species except sugar maple, second-year old seedlings were larger than first-year seedlings (Table 4.8; significant age and age \times species terms for individual seedling biomass). Nitrogen additions did not, however, significantly influence final seedling biomass in these plots (Table 4.8), and the result was no different whether I considered

individual seedling biomass or the combination of seedling abundance and biomass (total plot-level biomass).

Although final seedling biomass was not affected by increasing nitrogen availability, seedling allocation patterns did change significantly following nitrogen addition treatments. For allocation to leaves, significant effects of nitrogen were only observed when pooling across stand types (equivalent to no significant N x species x stand interaction), while there were clear differences in nitrogen-induced changes in root allocation between contrasting stand types. Red maple, white pine and red spruce all showed significant increases in allocation to leaves (when accounting for size) in response to nitrogen additions, and significant decreases in allocation to roots (but only in hemlock stands) (Figure 4.7).

Species also demonstrated some flexibility in leaf composition in response to increasing nitrogen availability in the understory. Nitrogen additions altered species' foliar chlorophyll concentrations (on both an area and weight basis), although the effects were contingent on stand type (Table 4.9, significant N x species x stand interaction). Specific leaf weight was unaffected by nitrogen treatments (Table 4.9), as was the ratio of chlorophyll a to b (data not shown). In red oak stands, increasing nitrogen availability led to significantly increased foliar chlorophyll for red maple, red spruce and hemlock (Figure 4.8b). In hemlock stands, in contrast, only white pine and hemlock showed significant increases in chlorophyll concentration, while foliar chlorophyll in red maple actually declines (Figure 4.8a).

DISCUSSION

Demographic impacts of nitrogen deposition

Simulated nitrogen deposition altered the structure and composition of early stages of the understory seedling bank in a mixed conifer broad-leaved forest in New England. For many tree species, maintaining an understory seedling bank is a critical component of their regeneration strategy, and thus nitrogen-induced changes in seedling bank structure will ultimately influence the future dynamics of these mixed temperate forests (Pacala *et al.* 1996). In the understory, I found that the demographic effects of nitrogen deposition were much larger than growth effects. Both seedling emergence and survival were significantly influenced by increasing nitrogen availability, while there were no detectable effects on seedling biomass. Much global change research focuses on physiological effects of novel perturbations (Bazzaz & Catovsky 2000), but my experiment clearly shows that effects on seedling demography might be equally as important, and in some cases, even more so, e.g., when mortality is high (but see Hättenschwiler & Körner 2000). When considering seedling regeneration under closed canopy conditions, it is now clear that survival in low light conditions arises as a more important determinant of understory seedling dynamics than growth rates (Pacala *et al.* 1996, Walters & Reich 1999).

Species-specific demographic responses to increased nitrogen availability differentially altered species' seedling abundance in the understory, and as a result nitrogen addition changed the composition of the seedling bank. Contributions of red maple and red spruce to the seedling bank frequently declined in response to increased nitrogen availability, while relative contributions of birch and hemlock both increased, leading to an overall reduction in seedling bank species diversity. These changes in seedling community composition were driven primarily by differential survival responses to nitrogen addition, and secondarily by emergence effects (for birch only). Experiments addressing community-level impacts of nitrogen deposition have frequently found nitrogen-induced changes in species composition (Bobbink *et al.* 1998), often with overall declines in species diversity (Berendse & Elberse 1990). Most studies,

however, have focused on communities dominated by short-statured and short-lived species, e.g., grasslands. It is only recently, however, that demographic mechanisms underlying nitrogen-induced community-level changes have begun to be addressed (Foster & Gross 1998).

Differential species' responses to nitrogen deposition

Nitrogen responsiveness is often correlated with particular species' traits (Chapin 1980). In my experiment, successional position emerged as a more important determinant of species' responses to increased nitrogen availability in the understory than did leaf habit (coniferous vs. broad-leaved). For example, red maple and red spruce (similar tolerance ranking but contrasting leaf habit) both showed similar declines in survival following nitrogen addition. In the present study, hemlock was the only species whose survival was increased by nitrogen additions in the forest understory, and also represents the only study species that is able to persist for decades in the deeply shaded forest understory as a sapling (Kobe *et al.* 1995). The notion that later successional species respond more strongly to novel perturbations under a closed canopy fits well with a number of CO₂ studies finding that shade tolerant forest species show the greatest CO₂ growth enhancements in low light conditions, while earlier successional species only respond positively to elevated CO₂ under high light conditions (Bazzaz & Miao 1993, Kubiske & Pregitzer 1997, Hättenschwiler & Körner 2000). In my study, I did find one earlier successional species (birch) that showed some positive increases in seedling understory abundance following nitrogen addition, but these effects were primarily as a result of enhancement of seedling emergence from the soil seed bank. Emergence effects are likely to be less important in the longer-term than effects on survival, as they are restricted to the first-year of a seedling's life, rather than accumulating over many years of understory persistence.

Influence of stand canopy composition

The contingency of species' responses to novel perturbations might be particularly marked in the forest understory, as canopy trees each create a unique combination of resource conditions beneath them (Boettcher & Kalisz 1990, Vesterdal & Raulund-

Rasmussen 1998). In the present study, seedling responses to nitrogen addition were often strongly dependent on canopy composition (hemlock vs. red oak stands). Environmental measurements in this current study and in an earlier study (see Chapter 2) clearly demonstrated that both light availability and pH were significantly lower in hemlock stands than in red oak stands. Nitrogen deposition might change the ability of species to grow and persist under different understory light levels in the future, and thus alter the prevalence of different species in contrasting stand types. Soil conditions have previously been shown to alter shade tolerance of certain species, e.g., sugar maple and white pine (Kobe 1996). In the current experiment, I found that these differences in resource environment increased species' sensitivity to nitrogen deposition in hemlock stands compared with red oak stands. Birch emergence was only enhanced by nitrogen addition in hemlock stands, while nitrogen-induced declines in survival were also more marked in hemlock stands, especially for red maple seedlings, and occasionally for white pine and red spruce seedlings. By the second-year of treatment, differences between nitrogen effects on survival in hemlock and red oak stands had accumulated to a considerable degree for white pine seedlings, with a significant nitrogen-induced increase in seedling abundance in red oak stands and a significant reduction in hemlock stands. Overall, nitrogen additions acted to enhance current positive feedback effects operating in hemlock stands by favoring hemlock survival in the understory over other seedling bank species, such as red maple and white pine (see Chapters 2 and 3).

Mechanisms underlying seedling responses to nitrogen

Species have been shown to differ in the degree to which low light availability may constrain seedling responsiveness to nutrients (Walters & Reich 1996, also see Chapter 3). Late successional species might have a better capacity to respond to increased nutrient availability under low light scenarios than earlier successional species (Walters & Reich 1997, Finzi & Canham 2000, Walters & Reich 2000). Hemlock was the only species to show consistent increases leaf chlorophyll concentrations across stand types in response to simulated nitrogen deposition. For less shade tolerant species, manufacturing additional chlorophyll in low light environments may represent a metabolic cost that is not offset by the resulting small increase in carbon gain.

The more marked nitrogen-induced declines in survival and abundance of a number of species in the understory of hemlock stands strongly suggest that resource imbalance may be driving the negative nitrogen effects on seedling regeneration. In hemlock stands, where light availability is particularly low, nitrogen additions are more likely to create an imbalance between above- and below-ground resource availability. Fertilization has been shown to hasten seedling mortality at low light levels (Grubb *et al.* 1996), although the actual mechanism has still not clearly established. In the present study, I found that the species whose survival significantly declined in nitrogen addition plots showed the greatest allocational flexibility in response to nitrogen. Red maple, red spruce, and white pine all allocated more biomass to leaves and less biomass to roots with increasing nitrogen availability. From an optimality stand-point, this strategy appears beneficial (Bazzaz 1997). As nitrogen becomes less limiting, plants allocate less below-ground and increase their leaf area ratio to improve their capacity for carbon gain above-ground (Peace & Grubb 1982). The greater allocation flexibility of the earlier successional species in the present study agrees with ecological theory on succession (Bazzaz 1996), and has been previously found for seedlings of these specific species growing under varying combinations of light and soil resources (Canham *et al.* 1996). This flexibility in response is often advantageous for responding to rapid increases in resource availability, but may be detrimental in a forest understory where resources are severely limiting. The reasons for shifts in allocation leading to increased mortality are not clear in this case, but could be related to seedlings allocating carbon to improve growth potential rather than survival (Walters & Reich 2000). Kobe (1997) has shown that more shade tolerant species had higher concentrations of non-structural carbohydrates in their roots than less tolerant species, and suggested that a trade-off between growth and survival exists. An alternative hypothesis is that species that allocate less biomass to roots in response to nitrogen deposition could be more sensitive to drought episodes (Canham *et al.* 1999).

The increased emergence of birch from the soil seed bank in response to nitrogen addition was likely the result of seeds using increased nitrogen availability (especially nitrate) as an environmental cue. Nitrification rates commonly increase following a disturbance event, and thus increased nitrate availability may represent a useful signal

for gap formation for earlier successional species (Pons 1989), which are particularly dependent on canopy openings to reach the overstory (Bazzaz 1996). My results that nitrogen addition led to significant increases in birch emergence only in hemlock stands and only in plots with seeds added point to the importance of adequate seed supply and microsite availability in controlling these responses. Birch emergence might be more responsive to increased nitrogen availability in stands where establishment is less limited by microsite availability, i.e., hemlock stands (see Chapter 2 of this thesis).

My experiment was not explicitly designed to test specific mechanisms underlying seedling responses to nitrogen deposition, so I cannot exclude other processes that might also be explaining the observed dynamics. Deer browsing, for example, is a major issue in limiting seedling regeneration in many forests in eastern North America. Higher tissue nitrogen concentrations could potentially make seedlings more susceptible to herbivory and thus reduce their survival in the understory (Crabtree 1992). In this experiment, however, deer browsing is unlikely to be an important determinant of seedling regeneration patterns in the understory. Deer densities are still at relatively low numbers in Massachusetts ($\sim 5 \text{ Km}^{-2}$) and there is no experimental evidence of extensive browsing in the understory at Harvard Forest (J. O'Keefe, *unpublished data*; further data in Harvard Forest archives).

Implications for future forest composition

Nitrogen deposition will influence future forest structure and dynamics in conjunction with a suite of other novel human-induced perturbations affecting natural ecosystems, such as increased frequency of biological invasions, changing human land-use patterns, and altered atmospheric chemical composition (Foster *et al.* 1997). Predicting the exact nature of any future impacts is challenging given the uncertainties in the magnitude and timing of these changes. For example, the future of hemlock populations in eastern North America is currently uncertain, as they are threatened by an exotic insect pest, the hemlock woolly adelgid (*Adelges tsugae*) (Orwig & Foster 1998). Loss of hemlock from the landscape will have major consequences for forest structure and dynamics (Jenkins *et al.* 1999) (see also Chapter 3), and for future forest responses to novel chemical perturbations, such as nitrogen deposition. A multiple resource perspective is useful in

this regard, as many novel perturbations involve changes in seedlings' resource environment (Field *et al.* 1992, Bazzaz & Catovsky 2000). If we can understand how species behave along a suite of resource axes, we should be able to predict patterns of future forest dynamics under a range of global change scenarios. In the current experiment, I examined how seedling responses to nitrogen deposition in the forest understory were contingent on environmental conditions determined by overstory canopy composition. My second experiment examining effects of nitrogen deposition on seedling responses to gap formation (see Chapter 5) should allow us to determine how increased nitrogen availability in the future will interact with human land-use patterns and frequency of disturbance events to influence future forest composition.

I have clearly demonstrated that increased nitrogen deposition will alter the structure and dynamics of early stages of the understory seedling bank in mixed temperate forests in eastern North America, but that the exact nature of the change will be dependent on future landscape stand composition. My results have shown that the contribution of hemlock, and possibly birch, to the understory seedling bank will likely increase, while contributions of red maple, red spruce, and possibly white pine, will decrease. These nitrogen-induced changes will be more marked if hemlock remains a significant component of these forests. As hemlock seedlings were favored in hemlock stands over other common seedling bank species, such as red maple and white pine, nitrogen deposition might accentuate current positive feedback effects acting in these stands, and thus encourage the persistence of these hemlock stands across the landscape, in the absence of any other disturbances.

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Table 4.1. Details of study species used for seedling and seed addition components of experiment.

| Species | Common name | Leaf habit | Successional position ^a | Average seed weight (mg) ^b | Years of seed collection |
|------------------------------|------------------------|------------------------|------------------------------------|---------------------------------------|--------------------------|
| <i>Tsuga canadensis</i> | Eastern hemlock | Evergreen coniferous | 5 | 2.5 | 1996, 1998 |
| <i>Picea rubens</i> | Red spruce | Evergreen coniferous | 4 | 3.5 | 1996 |
| <i>Pinus strobus</i> | White pine | Evergreen coniferous | 3 | 20 | 1996 |
| <i>Acer saccharum</i> | Sugar maple | Deciduous broad-leaved | 5 | 75 | 1996, 1998 |
| <i>Acer rubrum</i> | Red maple ^c | Deciduous broad-leaved | 4 | 15 | 1997, 1998 |
| <i>Betula alleghaniensis</i> | Yellow birch | Deciduous broad-leaved | 3 | 0.5 | 1996, 1997 |

^a Based on Baker's Table, where 1 is earliest and 5 is latest successional.

^b Based on empirical measurements of seed samples.

^c Red maple seeds collected in spring.

Table 4.2. Details of seed input and seedling emergence patterns for both seed addition (a) and natural regeneration (b) plots.

| a) Seed Addition Plots | | | | |
|------------------------------|------|------------|---|---|
| Species | Year | Stand type | Seeds added (m ⁻²) ^a | Emergence (m ⁻²) ^b |
| <i>Tsuga canadensis</i> | 1998 | Hemlock | 100 | 1.74 |
| | | Red oak | 100 | 0.22 |
| | 1999 | Hemlock | 250 | 18.41 |
| | | Red oak | 250 | 0.00 |
| <i>Picea rubens</i> | 1998 | Hemlock | 100 | 1.48 |
| | | Red oak | 100 | 0.10 |
| | 1999 | Hemlock | 200 | 0.72 |
| | | Red oak | 200 | 0.00 |
| <i>Pinus strobus</i> | 1998 | Hemlock | 50 | 0.26 |
| | | Red oak | 50 | 0.04 |
| | 1999 | Hemlock | 150 | 0.05 |
| | | Red oak | 150 | 0.00 |
| <i>Acer saccharum</i> | 1998 | Hemlock | 50 | 0.00 |
| | | Red oak | 50 | 0.00 |
| | 1999 | Hemlock | 75 | 0.00 |
| | | Red oak | 75 | 0.00 |
| <i>Acer rubrum</i> | 1998 | Hemlock | 100 | 0.67 |
| | | Red oak | 100 | 0.12 |
| | 1999 | Hemlock | 250 | 0.20 |
| | | Red oak | 250 | 0.01 |
| <i>Betula alleghaniensis</i> | 1998 | Hemlock | 500 | 26.12 |
| | | Red oak | 500 | 4.25 |
| | 1999 | Hemlock | 250 | 36.86 |
| | | Red oak | 250 | 1.33 |

Table 4.2 cont.

| b) Natural Regeneration Plots | | | | |
|-------------------------------|------|------------|---|---|
| Species | Year | Stand type | Seed rain (m ⁻²) ^{abc} | Emergence (m ⁻²) ^b |
| <i>Tsuga canadensis</i> | 1998 | Hemlock | 20 | 0.00 |
| | | Red oak | 0.1 | 0.00 |
| | 1999 | Hemlock | 2500 | 15.40 |
| | | Red oak | 60 | 0.00 |
| <i>Acer rubrum</i> | 1998 | Hemlock | 75 | 0.47 |
| | | Red oak | 45 | 0.06 |
| | 1999 | Hemlock | 12 | 0.04 |
| | | Red oak | 10 | 0.01 |
| <i>Betula spp.</i> | 1998 | Hemlock | 500 | 15.29 |
| | | Red oak | 100 | 0.36 |
| | 1999 | Hemlock | 2000 | 28.43 |
| | | Red oak | 120 | 0.37 |

^a As seed germination commonly takes place the year after seed fall, seed inputs refer to previous year, i.e. 1997 and 1998.

^b Values in bold represent significant differences between stand types for each year-species combination (*post hocs*, $p < 0.05$).

^c Based on seed trap sampling. Full details in Chapter 2.

Table 4.3. Nitrogen addition effects on plot environment, showing Manova results (a) and slope coefficients for individual N effect (b).

| a) Manova results | | | | | | | | | | | | | |
|-------------------|-------------------|-----------------|----------------|-----------------|-----|-----------------------------|-----|--------------------|----|---------------|-----|-----|----|
| Factor | d.f. ^b | NH ₄ | | NO ₃ | | Light (canopy) ^a | | Light (understory) | | Soil moisture | | pH | |
| | | F ^c | p ^d | F | p | F | p | F | p | F | p | F | p |
| Stand | 1 | 0.0 | NS | 0.0 | NS | 8.4 | ** | 2.7 | NS | 0.0 | NS | 8.4 | * |
| Site (Stand) | 4 | 0.4 | NS | 0.8 | NS | 43.6 | *** | 1.2 | NS | 12.3 | *** | 3.0 | * |
| N | 1 | 21.5 | *** | 44.6 | *** | 0.5 | NS | 0.7 | NS | 0.2 | NS | 0.5 | NS |
| N x Stand | 1 | 0.1 | NS | 1.9 | NS | 1.6 | NS | 0.3 | NS | 0.3 | NS | 0.6 | NS |

| b) Slopes for N effect | | | |
|------------------------|-------------------------------------|--------|-----|
| Factor | Units | Slope | p |
| NH ₄ | mg/g dry resin | 0.040 | *** |
| NO ₃ | mg/g dry resin | 0.144 | *** |
| Light (canopy) | % transmission | -0.200 | NS |
| Light (understory) | % transmission | -0.397 | NS |
| Soil moisture | g/g dry soil | -0.002 | NS |
| pH | log ₁₀ [H ⁺] | 0.005 | NS |

^a Light (canopy): % light transmitted from above canopy to 1 m; Light (understory): % light transmitted from 1 m to 5 cm.

^b Error degrees of freedom: 46.

^c Error mean squares: 0.040 (NH₄), 0.246 (NO₃), 0.466 (canopy light), 121.5 (understory light), 0.0072 (soil moisture), 0.030 (pH).

^d NS p>0.05, * p<0.05, ** p<0.01, *** p<0.001.

Table 4.4. Analysis of variance results (degrees of freedom, F ratios, p values) for seedling emergence (natural logarithm of square root transformed) in seed addition and natural regeneration plots.

| Factor | Seed Addition | | | Natural Regeneration | | |
|----------------------------|---------------|----------------|----------------|----------------------|-------|-----|
| | d.f. | F ^a | p ^b | d.f. | F | p |
| Year | 1 | 38.67 | *** | 1 | 5.74 | * |
| Stand | 1 | 0.75 | NS | 1 | 0.10 | NS |
| Stand x Year | 1 | 36.52 | *** | 1 | 3.23 | * |
| Site (Stand) | 4 | 5.02 | ** | 4 | 19.72 | *** |
| Plot (Site) | 46 | 1.96 | *** | 46 | 1.09 | NS |
| Species | 4 | 26.22 | *** | 2 | 53.69 | *** |
| Species x Year | 4 | 1.16 | NS | 2 | 25.56 | *** |
| Species x Stand | 4 | 5.46 | *** | 2 | 9.81 | *** |
| Species x Stand x Year | 4 | 2.36 | * | 2 | 11.23 | *** |
| N | 1 | 3.94 | * | 1 | 0.71 | NS |
| N x Year | 1 | 0.50 | NS | 1 | 0.29 | NS |
| N x Stand | 1 | 1.50 | NS | 1 | 2.85 | NS |
| N x Stand x Year | 1 | 1.13 | NS | 1 | 3.82 | * |
| N x Species | 4 | 0.54 | NS | 2 | 1.45 | NS |
| N x Species x Year | 4 | 0.92 | NS | 2 | 1.55 | NS |
| N x Species x Stand | 4 | 2.52 | * | 2 | 0.17 | NS |
| N x Species x Stand x Year | 4 | 0.85 | NS | 2 | 0.12 | NS |

^a Error mean square: 2.08, d.f. 450 (seed addition); 2.07, d.f. 250 (natural regeneration).

^b NS $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Table 4.5. Logistic analysis of variance results (degrees of freedom, F ratios, p values) for first-year seedling monthly survival (logit transformed) in different sub-plots.

| Factor | Seed Addition | | | Natural Regeneration | | | Planted Seedlings | | |
|------------------------------------|---------------|----------------|----------------|----------------------|------|----|-------------------|-------|-----|
| | d.f. | F ^a | p ^b | d.f. | F | p | d.f. | F | p |
| Year | 1 | 0.43 | NS | 1 | 0.25 | NS | 1 | 69.99 | *** |
| Month | 3 | 2.85 | * | 3 | 4.33 | ** | 2 | 43.87 | *** |
| Month x Year | 3 | 1.95 | NS | 3 | 2.72 | * | 2 | 1.44 | NS |
| Stand | 1 | 19.53 | * | 1 | 0.05 | NS | 1 | 0.12 | NS |
| Stand x Year | 1 | 0.03 | NS | 1 | 0.97 | NS | 1 | 13.58 | *** |
| Stand x Month | 3 | 3.11 | * | 3 | 1.37 | NS | 2 | 10.57 | *** |
| Stand x Month x Year | 3 | 3.84 | ** | 3 | 0.59 | NS | 2 | 3.78 | * |
| Site (Stand) | 4 | 0.13 | NS | 4 | 4.25 | ** | 4 | 11.96 | *** |
| Plot (Site) | 46 | 1.25 | NS | 45 | 1.11 | NS | 46 | 1.56 | * |
| Species | 4 | 2.87 | * | 2 | 3.57 | * | 5 | 19.51 | *** |
| Species x Year | 4 | 0.71 | NS | 2 | 0.44 | NS | 5 | 10.11 | *** |
| Species x Month | 12 | 4.07 | *** | 6 | 2.28 | * | 10 | 4.59 | *** |
| Species x Month x Year | 11 | 2.29 | ** | 6 | 2.50 | * | 10 | 3.23 | *** |
| Species x Stand | 4 | 2.42 | * | 2 | 1.94 | NS | 5 | 1.02 | NS |
| Species x Stand x Year | 3 | 0.24 | NS | 1 | 0.97 | NS | 5 | 1.02 | NS |
| Species x Stand x Month | 12 | 1.96 | * | 3 | 0.87 | NS | 10 | 1.12 | NS |
| Species x Stand x Month x Year | 7 | 1.16 | NS | 3 | 0.62 | NS | 10 | 1.22 | NS |
| N | 1 | 0.50 | NS | 1 | 1.20 | NS | 1 | 1.55 | NS |
| N x Year | 1 | 9.28 | ** | 1 | 0.34 | NS | 1 | 7.11 | ** |
| N x Month | 3 | 1.98 | NS | 3 | 2.03 | NS | 2 | 1.84 | NS |
| N x Month x Year | 3 | 0.95 | NS | 3 | 1.30 | NS | 2 | 0.02 | NS |
| N x Stand | 1 | 1.84 | NS | 1 | 0.45 | NS | 1 | 2.25 | NS |
| N x Stand x Year | 1 | 9.33 | ** | 1 | 1.71 | NS | 1 | 0.06 | NS |
| N x Stand x Month | 3 | 2.08 | NS | 3 | 0.76 | NS | 2 | 0.14 | NS |
| N x Stand x Month x Year | 3 | 1.93 | NS | 3 | 1.62 | NS | 2 | 0.78 | NS |
| N x Species | 4 | 0.91 | NS | 2 | 3.68 | * | 5 | 1.65 | NS |
| N x Species x Year | 4 | 3.92 | ** | 2 | 0.12 | NS | 5 | 0.47 | NS |
| N x Species x Month | 11 | 0.85 | NS | 6 | 1.55 | NS | 10 | 1.31 | NS |
| N x Species x Month x Year | 9 | 1.41 | NS | 4 | 0.85 | NS | 10 | 0.37 | NS |
| N x Species x Stand | 4 | 3.68 | ** | 2 | 1.22 | NS | 5 | 0.69 | NS |
| N x Species x Stand x Year | 3 | 2.02 | NS | 1 | 2.52 | NS | 5 | 1.16 | NS |
| N x Species x Stand x Month | 11 | 1.49 | NS | 3 | 0.44 | NS | 10 | 0.25 | NS |
| N x Species x Stand x Month x Year | 2 | 0.73 | NS | 1 | 0.04 | NS | 10 | 1.29 | NS |

^a Error mean square: 2.29, d.f. 1815 (seed addition); 5.60, d.f. 891 (natural regeneration); 6.13, d.f. 2350 (planted seedlings).

^b NS $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Table 4.6. Analysis of variance results (degrees of freedom, F ratios, p values) for first-year abundance (natural logarithm of square root transformed) in different sub-plots.

| Factor | Seed Addition | | | Natural Regeneration | | | Planted Seedlings | | |
|------------------------------------|---------------|----------------|----------------|----------------------|-------|-----|-------------------|-------|-----|
| | d.f. | F ^a | p ^b | d.f. | F | p | d.f. | F | p |
| Year | 1 | 5.339 | * | 1 | 7.486 | ** | 1 | 37.05 | *** |
| Month | 4 | 39.31 | *** | 4 | 13.47 | *** | 3 | 112.7 | *** |
| Month x Year | 4 | 5.211 | *** | 4 | 3.703 | ** | 3 | 5.472 | *** |
| Stand | 1 | 0.156 | NS | 1 | 0.139 | NS | 1 | 0.618 | NS |
| Stand x Year | 1 | 0.461 | NS | 1 | 0.838 | NS | 1 | 26.48 | *** |
| Stand x Month | 4 | 0.843 | NS | 4 | 1.359 | NS | 3 | 14.34 | *** |
| Stand x Month x Year | 4 | 0.715 | NS | 4 | 0.833 | NS | 3 | 4.642 | ** |
| Site (Stand) | 4 | 2.961 | * | 4 | 6.648 | *** | 4 | 4.669 | ** |
| Plot (Site) | 46 | 5.496 | *** | 45 | 3.053 | *** | 46 | 2.781 | *** |
| Species | 4 | 8.389 | *** | 2 | 7.607 | *** | 5 | 63.53 | *** |
| Species x Year | 4 | 3.712 | ** | 2 | 10.27 | *** | 5 | 31.17 | *** |
| Species x Month | 16 | 7.542 | *** | 8 | 4.815 | *** | 15 | 7.519 | *** |
| Species x Month x Year | 16 | 1.947 | * | 8 | 2.764 | ** | 15 | 4.523 | *** |
| Species x Stand | 4 | 10.06 | *** | 2 | 12.47 | *** | 5 | 5.838 | *** |
| Species x Stand x Year | 4 | 3.295 | * | 1 | 3.862 | * | 5 | 5.036 | *** |
| Species x Stand x Month | 16 | 1.812 | * | 8 | 2.538 | ** | 15 | 1.242 | NS |
| Species x Stand x Month x Year | 16 | 0.655 | NS | 4 | 1.103 | NS | 15 | 0.989 | NS |
| N | 1 | 1.006 | NS | 1 | 0.057 | NS | 1 | 0.674 | NS |
| N x Year | 1 | 0.272 | NS | 1 | 17.6 | *** | 1 | 2.371 | NS |
| N x Month | 4 | 1.106 | NS | 4 | 0.26 | NS | 3 | 0.079 | NS |
| N x Month x Year | 4 | 1.229 | NS | 4 | 2.152 | NS | 3 | 0.272 | NS |
| N x Stand | 1 | 0.319 | NS | 1 | 0.568 | NS | 1 | 0.023 | NS |
| N x Stand x Year | 1 | 1.227 | NS | 1 | 6.616 | ** | 1 | 9.081 | ** |
| N x Stand x Month | 4 | 1.577 | NS | 4 | 0.078 | NS | 3 | 0.298 | NS |
| N x Stand x Month x Year | 4 | 1.011 | NS | 4 | 1.21 | NS | 3 | 1.182 | NS |
| N x Species | 4 | 2.787 | * | 2 | 3.85 | * | 5 | 4.117 | *** |
| N x Species x Year | 4 | 1.789 | NS | 2 | 0.967 | NS | 5 | 3.546 | ** |
| N x Species x Month | 16 | 0.871 | NS | 8 | 0.269 | NS | 15 | 0.645 | NS |
| N x Species x Month x Year | 16 | 0.833 | NS | 8 | 0.767 | NS | 15 | 0.63 | NS |
| N x Species x Stand | 4 | 0.882 | NS | 2 | 0.862 | NS | 5 | 3.663 | ** |
| N x Species x Stand x Year | 3 | 3.095 | * | 1 | 3.859 | * | 5 | 1.554 | NS |
| N x Species x Stand x Month | 16 | 0.579 | NS | 8 | 0.105 | NS | 15 | 0.851 | NS |
| N x Species x Stand x Month x Year | 12 | 0.964 | NS | 4 | 0.909 | NS | 15 | 0.453 | NS |

^a Error mean square: 9.71, d.f. 761 (seed addition); 9.20, d.f. 376 (natural regeneration); 7.98, d.f. 1465 (planted seedlings).

^b NS p>0.05, * p<0.05, ** p<0.01, *** p<0.001.

Table 4.7. Multivariate analysis of variance results (degrees of freedom, F ratios, p values) for scores on the first two axes of detrended correspondence analysis (DCA) of first-year understory community composition, and for seedling bank species diversity, in different sub-plots.

| a) Seed Addition Plots | Overall Effect ^a | | | DCA Axis 1 | | DCA Axis 2 | | Species Diversity ^b | |
|--------------------------|-----------------------------|-------|----------------|----------------|-----|----------------|-----|--------------------------------|-----|
| | d.f. ^c | F | p ^d | F ^e | p | F ^f | p | F ^g | p |
| Year | 1 | 1.06 | NS | 1.94 | NS | 0.76 | NS | 81.12 | *** |
| Month | 4 | 18.8 | *** | 14.99 | *** | 25.25 | *** | 15.07 | *** |
| Month x Year | 4 | 2.6 | ** | 4.84 | *** | 1.38 | NS | 16.72 | *** |
| Stand | 1 | 3 | NS | 7.90 | * | 1.91 | NS | 0.15 | NS |
| Stand x Year | 1 | 25.6 | *** | 43.55 | *** | 0.15 | NS | 9.36 | ** |
| Stand x Month | 4 | 5.25 | *** | 8.90 | *** | 0.38 | NS | 1.69 | NS |
| Stand x Month x Year | 4 | 1.5 | NS | 1.07 | NS | 1.06 | NS | 1.72 | NS |
| Site (Stand) | 4 | 2.42 | * | 3.13 | * | 1.39 | NS | 1.95 | NS |
| Plot (Site) | 46 | 2.93 | *** | 3.04 | *** | 2.93 | *** | 3.77 | *** |
| N | 1 | 5.03 | ** | 6.87 | ** | 6.64 | * | 5.68 | * |
| N x Year | 1 | 0.221 | NS | 0.39 | NS | 0.00 | NS | 11.04 | ** |
| N x Month | 4 | 2.12 | * | 3.49 | ** | 0.77 | NS | 1.31 | NS |
| N x Month x Year | 4 | 0.56 | NS | 0.53 | NS | 0.86 | NS | 2.49 | * |
| N x Stand | 1 | 12.8 | *** | 24.68 | *** | 6.90 | ** | 4.04 | * |
| N x Stand x Year | 1 | 1 | NS | 1.00 | NS | 0.37 | NS | 1.29 | NS |
| N x Stand x Month | 4 | 1.11 | NS | 1.01 | NS | 0.73 | NS | 1.42 | NS |
| N x Stand x Month x Year | 4 | 0.954 | NS | 0.33 | NS | 1.34 | NS | 0.33 | NS |

Table 4.7 cont (i).

| b) Natural Regeneration Plots | d.f. | Overall Effect | | Axis 1 | | Axis 2 | | Species Diversity | |
|-------------------------------|------|----------------|-----|--------|-----|--------|-----|-------------------|-----|
| | | F | p | F | p | F | p | F | p |
| Year | 1 | 109.00 | *** | 4.44 | * | 79.65 | *** | 15.33 | *** |
| Month | 4 | 12.20 | *** | 12.26 | *** | 20.50 | *** | 2.86 | * |
| Month x Year | 4 | 5.62 | *** | 0.97 | NS | 8.46 | *** | 13.31 | *** |
| Stand | 1 | 9.65 | * | 14.78 | * | 2.25 | NS | 0.35 | NS |
| Stand x Year | 1 | 100.00 | *** | 57.66 | *** | 10.02 | ** | 2.19 | NS |
| Stand x Month | 4 | 7.24 | *** | 11.25 | *** | 3.73 | ** | 0.49 | NS |
| Stand x Month x Year | 4 | 6.78 | *** | 5.97 | *** | 5.54 | *** | 1.66 | NS |
| Site (Stand) | 4 | 1.59 | NS | 0.43 | NS | 0.37 | NS | 2.76 | * |
| Plot (Site) | 45 | 2.79 | *** | 3.46 | *** | 3.77 | *** | 1.80 | ** |
| N | 1 | 4.16 | * | 6.51 | * | 7.60 | ** | 0.91 | NS |
| N x Year | 1 | 3.55 | * | 0.70 | NS | 0.82 | NS | 15.30 | *** |
| N x Month | 4 | 0.80 | NS | 0.55 | NS | 1.23 | NS | 2.92 | * |
| N x Month x Year | 4 | 0.66 | NS | 0.88 | NS | 0.11 | NS | 3.06 | * |
| N x Stand | 1 | 3.57 | * | 4.01 | * | 4.72 | * | 0.14 | NS |
| N x Stand x Year | 1 | 2.42 | NS | 1.46 | NS | 0.21 | NS | 0.45 | NS |
| N x Stand x Month | 4 | 0.49 | NS | 0.59 | NS | 0.12 | NS | 0.16 | NS |
| N x Stand x Month x Year | 4 | 0.90 | NS | 0.68 | NS | 1.24 | NS | 0.42 | NS |

Table 4.7 cont (ii).

| c) Planted Seedling Plots | d.f. | Overall Effect | | Axis 1 | | Axis 2 | | Species Diversity | |
|---------------------------|------|----------------|-----|--------|-----|--------|-----|-------------------|-----|
| | | F | p | F | p | F | p | F | p |
| Year | 1 | 191.00 | *** | 349.90 | *** | 2.63 | NS | 18.05 | *** |
| Month | 3 | 35.00 | *** | 7.32 | *** | 48.41 | *** | 85.49 | *** |
| Month x Year | 3 | 13.40 | *** | 24.05 | *** | 0.15 | NS | 4.99 | ** |
| Stand | 1 | 1.95 | NS | 0.10 | NS | 0.05 | NS | 0.78 | NS |
| Stand x Year | 1 | 14.50 | *** | 20.09 | *** | 1.26 | NS | 22.78 | *** |
| Stand x Month | 3 | 0.45 | NS | 0.28 | NS | 0.55 | NS | 12.57 | *** |
| Stand x Month x Year | 3 | 2.57 | * | 2.74 | * | 0.28 | NS | 6.31 | *** |
| Site (Stand) | 4 | 1.42 | NS | 0.84 | NS | 1.52 | NS | 4.06 | ** |
| Plot (Site) | 46 | 2.71 | *** | 2.67 | *** | 2.49 | *** | 2.35 | *** |
| N | 1 | 1.41 | NS | 1.22 | NS | 0.59 | NS | 0.40 | NS |
| N x Year | 1 | 3.56 | * | 4.92 | * | 4.87 | * | 1.21 | NS |
| N x Month | 3 | 1.21 | NS | 2.14 | NS | 0.65 | NS | 0.10 | NS |
| N x Month x Year | 3 | 0.92 | NS | 0.72 | NS | 1.53 | NS | 0.15 | NS |
| N x Stand | 1 | 0.20 | NS | 0.35 | NS | 0.00 | NS | 0.19 | NS |
| N x Stand x Year | 1 | 9.53 | *** | 2.00 | NS | 10.98 | ** | 1.76 | NS |
| N x Stand x Month | 3 | 0.43 | NS | 0.55 | NS | 0.08 | NS | 0.12 | NS |
| N x Stand x Month x Year | 3 | 1.29 | NS | 0.34 | NS | 1.40 | NS | 1.23 | NS |

^a Based on Wilks' Lambda criterion.

^b Calculated from Shannon-Weaver Diversity Index

^c Error d.f.: 313 (seed addition), 263 (natural regeneration), 347 (planted seedlings).

^d NS $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

^e Error mean square for Axis 1: 2260 (seed addition), 1643 (natural regeneration), 432 (planted seedlings).

^f Error mean square for Axis 2: 2142 (seed addition), 1487 (natural regeneration), 482 (planted seedlings).

^g Error mean square for Species diversity: 0.093 (seed addition), 0.060 (natural regeneration), 0.035 (planted seedlings).

Table 4.8. Analysis of variance results (degrees of freedom, F ratios, p values) for final biomass (natural logarithm transformed) in planted seedling plots.

| Factor | Individual seedling biomass | | | Total plot-level seedling biomass ^a | |
|---------------------------|-----------------------------|----------------|----------------|--|-----|
| | d.f. | F ^b | p ^c | F | p |
| Stand | 1 | 7.95 | * | 0.36 | NS |
| Site (Stand) | 4 | 0.87 | NS | 5.01 | ** |
| Plot (Site) | 46 | 1.49 | * | 1.82 | ** |
| Species | 4 | 76.83 | *** | 39.47 | *** |
| Species x Stand | 4 | 1.23 | NS | 1.14 | NS |
| Age | 1 | 4.41 | * | 0.93 | NS |
| Age x Stand | 1 | 0.00 | NS | 0.29 | NS |
| Age x Species | 4 | 8.02 | *** | 9.00 | *** |
| Age x Species x Stand | 4 | 1.37 | NS | 1.73 | NS |
| N | 1 | 0.03 | NS | 0.13 | NS |
| N x Stand | 1 | 0.02 | NS | 1.33 | NS |
| N x Species | 4 | 0.25 | NS | 0.78 | NS |
| N x Species x Stand | 4 | 0.78 | NS | 0.87 | NS |
| N x Age | 1 | 0.30 | NS | 0.72 | NS |
| N x Age x Stand | 1 | 0.28 | NS | 0.65 | NS |
| N x Age x Species | 4 | 0.55 | NS | 0.63 | NS |
| N x Age x Species x Stand | 3 | 0.35 | NS | 0.70 | NS |

^a Combination of individual seedling biomass and final seedling abundance of species in each plot.

^b Error mean square: 0.24, d.f. 560 (individual biomass); 0.39, d.f. 210 (total biomass).

^c NS $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Table 4.9. Multivariate analysis of variance results (degrees of freedom, F ratios, p values) for foliar chlorophyll concentrations (on both area and dry weight basis) and specific leaf weight of second-year planted seedlings.

| Factor | d.f. ^a | Chlorophyll (as area) $\mu\text{g cm}^{-2}$ | | Chlorophyll (as weight) $\mu\text{g mg}^{-1}$ | | Specific leaf weight mg cm^{-2} | |
|---------------------------|-------------------|---|----------------|---|-----|--|-----|
| | | F ^b | p ^c | F | p | F | p |
| Stand | 1 | 10.89 | * | 2.11 | NS | 0.07 | NS |
| Site (Stand) | 4 | 0.55 | NS | 1.10 | NS | 1.42 | NS |
| Plot (Site) | 46 | 1.85 | ** | 1.82 | ** | 1.15 | NS |
| Species | 4 | 22.60 | *** | 28.85 | *** | 67.07 | *** |
| Species x Stand | 4 | 2.88 | * | 4.22 | ** | 1.09 | NS |
| Age | 1 | 0.10 | NS | 1.25 | NS | 1.27 | NS |
| Age x Stand | 1 | 7.22 | ** | 6.03 | * | 0.05 | NS |
| Age x Species | 3 | 0.99 | NS | 3.34 | * | 1.71 | NS |
| Age x Species x Stand | 3 | 3.29 | * | 4.54 | ** | 1.21 | NS |
| N | 1 | 2.26 | NS | 0.34 | NS | 0.58 | NS |
| N x Stand | 1 | 4.76 | * | 1.86 | NS | 1.37 | NS |
| N x Species | 4 | 4.74 | ** | 3.51 | ** | 0.61 | NS |
| N x Species x Stand | 4 | 3.01 | * | 3.48 | ** | 0.86 | NS |
| N x Age | 1 | 0.37 | NS | 1.20 | NS | 0.87 | NS |
| N x Age x Stand | 1 | 0.88 | NS | 1.64 | NS | 0.89 | NS |
| N x Age x Species | 3 | 0.83 | NS | 1.17 | NS | 0.21 | NS |
| N x Age x Species x Stand | 3 | 0.84 | NS | 1.13 | NS | 0.52 | NS |

^a Error d.f.: 197.

^b Error mean square: 32.91 (chlorophyll, as area), 2.01 (chlorophyll, as weight), 0.63 (specific leaf weight).

^c NS $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Figure 4.1. Effects of nitrogen addition on seedling emergence in seed addition plots in hemlock (a) and red oak (b) stands (mean \pm 1 SEM, pooled across years). Note the difference in scales for birch vs. other species. Values above each species represent slope coefficients calculated using transformed data. Slopes significantly greater than zero ($p < 0.05$) are shown in bold and with an asterisk.

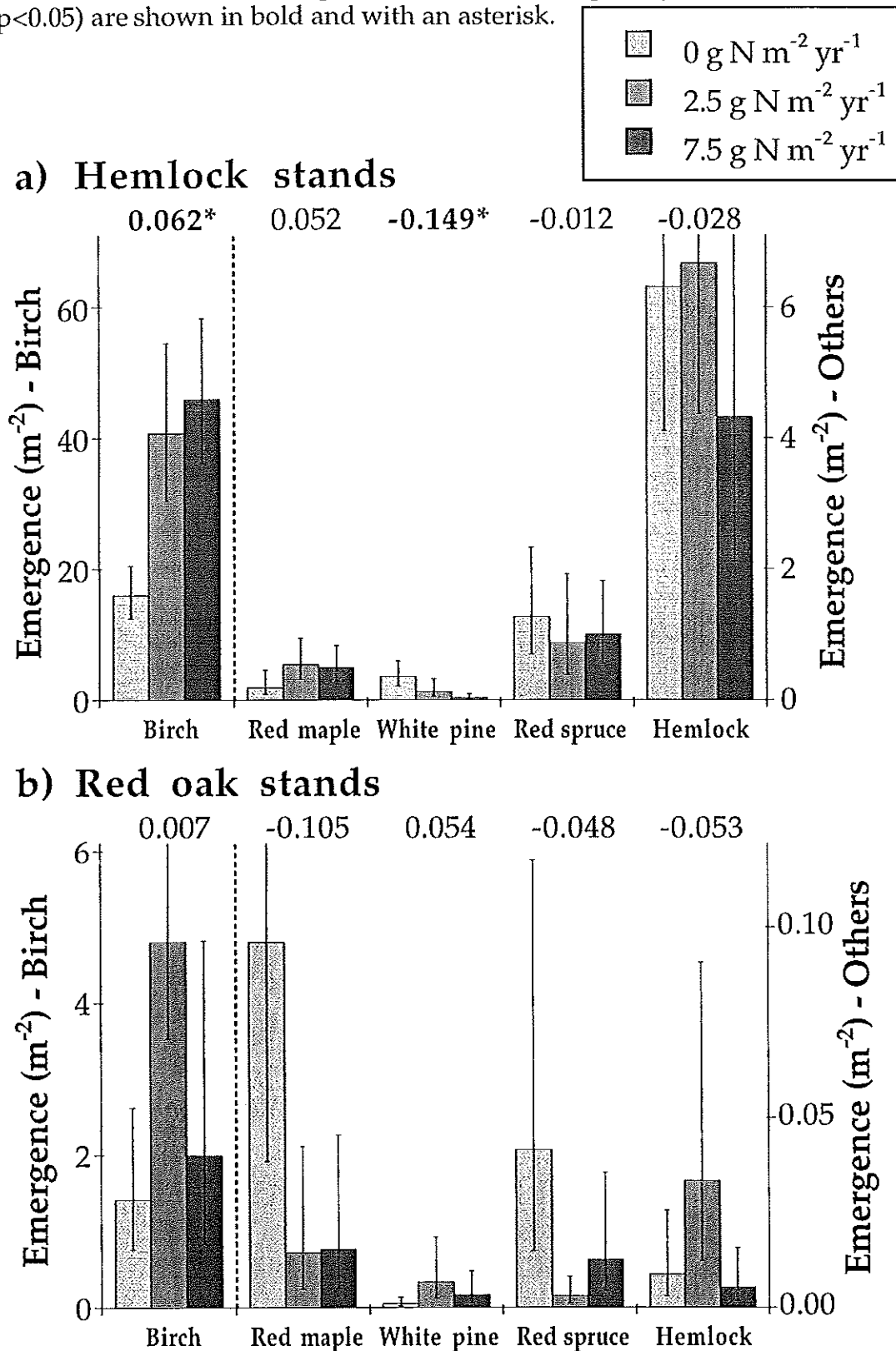
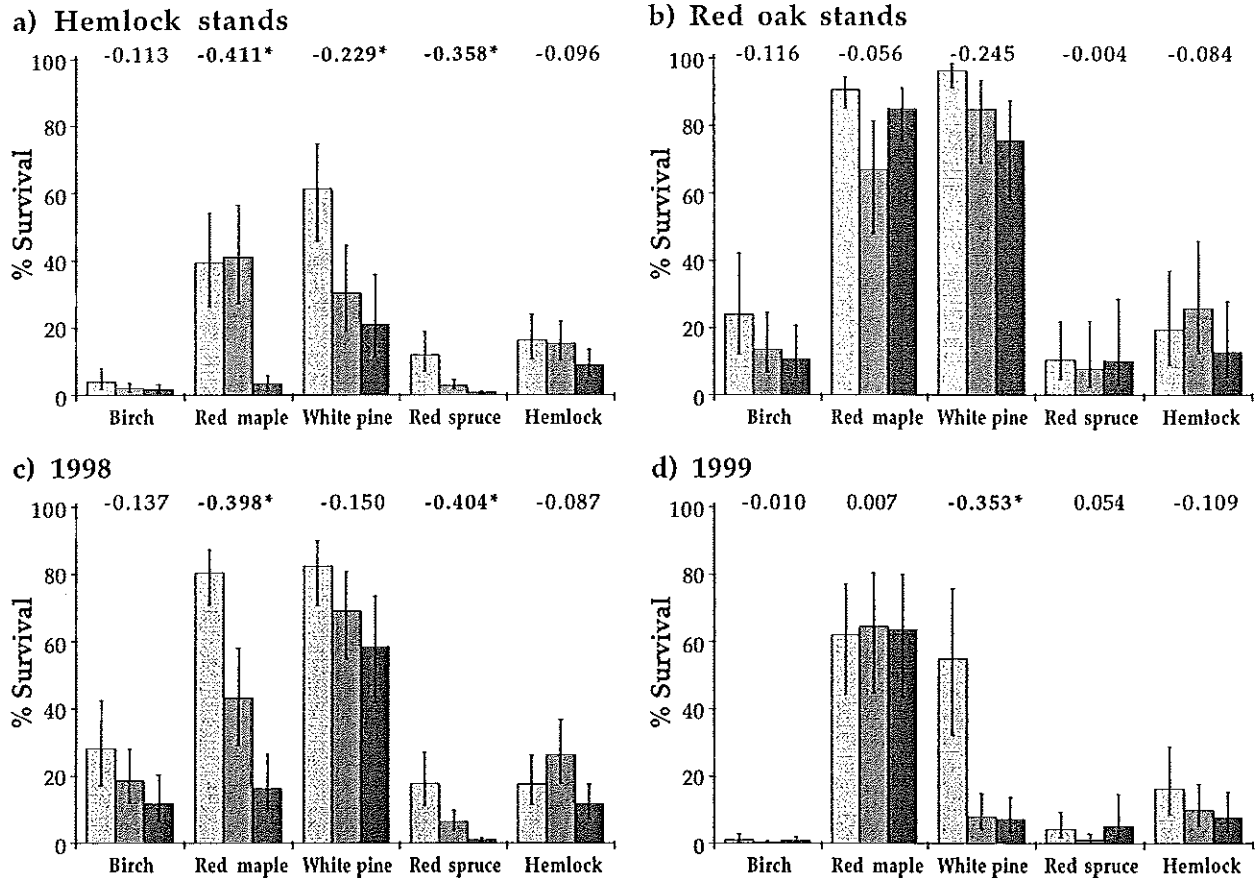


Figure 4.2. Effects of nitrogen addition on seedling survival (mean \pm 1 SEM, pooled across months). For seed addition plots, effects are shown for hemlock (a) and red oak (b) stands separately (pooled across years), and for 1998 (c) and 1999 (d) separately (pooled across stands). For natural regeneration plots (e), effects are shown pooled across stand types and years. Values above each species represent slope coefficients calculated using transformed data. Slopes significantly greater than zero ($p < 0.05$) are shown in bold and with an asterisk.

(a-d) Seed Addition Plots



(e) Natural Regeneration Plots

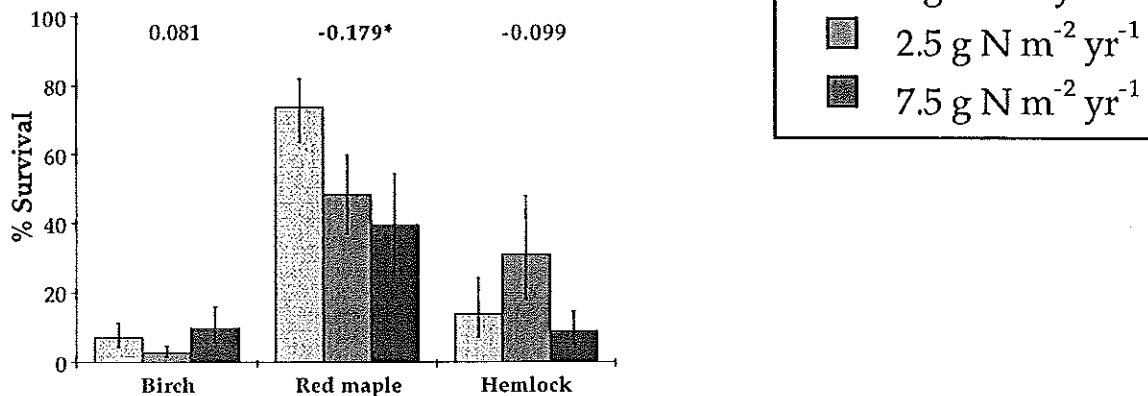


Figure 4.3. Effects of nitrogen addition on survival of planted seedlings after the first growing season (mean \pm 1 SEM). Effects are shown pooled across stand types for over-winter survival (a), and separately for second-year survival (across full length of growing season) in hemlock (b) and red oak (c) stands. Values above each species represent slope coefficients calculated using transformed data. Slopes significantly greater than zero ($p < 0.05$) are shown in bold and with an asterisk.

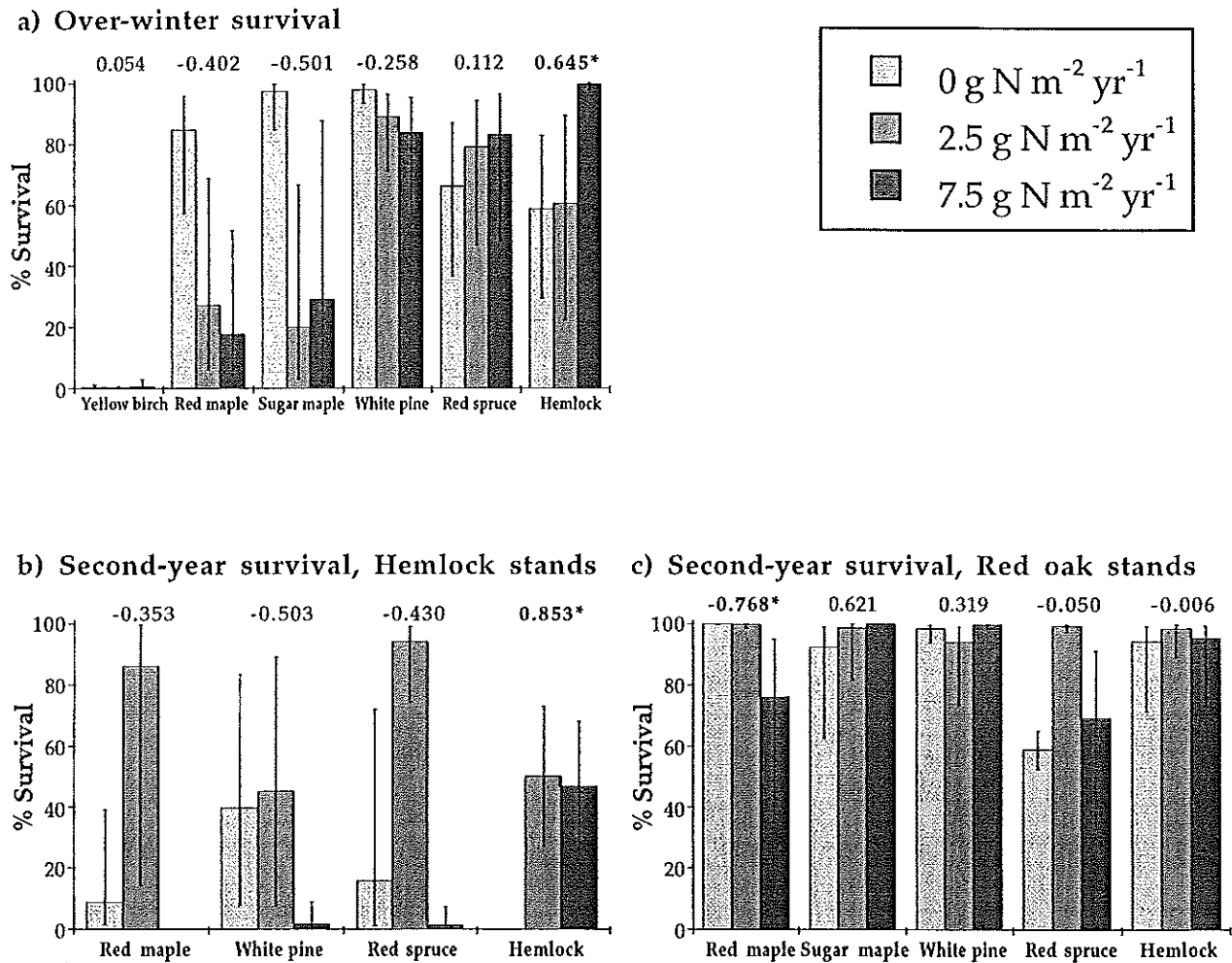
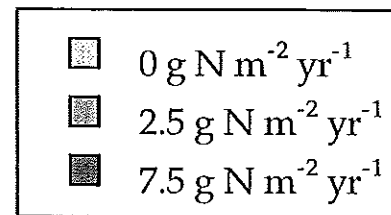
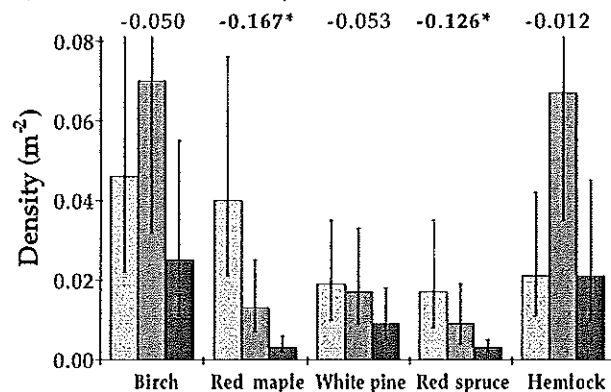


Figure 4.4. Effects of nitrogen addition on seedling understory abundance in seed addition and natural regeneration plots (mean \pm 1 SEM, pooled across months). Effects are shown separately for each stand \times year combination. Values above each species represent slope coefficients calculated using transformed data. Slopes significantly greater than zero ($p < 0.05$) are shown in bold and with an asterisk.

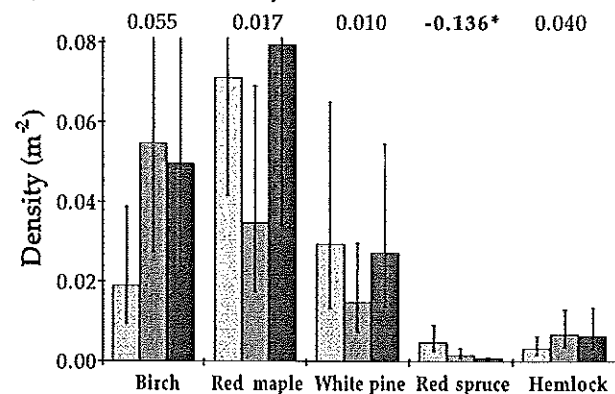
(a-d) Seed Addition Plots



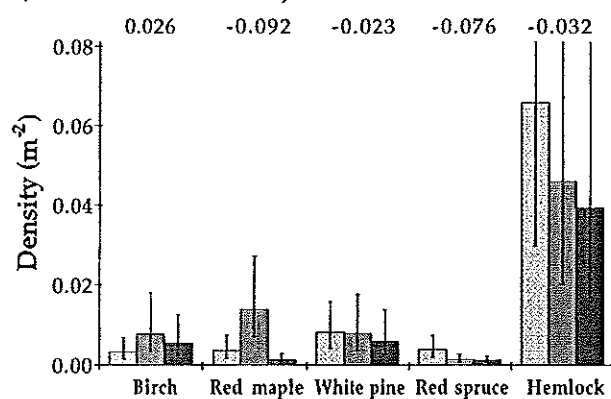
a) Hemlock stands, 1998



b) Red oak stands, 1998



c) Hemlock stands, 1999



d) Red oak stands, 1999

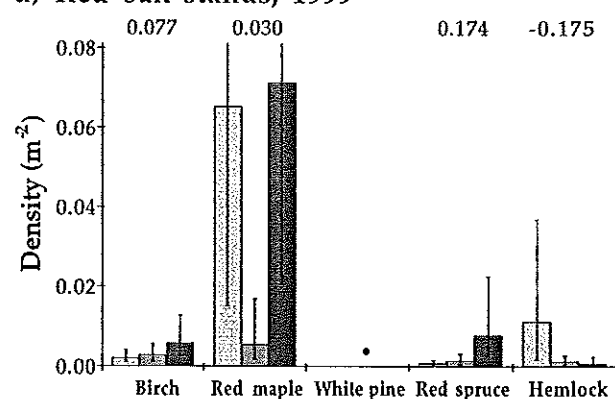


Figure 4.4. cont.

(e-h) Natural Regeneration Plots

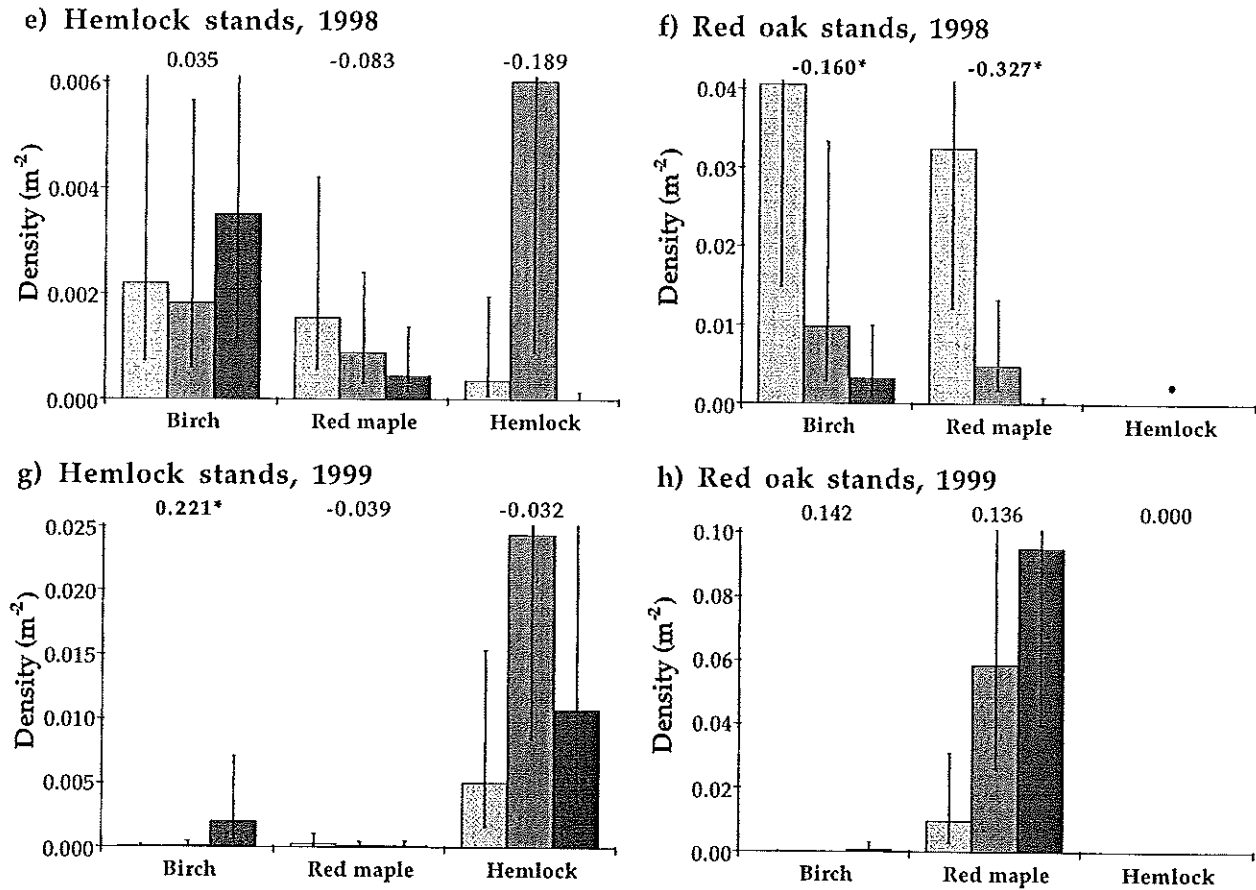


Figure 4.5. Effects of nitrogen addition on seedling understory abundance in planted seedling plots (mean \pm 1 SEM, pooled across months). For first-year abundance, effects are shown separately for each stand \times year combination, and for second-year abundance, effects are shown for each stand type. Values above each species represent slope coefficients calculated using transformed data. Slopes significantly greater than zero ($p < 0.05$) are shown in bold and with an asterisk.

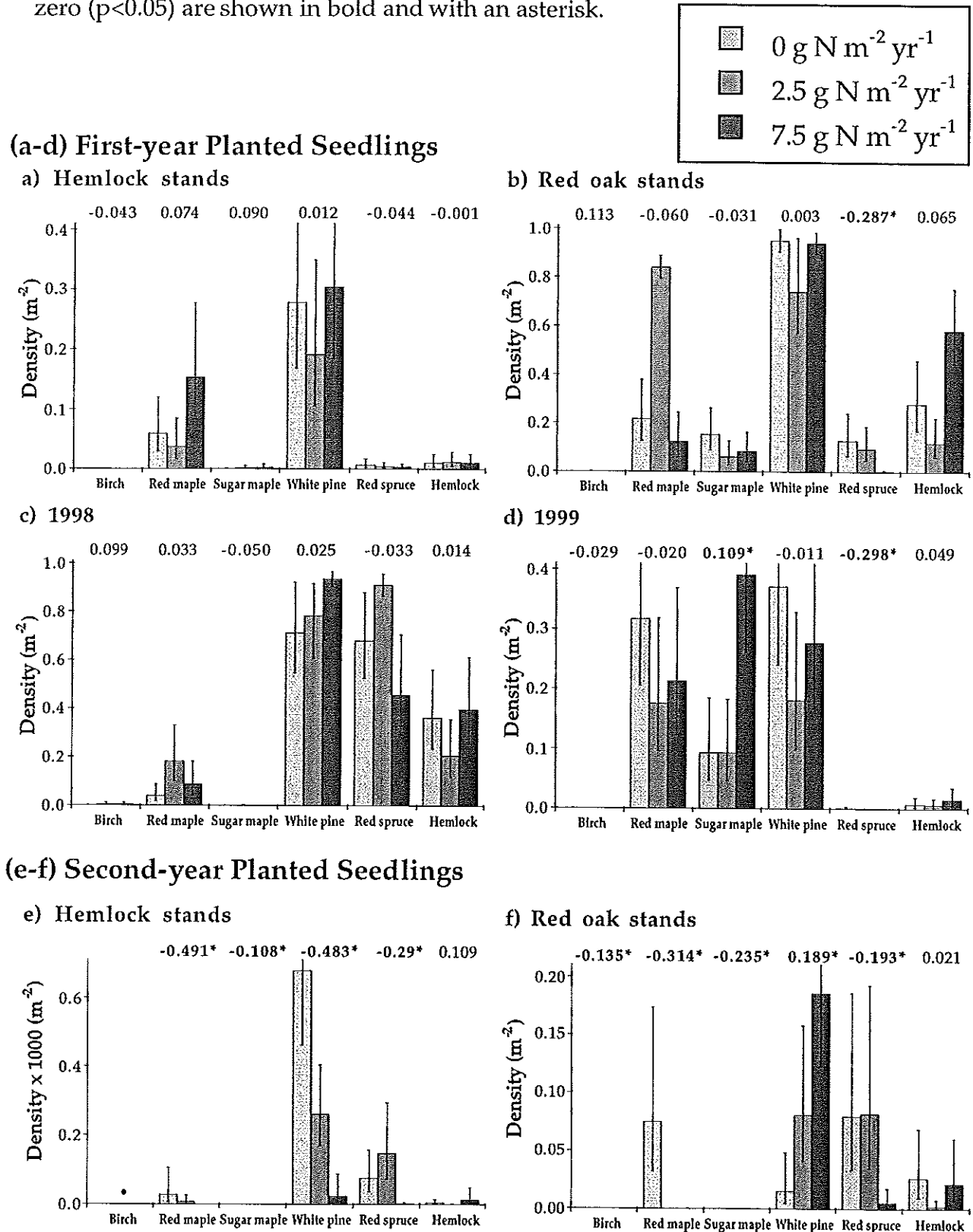
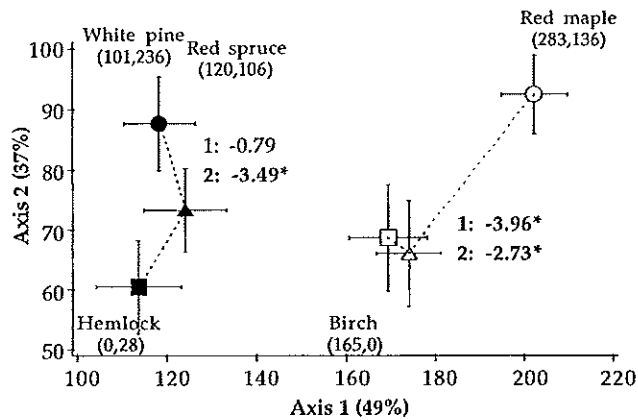


Figure 4.6. Effects of nitrogen addition on seedling community composition in different sub-plots, represented by mean treatment scores (± 1 SEM, pooled across months) on first two axes of detrended correspondence analysis (DCA). % variation explained by each axis is included for each DCA. For seed addition (a), natural regeneration (b), and second-year planted seedling plots (e), effects are shown separately for hemlock (black symbols) and red oak (white symbols) stands, and pooled across years for figs (a) and (b). For first-year planted seedling plots, a significant N \times stand \times year interaction is represented by separating growing seasons 1998 (c) and 1999 (d). Relative positions of species' scores are shown on each figure with species' names and their actual coordinates (x,y). Nitrogen plots within one stand type are connected with dashed lines, and values beside each stand type represent slope coefficients for each axis score against nitrogen addition. Slopes significantly greater than zero ($p < 0.05$) are shown in bold and with an asterisk.

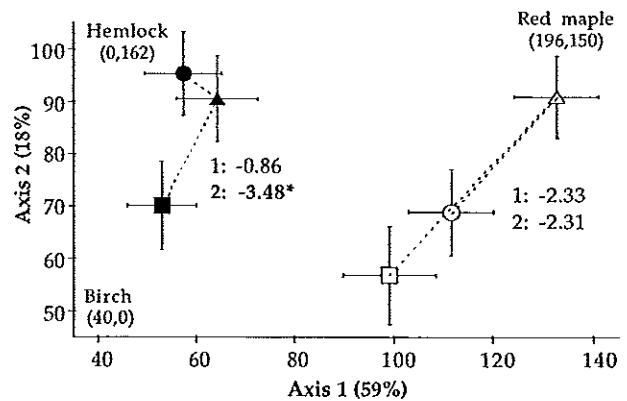
- Hemlock stands, 0 g N m⁻² yr⁻¹
- ▲ Hemlock stands, 2.5 g N m⁻² yr⁻¹
- Hemlock stands, 7.5 g N m⁻² yr⁻¹
- Red oak stands, 0 g N m⁻² yr⁻¹
- △ Red oak stands, 2.5 g N m⁻² yr⁻¹
- Red oak stands, 7.5 g N m⁻² yr⁻¹

Figure 4.6. cont.

(a) Seed Addition Plots

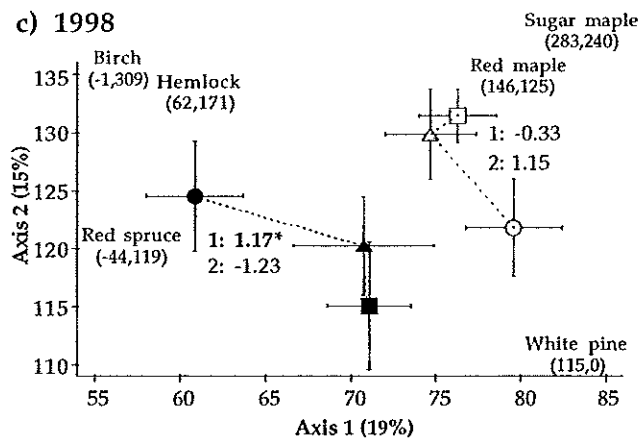


(b) Natural Regeneration Plots

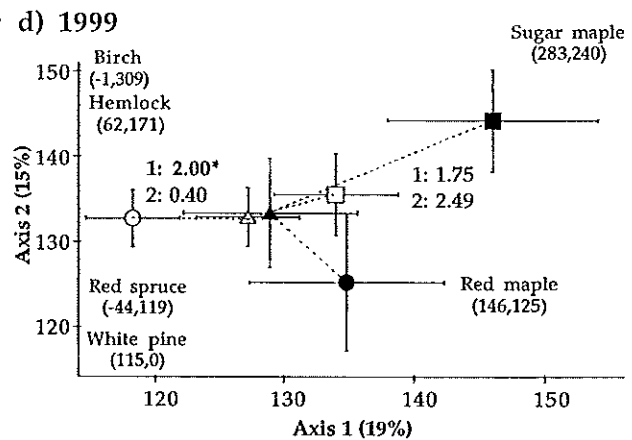


(c-d) First-year Planted Seedling Plots

c) 1998



d) 1999



(e) Second-year Planted Seedling Plots

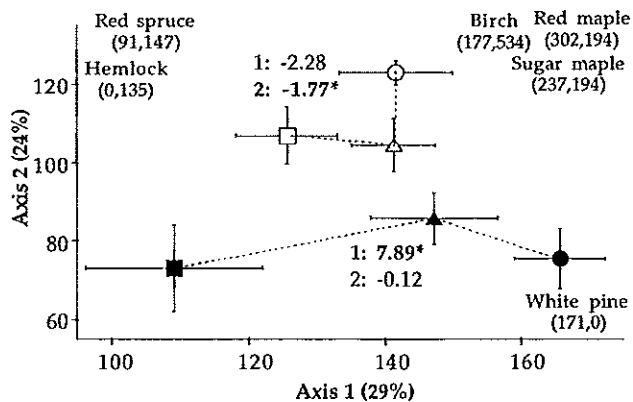
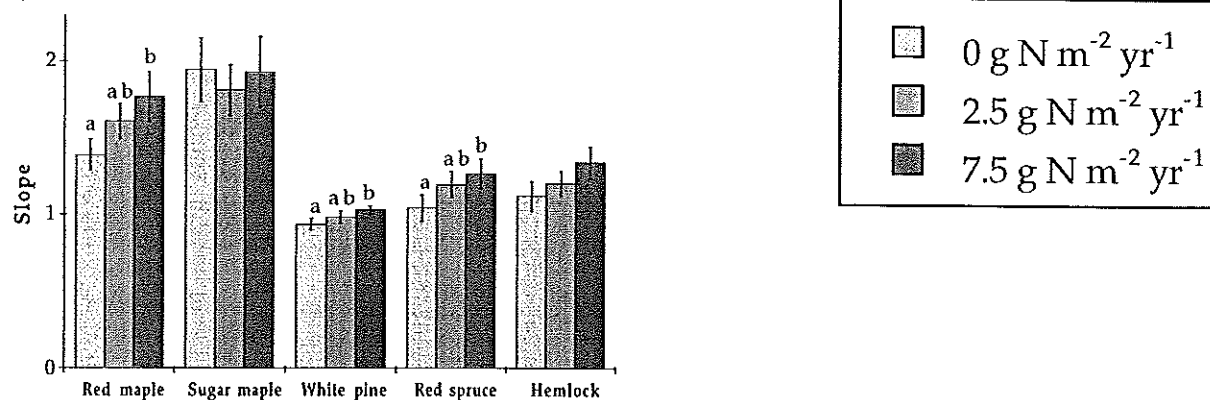
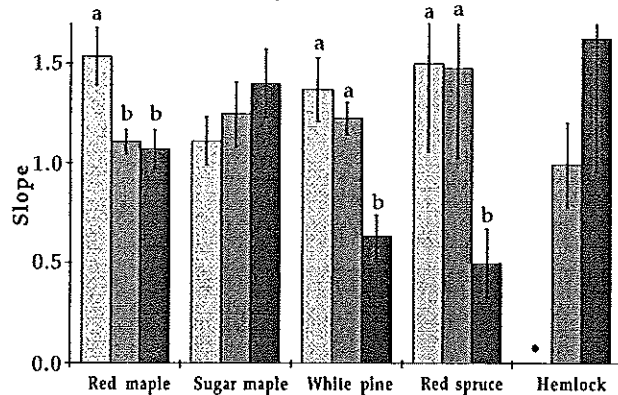


Figure 4.7. Effects of nitrogen addition on planted seedling allocation patterns (pooled across different seedling ages). Effects are shown as slopes (± 1 SE) from model II linear regression analysis of log leaf/root biomass vs. log total biomass for each species by nitrogen combination. For allocation to leaves (a), slopes are shown for regressions calculated on seedlings from both stand types, while for allocation to roots, effects in each stand type are shown separately. Slopes that were significantly different from one another within a species are shown by different letters ($p < 0.05$, planned comparisons, sequential Bonferroni corrected).

a) Leaf allocation



b) Root allocation, Hemlock stands



c) Root allocation, Red oak stands

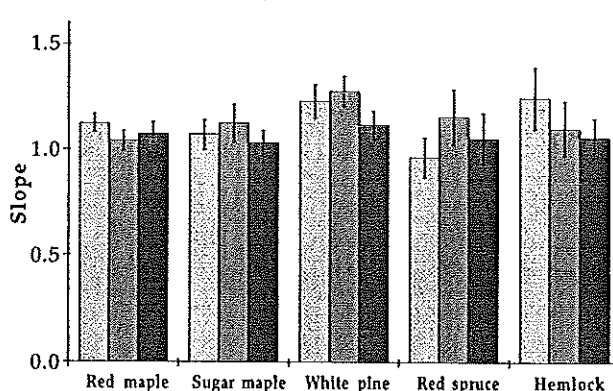
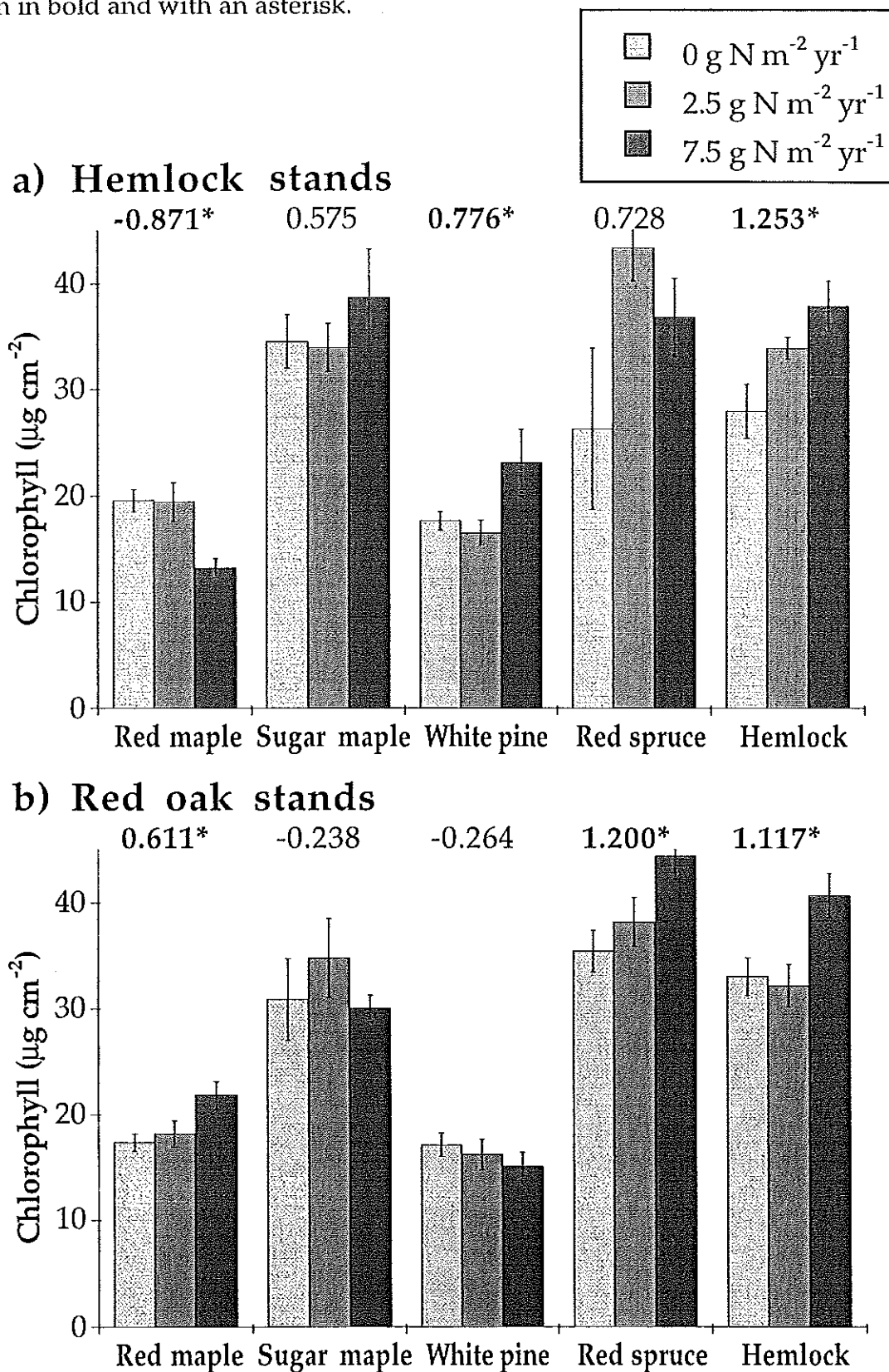


Figure 4.8. Effects of nitrogen addition on foliar chlorophyll concentrations (mean \pm 1 SEM, pooled across seedling ages), expressed on a leaf area basis, in both hemlock (a) and red oak (b) stands. Values above each species represent slope coefficients produced from linear models. Slopes significantly greater than zero ($p < 0.05$) are shown in bold and with an asterisk.



CHAPTER 5

NITROGEN DEPOSITION INFLUENCES REGENERATION OF CONIFEROUS AND BROAD-LEAVED TREE SPECIES. II. SEEDLING RESPONSES TO GAP FORMATION

Abstract. Increasing nitrogen deposition in temperate regions will likely have a profound influence on future forest structure and dynamics. These effects are expected to be particularly marked in transitional ecosystems, such as mixed conifer broad-leaved forests, which contain two distinct groups of tree species. To determine how nitrogen deposition may alter the future composition of such forests, I examined how seedlings of dominant coniferous and broad-leaved tree species in mixed temperate forests in eastern North America differ in their responses to increased nitrogen availability under simulated gap conditions (50 % irradiance). I grew seedlings of all six study species in a common garden for two years using forest soil collected in central Massachusetts (USA) from hemlock and red oak stands (dominant coniferous and broad-leaved tree species, respectively). When grown both individually and in mixed species competitive stands, the earlier successional broad-leaved species (yellow birch and red maple) consistently showed the greatest increases in biomass in response to nitrogen addition, while the most late successional of the broad-leaved species (sugar maple) and all the coniferous species examined did not grow significantly larger in treatments with higher nitrogen availability. At the community level, these changes led to concomitant declines in species diversity. I found a significant correlation between a species' growth rate during the first two years of its life and its growth enhancement following nitrogen addition, particularly for seedlings in competition, suggesting that growth rate, more than leaf habit or even successional position, may be a species' trait closely tied to nitrogen responsiveness. These patterns of species' responses to nitrogen addition were not contingent on the soil type on which seedlings were grown. I conclude that increased nitrogen deposition may interact with a number of other human-induced disturbance factors that are predicted to increase in frequency and further increase the contribution of earlier successional species to future forest composition.

INTRODUCTION

Increasing deposition of nitrogen into natural ecological systems has emerged as a major environmental perturbation in temperate regions of the world (Galloway *et al.* 1995, Vitousek *et al.* 1997). Temperate ecosystems are commonly limited by nitrogen availability (Vitousek & Howarth 1991), and thus increased nitrogen deposition is likely to have profound consequences for the structure and function of natural ecosystems in this region (Wedin & Tilman 1996). Research has particularly focused on the influence of nitrogen deposition on temperate forest ecosystem function, given the current importance of these forests as sinks in the contemporary global carbon cycle (Fan *et al.* 1998, Houghton *et al.* 1998). Large, long-term ecosystem-based experiments have been carried out both in the US (Magill *et al.* 1997) and in Europe (Emmett *et al.* 1998) to address the impact of nitrogen deposition on forest productivity and nutrient cycling. To date, however, remarkably few studies have considered how increased nitrogen availability may influence the structure and composition of temperate forests in the future (Crabtree & Bazzaz 1993). Mixed temperate forests may be particularly sensitive to nitrogen deposition in the future, as they contain two distinct groups of tree species (evergreen coniferous and deciduous broad-leaved) that may respond differently to increasing nitrogen availability, given their differences in leaf longevity and life-history strategy (Bond 1989). In the present experiment, I examine how some of the dominant coniferous and broad-leaved tree species in mixed temperate forests in eastern North America differ in their responses to increased nitrogen availability, and thus how nitrogen deposition may alter the composition and structure of such forests.

To determine potential impacts of nitrogen deposition on community composition, I focused on the influence of nitrogen availability on patterns of seedling regeneration. Given the pre-emptive nature of plant competition for resources (Weiner 1990), these early stages of a tree's life-cycle are a critical determinant of which individuals will successfully reach maturity and thus contribute to the future composition of the canopy stratum. In forests, primarily because of the height of the canopy, species are particularly dependent on disturbance events for regeneration

(Canham 1989, Bazzaz 1996). To incorporate this stage of regeneration into our understanding of forest responses to novel perturbations, I examined the influence of increased nitrogen deposition on seedling responses to canopy gap formation.

In addition, when considering responses of coniferous and broad-leaved tree species to nitrogen deposition, I accounted for the mosaic of stand types in mixed temperate forests (Pastor & Mladenoff 1992). In many temperate forests in north-eastern North America, hemlock (*Tsuga canadensis*) trees are clustered together on the landscape, forming hemlock-dominated stands in a matrix of predominantly broad-leaved tree species (Pastor & Broschart 1990). This landscape mosaic has been shown to be stable over many millennia (Davis *et al.* 1994) and is thought to be the result of a positive feedback between seedling regeneration and stand composition (Frelich *et al.* 1993). Regeneration of hemlock seedlings is favored over most broad-leaved tree seedlings in hemlock stands (see Chapters 2 and 3), as a result of hemlock's extreme tolerance of understory conditions, and thus stand composition may remain relatively constant over many regeneration cycles. Hemlock stands are typically characterized by lower rates of mineralization and nutrient turnover, and lower soil pH than the surrounding broad-leaved tree matrix (Finzi *et al.* 1998a,b). Contrasting patterns of nutrient availability in these two stand types may influence both current seedling regeneration responses to gap formation and future responses in an enhanced nitrogen environment. In the present experiment, I contrasted seedling responses to nitrogen addition on soil taken from stands dominated either by hemlock or by red oak, the dominant broad-leaved species in the region (Foster *et al.* 1998).

Thus, to test the hypothesis that nitrogen deposition differentially influences responses of coniferous and broad-leaved tree species to canopy gap formation in contrasting stand types, I examined growth and survival of seedlings of three coniferous and three broad-leaved species in response to nitrogen addition under simulated gap conditions. I chose coniferous and broad-leaved tree species that spanned the range of shade tolerance classes (Table 5.1), so that I could distinguish differences in species' responses due to evolutionary history (gymnosperm vs. angiosperm) from those due to life-history strategy (early vs. late successional). I

predicted that coniferous and late successional species would be less responsive to simulated nitrogen deposition than would broad-leaved and early successional species, as their evergreen habit and slow early growth rates would correlate with more conservative patterns of nutrient uptake and use (Reich *et al.* 1995, Bazzaz 1996, Reich *et al.* 1998b, Aerts & Chapin 2000). I also predicted that seedlings would be more responsive to nitrogen additions on soil from hemlock stands than on soil from red oak stands, as hemlock stands are often characterized by lower nutrient availability than broad-leaved tree stands (Boettcher & Kalisz 1990). As seedlings may regenerate in dense stands within forest gaps (Peet & Christensen 1987), I considered responses of seedlings grown both individually and in mixed species competitive stands. I expected that differences in species' responsiveness when grown as individuals would be exaggerated in mixed species stands, due to the asymmetric nature of much plant competition (Berntson & Wayne 2000).

MATERIALS AND METHODS

Soil and seed collection

Soil was collected from three hemlock- and three red oak-dominated forest stands at Harvard Forest (Petersham, MA; 42° 32' N, 72° 11' W, elevation 340 m) in April 1998. The stands were located in the Tom Swamp tract and were chosen so that hemlock and red oak contributed over 50 % of the basal area in each of three stands. Details of the stands are clearly described in Chapter 1. The soil was collected from one area in each stand as intact soil divots (40 x 50 cm, 15 cm depth to include all of O and some of A horizon), and was then transported back to the experimental garden at Harvard University (Cambridge, MA). Using a trowel, divots were divided vertically into smaller soil squares, which were placed over coarse silica sand in plastic containers. Individuals were grown in 12 L tree pots (16 x 16 cm, 48 cm deep), with approximately 8 L of sand beneath a 16 x 16 x 15 cm soil square. For the stands, I used wider but shallower containers (20 L; 30 x 35 cm, 20 cm deep), with a 5 cm layer of sand at the bottom.

Seeds of all study species (Table 5.1) were collected from multiple trees at Harvard Forest in the autumn of 1996 (most species) and spring of 1997 (red maple). Seeds were air-dried and stored at 4 °C until late autumn 1997, when they were placed in cloth bags and buried in trays of wet, coarse sand. These trays were placed outside through the winter to stratify the seeds and were collected the following spring. In 10 cm deep germination flats, seeds were spread out evenly over a peat-based potting mix with added perlite, and then covered with a thin layer of vermiculite. Flats were then placed in the experimental garden in mid-April and the seeds were left to germinate. The flats were monitored daily and watered when necessary. Seedlings began to germinate in early to mid-May, and were transplanted into their containers (individuals or stands) in mid-June when most seedlings had two to three true leaves. One seedling was planted per individual pot, and 42 seedlings were included in every mixed species stand. This represented a seedling density of 390 m⁻², which close to the mean density (300 m⁻², range: 30 – 1200 m⁻²) for seedlings establishing from the seed bank following a

canopy disturbance in this region (see Chapter 3). In the stands, seedlings were planted in a hexagonal array, such that each 'target' plant has six neighbors. Three individuals of each species were planted in the central 'target' 18 locations, and four individuals of each species were planted in the outer 'edge' 24 locations. Seedling positions were randomized within these 'target' and 'edge' locations, and the positions were established using a planting template with holes marked for each seedling.

Experimental treatments and growth conditions

I grew 54 individuals of each species and 54 mixed species stands for the experiment: 2 Soil types (hemlock vs. oak) \times 3 Sites \times 3 Nitrogen addition levels \times 3 Replicates. All containers for individuals and mixed stands were buried in the ground in the experimental garden underneath a large plastic greenhouse (30 m long, 6.5 m wide, 3.5 m tall), in which a continuous flow of air was maintained with the use of large embedded fans at one end. The covering of the greenhouse cut out 40 % of incoming photosynthetically active radiation (PAR) and was chosen to simulate light levels in a multiple tree fall gap in temperate forests (Bazzaz & Wayne 1994). Within the greenhouse, the individuals and mixed species stands were arranged in three large blocks, with one replicate of each treatment combination placed in each block. Seedlings were given daily watering treatments from automatic sprinklers within the greenhouse. Water was applied generously so that it would not be a limiting factor in this experiment.

Each individually grown seedling or mixed stand received one of three nitrogen addition treatments (0, 2.5, 7.5 g N m⁻² yr⁻¹). In both 1998 and 1999, seedlings were given nitrogen eight times per year at approximately three-weekly intervals, beginning mid-April and ending mid-September. At each addition, nitrogen was applied as dissolved ammonium nitrate solution of varying concentration. Individual seedlings were given 10 mL of 0, 0.016, and 0.048 mol L⁻¹, and mixed stands were given 0, 0.012, and 0.036 mol L⁻¹. Nitrogen addition treatments were chosen to reflect current and future levels of deposition. 2.5 g N m⁻² yr⁻¹ represents current high levels of deposition in parts of eastern North America (Ollinger *et al.* 1993), and 7.5 g N m⁻² yr⁻¹ reflects predicted increases in rates of deposition in the future (Galloway *et al.* 1995). Nitrogen was added

as ammonium nitrate as both ammonium and nitrate each compose close to half of the deposition in New England (Ollinger *et al.* 1993).

Seedling biomass and nitrogen measurements

In August 1999, a leaf sample was taken from every surviving seedling growing individually. Samples were photocopied and leaf area subsequently calculated using NIH Image software v1.6 (NIH, Bethesda, MD). The leaf samples were weighed after drying in an oven for 48 hours at 70 °C, and specific leaf weight calculated (SLW, g m⁻²). Once dried and weighed, leaf material was then ground up finely using a Mikro-Dismembrator (B. Braun Biotech International, Allentown, PA), and a small sample (2 – 5 mg) of the resulting powder was run through a Fisons CHN Analyzer 1500 Series 2 (Beverly, MA) to determine foliar nitrogen concentrations.

Season-long integrated nitrogen availability was determined using ion exchange resin bags placed in all mixed species stands and in a sub-set (one-sixth) of individually grown seedlings from June until September 1999 (Binkley & Vitousek 1989). The bags were constructed with 1.5 tablespoons (22 ml) of mixed bed strong acid (cation) and strong base (anion) gel resins (Sybron Chemicals, Birmingham, NJ) sealed in nylon mesh, and placed at a depth of 5 cm in the soil. After removal from the soil, 4 g of dried resin (70 °C, overnight) was extracted with 100 ml of 2 N potassium chloride solution (25 °C, 24 hours), and then frozen immediately following suction-filtration. Ammonium and nitrate in all soil and resin extracts were measured using a LaChat continuous flow ion analyzer using methods 12-107-06-1-A and 12-407-04-1-B (LaChat Instruments, Milwaukee, WI). Blanks were created from resin bags that had been sealed in polyethylene bags for the length of the growing season. These resins were extracted in the same way as the resins placed in the soil and were used to determine the lower threshold of detection.

Seedling mortality censuses were taken at the end of the first growing season (1998), and at the both the beginning and end of the second growing season (1999). Fallen litter of deciduous species was removed between the two growing seasons. In late September 1999, all seedlings were harvested after 16 months of growth. Leaves,

stems, and roots of all seedlings were separated. Isolated roots were obtained by carefully washing away the soil. For mixed species stands, every individual's root system was carefully separated by hand. Plant material was dried at 70 °C for seven days and then weighed.

Statistical analysis

Multi-factor analyses of variance were used to investigate influence of nitrogen addition on seedling growth and survival (Sokal & Rohlf 1995). Linear models included nitrogen addition as a continuous factor, soil type and species as fixed, discrete factors, and block within greenhouse as a random factor. All models also included a nested term for site (random factor), which was nested within stand, and the mixed species stand analysis included a nested plot term representing each mixed stand. Significant multi-factor interactions involving nitrogen were investigated by examining the magnitude and significance of regression slopes (dependent variable vs. nitrogen addition). Biomass data were natural logarithm transformed to ensure that the assumptions of analysis of variance were met (normality of residuals, homoscedascity).

Final community composition was investigated with multivariate analysis of variance on plot scores from the first two axes of detrended correspondence analysis (ter Braak 1995). Changes in allocation between roots and leaves under different nitrogen treatments were studied by examining model II linear regression slopes (geometric mean regression) for the natural logarithm of leaf/root biomass against natural logarithm of total biomass. In this way, I was able to distinguish between ontogenetic and true allocation responses to nitrogen addition (McConnaughay & Coleman 1999).

RESULTS

Soil nutrient availability

Nitrogen additions did lead to a significant increase in availability of both ammonium and nitrate in the soil matrix (Figure 5.1, $F_{1,93} = 45.85$ for ammonium, 48.43 for nitrate, $p < 0.001$ for both). Nitrogen availability did not differ between soil types ($F_{1,93} = 3.00$ for ammonium, 0.35 for nitrate, $p > 0.05$ for both) or between individually and competitively grown seedlings ($F_{1,93} = 1.36$ for ammonium, 0.23 for nitrate, $p > 0.05$ for both), and the relationship between nitrogen treatment and nitrogen availability was robust across soils and seedling densities (no significant higher order interactions in Anova, all $F_{1,93} < 1.21$, $p > 0.05$). Resin bags were more sensitive to nitrate concentrations than to ammonium (Figure 5.1), but in both cases, the high nitrogen addition treatment ($7.5 \text{ g m}^{-2} \text{ yr}^{-1}$) led to a seven- to nine-fold increase in nitrogen availability over control.

Seedling responses to nitrogen

For both individually and competitively grown seedlings, increased soil nitrogen availability only led to increased growth of the most fast growing species (Figure 5.2; Table 5.2, significant N x species interaction). Red maple showed significant nitrogen-induced growth enhancements both as an individual and in competition, while yellow birch only showed biomass enhancements when grown individually and not in mixed species stands. The other broad-leaved species, sugar maple, and all the conifers showed no significant growth responses to nitrogen addition. For competitively grown seedlings, there was a significant positive correlation ($r_6 = 0.92$, $p < 0.01$) between early seedling growth rates (as assessed by mean biomass in control treatments) and species' responsiveness to nitrogen (slope of the regression between biomass and nitrogen addition level). For individually grown seedlings, there was a close to significant positive correlation ($r_6 = 0.70$, $p = 0.12$). Species' responses to nitrogen were not contingent on soil type either as individuals or in stands (Table 5.2, no significant N x species x soil type interaction). When pooled across species, however, individually grown seedlings did show greater responsiveness to nitrogen when grown on soil from red oak stands (slope = 0.070, $F_{1,138} = 5.14$, $p < 0.001$) than on soil from hemlock stands

(slope = 0.045, $F_{1,122} = 1.41$, $p > 0.05$), as represented by a significant N x soil type interaction (Table 5.2).

Seedling survival was also influenced by nitrogen availability over the course of the two years. Individually grown seedlings only showed any significant mortality over winter (16 % between growing seasons, mainly as a result of wind damage and rodent up-rooting, vs. 3 % and 0 % during first and second growing seasons), while seedlings in mixed species stands showed more mortality during the growing season (16 % during the first, 4 % during the second) than over winter (0.5 %). Survival of slower-growing species (always canopy subordinates) was influenced by nitrogen additions in mixed species stands, but these responses were contingent on soil type (significant N x species x soil type interaction in Anova, $F_{5,250} = 2.57$, $p < 0.05$). On soil from hemlock stands, both red spruce and hemlock showed declines in survival with increasing nitrogen availability, while on soil from red oak, only hemlock showed any change in survival in response to nitrogen addition and in this case, survival increased with increasing nitrogen (Figure 5.3). All other species had higher overall survival than red spruce or hemlock and did not show any changes in survival following nitrogen addition.

Seedling growth was a larger determinant of species' overall contributions to final biomass in response to nitrogen addition than was seedling survival. Stand-level biomass of both red maple and yellow birch was significantly responsive to increased nitrogen availability (Figure 5.4), while no other species showed any biomass changes following nitrogen addition (significant N x species interaction in Anova, $F_{5,250} = 6.33$, $p < 0.001$). These responses did not vary between the two soil types (no significant N x soil type and N x species x soil type interactions, $F_{1,250} = 0.04$ and $F_{5,250} = 0.77$, $p > 0.05$ for both). Effects of nitrogen on survival of red spruce and hemlock subordinates were not reflected in stand-level biomass changes.

Nitrogen effects on individual species' growth within mixed species stands led to variation in stand community characteristics (Table 5.3). Nitrogen addition increased stand-level biomass (from 120 g in control to 200 g in 7.5 g N m⁻² yr⁻¹), and decreased overall community equitability, as measured by Shannon-Weaver diversity index (from

0.95 in control to 0.71 in $7.5 \text{ g N m}^{-2} \text{ yr}^{-1}$). Increasing nitrogen availability also led to a change in stand community composition (Figure 5.5). The first DCA axis separated the two dominant species in the stands (red maple and yellow birch), while the second axis separated these canopy dominant species from the subordinate species (sugar maple, all conifers). Nitrogen addition caused a significant movement down the second DCA axis (Figure 5.5, Table 5.3b), suggesting increased dominance by red maple and yellow birch with increasing nitrogen availability. None of these community responses to increasing nitrogen differed between soil types (Table 5.3, no significant N x soil type interaction).

Seedling allometry and foliar nitrogen concentrations

Nitrogen additions had small effects on seedling allometry, when I accounted for ontogenetic change (McConnaughay & Coleman 1999). As individually grown seedlings, red spruce was the only species to change its allocation between leaves and roots in response to simulated nitrogen deposition (Table 5.4a), with an unexpected decrease in allocation to leaves relative to total biomass with increased nitrogen availability. In mixed species stands, only the two largest of the subordinate species (sugar maple, white pine) changed their allocation patterns in response to nitrogen (Table 5.4b), but again in an unexpected directions. With increasing nitrogen additions, sugar maple decreased allocation to leaves and white pine increased allocation to roots (both relative to total biomass).

Nitrogen additions increased species' foliar nitrogen concentrations, expressed on either an area or weight basis (significant N terms in Manova, $F_{1,230} = 6.21$ and 5.52 respectively, $p < 0.05$ for both), although the response was not consistent across all species (significant species x N interaction, $F_{5,230} = 2.72$ for area and 2.39 for weight, $p < 0.05$ for both). Most species showed a 25 – 40 % increase in foliar nitrogen concentrations, except for red spruce, which experienced no change in foliar nitrogen with increasing nitrogen availability (Figure 5.6).

DISCUSSION

Species' responsiveness to increased nitrogen deposition

Seedling growth rates during the early stages of regeneration emerged as a good predictor of species' responsiveness to increased nitrogen deposition. When grown both individually and in competition, earlier successional broad-leaved species (yellow birch and red maple) consistently showed the greatest increases in biomass in response to nitrogen addition, while the most late successional of the broad-leaved species (sugar maple) and all the coniferous species examined did not grow significantly larger in treatments with higher nitrogen availability. I found a significant correlation between a species' growth rate during the first two years of its life and its growth enhancement following nitrogen addition, suggesting that growth rate, more than leaf habit or even successional position, may be a species' trait closely tied to nitrogen responsiveness. Of course, all of these traits (leaf habit, successional position, growth rate) are intimately related (Reich *et al.* 1998a), and thus all contribute in some way to determining the degree of nitrogen growth enhancement for a species. In this experiment, however, growth rate emerged as the single best predictor of a species' nitrogen responsiveness. This relationship was particularly strong for seedlings grown in mixed species competitive stands where nitrogen-induced fast early growth allowed certain seedlings to grow ahead of their competitors and thus experience further reduced competition for light (Berntson & Wayne 2000). Yellow birch showed lower responsiveness to increased nitrogen availability in stands than as individuals, as its small initial seedling size often placed it subordinate to red maple in mixed species stands. Plant competition often changes our predictions about species' responses to global environmental change, although the magnitude and direction of the change is highly variable (Catovsky & Bazzaz 2000).

Ecological theory addressing the relationship between species' functional traits and their responses to environmental gradients predicts that fast-growing species are more responsive to increases in resource availability (Grime 1979, Bazzaz 1996). Species' with high inherent growth rates typically have a suite of traits that give them the

capacity to take up nutrients rapidly from the soil (Lajtha 1994, Aerts & Chapin 2000) and utilize these nutrients effectively to increase carbon uptake and plant growth (Grime *et al.* 1997, Reich *et al.* 1998b), while slow-growing species place greater emphasis on high nutrient retention and high nutrient use efficiency, at the expense of a greater potential for resource capture (Chapin 1980, Aerts & Chapin 2000). Results of the present experiment support these basic predictions, as the faster-growing study species (the earlier successional broad-leaved tree species, yellow birch and red maple) were significantly more responsive to nitrogen addition in terms of biomass production than were slower-growing species.

The precise mechanisms underlying these responses were not clearly established, however. We might have expected responsive species to show greater flexibility in allocation patterns compared with non-responsive species, but there were no consistent trends between the fast- and slow-growing species. There was also little difference in species' abilities to take up additional nitrogen from the soil. Foliar nitrogen concentrations generally increased with increasing nitrogen availability, except for red spruce, and thus both responsive and non-responsive species took up nitrogen to the same degree. Species whose growth was not significantly affected by nitrogen amendment (conifers particularly) were clearly not able to utilize the additional nitrogen in their leaves. The photosynthetic capacity of evergreen coniferous species has been shown to be much less responsive to foliar nitrogen concentrations than that of deciduous broad-leaved species (Reich *et al.* 1995), although the physiological mechanisms for these differences are still equivocal. Conifers might be less responsive to increases in foliar nitrogen than broad-leaved species, if they were to allocate a greater proportion of the additional nitrogen to structural rather than photosynthetic proteins (Bazzaz 1997). Alternatively, leaf structure might impose a greater stomatal limitation on photosynthesis in conifers than in broad-leaved species (Sharkey 1985), so that conifers have a lower capacity to utilize additional nitrogen for photosynthesis. More detailed leaf-level physiological studies are clearly needed to ascertain what determines a species' capacity to make use of higher foliar nitrogen concentrations.

Many novel environmental perturbations involve changes in the basic resources essential for biological life (nutrients, CO₂, water, temperature) (Field *et al.* 1992, Bazzaz & Catovsky 2000). For one of these resource-based perturbations (increased nitrogen deposition), basic ecological theory was able to inform our predictions about future ecosystem responses to global environmental change. For some components of global environmental change, however, identifying species' functional traits that correlate with responsiveness to that perturbation has proved particularly challenging, e.g., elevated CO₂ (Poorter *et al.* 1996, Bazzaz & Catovsky 2000). Why might we be able to use current knowledge of species' biology to predict future responses to some global environmental changes but not others? In the case of nitrogen deposition, as nitrogen availability varies spatially and temporally within ecosystems (and has done so for millennia), soil nitrogen has been a critical resource axis upon which selection has acted over evolutionary time. As a result, there are clear links between particular species' life-history traits and responses to natural variation in soil nitrogen availability (Chapin 1980). These same traits are likely to be useful predictors of species' responses to novel increases in nitrogen availability in natural ecosystems. In contrast, for a novel perturbation such as elevated CO₂ where resource levels are taken beyond the natural range experienced by species' in their evolutionary past, it may be difficult to identify species' life-history characteristics (shaped by past selection pressures) that serve as good predictors for responses to future environmental changes.

Response consistency across soil types

Patterns of species' responsiveness to nitrogen addition were not contingent on the soil type on which seedlings were grown. Basic species' growth responses to nitrogen deposition were consistent across both hemlock and red oak soil types (no N x species x soil type interactions in Anova). I had expected a higher degree of nitrogen responsiveness for seedlings grown on soil from hemlock stands than on soil from red oak stands due to their hypothesized lower soil nitrogen availability (Boettcher & Kalisz 1990, Finzi *et al.* 1998b). I found, however, no difference in seedling responses in mixed species stands and greater nitrogen responsiveness on red oak soils than on hemlock stands for seedlings grown individually. Soil types did not differ significantly in

nitrogen availability, although there was a tendency for red oak stands to have lower nitrogen levels and lower stand-level productivity than hemlock stands (0.11 vs. 0.16 mg g⁻¹ for ammonium, 0.53 vs. 0.64 mg g⁻¹ for nitrate, 165.4 vs. 175.7 g for final biomass). Although under a closed canopy mineralization and nitrification rates are typically lower in hemlock stands than in broad-leaved stands, this pattern is often reversed following gap formation (Mladenoff 1987). Lower temperatures under hemlock stands may slow rates of decomposition in the understory (Daubenmire 1931), leading to greater organic matter accumulation in hemlock stands than in broad-leaved stands. Once the canopy opens up, however, this greater amount of organic matter in hemlock stands may lead to greater potential for mineralization and increased nutrient availability. Differences between hemlock and broad-leaved stands may be smaller in New England (my study region) than in midwestern states, as red oak is the dominant broad-leaved species in New England while sugar maple dominates in the Midwest. Litter and stand soil characteristics of red oak are much closer to those of hemlock than to those of sugar maple (Finzi *et al.* 1998a,b).

The tendency for soils from red oak stands to have lower nutrient availability than soils from hemlock stands in the present experiment may account for the higher overall responsiveness of seedling growth to nitrogen addition on oak soils than on hemlock soils, where nitrogen is perhaps less limiting. In addition, I found that, on the less productive red oak soils, simulated nitrogen deposition led to increases in the survival of subordinate coniferous species (hemlock and red spruce), while increasing nitrogen availability led to decreases in the survival of these species in mixed species stands grown on hemlock soils. Increased productivity commonly hastens seedling mortality during stand development (Harper 1977), and this effect might be more intense on hemlock soils that already have higher nitrogen availability.

Implications for future forest composition

Natural disturbance events are an integral part of the structure and dynamics of temperate forests (Jones 1945, Oliver & Stephens 1977, White 1979), but many forests are now threatened with increased frequency and magnitude of human-induced disturbance (Foster *et al.* 1997). Human effects on the forest landscape are more

substantial than ever before, through (1) direct management of forests and utilization of wood products (Foster *et al.* 1998), (2) introduction of invasive species, such as the hemlock woolly adelgid (*Adelges tsugae* Annand) (McManus *et al.* 2000), and (3) altered atmospheric composition leading to increased occurrence of extreme weather events (Houghton *et al.* 1996). In New England, we have already observed a substantial decline in late successional species, such as beech and hemlock, since European settlement (Foster *et al.* 1998, Fuller *et al.* 1998). In the future, these novel human-induced changes are likely to increase the frequency of canopy disturbance events and thus further increase the abundance of earlier successional species across the forest landscape (Bazzaz 1996). In the present experiment, I have demonstrated that increased nitrogen deposition may interact with these disturbance-mediated changes to increase further the contribution of earlier successional species to future forest community composition. Increasing nitrogen availability under simulated gap conditions led to increased community dominance of faster growing species, such as red maple and yellow birch, with concomitant declines in species diversity at the community level.

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Table 5.1. Details of experimental study species.

| Species | Common name | Leaf habit | Successional position ^a |
|-------------------------------------|-----------------|------------------------|------------------------------------|
| <i>Tsuga canadensis</i> (L.) Carr. | Eastern hemlock | Evergreen coniferous | 5 |
| <i>Picea rubens</i> Sarg. | Red spruce | Evergreen coniferous | 4 |
| <i>Pinus strobus</i> L. | White pine | Evergreen coniferous | 3 |
| <i>Acer saccharum</i> Marsh. | Sugar maple | Deciduous broad-leaved | 5 |
| <i>Acer rubrum</i> L. | Red maple | Deciduous broad-leaved | 4 |
| <i>Betula alleghaniensis</i> Britt. | Yellow birch | Deciduous broad-leaved | 3 |

^a Based on Baker's Table, where 1 is earliest and 5 is latest successional.

Table 5.2. Analysis of variance results (degrees of freedom, F ratios, p values) for final biomass of seedlings, either grown individually or in mixed competitive stands.

| Factor | Individually grown | | | Competitively grown | | |
|--------------------------------|--------------------|----------------|----------------|---------------------|----------------|-----|
| | d.f. | F ^a | p ^b | d.f. | F ^c | p |
| Soil Type | 1 | 1.74 | NS | 1 | 0.0023 | NS |
| Site (Soil Type) | 4 | 3.20 | * | 4 | 1.4471 | NS |
| Block | 2 | 0.92 | NS | 2 | 0.3208 | NS |
| Stand (Block) | • | • | • | 44 | 0.8822 | NS |
| Species | 5 | 35.74 | *** | 5 | 187.83 | *** |
| Species x Soil Type | 5 | 0.75 | NS | 5 | 1.5627 | NS |
| Nitrogen | 1 | 10.06 | ** | 1 | 0.0049 | NS |
| Nitrogen x Soil Type | 1 | 3.95 | * | 1 | 0.1258 | NS |
| Nitrogen x Species | 5 | 2.97 | * | 5 | 4.604 | *** |
| Nitrogen x Species x Soil Type | 5 | 1.13 | NS | 5 | 1.1108 | NS |

^a Error mean square for individually grown seedlings: 0.60, d.f. 232.

^b NS $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

^c Error mean square for competitively grown seedlings: 1.09, d.f. 707.

Table 5.3. Analysis of variance results (degrees of freedom, F ratios, p values) for community-level stand attributes (DCA ordination, diversity, productivity), showing main effects and interactions (a), and standardized regression coefficients for terms with significant nitrogen effects.

| a) Anova | DCA Axis 1 | | | | DCA Axis 2 | | Community Diversity ^a | | Stand-level Productivity ^b | |
|-----------------------|------------|----------------|----------------|--|------------|-----|----------------------------------|-----|---------------------------------------|-----|
| | d.f. | F ^c | p ^d | | F | p | F | p | F | p |
| Soil Type | 1 | 0.75 | NS | | 3.97 | NS | 1.12 | NS | 0.00 | NS |
| Site (Soil Type) | 4 | 0.33 | NS | | 1.53 | NS | 1.87 | NS | 1.81 | NS |
| Block | 2 | 0.69 | NS | | 2.35 | NS | 0.33 | NS | 5.54 | ** |
| Nitrogen ^e | 1 | 0.14 | NS | | 34.19 | *** | 15.45 | *** | 29.46 | *** |
| Nitrogen x Soil Type | 1 | 0.75 | NS | | 2.40 | NS | 2.19 | NS | 0.59 | NS |

| b) Standardized Regression Coefficients for Nitrogen Effect | |
|---|--------|
| Y-variable | b' |
| DCA Axis 2 | -0.593 |
| Community Diversity | -0.469 |
| Stand-level Productivity | 0.562 |

^a Calculated from Shannon-Weaver Diversity Index.

^b Biomass (g) of all 'target' and 'edge' seedlings in each stand.

^c Error mean squares (d.f. 44 in each case): 1432.70 (DCA Axis 1), 65.98 (DCA Axis 2), 0.03 (Diversity), 1739.50 (Productivity).

^d NS $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

^e Slope coefficients for y-variables with significant N effects shown in part (b) of table.

Table 5.4. Model II regression results examining changes in the slopes of regressions between leaf/root biomass (g) and total biomass (g) for (a) individually grown seedlings and (b) seedlings in mixed species stands, with data pooled across soil types and blocks.

| a) Individuals | Nitrogen (g m ⁻² yr ⁻¹) | Leaf (y) vs. Total (x) Biomass | | Root (y) vs. Total (x) Biomass | |
|----------------|---|--------------------------------------|---|--------------------------------------|---|
| Yellow birch | 0 | 1.115 | a | 0.841 | a |
| | 2.5 | 0.823 | a | 1.062 | a |
| | 7.5 | 1.056 | a | 1.295 | a |
| Red maple | 0 | 0.830 | a | 0.962 | a |
| | 2.5 | 1.077 | a | 1.014 | a |
| | 7.5 | 0.870 | a | 1.053 | a |
| Sugar maple | 0 | 0.950 | a | 1.039 | a |
| | 2.5 | 1.102 | a | 0.926 | a |
| | 7.5 | 1.047 | a | 1.007 | a |
| White pine | 0 | 1.084 | a | 0.896 | a |
| | 2.5 | 0.994 | a | 0.979 | a |
| | 7.5 | 0.886 | a | 1.022 | a |
| Red spruce | 0 | 1.471 | a | 0.786 | a |
| | 2.5 | 0.939 | b | 1.099 | a |
| | 7.5 | 0.745 | b | 1.628 | a |
| Hemlock | 0 | 1.455 | a | 0.489 | a |
| | 2.5 | 0.988 | a | 1.122 | a |
| | 7.5 | 1.125 | a | 1.026 | a |

Table 5.4 cont.

| b) Mixed stands | Nitrogen (g m ⁻² yr ⁻¹) | Leaf (y) vs. Total (x) Biomass | | Root (y) vs. Total (x) Biomass | |
|-----------------|---|--------------------------------------|----|--------------------------------------|---|
| Yellow birch | 0 | 0.847 | a | 1.086 | a |
| | 2.5 | 0.812 | a | 1.190 | a |
| | 7.5 | 0.888 | a | 1.108 | a |
| Red maple | 0 | 0.950 | a | 1.211 | a |
| | 2.5 | 0.904 | a | 1.058 | a |
| | 7.5 | 0.782 | a | 1.100 | a |
| Sugar maple | 0 | 1.682 | a | 1.232 | a |
| | 2.5 | 1.159 | ab | 1.166 | a |
| | 7.5 | 1.083 | b | 1.139 | a |
| White pine | 0 | 0.997 | a | 1.152 | a |
| | 2.5 | 0.914 | a | 1.444 | b |
| | 7.5 | 1.118 | a | 1.563 | b |
| Red spruce | 0 | 0.978 | a | 1.248 | a |
| | 2.5 | 1.049 | a | 1.263 | a |
| | 7.5 | 1.093 | a | 1.342 | a |
| Hemlock | 0 | 1.151 | a | 1.081 | a |
| | 2.5 | 1.292 | a | 1.211 | a |
| | 7.5 | 1.281 | a | 1.159 | a |

NOTES:

- (1) All biomass data were natural logarithm transformed.
- (2) Model II regression slopes were calculated using geometric mean regressions, with a larger slope indicating increased allocation to leaves/roots for a given total biomass.
- (3) Slopes followed by the same letter (within a species) were not significantly different from one another (sequential Bonferroni corrected planned comparisons, $p > 0.05$).

Figure 5.1. Effects of nitrogen addition on ammonium and nitrate soil availability (mean \pm 1 SE, pooled across soil types and across individually and competitively grown seedlings), assessed using resin bag extracts. Values above each species represent slope coefficients calculated using transformed data. Slopes significantly greater than zero ($p < 0.05$) are shown in bold and with an asterisk.

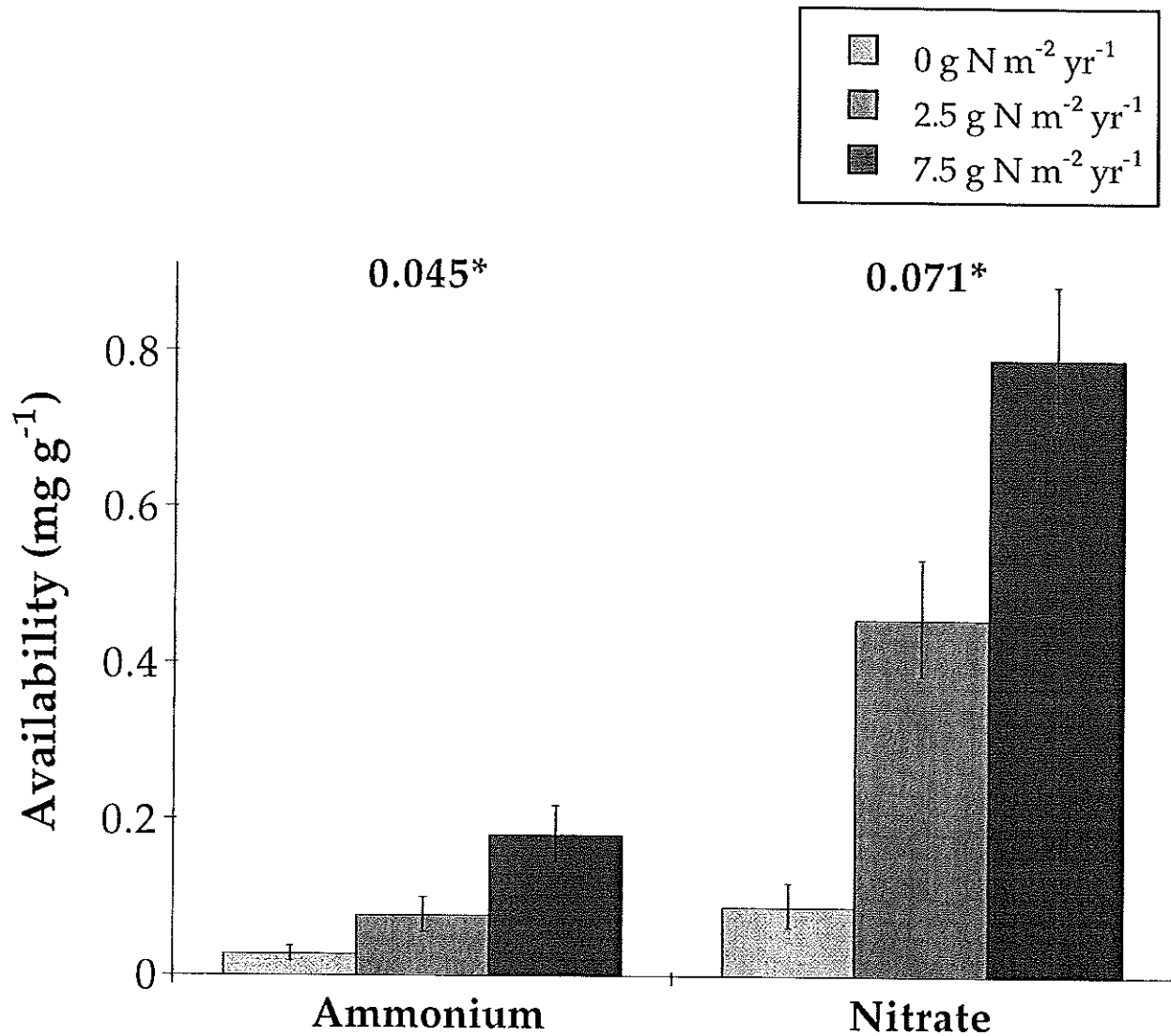


Figure 5.2. Effects of nitrogen addition on final biomass of seedlings after 16 months of growth (mean \pm 1 SE, pooled across soil types), grown either as individuals (a) or in mixed species stands (b) (note log scale). Values above each species represent slope coefficients calculated using transformed data. Slopes significantly different from zero ($p < 0.05$) are shown in bold and with an asterisk.

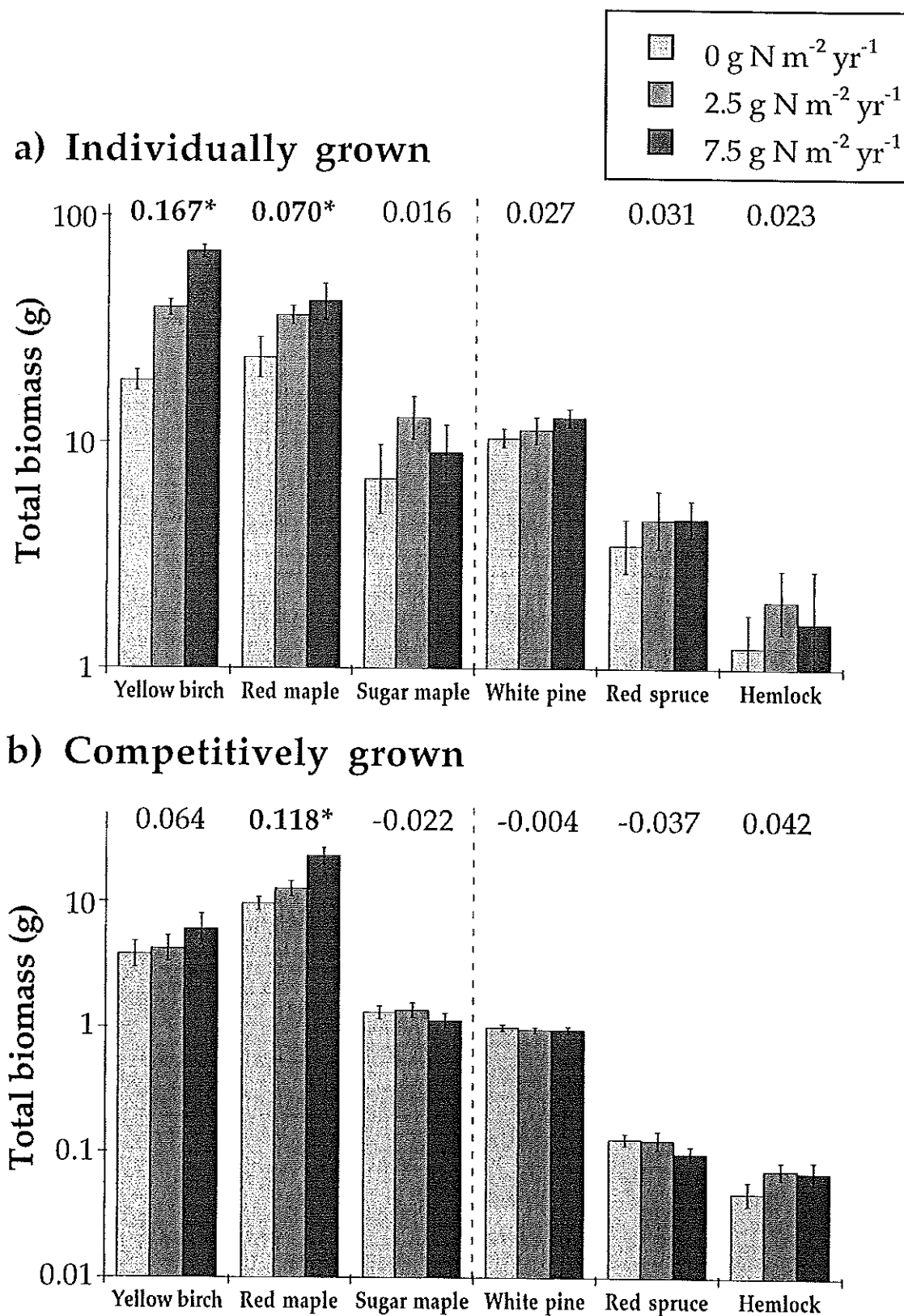


Figure 5.3. Effects of nitrogen addition on seedling survival in mixed species stands after 16 months of growth (mean \pm 1 SE), with seedlings grown on soil from hemlock (a) and red oak (b) stands shown separately. Values above each species represent slope coefficients calculated from the regression of survival against nitrogen treatment. Slopes significantly different from zero ($p < 0.05$) are shown in bold and with an asterisk.

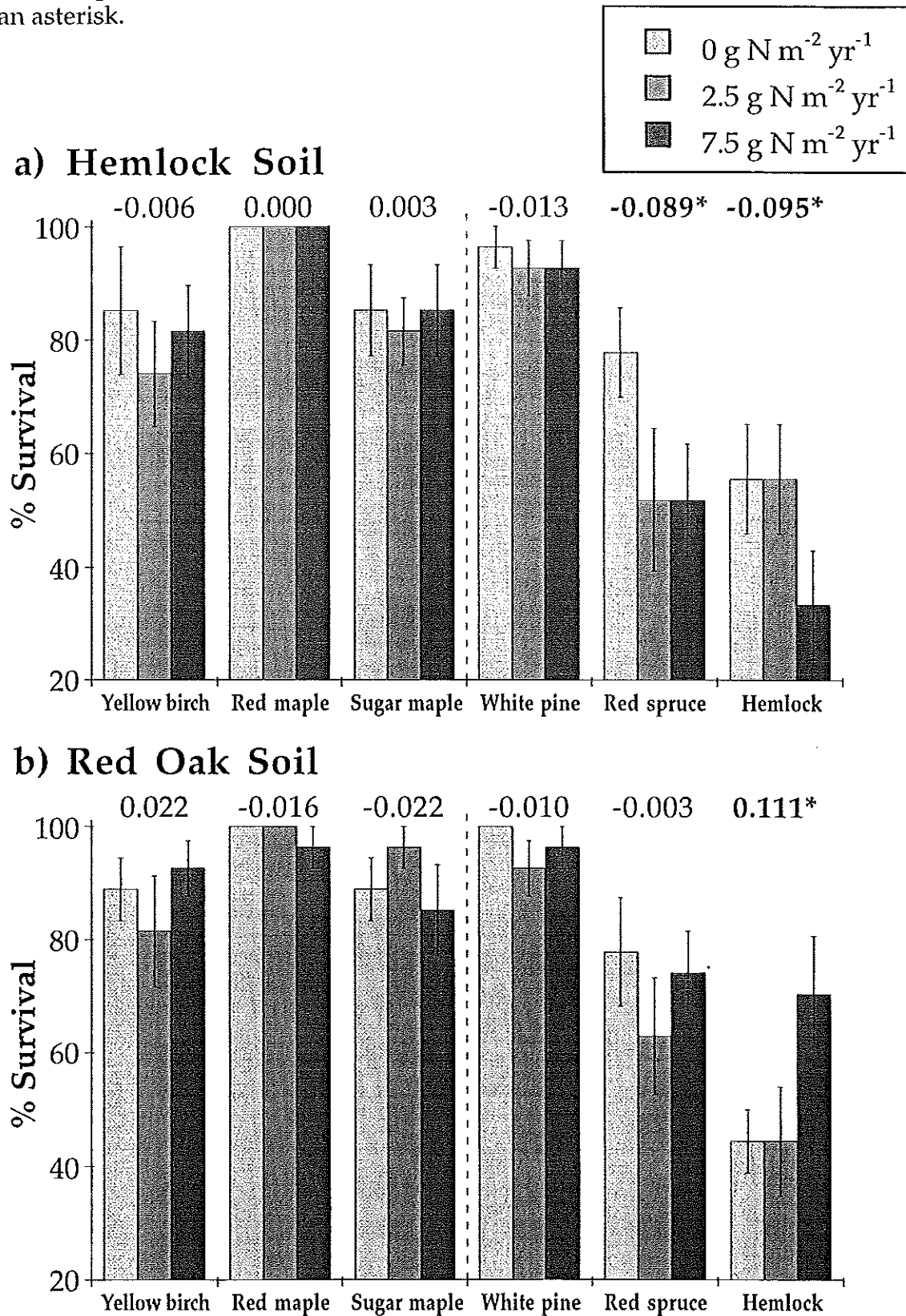


Figure 5.4. Effects of nitrogen addition on stand-level final seedling biomass after 16 months of growth in mixed species stands (mean \pm 1 SE, pooled across soil types) (note log scale). Values above each species represent slope coefficients calculated using transformed data. Slopes significantly different from zero ($p < 0.05$) are shown in bold and with an asterisk.

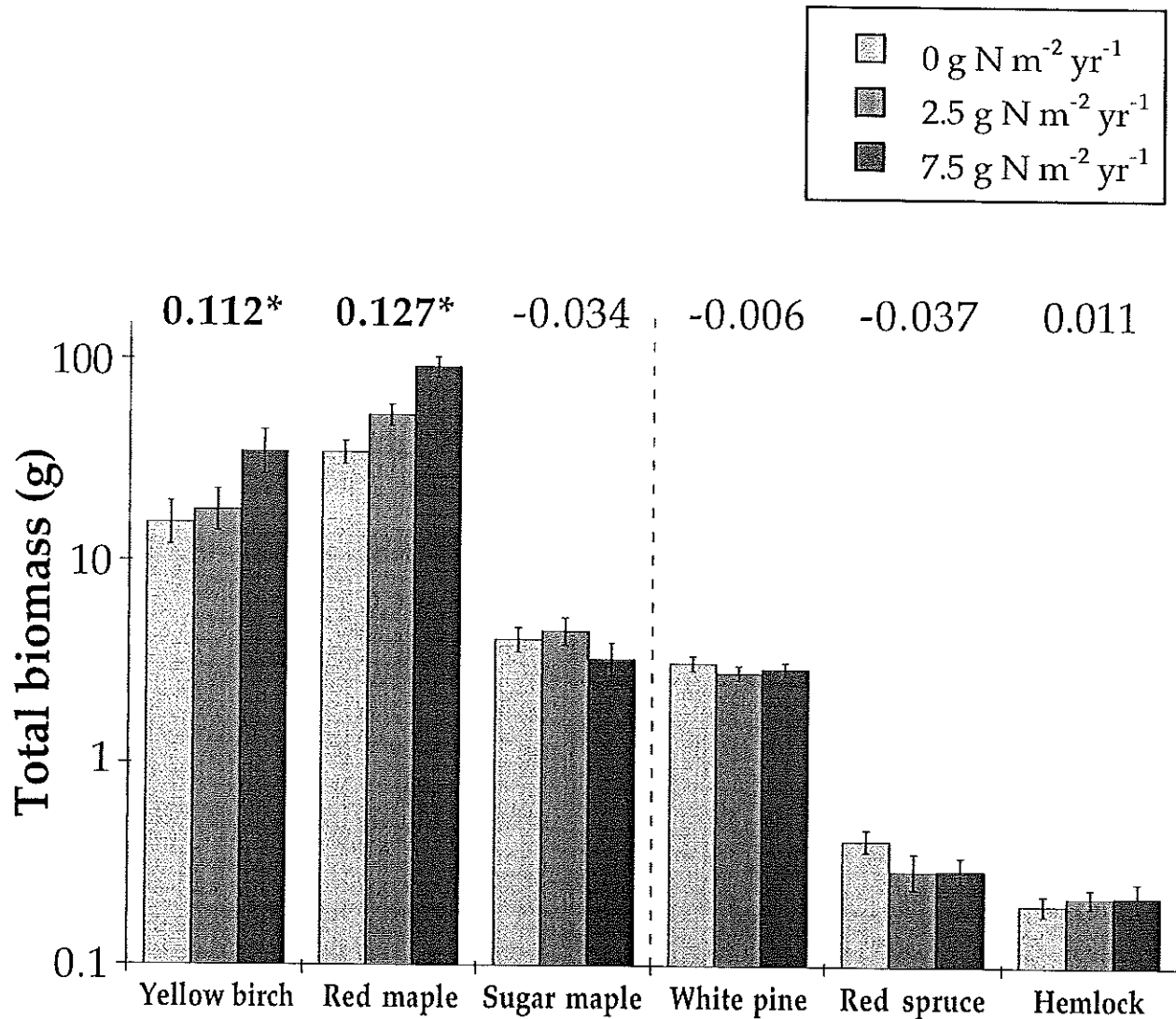


Figure 5.5. Results of detrended correspondence analysis (DCA) on stand-level community composition (biomass basis), showing (a) mean nitrogen treatment scores ± 1 SE on each axis, pooled across soil types, and (b) species scores on same two axes. Axis 1 explained 42 % of variation and axis 2 explained 23 % of variation in community composition.

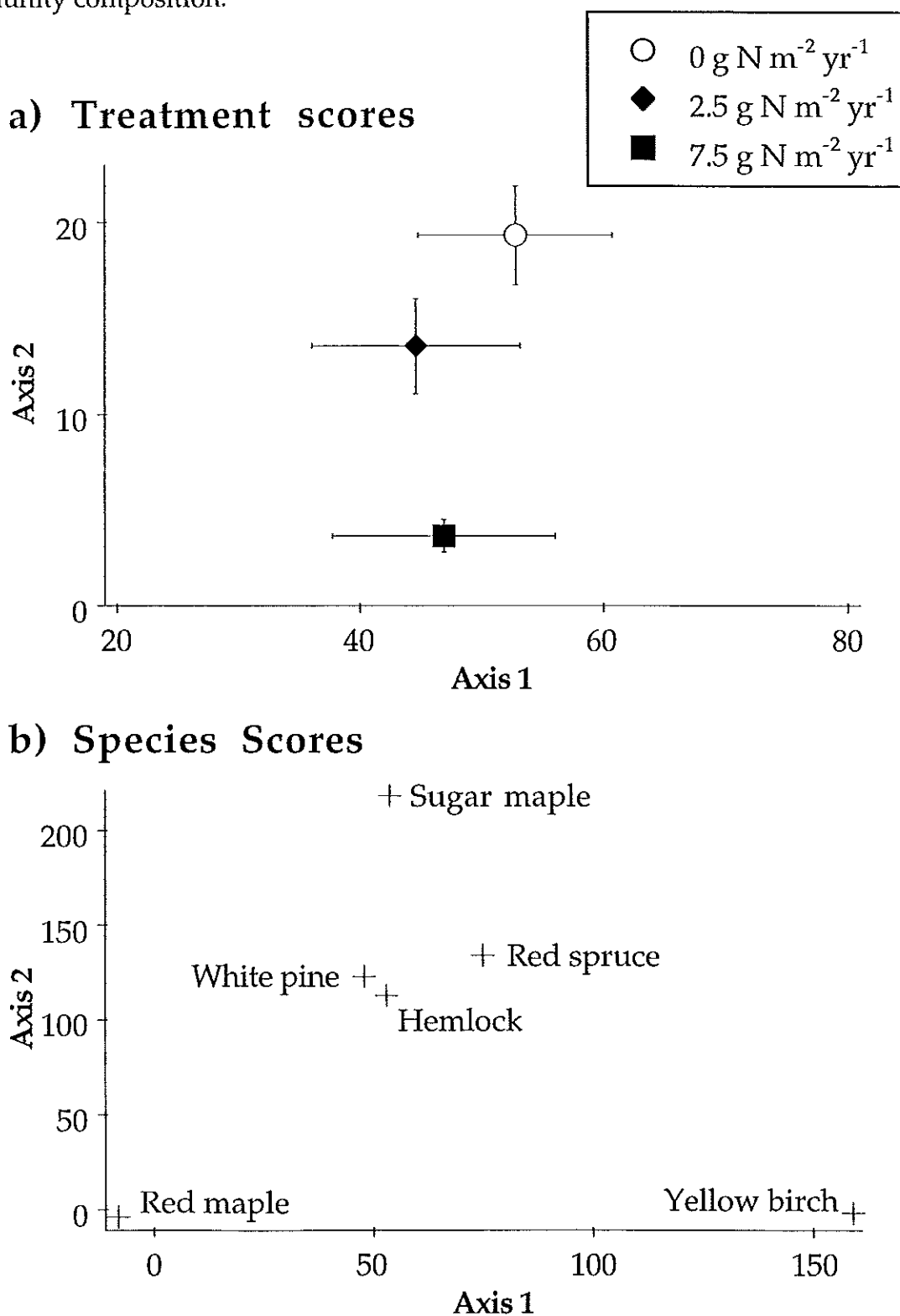
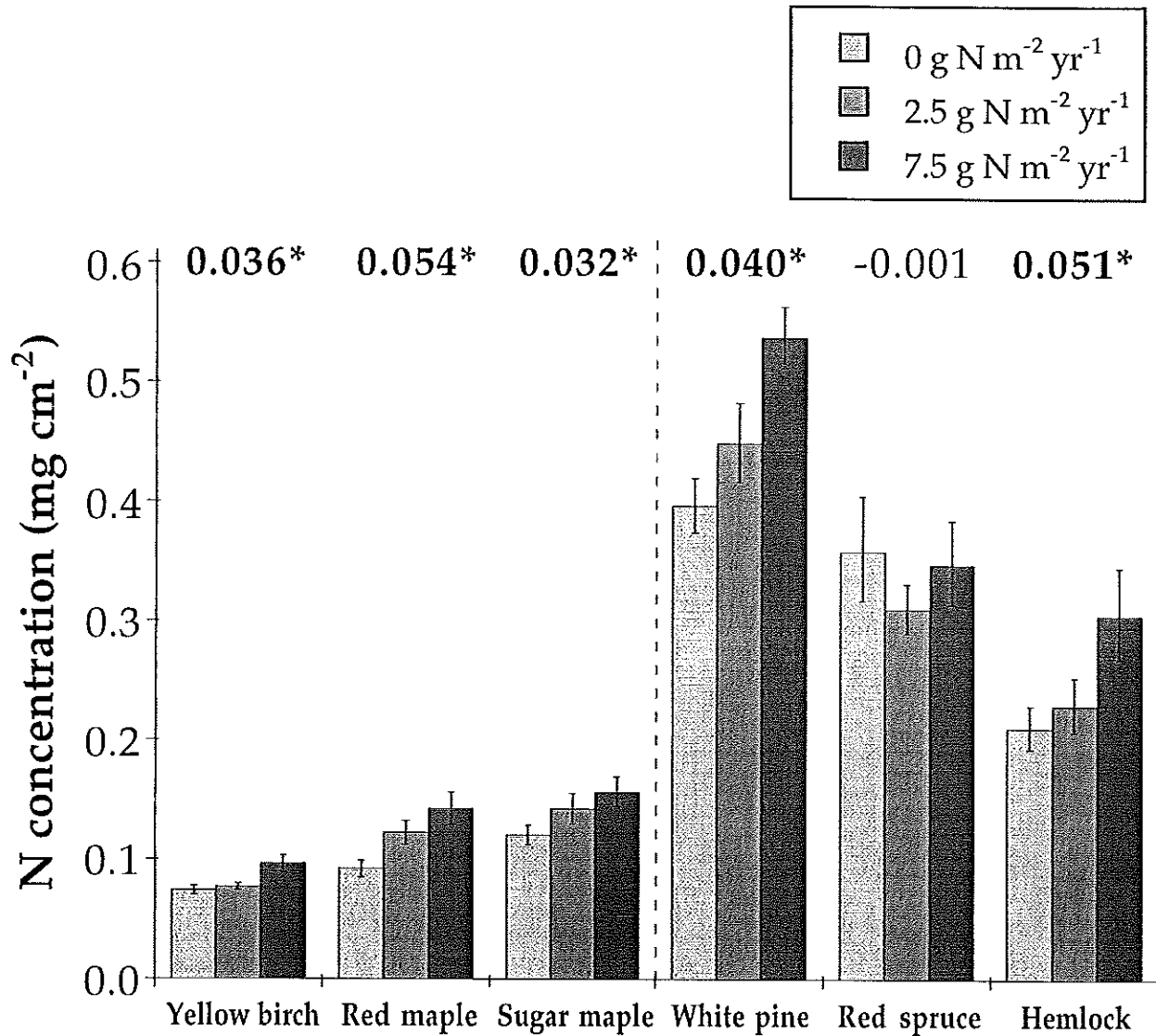


Figure 5.6. Effects of nitrogen addition on foliar nitrogen concentrations (expressed on an area basis) for individually grown seedlings (mean \pm SE, pooled across soil types). Values above each species represent slope coefficients calculated using transformed data. Slopes significantly different from zero ($p < 0.05$) are shown in bold and with an asterisk.



CHAPTER 6

CONTRIBUTIONS OF CONIFEROUS AND BROAD-LEAVED SPECIES TO TEMPERATE FOREST CARBON UPTAKE: A BOTTOM-UP APPROACH

Abstract. Changes in forest species composition could influence ecosystem carbon uptake rates. To understand how species differed in their contributions to canopy photosynthesis, I investigated how the dominant coniferous (eastern hemlock) and broad-leaved (red oak, red maple) species in a central Massachusetts forest differed in canopy carbon uptake rates. I considered what factors influenced *in situ* leaf-level photosynthesis, and then used a bottom-up summation approach to estimate species-specific total canopy carbon uptake rates. Variation in canopy light strongly influenced leaf-level photosynthetic rates—sunlit leaves had significantly higher rates than shaded leaves, and photosynthesis increased with canopy height. Species also differed in leaf-level photosynthetic rates, with the broad-leaved species having up to twofold higher rates than hemlock. Within hemlock, needles older than two years had lower photosynthesis than younger needles. Variation in leaf-level photosynthesis scaled up to influence canopy carbon uptake rates. Red oak consistently had the highest canopy photosynthetic rates, while, through the season, hemlock's relative contribution to carbon flux increased and that of red maple decreased. Thus, in such mixed forests, future changes in species composition could have substantial impacts on forest carbon dynamics, particularly if red oak is the primary broad-leaved species to expand at the expense of hemlock.

INTRODUCTION

Temperate forests are currently a significant terrestrial sink for atmospheric CO₂ and consequently play an important role in the contemporary global carbon cycle (Fan *et al.* 1998, Houghton *et al.* 1998). As forest systems have the potential to slow future increases in atmospheric CO₂ concentrations (Dixon *et al.* 1994, Woodwell *et al.* 1998), it is now critical to understand the factors that regulate forest ecosystem processes. Using eddy covariance, we can measure the total amount of carbon taken up by forests with a high degree of accuracy (Baldocchi *et al.* 1988), and we can relate carbon uptake to environmental conditions on different temporal scales (e.g., Grace *et al.* 1995, Goulden *et al.* 1996). These broad-scale measurements do not, however, allow us to predict future forest function should canopy composition change. As a result of natural and human-induced disturbance processes, and subsequent patterns of successional recovery (Bormann & Likens 1979, Bazzaz 1996), ecosystems are in a constant state of flux, and their composition is likely to vary over time. Functional differences between species may give rise to a close coupling between population and ecosystem processes (Jones & Lawton 1995, Chapin *et al.* 1997, Tilman *et al.* 1997). Thus, changes in forest canopy composition could directly affect forest productivity and carbon storage (Bolker *et al.* 1995, Canham & Pacala 1995, Bazzaz *et al.* 1996).

To predict patterns of carbon uptake and storage by forest ecosystems under a range of scenarios in the future, more mechanistic studies of controls on forest function are required to complement 'big leaf' approaches (Meinzer & Goldstein 1996, Bassow & Bazzaz 1998). In this study, I address the consequences of changes in temperate forest community composition for canopy carbon uptake. I investigate how the major species of a mixed conifer-hardwood forest in northeastern USA differ in their capacity for carbon uptake. Addressing links between community and ecosystem dynamics may be particularly important in these mixed forests where two contrasting groups of canopy trees co-occur. As evergreen coniferous and broad-leaved deciduous species differ from one another in their basic biology (Waring & Franklin 1979, Bond 1989, Smith & Hinckley 1995), they are likely to show contrasting responses to both natural

disturbance processes and to novel environmental perturbations currently threatening temperate forests, such as increasing atmospheric CO₂ concentrations and nitrogen deposition (Bazzaz *et al.* 1996, Magill *et al.* 1997, Saxe *et al.* 1998). Thus, we expect that forest community composition will change in the future. In addition, we expect that these changes in composition will significantly influence ecosystem-level processes, because these distinct groups of species have different functional roles within forest ecosystems (Baldocchi & Vogel 1996, Reich *et al.* 1997, Willis *et al.* 1997). As coniferous and broad-leaved species often have contrasting natural distributions, very few studies have directly compared these different groups in areas where they naturally co-occur.

In the present study, I address how canopy photosynthetic rates differ for mature trees of eastern hemlock (*Tsuga canadensis* (L.) Carr.), red oak (*Quercus rubra* L.) and red maple (*Acer rubrum* L.). These species represent the currently dominant coniferous (hemlock) and broad-leaved (oak, maple) species at the study site (Harvard Forest). To develop a mechanistic understanding of different components of total canopy carbon uptake, I first consider leaf-level gas exchange processes in temperate forest tree canopies. I ask what environmental, ontogenetic and phylogenetic factors are responsible for heterogeneity in canopy leaf-level photosynthetic rates. I hypothesize that light availability is the major determinant of leaf-level photosynthesis, and that carbon uptake is further modified by species identity and leaf age. I predict that the broad-leaved species will have higher leaf-level photosynthetic rates than hemlock (a conifer) (Bond 1989), and that, for hemlock, photosynthesis will decline with increasing needle age (Oren *et al.* 1986). These leaf-level measurements are then used to estimate instantaneous total canopy carbon uptake rates with a bottom-up summation approach (Ehleringer & Field 1993). I predict that hemlock will have higher canopy carbon uptake rates than the broad-leaved species, because of its evergreen habit and resulting deeper canopy (Schulze *et al.* 1977a, Bond 1989).

Because of the intensity of my canopy sampling scheme, I restrict my measurements to times when photosynthetic rates are likely to be maximal (clear, sunny days during the main growing season). In this way, I place considerable emphasis on understanding the photosynthetic capacity of each species, rather than on total carbon

gain throughout the whole year. The majority of carbon gain in temperate forests in this region, however, is between June and August (Goulden *et al.* 1996). Previously, with this approach, I have been able to account for a large portion of the flux in the system (Wofsy *et al.* 1993, Bassow & Bazzaz 1998).

MATERIALS AND METHODS

Canopy photosynthetic measurements

In situ leaf-level photosynthetic measurements were made in the canopies of mature trees of red maple, red oak and eastern hemlock at Harvard Forest (see Chapter 1 for full details of study site). Measurements were taken on three sunny days in both mid-June and mid-August 1996, from 8 am to 2 pm each day, before the late-day decline in photosynthesis often observed in temperate trees in this site (Bassow & Bazzaz 1998). Air temperatures did not differ significantly between months (average air temperature = 28 °C for both months). Each day, leaves from one tree of each species were measured. All trees measured on a particular day were located next to one another in mixed forest stands, and the order in which trees were sampled was random each day. Trees chosen were 30 - 50 cm diameter at breast height, and 15 - 20 m in height.

Canopy access was achieved using a mobile aerial lift with a 22 m boom (Shaughnessy, Worcester, MA). The rotation and extension of both boom and attached basket allowed access to parts of trees that were in closed forest. *In situ* photosynthesis was measured using a Li-Cor 6200 gas exchange system (Li-Cor, Lincoln, NB), with quarter-liter chamber. For each measurement, chamber orientation was adjusted to match natural leaf orientation, and conditions within the chamber were set to match external conditions (CO₂ concentration, 340-360 µL L⁻¹; air temperature, 20-25 °C; relative humidity, 30-60 %). Flow through the chamber was regulated such that chamber relative humidity was kept constant throughout each measuring period (1-2 minutes). Leaf areas of broad-leaved species were estimated from a grid in the leaf chamber, while hemlock needle leaf areas were obtained by running needles through a Li-Cor 3000A portable leaf area meter (Li-Cor, Lincoln, NB) at the end of the day. Measurements of photon flux density (PFD) falling on leaves were taken at the same time as gas exchange, using a Li-Cor PAR quantum sensor (Li-Cor, Lincoln, NB) attached to the chamber to match the orientation of leaves measured.

Canopy sampling

My sampling regime incorporated factors that I hypothesized would substantially contribute to heterogeneity in leaf-level photosynthesis within tree canopies. The first division separated tree canopies into different vertical strata. Red oak and red maple canopies were divided into three equivalent strata, while hemlock canopies, because they are deeper (see later), were divided into four strata. Within each canopy layer, I measured leaves that were either sunlit (intercepting direct beam radiation) or shaded (receiving only diffuse beam radiation). Canopy models have previously found that dividing leaves into sunlit and shaded classes at different canopy heights provided a good estimate of total canopy photosynthesis (Norman 1980, Caldwell *et al.* 1986, Hollinger 1992). In addition, for hemlock (an evergreen species), needles of different ages were sampled—those produced that season (current-season needles), one year old needles, and those two years old or more. As hemlock rarely retains needles older than three years, aggregating needles older than two years seemed very appropriate. For every layer x sun/shade (x leaf age) combination, three individual leaves were measured each day, giving a total of 18 measurements for each tree of red oak and red maple (3 layers x 2 sun/shade x 3 replicates) and 72 measurements for each hemlock tree (4 layers x 2 sun/shade x 3 ages x 3 replicates).

Scaling approach and sensitivity analysis

I scaled from leaf-level measurements of photosynthesis to total canopy carbon uptake by incorporating information on canopy structure into a bottom-up summation scheme (Norman 1980, 1993). I calculated leaf area index (LAI) of each canopy layer by dividing the total leaf area index of red oak/red maple and hemlock stands by the number of canopy layers, and assuming that foliage was distributed evenly through the canopy layers (Aber 1979, Ellsworth & Reich 1993). An LAI of $3 \text{ m}^2 \text{ m}^{-2}$ was used for mixed red oak/red maple stands in the area of Prospect Hill, based on previous extensive leaf litter trap data (Wofsy *et al.* 1993). For pure hemlock stands, I used an LAI of $4.4 \text{ m}^2 \text{ m}^{-2}$, obtained from destructive sampling of branches in the canopy of a hemlock stand in the vicinity (J. Hadley, *personal communication*). Non-destructive LAI measurements taken using an LAI 2000 (Li-Cor, Lincoln, NB) in the same summer as the photosynthesis

measurements fell within the range of the litter/destructive LAI estimates, assuming that 15-20% of canopy LAI is contributed by branches (Wofsy *et al.* 1993). The proportion of sunlit and shaded leaf area index within each canopy layer was derived from Norman's (1980, 1993) formulation, using a solar elevation angle of 70° for midday in the summer at 42° N. This relationship assumes that light attenuation follows Beer-Lambert's Law. In addition, for hemlock, the proportion of different needle age classes within each canopy layer was estimated from destructive branch samples. Three full branches were sampled in each canopy layer of each tree measured. For each canopy layer, the sunlit/shaded proportions and the different hemlock needle age classes were used to weight each of my leaf-level measurements according to their contributions to leaf area index. These weighted photosynthetic rates were then first summed within each canopy layer and subsequently across all canopy layers (see Norman 1993 for full discussion of Method). As my total canopy carbon flux estimates are scaled to ground area, they should represent appropriate measures of species contributions to forest carbon flux, provided canopy structure does not change dramatically between stand types.

In order to investigate the assumptions of my canopy summation scheme, I carried out a sensitivity analysis, where the inputs of each of the model parameters were varied, and the resulting output (total canopy carbon uptake) investigated. The assumptions tested were: (1) total LAI; (2) proportion of sunlit and shaded leaves; (3) vertical distribution of foliage; and (4) proportion of hemlock needle age classes in each canopy layer.

Statistical analysis

Leaf-level photosynthesis and PFD measurements were analyzed by pooling replicate measurements in each month x day x layer x sun/shade x species (or leaf age) class. To compare both photosynthesis and canopy light environment between species, I additionally pooled measurements for different hemlock needle age classes, and only considered the top three canopy layers. I performed multi-way analyses of variance, with month, species, layer, and sun/shade as fixed factors, and day as a random factor nested within month. I carried out an additional analysis of variance comparing

different hemlock needle age classes in a similar way, but replacing the species term with needle age. Light-saturated photosynthetic rates (A_{\max}) were compared using two-way analysis of variance (species/age class and month as main effects) on all gas exchange values measured at $>1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ PFD. Subsequent Bonferroni-corrected planned comparisons were made between species within each month for both leaf photosynthetic characteristics (Sokal & Rohlf 1995). Estimates of total canopy carbon uptake were compared in a three-way analysis of variance, with species and month as fixed factors, and day as a random factor nested within month. In all cases, I ensured that the data met the assumptions of Anova (normality of residuals, homoscedascity). PFD data were log-transformed, so that residuals would be normally distributed. Following each test, for each significant main effect with more than two levels and for each significant interaction, I examined the significance of individual treatment mean comparisons using Scheffé *post hoc* tests (Day & Quinn 1989, Sokal & Rohlf 1995). All statistical analysis was carried out with DataDesk v. 4.2 (Data Description Inc., Ithaca, NY).

RESULTS

Canopy light environment

The distribution of light through tree canopies varied with both sun/shade class and canopy position (Figure 6.1). Photon flux density (PFD) was significantly greater on sunlit leaves than shaded leaves (881 and $105 \mu\text{mol m}^{-2} \text{s}^{-1}$ respectively; $F_{1,62} = 961.5$, $p < 0.0001$) and decreased significantly with decreasing canopy height ($F_{2,62} = 63.5$, $p < 0.0001$; all *post hoc* comparisons, $p < 0.001$). Canopy light environment, however, did not vary significantly between species or between months ($F_{2,62} = 0.43$ and $F_{1,4} = 0.59$, $p > 0.05$). There were no significant higher-order interactions between any factors ($F_{1-4,62} < 2.0$, $p > 0.05$).

Leaf-level photosynthesis: species comparisons

Variation in canopy light environment strongly influenced leaf-level photosynthesis (Table 6.1). Sunlit leaves had substantially higher rates of photosynthesis than shaded leaves (Figure 6.2; 10.3 and $4.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ respectively; $p < 0.0001$), and classifying leaves as sunlit or shaded explained most of the variation in photosynthesis through the canopy ($F_{1,68} = 1101.5$; Table 6.1). Photosynthesis also significantly declined with canopy height (Table 6.1, Figure 6.2; $p < 0.0001$). The decline for sunlit leaves was significantly faster than for shaded leaves (Layer x Sun-Shade interaction, $p < 0.001$).

Species differed in their leaf-level photosynthetic rates (Table 6.1, Figure 6.2), with broad-leaved trees having higher rates of photosynthesis than hemlock trees (7.9 vs. $5.7 \mu\text{mol m}^{-2} \text{s}^{-1}$ respectively; *post hocs*, $p < 0.0001$). In addition, within broad-leaved species, red oak had consistently higher rates of photosynthesis in the sun than did red maple (significant Species x Sun/Shade interaction; *post hocs*, $p < 0.0001$). Leaves of broad-leaved species were more sensitive to variation in canopy light environment than were hemlock needles (Table 6.1; significant Species x Sun-Shade and Species x Layer x Sun-Shade interactions, $p < 0.0001$ and $p < 0.01$, respectively). Red oak showed particularly marked declines in photosynthesis from sunlit to shaded leaves (72 % decrease, vs. 53 % for red maple and 51 % for hemlock). In addition, red oak

photosynthesis declined faster with canopy height in the sun than in the shade, while red maple photosynthesis declined faster in the shade (Figure 6.2, Table 6.1). As a result of these changes, differences in photosynthesis between hemlock and broad-leaved species, and between red oak and red maple, were most evident for sunlit leaves and for leaves higher in the canopy (Table 6.1, *post hocs*).

Photosynthesis varied daily, but did not vary through the season (Table 6.1). Trees did, however, show species-specific seasonal changes in *in situ* photosynthesis (Month x Species interaction, $p < 0.0001$). Red oak photosynthesis did not change through the season (*post hocs*, $p > 0.05$), while that of hemlock increased from 5.1 to 6.3 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (*post hocs*, $p < 0.01$) and that of red maple declined from 8.4 to 6.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (*post hocs*, $p < 0.0001$). As a result, red maple photosynthesis was only significantly greater than that of hemlock in June, but not in August.

There were significant differences between species' light-saturated photosynthetic rates (A_{max}), and many of the differences varied through the season (significant Month x Species interaction, $F_{4,161} = 61.6$, $p < 0.0001$). Red oak leaves consistently had significantly higher A_{max} values than either red maple or hemlock leaves (Table 6.2; $F_{1,161} > 15.6$, $p < 0.05$, sequential Bonferroni). In June, red maple leaves had a significantly higher A_{max} than hemlock ($F_{1,161} > 31.9$, $p < 0.05$). Later in the season, however, there were no significant differences between red maple and hemlock needles younger than two years ($F_{1,161} < 5.4$, $p > 0.05$). Part of the change was driven by a marginal, but non-significant, decline in photosynthetic capacity of red maple leaves, and a marginal increase in photosynthetic capacity of one year old hemlock needles. Current-season hemlock needles showed the most marked increase in photosynthetic capacity (73 %) through the season ($F_{1,161} = 81.9$, $p < 0.05$).

Leaf-level photosynthesis: hemlock needle age comparisons

As in the previous multi-species analysis, hemlock leaf-level photosynthesis was influenced by canopy light environment (Table 6.3; significant Sun-Shade, Layer and Sun-Shade x Layer effects, $p < 0.01$) and by daily conditions ($p < 0.001$). In addition, in this more detailed analysis for hemlock, I found photosynthesis varied both with needle

age and seasonally (Figure 6.3, Table 6.3). Hemlock needles that were at least two years old had significantly lower rates of photosynthesis than younger needles (*post hoc*, $p < 0.05$). Hemlock photosynthesis increased significantly through the summer, and this change was driven by a seasonal increase in photosynthesis for current-season needles from 4.2 to $6.4 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Table 6.3; significant Month \times Age interaction, $p < 0.0001$). This increase was particularly strong for sunlit current-season needles higher up in the canopy (Figure 6.3), as shown by a number of significant higher order interactions - Month \times Sun-Shade, Month \times Layer, Age \times Sun-Shade, and Month \times Age \times Sun-Shade (Table 6.3).

Total canopy carbon uptake

I scaled leaf photosynthesis to total canopy carbon uptake by weighting my leaf-level measurements according to their contribution to LAI of each canopy layer (Figure 6.4), and then summing these weighted measurements together. Leaf area index was estimated from pure stands of oak/maple or hemlock and was used to assess species' contributions to total carbon flux on a ground area basis. I found that weightings varied with canopy height. The proportion of sunlit leaves and the proportion of current-season needles (for hemlock) increased with increasing canopy height (Figure 6.4).

Modeled total canopy carbon uptake varied seasonally in species-specific ways (Month \times Species interaction, $F_{2,8}=8.86$, $p<0.01$). In June, the broad-leaved species had significantly higher rates of total canopy carbon uptake than did hemlock (25.2 and $19.6 \mu\text{mol m}^{-2} \text{s}^{-1}$ respectively; Figure 6.5; $F_{1,8} = 13.6$ and 16.4 for maple-hemlock and oak-hemlock comparisons, $p < 0.05$ for both). Later in the season, however, hemlock total canopy photosynthesis increased significantly to $24.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ ($F_{1,8} = 9.6$, $p < 0.05$), and it no longer differed significantly from total canopy photosynthesis of broad-leaved species. Maple photosynthesis tended to decrease through the season. The decrease was only marginally significant ($F_{1,8} = 8.0$, $p < 0.1$), but did result in red maple having significantly lower canopy photosynthesis than red oak later in the season ($F_{1,8} = 13.9$, $p < 0.05$).

Sensitivity analysis

My estimates of total canopy carbon uptake were most sensitive to variation in stand leaf area index (Table 6.4). As LAI was a direct scaling factor in the summation scheme, any perturbation in this parameter strongly influenced estimates of total canopy carbon uptake (all relative LAI impacts between 0.7 and 0.8). Overall, perturbations to other model parameters had much smaller influences on canopy photosynthesis estimates (Table 6.4). Model sensitivity to the proportion of sunlit and shaded leaves in tree canopies varied with species, with total canopy photosynthesis most sensitive to this parameter for red oak.

DISCUSSION

Factors influencing leaf-level photosynthesis in tree canopies

As canopy microclimate is both spatially and temporally heterogeneous, many factors interact to influence the different leaf-level components of canopy photosynthesis (Norman & Jarvis 1975, Oker-Blom 1986). Leaves both respond to and modify their microenvironment, and these properties depend heavily on leaf characteristics. Amongst the study species, light availability was a major determinant of leaf-level photosynthesis. As expected, sunlit leaves had consistently higher rates of photosynthesis than shaded leaves for all species, and photosynthesis declined with decreasing height in the canopy for both sunlit and shaded leaves. Light has often been found to be the factor that varies most through tree canopies, and that most strongly influences leaf-level photosynthesis (Holbrook & Lund 1995). I did not directly relate photosynthesis to other environmental variables (e.g., air temperature and vapor pressure deficit), which may be additional determinants of canopy photosynthesis.

Species differed in their responses to canopy light environment. The broad-leaved species had significantly higher photosynthetic capacity than that of the conifer ($15.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ for red oak, $11.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ for red maple, and $7.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ for hemlock). As a result, in the sun, the broad-leaved species had up to twofold higher rates of photosynthesis than hemlock. The A_{max} values for these species fell in the upper end of the general range for broad-leaved and coniferous species, respectively (Jarvis & Leverenz 1983, Holbrook & Lund 1995). Many studies have previously found that conifers have consistently lower photosynthetic capacities than broad-leaved species (Bond 1989, Reich *et al.* 1995), although the basis for the generality of this finding is still unclear. Differences in leaf structural properties and in stem conductance to water movement have both been proposed as possible explanations (Bond 1989). The greater sensitivity of the broad-leaved species to light availability (especially red oak), however, reduced these between-species differences for shaded leaves.

Ontogenetic constraints additionally influenced hemlock leaf-level photosynthesis. Early in the season, needles produced the previous year had higher

rates of photosynthesis than either current-season needles or those produced at least two years before. The current-season needles, however, showed a dramatic increase in photosynthetic capacity through the season. Variation in needle nitrogen content and specific needle weight may have driven both the age-specific and seasonal changes in photosynthetic capacity (Field & Mooney 1986, Oren *et al.* 1986, Reich *et al.* 1991).

Species contributions to forest canopy carbon uptake

The large sizes of canopy trees present us with logistical problems for obtaining species-specific measurements of whole-tree carbon gain. In this study, I use a canopy aggregation model to scale leaf-level photosynthetic rates to total canopy carbon flux. The measurements were restricted to sunny days during the peak growing season (June and August), and thus do not fully represent the carbon dynamics for each species. Despite these limitations, I did find clear evidence that species differences in leaf-level photosynthetic rates scaled up to create distinctions between species in modeled canopy carbon uptake rates. These differences did not fall simply along a leaf habit axis (evergreen coniferous vs. deciduous broad-leaved), due to seasonal changes in canopy photosynthetic rates (see Figure 6.5). Earlier in the season, broad-leaved species had higher rates of total canopy carbon uptake than hemlock (25% greater). The deeper canopy of hemlock (higher LAI) compensated to some extent, but not completely, for its lower leaf-level photosynthetic rates. Hemlock canopies have additional standing foliage compared with broad-leaved species, but the approximately one unit increase in LAI was not sufficient to offset the lower photosynthetic capacity of its leaves. Moving down through the canopy, leaves contribute less and less to total canopy carbon uptake (Schulze *et al.* 1977b, Sprugel 1989, Ellsworth & Reich 1993), because: (1) a smaller proportion of the leaves receive direct beam radiation (Norman 1993), (2) even leaves that do receive direct beam radiation receive lower levels of PFD than leaves higher up (Oker-Blom 1986), and (3) the lower canopy contains a greater proportion of older needles. These phenomena may be particularly important in hemlock stands, as canopies of hemlock trees have very steep light attenuation curves (Canham *et al.* 1994), so that additional foliage provides diminishing benefits.

Red oak and red maple achieved equivalent rates of total canopy carbon uptake, but did so in different ways. Because red oak was particularly sensitive to changes in irradiance, sunlit leaves in red oak contributed more to total canopy photosynthesis than sunlit red maple leaves (80.5 % for red oak vs. 71.5 % for red maple). Bassow & Bazzaz (1998) found similar patterns for *in situ* photosynthetic rates of red oak and red maple. We might have predicted these patterns based on the species' life-history strategies (see Bazzaz 1979, 1996). Red oak is generally faster growing, and thus is likely to have higher light-saturated photosynthetic rates than red maple but lower carbon assimilation in the shade.

Information on canopy photosynthetic rates from only two points in time makes it difficult to draw many inferences about seasonal trends in carbon flux. I found, however, that at least between June and August, species' contributions to forest carbon uptake changed, even though air temperatures and relative humidity were not different between months. Hemlock showed a significant increase in modeled total canopy photosynthesis, because of changes in photosynthetic competence of its current-season needles. These needles may compose up to 30% of canopy leaf area (see Figure 6.4), and thus changes in their behavior will clearly influence total canopy carbon uptake. In parallel with these changes, red maple canopy photosynthesis declined, so that red maple and hemlock did not differ in their contributions to forest carbon uptake later in the season. Declines in red maple photosynthetic capacity through the season may be related to reduced stomatal conductance in response to reduced soil water availability and increased leaf-to-air vapor pressure deficits. Soil water content was particularly low in these stands by August in this year ($\sim 0.18 \text{ cm}^3 \text{ cm}^{-3}$; K.M. Newkirk, *unpublished data*), and red maple may be more sensitive to water deficits than oak (Abrams 1998, Tschaplinski *et al.* 1998).

These changes in canopy-level photosynthesis across the season reduced differences in modeled canopy carbon uptake rates between hemlock and red maple, whose overall carbon uptake rates did not differ from one another. In contrast, red oak, had consistently higher canopy photosynthetic rates than either of the other species. On an annual basis, hemlock carbon gain may be underestimated by my instantaneous

measures of canopy carbon gain on sunny days during the main carbon season. Hemlock's contribution to annual forest carbon gain may eventually surpass that of red maple, as hemlock may compensate to some degree for its lower photosynthetic capacity on clear summer days with higher carbon uptake on cloudy days and outside the main growing season. Previous studies have come to differing conclusions regarding the importance of winter carbon gain for conifer productivity (Schulze *et al.* 1977a, Schaberg *et al.* 1995). Chapter 7 considers a novel approach for measuring year-long carbon gain for hemlock.

Validity of bottom-up approach

Due to the large degree of heterogeneity and non-linearity inherent in canopy processes, forest canopy models are a particularly challenging method of ecological scaling (Holbrook & Lund 1995, Jarvis 1995, Baldocchi & Vogel 1996, Kruijt *et al.* 1997). My summation approach accounted for a large proportion of the heterogeneity by stratifying the canopy vertically and into sun/shade classes. This method has previously been found to describe canopy properties sufficiently well to accurately predict total canopy carbon uptake (Norman 1980). In contrast, my sensitivity analysis showed that direct scaling components are the largest source of error in bottom-up approaches. Leaf area index (LAI) was the principle scaling factor for the summations used in the present study, and outputs were particularly sensitive to perturbations in LAI estimates. In the present study, my LAI estimates were based on direct foliage sampling (litter traps and destructive branch sampling) and indirect analyses of canopy structure with a hemispherical lens, both of which should provide an accurate representation of canopy density for the stands sampled. My sensitivity analysis suggests, however, that obtaining accurate LAI estimates for other stands within the region would be the first step for extending these model results. Models that have effectively scaled canopy photosynthesis to the landscape level have often incorporated remotely sensed data covering broad geographic regions (Potter *et al.* 1993, Berry *et al.* 1997).

Implications for community and ecosystem dynamics

I have documented clear differences in canopy-level photosynthetic rates between the dominant coniferous and broad-leaved species in mixed forests in New England. I found that red oak consistently had the highest modeled canopy photosynthetic rates of the species studied, while, through the season, the relative contribution of hemlock to forest carbon flux increased and that of red maple decreased. A more complete analysis of species' contributions should include full annual carbon budgets for these species (see Chapter 7), and a broader range of species (e.g., white pine and yellow birch).

Changes in canopy composition are likely to occur in this region in the near future, as a result of both natural and anthropogenic disturbance processes (Foster & Motzkin 1998). Many of these perturbations may differentially affect coniferous and broad-leaved species, and thus alter the balance between these two groups of forest trees. There is growing evidence that both rising levels of atmospheric CO₂ and increased nitrogen deposition may favor broad-leaved species over conifers (Ceulemans & Mousseau 1994, Magill *et al.* 1997, but see Saxe *et al.* 1998; further discussion in Chapter 8). In addition, hemlock is specifically under threat from an exotic pest (the hemlock woolly adelgid, *Adelges tsugae* Annand), that has the potential to eliminate hemlock from the region (Orwig & Foster 1998). In the present study, I have demonstrated that many of these changes could have substantial impacts on forest carbon dynamics in the future, particularly if red oak is the primary broad-leaved species to expand at the expense of hemlock. Models of carbon sequestration for temperate forests should account for the different contributions that tree species make to ecosystem-level carbon uptake.

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Table 6.1. Summary results of analysis of variance comparing leaf-level photosynthetic rates for different species. Month, species, layer and sun-shade were fixed factors, and day was a random factor nested within month.. Significant effects are shown in bold, with symbols designating the level (^{NS} $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

| Effect | Degrees of freedom | F-ratio† | p |
|-------------------------------------|--------------------|----------------|-----|
| Month | 1 | 0.06 | NS |
| Day (Month) | 4 | 12.49 | *** |
| Species | 2 | 68.69 | *** |
| Layer | 2 | 82.26 | *** |
| Sun-Shade | 1 | 1101.50 | *** |
| Month x Species | 2 | 17.81 | *** |
| Month x Layer | 2 | 2.48 | NS |
| Month x Sun-Shade | 1 | 0.86 | NS |
| Species x Layer | 4 | 1.49 | NS |
| Species x Sun-Shade | 2 | 74.14 | *** |
| Layer x Sun-Shade | 2 | 8.35 | *** |
| Month x Species x Layer | 4 | 0.60 | NS |
| Month x Species x Sun-Shade | 2 | 2.87 | NS |
| Month x Layer x Sun-Shade | 2 | 2.16 | NS |
| Species x Layer x Sun-Shade‡ | 4 | 4.97 | ** |
| Month x Species x Layer x Sun-Shade | 4 | 1.13 | NS |

† The mean square of every effect was tested over the model error mean square (0.94, degrees of freedom 68), except for Month which was tested over day mean square (12.49).

Table 6.1 cont.

‡ For the highest order significant interaction, Scheffé *post hoc* comparisons involving a change in one single factor are shown below, with symbols showing significance of each comparison (as above).

a. Between sunlit and shaded leaves

| Species | Red maple | | | Red oak | | | Hemlock | | |
|-----------|-----------|-----|-----|---------|-----|-----|---------|-----|-----|
| Layer | 1 | 2 | 3 | 1 | 2 | 3 | 1 | 2 | 3 |
| Sun-Shade | Sun | Sun | Sun | Sun | Sun | Sun | Sun | Sun | Sun |
| Shade | *** | *** | *** | *** | *** | *** | *** | *** | *** |

b. Between species

| Sun-Shade | Sun | | | | | | Shade | | | | | |
|-----------|-----|-----|----|-----|----|-----|-------|----|----|----|----|----|
| Layer | 1 | | 2 | | 3 | | 1 | | 2 | | 3 | |
| Species | Ro | H | Ro | H | Ro | H | Ro | H | Ro | H | Ro | H |
| Rm | *** | *** | ** | *** | NS | *** | ** | * | NS | NS | NS | NS |
| Ro | — | *** | — | *** | — | *** | — | NS | — | NS | — | NS |

c. Between canopy layers

| Sun-Shade | Sun | | | | | | Shade | | | | | |
|-----------|-----------|-----|---------|-----|---------|-----|-----------|-----|---------|----|---------|----|
| Species | Red maple | | Red oak | | Hemlock | | Red maple | | Red oak | | Hemlock | |
| Layer | 2 | 3 | 2 | 3 | 2 | 3 | 2 | 3 | 2 | 3 | 2 | 3 |
| 1 | NS | *** | *** | *** | NS | *** | NS | *** | NS | NS | NS | * |
| 2 | — | NS | — | ** | — | NS | — | NS | — | NS | — | NS |

Table 6.2. Light-saturated photosynthetic rates (A_{\max}) derived from photosynthesis-light curves (standard errors shown in brackets).

| SPECIES | LEAF AGE (years) | Light-saturated photosynthetic rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$)† | |
|-----------|---------------------|--|-----------------------|
| | | June | August |
| Red maple | • | 11.27 (0.46) a | 10.26 (0.54) ab |
| Red oak | • | 15.45 (0.47) b | 14.35 (0.73) c |
| Hemlock | 0 | 6.51 (0.23) c | 11.25 (0.31) a |
| Hemlock | 1 | 8.58 (0.26) d | 9.16 (0.36) bd |
| Hemlock | 2+ | 7.27 (0.29) cd | 8.13 (0.51) d |

† Means that are significantly different ($p > 0.05$) either share no letters (between species within the month), or are shown in bold (between months within a species), based on sequential Bonferroni-corrected planned comparisons.

Table 6.3. Summary results of analysis of variance comparing leaf-level photosynthetic rates for different needle age classes of hemlock. Month, age, layer and sun-shade were fixed factors, and day was a random factor nested within month. Significant effects are shown in bold, with symbols designating the level (^{NS} $p > 0.05$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

| Effect | Degrees of freedom | F-ratio† | p |
|---------------------------------|--------------------|----------|-----|
| Month | 1 | 7.72 | * |
| Day (Month) | 4 | 5.85 | *** |
| Layer | 3 | 84.16 | *** |
| Age | 2 | 8.98 | *** |
| Sun-Shade | 1 | 588.71 | *** |
| Month x Layer | 3 | 3.70 | * |
| Month x Age | 2 | 14.72 | *** |
| Month x Sun-Shade | 1 | 22.46 | *** |
| Layer x Age | 6 | 0.59 | NS |
| Layer x Sun-Shade | 3 | 4.71 | ** |
| Age x Sun-Shade | 2 | 4.39 | * |
| Month x Layer x Age | 6 | 0.42 | NS |
| Month x Layer x Sun-Shade | 3 | 0.48 | NS |
| Month x Age x Sun-Shade† | 2 | 4.55 | * |
| Layer x Age x Sun-Shade | 6 | 0.51 | NS |
| Month x Layer x Age x Sun-Shade | 6 | 0.23 | NS |

† The mean square of every effect was tested over the model error mean square (0.80, degrees of freedom 92), except for Month which was tested over day mean square (5.85).

Table 6.3 cont.

‡ For the highest order significant interaction, Scheffé *post hoc* comparisons involving a change in one single factor are shown below, with symbols showing significance of each comparison (as above).

a. Between months

| Sun-Shade | Sun | | | Shade | | |
|-----------|------|------|------|-------|------|------|
| Leaf Age | 0 | 1 | 2+ | 0 | 1 | 2+ |
| Month | June | June | June | June | June | June |
| August | *** | NS | NS | NS | NS | NS |

b. Between sunlit and shaded leaves

| Month | June | | | August | | |
|-----------|------|-----|-----|--------|-----|-----|
| Leaf Age | 0 | 1 | 2+ | 0 | 1 | 2+ |
| Sun-Shade | Sun | Sun | Sun | Sun | Sun | Sun |
| Shade | *** | *** | *** | *** | *** | *** |

c. Between leaf ages (in years)

| Month | June | | | | August | | | |
|-----------|------|----|-------|----|--------|-----|-------|----|
| Sun-Shade | Sun | | Shade | | Sun | | Shade | |
| Leaf Age | 1 | 2+ | 1 | 2+ | 1 | 2+ | 1 | 2+ |
| 0 | *** | NS | NS | NS | NS | *** | NS | NS |
| 1 | — | ** | — | NS | — | *** | — | NS |

Table 6.4. Sensitivity of calculated total canopy carbon uptake (in both June and August) to variation in input parameters. Effects of each aggregation component are shown as relative changes in the output following perturbation (% change in output / % change in input). For all species (a), leaf area index (LAI), proportion of sunlit and shaded leaves (Sun/Shade), and vertical distribution of foliage (Layer) were varied. In addition, for hemlock (b), proportions of different needle age classes were varied (0, 1, and 2 or more years old).

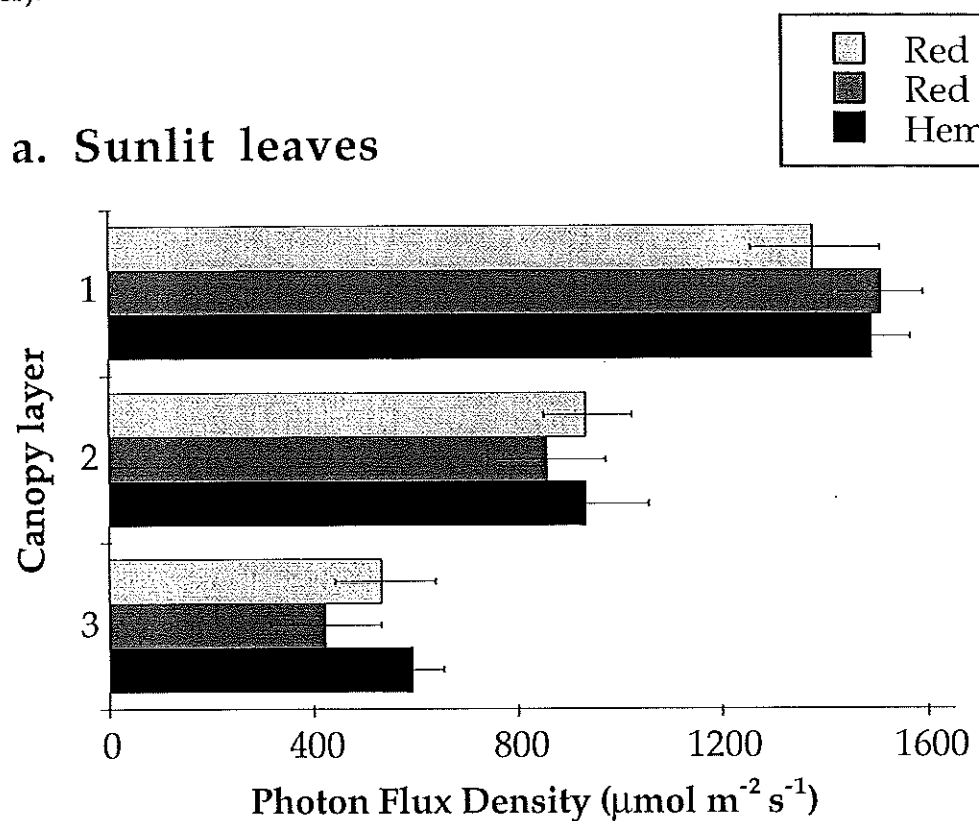
a. For all species

| Species | June | | | August | | |
|-----------|-------|-----------|-------|--------|-----------|-------|
| | LAI | Sun/Shade | Layer | LAI | Sun/Shade | Layer |
| Red maple | 0.807 | 0.314 | 0.106 | 0.778 | 0.401 | 0.148 |
| Red oak | 0.685 | 0.583 | 0.121 | 0.724 | 0.571 | 0.163 |
| Hemlock | 0.823 | 0.278 | 0.162 | 0.774 | 0.343 | 0.210 |

b. For hemlock only

| Needle Age (years) | June | August |
|--------------------|--------|--------|
| 0 | -0.049 | 0.086 |
| 1 | 0.041 | 0.001 |
| 2+ | 0.002 | -0.045 |

Figure 6.1. Photon flux density (PFD, mean \pm SE, pooled across months) falling on sunlit (a) and shaded (b) leaves of my study species in different canopy layers (1 is the top layer).



b. Shaded leaves

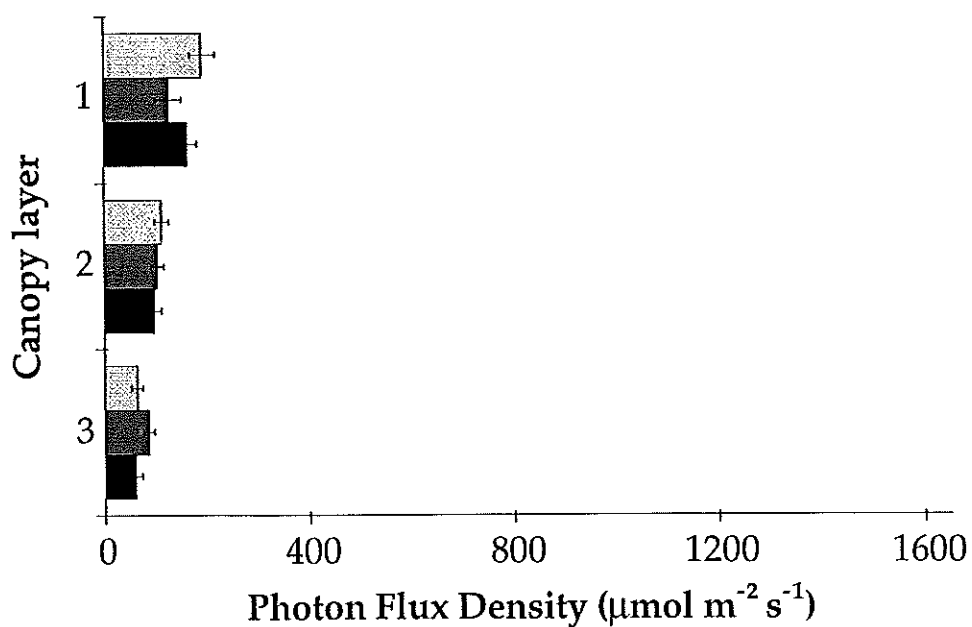


Figure 6.2. Leaf-level photosynthetic rates (mean \pm SE, $n = 3$) in June (a,b) and August (c,d) for sunlit (a,c) and shaded (b,d) leaves in different canopy layers (1 is the top layer) of mature red maple, red oak and hemlock trees.

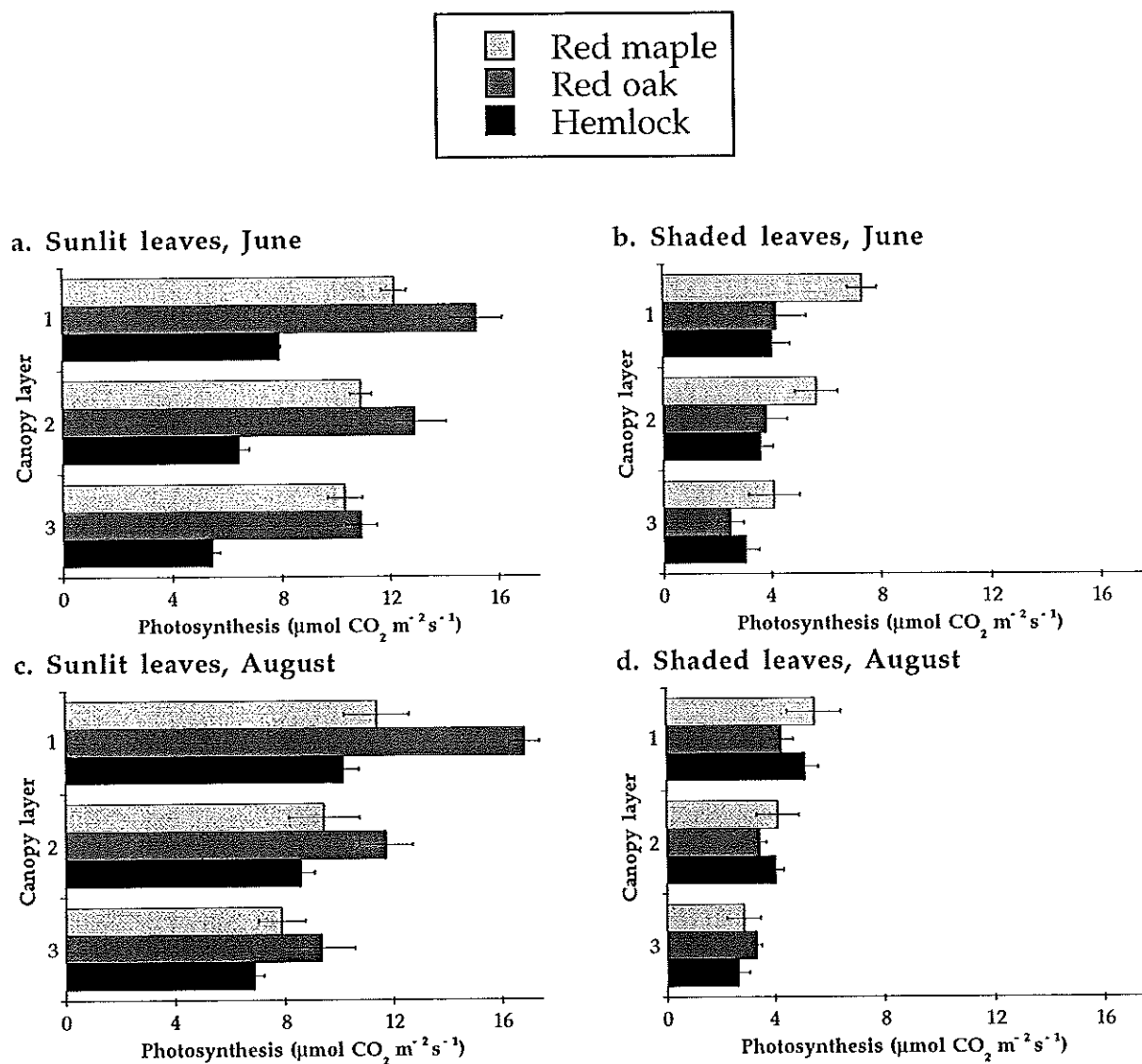


Figure 6.3. Leaf-level photosynthetic rates (mean \pm SE, $n = 3$) in June (a,b) and August (c,d) for hemlock sunlit (a,c) and shaded (b,d) leaves of different ages in different canopy layers (1 is the top layer).

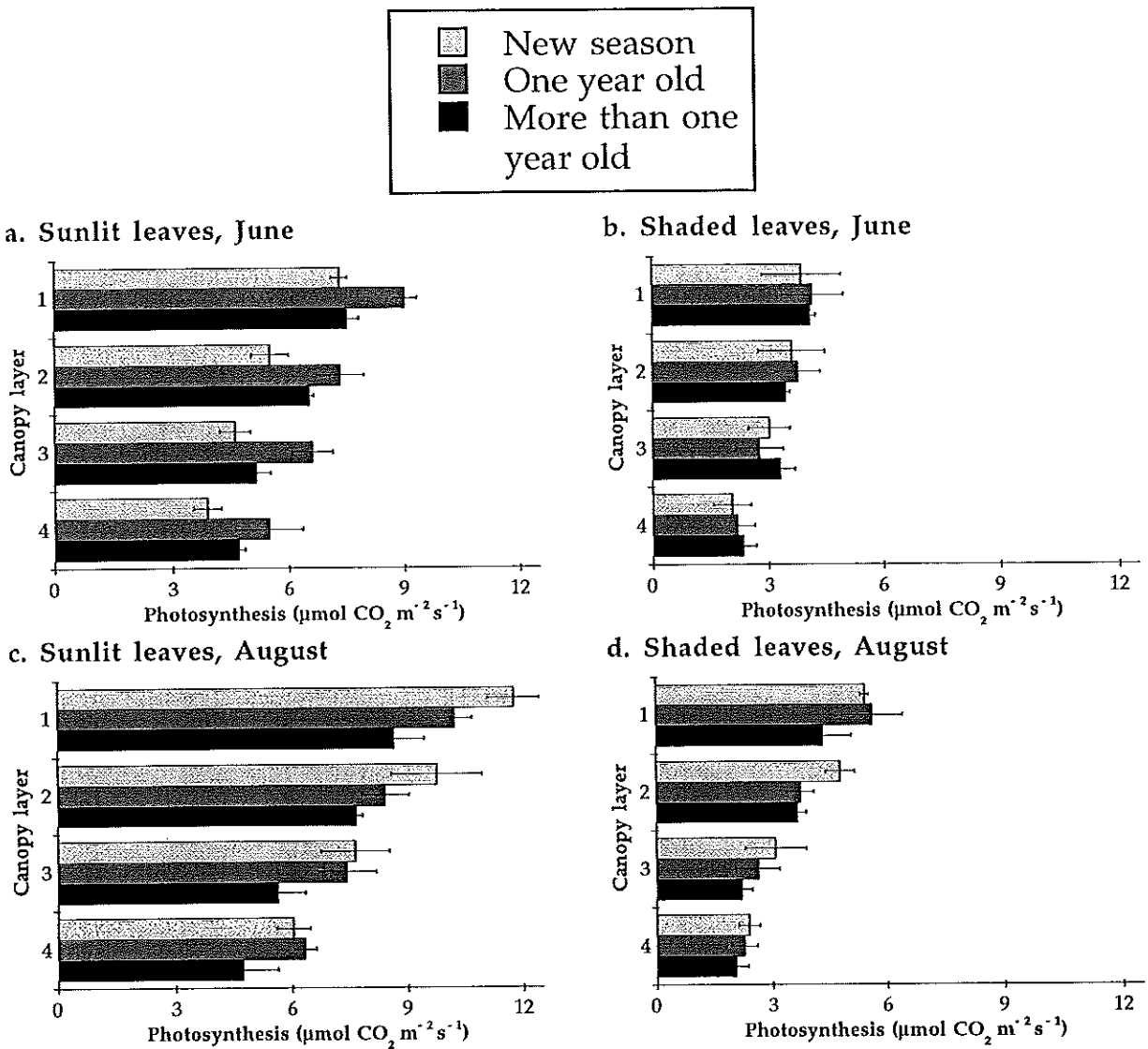


Figure 6.4. For different hemlock canopy layers (1 is top layer), (a) proportion of sunlit and shaded leaf area index at midday during mid-summer, and (b) proportion of different needle age classes. Red oak and red maple canopies show similar, but not identical, patterns for sunlit/shaded leaf proportions, with only three canopy layers recognized in this study.

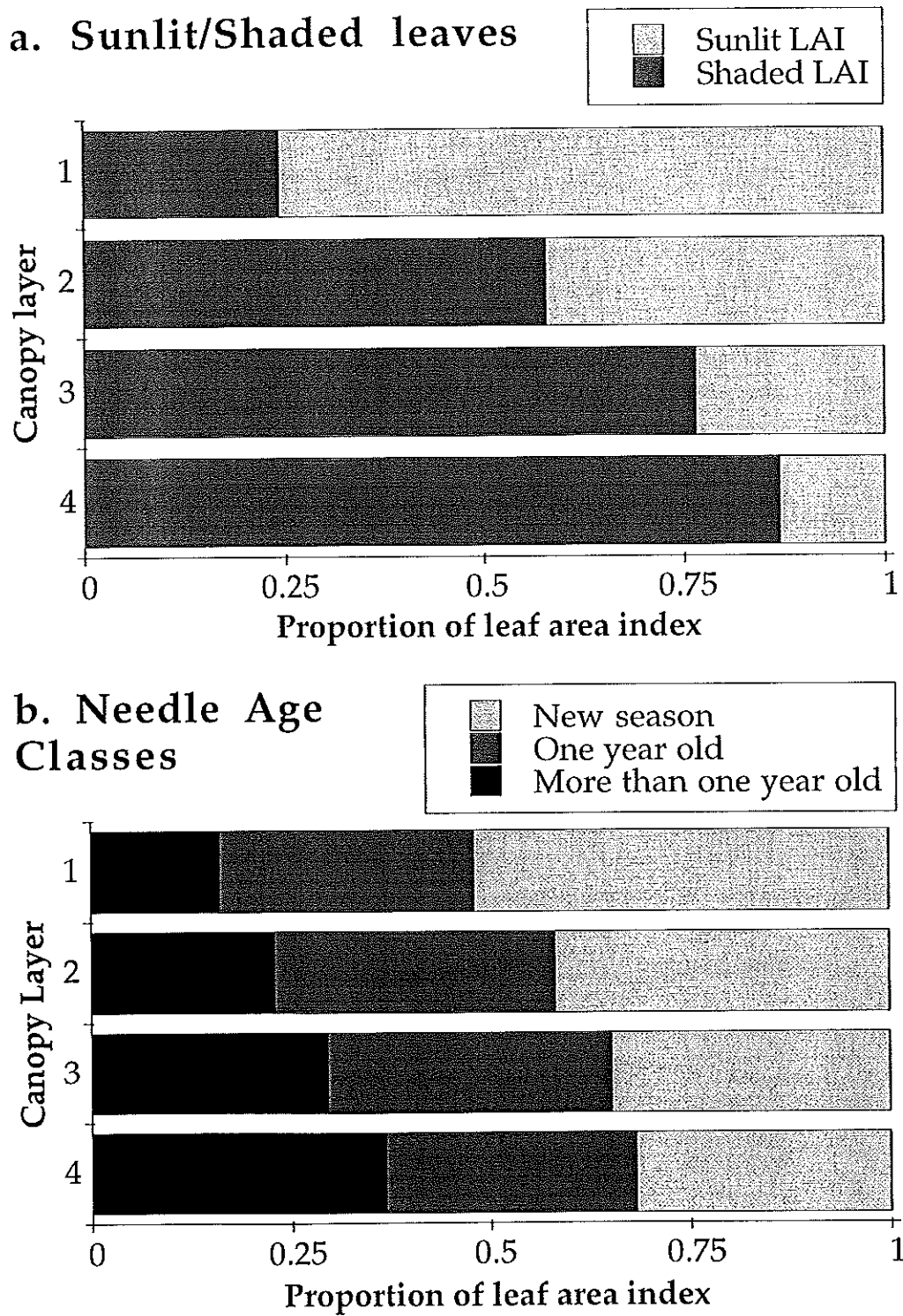
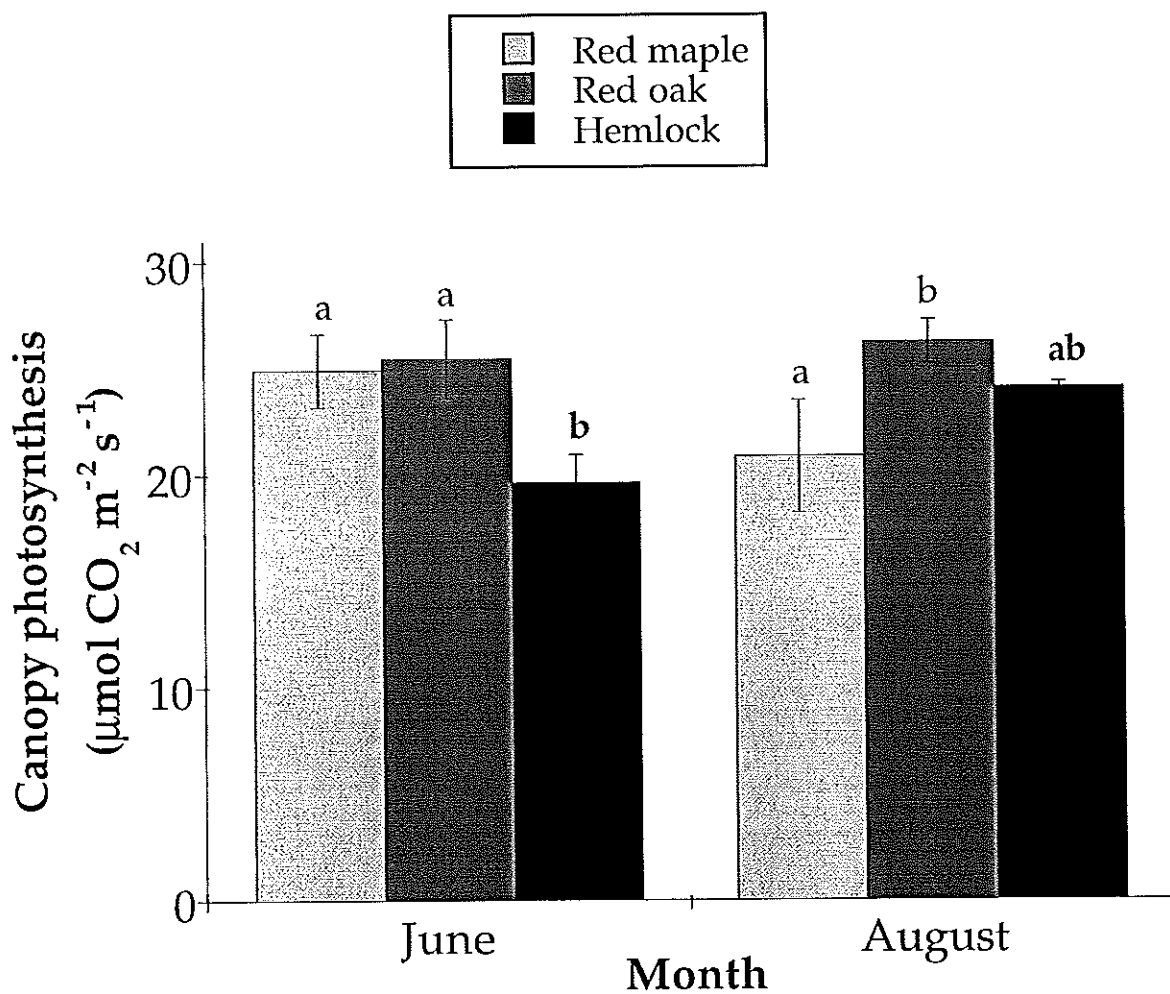


Figure 6.5. Modeled total canopy carbon uptake rates (mean \pm SE, $n = 3$) in June and August for red maple, red oak, and hemlock trees. Means that are significantly different from one another between species but within a month ($p < 0.05$) share no letters in common, while means that are significantly different from one another between months but within a species ($p < 0.05$) are shown with boldface letters (sequential Bonferroni-adjusted means comparisons).



CHAPTER 7

COUPLING WHOLE-TREE TRANSPIRATION AND CANOPY PHOTOSYNTHESIS IN CONIFEROUS AND BROAD-LEAVED TREE SPECIES

Abstract. Future changes in forest composition are likely to have major impacts on whole-forest ecosystem processes. I tested the hypothesis that the dominant coniferous and broad-leaved species in mixed temperate forests in New England differ in canopy-level transpiration and photosynthetic rates, and thus that changes in forest composition will influence water and carbon exchange between these forests and the atmosphere. I used heat dissipation probes to measure whole-tree sap flow in three species throughout one full year, and then combined these measurements with micro-meteorological monitoring (air and leaf temperatures, relative humidity, wind speed) to calculate canopy conductance. Leaf-level gas exchange measurements were then used to convert canopy conductance to whole-tree carbon gain throughout the year. Both broad-leaved species (red oak, *Quercus rubra*; red maple, *Acer rubrum*) had two- to four-fold greater annual fluxes of water and carbon on a ground area basis than did the conifer (hemlock, *Tsuga canadensis*). Among the broad-leaved species, there was also considerable variation, with red oak consistently showing 60–80 % higher fluxes than red maple. Although hemlock maintained a deeper canopy than the broad-leaved species and fixed one-third of its carbon outside the growing season (when broad-leaved trees were leafless), neither of these traits was sufficient to compensate for its low rates of leaf-level photosynthesis during the growing season. Net carbon accumulation estimates from annual growth rings and ecosystem-scale eddy covariance confirmed that using whole-tree sap flow as a scaling approach provided a good representation of both the magnitude of current forest fluxes and differences in individual species' fluxes. My results indicate that the predicted loss of hemlock from mixed temperate forests could increase whole-forest water loss and carbon gain by two- to four-fold, depending on the identity of the future dominant broad-leaved species.

INTRODUCTION

Temperate forests currently represent an important sink in the contemporary global carbon cycle (Fan *et al.* 1998, Houghton *et al.* 1998), and may serve to slow continued increases in atmospheric CO₂ related to human activities (Woodwell *et al.* 1998). These forests, however, are threatened by a suite of human-induced environmental perturbations that may affect their ability to function as a future carbon sink. Changes in atmospheric composition, increased incidence of exotic pests, and increased influence of natural and human disturbances will all likely affect the integrity of temperate forests in the future (Bazzaz 1996, Foster *et al.* 1997). To examine the potential influence of such changes, it is critical to understand the underlying processes controlling ecosystem function in temperate forests. In the present study, I ask how the species composition of mixed temperate forests influences whole-ecosystem function. Community structure is an important determinant of ecosystem function that has only recently received recognition (Tilman 1999). It is now clear that both the identity and number of species within a community could influence ecosystem processes (Hooper & Vitousek 1997, Hector *et al.* 1999). Changes in community composition could represent an important mechanism by which environmental perturbations affect future ecosystem functioning (Bolker *et al.* 1995, Wedin & Tilman 1996, Saleska *et al.* 1999).

Links between ecosystem structure and function should be particularly strong in mixed temperate forests, which contain two distinct groups of tree species (evergreen coniferous and deciduous broad-leaved) (Pastor & Mladenoff 1992). These two groups of trees have evolved distinctive traits over time and exhibit numerous biological differences, e.g., leaf habit, water transport capacity (Bond 1989, Smith & Hinckley 1995). Differences in basic physiology could ultimately scale up to influence species' contributions to ecosystem-level processes, such as forest carbon gain and nutrient cycling (Baldocchi & Vogel 1996, Reich *et al.* 1997, Bassow & Bazzaz 1998). As a result, basic forest ecosystem properties could be directly influenced by the relative abundance of different canopy tree species. In the present study, I tested the hypothesis that the dominant coniferous and broad-leaved species in mixed temperate forests in New

England differ in canopy-level transpiration and photosynthesis, and thus that a change in forest composition will influence the exchange of water and carbon between forests and the atmosphere. I predicted that, over the year, the main coniferous species (eastern hemlock, *Tsuga canadensis* (L.) Carr.) would lose more water and fix more carbon than would the major broad-leaved species (red oak, *Quercus rubra* L.; red maple, *Acer rubrum* L.). Conifers are often more productive as mature trees than broad-leaved species (Jarvis & Leverenz 1983), despite their lower instantaneous leaf-level photosynthetic rates (Reich *et al.* 1995), as a result of their higher leaf area index (Schulze *et al.* 1977, Bond 1989) and their ability to fix carbon outside the main growing season when broad-leaved species are leafless (Neilson *et al.* 1972, Waring & Franklin 1979).

Studies examining controls on ecosystem function are challenging as our ability to take large-scale mechanistic measurements on whole ecosystems is still limited. In the present study, I take advantage of a physiological technique that provides a simple measure of whole-tree function, and thus avoids many bottom-up scaling issues, but still contributes detailed species-level information. Whole-tree transpiration can now be monitored relatively easily using sap flow measuring devices (Granier *et al.* 1996, Wullschlegel *et al.* 1998), which provide information on very short time scales but which may be maintained over the long term. This ability to monitor plant function for long time periods becomes particularly important when comparing evergreen and deciduous species, because evergreen species can stay physiologically active outside of the main growing season when deciduous species have no leaves. If we wish to compare annual water fluxes for both kinds of tree species, we need to monitor transpiration for the whole year, not just at select points during the main growing season. As photosynthesis and transpiration are connected through the activity of stomata (Farquhar & Sharkey 1982), there is potential to use whole-plant sap flow to estimate annual patterns of total canopy carbon uptake. I combined measurements of sap flow taken throughout one full year with micro-meteorological monitoring (air and leaf temperatures, relative humidity, wind speed) to calculate canopy conductance (Meinzer *et al.* 1997). Leaf-level gas exchange measurements were then used to convert

canopy conductance to whole-plant carbon gain throughout the year. I compared my final estimates of tree productivity with net biomass growth rates calculated from tree ring widths and published dimension analysis values. In this way, I was able to test my hypothesis contrasting annual water and carbon fluxes for both coniferous and broad-leaved tree species.

MATERIALS AND METHODS

Sap flow

In autumn 1998, heat dissipation probes were installed in trees at three sites within the Prospect Hill tract of Harvard Forest (see further details in Chapter 1). At each site, one tree of each study species was chosen (Table 7.1), with all study trees at a site located within 5 m of each other. The study species represent the currently dominant conifer (hemlock) and broad-leaved (red oak, red maple) species both locally (Harvard Forest) and regionally (central Massachusetts) (Foster *et al.* 1998).

Heat dissipation probes (2 mm diameter, 3 cm length) were constructed following Granier's (1987) original design. Each study tree contained two pairs of probes, inserted radially at a height of 1.4 m on opposite sides of the trunk from each other. At each insertion point, the bark was removed, and two 2 mm diameter holes were drilled, one 10 cm above the other, for probe insertion. The upper (downstream) probe contained 60 cm of tightly coiled high resistance heating wire (0.005 mm diameter), used to heat the probe with a constant power of 0.2 W from a marine deep cycle battery. Each probe, whether downstream or upstream (reference), contained a T-type thermocouple junction embedded in blackened superglue. The thermocouples of each pair were connected in series at the constantan side, and the copper leads were connected to a 21X data logger (Campbell Scientific, Logan, UT) programmed to record the temperature difference between the probes. Once assembled, the probes were covered in a polystyrene housing and surrounded with silver bubble wrap to provide thermal insulation. The edges of each polystyrene holding were sealed with hardening foam to prevent water entry. The probes were run for one week in the middle of every month in 1999, logging data every 1 s and storing the average every 20 mins during each measurement interval.

Prior to insertion in the field, the heat dissipation probes were calibrated in the laboratory. Probes were inserted into excised branches (40 – 50 cm diameter, 25 – 40 cm long) of each study species (described above). Branches were clamped into a continuous

flow system where they were perfused with water from a reservoir. Flow rates of water through stems were determined by measuring the weight increase of water collected after leaving the branch per unit time. Flow rates were varied by adjusting the water reservoir height, and temperature differences at zero flow were determined two hours after flow was stopped. Provided the probes were fully in conducting sapwood (Clearwater *et al.* 1999), Granier's (1987) original empirical relationship between sap flux velocity (v , mm s⁻¹) and temperature difference between probes (ΔT , °C) was supported, as follows:

$$v = 0.119k^{1.231} \quad (1)$$

where k is related to the temperature difference between probes at some flow rate compared with the temperature difference at zero flow (ΔT_0)

$$k = \left(\frac{\Delta T_0 - \Delta T}{\Delta T} \right) \quad (2)$$

Regressions of $\log v$ against $\log k$ produced slope coefficients that varied from 1.19 to 1.25 ($r^2 = 0.90 - 0.95$), and these did not differ significantly from the original coefficient of 1.231 ($F_{1,28} < 0.01$, $p > 0.05$).

Based on this empirical relationship, continuous measurements of ΔT on the study trees were used to calculate sap flux velocity over 20-minute intervals throughout each measuring period. For calculation of k , the largest temperature difference from the previous night was used as ΔT_0 . Sap flux velocity measurements on the same tree were averaged and converted to whole-tree sap flow by multiplying by sapwood cross-sectional area (m²) in the tree's trunk (Granier *et al.* 1996), which itself was determined by measuring sapwood depth on increment cores taken in late 1999. Sapwood could be easily distinguished from the heartwood based on color differences, provided the measurements were taken straight after the core was removed from the tree. At this point, I noted the short sapwood depth of the red oak trees in the study (1.0 - 1.5 cm), a feature which is typical of ring-porous species. As the heat dissipation probes were not

fully in conducting sapwood in these trees, I applied the correction formulated by Clearwater *et al.* (1999):

$$\Delta T_{\text{actual}} = \frac{\Delta T_{\text{measured}} - (1 - a)\Delta T_0}{a} \quad (3)$$

where a is the proportion of probe in conducting sapwood. Whole-tree sap flow was scaled to ground area by dividing by projected canopy area (m^2), which was determined for each tree by locating the edge of the canopy in eight compass directions using a densitometer (Arneeth *et al.* 1996).

Micro-meteorology

Canopy conductance was determined from sap flow rates using:

$$g_c = \frac{F}{\text{vpd}} \quad (4)$$

where g_c is canopy conductance scaled to ground area ($\text{mol m}^{-2} \text{s}^{-1}$), F is sap flow scaled to ground area ($\text{mol m}^{-2} \text{s}^{-1}$), and vpd is vapor pressure deficit between the leaf interior and the bulk air (mol mol^{-1}), itself calculated as the difference between saturation vapor pressure at leaf temperature and the ambient vapor pressure (function of air temperature and relative humidity) (Pearcy *et al.* 1989). Leaf temperatures were measured with fine-wire copper-constantan thermocouples attached to leaves of all study species from two canopy access towers located within 500 m of all study sites (Bassow & Bazzaz 1998, Hadley 2000). Thirty thermocouples were placed in the canopies of each study species. Due to temperature differences between sunlit and shaded leaves, tree canopies were stratified into two layers of approximately equal leaf area – the upper canopy containing mostly sunlit leaves and the lower canopy containing mostly shaded leaves. Thermocouples were divided equally between both strata, and temperatures were recorded separately for each stratum. Stratification based on sunlit/shaded leaf conditions often captures much of the variation in canopy processes (Norman 1993, and see Chapter 6). I aimed to ensure good contact between thermocouple junctions and leaves. For hemlock, thermocouple junctions were

positioned within a tight constantan loop slipped around each needle. For the broad-leaved species, thermocouple leads were attached to leaf petioles with cable ties and then thermocouple junctions were held to leaf under-sides using small strips of medical tape, which permitted continued water loss from leaves. In addition, a CS500 sensor (Vaisala, Woburn, MA) was installed on the hemlock canopy access tower to measure both air temperature and relative humidity.

All temperature/humidity sensors were connected to 21X loggers (Campbell Scientific, Logan, UT), which recorded data over the same sampling interval as did those measuring sap flow (1 s sampling averaged every 20 mins, one week every month for a year). No apparent time lags existed between sap flow near the base of the tree and vpd in the canopy (highest correlations between F and vpd were obtained with no time lag, $r_{70} = 0.78 - 0.95$, vs. $0.62 - 0.88$ with a one-hour lag), and so g_c could be calculated from F and vpd measurements taken over the same time intervals. Due to differences in temperature between upper and lower canopy leaves, canopy conductance values were calculated separately for each strata. Sap flow was divided between strata (equal leaf areas) based on differences in conductance ratios determined from *in situ* measurements of gas exchange (see next section and Table 7.2). The ratio of sap flow through upper and lower strata was assumed to be 2/1 for hemlock, 1/1 for red maple, and 3/2 for red oak.

Stomatal conductance was calculated from canopy conductance using the following relationship:

$$g_s = \frac{1}{\left(\frac{1}{g_c} - \frac{1}{g_b}\right)} \quad (5)$$

where g_s is stomatal conductance and g_b is boundary layer conductance, both scaled to ground area ($\text{mmol m}^{-2} \text{s}^{-1}$). Boundary layer conductances in the upper and lower canopies were determined from wind speed, measured using O14A anemometers (MetOne, Grants Pass, OR) attached to the hemlock canopy access tower at two heights, and from leaf size, according to the relationship proposed by Nobel (1999):

$$g_b = \frac{255}{\sqrt{\frac{d}{w}}} \quad (6)$$

where d is mean leaf length/width (0.5 cm hemlock, 7.5 cm red maple, 10 cm red oak) and w is wind speed (cm s^{-1}).

Gas exchange

To convert stomatal conductance values to carbon uptake rates, I took *in situ* gas exchange measurements in the canopies of each of the study species. Trees of all species were sampled in July and September 1999, with an extra sampling interval for hemlock in May (before broad-leaved species had leafed out). At each sampling time, gas exchange measurements were taken throughout the day (0800 – 1800 h) over four consecutive days on trees that could be reached from the canopy access towers at Harvard Forest (four hemlock individuals, two individuals of both maple and oak). 8 - 10 leaves were sampled within each canopy layer (upper and lower) each day, and additionally for different needle age classes for hemlock (see details in Chapter 6). *In situ* leaf-level photosynthesis and conductance were measured using a Li-Cor 6400 open gas exchange system (Li-Cor, Lincoln, NB). The system was set up to match current environmental conditions as closely as possible. Ambient air was drawn in from a dry, empty carboy (to stabilize gas concentrations), so that temperature and $\text{CO}_2/\text{H}_2\text{O}$ concentrations corresponded with those of bulk air. In addition, in order to make measurements under ambient light levels, the gas exchange chamber was fitted with a clear lid and its orientation set to match that of each leaf. Due to the irregular shape of hemlock needles, sampled needles were scanned into the computer after measurement and their area determined using NIH Image software v1.6 (NIH, Bethesda, MD).

Linear models examining the influence of sampling month, canopy layer, and leaf age class (for hemlock only) on the relationship between stomatal conductance and *in situ* leaf-level photosynthesis revealed that, for the broad-leaved species, the relationship differed between upper and lower canopy layers ($F_{1,125} = 133.60$ for red maple, 62.17 for red oak, both $p < 0.001$), but not between sampling months ($F_{1,125} = 0.72$

for red maple, 0.67 for red oak, both $p > 0.05$). In contrast, for hemlock, both canopy layer and sampling month influenced the photosynthesis-conductance relationship ($F_{2,437} = 10.18$, $p < 0.001$), but this relationship did not differ between needle age classes ($F_{2,437} = 0.81$, $p > 0.05$). The actual parameters used to convert stomatal conductance to canopy carbon uptake rates were generated from Model II linear regression analysis (Table 7.2) (Sokal & Rohlf 1995). As there was no seasonal variation in the relationship for either maple or oak, these parameters were used across all months during which the trees were foliated (June – October). For hemlock, May parameters were used for both April and May, July parameters were used for June – August, and September parameters were used September – November. For all species, there was no measurable sap flow from January until March, and in December, and so canopy photosynthesis was assumed to be zero at these times as well.

Above-ground biomass gain

Measurements of gross canopy carbon gain in 1999 for hemlock, red maple, and red oak were compared with estimates of net above-ground biomass gain over the previous decade. The tree cores taken to determine sapwood depth/area (see earlier) were mounted and sanded to reveal annual rings. The widths of rings produced in the last ten years were measured using a Unislide tree ring measuring system (Velmex, New York, NY) and a dissecting microscope. Annual growth increments were used to calculate annual above-ground biomass growth based on dimension equations specific to each of the study species (ter Mikaelian & Korzukhin 1997). All equations were of the form:

$$M = aD^b \quad (7)$$

where M is the dry weight of the above-ground biomass (Kg), D is DBH (cm). For the species-specific parameters, a and b , I used averages of published values for each study species (0.11 and 2.32 for hemlock, 0.13 and 2.38 for red maple, 0.10 and 2.51 for red oak).

RESULTS

All species showed a clear diurnal signal in water flux during months when sap flow could be detected (April – November) (Figure 7.1). Broad-leaved species had very low rates of sap flow in the months prior to leaf out and after leaf fall (April, May, November), but had much greater fluxes of water than hemlock during summer months (June – October). Sap flow remained low at night, typically began to increase around 0700 h, hit a peak close to 1200 h (up to $6.8 \text{ mmol m}^{-2} \text{ s}^{-1}$ for red oak, $4.7 \text{ mmol m}^{-2} \text{ s}^{-1}$ for red maple, and $1.4 \text{ mmol m}^{-2} \text{ s}^{-1}$ for hemlock, during summer months), and then declined until a little before midnight, after which no measurable sap flow was recorded (Figure 7.1). Canopy photosynthesis was calculated from sap flow rates using (1) measurements of vapor pressure deficit to determine canopy conductance, (2) wind speed measurements to determine boundary layer conductance, (3) gas exchange parameters to determine photosynthesis for a given stomatal conductance. Canopy photosynthesis showed similar diurnal trends to sap flow (Figure 7.2), except that there was a more pronounced midday decline in photosynthesis for most species during the summer months. This trend arose as vapor pressure deficit often continued to increase after midday while sap flow leveled off, so that, although the driving force for water movement was increasing, water flux did not increase as stomata closed and canopy conductance declined. Maximal instantaneous canopy photosynthetic rates ranged from $33 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$ for red oak, to $19 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$ for red maple, and $7 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$ for hemlock. Species-specific differences in water flux were matched in carbon gain patterns, with broad-leaved species having substantially greater rates of canopy photosynthesis than hemlock during summer months, and with hemlock compensating to some degree by fixing carbon in spring and late autumn (Figure 7.2).

Sap flow, canopy conductance, and carbon uptake rates all showed distinct seasonal patterns for the different study species (significant species \times month interactions in Manova, $F_{14,42} = 26.9$ for sap flow, 238.6 for canopy conductance, 120.1 for canopy photosynthesis, $p < 0.001$ for all). During the main growing season when all species had foliated canopies (June – October), the broad-leaved trees had significantly greater rates

of water loss and carbon gain than did hemlock trees (2- to 10-fold greater for water loss, 3- to 12-fold greater for carbon gain) (Figure 7.3). During the main summer months (July – Sept), the broad-leaved species also differed in canopy fluxes, with red oak showing significantly greater rates of water loss, canopy conductance, and carbon gain than red maple (e.g., water loss and carbon gain for red oak averaged $142.7 \text{ mol m}^{-2} \text{ day}^{-1}$ and $644.0 \text{ mmol m}^{-2} \text{ day}^{-1}$, while equivalent values for red maple were $78.7 \text{ mol m}^{-2} \text{ day}^{-1}$ and $350.7 \text{ mmol m}^{-2} \text{ day}^{-1}$; *post hocs*, $p > 0.05$). Hemlock was able to maintain relatively constant rates of both water loss ($\sim 18.8 \text{ mol m}^{-2} \text{ day}^{-1}$) and carbon gain ($\sim 85.7 \text{ mmol m}^{-2} \text{ day}^{-1}$) from early spring (April) until late autumn (November). Hemlock compensated to some extent for its lower carbon gain during the main growing season by fixing carbon before and after the broad-leaved trees were foliated (April, May, November). Photosynthesis outside the main growing season contributed 32 % of hemlock's annual carbon budget.

Canopy photosynthesis, as determined from whole-tree transpiration, represents species' contributions to forest gross primary productivity, since it does not account for plant/soil/microbe carbon respiratory losses. In contrast, tree rings measure net annual biomass increments. Using dimension analysis, I calculated above-ground growth (scaled to projected ground area) for each study tree over the last ten years (Figure 7.4). There was a limited amount of inter-annual variation (significant year term in Anova, $F_{9,54} = 2.41$, $p < 0.05$), most notably with species having lower growth rates in 1993 than in 1999 (*post hocs*, $p < 0.05$), but no other significant changes. These trends did not vary between species (no significant species x year interaction in Anova, $F_{18,54} = 1.27$, $p > 0.05$). Overall, however, the species did differ in net primary productivity (species term in Anova, $F_{2,6} = 8.70$, $p < 0.05$), with red oak having significantly greater net biomass gains than hemlock (*post hocs*, $p < 0.05$), but no significant difference between red maple and either of other species.

Species showed a consistent ranking in their annual totals for water loss, and gross and net carbon gain, all scaled to projected canopy area (species term in Manova, $F_{2,6} = 15.7 - 21.3$, $p < 0.01$) (Table 7.3). Most interspecific comparisons were significant

(*post hoc*s, $p < 0.05$), except for oak-maple and hemlock-maple contrasts for net primary productivity. Red oak had 60 – 80 % greater fluxes than did red maple, and 3 – 4 times greater fluxes than did hemlock, while red maple had a little over twice the fluxes than did hemlock. All species lost 200 - 250 times more water than they gained in carbon (on a mole for mole basis), and net above-ground primary productivity was typically 25 – 30 % of gross primary productivity.

DISCUSSION

Impacts of community change on ecosystem properties

Both broad-leaved species (red oak and red maple) had substantially higher fluxes of water and carbon on an annual basis than did the coniferous species (hemlock). Even among the broad-leaved species, there was considerable variation in transpiration and canopy photosynthesis, with red oak consistently showing 60–80 % higher fluxes than red maple. Clearly, a change in forest composition between the three dominant species in mixed forests in New England will have major impacts on both carbon and water ecosystem budgets. For example, continued human impacts on temperate forests are predicted to result in the loss of hemlock from stands currently dominated by the species (see below). This change, in turn, will lead to a two- to four-fold increase in canopy carbon uptake rates, depending on which species replace hemlock. A switch from hemlock to red oak would have a much larger impact on forest canopy processes than would a switch from hemlock to red maple. Other studies have documented differences in co-occurring species' impacts on ecosystem properties in temperate forests, such as canopy carbon gain (Sullivan *et al.* 1996, Bassow & Bazzaz 1997) and soil nutrient cycling (Turner & Franz 1985, Finzi *et al.* 1998), but rarely to the same degree as in the present study (four-fold differences).

Interspecific comparisons of water and carbon flux

Coniferous forests are typically more productive than broad-leaved forests (see survey in Jarvis & Leverenz 1983), and so the lower annual rates of canopy photosynthesis recorded for hemlock in this study in comparison with co-occurring broad-leaved species (red oak and red maple) were unexpected. For coniferous species, thick leaf structure (so leaves survive more than one growing season) and limited water transporting capabilities through tracheids restrict their leaf-level photosynthetic rates (Smith & Hinckley 1995). Broad-leaved tree species that co-occur with hemlock typically have more than two-fold greater rates of carbon uptake on a leaf-level than hemlock itself (see Chapter 6). Often, however, conifers are able to compensate for their lower

leaf-level photosynthetic rates on the whole-tree level by maintaining deep canopies (Schulze *et al.* 1977, Bond 1989), and by fixing carbon outside the main growing season (Waring & Franklin 1979). For hemlock, though, neither of these traits was sufficient to compensate for its very low rates of canopy photosynthesis during the growing season.

The evergreen habit of hemlock did not benefit the species much in terms of increasing leaf longevity and thus producing a deeper canopy (compare with Schulze *et al.* 1977), as the planar arrangement of its needles keeps hemlock at a lower leaf area index (LAI of 4) than many coniferous species (LAI can be as high as 15) (Waring *et al.* 1978, Holbrook & Lund 1995). Nevertheless, hemlock was able to take some advantage of maintaining a fully foliated canopy year-round. In three of the seven months when the broad-leaved species were leafless, conditions were favorable for hemlock to fix carbon, and almost one-third of its annual carbon uptake was obtained during this time (Figure 7.3). This additional carbon fixation, however, was still not sufficient to allow hemlock's canopy photosynthesis to match that of broad-leaved species on an annual basis. In eastern North America, the harsh winter conditions only allow conifers to fix limited amounts of carbon outside the main growing season (Jurik *et al.* 1988, Schaberg *et al.* 1998). Conifers are able to profit more from their evergreen habit in temperate forests in western North America, where the winters are mild (advantage for evergreen species) and the summers are dry (disadvantage for deciduous species) (Waring & Franklin 1979).

While hemlock consistently had lower fluxes of carbon and water than either red oak or red maple, there were also significant differences in canopy photosynthesis between the broad-leaved species. In the study year, red oak fixed 60 – 80 % more carbon annually than did red maple. Red oak was able to make a large contribution to ecosystem-level carbon flux by sustaining higher photosynthetic rates throughout the growing season. Oak (*Quercus*) typically exhibits the highest maximal photosynthetic rates of co-occurring species, both in New England forests (Bassow & Bazzaz 1997, 1998, and see Chapter 6 in this thesis), and more generally (Reich *et al.* 1991, Morecroft & Roberts 1999). The substantial carbon uptake capacity of red oak may arise, in part,

from its ability for rapid water transport through its ring porous xylem vessel elements. To sustain high photosynthetic rates, trees must be able to deliver a constant supply of water to the leaves, so that stomata can stay open and maintain a high canopy conductance without causing cavitation (Sperry 1995). Low hydraulic conductance caused by differences in vascular architecture may limit maximal photosynthetic rates of tree species (Ryan & Yoder 1997). Mature red oak trees are also deeply rooted, which may allow them to access ground water, and thus gain a relatively constant water supply that is unaffected by periods of low soil moisture availability (Cavender-Bares & Bazzaz 2000).

Value of sap flow as a measure of whole-tree function

The large size of canopy trees makes it difficult to make physiological measurements at the whole-plant level. Chambers that fully enclose mid-sized trees have been used previously (Goulden & Field 1994), but even these have the problem of altering environmental conditions around the tree. Most studies take some kind of scaling approach to measure whole-tree function (Jarvis 1995), either aggregating weighted leaf-level measurements (bottom-up) (Norman 1993) or using process-based measurements of leaf and canopy energy/nutrient budgets (top-down) (e.g., Jarvis & McNaughton 1986, Aber *et al.* 1996). Both kinds of approach, however, have problems arising from scaling between different spatial and temporal scales, and thus may only be of limited use.

Top-down approaches for understanding ecosystem function have the benefit of measuring integrated ecosystem-level processes over large spatial and temporal scales, but only present a static picture of ecosystem properties for one forest over one particular time interval. In contrast, bottom-up scaling investigates ecological processes at smaller spatial and temporal scales, and then aggregates these calculations to larger scales. Such approaches provide a more mechanistic understanding of controls on ecosystem function (Hollinger 1992) and contribute species-level data to ecosystem models (Bassow & Bazzaz 1997, 1998, and see Chapter 6 in this thesis). As a result, bottom-up approaches can be used to determine how ecosystem function might

respond to a change in environmental conditions or even community structure. The heterogeneous nature of plant canopies in space and time, however, requires that sampling schemes for bottom-up models are typically highly stratified and intense (Holbrook & Lund 1995, Jarvis 1995). In addition, the results of such approaches are extremely sensitive to the major scaling parameters used in the model, e.g. leaf area index (see Chapter 6). Sap flow measurements overcome some these challenges by providing a whole-plant non-disruptive measure of tree function on both short and long time scales (Granier *et al.* 1996, Wullschleger *et al.* 1998). I was able to use sap flow to calculate individual species' contributions to canopy water and carbon fluxes, and thus determine the consequences of changes in community species composition for whole-ecosystem properties.

Based on comparisons with other methods for measuring ecosystem-level productivity, we can clearly see that this whole-tree scaling approach provided a useful and relatively accurate way to evaluate species' contributions to ecosystem carbon and water fluxes. My estimates of total annual carbon uptake rates were consistently about four times greater than species' net above-ground carbon gain determined from annual growth rings. Species' typically retain 50 % of their gross carbon gain as net biomass growth (Ryan 1991), approximately half of which will be allocated to above-ground parts. Thus the consistent and realistic difference between gross and net productivity among species gives added support to the accuracy of my measurements. Both sap flow and growth ring methods produced identical species' rankings (red oak, red maple, then hemlock) and maintained the same magnitude of differences between species (Table 7.3). From eddy covariance measurements taken during my sampling intervals (C. C. Barford and S. Wofsy, *unpublished data*), gross ecosystem productivity for the forest stand containing the study trees in 1999 was calculated as $1.173 \text{ Kg C m}^{-2}$. This value matched closely with my calculated value of total annual carbon gain for red oak ($1.055 \text{ Kg C m}^{-2}$). While red oak currently dominates the stand (45 % based on basal area), it is not the only component, with red maple and hemlock both making significant contributions to basal area (23 % and 11 %, respectively). The presence of these species in the community would bring estimates of ecosystem-scale primary

productivity down below 1 Kg C m⁻², as both species had significantly lower annual carbon uptake rates than red oak (Table 7.3). This small discrepancy might arise in part from the manner in which sap flow and carbon gain were scaled to ground area. I used canopy projected area as a measure of each tree's spatial extent, but overlap between tree canopies means that ecosystem productivity cannot be directly calculated as the average of individual species' productivity weighted by their contribution to forest canopy area.

My laboratory calibrations and those of others (Clearwater *et al.* 1999) confirmed that heat dissipation probes give accurate estimates of sap flux velocities, suggesting that any errors are likely to have arisen only during the scaling process itself. Sapwood area and canopy projected area were both primary scaling factors in my approach (to calculate fluxes on whole-tree and ground area bases, respectively), and thus the accuracy of my flux estimates depends strongly on the precision of these measurements (as demonstrated in Chapter 6). In addition, my scaling approach assumed a degree of homogeneity in canopy microclimate, while the reverse is likely true (Oker-Blom 1986). I stratified the canopy into only two layers, and assumed that average measurements in each layer were sufficient to represent canopy environmental conditions adequately (Parker & Brown 2000). While vertical stratification captures much of the heterogeneity in canopy microclimate (Norman 1993, see also Chapter 6), non-linearities in canopy processes can produce unexpected errors during scaling (Jarvis 1995). For example, calculation of leaf-to-air vapor pressure deficit is highly sensitive to accurate measurement of leaf temperature (Tyree & Wilmot 1990). My sampling information incorporated leaf temperature in the upper and lower canopy strata, but did not account for variation in leaf temperatures within each canopy layer.

Nevertheless, the overall conclusions of the present study should be robust to most of these relatively small errors introduced during the scaling process. Annual growth rings and eddy covariance both confirmed that my scaling approach provides a good representation of the magnitude and direction of current fluxes, and that measured variation in species' fluxes reflect real differences in species' contributions to

ecosystem processes in mixed temperate forests. Results from the present study, however, cannot be directly used to make predictions about the carbon storage capacity of temperate forests. Long-term net carbon exchange of forests will not only depend on the productivity of individual species, but also on their mean life-span (and thus turnover time) (Phillips *et al.* 1998), and their impact on soil respiration (Goulden *et al.* 1996, Valentini *et al.* 2000).

Prospects for future forest ecosystem properties

Novel environmental perturbations and land-use change are likely to interact in the future to reduce the abundance of hemlock on the landscape, and increase the abundance of earlier successional broad-leaved species, such as red oak and yellow birch. Hemlock forests are currently threatened by an invasive insect pest (hemlock woolly adelgid, *Adelges tsugae* Annand), which is likely to cause widespread mortality throughout hemlock's north-eastern range (McManus *et al.* 2000). After infestation, former hemlock forests are often taken over by fast-growing broad-leaved species, such as black birch (Orwig & Foster 1998). Human-induced changes in atmospheric composition (elevated CO₂, increased nitrogen loading) are also predicted to favor faster-growing broad-leaved species over late successional species, such as hemlock, in the future (Bolker *et al.* 1995, see further discussion in Chapter 8). All these changes may be exacerbated by increased incidence of canopy disturbance (Bazzaz 1996), as a result of increased frequency of extreme weather events (Houghton *et al.* 1996) and continued human dominance of the landscape (Foster & Motzkin 1998). By changing the structure of the forest, these human-induced disturbances will also affect forest ecosystem properties. Results of the present study demonstrate that a switch from a forest dominated by hemlock to one dominated by broad-leaved species (particularly red oak and red maple) could increase canopy transpiration and photosynthetic rates by two- to four-fold, depending on the identity of the future dominant broad-leaved species.

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Table 7.1. Characteristics of trees used in the study, showing measured dimensions and positions relative to EMS tower.

| Site | Distance to tower (m) | Direction from tower | Species | DBH (cm) | Height (m) | Projected canopy area (m ²) | Sapwood area (cm ²) |
|------|-----------------------|----------------------|-----------|----------|------------|---|---------------------------------|
| 1 | 500 | W | Hemlock | 30.5 | 23 | 19.1 | 136.4 |
| | | | Red maple | 23.5 | 22 | 18.7 | 194.3 |
| | | | Red oak | 32.7 | 21 | 13.9 | 55.8 |
| 2 | 150 | W | Hemlock | 36.9 | 21 | 21.8 | 176.2 |
| | | | Red maple | 38.1 | 21 | 20.3 | 287.7 |
| | | | Red oak | 29 | 23 | 17.6 | 40.5 |
| 3 | 150 | NW | Hemlock | 29.6 | 18 | 13.1 | 131.4 |
| | | | Red maple | 23.3 | 23 | 18.1 | 190.3 |
| | | | Red oak | 23.5 | 22 | 4.8 | 21.1 |

Table 7.2. Model II regression coefficients for the relationship between leaf-level photosynthesis ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and conductance ($\text{mol m}^{-2} \text{s}^{-1}$) for different canopy layers and different species.

| Canopy layer | Species | Month | n | r^2 | Slope ^a | Intercept | Mean Conductance | Mean Photosynthesis |
|--------------|----------------------|-------|-----|-------|--------------------|-----------|------------------|---------------------|
| Upper | Hemlock ^b | May | 46 | 78.82 | 17.77 | 0.79 | 0.207 | 6.43 |
| | | July | 108 | 67.09 | 77.89 | -0.13 | 0.082 | 5.68 |
| | | Sept | 81 | 80.28 | 57.30 | -0.10 | 0.117 | 5.72 |
| | Red maple | - | 69 | 76.32 | 68.28 | 0.62 | 0.085 | 6.40 |
| | Red oak | - | 69 | 84.72 | 46.99 | 0.39 | 0.249 | 12.61 |
| Lower | Hemlock | May | 48 | 70.77 | 25.69 | 0.63 | 0.110 | 3.35 |
| | | July | 108 | 57.07 | 45.43 | -0.20 | 0.039 | 1.47 |
| | | Sept | 81 | 66.97 | 20.43 | -0.21 | 0.048 | 0.77 |
| | Red maple | - | 69 | 75.22 | 31.27 | -0.07 | 0.094 | 1.92 |
| | Red oak | - | 69 | 65.60 | 24.07 | -0.46 | 0.156 | 1.74 |

^a Based on Model II geometric mean regression.

^b As hemlock leaves exhibited significant seasonal variation in photosynthesis-conductance relationship, regression parameters were calculated for separate months.

Table 7.3. Annual totals (1999) of water loss, gross and net primary productivity for each study species, scaled to projected canopy area, expressed as means (with SEM in brackets, $n = 3$).

| Species | Water loss (Kg m ⁻²) | Gross Primary Productivity (Kg C m ⁻²) | Net Primary Productivity (Kg C m ⁻²) ^a |
|-----------|-------------------------------------|--|---|
| Hemlock | 92.6 (32.6) a | 0.301 (0.113) a | 0.071 (0.023) a |
| Red maple | 230.2 (30.7) b | 0.630 (0.089) b | 0.166 (0.031) ab |
| Red oak | 359.4 (22.4) c | 1.055 (0.107) c | 0.295 (0.054) b |

NOTE: Letters indicate significant differences between species for a given column (Scheffé *post hoc*s, $p < 0.05$).

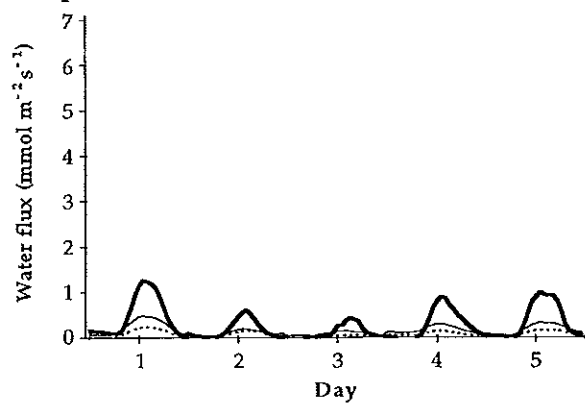
^a Above-ground NPP, calculated as 50 % of above-ground net biomass gain (determined from tree ring growth).

Figure 7.1. Diurnal changes in sap flow (scaled to projected canopy area), shown for five days every month that sap flow could be detected. Day numbers mark 1200 h on each day, and each line represents the mean ($n = 3$) for each study species (hemlock, red maple, red oak)

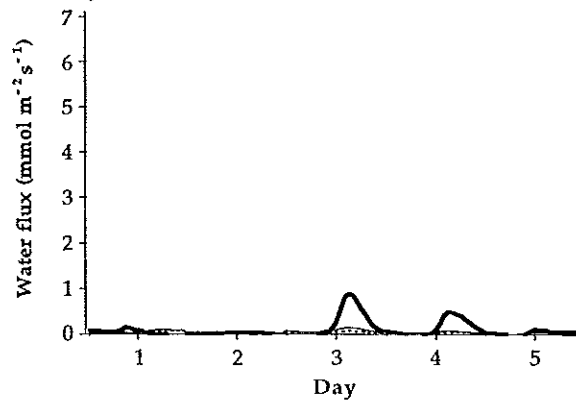
| |
|---|
| —— Hemlock —— Red maple Red oak |
|---|

Figure 7.1. cont.

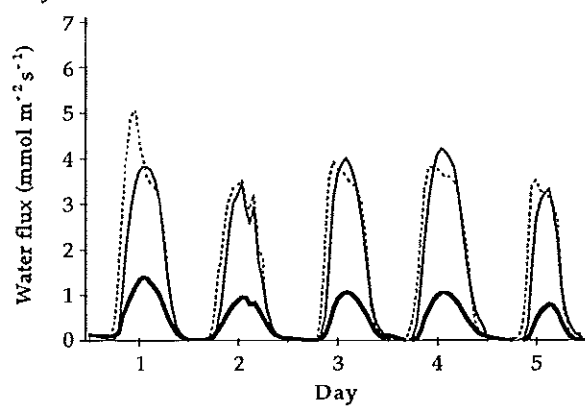
a) April



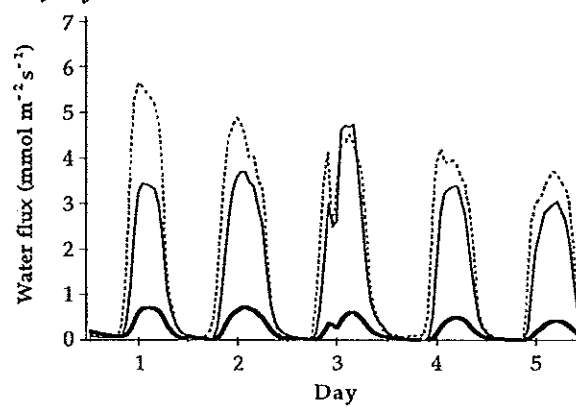
b) May



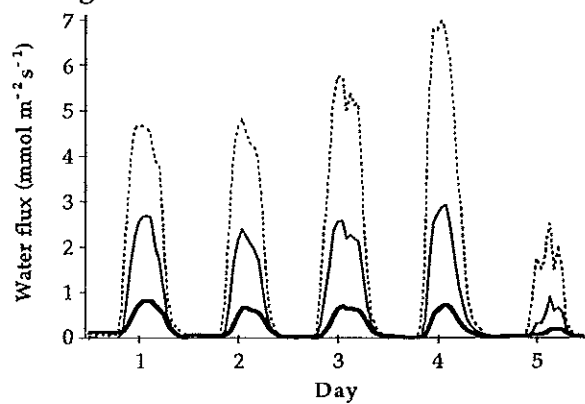
c) June



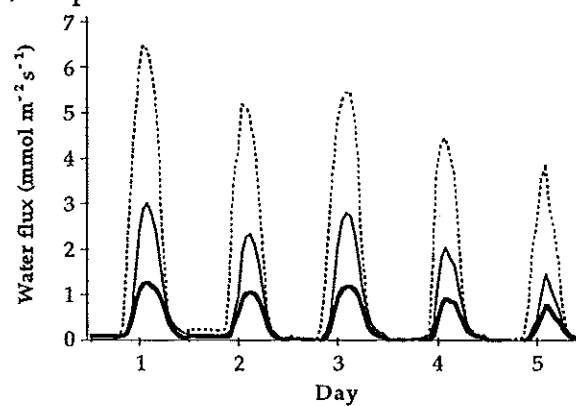
d) July



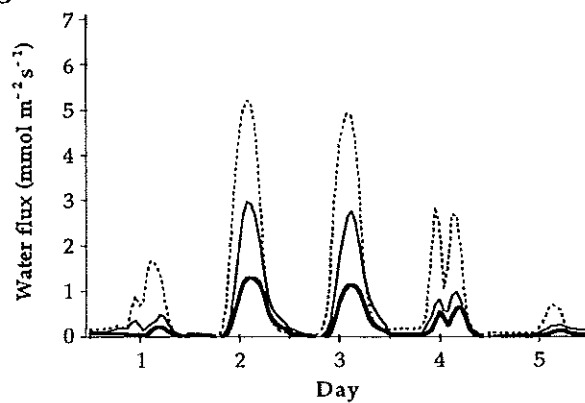
e) August



f) September



g) October



h) November

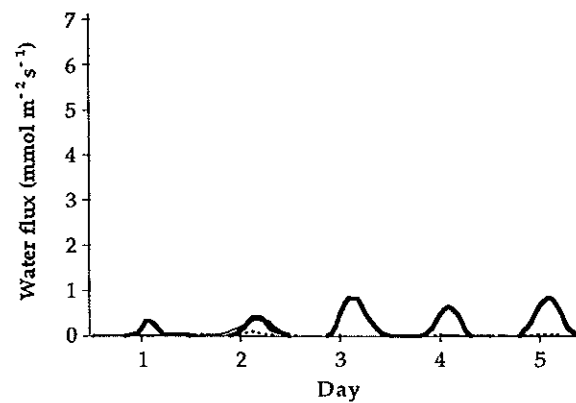
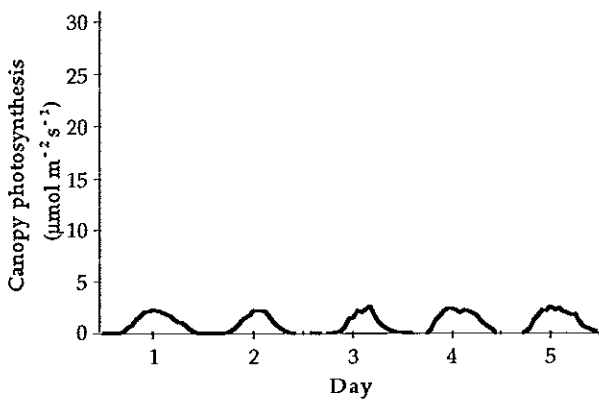


Figure 7.2. Diurnal changes in canopy photosynthesis (scaled to projected canopy area), shown for five days every month that sap flow could be detected. Day numbers mark 1200 h on each day, and each line represents the mean ($n = 3$) for each study species (hemlock, red maple, red oak)

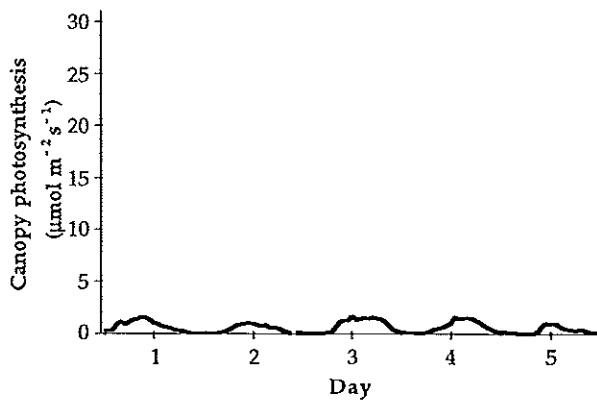
| | | | | | |
|---|---------|---|-----------|-------|---------|
| — | Hemlock | — | Red maple | | Red oak |
|---|---------|---|-----------|-------|---------|

Figure 7.2. cont.

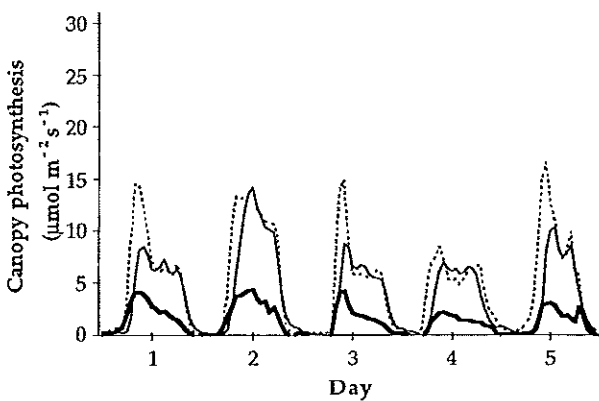
a) April



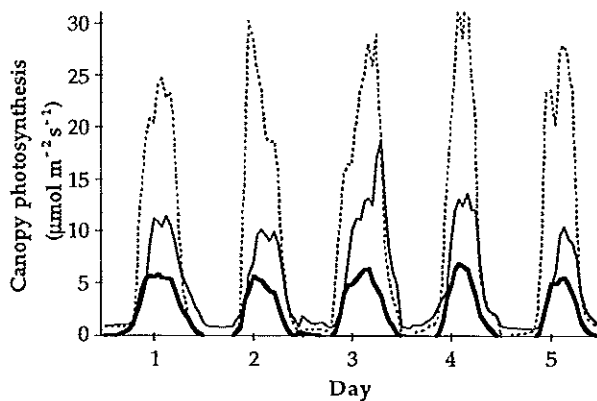
b) May



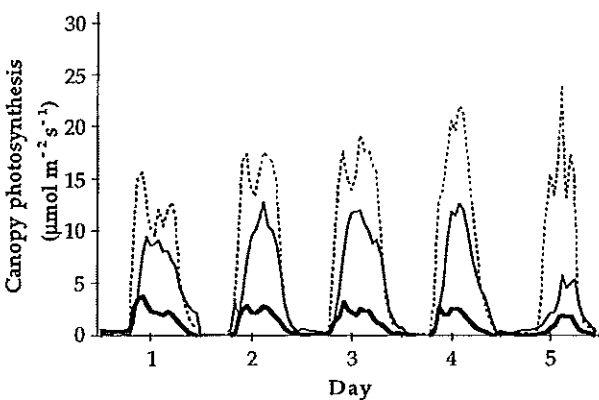
c) June



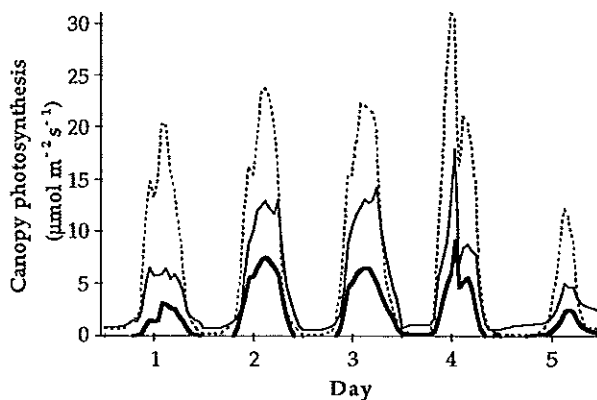
d) July



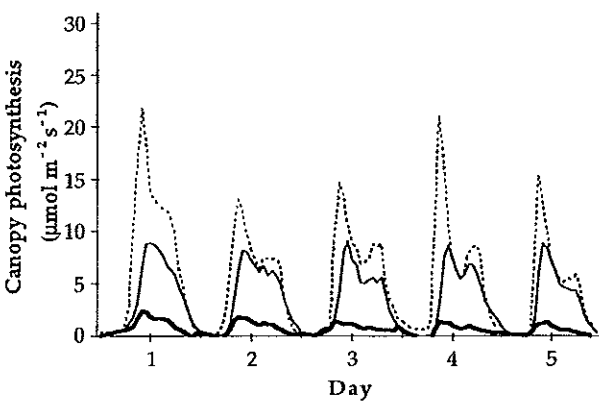
e) August



f) September



g) October



h) November

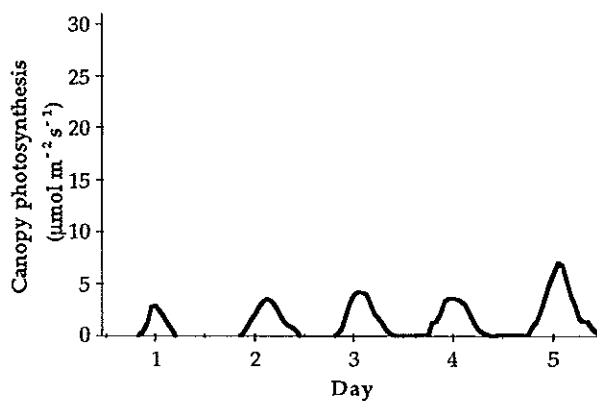


Figure 7.3. Seasonal changes in sap flow (a), canopy conductance (b), and photosynthesis (c) (mean \pm SE, $n = 3$), all scaled to projected canopy area. Letters above each month identify which species have the significantly highest rates at that time (Scheffé *post hoc* comparisons, $p < 0.05$; h – hemlock, m – red maple, o – red oak).

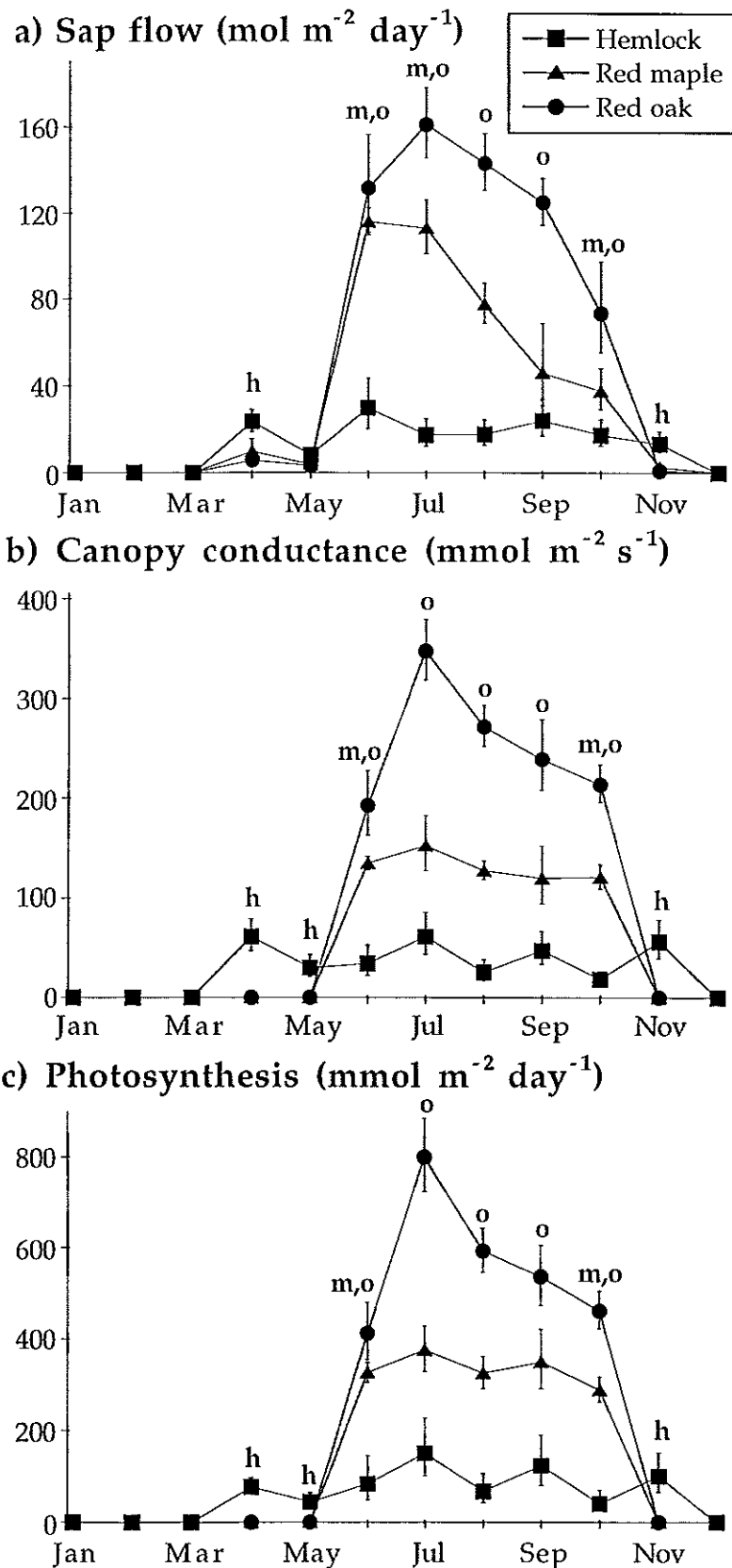
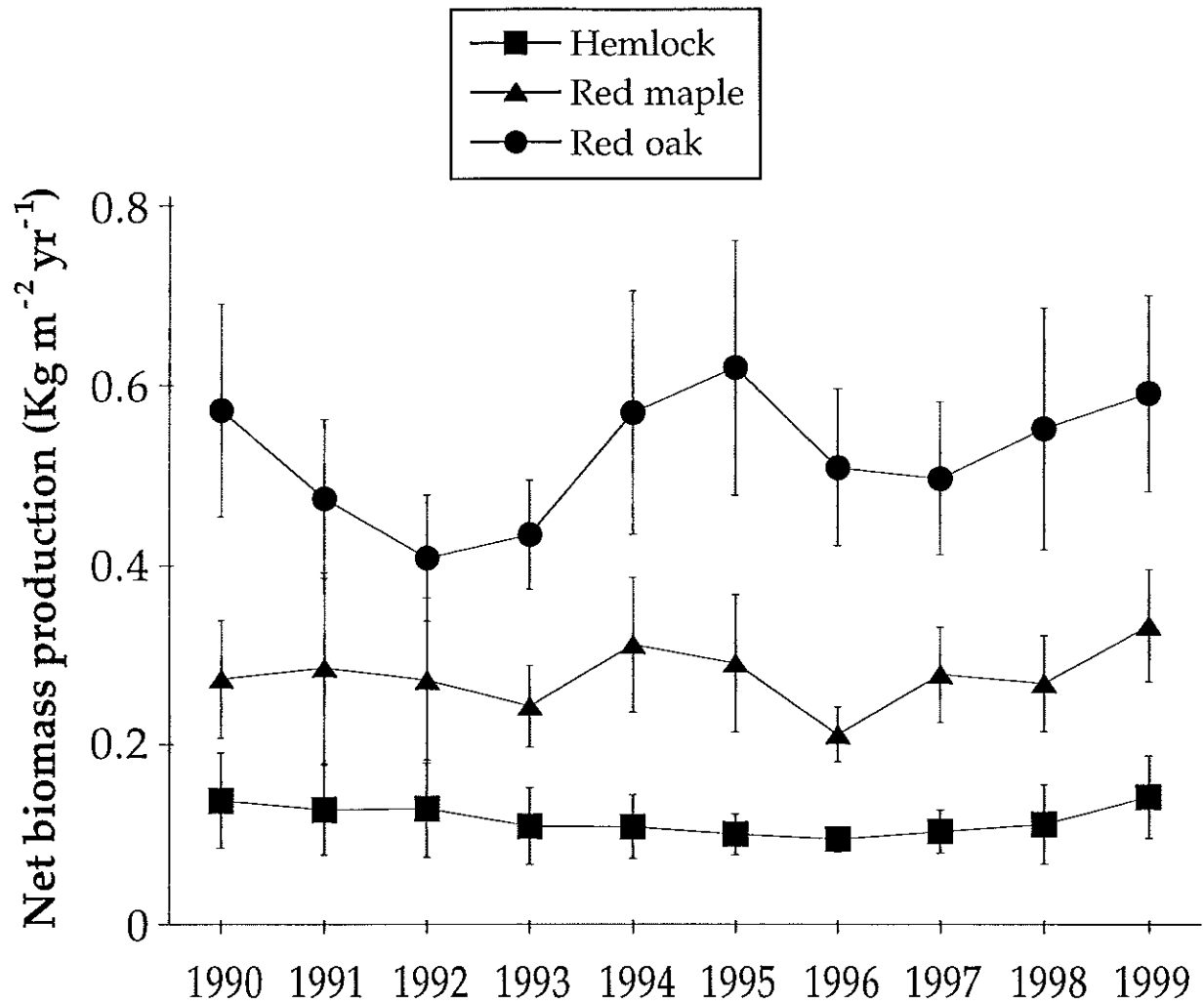


Figure 7.4. Annual changes in net biomass production (mean \pm SE, $n = 3$ for each species), scaled to projected canopy area.



CHAPTER 8

CONCLUSION: CURRENT AND FUTURE ECOSYSTEM DYNAMICS IN MIXED TEMPERATE FORESTS

A resource-based approach to community and ecosystem dynamics

Given the complexity of natural ecosystems, and the multitude of natural and human-induced factors that influence their structure and function, developing a clear understanding of current and future ecosystem dynamics presents ecologists with a major challenge. In my thesis, I determined some of the primary resource-based mechanisms underlying community and ecosystem dynamics in mixed conifer broad-leaved forests in eastern North America. As interactions between organisms and their resource environment underpin most ecological dynamics, a resource-based approach allows us to understand better the major processes controlling current forest structure, and also to predict forest responses to novel environmental perturbations threatening their future integrity. My thesis research established that (1) current community dynamics in mixed temperate forests could be understood in large part from seedling responses to canopy-mediated changes in understory resource environment (particularly light and soil pH) in both coniferous and broad-leaved stand types, (2) nitrogen deposition will exaggerate these successional dynamics in the future, and ultimately lead to a further increase in the early successional character of these forests, and (3) nitrogen-mediated changes in forest community structure will likely increase the flux of carbon into temperate forests in the future by two- to four-fold.

Current community dynamics

The first part of my research took a mechanistic approach to understanding factors influencing community dynamics in mixed conifer broad-leaved forests. I examined how canopy-mediated differences in understory resource environment influenced seedling performance, and created different regeneration dynamics in coniferous and broad-leaved stand types (compare with Collins 1990, Cornett *et al.* 1997). Community dynamics in these mixed temperate forests could be interpreted to a large degree by determining how canopy trees altered understory conditions and how seedlings responded to variation in resource environment between hemlock and red oak stands. Using a demography experiment (Chapter 2), I demonstrated that hemlock seedlings were favored in hemlock stands (a true positive feedback), as a result of high seed inputs, high seedling emergence and relatively high seedling survival, while a suite of mid-successional species were favored in red oak stands, through adequate seedling

emergence and high overall seedling survival. These canopy-seedling dynamics may act to slow successional trajectories in these mixed forests, either by reducing successful hemlock establishment in red oak stands, and thus inhibiting the natural course of succession, or by allowing hemlock to develop an extensive understory seedling bank in hemlock stands, and thus encouraging self-replacement of hemlock by hemlock following a canopy disturbance. Hemlock stands were characterized by much lower light availability and more acidic soils than red oak stands, and these canopy-mediated variations in both light and pH were found to be the primary causes of stand-level differences in understory seedling bank dynamics. Experimental manipulations of stand understory conditions (Chapter 3) emphasized the importance of light availability as a driver of positive feedback effects in hemlock stands. Differential species' responses to resource availability led to dominance of final seedling communities by hemlock in low light, unamended soils (i.e., under conditions naturally found in hemlock stands), but by birch in high light.

This part of my research emphasizes the value of mechanistic studies at the community level itself (Leps *et al.* 1999). Predictive models of community dynamics can only be developed once the underlying physiological and population-level processes have been established. My work in mixed conifer broad-leaved forests highlights the importance of canopy-mediated effects on seedling resource environment, and the resulting feedbacks between stand composition and patterns of seedling regeneration. I was able to establish how canopy trees alter understory conditions, and how regeneration responses of different species are affected by variation in resource conditions between contrasting stand types. It is only recently that both species' effects on and responses to their environment have been incorporated into our understanding of vegetation dynamics (van Breemen & Finzi 1998). In contrast to the many studies addressing species' responses to local environmental conditions, little research has directly considered the role played by species' effects in the structure and dynamics of plant communities. As these species' effects are likely to be an important component of many ecological communities (especially those with long-lived, large individuals, such as forests), the results of my experiments have direct implications for our fundamental understanding of plant community structure and dynamics.

Nitrogen deposition impacts on future community dynamics

Seedling responses to different resource combinations can be used to predict spatial and temporal variation in forest community composition (Kobe 1996). In addition, an understanding of the resource-based mechanisms controlling current community patterns in mixed conifer broad-leaved forests makes it possible to determine how novel perturbations will alter forest community structure. Many global changes directly influence environmental conditions and resources essential to basic plant functioning. Plant responses to a change in availability of a particular resource depend on the levels of other resources (Chapin *et al.* 1987, Bazzaz & Miao 1993), and so it is critical that we understand species' responses to their current resource environment if we wish to predict effects of future changes. My thesis research focused on nitrogen deposition as a critical environmental perturbation threatening the future integrity of mixed temperate forests. Nitrogen is an essential resource for plants, and is particularly limiting in temperate regions where the soils are relatively young (Vitousek & Howarth 1991). Nitrogen is likely to interact with other resources to influence seedling performance under different environmental conditions. To determine how increased nitrogen loading will alter forest community composition, I examined how nitrogen availability influenced seedling growth and survival both under closed canopy conditions (conifer vs. broad-leaved) (Chapter 4) and following a canopy disturbance (Chapter 5).

Contrary to expectations, in both experiments, successional position emerged as a more important determinant of species' responses to increased nitrogen deposition than did leaf habit (coniferous vs. broad-leaved). In the understory, only survival of the most late successional species (hemlock) was increased by nitrogen additions, while a number of mid-successional species (red maple, white pine, red spruce) all showed nitrogen-induced declines in survival. Effects were particularly marked in hemlock stands (characterized by very low light availability), suggesting nitrogen-induced declines in seedling abundance were due to an imbalance between above- and below-ground resources. In the simulated gap experiment, I found a significant positive correlation between a species' growth rate during the first two years of its life and its nitrogen-induced growth enhancement, again demonstrating that successional position (related to early growth rate) more than leaf habit may be a species' trait closely tied to nitrogen responsiveness. With increased nitrogen loading in the future, successional

dynamics in mixed temperate forests are likely to become more exaggerated, as earlier successional species are further favored following canopy disturbance events, while later successional species (particularly hemlock) are able to maintain a more persistent seedling bank, and thus remain a dominant component of late successional forests.

On balance, nitrogen deposition is likely to increase the early successional character of temperate forests in the future, as the high light effects of increased nitrogen availability predominate in the longer term. In collaboration with Richard Kobe (Michigan State University, MI), I used the data from both my nitrogen experiments to re-parameterize SORTIE, an individual-based forest dynamics model designed for mixed temperate forests in eastern North America (based on Pacala *et al.* 1996). The results of these simulations show that increased nitrogen loading will lead to yellow birch dominance of the forest community, with scattered individuals of canopy hemlock and red spruce trees, reducing both the relative contribution of late successional species to forest community structure and overall species diversity (Figure 8.1). These results can be understood more clearly by returning to the original empirical data. Only three of my study species showed enhanced performance with increasing nitrogen availability – yellow birch and red maple (increased growth in high light, Chapter 5), and hemlock (increased survival in the understory, Chapter 4). Red maple, however, showed declines in survival in low light, which ultimately outweighed the regeneration benefits afforded by the nitrogen-induced increased growth in high light. Thus, an earlier successional broad-leaved species (yellow birch) and a late successional coniferous species (hemlock) could both potentially profit from increased nitrogen loading in temperate forests. On balance, though, the nitrogen-induced growth benefits for yellow birch seedlings in high light predominated over the marginal benefits for hemlock of a further increase in low light survival, which is already high in the model due to hemlock's extreme shade tolerance (Kobe *et al.* 1995). The model's predictions for an increase in the abundance of earlier successional species will be further compounded by the likelihood of increased human-induced disturbances in the future (see below).

This part of my thesis research expands on the mechanistic studies of forest community dynamics presented earlier by examining the population-level processes underlying forest responses to a novel environmental perturbation. I examined seedling responses to increased nitrogen deposition under a range of regeneration conditions to

characterize changes at a number of life-cycle stages – understory seedling bank dynamics in contrasting stand types (hemlock vs. red oak), and seedling responses to canopy gap formation. Most global change research focuses on one component of community dynamics, even though other population processes may respond in a different way to the perturbation and thus alter our conclusions. This is best exemplified by the multitude of elevated CO₂ experiments that have examined plant growth responses to atmospheric CO₂ under high light (Wullschleger *et al.* 1995), without considering survival responses or effects under a range of other environmental conditions that the plant might experience through its life-cycle (Catovsky & Bazzaz 1999). It is clear that plant responses to environmental changes depend both on the plant's complete resource environment (Bazzaz 1990, Bazzaz & Catovsky 2000) and on its full suite of physiological and demographic responses (Bazzaz 1993). My thesis research overcomes some of these problems by following both growth and survival responses of seedlings to increased nitrogen loading, and by examining these responses under realistic field conditions. There are still short-comings with this approach, however, so some caution must be exercised when interpreting the results. For example, the length of the experiments was relatively short (two years) compared with the full life-cycle of a tree, and I simulated a disturbance rather than using a natural forest gap.

Ecosystem consequences of changing community composition

The third part of my thesis considered how changes in mixed forest community structure would influence whole-ecosystem properties. As a result of natural and human-induced disturbance processes, and subsequent patterns of successional recovery (Bormann & Likens 1979, Bazzaz 1996), forest ecosystems are in a constant state of flux, and their composition is likely to vary over time. Research reconstructing community dynamics in the past has shown that temperate forests typically have a history characterized by change rather than stasis (Foster *et al.* 1996). This legacy of change was exacerbated in North America after European settlement when forests were threatened by a suite of novel human-induced perturbations primarily related to land-use change (Foster *et al.* 1998, Fuller *et al.* 1998). These forests face further threats in the future as human activities continue to dominate the landscape (Foster & Motzkin 1998), as well as imposing novel chemical and climatic stresses on natural ecosystems (Bazzaz

et al. 1996, Foster *et al.* 1997, Vitousek *et al.* 1997). I evaluated the influence of these community-level changes on the future productivity of mixed temperate forests.

Using two separate scaling approaches (leaf-level aggregation, Chapter 6; whole-tree sap flow, Chapter 7), I examined how tree species differed in their contributions to canopy-level carbon uptake, focusing on the dominant coniferous and broad-leaved tree species at Harvard Forest. Species' differences in total canopy carbon uptake rates did not fall simply along a leaf habit axis (evergreen coniferous vs. deciduous broad-leaved), but rather fell out along a continuum – red oak consistently had the highest rates of canopy carbon uptake, followed by red maple, and then hemlock typically had the lowest rates. Hemlock was able to compensate to some extent, but not completely, for its lower leaf-level photosynthetic rates by maintaining a deeper canopy (Chapter 6) and by taking up one-third of its carbon annually in the spring and autumn when the broad-leaved canopies were not foliated (Chapter 7). A lower than average leaf area index (for conifers) and cold winter temperatures, however, meant that hemlock only gained limited benefits from maintaining an evergreen canopy, and overall the broad-leaved species (particularly red oak) finished with higher rates of annual carbon gain.

Species' differences in carbon uptake rates on a range of time-scales (seasonal, annual, decadal) have implications for future forest productivity should community composition change. The study species ranked in the same order in all scaling approaches (red oak, red maple, then hemlock), but the magnitude of differences between species varied between approaches. The bottom-up aggregation method (Chapter 6) consistently over-estimated hemlock's contribution to canopy carbon uptake relative to the broad-leaved species when compared with the sap flow and annual ring methods (Chapter 7). Bottom-up scaling calculated maximum potential photosynthetic rates during the main growing season, while the other methods provided a more integrated estimate of canopy carbon gain on annual and decadal time-scales. If the relative abundance of hemlock in temperate forests does indeed decline (e.g., as a result of nitrogen deposition, Figure 8.1) to be replaced by common broad-leaved species, such as red oak, red maple, or yellow birch, my experiments suggest that forest productivity could increase by two- to four-fold. The size of the increase will depend on the exact composition of broad-leaved species that replace hemlock, with red oak and red maple representing the upper and lower limits,

respectively, and yellow birch falling between the two (Bassow & Bazzaz 1997, 1998). The present research, however, cannot be directly used to make predictions about the carbon storage capacity of temperate forests. Long-term net carbon exchange of forests will not only depend on the productivity of individual species, but also on their mean life-span (Phillips *et al.* 1998), and their impact on soil respiration (Goulden *et al.* 1996).

My research presents a conceptual framework for examining the impacts of novel environmental perturbations on both the structure and function of natural ecosystems. There is now a considerable body of work showing that ecosystem properties can be a direct function of community composition (Hooper & Vitousek 1997, Hector *et al.* 1999, Tilman 1999), and thus global change studies cannot address the impacts of perturbations on ecosystem function without considering concomitant changes in structure. Only a few studies have examined how alteration of community composition brought about by a novel environmental perturbation will influence ecosystem properties. Most of these studies have empirically tested this question in communities with small, short-lived individuals, such as grasslands (Wedin & Tilman 1996, Saleska *et al.* 1999). Research in forest systems has, to date, been limited to modeling studies (Pastor & Post 1988, Bolker *et al.* 1995). By examining the responses of individual tree species to a novel environmental perturbation (nitrogen deposition) and by quantifying species' individual contributions to ecosystem carbon uptake, my research directly examines links between community/ecosystem dynamics and global environmental change, and thus provides an integrated framework for predicting future impacts of human-induced perturbations on forest communities.

Putting ecological research into a more practical context

In light of the many forces shaping current and future forest dynamics, it is important to consider how results of ecological research apply to our understanding of 'real forests'. Nitrogen deposition will likely interact with a suite of other natural and human disturbances that threaten forests in the future (Aber *et al.* 1998). In this case, how valid are our predictions about nitrogen impacts on future forest structure and function? One advantage with taking a mechanistic resource-based approach to community and ecosystem dynamics is that it allows us to generate predictions for a range of future scenarios. As all disturbances ultimately affect a plant's resource base, we can interpret

future changes in the context of modification of spatial and temporal variation in forest resource environment. If we know how disturbances alter the physical, chemical and biotic environment, and we know how seedlings respond to a range of interacting resources, we should be able to predict how a suite of novel environmental perturbations will influence future forest structure and function.

For example, my earlier predictions about how nitrogen deposition will influence forest community dynamics are contingent on both landscape structure and disturbance regimes, both of which may change in the future. The sensitivity of my predictions to future conditions can be evaluated using SORTIE, the forest dynamics model discussed previously. My nitrogen deposition experiment in the forest understory (Chapter 4) revealed that most of the negative effects of increasing nitrogen availability on seedling survival occurred as the result of resource imbalance and were most pronounced in hemlock stands where light levels are considerably lower (Chapter 2). I ran SORTIE under two separate scenarios – one where hemlock dominated the canopy layer and one where red oak dominated (Figure 8.2). If hemlock trees dominate, the negative effects of nitrogen deposition on seedling survival in the understory become more pronounced, and hemlock increases its relative abundance within the community. Hemlock was the only species whose survival was positively affected by nitrogen under very low light conditions. Under the red oak canopy scenario, differences between hemlock and a suite of mid-successional species (white pine, red spruce, red maple) become less pronounced, and hemlock remains less persistent in the long term.

Forest stand structure is likely to change in the future, and so developing predictions for a range of landscape scenarios becomes important. Currently, hemlock forests in eastern North America are threatened by an exotic insect pest, the hemlock woolly adelgid (*Adelges tsugae* Annand), which has already caused widespread mortality in parts of hemlock's southern range (Royle & Lathrop 1997). After adelgid-induced death of hemlock trees, former stands become dominated by earlier successional broad-leaved species, such as black birch (Orwig & Foster 1998), thus altering subsequent forest ecosystem dynamics (Jenkins *et al.* 1999). This biological invasion will clearly reduce the late successional character of mixed temperate forests by eliminating hemlock, which in turn will interact with nitrogen deposition to reduce further hemlock's contribution to the forest community (Figure 8.2).

As well as acting as a direct threat to hemlock forests in eastern North America, the hemlock woolly adelgid represents a novel canopy disturbance agent. A number of natural and human disturbances threatening mixed temperate forests are predicted to increase in the future (Foster *et al.* 1997). Human effects on the forest landscape are more substantial than ever before, through (1) direct management of forests and utilization of wood products (Foster & Motzkin 1998), (2) introduction of invasive species (Mack *et al.* 2000), and (3) altered atmospheric composition leading to increased occurrence of extreme weather events (Houghton *et al.* 1996, Timmermann *et al.* 1999). In New England, late successional species, such as beech and hemlock, have already shown substantial declines in abundance since European settlement (Foster *et al.* 1998, Fuller *et al.* 1998). In the future, these novel human-induced changes are likely to increase the frequency of canopy disturbance events and thus further increase the abundance of earlier successional species across the forest landscape (Bazzaz 1996). Once again, using SORTIE to assess the consequences of changing disturbance regimes on forest community dynamics, we can see that increasing disturbance frequency interacts with nitrogen deposition to increase yellow birch's contribution to community composition in the future (Figure 8.3). Loss of later successional species from the landscape may be further exacerbated with another global change, elevated CO₂, which will likely favor yet another mid-successional species (red oak) (Bolker *et al.* 1995).

Based on current knowledge, my thesis results provide strong evidence that nitrogen deposition, in concert with other human-induced physical and chemical disturbances, will increase the early successional character of forests by promoting faster growing species, such as yellow birch, at the expense of later successional species, such as hemlock and red spruce, with a concomitant decline in overall species diversity. Alteration in community composition, in turn, will increase forest productivity two- to four-fold, although the consequences for long-term carbon storage are still uncertain. Understanding the nature of future environmental changes is the first step towards mitigation. It is the role of ecologists to highlight potential environmental problems that we may face in the future. Then, given the best information available, it is up to all of us, policy-makers and the public alike, to decide what kind of world we want for ourselves and for future generations.

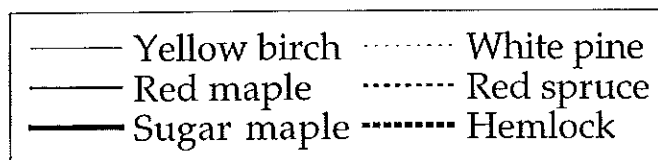
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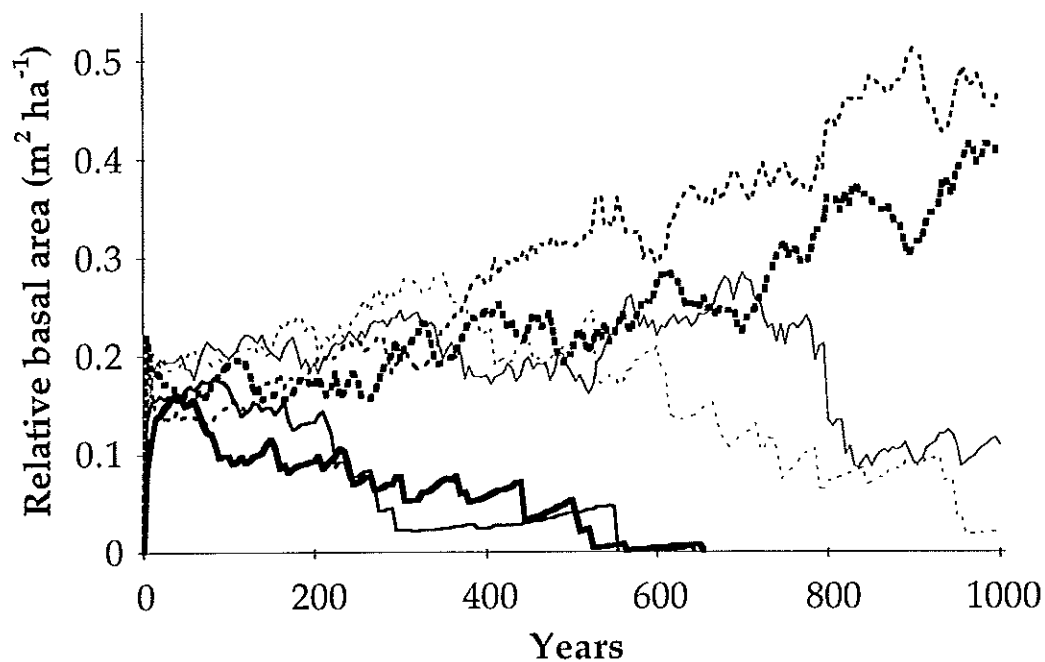
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Figure 8.1 SORTIE simulation results showing change in community composition over time under control (a) and nitrogen deposition (b) conditions.



a) Control run



b) N deposition run

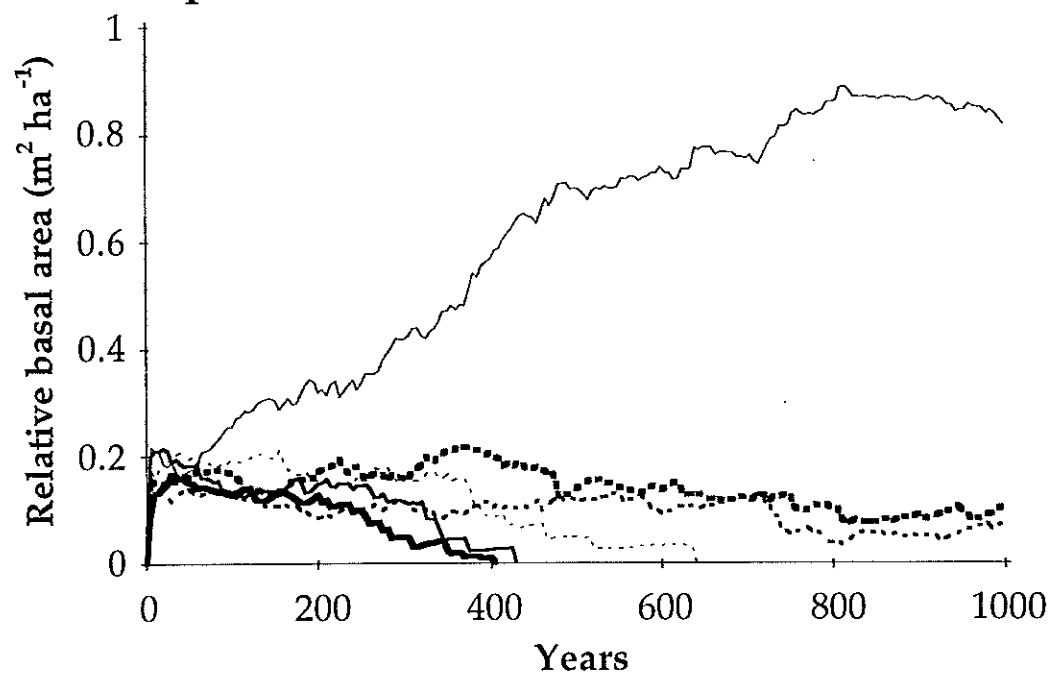


Figure 8.2 SORTIE simulation results showing nitrogen deposition effects on community composition when hemlock (a) or red oak (b) dominate the canopy.

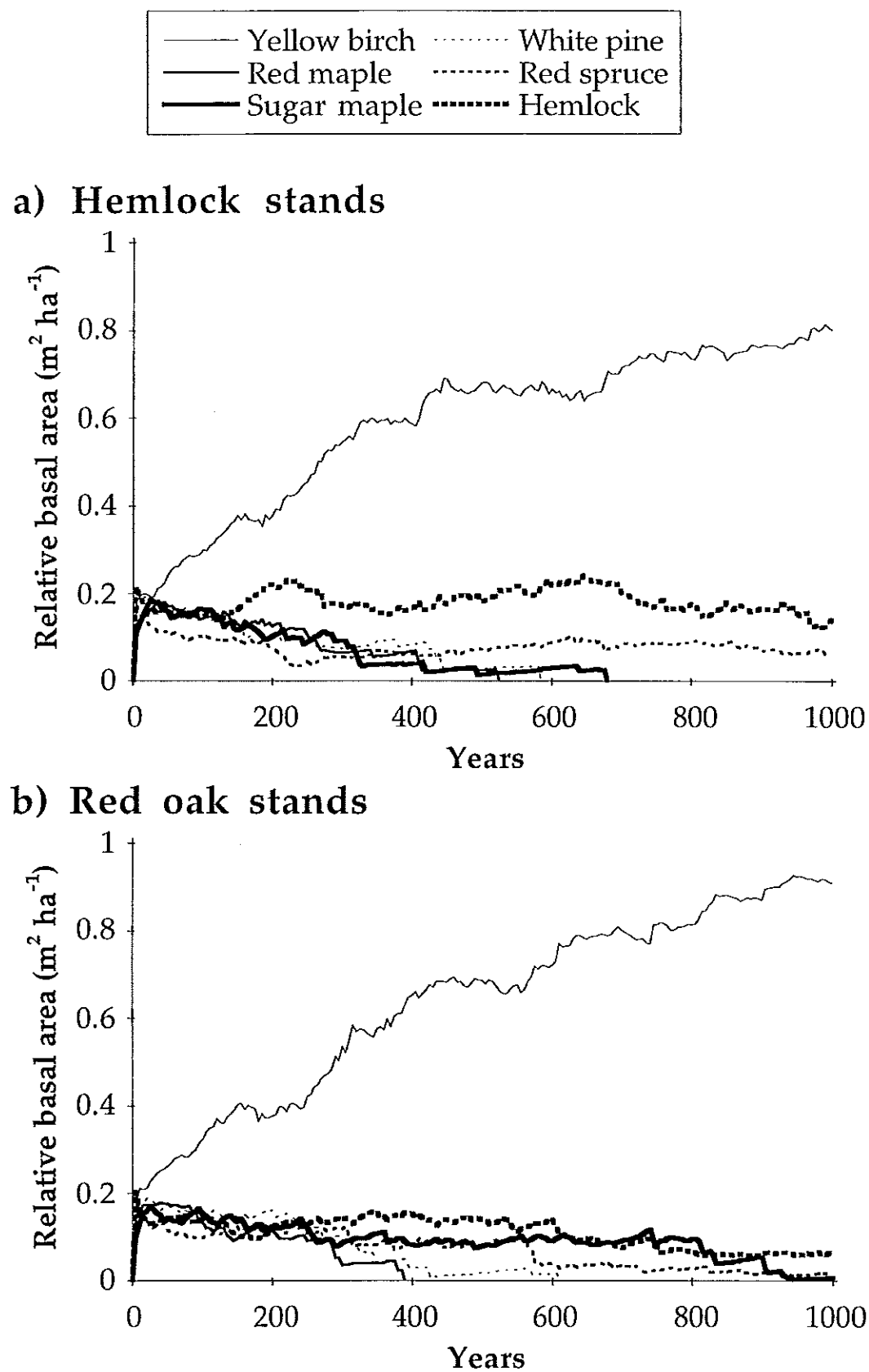


Figure 8.3 SORTIE simulation results showing how disturbance intensity and nitrogen deposition may interact to influence forest community dynamics.

