Comparisons between Physical Disturbances and Novel Stresses

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The three experimental treatments—hurricane pulldown, chronic nitrogen addition, and soil warming—simulate and enable us to begin to contrast the effects of important processes that have exerted and will continue to exert significant impacts on the forests of New England. Because we seek to understand long-term forest dynamics and work closely with land-management, conservation, and environmental organizations that develop forest and environmental policies, we are keenly interested in evaluating the long-term effects of these disturbances and stresses on forest ecosystem structure and function.

The results of our experiments yield surprises and a paradox. The different treatments generate strikingly different physical effects, ranging from apparent catastrophic disturbance in a jumble of uprooted trees to seemingly healthy ecosystems subjected to altered nitrogen and temperature regimes. And yet the long-term functional differences among forests subjected to these different treatments run in direct opposition to these first appearances. Functionally, nitrogen deposition and soil warming move forest ecosystem function in novel directions that contrast strongly with the intact forest in adjacent controls or the physically disturbed forest in the hurricane experiment. In contrast to the long-term changes initiated from chronic additions of nitrogen, recovery of key forest processes after the hurricane simulation was remarkably rapid. The unseen changes generated by nitrogen deposition and soil warming have important ramifications on local, regional, and global scales for our New England forest; however, the hurricane is very much "business as usual."

Despite the dramatic appearance of the hurricane blowdown, the major ecological effect was a vertical reorganization of the canopy and foliage from more than 20 meters in height to 1 to 5 meters above the ground surface. The combination of high survival and sprouting rates of damaged trees and rapid understory plant growth resulted in little change in leaf area and soil microenvironment. Most important for a
range of ecosystem processes, soil temperature and moisture did not change detectably, as the prolific growth of plants shaded the ground and apparently maintained active uptake of moisture and nutrients. Diverse morphological responses of the surviving trees (for example, epicormic branching and stem, basal, and root sprouts) resulted in rapid redevelopment of leaf area and continuity in composition and foliage cover. As damaged trees have died off gradually, the growth of saplings and understory plants has provided additional leaf area. Because of the high rates of survival and vegetative reproduction, floristic composition has changed less than might be expected based on successional theory and on previous studies of the 1938 storm. Specifically, instead of a rapid influx of early-successional and weedy species, the site continues to be dominated by species characteristic of mature forests.

From an ecosystem perspective, 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 after the disturbance but recovered to 71 percent of predisturbance rates within four years. The similarity of nitrogen cycling, soil respiration rates, and nitrous oxide effluxes in the control and blowdown plots indicates that changes in nutrient availability were minimal. Continuous plant production and cover provided a high degree of biotic control over critical microclimatic factors and important ecosystem processes.

In contrast to damage in the blowdown experiment, the chronic nitrogen and soil-warming experiments simulate novel environmental stresses to which no visible, large-scale, integrated community responses occur. Tree growth and litterfall, for example, have changed slowly; vegetation composition and structure have not been altered. However, despite the absence of obvious community responses and every visible indication of ongoing health of the forest, measurable changes in ecosystem function are occurring (Table 14.1). In the chronic nitrogen addition plots, nitrate leaching is being induced, major changes in trace gas balances have occurred, and forest productivity has

<table>
<thead>
<tr>
<th>Ecosystem Process</th>
<th>Blowdown</th>
<th>Chronic Nitrogen Addition</th>
<th>Soil Warming</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mineralization</td>
<td>+15.9 (1)</td>
<td>+1.38 (6)</td>
<td>+50 (2)</td>
</tr>
<tr>
<td>Methane uptake</td>
<td>-2.4 (1)</td>
<td>-3.6 (2, 3, 6)</td>
<td>+20 (2)</td>
</tr>
<tr>
<td>Soil respiration</td>
<td>+6.2 (1)</td>
<td>0</td>
<td>+76 (1)</td>
</tr>
<tr>
<td>Nitrate leaching</td>
<td>—</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>


Note: The chronic nitrogen results compare the hardwood control plot with high-nitrogen plots. Numbers in parentheses refer to the year posttreatment for which data are shown.
declined. In the soil-warming plots, soil CO$_2$ balances have become negative, nitrogen cycling has increased dramatically, and nitrogen losses (as nitrate) are increasing. In time, altered chemical or physical environments caused by these novel stresses create altered nitrogen concentrations and altered rates of carbon and nitrogen cycling, which in turn alter ecosystem productivity. Although we cannot predict what future course these changes will follow because there is no historical analogue for these experiments, we expect that ecosystem function will be disrupted more in the long run by these novel disturbances than by physical disturbances because none of the major species present has evolved in an environment that contains these stresses. The type of plant response mechanisms seen in the hurricane experiment apparently do not exist for the stresses induced by the chronic nitrogen or soil-warming experiments.

Which of these treatments, physical 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? Whereas the blowdown site appears severely disturbed, internal processes have not been altered significantly, and the stand is on a path to recovery of structure and function in keeping with the cyclic pattern of disturbance and development of this forest type. By contrast, the chronic nitrogen and soil-warming plots are visually intact and apparently healthy (with the exception of the decline in the pine stands receiving high nitrogen), 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 environment.

**Reinterpreting the Role of the 1938 Hurricane**

The understanding of temperate forest response to tropical storms is strongly influenced by studies of the 1938 hurricane. However, a comparison of our hurricane manipulation with the 1938 hurricane illustrates important differences and highlights critical issues that argue for a reevaluation of some interpretations based on the 1938 event.

The 1938 hurricane produced dramatic changes in forest composition that involved major increases in early-successional species, in striking contrast to the blowdown experiment. The 1938 hurricane also generated major changes in regional hydrology (see Figure 11.3). For a five-year period after the hurricane, stream flow increased greatly from the damaged watersheds, such as the Connecticut and Merrimack Rivers, as compared with the undamaged Androscoggin River, a result that has been interpreted historically as a natural consequence of hurricane-induced reduction in evapotranspiration. The lack of major compositional change, the relatively unimportant role of successional species, and the
absence of a change in soil moisture in our experimental hurricane plot encouraged us to reanalyze the information and interpretation of the effect of the 1938 hurricane on the New England landscape.

The 1938 storm severely damaged a landscape in which white pine, a species that is highly susceptible to windthrow, covered extensive areas that had been abandoned from agriculture in the previous century (see Chapter 4). The storm was followed by the single largest timber-salvage operation in U.S. history, as more than 4.5 million workdays were expended in harvesting more than 1.5 billion board feet of timber—approximately 40 percent of the damaged timber across the New England states (see Figure 11.13). Salvage activity was associated with road development, soil scarification, and burning of residual slash. Loggers commonly cut broken, leaning, uprooted, and even undamaged stems. Consequently, given the novel forest composition of the region and the geographical extent of the salvage effort, the 1938 hurricane may be interpreted more accurately as a regional logging operation of a cultural landscape than as a natural disturbance. Logging-associated tree mortality, removal of leaf area and biomass, and disruption to the forest floor resulted in substantial modification of the understory and soil environment and prevented the rapid recovery observed in the blowdown experiment. In addition, loss of biotic control over ecosystem processes resulted in major changes in hydrology and, presumably, biogeochemistry.

In the simulated hurricane blowdown, by contrast, increases in resource availability were used quickly by survivors—sprouts and seedlings of many species adapted to natural disturbance. This rapid utilization of resources led to minimal change in vegetation composition and rapid recovery of critical ecosystem processes. The chaotic appearance of the recovering community results directly from a wide range of regenerative responses by the species in the system.

These results may have relevance for land managers in the face of many natural disturbances. As has been shown through many studies of fire in forest ecosystems and a recent investigation of forest mortality from the hemlock woolly adelgid, human attempts to salvage or minimize forest damage may often lead to more severe and long-lasting effects than the disturbance itself. If environmental integrity and ecosystem function, measured by biotic control of nutrient cycling, transpiration, etc., are major objectives, then allowing the disturbance to take its course and leaving the damaged ecosystem intact may be the preferred strategy.