

Comparing Deterioration and Ecosystem Function of Decay-resistant and Decay-susceptible Species of Dead Trees¹

Paul E. Hennon,² Michael H. McClellan,³ and Patricia Palkovic⁴

Abstract

The pattern and rate of deterioration of dead trees vary by species, which leads to important differences in their ecosystem function. This is illustrated by two species with different modes of death and decay: yellow-cedar (*Chamaecyparis nootkatensis*) and western hemlock (*Tsuga heterophylla*). The heartwood of yellow-cedar contains compounds that inhibit decay. Most yellow-cedar trees die standing and persist as snags with intact tops for 80 years or more. Western hemlock lacks these specialized heartwood compounds and exhibits a more rapid deterioration. Also, modes of tree death, heart rot levels, and type of saprophytic decay may differ considerably by stand age for western hemlock. A greater diversity of structures is produced by the death and deterioration of western hemlock than yellow-cedar.

Introduction

Our research on dead trees in southeast Alaska has two origins. For yellow-cedar (*Chamaecyparis nootkatensis*), we developed a snag class system and conducted ground surveys in an attempt to reconstruct the epidemiology (i.e., timing of onset and population changes) for the extensive mortality problem that this species is experiencing. A more applied continuation of that research led us to describe the patterns of deterioration and recovery of the dead yellow-cedar resource. A separate line of research has focused on the mortality of trees in the western hemlock (*Tsuga heterophylla*) dominated old-growth forests. Here, it was necessary to reconstruct mortality of canopy-level trees so that we could interpret the factors that were driving small-scale disturbance in these forests. An applied aspect of this latter research is to evaluate the extent to which the factors that contribute to structural diversity and small-scale disturbance are maintained after different silvicultural treatments.

The objective of this paper is to contrast what we have learned about the death, decay, and ecosystem function of these two tree species: yellow-cedar and western hemlock.

¹ An abbreviated version of this paper was presented at the Symposium on the Ecology and Management of Dead Wood in Western Forests, November 2-4, 1999, Reno, Nevada.

² Research Pathologist, State and Private Forestry and Pacific Northwest Research Station, USDA Forest Service, 2770 Sherwood Lane, 2A, Juneau, AK 99801 (e-mail: phennon@fs.fed.us)

³ Research Ecologist, Pacific Northwest Research Station, USDA Forest Service, 2770 Sherwood Lane, 2A, Juneau, AK 99801 (e-mail: mmcclellan@fs.fed.us)

⁴ Forester, Department of Natural Resources, Division of Forestry, 2030 Sealevel Dr. #217, Ketchikan, AK 99901.

Snag and Log Classification Systems

Existing snag and log classification systems proved to be inadequate for our use in both tree species. Such schemes (Cline and others 1980, Maser and others 1979) typically have classes in which tops progressively break, gradually reducing the heights of snags through time. For yellow-cedar, our early observations indicated that dead trees do not appear to have their tops break repeatedly as they deteriorate. For western hemlock, a tree species that contains considerable heart rot as a live tree in old forests, classifying snags and logs based on the decay levels of wood was not appropriate. Otherwise, some live trees or recently-killed trees would be classified as dead long ago. One of our objectives is to reconstruct tree mortality patterns through time (i.e., establish epidemiology rather than simply report structural condition of dead trees). Thus, we needed to use characteristics other than wood decay to distinguish groups of dead trees. We chose to develop a new system where we focused on the presence of primary limbs, secondary limbs, and twigs; we suspected that their presence was a more reliable indicator of how long trees had been dead. For western hemlock, our classes were aligned with an established snag and log decomposition system (Maser and others 1979, *table 1*).

Table 1—Description of the snag/log class system and time-since-death estimates for each class of dead overstory trees of yellow-cedar (Hennon and others 1990) and western hemlock.¹

Structures retained, soil contact	Yellow-cedar		Western hemlock	
	Snag/log class #	Mean, time-since-death (yrs)	Snag/log ² class #	Range, time-since-death (yrs)
Foliage	1	4	-	-
Twigs	2	14	1	0-12
Secondary branches	3	26	2	12-33
Primary branches	4	54	3	33-63
No limbs	5	81	4	63-117
Bole broken at soil level	6	Not dated	-	-
Integrated into soil	-	-	5	Not dated

¹ Unpublished data on file at the Department of Natural Resources, Division of Forestry, Ketchikan, AK.

² For western hemlock, our snag/log classes 1 through 4 align with snag stages 3 through 6, respectively, as described by Maser and others 1979; for downed material, our snag/log classes align with their log decomposition classes as follows, respectively: 1=1; 2 and 3=2; 4=3; 5=4 and 5.

We used two methods to date the death of yellow-cedar snags (Hennon and others 1990b): determining radial growth release of previously suppressed western hemlock and mountain hemlock (*Tsuga mertensiana*) that grew directly beneath larger yellow-cedar snags, and counting annual growth rings from a strip of callus tissue that connected one or more live roots to a single live branch in yellow-cedar trees that had a dead top and most of the bole was dead. For dead western hemlock, we determined time-since-death by finding trees cut and left at known times of partial timber harvesting (n=16), counting annual rings in wounds of adjacent trees that were scarred when live trees were windthrown (n=20), and aging conifer regeneration that had established on downed logs (n=15).

The snag/log classification systems that we develop for yellow-cedar and for western hemlock and average time-since-death for each class are given in *table 1*.

Note the comparable time-since-death for dead cedar and hemlock with similar branch conditions. The condition of the wood and persistence of snags standing for the two species are extremely different, however.

Patterns of Deterioration

The difference in heartwood chemistry between yellow-cedar and western hemlock is the key to understanding the vastly different pattern and rate of wood deterioration. Yellow-cedar has generally received little research attention until recently, but its heartwood chemistry is quite well known. Of the compounds reported in yellow-cedar heartwood (*table 2*), only nootkatin and chamic acid have been tested for their biological activity against fungi. Nootkatin is active at concentrations as low as 0.001 percent (Rennerfelt and Nacht 1955). These various compounds give the heartwood its color and aroma, as well as the wood's classification as being "resistant or very resistant" to decay (Forest Products Laboratory 1987). Western hemlock heartwood lacks these specialized compounds and is known as "slightly or non-resistant" to decay (Forest Products Laboratory 1987).

Table 2—*The known heartwood constituents of yellow-cedar (Hennon and Harris 1997).*

Compound	Identification, conformation, synthesis, or assay
Alaskene	Marx and Lewis 1973
Carvacrol	Erdtman 1952, Carlsson and others 1952
Chamic acid ¹	Carlsson and others 1952, Erdtman 1955, Rennerfelt and Nacht 1955, Erdtman and others 1956, Nordin 1964, Gensler and Solomon 1973, Nordin and others 1982
Chaminic acid	Erdtman 1955, Erdtman and others 1956, Nordin 1964
Chanootin	Nordin 1964, Karlsson and others 1973
Isochamic acid	Nordin 1964
Nootkatene	Erdtman and Topliss 1957
Nootkatin ²	Aulin-Erdman 1950, Campbell and others 1952, Erdtman and Harvey 1952, Carlsson and others 1952, Duff and Erdtman 1954, Duff and others 1954, Johnson and Cserjesi 1975
Nootkatone	Erdman and others 1962, Ishida and others 1970, Odom and Pinder 1972, Dastur 1974, Yanami and others 1980
Valerianol	Odom and Pinder 1972
Vetivone	Dastur 1974

¹ Active against fungi at 0.01 percent (Rennerfelt and Nacht 1955).

² Active against fungi 0.001 percent (Rennerfelt and Nacht 1955).

For trees that die standing, yellow-cedar and western hemlock show differences soon after death. The needles on dead western hemlock trees are shed within a few months after trees die, but the scale-like foliage of yellow-cedar trees adheres to twigs for several years (*table 1*). Bark becomes loose and begins to slough away within several years for both species. The sapwood of both cedar and hemlock is colonized by fungi that initiate stain and wood decay. These sapwood fungi and other wood decay fungi continue their decay in the heartwood of western hemlock. Until this stage, the deterioration of the wood for the two tree species does not differ appreciably, but profound differences appear later. Eighty years after death, the

penetration of decay in yellow-cedar wood is typically limited to less than 4 cm (fig. 1). Finally, approximately a century after death, soil-borne fungi create sufficient decay in the wood at the ground level so that the limbless tree boles of yellow-cedar break and fall. Soil-borne fungi are less influenced by yellow-cedar's heartwood compounds than other fungi (DeGroot and others 2000).

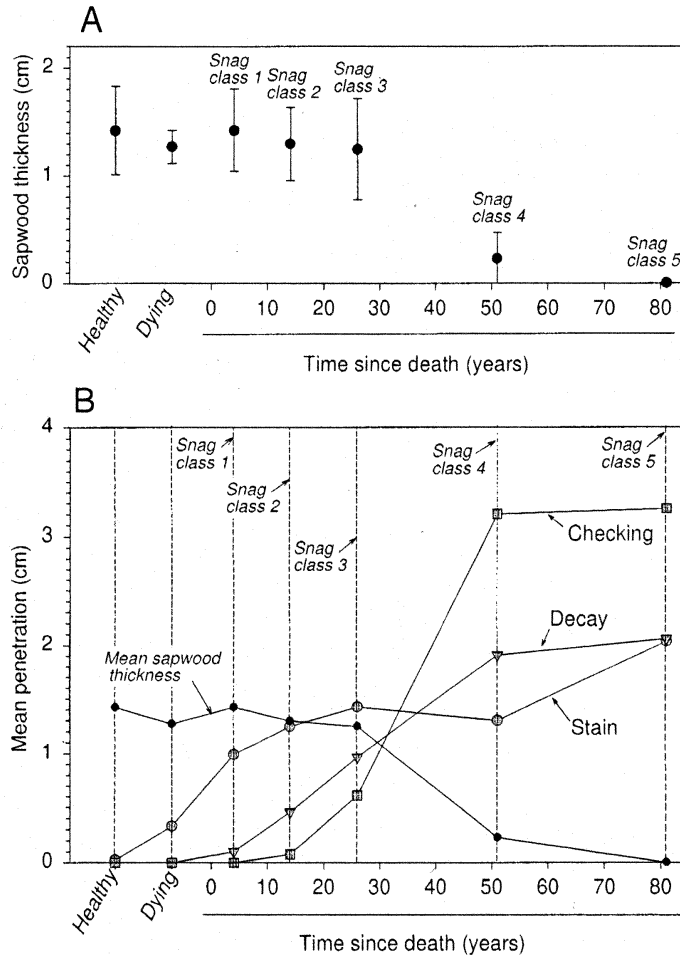


Figure 1—(A) Sapwood width, and (B) radial penetration of stain, decay, and checks (cracks) into the wood of yellow-cedar trees by classes of live trees, dying trees, and five snags.

For western hemlock, the decay process continues relatively unchecked as fungi penetrate into the heartwood. One fungus, *Fomitopsis pinicola*, causes a great amount of the decay in both the sapwood and heartwood. It degrades wood chemically in a process that selectively removes cellulose (i.e., brown rot) and leaves a residue of partially-modified lignin. A white rot fungus, *Ganoderma applanatum*, is also common as a wood decomposer of dead hemlock. As decay develops in the bole of dead hemlocks, the tops break, reducing the heights of snags in a pattern similar to many other conifers. We observed dead hemlocks 38 years after they were killed standing on Cat Island in southeast Alaska (Hennon and Loopstra 1991). Only one of

42 hemlocks had a standing portion taller than 10 m and most had broken within a few meters of the ground. The wood from all of these dead hemlocks was in a condition of advanced decay, most commonly colonized by *F. pinicola* or *G. applanatum* or both. These logs were all in the class 3 to 4 conditions (*table 1*). In the final stages of decomposition, tree boles of western hemlock become fully incorporated into the soil (Graham and Cromack 1982).

Which Trees Die? How Do They Die?

Most dead yellow-cedar trees within the stands experiencing yellow-cedar decline are overstory trees that died standing (Hennon and Shaw 1997). Of the more than 250 dying yellow-cedars that we have monitored for nearly 20 years, fewer than 2 percent have died by uprooting or bole breakage. Declining yellow-cedar forests cover more than 200,000 ha in Southeast Alaska. In declining stands, dead yellow-cedars in all five standing snag classes made up two-thirds of the yellow-cedar basal area (Hennon and others 1990a).

The type of tree death for western hemlock is more variable and is influenced by stand age. Hemlocks dying in young-growth forests are predominantly small, suppressed trees that die standing from competitive stresses. Biotic agents are not generally important tree mortality factors in these stands. Uprooting of young trees is usually caused by the collapse of unstable organic rooting substrates (such as decaying logs or stumps) and not by wind.

Recently, we sampled tree mortality in a maturing even-aged stand near Sitka, the oldest known clearcut in Southeast Alaska. Many western hemlock trees had died standing, but many also died through bole breakage (*table 3*). Unlike in younger stands, much of the mortality in this stand was of the largest dominant trees. We suspect that much of this damage was from wind or snow loading and that these trees were predisposed to break because of their excessive height: diameter ratio. Heart rot was not involved with tree death in this stand.

In old-growth forests, western hemlock trees die standing, by bole breakage, and by uprooting. Many agents kill standing hemlocks; heart rot and gravity or wind often lead to bole breakage; and storms with associated heavy precipitation and wind cause much of the uprooting in upland forests. When large trees die by any of these mechanisms, gaps appear in the canopy and contribute to small-scale disturbance. We sampled 1180 dead hemlock trees in 27 old-growth stands in Southeast Alaska (Hennon and McClellan 1999) and found that uprooting is not the principal form of tree mortality, unlike in Washington (Graham and Cromack 1982). In reconstructing tree mortality, death by uprooting can be interpreted long after tree death because of the presence of the upturned root system. Distinguishing death as a standing tree or by bole breakage is more challenging because dead standing trees deteriorate and are reduced in height until they acquire the same broken-off, stump-like structure as that of trees that die by bole breakage. Our reconstruction showed that western hemlock trees most frequently die standing, fewer died from bole breakage, and fewer yet died from uprooting (*table 3*).

Table 3—Origins and functional characteristics of woody debris produced by three forms of tree mortality of western hemlock in different stages of stand development of upland forests in southeast Alaska. Type of tree mortality is very common (++) , common (+) , or uncommon (-) for each forest stage.

Stage of stand development	Dead standing	Bole breakage	Uprooting	Predisposing factors	Relative size of affected trees	Decay condition upon falling ¹	Primarily brown or white rot ²	Hollow logs ³	Root system attached ⁴	Soil mixing ⁵
Early young-growth (< 100 yrs)	++			Competition-suppression	smallest	decayed	brown, white?	no	no	no
		-								
			+	Unstable rooting substrate	smallest	undecayed	brown, white?	no	yes	no
Maturing young-growth (100 to 250 yrs)	++			Competition, other	all sizes	decayed	brown	no	no	no
		++		Small diameter/height ratio	tallest	undecayed	brown	no	no	no
Old-growth (>250 yrs)	++			Competition, diseases, insects	all sizes	decayed	brown, white	some	no	no
		+		Heart rot, gravity, wind, snow/ice	large	decayed	white, brown	frequent	no	no
			+	Wind, saturated soils, snow/ice	all sizes	undecayed	brown, white	some	yes	yes

¹ Standing trees become partially decayed before falling to the forest floor and into streams; bole breakage in old-growth often produces logs that are pre-decayed by either white or brown rot before falling; trees that uproot likely have less extensive heartrot while live

² Most deterioration of dead western hemlock is by the brown rot process, but, in Washington, Edmonds (1998) reports more white rot than brown rot in dead young-growth conifers. White rot may occur in old trees before any form of tree death.

³ Hollow logs are produced by white rot fungi in live trees, are common in hemlocks with all 3 types of mortality, but most common in trees that die by bole breakage

⁴ Attached root systems can function as an anchor for less mobility of woody debris in streams and rivers; birds may nest in upturned root systems

⁵ Soil mixing of organic and inorganic layers produced by uprooting may improve site productivity for tree growth

Ecosystem Roles of Dead Yellow-cedar and Western Hemlock

For yellow-cedar, three insects (a bark beetle [*Phloeosinus cupressi*], one or more longhorned beetles [e.g., *Opsimus quadrilineatus*], and a woodwasp [*Sirex* sp.]) are common in dying trees and class 1 snags but have completed their life cycles and abandoned the snags just 2 years after tree death (Schultz, pers. comm.) (fig. 2). The larvae residing under bark and the emerging adults are both potential food items for foraging birds. Little insect activity appears to occur in dead standing trees after they reach the class 2 stage. Loose and hanging bark could provide habitat for roosting bats on snags dead up to 14 years. We are beginning to evaluate these possible wildlife uses of each of the snag classes, but little is currently known about the extent to which dead cedars are used. Cavity nesting is apparently rare in dead yellow-cedars, likely because of the undecayed condition of heartwood even 81 years after death (fig. 1).

Johnson (1997) found a high rate of landslides associated with dead yellow-cedar forests on steep slopes where most of the trees were in snag class 4 (dead approximately 54 years). This probably occurs because the roots of these snags are decayed to the extent that hillsides become unstable (Johnson and Wilcock 1998). We know little about the deterioration of dead yellow-cedar trees and their interaction with soil processes and vegetation once they reach class 6, roughly 100

years after death. Possible roles of these downed yellow-cedar logs as they decay could be hiding cover for small mammals, seedling establishment for trees and other vegetation (i.e., nurse logs), and a nutrient source and substrate for roots, mycorrhizae, and soil invertebrates. Where yellow-cedar grows and dies in riparian areas, woody debris produced by this tree would likely persist as long or longer than any other wood in southeast Alaska. Thus, ecosystem function for dead yellow-cedar appears to be greatest immediately after tree death, is limited for above-ground processes as snags remain standing, and may increase about 100 years after tree death when snags break and fall to the forest floor.

Understanding the type of tree death for western hemlock is important because of the dominance of this species in the forests of coastal Alaska and the wide range of structures and processes that result from the different forms of tree mortality (*table 3*). Some structures are uncommon or absent during particular stages of forest stand development; also, several structures can only be produced by a specific form of tree death.

For example, uprooting of large conifers is the only form of tree mortality that produces large, dead trees with an attached root system. Uprooting mixes the inorganic and organic soil layers, counteracts some effects of soil development, and may maintain site productivity (Bormann and others 1995). In contrast, there is no soil mixing with trees that die standing or by bole breakage. When small trees in young-growth forests sometimes uproot on unstable, decayed woody substrates, they do not affect inorganic soil layers. The large anchoring root system attached to dead conifers that uproot in old-growth riparian forests may limit their mobility as woody debris and thereby enhance their function in streams and rivers.

Hollow logs develop with the combination of white rot fungi and tree response (i.e., “compartmentalization”) in live trees. Heart rot of western hemlock is extremely common in old-growth forests of southeast Alaska where 30 to 40 percent of the volume of live trees is defective and 62 percent of this decay is white rot (Kimme 1956). Heart rot levels are directly proportional to tree and stand age in southeast Alaska (Farr and others 1976) with little to none occurring in forests younger than 100 years (Kimme 1956).

Dead standing trees and downed logs, whether colonized by heart rot fungi before death or decayed after death, can function as important habitat for a wide range of wildlife species, both large and small (Maser and others 1979, 1988). At least twelve species of birds rely on tree cavities for roosting and nesting in southeast Alaska (Hughes 1985). But snags of western hemlock have a limited persistence as a dead standing tree. Our observations on 42 western hemlocks made 38 years after they were intentionally killed indicate two outcomes: 37 percent broke at the lower bole before developing extensive decay and then they decomposed intact on the ground, and 63 percent developed decay as a standing dead tree and then shattered into many fragments upon impact with the ground (Hennon and Loopstra 1991).

Most hemlock mortality in young forests involves small trees that die standing from suppression. Fungi colonize these small dead stems and their wood is partially decomposed before falling to the forest floor or into streams. Thus, woody debris produced in these young forests may provide a limited function compared with old-growth forests because of small piece size and lack of an attached root system. The decomposition process of conifer wood may differ between young and old forests as well; Edmonds (1999) reports that wood decay of conifers in young-growth forests

may favor white rot fungi over the more common brown rot found in old-growth forests. Repeated short rotations of young-growth forest could reduce the effects of brown rot, which produces stable residues that can contribute 30 percent of the volume in the upper layers of soil (McFee and Stone 1966). Generally, the variable type of tree mortality and the responding number of structures and processes in old-growth forests probably contributes to the structural diversity present in old-growth forests of southeast Alaska (Alaback 1982).

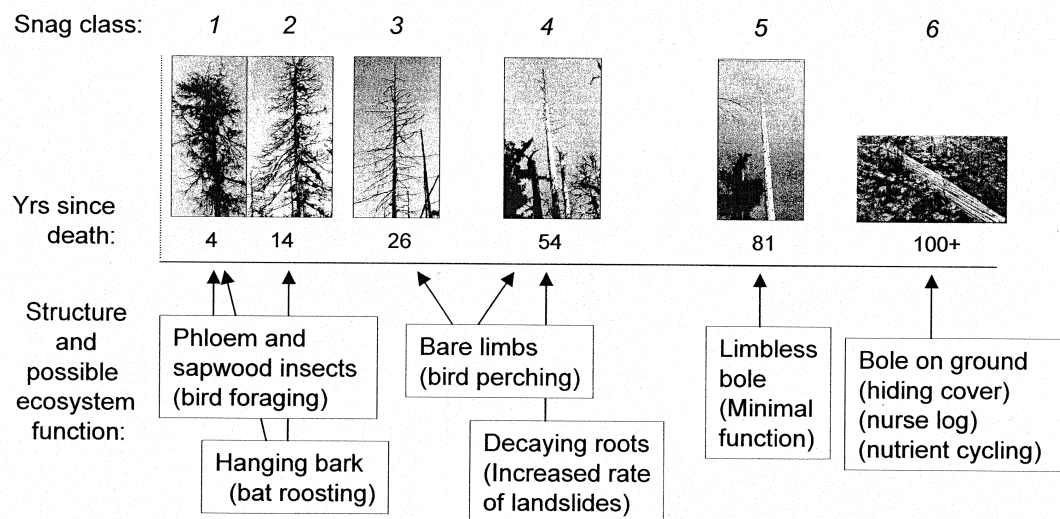


Figure 2—Potential ecosystem function of dead trees in each of the snag classes for yellow-cedar in southeast Alaska.

Summary

The defensive compounds in the heartwood of yellow-cedar alter the rate and pattern of deterioration in dead trees. Perhaps one compound, nootkatin, is responsible for the differences in decay between dead yellow-cedar and western hemlock trees and the corresponding structures that are produced. The tree containing this compound in its heartwood stands after death for nearly a century, possibly producing little in the way of terrestrial wildlife habitat, and finally breaks at the ground level to be decayed by soil organisms. The tree whose heartwood lacks this compound deteriorates rapidly, standing for a few decades at most, is used by many organisms in the complex number of structures produced, and falls to the forest floor where it becomes an integral part of the humus layer of soils.

Acknowledgments

Some results presented in this paper are from the USDA Forest Service study, “Alternatives to Clearcutting in the Old-Growth Forests of Southeast Alaska,” a joint effort of the Pacific Northwest Research Station, the Alaska Region, and the Tongass National Forest. We thank Mark Schultz and Adelaide Johnson for helpful suggestions on a draft of this manuscript.

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