

Tree Death as an Ecological Process

The causes, consequences, and variability of tree mortality

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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. Ecolo-

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

gists 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. The problem is compounded by attempts to define many ecological problems rigidly in terms of either/or hypotheses. Many of the ecological processes and systems are not sufficiently well understood, or are too complex, to be described in such limited terms.

It is tempting to use simple systems and models to circumvent the com-

plexity introduced by the varied natural histories of species and natural ecosystems. Unfortunately, such simplifications can also mislead the unwary about important ecological processes.

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.

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

Altered tree population structure
Altered community structure
Shift from biomass to necromass
Resources released (light, nutrients, moisture)
Resources stored by decomposers
New resources created
Structures (snags or logs) for wildlife
Habitat for decomposer organisms
Complex organic compounds
Work carried out
Kills other trees or organisms by crushing
Mixes soil (in case of uprooting)

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, physiologically, 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 boles). The dead tree may also function as a sink where nutrient resources brought in by the decomposer

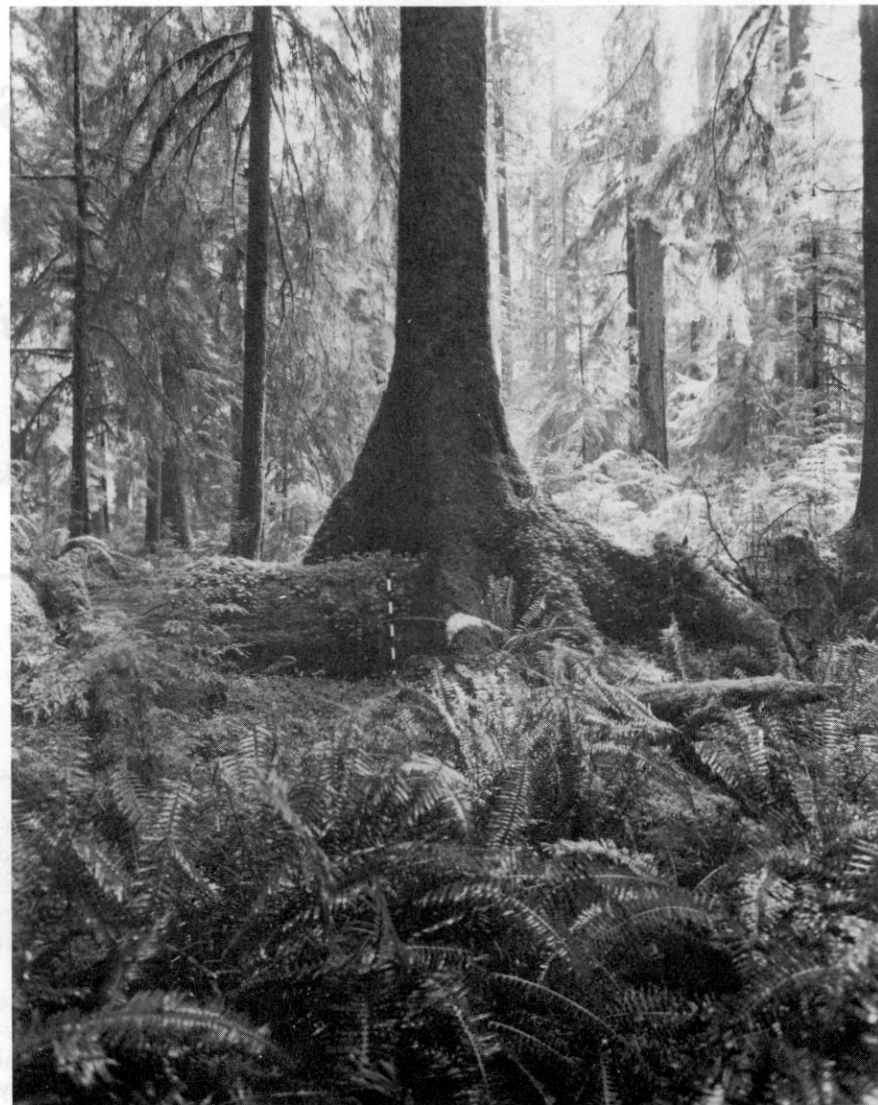


Figure 1. Logs provide habitat for tree seedlings and other higher plants. In ecosystems such as the alluvial Sitka spruce-western hemlock forests of the Olympic Peninsula, Washington, essentially all tree reproduction is confined to rotten wood seedbeds, primarily nurse logs.

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 wood structures to the geological and 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 seedbeds 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 (in terrestrial habitats) and on (in stream habitats) the wood itself (Harmon et al. 1986).

Woody 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), allogenic and autogenic, and extrinsic and intrinsic. All these classifications fail to portray the complicated 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 also, in large measure, allogenic and extrinsic in nature. Environmental stresses, such as flooding, drought, heat, low temperatures, ice storms, 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, volcanic eruptions, may be too random in its timing and impact to have an 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 post-eruptive forest recovery (Franklin et al. 1985).

Biotic factors are highly variable and difficult to define as being either extrinsic or intrinsic. Most effects of competition fall in the category of starvation, 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 tissue and sap.

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 schweinitzii*). 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-



Figure 2. Even death can contribute important ecological work. Uprooting of trees in coastal Alaskan Sitka spruce-western hemlock forests is an important factor retarding development of iron pans (impervious layers of mineral deposits) and consequent paludification of forest sites.

Table 2. Some common contributors to or causes of tree death.

Abiotic
Fire
Lightning
Chemical pollution (e.g., ozone)
Environmental stress (e.g., flooding, drought, heat)
Wind
Volcanic eruption
Climatic change
Biotic
Old age, senescence
Mechanical imbalance (e.g., top heavy)
Starvation (inadequate photosynthesis)
Consumption (includes insects, ungulates, and humans)
Disease

signed elsewhere. Humans are, of course, a major biotic cause of tree death, acting both directly (tree cutting) and indirectly in influencing almost all other agents.

The issue of tree senescence and its contribution to mortality is a very interesting one. Does old age—an intrinsic physiological alteration in the tree—contribute to tree death? Some biologists have proposed that trees have the potential to be immortal, i.e., they must be killed by some external agent (Molisch 1938). But, inherent declines in vigor and in growth do detract from a tree's ability to resist a variety of damaging agents. Families and genera differ markedly in the timing of these declines; for example, trees in the families *Cupressaceae* and *Taxodiaceae* typically can live for millenia. There is also an environmental component of tree longevity. Some trees live longer where site conditions restrict growth rates. Bristlecone pine, *Pinus aristata*, growing under stressful conditions on mountains, can live for more than 3000 years.

Tree death thus is generally the result of complex interactions among multiple factors. As Shigo (1985) notes, most "disease-causing agents injure organisms that have been predisposed to diseases." He emphasizes the importance of energy reserves in disease resistance of trees and the cumulative effect of many seemingly unimportant injuries. Manion's (1981) "decline disease spiral" can be generalized to a *mortality spiral* reflecting the cumulative, sequential contributions of various events and factors (Figure 3).

A probability transition matrix may provide a useful mathematical construct of the mortality spiral. While at first glance this approach would seem to allow an infinite number of causal combinations, it is likely that there is a limited number of mortality spirals (or transitions in the matrix), each with strongly linked factors. We have already described a number of well-known spirals, such as butt rot and wind. Other spirals may be less strongly linked and less predictable. This approach also allows biologists to consider the mechanisms allowing trees to escape various spirals. In addition, the optimal point to apply management actions could

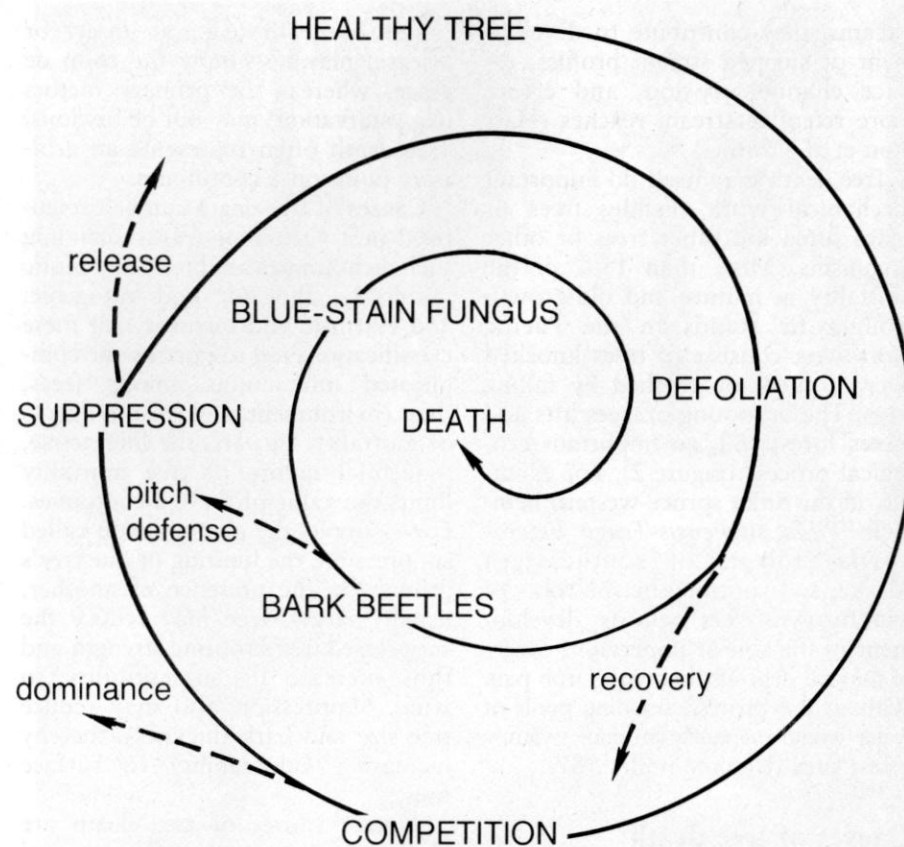


Figure 3. Mortality spiral for a Douglas-fir tree illustrates the series of events leading to its death. The spiral is based upon the decline disease spiral of Manion (1981). In this example, a healthy tree is suppressed by larger trees. If not released from competition, the tree is predisposed to attack by defoliators. Once partially defoliated, the weakened tree is attractive to bark beetles (Wickman 1978) and is unable to resist the beetles, which carry blue-stain fungus (Berryman 1982). The fungus blocks the transpiration stream in the tree and causes desiccation of the leaves. As the tree progresses along this spiral, its opportunities to escape death become more limited.

be identified. This perspective should receive more attention in future mortality studies.

The way in which a tree dies strongly influences its subsequent effect on the ecosystem. For example, instantaneous death may result in rapid understory response, whereas a slow decline would allow gradual adjustments to freed resources. Trees that die standing upright provide different animal habitats than downed logs and also differ in rates and dominant processes of decomposition. The differences in decay rates have important ecosystemic 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 temporal variation is influenced by physiology, such as the age of the individual or of entire cohorts (Mueller-Dombois, p. 575, this issue); succession, that is, the progression of the community through time; and chance.

The rates and causes of tree mortality show dramatic variation with succession (Harcombe p. 557, and Peet and Christensen, p. 586, this issue). This variation is well illustrated by a successional stage after wildfire or clearcutting in the Douglas-fir region of the Pacific Northwest (Table 3).

Mortality rates, primarily due to

Table 3. Changes in causes and rates of tree mortality during forest successional stages in the Douglas-fir region of the Pacific Northwest.

	Stage				
	Prevegetative closure	Full vegetative cover	Closed tree canopy	Mature forest	Old forest
Approximate period (years)	0-5	5-20	20-100	100-200	>200
Mortality rate	Very high	High	High to medium	Medium to low	Medium to low
Typical mortality causes	Environmental stress, predation, pathogens	Interspecific competition, environmental stress, pathogens, predation	Intraspecific competition, pathogens, wind	Pathogens, wind, competition	Wind, pathogens, physiological disorders

heat and drought, are high among colonizing tree seedlings. Herbivory and pathogens may also be considered important factors in tree mortality at this stage. As herb and shrub coverage increases, competition between trees and other plants becomes important; this process may dominate for 10-20 years.

Competition among trees becomes important with development of a closed forest canopy, and so-called thinning mortality begins. This competition dominates for a long period in Douglas fir; for example, stands 100-150 years old still exhibit this pattern of mortality,¹ although the effects of pathogens may also be significant. The period of competitive mortality may occur earlier and be briefer for tree species that mature more rapidly, such as loblolly pine (*Pinus taeda*) (Peet and Christensen, p. 586, this issue). Finally, wind and pathogens tend to become the proximate causes of death, to which senescence, competition, and environmental stresses may contribute.

Some important generalities can be associated with tree death along this successional gradient (Table 3). 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.² 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 individual and stand mortality.

Much tree death is episodic and irregular. Catastrophic destruction of stands represents the extreme form of a mortality episode, in which rates of mortality rise above the background levels for the stand or cohort of trees. But mortality episodes also occur within stands remaining essentially intact. Such episodes may involve individual trees scattered through the stand or together in small groups. Criteria defining such episodes may be either quantitative (e.g., mortality beyond two standard deviations from the long-term mean) or more subjective. The episodic mortality rate varies with tree species, forest type, and successional stage. Some episodes of mortality are predictable, based for example, on developing stand structure, whereas other episodes, such as those associated with unusual climatic events, are determined by chance.

Episodes of tree death are often due to bark beetle epidemics, wind, climatic stresses (e.g., drought), or anthropogenic influences (e.g., pollutants). At least some of these episodes, such as bark beetle outbreaks, appear

to be related to successional stage and other predisposing factors. Stands may develop beyond the long-term carrying capacity of the site during favorable periods, undergo stress during an unfavorable climatic period, and then be subject to a major outbreak of insects. In the Douglas-fir region an extensive windthrow created conditions for epidemic outbreaks of the Douglas-fir bark beetle (*Dendroctonus pseudotsugae*) and subsequent elevated tree mortality (Wright and Lauterbach 1958).

Spatial variation

Mortality is not evenly distributed in space. The rates and mechanisms of tree death differ dramatically over a landscape. Systematic differences may exist on different landforms or on adjacent sites of different productivity levels. In the Pacific Northwest, for example, mortality rates in mature and old-growth stands are generally higher on habitats of high productivity than on those of low productivity.³ A regional gradient is also apparent (Table 4), reflecting, at least in part, differences in productivity. Mortality is higher for the coastal Sitka spruce-western hemlock than for the Cascade Range Douglas fir, which in turn has higher productivity than the interior ponderosa pine (*Pinus ponderosa*).

Many agents of tree mortality have distinct spatial patterns at the landscape level. Windthrow is most important on wet soils where rooting zones are restricted and in particular topographic positions (Gratkowski 1956). Regional gradients in intensity of wind damage also occur, as in the Pacific Northwest where wind-related mortality drops from about 80% in coastal spruce-hemlock stands to less than 15% in interior ponderosa pine stands (Table 4).

Wildfires are known to occur with different frequencies in different parts of a landscape or region (Hemstrom 1982, Kessell 1979). Mortality from atmospheric pollutants is often most severe in ridgetop, cloud, or fog forests (Johnson and Siccama 1983, Lovett et al. 1982, Manion 1981). Mortality caused by fluvial processes, such as bank cutting or flooding, also

¹J. F. Franklin, M. Klopsch, K. J. Luchessa, and M. E. Harmon, 1987. Manuscript submitted.

²J. F. Franklin and D. S. DeBell, 1987. Manuscript submitted.

³See footnote 1.

has a strong spatial pattern (Swanson and Lienkaemper 1982). Because such landscape-level 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 completely accounted for by the landscape perspective. Knowing 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; is tree death dispersed throughout or is it occurring in patches or even as complete stands? The number of trees that die may be identical, but the ecological implications very different.

Importance of natural history

Knowledge of the ecology and natural history of individual species and ecosystems is essential for understanding and predicting what will occur in forests. The only way to contemplate the near-infinite array of possibilities of species and systems 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. This variety is apparent in regional patterns of tree mortality (Buchman et al. 1983) as well as among species in the same stand.

Tree species can be grouped into types with similar patterns of death (Franklin and Hemstrom 1981, Shugart 1984); such functional groups may be particularly useful in modeling exercises where detailed species-specific information is not available. One paradigm often used in modeling—in which an individual's probability of death increases as it approaches the maximal size or age for the species—should probably be avoided whenever possible. There is

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 Sitka spruce-western hemlock to interior ponderosa pine forests.

Forest		Annual mortality rate (% of cohort)	Wind-related mortality (% of total)
Sitka spruce-western hemlock	Cascade Head, OR*	2.95	83
	Olympic Peninsula, WA†	0.81	
Douglas fir-western hemlock	H. J. Andrews Experimental Forest, OR‡	0.70	33
	Mount Rainier, WA‡	0.52	41
	Wind River Experimental Forest, WA§	0.75	46
Ponderosa pine	Metolius Research Natural Area, OR*	0.31	10
	Pringle Falls Research Natural Area, OR†	0.52	18

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

†Data on file at the Forestry Sciences Laboratory, Corvallis, OR 97331.

‡Franklin et al. submitted manuscript.

§Franklin and DeBell 1987.

evidence that rates of mortality differ (Hibbs 1979) and may actually decline with size and age in at least some species (Harcombe, p. 557, this issue).

Near-simultaneous death of entire tree cohorts, as reported by Mueller-Dombois (p. 575, this issue), is an extreme case exemplifying the importance of considering individual species and their ecologies. Synchrony in senescence of even-aged tree cohorts is probably widespread but rarely to the degree seen in the *Metrosideros* spp. of Hawaii and New Zealand (Allen and Rose 1983, Mueller-Dombois 1983, Stewart and Veblen 1983), the *Nothofagus* forests of New Zealand (Jane and Green 1983, Wardle and Allen 1983), and the *Abies* spp. of Japan and New England (Iwaki and Totsuka 1959, Sprugel 1975).

Tree mortality has important implications for succession because the individuals it removes may not be replaced. In an attempt to add scientific structure and mathematical rigor to the understanding of ecological succession, Tansley (1929) proposed classifying ecological successions according to apparent causes of the change in the vegetation pattern. Thus he identified allogenic successions, in which change was driven mostly by external features, and contrasted these with autogenic successions in which the change was driven

from within. Unfortunately, the logic of this dichotomy did not alter the fact that, in reality, both autogenic and allogenic causes seem to frequently share (or alternate) the control of the successional direction of any given ecological system. Tansley came to recognize this and retracted the idea of the dichotomy in the classic paper (Tansley 1935) in which he defined the ecosystem concept.

The Gordian knot of intertwined causality that made it difficult for Tansley to design a clean, useful dichotomy in the successional dynamics of ecosystems in the 1920s and 1930s remains tightly tied today. Perhaps recognizing that such dynamics are the consequence of multiple contributing factors is more useful than clinging to an artificial autogenic-allogenic dichotomy.

Conclusions

The consequences of tree death, in terms of effects on other ecosystem components and processes, depend on many variables including the species, mortality agent, position, spatial pattern (dispersed or aggregated), and numbers that have died. Tree death is an important indicator of ecosystem health and can assist recognition of stresses caused by pollutants, such as acid rain and ozone. However, the value of tree death as an indicator of

anthropogenic disturbance depends 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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