Tree Death as an Ecological Process

The causes, consequences, and variability of tree mortality

Jerry F. Franklin, H. H. Shugart, and Mark E. Harmon

Tree death is so commonplace that the casual observer might logically assume it to be well understood by biologists. Some causes of tree mortality are obvious and even spectacular events, such as wildfires and hurricanes. But overall the patterns and causes of tree death typically are complex, and we are only beginning to appreciate the complexities.

Understanding and predicting tree mortality is critical in both applied and basic ecology. Practically speaking, information on mortality is essential in calculating forest stand yields and allocating efforts in tending and protecting forests. A thorough knowledge of tree death is also necessary to interpret correctly the dying back of forests. Yet, despite its long history, forest husbandry lacks a comprehensive understanding of tree mortality.

In basic ecology, tree death is relevant to a broad array of topics. Ecologists focusing on ecosystems, communities, populations, physiology, and evolution all find tree death significant to their perspectives. Tree mortality exemplifies several important principles of ecological complexity.

Tree death can be used to illustrate the variability of an ecological process in terms of rates, as well as causal factors or mechanisms; the necessity for defining the spatial and temporal scales of interest; and the importance of the natural history of species and ecosystems in understanding ecological processes. Studies of tree death can also illustrate the relevance and validity of differing viewpoints—those of different disciplines or scales—on the same process.

An emphasis on these general features of ecological processes and systems is especially appropriate in view of the all-too-human tendency of ecologists to seize upon one viewpoint to the exclusion of all others.

We are only beginning to appreciate the complexity of patterns of tree death.

In this article, intended to provide a context for the other articles in this issue of BioScience, we provide an overview of tree death as a rich ecological process. We include its consequences and causes, its variability, and the importance of species' natural histories. We also use tree death to illustrate some general aspects of ecological processes.

Consequences of tree death

Tree death's importance in ecology reflects the multiple roles that a tree plays. It is a primary producer, a storage compartment, and a support structure. Tree death removes a genetically distinct individual from the stand, but it also provides additional resources to the ecosystem. In this way, the death process itself does important work (Table 1).

The function of dead trees in the ecosystem has rarely received the consideration that it deserves. At the time a tree dies, it has only partially fulfilled its potential ecological function. In its dead form, a tree continues to play numerous roles as it influences surrounding organisms. Of course, the impact of the individual tree gradually fades as it is decomposed and its resources dispersed, but the woody structure may remain for centuries and influence habitat conditions for millennia.

Jerry F. Franklin is the chief plant ecologist, USDA Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, Corvallis, OR 97331, and Bloedel Chair of Ecosystem Analysis, College of Forest Resources, University of Washington, Seattle, WA 98195. H. H. Shugart is Corcoran Professor of Environmental Sciences, University of Virginia, Charlottesville, VA 22903. Mark E. Harmon is a research associate, Forestry Sciences Laboratory, Oregon State University, Corvallis, OR 97331. © 1987 American Institute of Biological Sciences. All rights reserved; the US government retains a nonexclusive royalty-free license to publish or reproduce this article.
Altered tree population structure

Table 1. Some ecological changes brought about by the death of a tree.

<table>
<thead>
<tr>
<th>Resources released (light, nutrients, moisture)</th>
</tr>
</thead>
<tbody>
<tr>
<td>New resources created (e.g., decompositions) for wildlife</td>
</tr>
<tr>
<td>Habitat for decomposer organisms</td>
</tr>
<tr>
<td>Complex organic compounds</td>
</tr>
<tr>
<td>Work carried out</td>
</tr>
<tr>
<td>Kills other trees or organisms by crushing</td>
</tr>
<tr>
<td>Mines soil in case of uprooting</td>
</tr>
</tbody>
</table>

While many organisms display a continuum of ecological roles between the living and dead forms, with a gradual fading of influence after death, in trees this continuum is more apparent because of their size, durability, and multiplicity of roles in the ecosystem.

Although from an ecosystem perspective the tree is shifted from the category of living to dead matter, physiological states (some even most) of a tree (e.g., the heartwood) could be considered dead much earlier and significant portions of a live tree may already have been decomposed. In a live conifer, only about ten percent of the cells are actually alive; the leaves (three percent), inner bark (phloem and cambium, five percent), and ray cells in sapwood (two percent). Some processes associated with dead trees begin while the tree is still alive. For example, fungi are already at work rotting the woody material, and animals excavate the dead parts of living trees. In contrast, a dead tree or log in an advanced state of decay may include a considerable number of living cells, as much as 35% of the biomass may be live fungal cells alone (Swift 1973).

Tree death substantially increases the resources (e.g., light, nutrients, water, and energy) available to other organisms in the ecosystem. The amount of resources made available depends on the number and size of trees that die. The resources may be made available instantaneously (e.g., light) or very slowly (e.g., nutrients and energy contained within the logs). The dead tree may also function as a sink where nutrient resources brought in by the decomposer organisms are immobilized for a period of time. The dead tree is itself a major new resource for the ecosystem, whether as a snag (standing dead tree) or as a downed log. The importance of dead trees to the ecological and functional ecological functions of forest and stream ecosystems has been thoroughly reviewed (Harmon et al. 1986, Maser and Trappe 1984).

With the large array of organisms present in the decaying log, it may be more "alive" than a living bole. In addition to being the habitat of decomposer organisms, dead trees provide critical habitat for sheltering and feeding a variety of animal species (Brown 1985, Thomas 1979). Snags and logs also provide habitat for plants of higher orders. Indeed, the seedlings provided by "nurse logs" may be the primary sites for tree reproduction in some ecosystems (Figure 1) (Harmon et al. 1986). Along with the nutrients and energy released by the decomposition process, there is also significant nitrogen fixation by organisms living within the habitat (Harmon et al. 1986).

Woozy structures also influence geomorphic processes. For example, they serve as erosion barriers on forest slopes and, in smaller forest streams, they contribute to development of stepped stream profiles, reduce channel erosion, and create more retentive stream reaches (Harmon et al. 1986).

Tree death may itself do important mechanical work. Falling trees or snags often kill other trees or other organisms. More than 15% of the mortality in mature and old-growth Douglas-fir stands in the Pacific Northwest consists of trees knocked over, broken, or crushed by falling trees. The uprooting of trees lifts and mixes forest soil, an important ecological process (Figure 2). For example, in the Sitka spruce-western hemlock (Picea sitchensis-Tsuga heterophylla) forests of southeastern Alaska, soil churning by the roots of windthrown trees retards development in the soil of impervious layers of mineral deposits, known as iron pan. Without this process, standing pools of water would eventually produce swampy forest sites (Ugolini et al. 1987).

Causes of tree death

Although tree death is sometimes abrupt, it is more frequently a complex and gradual process with multiple contributors (Waring, p. 569, this issue). For example, the proximate causes of death (e.g., an insect or disease) may be simply the coup de grace, whereas the primary factors (e.g., starvation) may not be obvious. Tree death often represents an arbitrary point on a continuum.

Causes of tree death can be categorized in a variety of ways, including such dichotomies as abiotic and biotic (Table 2), allochthonous and autogenic, and extrinsic and intrinsic. All these classifications fail to portray the complex interactions among trees, their environment, and various agents of mortality. In part, the interactive, sequential nature of tree mortality limits the value of these dichotomies. For example, the phenomenon called suppression, the limiting of one tree's growth by the presence of another, usually larger, tree may reduce the suppressed tree's rooting strength and thus increase its susceptibility to wind. Suppression also may reduce tree size and bark thickness, thereby increasing vulnerability to surface fires.

Abiotic causes of tree death are those of large measure, allochthonous, and extrinsic in nature. Environmental stresses, such as flooding, drought, heat, low temperatures, ice cover, and excess sunlight, tend to be particularly important in the death of tree seedlings. We place most pollutant stresses (e.g., acid precipitation, ozone, and acid-forming oxides of nitrogen and sulfur) into the abiotic category, although the proximate cause of death may be biotic agents or physiological failure. Most of the abiotic agents could be strong selective forces in evolution, but at least one, windthrow, may be too random in its timing and impact to have a significant evolutionary effect. Research at Mount St. Helens, for example, has shown dramatic differences, depending on the season of eruption, in the survival of organisms and the rate and composition of posteruptive forest recovery (Franklin et al. 1985).

Biotic factors are highly variable and difficult to define as either extrinsic or intrinsic. Most effects of competition fall in the category of stovatiation, where light, nutrients, or water limit photosynthesis. The most drastic effects of herbivory occur when insects, ungulates, or humans eat tissues essential for growth (e.g., cambium). Herbivory of roots may kill trees or predispose them to mechanical failure. But trees can tolerate significant herbivory of photosynthetic tissues without apparent effect. Diseases may also kill trees or may predispose them to mechanical failure. For example, a large percentage of windthrown old-growth Douglas firs (Pseudotsuga menziesii) contain significant butt rot (Polyporus squamosus). Both insects and disease may be the proximate agent of death in trees already weakened by other factors; as such, they often are blamed for deaths more properly as...
be identified. This perspective should receive more attention in future mor-tality studies. The way in which a tree dies strongly influences its subsequent ef-fect on the ecosystem. For example, an instantaneous death may result in rapid understory response, whereas a slow decline would allow gradual adJUSTments to freed resources. Studies of different animal habitats than downed logs and also differ in rates and domi-nant processes of decomposition. The differences in decay rates have impor-tant ecosystentic implications. For example, Douglas-fir snags and their debris in the Pacific Northwest may disappear at two to three times the rate of comparable windthrown trees due to high rates of fragmentation (Graham 1982).

Temporal variability

The timing of tree death, like many other ecological processes, is highly variable and unpredictable. The tem-poral variation is influenced by physi-
ology, such as the age of the individ-
ual or of entire cohorts (Mueller- sled, 2000). Severe weather years may contribute. Some important generalities can be associated with tree death along this successional gradient (Table 1). First, mortality rates generally decline, and causes of death appear to become more complex throughout the successional stage. Second, the forest is at an approximate equilibrium for long periods of time, that is, mortality rates are essentially constant and change in forest structure and compo-
sition is slow. An organism or an ecologist observing such a forest over a 50-year period would appropriately view it as in equilibrium; one with a 500-year perspective would not. Third, probability functions based on such factors as species and relative size are required for predicting indi-
vidual and stand mortality. A regional gradient is also apparent (Table 4), reflecting, at least in part, differences in productivity. Mortality probabilities may vary, as found in coastal Sitka spruce-western hemlock than for the Cas-cade Range Douglas fir, which in turn has higher productivity than the inte-
rior ponderosa pine (Pinus ponderosa).

Many agents of tree mortality have distinct spatial patterns at the land-
scape level. See for example Figure 4, which is most impor-tant on wet soils where rooting zones are restricted and in particular on stream banks. Regional gradients in intensity of wind damage also occur, as in the Pacific Northwest, where wind-related mortality drops from about 80% in coastal stands to less than 15% in interior ponderosa pine stands (Table 4). Wind mortality is known to occur with different frequencies in different parts of a landscape or region (Hemstrom et al. 1983). Mortality from atmospheric pollutants is often most severe in ridgetop, cloud, or fog for-es (Johnson and Sicama 1983, Lo-
vet et al. 1982, Manion 1981). Mor-
tality caused by fluvial processes, such as bank cutting or flooding, also...
has a strong spatial pattern (Swanson and Lienkaemper 1982). Because such landscape-patterns in rates and causes of mortality are so common, positions of study sites need to be recognized and defined in research on tree death. The spatial patterning in tree mortality is not distinctly accounted for by the landscape perspective. Knowning the degree to which tree death is dispersed or aggregated within the study area is often important. If in a stand, for example, dying trees scattered rather than clustered, the consequences of the tree death may be quite different. This patterning will determine, for instance, the size of gaps that are created. Similar information is needed at the landscape level; i.e., tree death dispersed throughout or is it occurring in patches or even in complete stands? The number of trees that die may be identical, but the biological ecologies very different.

Importance of natural history
Knowledge of the ecology and natural history of individual species and ecosystem dynamics is essential for predicting what will occur in forests. The only way to contemplate designing a temporal array of possibilities and species is through systematic observations under natural conditions. The study of ecosystem dynamics requires such natural history research. The variety in patterns of death among tree species reflects such factors as differences in life-spans, vulnerability to various agents, and distribution in the landscape. The study of ecosystem dynamics requires such natural history research.

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Table 4. Differences in rates of mortality and percentage of tree death associated with wind in mature and old-growth conifer forests along a geographic gradient from coastal to interior ponderosa pine forests.

<table>
<thead>
<tr>
<th>Forest</th>
<th>Annual mortality rate (%)</th>
<th>Wind-related mortality (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sitka spruce-western hemlock</td>
<td>Cascade Head, OR</td>
<td>0.81</td>
</tr>
<tr>
<td>Douglas fir-western hemlock</td>
<td>Olympic Peninsula, WA</td>
<td>1.35</td>
</tr>
<tr>
<td>Mount Rainier, WA</td>
<td>0.52</td>
<td></td>
</tr>
<tr>
<td>Wind River Experimental, WY</td>
<td>0.75</td>
<td></td>
</tr>
<tr>
<td>Ponderosa pine</td>
<td>Mendenhall Research Natural Area, OR</td>
<td>0.31</td>
</tr>
<tr>
<td>Pinion Pinyon Research Natural Area, OR</td>
<td>0.52</td>
<td></td>
</tr>
</tbody>
</table>

Data courtesy of S. Greene, Forestry Sciences Laboratory, Corvallis, OR 97331.

Franklin et al. submitted manuscript.

Franklin and Deyell 1987.

antihypertensive and antidiabetic activities depend on a thorough understanding of patterns of tree death under natural conditions. At the present time, adequate understanding of this is woefully lacking.

Tree death also demonstrates some principles of ecological processes: the importance of defining the spatial and temporal context of a study, the importance of stochastic processes, the fact that most ecological processes are driven by multiple mechanisms and that the relative importance of these mechanisms changes in time and space, and the importance of species' and ecosystems' natural histories. Tree death illustrates that many valid and useful perspectives on a single, presumably simple process exist. Further, it makes clear that we need to give more consideration to the biology of organisms and ecosystems in developing, evaluating, and applying theoretical constructs.

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