CHAPTER 16

Experimental Approaches to Understanding Forest Regeneration

S. CATOVSKY, R. CRABTREE, T. SIPE, G. CARLTON, S. BASSOW, L. GEORGE, and F. BAZZAZ

Introduction: Disturbance, Heterogeneity, and Regeneration

Major changes in forests are initiated by disturbance. The previous chapters have presented both historical and novel forms of disturbances that are part of the New England landscape. Each of these will induce changes in the quantity and spatial distribution of resources required by plants as well as substantially alter vegetation structure and composition. Consequently, a single disturbance may initiate a highly complex chain of events that affect processes within a forest at many levels of organization and over long periods of time. Changes in species composition resulting from disturbance and succession may include important feedbacks between site and species characteristics, altering ecosystem function (Figure 16.1).

In order to explore the ecological mechanisms underlying the changes witnessed across New England, we have used a combination of field and glasshouse experiments to understand this dynamic interplay between species and site. A total of six different experiments are presented here that form the core of our Harvard Forest research. They address different aspects of environmental heterogeneity and change but share a common approach, which includes the use of tightly controlled experiments with a range of species drawn from the same genus. The species chosen for each experiment represent a range of successional characteristics. For example, with maples we use a very tolerant canopy tree (sugar maple), a canopy species of intermediate tolerance (for example, red maple), and a very shade-tolerant subcanopy tree (for example, striped maple). Variation in life-history strategies among the species allows examination of differences in responses to experimental environments while minimizing other evolutionary constraints.

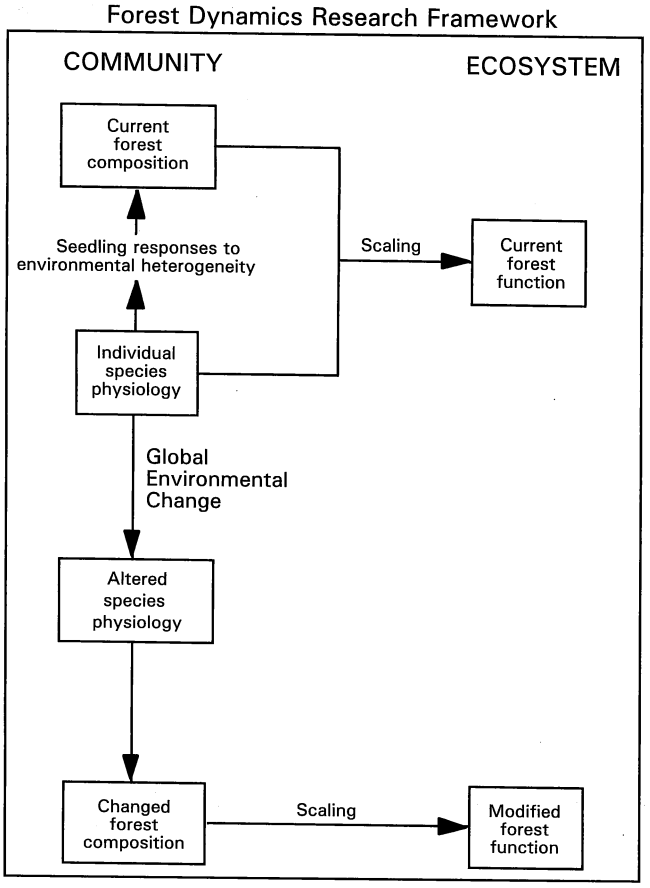

Figure 16.1. Research framework for studying forest dynamics, highlighting approaches for incorporating heterogeneity into the understanding of current forest composition and future forest responses to global environmental change, and for scaling from forest community structure to ecosystem function.

The experiments include the following:

- Plant response to experimental gap size and placement in the field
- Seedling response to temporal patterns of light availability in gaps
- Plant response to resource congruence in gaps
- Seedling responses to hurricane disturbance—consideration of multiple resources
- The influence of herb–tree seedling interactions and forest spatial structure
- Seedling regeneration and global environmental change

Experiment 1: Plant Response to Gap Size and Placement

Rationale

Ecological theory has suggested that fine-scale variation in environment and resources may enable a greater diversity of plant species to coexist in what are otherwise rather homogeneous forest conditions. Our research using experimentally created gaps in the forest canopy sought to test what has become known in the ecological literature as the *gap partitioning hypothesis*—that different species are adapted to different subsets of the entire range of environmental conditions to be found in a forest.

Experimental Design

We created three small (75 square meters) and three large (300 square meters) gaps in October 1987 in a 4-hectare stand of mixed oak, birch, and red maple on the Prospect Hill tract. In this study, which preceded our development of hurricane manipulations, we produced gaps by felling selected canopy trees with a chain saw and then cutting and removing all logs and branches manually with minimal disturbance to the soil. To minimize additional (albeit natural) heterogeneity, we cut back the understory vegetation to the ground each year. Each gap was broadly elliptical, with its long axis oriented in an east-west direction. Experimental plots were placed in the center of each gap, and in the northwest, northeast, southwest, and southeast corners. Equivalent plots in the same spatial arrangement were created as controls in adjoining areas of intact forest. Environmental monitoring stations were established at each plot to measure daily and seasonal variation in light (photon flux density, PFD), air and soil temperature, relative humidity, and wind speed. Seedlings of three maple species were planted, and physiological and demographic responses to the gap-understory continuum were measured for two years after gap creation.

Results

Light varied most among the resources measured, through both the day and the season, and between and within gaps, as would be predicted from the movement of the sun across the sky and the geometry of experimental gaps. In the northern hemisphere, the sun tracks across the southern part of the sky and thus exposes the north side of a gap, and the adjoining understories, to greater direct light. In contrast, the south side of the gap, although open to the sky, receives no direct light. Consequently, the number of days that direct beam radiation reached the forest floor decreased from north to south across the gaps, and in small gaps direct light fell only in the north half of each gap (Figure 16.2).

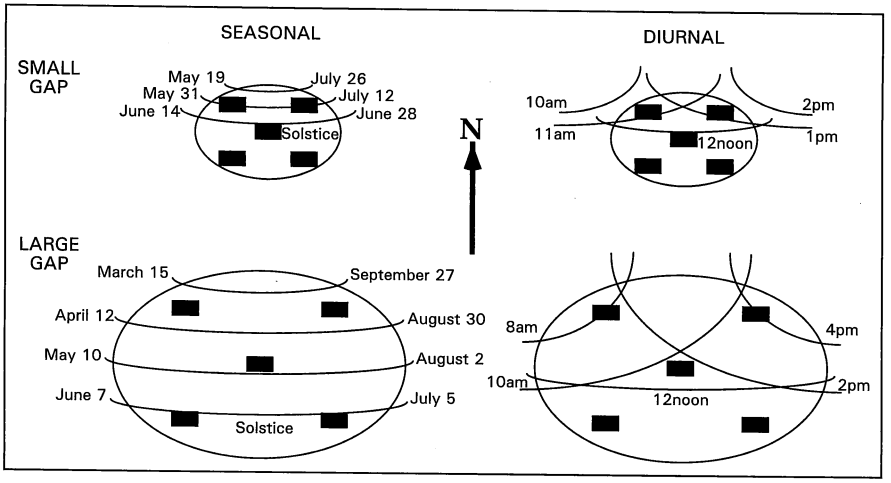

Figure 16.2. Seasonal and diurnal movement of direct beam radiation (direct sunlight) arcs in small and large gaps, based on field measurements and geometric calculations. Seasonal changes are shown with solar noon arcs, and diurnal changes are shown close to the summer solstice (hours are solar time). Modified from Bazzaz and Wayne 1994, 359–60, with permission from Elsevier Science (copyright 1994).

Superimposed on this north-south light gradient there occurred a strong east-west gradient in the diurnal light environment. As the sun rises in the east, west sides of gaps received morning sun, whereas east sides received beam radiation in the afternoon (Figure 16.2). Around the summer solstice, when the sun is highest in the sky, small gaps received direct light for only a little more than two hours each day, in contrast to large gaps, which received more than eight hours of direct light. These diurnal and seasonal patterns in light availability were observed only on clear days. On overcast days, the centers of gaps received marginally more diffuse light than the sides, and there were no differences among the four gap corners. Over the entire growing season there was significant spatial variation in light availability according to the following ranking: NW > NE > Center > SW > SE (Figure 16.3).

Species responses differed among large gaps, small gaps, and understory plots. Red maple seedlings showed a large increase in leaf area and in the rate of CO_2 assimilation with increasing gap size (Figure 16.4a and 16.4b). This flexibility in response gave red maple the highest survival overall and the largest increases in growth from the forest understory to large gaps (Figure 16.4c and 16.4d).

In contrast, striped maple showed a preference for small canopy gaps, as it grew better there than in large gaps or the understory. It also showed a modest increase in leaf area and a very substantial decline in

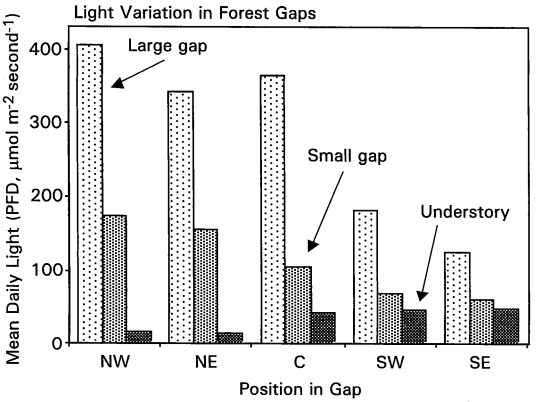

Figure 16.3. Variation in light availability (photon flux density, PFD) at different positions (northwest [NW], northeast [NE], center [C], southwest [SW], southeast [SE]) within the three different sizes of gap. Data represent daily means of both clear and overcast days through the 1989 growing season. Data from Sipe and Bazzaz 1995.

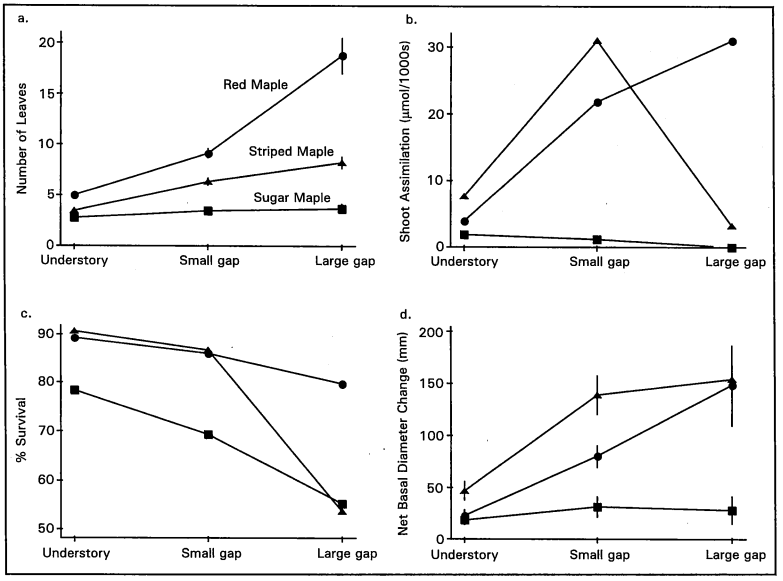

Figure 16.4. Responses of three co-occurring maple species seedlings to canopy gap size, in terms of the number of leaves (a), shoot assimilation rates (b), percent survival (c), and net basal diameter change after gap formation (d). For a and d, means (± standard error) were taken by pooling across plots within sites. Overall, red maple exhibits the greatest growth and performance. Data from Sipe and Bazzaz 1994 and 1995.

shoot growth rates from small to large gaps (Figure 16.4a and 16.4b). The decrease in photosynthesis for striped maple with increasing gap size may have been the result of the higher levels of direct light and possibly greater water stress in larger gaps. This conclusion is supported by the pattern of growth and survival. Seedlings of striped maple declined slightly in survival from the forest understory to small gaps, and greatly from small to large gaps (Figure 16.4c). Meanwhile, seedling growth increased substantially from the understory to small gaps, but only moderately in large versus small gaps (Figure 16.4d).

Sugar maple seedling performance decreased with increasing gap size. Shoot growth and percent seedling survival were both greater in the understory than in canopy gaps, whereas leaf area and seedling growth were unchanged.

Surprisingly few variables demonstrated significant differences in species' responses to different parts of gaps, despite large variation in the light environment across these locations. The clearest trend was red maple's strong preference for the center of large gaps (Figure 16.5). Gap centers received the greatest amounts of diffuse light but did not suffer the very high radiation loads experienced by north sides of gaps that may lead to photoinhibition and water stress.

Experiment 2: Seedling Response to Temporal Patterns of Light Availability in Gaps

Rationale

Differences in the timing of light availability is another aspect of gap heterogeneity. Plants may respond differently if the same amount of

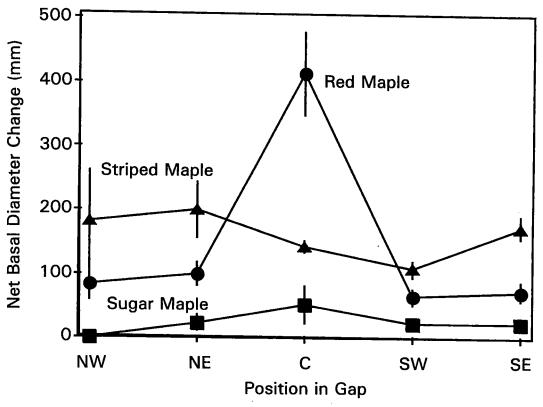

Figure 16.5. Growth responses of co-occurring maple species seedlings to canopy gap position, as determined by net basal diameter change after gap formation. Means (± standard error) were taken by pooling across seedlings within plots. NW, northwest; NE, northeast; C, center; SW, southwest; SE, southeast. Data from Sipe and Bazzaz 1995.

total radiation is received as intense light for a short period of time or diffuse light over the course of a whole day.

Experimental Design

We tested the effect of variable timing and intensity of radiation by simulating gap conditions and understory conditions and comparing seedling growth. Gap conditions were established using plywood walls (1.8 meters high) oriented north-south to control the timing and duration of direct radiation. The diffuse light in the understory was simulated using shade cloth of different thickness. Seedlings of birch were grown in each environment.

Seedlings of both early-successional gray birch and mid-successional yellow birch consistently grew larger in the shadehouses than in simulated gaps receiving equivalent amounts of light but in varying intensity (Figure 16.6). Gray birch was more sensitive to light availability in gaps than was yellow birch, while there was little difference between species' sensitivities in shadehouses.

The physiological mechanisms generating these response patterns are poorly understood, although a number of hypotheses have been proposed, including the following:

- Inefficient use of light: At levels higher than approximately 800 micromoles per square meter per second, light becomes saturating; any additional light intensity does not improve a plant's photosynthetic perfor-

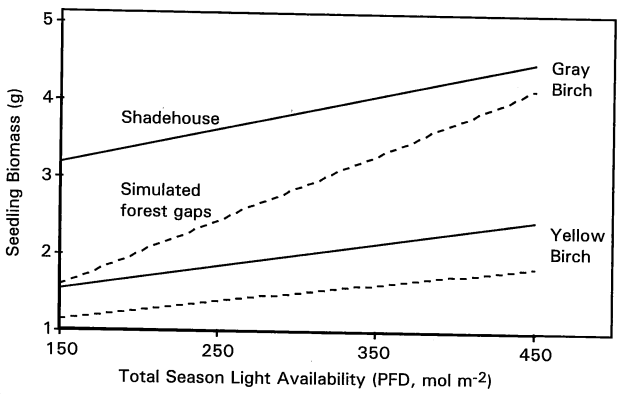

Figure 16.6. Growth responses of gray birch and yellow birch to differing diurnal distributions of light availability (photon flux density, PFD) after one growing season in simulated gaps (dotted lines) and shadehouses (continuous lines). Lines represent results of linear regressions fit to all data points. Modified from Wayne and Bazzaz 1993b, with permission from the Ecological Society of America.

mance. By concentrating a seedling's available light regime into a few hours in the middle of the day, the amount of excess light is increased.

- Trade-offs in biochemical processes within leaves: We might expect that seedlings receiving a relatively uniform distribution of light could adjust the photosynthetic machinery in their leaves to this rather narrow range of light levels, while seedlings receiving a more fluctuating light pattern would be forced into a more generalist and less efficient leaf biochemistry in order to cope with both high and low light. We did find that seedlings in simulated gaps showed greater reductions in leaf area ratio and increases in root weight ratio and leaf nitrogen and chlorophyll concentrations with increasing light than did seedlings in shadehouses. These adjustments to high light may have reduced seedling performance in low light, thereby decreasing their overall performance relative to plants grown in more uniform light conditions.
- Lack of congruence in resource availability: Plant responses to a particular resource are contingent on prevailing local environmental conditions, so the temporal pattern of resource availability could critically determine a plant's performance. We investigate this option in the next experiment.

Experiment 3: Plant Response to Resource Congruence in Gaps

Rationale

Plant responses to a particular resource are contingent on the availability of other resources. If high light coincides with abundant soil moisture (that is, resources are *congruent*), then plants will make better use of that light than if water availability is low. For seedlings in a canopy gap, where environmental conditions show distinct daily and seasonal patterns, resource congruency could play a major role in determining plant performance. These effects may be particularly marked between the west and east sides of a gap, which respectively receive morning and afternoon sun.

In particular, we hypothesized that seedling performance on the west side of a gap would be greater than on the east because western seedlings receive direct sunlight in the morning when other conditions are more favorable. In the hours before noon, vapor pressure deficit and temperatures are lower, imposing less stress on leaf function than afternoon conditions.

Experimental Design

We tested this hypothesis by placing birch seedlings on the east and west sides of simulated gaps so that they would receive direct light at different times of the day. A water treatment was also included, as diurnal changes in plant water status and moisture stress were expected to drive responses.

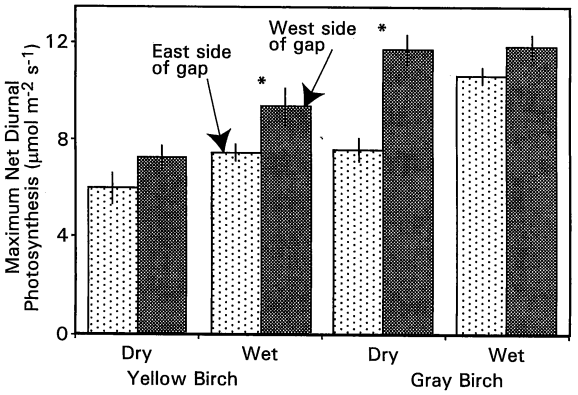

Figure 16.7. Maximum net photosynthetic rates measured during daily time courses of leaf-level gas exchange for gray birch and yellow birch seedlings grown on the east (afternoon sun) and west (morning sun) sides of simulated forest gaps and exposed to dry or wet soil treatments. Means (± standard errors) are pooled across blocks, with significant post hoc comparisons ($p < .05$) between east and west treatments denoted with an asterisk. Data from Wayne and Bazzaz 1993a.

Results

In the second year of the experiment, the rate of carbon uptake by leaves was indeed higher for plants on the west side of gaps, which received morning sun, than for plants on the east side, which were not in full sun until after noon. These differences, however, varied with species and water availability (Figure 16.7). Gray birch seedlings grew larger on the west than on the east in dry soils, whereas yellow birch performed better on the west in well-watered soils. Gray birch has a high level of drought tolerance, and may only have experienced incongruent resources when water stress was particularly strong. In contrast, yellow birch is quite drought sensitive and may have suffered water deficits in all drought treatments regardless of the timing of light availability.

These differences in photosynthetic rates were not, however, reflected in the overall growth responses at the end of the experiment. In particular, seedling biomass did not differ significantly between morning and afternoon sun treatments. This result highlights the importance of whole-plant processes that may compensate for leaf-level photosynthetic differences. Differences between east and west sides will be evident only on clear, sunny days, and any effects may become masked when integrated with seedling growth on overcast days.

Experiment 4: Seedling Responses to Hurricane Disturbance—Consideration of Multiple Resources

Rationale

Hurricanes are the most important natural disturbance in New England forests. Wind damage generates canopy gaps such as those we have studied, but also much larger openings with greatly altered physical structure. As trees fall, they create a wide variety of microsites due to uprooting of trees (for example, pits and tip-up mounds) and the distribution of prostrate tree boles and crowns (see Chapter 11). This profound alteration affects belowground processes and resource availability, as well as the distribution of light.

To understand the role of forest structure on dynamics, we developed a series of studies investigating seedling regeneration patterns at the simulated hurricane experiment. These studies address changes in both aboveground and belowground conditions and related seedling responses. As well as re-creating a disturbance that is a critical determinant of forest structure and composition in this region, taking this multiple resource perspective allowed consideration of a broader range of potential opportunities for species' niche specialization. Thus, this experiment offered the potential for developing a better understanding of species coexistence and maintenance of diversity in New England forests.

Experimental Design

We conducted this work at the two experimental hurricane blowdowns in the Tom Swamp and Prospect Hill tracts (see Chapter 11). Environmental conditions and resource availability were characterized across the range of microsites created by the uprooted and fallen trees. The physical and environmental characteristics of these microsites were then related to patterns of seedling regeneration. Our assessment of the availability of various resources such as light, moisture, and nutrients revealed significant differences among microsites, and this heterogeneity had striking effects on patterns of seedling regeneration.

In these detailed studies we focused particularly on the regeneration of co-occurring birch species, as their differential performance on such microsites may play an important role in determining their contrasting roles in New England forests. Birch species rarely sprout after wind damage but instead rely on seedling establishment. The small size and wide dispersal capabilities of birch seeds mean that they can easily reach and potentially establish on a broad range of sites. The small size also means that energy reserves in each seed are small, and new seedlings must reach mineral soil in a short period of time. This gener-

ally limits successful establishment to areas of bare soil without surface organic matter.

Results

On the hurricane blowdowns, open microsites without vegetation and shade were most favorable for birch seedling establishment because these open areas created many small patches of exposed soil. A significant proportion of seeds also reached tip-up mounds, and the emergence of new seedlings was relatively high on these microsites, although it varied between years. Emergence was lower on the tops of tip-ups and especially in pits, where litter tended to collect, making it difficult for seedlings to establish. As well as differing in amounts of seed rain and seedling emergence, microsites had contrasting degrees and types of mortality (Figure 16.8). Open microsites had the lowest mortality, with snowshoe hare browsing as the main cause. Similarly, mound microsites had modest mortality, largely due to frost-heaving and physical displacement. Seedlings on tops of tip-ups had high mortality primarily due to low light levels. Almost no seedlings survived in pits, as the few seedlings that did emerge were eventually buried by litter.

Microsite type affected seedling growth as well as establishment. Mounds and tops of tip-ups supported the highest rates of seedling growth on account of high light availability and high nutrient availability, respectively (Figure 16.9). Within the tops, seedlings grew best at higher vertical positions, perhaps because light varied because of over-

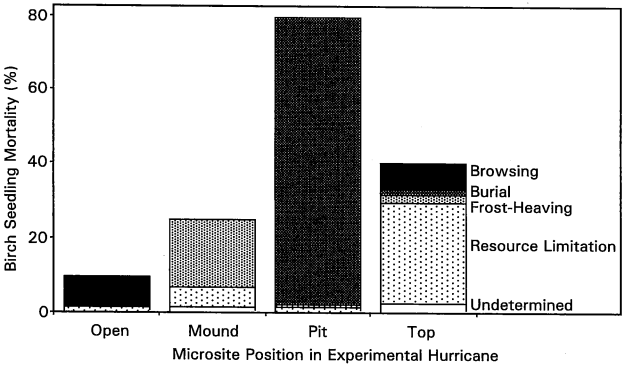

Figure 16.8. Mortality rate and cause of death (browsing, burial, frost-heaving, resource limitation, undetermined) for birch seedlings on different experimental microsites (see Figure 11.10 for diagram of microsites) over three growing seasons. Modified from Carlton and Bazzaz 1998a, with permission from the Ecological Society of America.

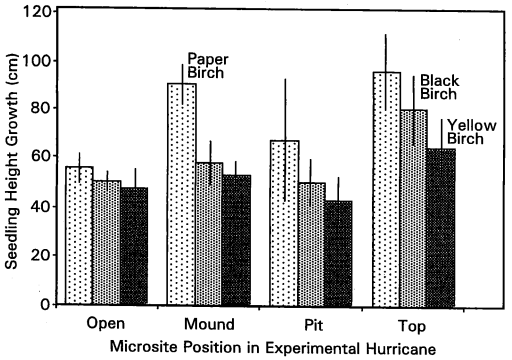

Figure 16.9. Mean height growth (± standard error) of paper birch, black birch, and yellow birch after three years of growth on different experimental microsites (see Figure 11.10 for diagram of microsites). Data from Carlton and Bazzaz 1998a.

hanging branches and residual understory vegetation. Paper birch responded most to the increased light and soil resource availability on mounds and tops, which might be expected from its early-successional status in New England forests. Seedlings were most responsive to increasing light availability at lower light levels and to increasing nitrogen availability at higher nutrient levels. Light responses were generally contingent on the level of soil nitrogen, with greater responsiveness at higher soil nitrogen availability. Nitrogen responses were less sensitive to prevailing light levels, except in very deep shade where all responses are severely limited.

Although seedling growth was enhanced on the mounds and tops of hurricane-created tip-ups, seedling establishment was very limited. Nevertheless, it appears that these growth responses could be important components of regeneration strategies for paper, black, and yellow birch as all three species maintain a seedling bank in undisturbed forests. After a hurricane, birch seedlings growing near a fallen tree's root mat will be raised up from the forest floor and exposed to high levels of light, substantially improving their chances of reaching the canopy. We included all the different components of seedling regeneration in projection matrix models to investigate the importance of hurricane events for the population dynamics of a number of forest species. These models showed that population growth rates of all species increase after a hurricanelike disturbance but that paper birch is particularly dependent on such events for long-term persistence in these forests (Figure 16.10). This analysis also revealed that regeneration in open microsites makes the largest contribution to population responses to a hurricane event, whereas regeneration on tip-up mounds themselves makes a much

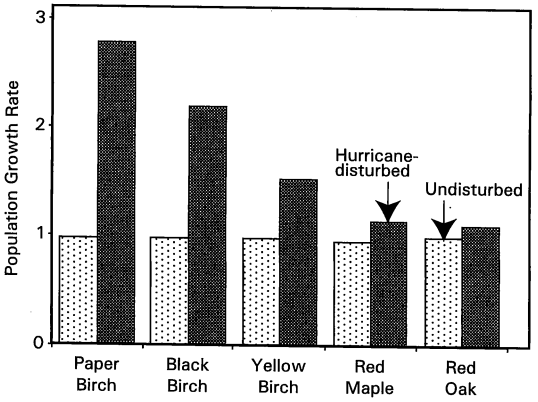

Figure 16.10. Population growth rates derived from the dominant eigenvalues of a projection matrix model of species' dynamics in undisturbed and hurricane-disturbed forests for five common temperate forest species. Data from Carlton 1993.

smaller contribution, primarily due to the small area covered by such microsites.

The work on seedling regeneration after a blowdown demonstrated that the complexity of forest responses to a large disturbance may be understood largely in terms of fluxes of the major resources in the forest ecosystem and seedling responses to these fluxes. Hurricanes increase heterogeneity in the availability of light, moisture, nitrogen, and space at the scale of individual seedlings by creating a wide variety of microsites at the forest floor. These microsites differ in both aboveground and belowground resource availability. Absolute differences in the levels of different resources, as well as congruency between different resources, may influence many stages of seedling regeneration, including dispersal, emergence, survival, and growth. Effects of disturbance on multiple environmental conditions may provide further resource axes, by which species may partition the environment.

Experiment 5: The Influence of Herb–Tree Seedling Interactions and Forest Spatial Structure

Rationale

Species differ in their ability to persist as seedlings and saplings in the shaded forest understory. For many species, development of a seedling bank forms a critical part of their regeneration strategies, as the size and status of seedlings in the understory may determine a species' response to a disturbance that will allow seedlings to reach the overstory.

Table 16.1. Environmental Conditions, Understory Vegetation Patterns, and Seedling Regeneration Dynamics between Contrasting Stand Types

Factor	Stand Type	
	Hemlock	Broad-leaved
Environment		
Light (mol day^{-1})	0.39*	0.94*
N (mg/kg soil)	90.6	112.8
Water (g g^{-1})	1.12	0.81
Soil pH	3.67	3.96
Herb/shrub species		
Density (m^{-2})	2.0*	28.6*
Species richness	8.3*	25.7*
Seedling demography		
Mean age (yr)	1.04*	1.53*
Emergence (m^{-2})	88.8*	19.6*
Survival (%)	28.1*	46.9*

Source: Unpublished data from S. Catovsky and F. A. Bazzaz.
*Significant difference.

Conditions in the understory can be both spatially and temporally heterogeneous due to site conditions, human disturbance, or differences in canopy trees overhead. One of the most striking patterns is the contrast between conditions under deciduous broad-leaved species (for example, red oak, red maple, and birch) and hemlock, an evergreen coniferous species. Hemlock-dominated stands have significantly less light at the forest floor than do broad-leaved tree stands, which leads to a sparse understory vegetation and higher seedling turnover and lower average age in the hemlock stand (Table 16.1).

Variation in the distribution and abundance of understory species may also influence seedling regeneration dynamics. Within temperate forests, herb and shrub species can form fairly stable patches that differ in species composition and density across different stand types. As all tree seedlings must pass through this herb and shrub layer before they reach the overstory, these understory plants may act as an ecological filter, determining the composition and spatial structure of the seedling bank and ultimately controlling future canopy composition. Ferns are one of the most important components of this ecological filter. They are widely distributed, have dense growth patterns, and tend to increase under conditions of increasing light.

Experimental Design

To investigate the influence of the major fern species (hay-scented fern, *Dennstaedtia punctilobula;* and interrupted fern, *Osmunda*

claytoniana) on forest regeneration, we removed ferns chemically (glyphosate application), pinned them back (shade-free treatment), or left them intact in a total of six plots. By comparing removal and shade-free plots, and by comparing shade-free and intact plots, it was possible for us to decouple competition for light from competition for water and nutrients. At each plot, the microenvironment and demographic responses of both naturally regenerating seedlings and planted seeds/seedlings were characterized.

Results

The two fern species did not differ in their influence on the understory microenvironment, but the presence of a full fern cover significantly reduced the levels of light reaching seedlings in the understory, from 3.4 percent to 1.1 percent of light reaching the top of the canopy (Figure 16.11a). Fern fronds also increased litter accumulations onto the

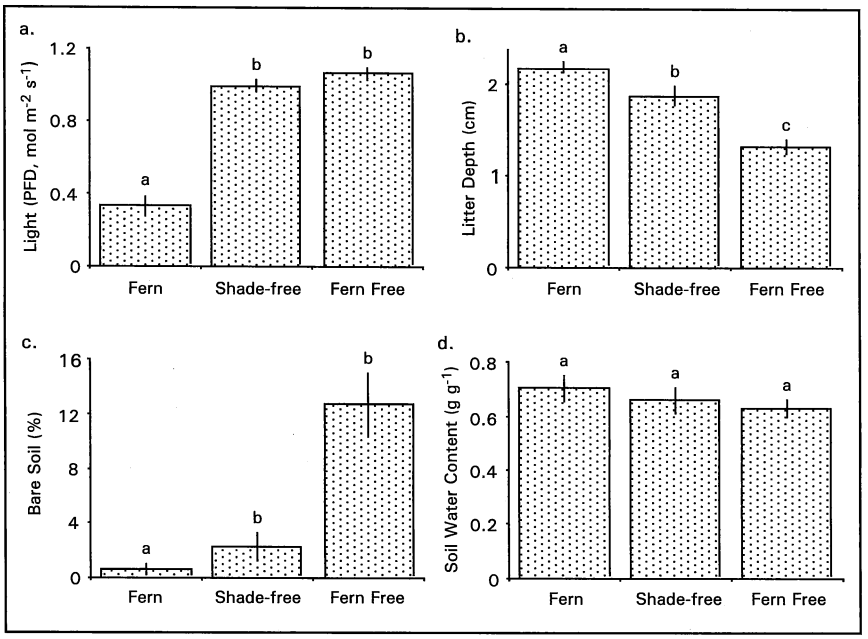

Figure 16.11. Microenvironmental characteristics of fern manipulation plots: light (photon flux density, PFD) (a), litter depth (b), percent exposed soil (c), and soil water content (d). Means ± standard error were calculated across all experimental sites ($n = 60$ plots). Within each panel, columns that share a letter are not significantly different ($p < .05$, Fisher's protected LSD) from one another. Modified from George and Bazzaz 1999a, with permission from the Ecological Society of America.

ground surface and decreased the degree of soil exposure, but they did not affect soil water content (Figures 16.11b, 16.11c, and 16.11d). Patterns of seedling emergence, survival, and growth were affected by the presence of a fern cover due to influences both on understory microenvironmental conditions and on the movement and activity of seed and seedling predators.

Emergence of yellow and black birch, white pine, and red oak seedlings was significantly reduced in fern plots, while red maple and white ash were unaffected (Figure 16.12a). Further analysis and experimental

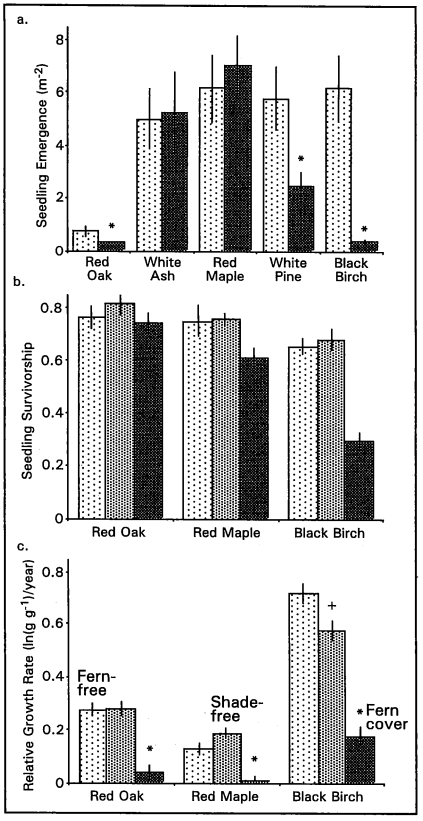

Figure 16.12. Variation in seedling emergence (a), survivorship (b), and relative growth rate (c) in experimental fern plots (fern-free, light shading; shade-free, moderate shading; and fern cover, dark shading) for different tree species. Species are shown in decreasing order of seed size. Panel a is from naturally established seedlings, while panels b and c are from planted seeds and seedlings, respectively. Bars represent means (± standard error) pooled across six study sites. Symbols (*, +) designate bars that are significantly different from one another within a species ($p < .05$, Fisher's protected LSD). Data from George and Bazzaz 1999a and 1999b.

manipulation (for example, removal of litter, caging of the seedlings from herbivores) revealed that the factors leading to reduced emergence under ferns differed among species. Fewer white pines emerged under ferns mainly because of the reduced light levels. Birch emergence was also partially related to light levels but was primarily affected by the degree of litter accumulation in plots; the generally thick litter layer under ferns strongly inhibited emergence of very small-seeded birch. Red oak emergence was low in plots with ferns because of increased activity of small mammals that eat acorns and prefer the shelter and protection offered by fern-dominated areas. Again, because of small seed size, birch seedling survival was most sensitive to fern presence, whereas red maple survival was only marginally affected by ferns (Figure 16.12b). Red oak survival was not influenced overall by the presence of ferns, as the detrimental effect of lower resource availability under ferns was balanced by the protective advantage conferred by ferns against insect herbivory. Seedling growth in fern plots was consistently lower than in fern-free plots mainly as a result of reduced light availability (Figure 16.12c).

Ferns may have substantial effects on conditions in the forest understory, in terms of both microenvironmental characteristics (especially light and litter) and the activity of seed/seedling predators. All these factors may selectively influence seedling emergence, survival, and growth of different species, and thus affect forest composition. Projecting the results of this study forward suggests a strong selectivity of the fern layer and a strong role of this ecological filter. Red maple seedlings dominate in fern areas, whereas the contribution of birch and red oak to seedling bank composition increases in fern-free areas. The heterogeneous distribution and abundance of fern species across the forest may strongly influence the spatial structure of seedling regeneration. These spatial dynamics have important implications for neighborhood interactions between individuals and the genetic structure of tree populations.

Experiment 6: Seedling Regeneration and Global Environmental Change

Rationale

The responses to light, water, and nutrients described above may all be altered by the novel perturbations of elevated CO_2 and nitrogen deposition resulting from widespread human activity. As a result of fossil fuel combustion and extensive fertilizer production and use, forests across New England are experiencing high levels of nitrogen deposition (see Chapter 12). More than half the nitrogen currently deposited across New England is nitrate, whereas forest soils in this region are predominantly ammonium based. This switch in the nitrogen

species available to seedlings clearly has the potential to influence forest regeneration dramatically

Also as a result of the use of fossil fuels, CO_2 in the global atmosphere has risen from 280 to 360 microliters per liter over the past century. Carbon dioxide is a primary substrate for photosynthesis, and changes in atmospheric CO_2 concentrations are likely to affect plant function profoundly. Early work in this area demonstrated striking differences in tree species' responses to elevated CO_2, suggesting the possibility of substantial change in forest regeneration dynamics in the future. Elevated CO_2 may also influence plant responses to spatial and temporal heterogeneity in environmental conditions, leading in turn to alterations in the distribution and abundance of species across the landscape and to changes in forest species composition and spatial structure.

Experimental Design

To explore the implications of changing resource interactions further, we have run a series of experiments on the individual and combined effects of nitrogen (quantity and form) and CO_2 on regeneration and physiology. Our central hypothesis is that seedling responses depend on both species' characteristics (for example, leaf habit and life-history strategy) and environmental conditions (for example, light and soil resources) and that coniferous and broad-leaved species may respond differently due to fundamentally contrasting patterns of nutrient use.

Results

There were surprises in the results from these experiments. For example, the light environment exerted a strong effect on black birch response to the form of nitrogen addition. In contrast to predictions from the physiology of nitrogen metabolism, black birch seedlings showed a clear preference for ammonium over nitrate in high versus low light (Figure 16.13).

Although early-successional species tend to be characterized by greater flexibility in response to changing environmental conditions, our studies indicated that later-successional species showed the greatest growth enhancements in response to elevated CO_2 (Figure 16.14). More recent work at the Harvard Forest comparing eight coniferous and eight broad-leaved tree species suggests that leaf habit may alter the relationship between shade tolerance and CO_2 responsiveness. Growth enhancement in elevated CO_2 increased with increasing shade tolerance for coniferous seedlings, while CO_2 growth enhancement decreased with increasing shade tolerance for broad-leaved species seedlings.

We found that elevated CO_2 caused the greatest enhancement of

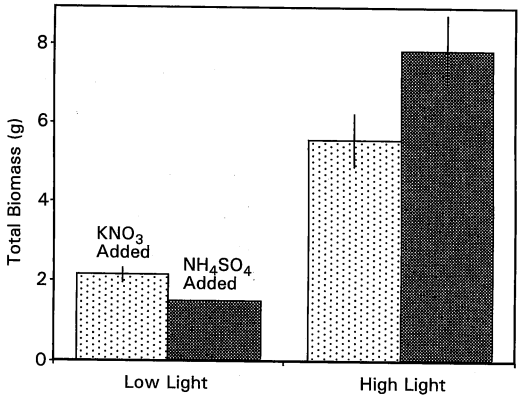

Figure 16.13. Black birch growth responses to the form of nitrogen addition (KNO_3 and NH_4SO_4) under low (8 percent photosynthetically active radiation [PAR]) and high (70 percent PAR) light treatments. Means (± standard error) were pooled across block and nitrogen addition rates (2.5 and 5 grams per square meter per year). Data from Crabtree and Bazzaz 1993a.

growth in treatments with high nutrients and low light availability. The nutrient interaction was most noticeable in earlier-successional species such as gray birch and white ash, whereas the low light effect was particularly striking in mid-successional species, including red oak and yellow birch. The low-light, high-nutrient combination may produce the greatest CO_2 growth enhancements because it is the treatment in

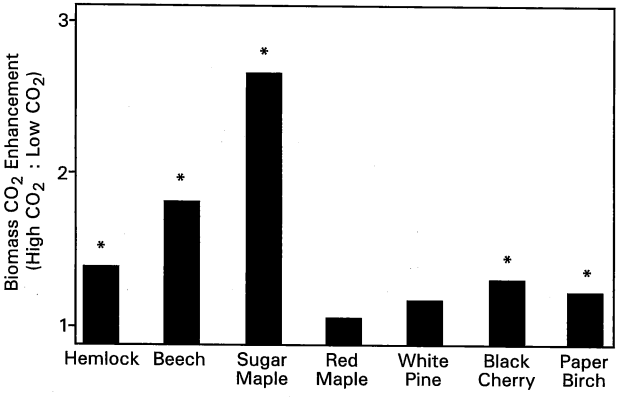

Figure 16.14. CO_2 enhancement ratios of total seedling biomass (biomass at 700 microliters per liter/biomass at 400 microliters per liter) after one growing season for seven co-occurring temperate forest species, ranked from left to right in order of decreasing shade tolerance. Asterisks designate significant differences between growth at ambient and elevated CO_2 for that species. Data from Bazzaz et al. 1990.

which plants undergo the least photosynthetic down-regulation after prolonged exposure to elevated CO_2. Down-regulation is thought to occur when carbohydrate supply (that is, photosynthesis) exceeds a plant's demand. Capacity to utilize carbohydrates is a function of the size and number of sinks within a plant. High nutrient availability may increase sink strength, while low light availability may reduce carbohydrate supply rates, and thus both factors may reduce the degree of down-regulation in response to elevated CO_2. The reasons for differences in species' sensitivity to down-regulation, however, are currently unclear. Importantly, we noticed one major consequence of down-regulation: substantial declines in CO_2 responsiveness were observed over three growing seasons for a number of temperate forest species, although the extent and rate of decline differed among species.

Although no consistent effects of CO_2 on species' niche breadths relative to drought stress were found, significant shifts in species' responses across moisture gradients did occur. Species that are more tolerant of drought, such as gray and paper birch, increased their representation in dry soil treatments, while drought-intolerant species, including yellow birch and red maple, were more responsive to CO_2 in well-watered treatments (Figure 16.15). These patterns may reinforce current distributions of these species in relation to soil moisture.

Synthesis and Extrapolation

Extrapolating from short-term seedling experiments to the longer-term effects of novel environmental perturbations on forest struc-

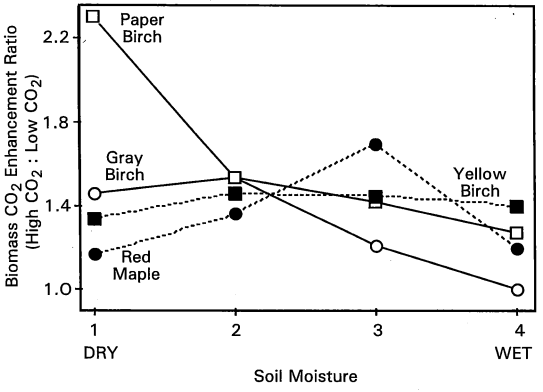

Figure 16.15. CO_2 enhancement ratios of total seedling biomass (biomass at 700 microliters per liter/biomass at 375 microliters per liter) after one growing season for two drought-tolerant (gray birch and paper birch) and two drought-intolerant (red maple and yellow birch) species under different water treatments. Data from Miao et al. 1992 and Catovsky and Bazzaz 1999a.

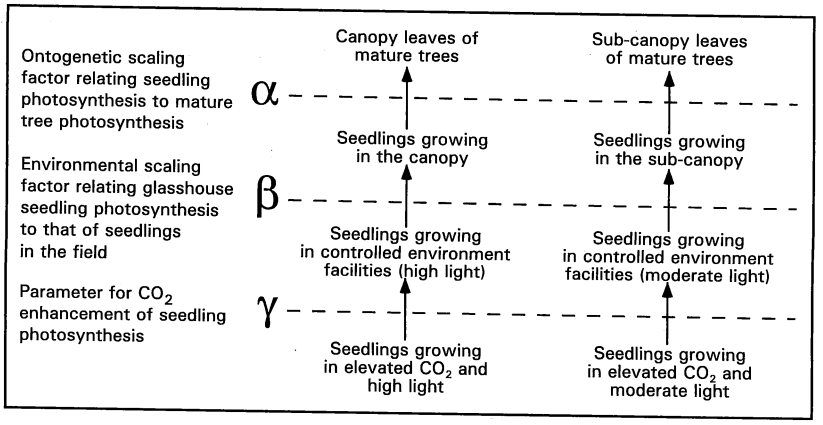

Figure 16.16. Approach for predicting future responses of mature canopy trees to atmospheric CO_2 levels based on scaling seedling photosynthetic responses to elevated CO_2. Based on Bassow 1995 and Bazzaz et al. 1996.

ture and function is one of the most challenging aspects of global change research. We have developed a scaling approach that allows us to estimate how mature tree photosynthesis may respond to elevated CO_2 based on seedling responses in controlled environment facilities (Figure 16.16).

We measured the α effect by growing seedlings on canopy access towers in the canopy and subcanopy strata of mature trees, so that microenvironmental conditions are identical, and measuring leaf photosynthetic characteristics. The β effect is calculated by comparing seedlings growing in a forest canopy with seedlings in controlled environment facilities, where similar microenvironmental conditions are simulated (high versus low light, matched temperature and vapor pressure deficit). The final factor, γ, is measured by comparing seedling photosynthetic responses with ambient and elevated CO_2. Our results suggest that such a scaling approach is feasible provided that the developmental scaling factor α is not too large. For species like red maple and birch, seedlings and mature trees did not differ greatly in photosynthetic responses, whereas red oak and yellow birch showed much larger photosynthetic differences. For these latter species, nonlinearities in photosynthetic responses between scaling components may limit the utility of such an approach.

As part of a second scaling approach, we incorporated our results on variation in CO_2 responsiveness as a function of species and resource availability into a spatially explicit temperate forest dynamics model (SORTIE) in conjunction with collaborators at Princeton to investigate the community- and ecosystem-level consequences of rising CO_2 levels.

The model is driven by canopy tree species effects on light environment at the forest floor and seedling growth and survival responses to this variation in light availability. By re-parameterizing the model, we showed that differences in species' responses to elevated CO_2 can lead to dramatic changes in future forest species composition. The model predicted particularly large increases in the contribution of red oak to community biomass (Figure 16.17), with a simultaneous decrease in species diversity. This alteration of community structure was also a primary determinant of ecosystem-level change in the future. The model predicted an additional 35 percent in basal area if species composition was allowed to change over time, compared with runs where composition was constrained.

The experiments outlined above demonstrate that substantial alteration of forest species composition could occur as a result of future environmental changes, in particular, elevated atmospheric CO_2 and nitrogen deposition. Novel environmental perturbations will interact with current spatial and temporal patterns of resource availability to influence forest regeneration dynamics. Species' responses to different resource combinations will determine which species come to dominate the future forest. In central New England, model results predict a noticeable increase in red oak abundance in response to elevated CO_2, with accompanying decline in overall species diversity. The exact nature of the change, however, will depend on the degree of future forest disturbance. Human activities, such as land-use management, pathogens, and the introduction of exotic species, may influence disturbance regimes and determine the kinds and rates of future changes.

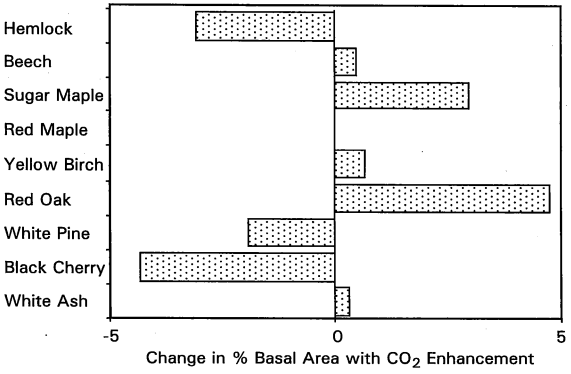

Figure 16.17. Projected relative change in species composition after 100 years of CO_2 enrichment. Species are ranked from top to bottom in order of decreasing shade tolerance (hemlock to white ash). Data from Bolker et al. 1995.