# Forest Response to Natural Disturbance Versus Human-Induced Stresses

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Retrospective studies, which employ historical, archaeological, paleoecological, and dendrochronological techniques to unravel past changes in landscapes and the environment, provide one of the few opportunities for comparing forest disturbance and vegetation dynamics across major cultural and temporal boundaries. By extending our perspective from decades to millennia, historical forest reconstructions permit us to assess the effects of infrequent events, long-term trends, and gradual environmental change. They also enable us to document the successional or developmental changes in forest ecosystems that are often comprised of tree species that can live many centuries. Therefore, these assessments provide important insights into fundamental ecological processes and the provenance of modern conditions and can also serve as the basis for informed management decisions.

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*Saplings grow between moss-covered logs of old-growth white pine and hemlock downed in the hurricane of 1938*

One important source of long-term information on forest history and dynamics in response to natural environmental change and disturbance are old-growth forests and other sites on which human impact has been minimal. Recent surveys have discovered surprisingly large numbers of old-growth stands—even in the densely populated eastern U.S.—and these forests have become an important focus of reconstructive studies on both basic and applied issues. The presence of old trees with lengthy tree-ring records of growth, and undisturbed sediments and soils that contain stratigraphic records of pollen, charcoal, and other semi-fossilized plant and animal materials, enable us to develop long-term site histories of disturbance and forest change.

Reconstructive studies of old-growth and other sites have revealed the remarkable resiliency of the temperate forests in the Northeast to a wide range of physical disturbances, including windthrow, fire, ice damage, and pathogens. However, a question of great interest to ecologists and with major implications for policymakers is whether these forests will be equally resilient in the face of chronic chemical and climatic stress brought on by changes in the global earth-atmosphere system. To address this question, the Harvard Forest initiated its Long Term Ecological Research (LTER) program in 1988 to analyze the effects on ecosystem structure and function of historically important natural disturbances in comparison with those of recent and projected chemical and climatic stresses.

Three disturbance and stress processes are being investigated in considerable detail: hurricane blowdowns, the chronic additions of nitrogen that occur presently as a consequence of acid rain and the burning of fossil fuels, and the warming of the soil environment that will occur as global temperatures rise with predicted climate change. To develop meaningful comparative results, we designed experimental treatments that closely simulate the major impacts of the relevant disturbances and stresses, and we chose sites in typical second-growth forests on widespread upland soils with similar forest and environmental conditions.

### The Experimental Blowdown

Hurricane blowdowns cause catastrophic damage in New England forests every fifty to one hundred and fifty years. The LTER studies undertook to evaluate the effects of a storm similar to that of the 1938 hurricane on an eighty-year-old hardwood forest. To simulate a hurricane on an experimental plot, researchers used a power-driven winch to pull over in one direction, as would occur in a natural windstorm, a subset of trees comparable to those blown down in 1938.

The experimental blowdown had an immediate and dramatic impact on forest structure: the basal area (cross-sectional area of wood) and density of trees declined more than 70 percent; the average distance between canopy trees increased from 3.3 to 7.6 meters, and the maximum distance increased from 7.8 to 20.9 meters; and more than 260 new mounds and pits resulting from the uprooting of trees covered 8 percent of the soil surface.

Nonetheless, as a result of releafing and sprouting, more than 75 percent of uprooted and broken trees survived the first year and more than 40 percent continued growing after four years. Survival varied considerably according to species and extent of damage: 60 percent of yellow and black birch *(Betula alleghaniensis* and *B. lenta)* survived, as did approximately 50 percent of white pine *(Pinus strobus)* and red maple *(Acer rubrum)*, and approximately 30 percent of red oak *(Quercus rubra)*, white birch *(B. papyrifera)*, and white ash *(Fraxinus americana)*. The standing and relatively undamaged trees remaining after the blowdown showed the same low mortality rate (4 percent) as the control site for the first four years.

The extent of tree regeneration in the "blowdown" understory was high. Saplings and

*A skidder's winch and cable were used at the Harvard Forest to pull down trees across a two-acre area to simulate the effects of a hurricane in 1990.*

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*Researchers attach markers to a root mound upended in a simulated hurricane, 1992 The many microsites created by the uprooting of trees provide important habitat and microenvironmental diversity in the forest*

sprouts increased from fewer than 6,000 per hectare before the blowdown to nearly 8,000 per hectare one year later and to over 25,000 per hectare after three years, with only slight compositional change (birches increased, black cherry *[Prunus serotina]* and white pine declined). Increased light levels one to three meters above the ground resulted in greater growth in diameter and height of existing saplings and new sprouts on the blowdown site than on the control site.

Net ecosystem productivity declined following the experimental blowdown: in the second year, litterfall in the blowdown was only 59 percent of that found in the control site; by the fourth year, however, that number had increased to 71 percent. In general, the blowdown site underwent major reorganization of forest structure and a subtle compositional change along with rapid redevelopment of canopy cover. In contrast, and contrary to general expectation, the soil environment showed no major changes. Temperature and moisture remained the same, as did the nitrogen cycling pattern and net exchanges of important greenhouse gases between soils and the atmosphere.

The hurricane blowdown caused a marked change in the appearance of the forest, but the long-term impact on important processes was far less dramatic: it was limited to a vertical reorganization of the canopy and foliage from the top of the canopy to one to five meters above the ground. The combination of high survival rates and prolific sprouting by broken and uprooted trees, coupled with rapid growth by understory plants, resulted in rapid recovery of total leaf area and little change in the soil microenvironment, including temperature and moisture: as damaged trees died off, the growth of saplings and understory plants has provided additional leaf area. By ensuring the continuity of shade on the forest floor, floristic composition has changed less than might be expected based on successional theory and on previous studies of the 1938 storm.

From an ecosystem perspective, which seeks to examine the structure and function of forests, the blowdown experiment is highly instructive. Despite massive structural alteration of the forest, net energy and nutrient processes remained largely intact. Productivity, as measured by litterfall, declined immediately following the disturbance, but recovered rapidly within four years. The similarity of nitrogen cycling patterns, soil respiration rates, and gaseous effluxes in the control and blowdown plots indicates that changes in nutrient availability were minimal. Importantly, the maintenance of efficient cycling of nutrients suggests that the forest was able to retain these constituents despite the major physical change. Continuous vegetation production and cover provided a high degree of control by the vegetation over critical microclimatic conditions and ecosystem processes.

### The Experimental Nitrogen Increases

In industrialized parts of North America and Europe, the atmospheric deposition of nitrogen has vastly increased since the 1940s as a consequence of fossil fuel combustion. In the high elevation forests of New York and New England and throughout central Europe, nitrogen deposition has been implicated in tree mortality and forest dieback. This conclusion is somewhat paradoxical because nitrogen is limiting in most terrestrial ecosystems and an increase might be expected to simply increase growth rates. How-

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*After the experimental blowdown, gridded frames were used to map fine-scale microtopography and to release and track tree seed as part of a study of seed dispersal. The root mound stands nearly two meters high.*

ever, as nitrogen availability through acid rain exceeds demand, the ecosystem may become "saturated," basic processes may change in deleterious ways, and the excess nitrogen may leak through soils into streams and lakes. There is strong concern that this increased nitrogen will damage water quality and alter critical soil processes, including nutrient cycling and trace gas fluxes, throughout the temperate zone.

The chronic nitrogen, or nitrogen saturation, experiment was designed to examine the effects of continuous, low-level additions of nitrogen caused by acid deposition or forest ecosystem structure and function. Two stands were selected for study: a second-growth hardwood stand and a mature red pine *(Pinus resinosa)* stand. Importantly, the eighteenth- and nineteenth-century land-use history of the hardwood forest involved repeated cutting, which probably depleted nutrients on the site, whereas the red pine stand had been planted in the 1920s on an old agricultural field that had been plowed and fertilized, thereby maintaining or enhancing its natural abundance of nitrogen.

Three 30-by-30-meter plots—control (no nitrogen), low nitrogen-addition, and high nitrogen-addition—were established in each stand; nitrogen was applied in the form of ammonium nitrate in six equal monthly doses from May to October beginning in 1988. The high nitrogen-addition plots receive doses similar to levels occurring in central European countries today.

In marked contrast to the blowdown experiment, the chronic nitrogen experiment has so far produced only minimal structural changes. Tree mortality has not been affected, and species composition and canopy structure remain similar to those in control plots. However, dramatic changes in ecosystem function have occurred that may foreshadow future changes in structure.

For example, whereas the control plots retain essentially all of their nitrogen and lose none through soil leaching, the high-nitrogen pine plot has shown accelerated nitrate loss, indicative of nitrogen saturation, since year three. In the sixth year of treatment, the low-nitrogen pine plot also began showing nitrate losses. By contrast, the more nitrogen-limited hardwood stand has shown nearly total retention of nitrogen; detectable nitrate losses were not measured until year six, and then only in the high-nitrogen plot. Changes in internal carbon- and nitrogen-cycling rates and in net exchanges of methane between soils and the atmosphere have also been substantial. This result is important as it demonstrates that nitrogen excess and saturation triggers very fundamental changes in a range of ecosystem processes.

Ecophysiological theory predicts that higher concentrations of a limiting nutrient like nitrogen will lead, in turn, to higher rates of net photosynthesis and tree growth through a fertilizer effect. Indeed, more tree growth has occurred in the hardwood stand (originally nitrogen-limited), with a 45-percent increase in wood production. However, in the pine stand—where high losses from leaching suggested that nitrogen saturation occurred very rapidly—wood production over six years has been 28 percent lower than that of the control plot. Combined with even more dramatic growth declines and mortality increases in conifer stands located in high nitrogen-deposition regions of the world, these results suggest a general decrease in the vigor and wood production of conifer stands, and perhaps even the onset of serious forest decline, in response to nitrogen saturation.

## The Soil-Warming Experiment

The rate of increases in global temperature that are currently projected far exceed the changes that occur naturally through glacial-interglacial cycles. One consequence of global warming may be changes in the rates of critical temperature-dependent ecosystem processes, which in turn control forest growth and health. Important soil processes that may be expected to change with increasing global temperatures include decomposition, methane production, nitrogen mineralization and nitrification, and phosphorus availability. Since many of these changes may result in the release of greenhouse gases, soil warming may itself exacerbate soil warming.

The soil-warming experiment at the Harvard Forest was designed to assess the response of a second-growth hardwood forest to elevated soil temperatures. We paid particular attention to the effects of warming on soil processes that may alter ecosystem function, atmospheric chemistry, and global climate. Eighteen 6-by-6-meter plots were established in April 1991; each was randomly assigned to one of three treatments: heated plots, in which the average soil temperature was raised 5 degrees Centigrade above ambient using buried heating cables; disturbance control plots, in which buried cables were installed but received no electrical power; and undisturbed control plots.

Initial results from the first growing season of the study indicated that heating increased emissions of carbon dioxide by 40 percent. Nitrogen cycling was also affected dramatically, with a doubling of mineralization rates in the upper soil layers. During the second and third growing seasons, warming had a much less dramatic effect on carbon dioxide emissions but a sustained dramatic effect was seen in nitrogen mineralization, which again doubled in rate.

The following scenario provides one interpretation of why the rate of carbon dioxide emissions in the heated plots relative to that of control plots decreased between the first and second years relative to disturbance control plots, whereas the rate of nitrogen mineralization continued to increase. There are two major pools of organic matter in soils, a "fast" pool and a "slow" pool. The fast pool contains material with a high ratio of carbon to nitrogen (for instance, recently fallen litter), whose decay results in relatively large losses of carbon dioxide but a small net loss of nitrogen. In contrast, the slow pool contains material with a low ratio of carbon to nitrogen (such as partially decomposed and relatively stable humus), whose decay results in a smaller loss of carbon dioxide and a larger net loss of nitrogen.

Because elevated soil temperature increases the rate of decay in the slow pool, increased amounts of both carbon and nitrogen are released. The nitrogen then becomes available for uptake by plants. However, the carbon-to-nitrogen ratio of living plant material is substantially higher than that of organic matter in the soil of the slow pool, and because of that, warming may lead to increased carbon storage in the ecosystem without increased nitrogen storage.

The study highlights the importance of long-term experiments while underscoring the potential for complex changes resulting from global climate change. Although the immediate result of soil warming is carbon release—and

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*One of the eighteen 6-by-6-meter plots used in the soil-warming experiment at the Harvard Forest Heating coils placed below the soil surface raised the average temperature by five degrees Centigrade and caused subtle changes in the environment.*

feedback on global change—this effect is transient. Over the longer term, the net release of nitrogen might be a much more important effect and might signal fundmental though subtle shifts in ecosystem processes.

**Comparison Between the Effects of Natural Disturbances and Those of Novel Stresses**

Which of these changes—"natural" disturbance or climatic and chemical stress—is actually most disruptive to the integrity of the community and most likely to lead to long-term changes in ecosystem function? Comparison of results from the three experiments led to the surprising conclusion that structural integrity—that is, the actual appearance of a forest—is not a good indicator of forest ecosystem function. Whereas the blowdown site appeared severely disturbed, fundamental internal processes were not altered significantly, and the stand is on a path to recovery of structure and function in keeping with the cyclic pattern of disturbance and regeneration in this forest type.

By contrast, the nitrogen-addition and soil-warming plots are visually intact and apparently healthy, yet the subtler measures of ecosystem function suggest serious imbalances with possible future implications for community structure, internal ecosystem processes, and exchanges with the global atmosphere.

In the nitrogen-addition plots, nitrogen losses into the deeper soil are being induced and major changes in the amounts of trace gases (carbon dioxide, methane, nitrous oxide) released from the soil to the atmosphere have occurred. In the soil-warming plots, carbon dioxide exchanges have become negative, nitrogen cycling has increased dramatically, and nitrogen losses (as nitrate) are increasing. In time, alterations in chemical or physical environments caused by these novel stresses will create changes in nitrogen concentrations and in the rates of carbon and nitrogen cycling, which in turn will alter ecosystem productivity.

We cannot predict what the ultimate trajectory of these changes will be because there is no historical analog for these experiments and none of our present-day species evolved in an environment that included these stresses. It is reasonable to believe, however, that in the long run system function will continue to be disrupted more by these novel disturbances than by natural disturbances. The plant-response mechanisms seen in the hurricane experiment, which have presumably evolved as a consequence of natural selection for recovery from natural, physical disturbance, may not exist for situations where large quantities of nitrogen are added to the soil because of human activity, or soil becomes warmer very rapidly because of climate change.

Several conclusions emerge from studies of natural ecosystems and from our experimental study of "natural" physical disturbance and novel climatic and chemical stresses: (1) all ecosystems are dynamic as a consequence of natural disturbance, natural environmental change, and human impacts; (2) as a consequence of natural changes there are no static baseline conditions for assessing current ecosystems or for establishng correct goals for environmental management; (3) ecosystems are incredibly resilient, but the rate and novel character of modern human disturbances raises the question of whether they exceed this threshold of resiliency; and (4) a comparison of hurricane disturbance, nitrogen deposition, and global change (soil warming) suggests that physical appearance is a poor indicator of ecosystem integrity and that major and deleterious changes in ecosystem function may occur as a consequence of these novel stresses.

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This research is reported in full in "Forest Response to Disturbance and Anthropogenic Stress," published in BioScience (1997) 47(7) 437–445. This summary also draws on "Ecological and conservation insights from reconstructive studies of temperate old-growth forests" by D. R. Foster, D. A Orwig, and J S. McLachlan, published in *TREE Trends in Ecology and Evolution* (1996) 11(10): 419–424.