CHAPTER 11

Simulating a Catastrophic Hurricane

D. FOSTER, S. COOPER-ELLIS, A. BARKER PLOTKIN, G. CARLTON, R. BOWDEN, A. MAGILL, and J. ABER

Background and Major Questions

In 1635, fifteen years after the establishment of Plymouth Plantation on the eastern shore of Massachusetts, Governor William Bradford awoke one August morning to witness the arrival of one of the great hurricanes in New England history: "It began in the morning a little before day, and grew not by degrees but came with violence in the beginning, to the great amazement of many. It blew down sundry houses and uncovered others. . . . It caused the sea to swell to the south of this place above 20 foot right up and down, and made many of the Indians to climb into trees for their safety. It blew down many hundred thousands of trees, turning up the stronger by the roots and breaking the higher pine trees off in the middle. And the tall young oaks and the walnut trees of good bigness were wound like a withe, very strange and fearful to behold."

Since the day that this awe-inspiring storm struck, New Englanders have been occasionally reminded of the impacts that tropical storms can exert on their landscape. Through time this awareness has led to many questions concerning the importance of hurricanes in controlling the structure, composition, and function of forest ecosystems across the region. As our understanding of the historical frequency and distribution of these storms has improved through our reconstructions and modeling, we have also sought to understand the patterns of forest damage from wind disturbance, the rate of recovery of the vegetation and ecosystem function, and the differences between hurricane damage and the effects of other types of natural and human disturbances. This interest in the ecological role of hurricanes has been paralleled by a desire to apply this information to the conservation and management of forests and other ecosystems across New England.

Interpretations of the effects of intense wind disturbance on the northeastern United States have been strongly shaped by observations and experiences related to the Great Hurricane of 1938, the most destructive storm to hit the region in the past 175 years. This storm struck Long Island, New York, on September 21 and then passed northward across central Connecticut and Massachusetts to the northwest corner of Vermont, bringing wind speeds exceeding 130 miles per hour as well as 6 to 14 inches of rain. Forest damage, which included the destruction of more than 4 billion board feet of timber along a 100-mile-wide path, was most intense east of the storm track where the forward momentum and rotational velocity of the storm coincided (see Figure 1.4). In the aftermath of the hurricane, the federal government organized a regional timber program that salvaged more than 1.5 billion board feet of lumber. This salvage operation sought to reduce the immediate threat of wildfire and recoup lost investment, but it also had the indirect consequence of promoting extensive road construction, soil scarification, and burning of logging slash.

At the Harvard Forest, research on wind disturbance evolved around the effect of this storm. Even before 1938, R. T. Fisher and his students had recognized that natural disturbance by wind, as well as fire, ice, snow, and pathogens, was important to the maintenance of a shifting mosaic of vegetation and the retention of early-successional species in the landscape. However, the unanticipated severity of the 1938 storm and its catastrophic effect on forests, research experiments, and regional economic prospects promoted a rethinking of forest-management approaches and ecological interpretations across the northeastern United States (Figures 11.1 and 11.2).

Surveys conducted immediately after the hurricane concentrated on such practical issues as efficient salvage methods and fire prevention, but research attention gradually turned toward seeking silvicultural and ecological insights from the widespread pattern of uprooted and broken trees. Three questions loomed above all others: Was there a predictable return interval for these storms, and if so, how did this vary across New England? Did strong relationships exist between forest composition and age and susceptibility to wind damage? What were the patterns of forest recovery and the long-term effects on forest conditions? Answers to all three questions were deemed critical if ecologists were to understand the spatial and temporal variations in vegetation across New England and if foresters were to incorporate an understanding of tropical storms into long-term forest planning. While a graduate student (and future leader of temperate forest silviculture) named David (D. M.) Smith addressed the first question in a classic master's thesis at Yale University (1946), his counterpart at Harvard, Willett Rowlands, clambered through the tangle of windthrown trees on the Harvard Forest to address the second (1941), and a succession of graduate students and researchers at Harvard tackled the last.

Although Smith's work was never published beyond the original thesis, it is a beautiful piece of regional reconstructive research. In fact, his

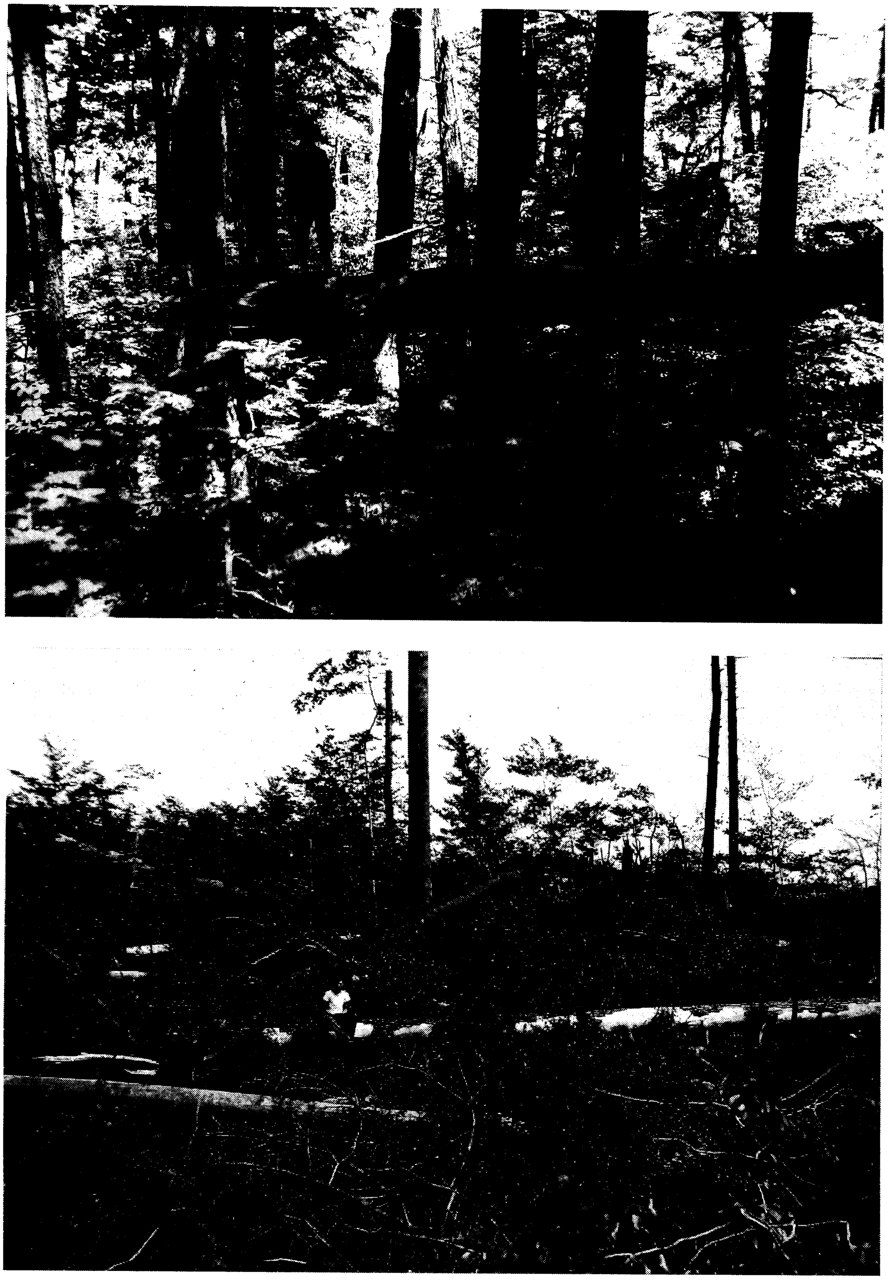

Figure 11.1. The old-growth forest on the Harvard Forest Pisgah tract in southwestern New Hampshire before (top) and after (bottom) the 1938 hurricane. Photographs from the Harvard Forest Archives.

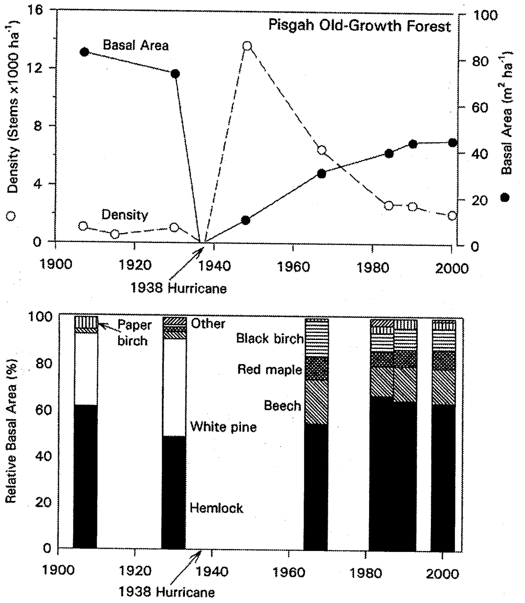

Figure 11.2. Changes in forest structure (top) and composition (bottom) at the Pisgah Forest from the early 1900s to 2000, showing the forest response to the 1938 hurricane. The original old-growth forest was composed of widely spaced but massive white pine and hemlock, which were nearly all blown down by the storm. A young and dense stand of hemlock, beech, red maple, and birch has been undergoing a process of thinning in density and gradual increase in basal area over the past sixty-five years. White pine was essentially eliminated from the stand by the windstorm. Updated from Foster 1988b and Foster, Orwig, and McLachlan 1996 by A. Barker Plotkin (Harvard Forest Archives).

study presages our hurricane modeling work by using a knowledge of historical sources and meteorology to interpret all storms since 1635. Smith's study clearly defined the south-to-north regional gradient in hurricane return interval and average intensity. Meanwhile, Rowlands looked at sites across Petersham that were topographically exposed to the strong winds from the hurricane and documented the type and extent of damage to trees in forests of different age and composition. He discovered that the even-aged white pine that were abundant on old-field sites were much less windfirm than the hardwoods. For all species, he found that wind damage increased linearly with tree height and that open-grown trees survived better than those growing in densely stocked stands. Rowlands also concluded that even-aged stands were more wind-resistant than mixed-aged stands as a consequence of lower turbulence in the canopy. Furthermore, he suggested that soil moisture was correlated with a tree's proneness to uprooting. As moisture increased, rooting strength declined, and the trees toppled over more readily. Rowlands's results had immediate implications for forest managers concerned with producing windfirm stands, and they provided new insights into the natural dynamics of forests in response to wind.

The extensive and preferential damage to white pine forests gave impetus to additional studies and interpretations of forest dynamics. The emphasis of most early New England forest management, including much of the research at the Harvard Forest, was aimed at the sustained production of white pine. By 1938 it was evident that most of the mature white pine forests that uprooted were the product of natural succession on abandoned agricultural fields. What would replace the blown-down pine forests? This important ecological and silvicultural question was addressed by Ralph Brake and Howard Post, graduate students at the Harvard Forest, who assessed patterns of natural regeneration on sites with different soils, contrasting amounts of prehurricane pine and hardwoods and varying intensities of posthurricane logging. They found that despite heavy damage to hardwood seedlings and saplings by the hurricane and subsequent salvage logging, the windthrown areas were often densely filled with rapidly growing hardwoods. The density, species composition, and type of tree regeneration varied by soil type. For example, red maple, red oak, and various birches predominated on mesic sites, whereas gray birch and white pine were more common on sandier soils. Nonetheless, despite this excellent work many questions remained concerning explicit connections between local site conditions and revegetation, the long-term changes that would occur in the forests and their environment in the years after a storm, and the influence of windstorms on the natural, hardwood forests.

One critical element was also largely missing from these early studies of the 1938 hurricane: investigations of disturbance impacts on fundamental ecosystem processes such as carbon accumulation, hydrology, and nutrient dynamics. Some related issues were partially addressed by Jim Patric's ingenious investigation of long-term response of river flow to the 1938 hurricane (Figure 11.3). Patric, a soil scientist and Bullard Fellow at the Harvard Forest in the 1960s, reasoned that the broadscale reduction in forest canopy caused by the storm might produce a regional change in river discharge. By comparing long-term flow records from the Connecticut River, whose watershed was intensively damaged by the storm, with those from the Androscoggin River, where little damage occurred, he was able to demonstrate that a substantial increase in river flow was sustained for five years after the 1938 hurricane. Patric concluded that interception of precipitation by the vegetation, evaporation from leaf surfaces, and transpiration of moisture from the forest canopy were all reduced when the storm abruptly altered the forest cover. With less moisture returning to the atmosphere, more was delivered to groundwater and small tributaries and eventually into the larger river. The cumulative effect on regional hydrology of changes in forest struc-

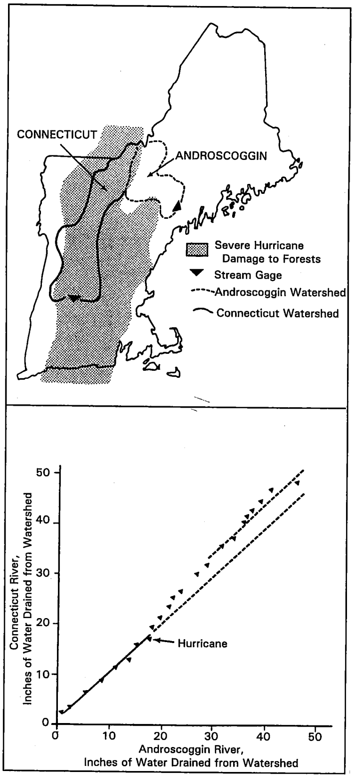

Figure 11.3. Analysis by Jim Patric (1974) of changes in major river flow as a long-term consequence of the 1938 hurricane. Top: Distribution of severe damage in relation to New England forest watersheds. Bottom: Cumulative summer flow (July to September) for the Androscoggin and Connecticut Rivers. After the storm there was a substantial increase in flow from the damaged Connecticut River watershed that persisted for nearly five years. The Androscoggin watershed was undamaged. Reprinted from Foster and Boose 1995, with the permission of Cambridge University Press.

ture across this enormous watershed was a major consequence of the hurricane (Table 11.1). Patric likened the phenomenon to the increased runoff measured at watersheds like Coweeta and Hubbard Brook after experimental logging, and he described the hurricane as a "forest treatment of regional proportions." Patric's findings on stream flow, observations of increased nutrient export associated with experimental cuttings and herbicide treatments at Hubbard Brook, and documentation of increased fluxes of trace gases after Hurricane Hugo in Puerto Rico have raised many new questions about the effects of hurricanes on hydrology, soil chemistry, and ecosystem dynamics. All of these results and emerging questions motivated the Harvard Forest hurricane experiment.

Table 11.1. Increased River Flow and Decreased Evaporative Loss from Hurricane-Damaged Watersheds in Comparison to the Undamaged Watershed of the Androscoggin River (inches per hydrologic year)

	Flow Increase		Evaporative Decrease	
Year	Connecticut	Merrimack	Connecticut	Merrimack
1939	+4.8*	+5.1	−5.8	−5.0
1940	+2.4	+2.9	−1.6	+1.6
1941	+2.5	+3.8	−3.4	−4.2

Source: Patric 1974, copyright 1974 by the Society of American Foresters, reproduced with permission of the Society of American Foresters in the format Other Book via the Copyright Clearance Center, Inc.
*Significant at the .05 level of probability.

Rationale for the Hurricane Experiment

Few disturbances have the potential to rearrange forest biomass on a broad scale as abruptly or as dramatically as severe windstorms. Unfortunately, our understanding of the ecological effects of these events has been based almost exclusively on post-hoc assessments of storm impacts on sites where little baseline data have been available. With the exception of Hurricanes Hugo and Mitch in Puerto Rico, where the existence of the Luquillo LTER project enabled a range of continuous measurements, the lack of baseline information has precluded good integrated studies of forest response to hurricanes. Consequently, to investigate vegetation and ecosystem response to severe wind disturbance in a controlled setting, we designed an experimental hurricane as a core part of our comparative study of ecosystem dynamics. The hurricane experiment, like our other manipulations and long-term measurements, was situated in the most prevalent forest type in our landscape, a mature red oak–red maple stand. To maximize the realism of the manipulation, we based the damage design on empirical studies of the 1938 hurricane, especially those by Willett Rowlands, Howard Post, and Ralph Brake, and we initiated the experiment during the height of hurricane season.

Experimental Design

The hurricane experiment was designed to examine both forest responses to and recovery from major wind damage in a comprehensive way. We sought to (1) identify changes in important plant resources such as light, moisture, and nutrients resulting from changes in forest structure; (2) document patterns of species damage, repair, regeneration, and growth; and (3) explore the relationships among vegetation dynamics, environmental conditions, and ecosystem processes. To quantify changes accurately, our design allowed for extensive measurement before the manipulation in both the disturbed area and in a nearby control area.

Measurements were made to further our understanding of the relationship between wind disturbance and ecosystem function, with an emphasis on such critical environmental processes as the movement of materials among the biota, the soil, and the atmosphere. Included were measurements of soil environment conditions such as moisture and temperature that can affect decomposition, respiration, and other belowground processes; changes in soil nutrient availability and cycling, with an emphasis on nitrogen; and concentrations and fluxes of the trace gases nitrous oxide, CO_2, and methane, which are important greenhouse gases. The experiment also provided an opportunity for us to examine vegetation responses, including the type and distribution of damage and patterns of mortality among tree species; changes in the structure of the canopy and forest floor; the importance of different modes of tree regeneration (for example, seedlings versus saplings or sprouts) in controlling species composition and abundance; and changes in understory composition as a result of damage to the overstory and forest floor structure. Finally, in addition to detecting changes in ecosystem functioning across the area, we were also interested in quantifying environmental resource conditions such as light and soil moisture at the scale of the microsites created by the disturbance. This we sought in order to contrast the patterns of resource availability in the experimental study area with those in the undisturbed forest understory and to relate these to plant performance.

Mimicking a Hurricane

The seventy-five-year-old red oak–red maple forest selected for the experiment is typical of the most common forest type in central New England. In addition to oak and maple, the relatively homogeneous stand includes white pine; white ash; black, yellow, and paper birch; hickory; and other species. The site occupies a gentle northwest slope, and soils are moderately well-drained with a discontinuous hardpan. We surveyed the rectangular experimental area, which is roughly the size of a soccer field (0.8 hectares), and the nearby control area and mapped and tagged all trees. We established plots on transects across the experimental and control areas to monitor regeneration and understory vegetation and made baseline measurements of the forest environment, soils, and ecosystem processes.

In designing the experiment, we sought to mimic damage from the 1938 storm, when approximately 80 percent of canopy hardwood trees and all mature white pine on exposed sites were damaged. We used data collected by Rowlands to determine the proportion of trees to pull down, based on the size and type (conifer or hardwood) of tree. Using observations from 1938 and some preliminary attempts by our woods crew to simulate the damage from a hurricane, we determined that

Figure 11.4. The edge of the experimental "blowdown" in the second year after the manipulation. Most of the trees uprooted, producing large mounds, and many of these produced thick crowns of leaves the following summer. Photograph by M. Fluet.

pulled trees account for fewer than 40 percent of total trees damaged and that the majority of broken and uprooted trees are actually damaged indirectly as pulled trees fall against other, generally smaller, trees in their path. In early October 1990, we pulled more than 235 canopy trees toward the northwest using a cable attached to a large winch on a logging skidder located outside the study area. This method simulated the lateral force of wind against the crown of a tree and allowed the structure of the tree to determine whether the actual damage would be by uprooting or breakage. By keeping heavy equipment off the site and by generating a range of direct and indirect damage to plants and soil, this treatment effectively reproduced many of the natural consequences of a hurricane (Figure 11.4). We made no effort to pull trees beyond their initial point of repose if they were hung up on other trees, and we left all trees, including those indirectly damaged by falling trees, where they fell.

Assessing the Consequences and Limitations of the Manipulation

As expected, the manipulation produced dramatic changes in forest structure, including a redistribution of biomass from a canopy nearly 30 meters tall to a thick tangle of subparallel and prostrate boles and branches resting a few meters above the forest floor (Figure 11.5). Nearly 70 percent of all trees were damaged, and the basal area and density of standing trees declined by more than 50 percent. Interestingly, the proportions of uprooted and snapped trees (approximately 70 to 30) closely approximated the damage produced by the 1938 hurricane and documented by Rowlands. A range of new tree and ground-surface structures was produced by the manipulation, including bent and broken understory trees and a heterogeneous array of forest floor microsites. Although more than two-thirds of all trees were uprooted, the majority of these came to rest in the crowns of other trees or on mounds. Consequently, the damaged trees lay at a wide range of angles with respect to the ground surface. Uprooted boles covered about 13 percent of the ground surface, and disturbed soil from the resulting complexes of pits and mounds covered about 8 percent.

The experimental area appeared to produce initial consequences that were strikingly similar to those from the 1938 hurricane. However, there are differences between our manipulation and a natural storm that may be important to consider as we follow the experiment through time. Hurricanes are often preceded or accompanied by heavy rains that, depending on timing and amount, may affect the response of the soil and vegetation to intense winds. It was not feasible to simulate this effect, although we were able to conduct the manipulation during the first week

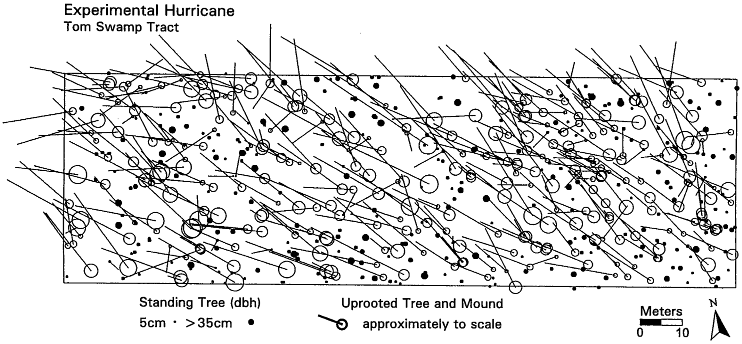

Figure 11.5. The experimental hurricane study area showing standing trees (solid circles; dbh, diameter at breast height), uprooted trees (open circles), and the length and orientation of downed trees. Mound sizes and downed tree lengths approximate their true size. Modified from Cooper-Ellis et al. 1999, with permission from the Ecological Society of America.

of a rainy October hurricane season. In addition, we did not replicate the effect that high winds have in stripping foliage and small branches from remaining trees and producing a wide range of damage to tree crowns. The manipulation, however, took place within two weeks of seasonal leaf-fall, and most of the surviving trees did sustain some damage to their branches as surrounding trees fell. Otherwise, the overall pattern of damage, including the percentage of damaged trees, the distribution of damage among size classes, and the orientation and distribution of boles and woody debris, matched the effects of the historical hurricane. Finally, the size of the resulting gap greatly exceeded the single-tree gaps of many simulations, although it was smaller than many damage patches created by hurricanes. Indeed, the sharp transition between the edge of the experimental area and the surrounding forest is more like the pattern produced by a tornado. Despite these differences, the large extent of the experimental area allowed us to measure most of the important attributes of a posthurricane environment.

Vegetation Response

We were interested in documenting the effect of the manipulation on trees and understory plants. The extent and type of damage were of immediate interest, as these clearly set the trajectory for long-term changes in forest structure (Figure 11.6). Understanding the variation in damage by species and size would also help predict the initial impacts of hurricanes in other areas with similar species composition. In addition, the initial and long-term rates of mortality among injured trees could have important consequences for ecosystem processes. Finally, the capacity of various plant species to respond opportunistically to altered conditions created by the disturbance helps to determine both the rate of stabilization of environmental conditions and the degree of change in composition of the postdisturbance community.

The majority of the largest trees in the predisturbance forests were red oaks up to 60 centimeters in diameter, whereas red maples were typically 5 to 10 centimeters in diameter. In general, the proportion of trees damaged increased with size up to 15 centimeters across and then decreased above 15 centimeters. Smaller trees tended to bend, larger trees uprooted, and trees that were previously standing but dead or decaying mostly snapped. Nearly 95 percent of the damaged red oak uprooted, and damage to red maple was more evenly distributed between uprooting, snapping, bending, and leaning (Figure 11.6). This variation in damage type by species suggests that differential survival of the different sizes and species of trees will be important in determining long-range compositional changes for the stand.

Despite the dramatic reorganization of forest structure caused by the manipulation, the vegetation exhibited a remarkable capacity for sur-

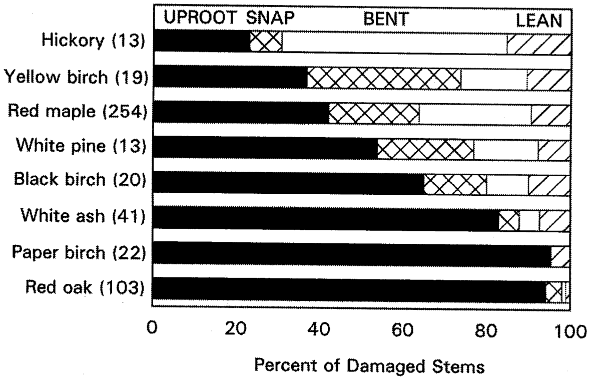

Figure 11.6. Distribution of damage types among major tree species in the experimental hurricane for all damaged stems greater than 5 centimeters in diameter at breast height. Numbers in parentheses indicate tree sample sizes. Modified from Cooper-Ellis et al. 1999, with permission from the Ecological Society of America.

vival and growth under the altered conditions. In fact, the capacity of injured hardwoods to survive for one to many years despite intense damage and then to generate sprouts from the roots, root crown, or trunk was a major factor in maintaining vegetation and canopy continuity through time. Although the manipulation displaced more than 80 percent of canopy trees from their vertical positions, nearly 90 percent of these survived the first growing season, and many leafed out again even in a prostrate position (Figure 11.7). Mortality occurred gradually but progressively; despite high survival rates the first season, after six years fewer than 20 percent of damaged trees survived. Persistence varied strongly by species, with approximately 30 percent of oaks and 70 percent of red maples releafing or sprouting after six years. Because oaks were generally larger, however, these differences have not resulted in major changes in the relative importance of species in the stand. In contrast to the New England forests of 1938, our study area contained only a handful of white pines, most of which were understory trees. These largely uprooted, and overall survival for pines was low.

Environmental conditions at the ground surface did not change much in areas other than the pits and mounds. This is because a dense, though low, canopy was maintained by the strong sprouting and releafing response of damaged trees, the growth of saplings already present in the understory, and the establishment of new seedlings. The density of sprouts and saplings increased from fewer than 6,000 per hectare before the manipulation to nearly 25,000 three years after the pulldown, and then decreased to 17,500 per hectare in 1999. These understory trees now compose slightly more than a third of the total woody basal area of the stand (Figure 11.8). Although nearly half of the saplings present af-

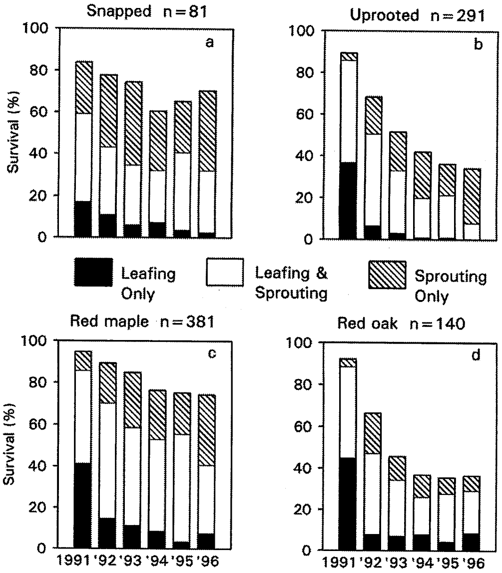

Figure 11.7. Survival (releafing and sprouting) of trees by damage type (a and b) and species (c and d) in the experimental hurricane area. Considerable variation in these responses underscores the potential for great variation in vegetation response to disturbance depending on the type and intensity of damage and the original forest composition. Modified from Cooper-Ellis et al. 1999, with permission from the Ecological Society of America.

ter six years became established after the manipulation, they represent a minor part of the stand basal area since they grow much more slowly than either the older saplings or new sprouts. If we assume that natural mortality will continue to thin these crowded understory stems, density will continue to drop rapidly. However, because many birch seedlings became established on tip-up mounds where they will have a height advantage and reduced competition, birch may increase in importance in the overstory.

With the majority of standing trees felled, the new forest canopy was initially characterized by multilevel, heterogeneous cover, with broad areas of thick foliage generating dense shade that alternated with occasional open areas where light penetrated to the forest floor. The understory vegetation responded strongly to these changes, especially increases in light. Saplings have increased from less than 10 percent to nearly 40 percent cover. Shrubs have also increased in cover and average height. Ferns present before the experiment spread to form dense patches in some areas. Meanwhile, the vegetation at the forest floor has remained relatively stable. Understory species richness increased for two years but decreased by year four. Prior land-use activity, primarily pasturing, had generated a seed bank of disturbance-related species that has persisted

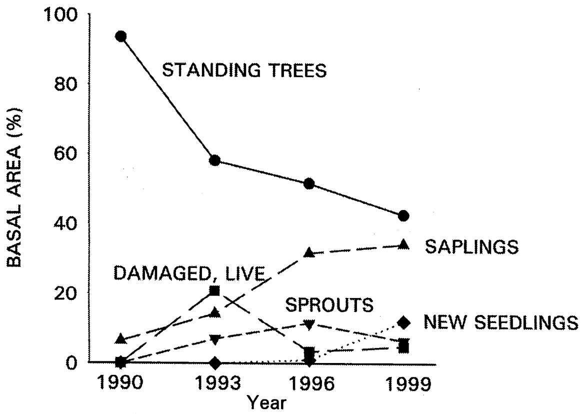

Figure 11.8. Through time, the relative contribution of survival versus different types of regrowth (damaged trees, saplings, sprouts, and seedlings) has varied in the experimental hurricane. Initial high levels of tree survival and rapid regrowth provided great control over environmental factors and ecosystem processes in the developing forest. Updated from Cooper-Ellis et al. 1999.

for more than a century. Thus, scattered colonists such as blackberry, raspberry, staghorn sumac, pin cherry, European honeysuckle, and fireweeds appeared in the pulldown, mostly in areas with soil disturbance. However, only the blackberries, raspberries, and some tussock-forming sedges have persisted. Consequently, compositional changes in the understory, like the overstory, have been minor.

To summarize, the hurricane manipulation initiated profound changes (Figure 11.9). The extent and types of damage paralleled the dramatic effects of the 1938 hurricane, but environmental conditions were stabilized by the persistence of damaged hardwoods and the rapid growth of sprouts and saplings. Forest structure, which was dramatically changed by the dislocation of standing trees, has become more complex and multilayered and continues to reorganize over time. However, the composition of the forest community has remained remarkably stable. Therefore, the imprint of the disturbance—as evidenced by the presence of uproot mounds and pits, bent and misshapen trees, and scattered weedy or early-successional species—will likely be evident well into the future, despite the fact that the dominant species will remain largely unchanged.

Heterogeneity in Environmental Resources: A Major Consequence of Wind Damage

The disturbance created a range of microsites that vary in important characteristics that affect ecosystem processes and the ability of

Figure 11.9. The edge of the experimental blowdown in 2002, nearly twelve years after the manipulation. The uproot mounds have eroded considerably, and the regrowing vegetation is tall and thick. Photograph by D. R. Foster.

plants to establish and grow (Figure 11.10). However, overall differences between the manipulation and the undisturbed forest understory were relatively minor as a consequence of the small extent of ground area directly affected by tree uprooting (about 8 percent), the releafing of damaged vegetation, and vigorous growth of new plants. Nonetheless, the different microsites—uproot mounds, pits, and areas of dense fern—constitute distinct environments from the intact forest understory in terms of light levels, substrate type, stability, and composition and thus contribute to the small-scale heterogeneity of the forest environment. They may provide contrasting opportunities for different species in the postdisturbance forest community.

Although light levels within 50 centimeters of the forest floor increased immediately in some places and remained elevated for at least three years, light was extremely variable among the different microsites. Soil moisture, organic matter content, and nitrification rates were rela-

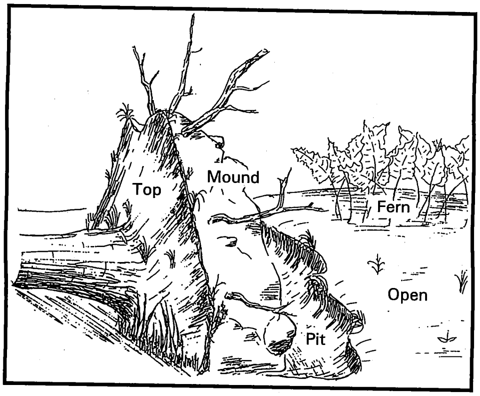

Figure 11.10. The range of microsites that develops after the uprooting of a large canopy tree. Resources such as light, nutrients, moisture, and competition among plants vary tremendously among these small-scale habitats. Modified from Carlton and Bazzaz 1998a, with permission from the Ecological Society of America.

tively similar between the disturbed and undisturbed forest, but also varied substantially among microsites. Similarly, although the soil in pits had lower temperatures and respiration rates than that on mounds or intact sites, the limited area of pits and mounds resulted in virtually no impact on ecosystem-wide rates of CO_2 flux from soils to the atmosphere.

Mounds and tops of tip-ups had contrasting patterns of resource availability, despite being very close to one another spatially (Figure 11.11). Mounds had high levels of light availability but much lower levels of soil resources, for instance, water and nitrogen. In contrast, tops received very low amounts of light, mainly because they were north-facing, and had high rates of nitrogen mineralization and nitrification. Pits generally had average resource levels (compared with open sites) but had much thicker litter layers than other sites because of the ongoing erosion of material. Contrasting patterns of resource availability indicated that resource congruency was lower in blowdown plots than in undisturbed forest, especially for light versus soil resources.

Because light, CO_2, and soil resources vary at different temporal scales after disturbance, plants are exposed to various combinations of resources over time. Differences in the ability among species to tolerate or to capitalize on these resources will influence their survival, growth rates, and future success. Fast-growing, colonizing species like paper birch thrive on the mineral soil seed bed, high light conditions, and reduced competition characteristic of the mounds; they thereby gain an early height advantage over seedlings established on the intact forest floor. Yellow birch, which is more shade tolerant and was present as a seedling in the understory before the experiment, occurred frequently

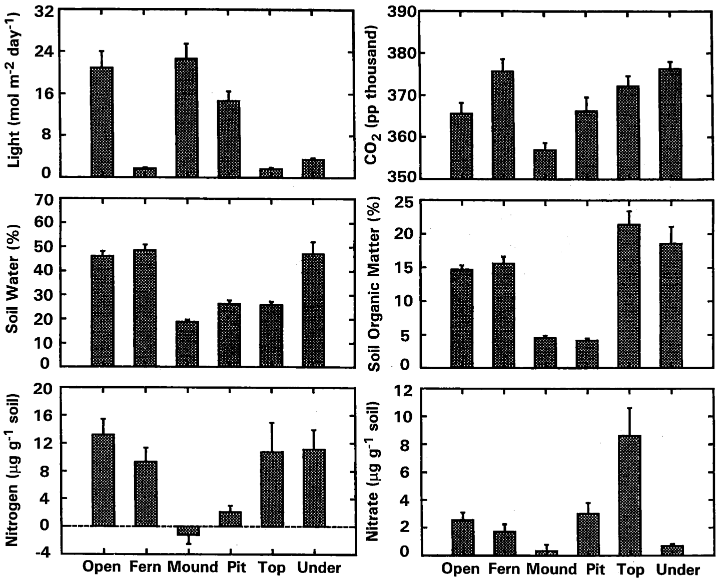

Figure 11.11. Resource availability in hurricane blowdown microsites. Means for each microsite were pooled across experimental plots. The availability of plant resources varies tremendously across the different microsites produced by the windthrow of trees in the experimental hurricane. Modified from Carlton and Bazzaz 1998b, with permission from the Ecological Society of America.

on the mound "top" (that is, the side of the root plate closest to the tree). These seedlings become elevated as the tree falls and creates a mound, and respond to the increased light and leaning orientation with a vertical (perpendicular) growth spurt. The relative hospitality of the different microsites varies considerably depending on overall soil and climatic conditions. Thus, in a particularly dry climate mounds may be less favorable seed beds than we observed. Conversely, in areas where accumulation of litter and water and slumping of mound materials into pits are not as extensive as in our study, pits may provide favorable resource conditions and establishment opportunities.

Soils and Biogeochemistry

The massive rearrangement of forest structure, the large number of broken and damaged tree boles, and the striking appearance of the pit-and-mound topography strongly suggested that the blowdown would greatly alter physical soil conditions and biogeochemical cycling. On the basis of the extent of forest damage and the results of studies from the Hubbard Brook watershed and the Puerto Rican landscape after Hur-

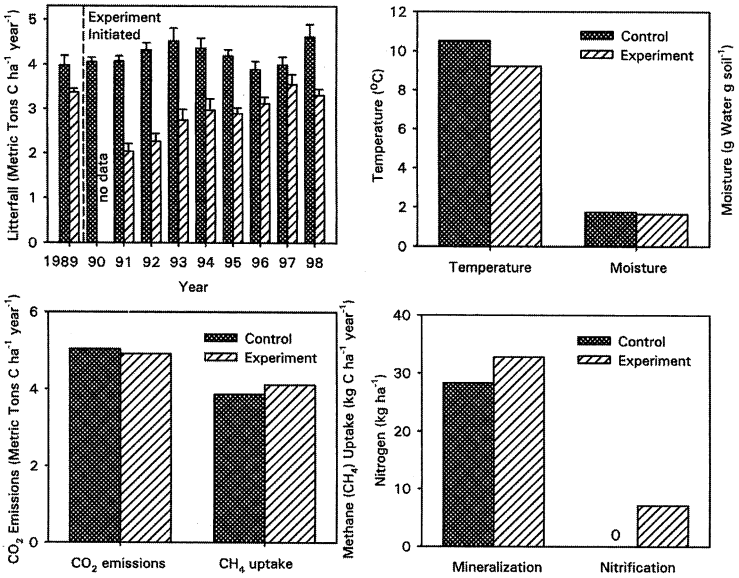

Figure 11.12. Summary of the major ecosystem and biogeochemical changes after the experimental hurricane blowdown. As a consequence of releafing of the windthrown canopy and rapid recovery of leaf area (litterfall), there were only slight changes in microenvironment (temperature and moisture) and nitrogen and carbon dynamics. Modified from Foster, Aber et al. 1997; unpublished litterfall data from A. Magill.

ricane Hugo, we anticipated that the experimental manipulation might be disruptive to the soil environment and reduce biotic control of biogeochemical processes. Thus, we looked closely at the soil environment, including soil temperatures and moisture content, changes in the rate of nitrogen cycling and available nitrogen content, and altered fluxes of gases between soils and the atmosphere.

Remarkably, few ecosystem-level changes in soil conditions or biogeochemical processes were detected (Figure 11.12). Average annual soil temperature in the upper 2.5 centimeters of soil was unchanged, probably because of shading of the soil surface by the leafing and resprouting of downed trees during the summer after the blowdown. Survival of damaged trees and the rapid recovery of leaf area across the experimental blowdown maintained evapotranspiration, which kept soil moisture at predisturbance levels. The stabilization of physical conditions at the soil surface by living vegetation mitigated effects of the disturbance on soil nutrient processes. Soil respiration, a function of both root respiration and organic matter decomposition, was unchanged. Active root systems in damaged trees ensured the continued contribution of root respiration to total soil respiration rates. In addition, the manipulation did not affect organic matter decomposition, which is particularly sensitive to temperature and moisture availability in temperate forests.

We did record changes in nitrogen processing, but these were local in scale and minor in terms of the overall nitrogen economy of the site. Net nitrogen mineralization (conversion of organic nitrogen to ammonium and nitrate) was unchanged in the summer immediately following the manipulation. We detected a large relative increase in the net conversion of soil ammonium to nitrate (nitrification); however, given the low absolute levels of nitrification in forests in central Massachusetts, such changes were extremely modest. Soil nitrate generally remained low, whereas available soil ammonium increased to levels nearly double those in the control site. This change was probably due to decreased production of leaf litter, which declined by about 60 percent in the first two years after the experiment and recovered to nearly 75 percent by the fourth year. Net release of nitrous oxide by soils to the atmosphere was lower in the experimental area than in the control, but again, overall flux rates were low compared with the range of levels measured in other temperate and tropical forests and after other disturbances.

Had nitrogen cycling been altered to a large degree, soil fluxes of nitrous oxide to the atmosphere would have increased dramatically. Another strong indicator that the physical and biogeochemical environment was not severely altered by the experiment was the overall stability in methane levels. Methane uptake by soil is quite responsive to the availability of ammonium and to changes in soil moisture, which controls methane diffusion through soil pore spaces. There was no detected reduction in methane consumption.

Consequently, despite the physical damage to the forest and the soil by the experimental hurricane, including the massive vertical redistribution of biomass, a number of forest responses mitigated changes in the soil environment. In turn, as the survival and releafing of damaged trees and rapid growth of sprouts and understory plants maintained the soil microenvironment, they also led to a rapid recovery of leaf area and root biomass and presumably active root uptake. These biotic responses provided strong biological control over biogeochemical processes, resulting in relatively minor changes in ecosystem processes. In the face of apparent forest destruction, many fundamental processes were maintained.

Interpretation and Insights from the Experimental Hurricane

In important ways, the results of the blowdown experiment have led us to modify our interpretations of the response of temperate forest ecosystems to intense wind events and to reevaluate the role of tropical storms in structuring our forest landscape. The surprising vegetation and ecosystem responses also required us to reexamine some earlier interpretations of the impact of historical events such as the 1938 hurricane. Collectively, these results enable us to offer some insight into the consequences of management efforts after natural disturbances.

Three aspects of the vegetation response to the experiment stand out: the high rate of initial survival in damaged (including broken and uprooted) trees; the importance of vegetative reproduction during the initial period of forest recovery; and the minor compositional changes that have occurred. Survival by damaged trees, sprouting along the trunk, stump, and roots, and growth of advanced regeneration produced a large leaf area and maintained fairly constant soil and microenvironments. In turn, this continuity in microenvironmental conditions and the relatively small amount of soil disturbance minimized the importance of fast-growing early-successional trees in the revegetation process. The resulting forest, therefore, includes a wide range of growth forms and age cohorts: relatively undamaged survivors from the mid-canopy and understory of the original stand; a wide array of bent, misshapen, and reiterating stems; and sprouts and seedlings concentrated on the ground, tip-up mounds, and pit margins (see Figure 11.8).

This response stands in striking contrast to the conditions that developed after the 1938 hurricane, in which even-aged stands of paper birch and pin cherry were common. The differences may be largely attributed to two historical conditions arising from human land use: the predominance of young stands of old-field white pine in New England in 1938 and the regionwide salvage logging that followed the hurricane (Figure 11.13). Given the history of farm abandonment and ongoing forest cutting into the twentieth century, forests in 1938 were generally young and even-aged. Across this landscape, the forests that were most susceptible to wind damage were the extensive stands of white pine that had established on old fields. More than half of the volume of timber damaged by the 1938 storm was pine. White pine forests differ in important ways from the mixed hardwood stands that predominate naturally in this region and that were studied in our experimental manipulation. Unlike the hardwoods, white pines die rapidly after uprooting or breakage, and they lack the ability to sprout or releaf. In addition, in fairly dense stands of young pines, advanced regeneration is limited and generally doesn't include the shade-intolerant pine. Consequently, following the intensive damage experienced by pine stands in 1938, continuity of forest cover was interrupted, as the pine overstory died abruptly and was replaced by a new cohort of seedlings and sprouts, dominated by fast-growing and early- and mid-successional hardwoods. Because forest conditions in 1938 resulted from two centuries of prior land use, the hurricane of 1938 elicited a very different response from what we observed in our experiment.

Logging after the 1938 hurricane, which was the largest timber sal-

Figure 11.13. Salvage logging after the 1938 hurricane. Photograph from the Harvard Forest Archives.

vage operation in U.S. history, exacerbated the tendency toward dramatic environmental change and an increase in early-successional species. Logging involved cutting and removal of uprooted, damaged, and even many sound trees; burning of resulting slash; and extensive scarification of forest soils. These effects further reduced the density of the remaining canopies and the survival of damaged trees. Logging also greatly increased light penetration to the forest floor and altered the soil environment and seed-bed conditions. Under these open and highly disturbed conditions, the previous vegetation was largely replaced by early-successional and sprouting hardwoods. A legacy of this history may be seen in the even-aged stands of hardwoods that dominate the New England landscape today. In these forests, species such as paper birch and black birch are widely distributed and are not restricted to the mounds and pits as they are in the experimental blowdown. Widespread soil scarification, burning of logging slash and forest litter layers, and open conditions in 1938 allowed these small, light-seeded species to achieve an unusual prominence and distribution.

We have strong evidence that these striking vegetation changes in 1938 were accompanied by soil and biogeochemical changes that differed from the results of the experiment. As shown by Jim Patric, for nearly five years after the 1938 hurricane the Connecticut River experienced a major increase in flow in comparison with rivers that received little damage to their watersheds. This effect is undoubtedly a consequence of the regional decrease in evapotranspiration due to the massive reduction in leaf area, resulting in an increase in soil moisture and, presumably, major alterations of biogeochemical processes. However, although many interpreted this effect as a natural response of the forest landscape to a natural disturbance, an alternative explanation is prompted from awareness of regional history, namely, the history of land use that led to the dominance by white pine and the extensive salvage logging. Indeed, it is quite likely that the response of increased river flow was an indirect consequence of human activity. The very young age of the 1938 forest, the dominance by white pine that was susceptible to blowdown and unable to sprout, the removal of leaf area, and extensive soil disruption by logging and burning all greatly reduced biotic control by the vegetation over soil and biogeochemical processes.

These results broaden the basis for decision making in forest management with regards to storm damage. The minimal change that we observed in soil, microenvironment, and important biogeochemical processes after the experiment suggests that natural hurricane disturbance is actually not highly disruptive to ecosystem integrity. In contrast, postdisturbance salvage logging may generate stronger ecosystem-level responses than the disturbance itself. If maintenance of biotic control over hydrology, soil environment, and nutrient fluxes is a priority of management, and if rapid forest recovery is sought, then leaving the site intact may be a preferred approach. This may be the approach taken, for example, in a municipal watershed where water quality is a primary objective or in natural areas or wildlife management areas in which natural conditions and structures such as standing and dead trees are objectives. Such an approach will also lead to the natural development of a diversified forest structure in which a range of classes and growth forms, including bent, misshapen, and broken trees, occurs along with quantities of downed wood.

In contrast, the desires to recoup value from windthrown timber and to influence the future composition and structure of the forest are major motivations for salvage logging. Salvage allows the elimination of leaning, bent, and broken trees and enables the promotion of low stump sprouts as opposed to stem sprouts. However, logging after extensive windstorm also increases soil disturbance and open conditions that will favor the establishment of early-successional species.

On one subject regarding salvage logging, namely, fire hazard, there are strong opinions but few data or little long-term study. Windstorms are often implicated as one of the catalysts of major forest fires in the New England landscape; indeed, a major motivation driving salvage, including the effort in 1938, is a desire to reduce fuel loading. However, there are essentially no studies of the changes in fuel loading after windstorms from New England forests, nor is there good historical research that links windstorm events and fire. Most of the support for salvage operations is actually predicated on the intuitive notion that the downed woody debris associated with windstorms necessarily enhances long-term fire hazard. Although blowdowns in conifer stands may produce a short-lived increase in hazard, data from the hurricane experiment suggest that fine fuels, which are the main fire concern, are unevenly distributed and highly transient because of the rapid decay of fine material and extended period over which the damaged trees die. As a consequence, overall fire hazard was only slightly increased in the experimental study and for a relatively short time. The decomposition of fine fuels and the rapid growth of new sprouts and understory plants quickly reduced the fire hazard.

Another approach to forest planning in a landscape subjected to infrequent tropical storms is to incorporate an understanding of hurricane disturbance regimes and forest response to winds into the harvesting regime in order to minimize damage and to increase long-term yields. Such considerations stimulated considerable research and discussion in the aftermath of the extreme losses suffered in 1938 and led to many studies, including the research by D. M. Smith. However, this burst of interest resulted in few significant changes in silvicultural practices across the region. Quite recently, however, the Metropolitan District Commission, the Massachusetts state agency responsible for metropolitan Boston's water supply, has taken this approach to heart in its management of the watershed of the Quabbin Reservoir, a 32,000-hectare area of forest and water. By cutting to decrease the average age of forests and to favor a diverse forest of wind-firm species, forest managers are seeking to minimize damage from the next storm, pathogen, or other disturbance. Although few data, including our own studies on the hurricane or hemlock woolly adelgid, suggest that these disturbances have negative effects on water quality, for areas in which logging is a management objective it should be quite feasible to direct silvicultural activities so as to mitigate other disturbances.

Many questions remain about the impacts of hurricanes on New England forests. In particular, we lack the ability to anticipate the effects of posthurricane management strategies on ecosystem function and vegetation development. Our experiment simulated the effects of intensive wind in the most common forest type on the central New England landscape today, and we found that at the scale of approximately 1 hectare, the forest has a remarkable ability to maintain internal functioning and resist major compositional changes. However, matched experimental treatments such as blowdown followed by fire, blowdown followed by salvage, and standard silvicultural treatments on comparable sites in hardwood and conifer forests could help to answer many remaining questions about the relationship between vegetation and environment, controls on regeneration after various types of disturbance, and the challenges of management in the face of the certainty of future hurricanes.