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Death and Decay: A Vital Part of Living Canopies

Abstract

Wood decay is a significant ecological process affecting Northwest forest canopies. Standing dead trees (snags) and partially decayed living trees offer five primary functions in the forest canopy: they increase structural diversity, alter canopy microenvironment, promote biological diversity, provide critical habitat for wildlife, and act as storehouses for nutrient and organic matter recycling agents. In this paper we do not discuss traditional measurement of wood decay in the canopy as a silvicultural loss of standing timber, but review current literature of forest ecology and define wood of dying and dead trees as an important component of the aboveground ecosystem.

Introduction

In the last two decades, considerable research has helped elucidate the role of "dead and down" wood in forest ecosystems (Graham and Cromack 1982, Erickson et al. 1985, Harmon et al. 1986, Sollins et al. 1987, Means et al. 1992). Earlier, in his classic pioneering work on the subject, *The Pattern of Animal Communities*, Charles Elton stated that the wood of dying and dead trees provides one of the greatest resources for animal species in natural forests (Elton 1966). In temperate forests, Elton estimated if fallen timber and slightly decayed trees are removed from the system "the whole system is gravely impoverished of perhaps more than a fifth of its fauna." Although insightful for the era, Elton's appraisal of the importance for this ecosystem component likely falls short. Even with our current understanding of ecosystem function, we cannot adequately assess consequences to the system of having decayed and dead trees removed or not available (i.e., through several forms of forest management).

The wood of dying and dead trees helps to vary the pattern of forest communities, not only on the ground but also at all levels of the canopy. Many organisms share dependence on the wood of dying and dead trees, but little is known of their inter-dependence and how they interact within the larger system. The general stages by which standing timber is invaded by insects and fungi are well known from the extensive work of forest entomologists, pathologists, and mycologists,

but little effort has been applied to clarifying the ecosystem function of the standing dead. Research efforts presumably have been hindered not only by the difficulty of safely working in standing decaying trees, but by the inherent complexity of the effects. Generally, ecologists have underestimated that the way trees die can markedly influence several ecological processes.

Decay of a tree progresses until, ultimately, its residues are fully integrated into the soil. Standing dead trees may be susceptible to windthrow, which uproots the tree, or to bole breakage close to the ground that prostrates the entire bole. Just as frequently, much of the decay process takes place while the tree is standing and an integral part of the living canopy (Graham and Cromack 1982). Living trees with partial decay may remain upright for decades, their dead, decaying branches intermingling with living branches (Figure 1).

Distribution and Causes of Dead Wood in the Canopy

Much of the decayed wood in canopies is within the main bole and stems of live trees. This "heartrot" can account for 20% or more of the total volume of wood in a stand of trees. As a function of stand age, older stands have more decay as a total percentage of the volume (Childs and Shea 1967, Aho 1977). When estimating for timber production, a measure of annual volume growth increment is calculated; from that amount is

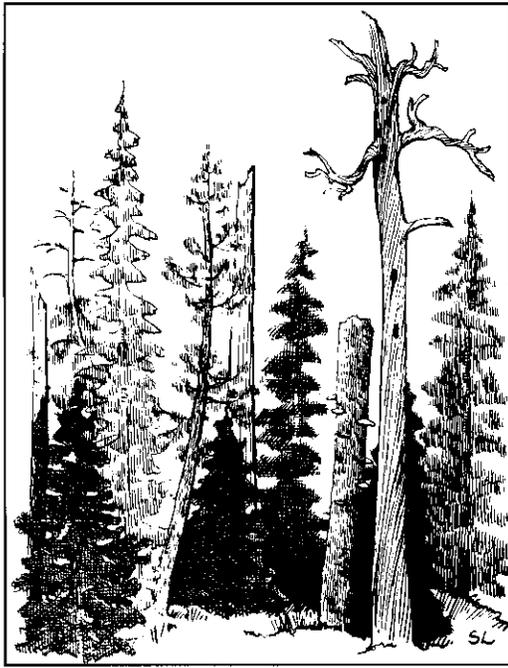


Figure 1. Dead boles and branches are an integral part of the living canopy.

subtracted the increasing increment of defect caused by heartrot fungi to get a realistic estimate of volume growth. At some point in the life of trees the increment produced by annual growth equals the amount of wood destroyed by heartrot fungi. This point is a theoretical age of maximum volume of merchantable wood. It is referred to as the "pathological rotation age" (Manion 1981). For obvious reasons, the timber producers aim to harvest the stand long before this point is reached. Intensive management involving even-aged, short-term rotations, harvests trees while wood decay in the canopy is minimal.

Dead wood is not randomly distributed across the forest canopy. Incidence of wood decay has been correlated with stand age, climatic zones (Setliff 1986), elevation and soil type (Hobbs and Partridge 1979), and habitat type (Byler et al. 1990). Some disturbance agents may cause wide-scale mortality throughout a forest landscape, but certain insects, parasitic plants, and root and stem fungi affect patches of trees and exhibit spatial patterns that are aggregated or clumped in the forest canopy (Knight 1987, Geils 1992).

Fire may be a major contributor to subsequent canopy tree decay. Trees are fire-killed directly

by stem girdling, crown scorching, and burning of the root systems. Trees can be fire-killed indirectly through basal wounds. Wounding events such as fire scars, broken tops, or other stem injuries create infection courts for stem- and root-decay organisms. Trees respond to wounding and infection by compartmentalizing the infection and wounds, which can result in hollow or soft inner cores and hard outer shells after many years. This "hard outer shell and soft core" is critically important to cavity-nesting vertebrates. This process of compartmentalization helps trees limit wood decay (Shigo and Marx 1977).

Wood-boring arthropods also may initiate the decay process or act as secondary agents of decay. Repeated defoliation of conifers can cause mortality, or weaken trees and allow successful attack by secondary bark beetles (Wickman 1978). Healthy trees also can be killed by insects that came from adjacent trees killed by fire, insects, or root diseases (Furniss 1936, Childs 1960).

Perpetual natural thinning of trees growing in subordinant canopy positions is known as suppression mortality. Natural senescence of all sizes of branches, especially in mature trees, translates to a large biomass of dead and decaying wood located in the canopy (Pike et al. 1977).

The Decomposer Community

Wood is a bulky, spatially determinate resource that decomposes slowly relative to most plant litter; it takes on average 15-20 years for small (>5-cm diameter) branches and over 300 years for large trunks to decay in temperate forests (Boddy 1992). As wood decay organisms colonize and use wood they encounter continually changing conditions, *e.g.* an increase of porosity, decrease of apparent density, and so forth. The changes may, in turn, affect the activity and development of the decomposer community (Yoneda 1975).

Dying and dead wood in the canopy is broken-down by the combined action of the decomposer community, which is composed predominantly of micro-organisms (bacteria and fungi) and invertebrate animals (Käärik 1974, Swift 1977). These organisms "feed" on the dead wood, using its carbon, and other nutrients for their own growth and development. Eventually the decomposers die, their carcasses become integrated with the dead wood, and they are acted upon by other decomposers.

As with successional changes in seed plant communities, directional trends in the decomposer community are associated with wood decay in forest canopies (Hudson 1968, Blanchette and Shaw 1978). Much is known of the substratum succession of decay organisms in the dead and down tree (Swift 1982a, Swift 1982b, Harmon et al. 1986), but the studies of decay organism succession in canopy wood has lagged far behind.

Five Primary Functions of Decaying and Dead Trees in Forest Canopies

Five primary functions of aboveground decaying wood in the forest system are to increase structural diversity, alter canopy microenvironment, promote biological diversity, provide critical habitat for wildlife, and act as a storehouse for nutrient and organic matter recycling agents. These functions are highly correlated with complex interactions but will be discussed separately in the following text.

Increase Structural Diversity

The structure provided by boles and branches of trees that are dead, decaying, or both is a distinctive and dynamic feature of the canopy (Figure 2). Stand structure is altered by canopy gaps caused by the partial or complete mortality of an individual tree or group of trees.

The lag time between tree death and the onset of fragmentation is influenced by species, size, microclimate, and type of mortality (Harmon et al. 1986). Lag times for snags to begin falling are reported to be <3 years (Harmon et al. 1986). Hennon et al. (1984, 1990) found that some Alaskacedar (*Chamaecyparis nootkatensis* (D. Don) Spach) snags were persistent in forest canopies of southeastern Alaska for over 100 years.

Decay of boles differs from that of small branches and twigs. The bole is a denser substrate and is likely to house a different community of organisms than the fine twigs and small branches, which are less dense and have a greater surface

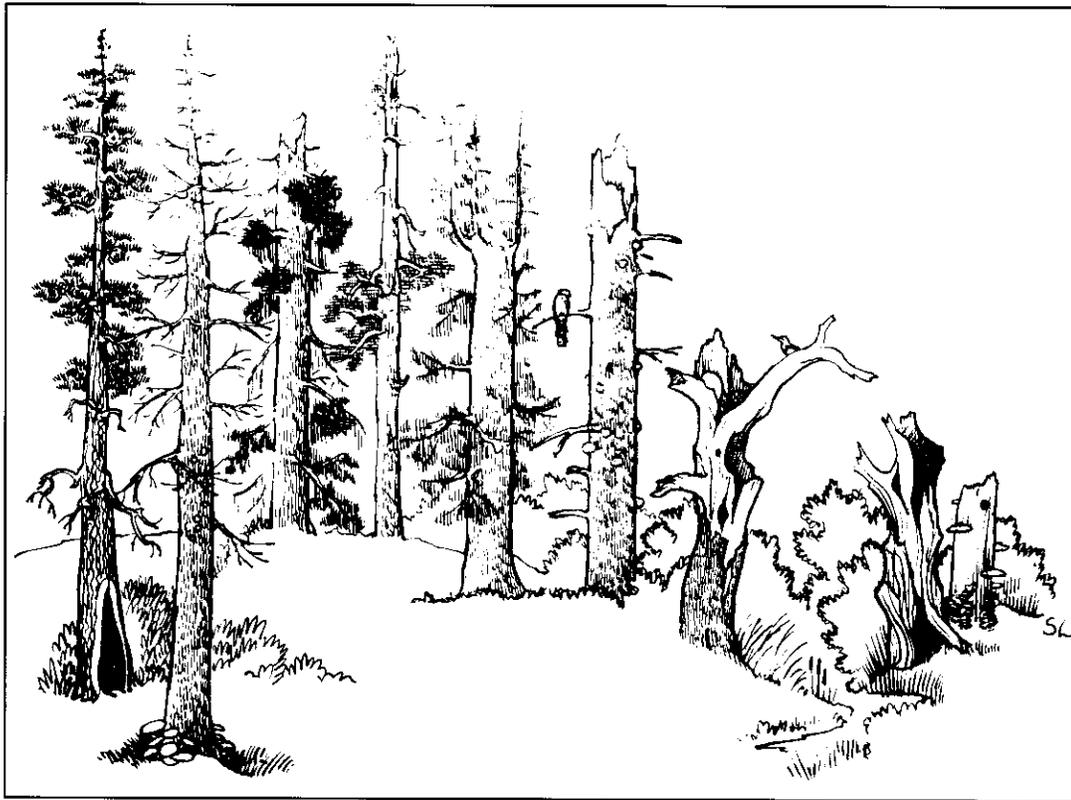


Figure 2. Various stages of tree decay provide dynamic diversity in canopy structure

area than the wood of the bole. Most studies of canopy biomass seem to ignore the dead wood component—either ignore that it is dead or simply omit dead branches from the sample. In one old-growth stand (>400 years), the biomass of dead twigs in the canopy of living trees was equal to roughly 18% of the total twig biomass and about one-third of the needle biomass (Pike et al. 1977). Even more surprising, dead twigs represented 47% of the total twig surface area.

Alter Canopy Microenvironment

The microenvironment within the vertical profile of the canopy is controlled to a large degree by the structure of the canopy. Death of whole or partial tree crowns plays an important role in defining the nature of that structure. Gaps in the living canopy also alter its structure by varying the patterns of light, moisture, wind, and thermal properties (Oliver and Stephens 1977, Oliver and Larson 1990). These gaps also increase the heterogeneity or "roughness" of the upper canopy, which creates a broader gradient of light, temperature, and humidity. In rough, deep, canopies of older forests in the Pacific Northwest the diverse forest microclimate is reflected in the vertical distribution of epiphytes (McCune 1993).

Patches of dead trees within old-growth stands provide habitat for wildlife that require grass-forb or shrub conditions for reproduction and feeding. Immense tree mortality may be disadvantageous to deer and elk, however, because of loss of canopy cover traits. Under full canopy cover, the animals are less subject to extremes in temperature, solar radiation, windspeed, humidity, rain throughfall, snow accumulation, predation, and human disturbance (Witmer et al. 1985).

Promote Biological Diversity

Dead and decaying wood provides an exceptional environment in the forest canopy. On a stand scale, even small modifications to canopy structure may allow previously nonresident species to grow and occupy a niche. On a smaller scale, the special microenvironment caused by dead and decaying wood contributes to the life support system for many canopy-dwelling microorganisms, invertebrates, birds, mammals, and plants.

Wood-attacking fungi are mainly basidiomycetes (Hawksworth et al. 1983), although some ascomycetes and other fungi may be present and

attack cellulose or other substrates (Hudson 1968). Although fungi act as the main agents of wood decomposition, other organisms also use rotting wood. These include bacteria, yeasts, myxomycetes, and invertebrates, particularly insects but also oligochaetes, mites, and nematodes (Harmon et al. 1986). Their major influence is in interacting with mycelial fungi, which can alter community structure, community dynamics, and rates of decay. These interactions may be direct, as with grazing of fungal mycelium, antibiosis, and nutrient competition, or indirect, by operating through alterations to the wood substratum and microclimate (Boddy 1983).

Invertebrate use of and dependence on canopy dead-wood is well known to entomologists. By chewing, ingesting, and excavating, invertebrates create a dust that decays more rapidly than the original wood because of an increased surface-to-volume ratio (Ausmus 1977, Harmon et al. 1986). Depending on the species, invertebrates either transport these particles from the wood or leave them inside. The galleries made by invertebrates allow microbes to colonize dead wood more rapidly (Ausmus 1977, Swift 1982a). Some invertebrates are fungivorous, and the decomposer fungi produce abundant resources for grazing. Furthermore, invertebrates are an important food source for vertebrates, such as bears and birds, that fragment the material while foraging (Almack 1985, Beckwith and Bull 1985).

In the Pacific Northwest, more than one hundred species of wildlife depend on snags for habitat (Thomas et al. 1979, Neitro et al. 1985). The listing includes representatives from all classes of terrestrial animals. The dependency of these species on trees that are dead, decaying, or both ranges from absolute to incidental, but for some species the presence of dead trees can spell the difference between local extinction and the perpetuation of existing populations (Thomas et al. 1979, Neitro et al. 1985).

Dead wood also provides a unique canopy substrate for plants. For example, some lichens are associated almost exclusively with dead trees or branches in the canopy. Members of the "pin lichens," in particular, are most often found using dead, bare wood versus bark as structural habitat. Once this wood fragments and falls to the forest floor, the lichens fail to thrive under the new environmental conditions and die (B. McCune, Oregon State University, pers. comm.).

Stephen Sillett (Oregon State University, pers. comm.) has observed dead wood in giant sequoia (*Sequoiadendron gigantea* (Lindl.) Buchholz.) acting as a stable substrate for epiphytes. Giant sequoia has a bark that characteristically sheds and flakes. In his survey of sequoia for epiphytes, dead wood and old persistent seed-cones were the primary areas where epiphytes were growing.

Provide Critical Habitat for Wildlife

As wildlife habitat, dead and dying trees function in a variety of ways (Table 1). Decaying wood is particularly important to cavity-nesting birds because wood decay in stems is an essential precursor to use by cavity excavators (McClelland and Frissell 1975, Cline et al. 1980). Large trees that contain heartrot before they die may be particularly important because they may be used by primary excavators before and long after tree death (Hennon and Loopstra 1991).

Recent findings by Akenson and Henjum (1994) suggest that black bear in the Blue Mountains of Oregon are intimately associated with canopy wood decay. They report that of 23 den sites used by radio-instrumented bears, 20 are tree-associated. Among these, 10 are top entry into hollow centers. All 10 trees are standing and 6 are living. The internal cavities within these trees resulted from stem decay by fungi.

In the past, in intensively managed forests of the Pacific Northwest, most snags were cut to reduce safety and fire hazards, and to increase the yield of woody fiber (Woodfin 1976). Current recommendations (USDA Forest Service R6, amendments to Forest Plans, 1994) for managed forests include a broader approach to habitat management for dead-wood-dependent wildlife that retains snags and other woody debris.

Act as Storehouses for Nutrient and Organic Matter Recycling Agents

The notion that down woody debris improves long-term site productivity by enhancing the nutrient capital, water economy, and soil organic reserves is well documented (Franklin and Waring 1980, Maser and Trappe 1984). The concept that the decomposition process is often initiated and dependent on conditions in the canopy zone before the fall of the material is often ignored.

The role of decay within standing trees associated with cycling of nitrogen (N) is particularly interesting from an ecosystem perspective. In the

short-term, decaying trees may be a nutrient sink, but over the long run they are a source of nutrients (Harmon et al. 1986). For example, Harvey et al. (1989) reported that N-fixing bacteria populations accompany common fungal-initiated wood decay processes in living trees. Nitrogen fixation was demonstrated in decay columns caused by various fungi in several western conifers. They used these data to approximate the nitrogen fixation potential in the forest ecosystems of northern Idaho. Their calculations propose that the N gains in decaying, live trees on northern Idaho sites amount to between 0.06 and 4.91 kg/ha per year and primarily depend on volume of decay in live standing trees on site. Such large N gains on some sites could equal or surpass the amounts of N fixed in downed woody residues on forest soils in the northern Idaho region (Jurgensen et al. 1989).

Wood decay fungi can be grouped into two categories according to the way in which they decay wood. These two groups are referred to as white rot fungi and brown rot fungi. White rot fungi have cellulase and lignase enzyme systems that enable them to degrade all components of woody cell walls. Most of these fungi apparently remove the lignin and polysaccharides at about the same rate (Gilbertson and Ryvardeen 1986). White rot fungi eventually decay wood completely, and white rot residues are not stable components of forest soils.

Brown rot fungi selectively remove cellulose and hemicellulose from wood. In advanced stages, wood is reduced to a residue of amorphous, crumbly, brown cubical chunks composed largely of only slightly modified lignin. Brown rot residues are extremely stable and are major organic components in forest soil (Gilbertson and Ryvardeen 1986).

Both white and brown rot fungi decay wood in the canopy zone (Hepting 1971). Brown rot fungi may be particularly important organisms in forest ecosystems of the Pacific Northwest. Considering all wood-decaying fungi, species of brown rot fungi are relatively few when compared to numbers of species of white rot fungi (only about 7%) (Gilbertson and Ryvardeen 1986). Brown rot fungi occur primarily on conifer wood. On a geographic basis, brown rot fungi are primarily distributed in coniferous forest ecosystems. Gilbertson and Ryvardeen (1986) suggested that because fossil records indicate brown rot fungi

TABLE 1. Some uses of snags by selected wildlife species (as modified from Neitro et al. 1985)

Use	Pileated woodpecker	Red-breasted sapsucker	Acorn woodpecker	Turkey vulture	Owls and raptors	Osprey	Bald eagle	Flycatchers	Brown creeper	Bats	Raccoon and black bear	Small mammals
Cavity nest sites	X	X	X		X							X
Nesting Platforms						X	X					
Feeding substrate	X	X	X						X			
Plucking posts					X							
Singing or drumming (communication)	X	X	X									
Food cache or granary			X									X
Location of courtship	X	X	X									
Overwintering sites	X		X		X					X	X	X
Roosting	X	X	X	X	X	X	X			X		
Lookout posts				X	X	X	X	X				
Hunting and hawking perch					X	X	X	X				
Fledgling site						X	X					
Dwelling or dens											X	X
Loafing sites				X		X	X					
Nesting under bark									X			
Communal nesting or nursery colonies			X							X		
Anvil sites			X									
Thermally regulated habitat	X	X	X		X					X		X

were present about 300 million years ago during the carboniferous age when the development of woody gymnosperms began, brown rot fungi evolved along with conifers and probably played an important ecological role in the evolution of coniferous forest ecosystems.

We know that, on the forest floor, brown rot residues remain essentially unaltered in the soil for hundreds of years. They may comprise up to 30% of soil volume in the upper layers, are major sites of ectomycorrhizal development and nonsymbiotic nitrogen fixation, may increase the

water-holding capacity of the soil, ameliorate soil temperatures, and increase the soil cation exchange capacity (Gilbertson and Ryvardeen 1986). The extent of specialized roles that brown rot fungi may play in the canopy zone is largely unknown.

Conclusions

Death and decay of woody components of tree crowns, including heartrot of living stems, dead branches, and dead trees, are important, functional aspects of forest canopies that have been largely ignored in forest canopy studies because of the difficulty of access and quantification. Generally, ecologists have underestimated that the way trees die can markedly influence numerous ecological processes. Most study of this important resource has been by wildlife biologists interested in habitat associations, and by forest pathologists interested

in reducing losses of timber value. In no way do we intend to question the need to reduce losses of timber volume in forest plantations where economy is the driving factor; we only want to elucidate the importance and functional aspects of decaying and dead trees in the forest canopy because we believe it is critical and not well understood. Canopy studies must include decaying and dead trees as subcomponents of the ecosystem if we are to more thoroughly understand what is occurring aboveground.

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Literature Cited

- Aho, Paul E. 1977. Decay of grand fir in the Blue Mountains of Oregon and Washington. USDA For. Serv. Res. Paper PNW-229. Pac. Northw. For. and Range Exp. Sta. Portland, Oregon. 18 p.
- Akenson, J. J., and M. G. Henjum. 1994. Black bear den site selection in the Starkey study area. *In* L. Starr (ed.) Natural Resource News. Blue Mountains Natural Resources Institute, La Grande, Oregon. 4(2):1-2.
- Almack, J. A. 1985. Grizzly bear habitat use, food habits, and movements in the Selkirk Mountains, northern Idaho. *In* G. P. Contreras and K. E. Evans (tech. comps.) Proc. Grizzly Bear Habitat Symp. USDA For. Serv., Gen. Tech. Rep. INT-207. Intermountain Res. Sta., Ogden Utah. Pp. 150-157.
- Ausmus, B. S. 1977. Regulation of wood decomposition rates by arthropod and annelid populations. *Ecol. Bull.* 25:180-192.
- Beckwith, R. C., and E. L. Bull. 1985. Scat analysis of the arthropod component of pileated woodpecker diet. *Murrelet* 66:90-92.
- Blanchett, R. A., and C. G. Shaw. 1978. Associations among bacteria, yeasts and basidiomycetes during wood decay. *Phytopathology* 68:631-637.
- Boddy, L. 1983. Microclimate and moisture dynamics of wood decomposing in terrestrial ecosystems. *Soil Biol. Biochem.* 15(2):149-157.
- Boddy, L. 1992. Development and function of fungal communities in decomposing wood. *In* G. Carroll and D. Wicklow (eds.), *The Fungal Community: Its Organization and Role in the Ecosystem*. Marcel Dekker, Inc., New York. Pp. 749-782.
- Byler, J. W., M. A. Marsden, and S. K. Hagle. 1990. The probability of root disease on the Lolo National Forest, Montana. *Can. J. For. Res.* 20:987-994.
- Childs, T. W. 1960. Laminated root rot of Douglas-fir. *USDA For. Serv. Forest Pest Leaflet*, 48:6.
- Childs, T. W., and K. R. Shea. 1967. Annual losses from diseases in Pacific Northwest Forests. *USDA For. Serv. Resource. Bull. PNW-20*. Pac. Northw. Res. Sta., Portland, Oregon. 19 p.
- Cline, S. P., A. B. Berg, and H. M. Wight. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. *J. Wildl. Manage.* 44:773-786.
- Elton, C. 1966. *The Pattern of Animal Communities*. Wiley and Sons, New York.
- Erickson, H. E., R. L. Edmonds, and C. E. Peterson. 1985. Decomposition of logging residues in Douglas-fir, western hemlock, Pacific silver fir, and ponderosa pine ecosystems. *Can. J. For. Res.* 15:914-921.
- Franklin, J. F., and R. H. Waring. 1980. Distinctive features of the Northwestern coniferous forest: development, structure, and function. *In* R. H. Waring (ed.), *Forests: Fresh Perspectives from Ecosystem Analysis*. Oregon State University Press, Corvallis, Oregon Pp. 59-85.
- Furniss, R. L. 1936. Bark beetles active following Tillamook fire. *Timberman* 37:21-22.
- Goils, B. 1992. Analyzing landscape patterns caused by forest pathogens: review of the literature. *In* Proceedings of the 40th Annual Western International Forest Disease Work Conference, July 13-17, Durango, CO. USDA For. Serv. PSW-FPM, San Francisco, California. Pp. 21-32.
- Gilbertson, R. L., and L. Ryvardeen. 1986. *North American Polypores*, Vol. 1. Fungiflora, Oslo, Norway. 433 p.
- Graham, R. L., and K. Cromack, Jr. 1982. Mass, nutrient content, and decay rate of dead boles in rain forests of Olympic National Park. *Can. J. For. Res.* 12:511-521.
- Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. Cromack, Jr., and K. W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. *Adv. Ecol. Res.* 15:133-301.

- Harvey, A. E., M. J. Larsen, M. F. Jurgensen, and E. A. Jones. 1989. Nitrogenase activity associated with decayed wood of living northern Idaho conifers. *Mycologia* 81(5):765-771.
- Hawksworth, D. L., B. C. Sutton, and G. C. Ainsworth. 1983. Dictionary of the Fungi. Commonwealth Mycological Inst., Kew, Surrey, Commonwealth Agricultural Bureaux, Slough, England.
- Hennon, P. E., and E. M. Loopstra. 1991. Persistence of western hemlock and western redcedar trees 38 years after girdling at Cat Island in southeast Alaska. USDA For. Serv. Res. Pap. PNW-RN-507. Pac. Northw. Res. Sta., Portland, Oregon. 5 p.
- Hennon, P. E., C. G. Shaw III, and E. M. Hansen. 1984. Is a pathogen the primary cause of decline and mortality of *Chamaecyparis nootkatensis* in southeast Alaska? In Proceedings for 32nd Western International Forest Disease Work Conference, September 25-28, 1984, Taos, New Mexico. Can. For. Serv. Victoria, B.C., Canada. Pp. 15-23.
- Hennon, P. E., C. G. Shaw III, and E. M. Hansen. 1990. Dating decline and mortality of *Chamaecyparis nootkatensis* in southeast Alaska. *For. Sci.* 36:502-513.
- Hepting, G. H. 1971. Diseases of Forest and Shade Trees of the United States. USDA For. Serv. Agric. Handb. 386. Washington, D.C.
- Hobbs, S. D., and A. D. Partridge. 1979. Wood decays, rootrots, and stand composition along an elevation gradient. *For. Sci.* 25:31-42.
- Hudson, H. J. 1968. The ecology of plant remains above the soil. *New Phytol.* 67:837-874.
- Jurgensen, M. F., A. E. Harvey, M. J. Larsen, and J. R. Tonn. 1989. Soil organic matter, timber harvesting, and forest productivity in the Inland Northwest. In Proceedings, Symposium on Forest Productivity, 7th North American Forest Soils Conference, July 25 to 27, 1988, Vancouver, B.C., Canada.
- Käärik, A. A. 1974. Decomposition of wood. In C. H. Dickson and G. J. E. Pugh (eds.), *Biology of Plant Litter Decomposition*, Vol. I. Academic Press, London. Pp. 129-174.
- Knight, D. H. 1987. Parasites, lightning, and the vegetation mosaic in wilderness landscapes. In M. G. Turner (ed.), *Landscape Heterogeneity and Disturbance*. Springer-Verlag, New York. Pp. 59-83.
- Manion, P. D. 1981. *Tree Disease Concepts*. Prentice-Hall, Inc., Englewood Cliffs, N.J. 399 p.
- Maser, C., and J. M. Trappe (tech. eds.) 1984. The seen and unseen world of the fallen tree. USDA For. Serv. Gen. Tech. Rep. PNW-164. Pac. Northw. For. and Range Exp. Sta., Portland, Oregon.
- McClelland, B. R., and S. S. Frissell. 1975. Identifying forest snags useful for hole-nesting birds. *J. For.* 73:414-417.
- McCune, B. 1993. Gradients in epiphyte biomass in three *Pseudotsuga-Tsuga* forests of different ages in western Oregon and Washington. *The Bryologist* 96:405-411.
- Means, J. E., P. C. MacMillan, and K. Cromack, Jr. 1992. Biomass and nutrient content of Douglas-fir logs and other detrital pools in an old-growth forest, Oregon, USA. *Can. J. For. Res.* 22:1536-1546.
- Neitro, W. A., R. W. Mannan, D. Taylor, V. W. Binkley, B. G. Marcot, F. F. Wagner, and S. P. Cline. 1985. Snags. In E. Reade Brown (ed.), *Management of Wildlife and Fish Habitats in Forests of Western Oregon and Washington*. Part 1—Chapter narratives, Chap. 7. R6-F&WL-192. USDA For. Serv., Pac. Northw. Region, Portland, Oregon. Pp. 129-169.
- Oliver, C. D., and B. C. Larson. 1990. *Forest Stand Dynamics*. McGraw-Hill, Inc. San Francisco.
- Oliver, C. D., and E. P. Stephens. 1977. Reconstruction of a mixed species forest in central New England. *Ecology* 58:562-572.
- Pike, L. H., R. A. Rydell, and W. C. Denison. 1977. A 400-year-old Douglas-fir tree and its epiphytes: biomass, surface area, and their distributions. *Can. J. For. Res.* 7(4):680-699.
- Setliff, E. C. 1986. Wood decay hazard in Canada based on Scheffer's climate index formula. *For. Chron.* (October):456-459.
- Shigo, A. L., and H. G. Marx. 1977. Compartmentalization of decay in trees. (CODIT). USDA For. Serv. Agric. Inf. Bull. 405. 73 p.
- Sollins, P., S. P. Cline, T. Verhoeven, D. Sach, and G. Spycher. 1987. Patterns of log decay in old-growth Douglas-fir forests. *Can. J. For. Res.* 17:1585-1595.
- Swift, M. J. 1977. The ecology of wood decomposition. *Sci. Prog. Oxf.* 64:175-199.
- Swift, M. J. 1982a. Microbial succession during the decomposition of organic matter. In R. G. Burns and J. M. Slater (eds.), *Experimental Microbial Ecology*. Blackwell Sci. Publ., Oxford, England. Pp. 164-177.
- Swift, M. J. 1982b. Basidiomycetes as components of forest ecosystems. In J. C. Frankland, J. N. Hedger, and M. J. Swift (eds.), *Decomposer Basidiomycetes: Their Biology and Ecology*. Cambridge University Press, New York. Pp. 307-337.
- Thomas, J. W., R. G. Anderson, C. Maser, and E. L. Bull. 1979. Snags. In J. W. Thomas (tech. ed.), *Wildlife Habitats in Managed Forests: the Blue Mountains of Oregon and Washington*. USDA For. Serv. Agric. Handb. 553. Pp. 60-77.
- Wickman, B. E. 1978. Tree mortality and top-kill related to defoliation by the Douglas-fir tussock moth in the Blue Mountains outbreak. USDA For. Serv. Res. Pap. PNW-233. Pac. Northw. For. and Range Exp. Sta., Portland, Oregon. Pp. 47.
- Witmer, G. W., M. K. Kuttel, M. Wisdom, I. D. Luman, E. P. Harshman, R. J. Anderson, R. W. Scharpf, C. Carey, and D. Smithey. 1985. Deer and Elk. In E. Reade Brown (ed.), *Management of Wildlife and Fish Habitats in Forests of Western Oregon and Washington*. Part 1—Chapter narratives, Chap. 11. USDA For. Serv., Pacific Northwest Region, Portland, Oregon. Pp. 231-258.
- Woodfin, R. O. 1976. Potentials from salvage timber. In R. Mosley (chair), *The wood product industry in the Rocky Mountain area—today and tomorrow*. Rocky Mountain Forest Industries Assoc., Missoula, Montana. Pp. 89-95.
- Yoneda, T. 1975. Studies on the rate of decay of wood litter on the forest floor. II. Dry weight loss and CO₂ evolution of decaying wood. *Jap. J. Ecol.* 25(3):132-140.