

Are Heart Rot Fungi Major Factors of Disturbance in Gap-Dynamic Forests?

Abstract

Heart rot fungi cause substantial economic loss in many forests, but their ecological roles in altering the speed or direction of succession are frequently overlooked. As heart rot induces trees to die standing or, more commonly, by bole breakage, the fungi that cause heart rot can be viewed as both pathogens and agents of disturbance. Many forests that do not experience frequent, large-scale disturbance, such as those where fire is rare, are composed of old trees. Heart rot fungi are abundant in these old forests and are important ecologically as disturbance agents by initiating and sustaining canopy gaps. Heart rot fungi also have profound influence on numerous structures and processes such as nutrient cycling, vegetation composition, and wildlife habitat. This paper uses the temperate rainforest of southeast Alaska to explore ecological consequences of heart rot, including the role of heart rot fungi in canopy gap formation. A thorough understanding of disturbance ecology in such forests must involve closely integrated research among ecologists, mycologists, and pathologists.

Introduction

Virtually every important timber species in North America is invaded and decayed by one or more species of heart rot fungi (Gilbertson and Ryvarden 1986). The same undoubtedly applies for other tree species throughout the world. A considerable body of literature on commercial loss by heart rot has been developed since Hartig (1874) described the causal relationship of fungi. But the ecological role of heart rot fungi as disturbance factors in forests has received very little attention. The purpose of this paper is to explore this concept.

I use the western hemlock (*Tsuga heterophylla* (Raf.) Sarg.)-Sitka spruce (*Picea sitchensis* (Bong.) Carr.) temperate rainforest of coastal Alaska to illustrate how heart rot fungi may influence disturbance ecology. These forests provide an excellent setting to explore the ecological function of such pathogens and the concept of forest health in an ecosystem because of the large forested areas present with little direct impact by humans. Vast forests still exist that have not been subjected to timber harvesting, forest management, or fire suppression. Other pathogens, such as hemlock dwarf mistletoe (*Arceuthobium tsugense* (Rosendahl) G.N. Jones) and fungi that cause root diseases, are not the major focus of this paper even though they cause some, but as yet unmeasured level of disturbance-mortality or alter stand structure or species composition in these forests.

Initial observation and knowledge of their intensive infection levels and more extensive distribution suggest that heart rots play more important ecological roles, particularly in causing disturbance. I hope that the ideas that follow, some of which are hypothetical and speculative, will stimulate thinking and encourage a better working relationship among ecologists, mycologists, and pathologists.

Forest Dynamics in Coastal Alaska

The forests of the southeast portion of coastal Alaska are composed by volume of approximately 61% western hemlock, 33% Sitka spruce, and 6% cedars and other species (Harris and Farr 1974). An estimated 31% of the overall gross volume of old-growth forests in southeast Alaska is defective (Farr et al. 1976). Several factors have probably contributed to such a high proportion of defect including hemlock and spruce's susceptibility to decay, their thin bark that is easily wounded, and a wet, mild climate favorable for the development and spread of fungi. Time may also be a critical factor. Many forests in coastal Alaska are composed of old trees because of the infrequency of large-scale catastrophic disturbance. Fires are uncommon and not considered an important disturbance factor in most areas (Harris and Farr 1974, Alaback 1988). Landslides, glacial rebound, and large-scale windthrow appear to be more common disturbances on sites where topography and

other factors are favorable for their occurrence (Ruth and Harris 1979). The more frequently disturbed sites host one of the several stand development phases leading to the true "old growth" stage as described by Oliver and Larson (1990). But on other sites, perhaps centuries or even millennia elapse between large-scale disturbance events. Without frequent disturbance, forests are allowed to reach and persist in the old-growth stage where fungi apparently have ample time to cause their slow, but persistent heart rot decay.

Succession in these old-growth forests appears to be occurring on many sites as the result of small-scale disturbance in the form of gap-phase development (Alaback 1988). Canopy gaps form when one or more trees die standing, when boles break (sometimes called windbreak or stem snap), when trees are uprooted (sometimes called windthrow), or combinations of these. The incidence of the various causes of tree mortality leading to gap formation is only now being measured. Preliminary results and observation in the region by ecologists and me suggest that all three types are common and bole breakage is often the leading cause of tree death. High winds, water-saturated soils, and shallow root systems lead to susceptibility for uprooting (Alaback 1988). Until now, the consequences of uprooting is the only effect of small-scale disturbance mortality that have received much study in these forests.

Heart rot fungi may also facilitate the change from the maturing even-aged stage (i.e., understory reinitiation, to use Oliver and Larson's (1990) terminology) that is in transition to the true old-growth stage. Mortality of dominant trees may be necessary for this transition or at least it speeds the rate of change. In the four forests in southeast Alaska at this stage of development (150 to 165 years old) in which I have made observations, each had substantial levels of heart rot and many large trees were dying as a result of bole breakage. By contrast, earlier stages (i.e., stand initiation and stem exclusion) of stand development lack both high levels of heart rot and bole breakage. Disease levels are generally low at these early stages; most trees die standing from factors associated with competition (Hennon et al. 1994).

Heart Rot Fungi in Coastal Alaska

The dominant species of heart rot fungi of western hemlock and Sitka spruce in coastal Alaska

(Table 1) are well known to mycologists and pathologists, all are found in conifers throughout the Pacific Northwest of North America. Brown and white rot species are well represented in both hosts. Western hemlock and Sitka spruce host a large number of fungi (Hepting 1971). These fungi have been shown by regional studies to vary widely in the amount of decay caused throughout the ranges of their hosts. For example, the fungus *Echinodontium tinctorum* (Ellis & Everh.) Ellis & Everh. is known to cause heavy losses in portions of the range of western hemlock (Foster et al. 1954) but is absent on this host in coastal Alaska.

TABLE 1. Decay fungi of living of Sitka spruce and western hemlock in forests of coastal Alaska listed in descending order of importance (modified from Kimmey (1956).

Sitka spruce
<u>White rot fungi</u>
<i>Phellinus pini</i> (Thore:Fr.) Pilat
<i>Armillaria</i> spp.
<i>Heterobasidion annosum</i> (Fr.) Bref.
<i>Merulius</i> sp.
<i>Phellinus nigrolimitatus</i> (Rom.) Bourd. & Galz.
<u>Brown rot fungi</u>
<i>Fomitopsis pinicola</i> (Schwartz:Fr.) Karst.
<i>Phaeolus schweinitzii</i> (Fr.) Pat.
<i>Laetiporus sulphureus</i> (Bull.:Fr.) Murr.
<i>Antrodia heteromorpha</i> (Fr.) Donk.
<i>Lentinus kaufmanii</i> A.H. Smith
Western hemlock
<u>White rot fungi</u>
<i>Armillaria</i> sp.
<i>Heterobasidion annosum</i>
<i>Pholiota adiposa</i> (Fr.) Kumm.
<i>Phellinus hartigii</i> (Allesch. & Schnabl) Bond.
<i>Phellinus pini</i>
<i>Ganoderma applanatum</i> (Pers.:Wallr.) Pat.
<u>Brown rot fungi</u>
<i>Fomitopsis pinicola</i>
<i>Laetiporus sulphureus</i>
<i>Phaeolus schweinitzii</i>
<i>Hericium</i> sp.

Heart rot fungi are specialized organisms that attack the heartwood of trees that are still living. They colonize and begin the decomposition process of wood before the tree is dead. Ecologically, some are pioneers of the wood substrate, the first organisms to inhabit wood. In other cases, a heart rot fungus, although causing the most destructive decay, may follow others in a succession of organisms colonizing the wood of living trees (Shigo 1967, Etheridge 1973).

These fungi have different degrees of specialization and modes of attack. Several species (e.g., *Fomitopsis pinicola* (Schwartz:Fr.) Karst. and *Laetiporus sulphureus* (Bull.:Fr.) Murr.) are common and ecologically important as brown rot decomposers of downed woody debris. These are opportunists, they spread by aerial dissemination of spores and, presumably, invade hemlock and spruce through wounds with exposed wood, first as a sap rot and then heart rot of live trees (Etheridge 1973). Other species (e.g., *Armillaria* spp. and *Phaeolus schweinitzii* (Fr.) Pat.) produce decay in roots and spread into the butt portion of trees' boles. These so called "butt rot fungi" are believed to initially enter trees through root infection (Kile et al. 1991). Some species (e.g., *Heterobasidion annosum* (Fr.) Bref.) are able to spread both by vegetative growth from the root system into the lower bole and by spores to invade wounds. All of these fungi are capable of continuing to decompose wood after their host tree has died, standing or down.

Several other heart rot fungi are restricted to causing decay only in living trees and have specialized modes of attack. Etheridge (1972) called these fungi the "true heart rots." The heart rot fungus *Echinodontium tinctorium* infects conifers through small twigs then remains dormant, perhaps for decades, until the tree is stressed or injured (Etheridge and Craig 1976). Large bole wounds are not infection courts for the true heart rot fungi but these injuries do stimulate their growth and decay activity. Several heart rot fungi do not confine their assault to heartwood inside the boles of live trees. Species such as *Phellinus hartigii* (Allesch. & Schnabl) Bond., *P. pini* (Thore:Fr.) Pilat, and *P. chrysoloma* (Fr.) Donk. (Owens 1936, Boyce and Wagg 1955) may grow into the sapwood and phloem, killing tissues as they advance. This type of attack can result in death of a side of the tree or of the entire tree.

The true heart rot fungus *P. pini* is a leading cause of heart rot in many living western conifers, including all species of spruce and hemlock in Alaska (Holsten et al. 1985). Its primary avenue for infecting heartwood is probably through dead branch stubs (Boyce 1961) or very small twigs (Haddow 1938). Boyce and Wagg (1955) suggest that this heart rot fungus has a cyclical pattern of infection throughout the developmental stages of old Douglas-fir (*Pseudotsuga menziesii* (Murb.) Franco) forests. It infects vigorously growing Douglas-fir trees at about 50 years of age and, after most heartwood has been colonized, it attacks sapwood. Such trees experience a slowed radial growth and often die standing, sometimes 150-170 years after initial infection (Boyce and Wagg 1955). Because of its common occurrence (*P. pini* causes more than 80% of the heart rot in old-growth Douglas-fir) and through its habit of killing trees, this fungus may be a factor in the succession to shade-tolerant species such as western hemlock when stands reach 300-400 years of age.

What about heart rot in conifers with extremely decay resistant heartwood? Tree species in the Cupressaceae and Taxodiaceae, for example, have evolved to produce heartwood with high concentrations of compounds that retard the growth of decay fungi. Interestingly, each tree species has a complement of compounds which imparts its own unique aroma. These compounds have led to relatively little heart rot in some species, such as redwood (*Sequoia sempervirens* (D. Don) Endl.), which has great potential longevity. Or, when one or two fungal pathogens have become highly adapted to growth in such hosts, and presumably are tolerant of or able to detoxify the anti-fungal compounds, heart rot is extremely common and intensive. This is the case for western redcedar (*Thuja plicata* Donn ex D. Don) in coastal Alaska where more than half of its volume is rotten, 85% of which is caused by two fungi (*Phellinus weirii* (Murr.) Gilbt. and *Ceriporiopsis rivulosa* (Berk. & Curt.) Gilbn. & Ryv.) (Kimmey 1956).

"Pathological Rotation"

Numerous authors report that heart rot in various forest systems only becomes commercially threatening in older stands. In southeast Alaska, for example, conifers less than 100 years old have little decay, but by 200 years, 65% of western

redcedar, 50% of western hemlock, and 20% of Sitka spruce trees contain decay (Kimmey 1956). Farr et al. (1976) reported a significant correlation between tree age and the percentage of decayed wood volume.

The age of a stand when decay losses exceed annual increment was dubbed the "pathological rotation age" by Meinecke (1916). This age varies widely for different tree species and for a single species in different regions. Western hemlock, for example, reaches "unacceptable" decay losses at stand ages of 225 to 275 years in western British Columbia (Buckland et al. 1949) and 100 to 120 years in Idaho and Montana (Weir and Hubert 1918). The less subjective definition of pathological rotation is sometimes used, which is the stand age at which the decay rate is in equilibrium with the volume of wood produced annually (net wood volume produced is zero). Although this concept was developed for even-aged managed forests, it has ecological relevance to other forests. Many old-growth forests of coastal Alaska are probably near or past that equilibrium. Within age classes of trees, young-trees may be producing positive net volumes of wood each year, but many of the larger, older trees likely have decay losses that exceed wood volume produced.

Are Heart Rot Fungi Pathogens?

Clearly, the destruction of sapwood or phloem directly disrupts a tree's physiology and qualifies the causal organism as a pathogen. With the exception of a few heart rot fungi that continue to advance on the sapwood and cambium, however, most colonize only heartwood and injured sapwood. Although the heartwood is composed primarily of dead xylem cells, it contributes structural support—a vital function to large trees. Heart rot fungi may not always directly alter the physiology of a tree, but, by weakening the structural support of wood, they are frequently the cause of death by bole failure, thus also qualifying them as pathogens.

The relationship between heart rot and bole breakage has been frequently documented, although rarely interpreted ecologically. For obvious reasons, tree failure has been of particular interest to those concerned with potentially hazardous trees around recreation areas and homes. Wood decay is the leading cause of tree failure in such areas (Johnson 1981, Hadfield 1976). The

thickness of sound wood in the outer cylinder in trees with a central heart rot determines structural strength. Several models involving tree diameter and remaining sound wood have been designed to predict tree failure (Wagener 1963, Ossenbruggen et al. 1986, Harvey and Hessburg 1992).

Harris (1989) describes "windfirmness" in trees as the force of the wind on the crown and stem acting in opposition to the resistance of the tree to uprooting or breakage. In general, trees become less windfirm as they grow taller and larger because the force exerted on them by wind increases; and as trees become taller, the turning moment increases with the length of the lever arm (i.e., tree height). When a tree leans with the wind, the force of gravity on the crown and stem adds to the turning moment. Stem decay can provide a weak point in the stem which leads to failure through buckling.

The Heart Rot-Bole Breakage-Wound Cycle

Many of the fungi responsible for the considerable level of heart rot in conifers of coastal Alaska are likely spread by infectious spores colonizing large wounds. One such fungus, *F. pinicola*, is extremely common and causes an estimated 73% of cull in Sitka spruce and 22% of cull in western hemlock in coastal Alaska (Kimmey 1956). In British Columbia, wounding is associated with up to 65% of decay in live western hemlock trees (Buckland et al. 1949). Causes of wounds on trees in Alaska include porcupines, bears, beavers, logging, and road building, but falling trees appear to be the most common form of bole injury in western hemlock old-growth forests (Kimmey 1964). Scars are frequently colonized by decay fungi, particularly when wounds are greater than 0.1m² in surface area (Wallis et al. 1971).

The volume of decay is strongly correlated with wound size and scar age of western hemlock and Sitka spruce (Wright and Isaac 1956). Vertical and radial development of decay in wounded boles is quite variable and dependent, in part, on the causal fungus. Silverborg and Larsen (1967) measured the vertical spread of decay by *Phellinus pini* to be 0.26 m/yr, which is generally greater than that of various other tree species reported by Boyce (1961). Data from a study in progress on the rate of decay in wounded western hemlock

and Sitka spruce in Alaska suggest that very little decay develops 20 years after wounding and estimates of time from wounding to substantial radial and vertical decay development should be measured in decades (Hennon, unpublished data).

Thus, at some undetermined time after wounding, perhaps as long as a century or more, wood in the bole of the wounded tree may lose sufficient support and fail. As the bole breaks and the tree falls to the ground or lodges in other trees, one or more adjacent trees are likely to be wounded by having a portion of their bark scraped off. The bark of all coastal Alaskan tree species is thin, perhaps as a result of the rarity of fire, and offers little protection against wounding. Besides wounding, falling trees or snags often kill other trees; 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 (Franklin et al. 1987).

Assuming equal amounts of decay, trees with wounds and associated decay may be much more likely to experience bole breakage than unwounded trees with a central column of heart rot. Trees with heart rot limited to the central portion of their boles still maintain the integrity of the outer cylinder (Harvey and Hessburg 1992), whereas, trees with a wound and associated decay lose strength on one side. Piirto et al. (1984) examined large fallen giant sequoia trees (*Sequoiadendron giganteum* (Lindl.) Buchholz) and reported 21 of 33 trees had substantial decay in the area of failure. All but one of twenty seven trees with scars and decay fell in the direction of the scarred side.

The wound-invading heart rot fungi may thus be directly involved in causing gaps, probably by "fine-scale" or minor disturbance in which just one or a few trees are killed as described by Spies and Franklin (1989). The largest, oldest trees may be those most frequently affected by heart rot and bole breakage; their death would tend to create a substantial opening in the canopy. Because such a long period of time elapses between the wounding event and sufficient heart rot development to predispose a tree's bole to break, this heart rot-bole breakage-wound cycle (Fig. 1) may not perpetuate a simple expanding canopy gap. Rather, bole breakage occurs long after invasion, other vegetation responds, and canopy reclosure. Thus, gaps could be continually opening and closing in a scattered spatial pattern across the forest landscape.

Consequences of Mode of Death

Ecological studies on gaps should document how trees die because different types of tree mortality affect vegetation response (Putz et al. 1983, Franklin et al. 1987). For example, different opportunities exist for vegetation to respond in gaps where tree crowns thin slowly and trees die standing, compared to those where trees die suddenly by uprooting or bole breakage (Lertzman and Krebs 1991). In coastal Alaska, windthrow of trees by uprooting exposes mineral soil and mixes it with organic layers. This favors the reproduction of Sitka spruce (Deal et al. 1991). Uprooting also creates mounds which are important sites for regeneration and exploitation for both conifers and other vegetation. The decaying boles of uprooted and snapped trees enhance the regeneration of hemlock by serving as nurse logs (Ruth and Harris 1975, Harmon and Franklin 1989), but how previous heart rot in logs affects this regeneration is not known. Perhaps heart rot makes logs suitable for tree colonization more quickly but, because they are partially decomposed before tree death, these logs may not be as persistent as logs from living trees that had no heart rot. Uprooted trees and trees that die with broken boles usually fall to the ground and decay in place, slowly sinking into the forest floor. Trees that die and partially decompose standing finally fall to the ground and shatter, frequently scattering fragments of decayed wood across the forest floor (Hennon and Loopstra 1991).

The type of decay caused by heart rot fungi, whether white rot or brown rot, has ecological significance. Both types of decay occur in stages, first as a visible stain with little-to-no loss of wood strength followed by advanced decay with substantial loss of strength. The "white rot fungi" produce enzymes that diffuse relatively short distances, but enable them to degrade all major components of the cell walls of wood, sometimes resulting in pockets of decay surrounded by sound wood. In the late stages of some white rots, tree boles become entirely hollow. The "brown rot fungi," however, remove cellulose and hemicellulose from wood, but do not decompose lignin. Wood attacked by the brown rot fungi loses almost all of its strength, but persists as cubical pieces composed primarily of partially modified lignin. Brown rot residues are extremely stable and provide important properties to the organic compo-

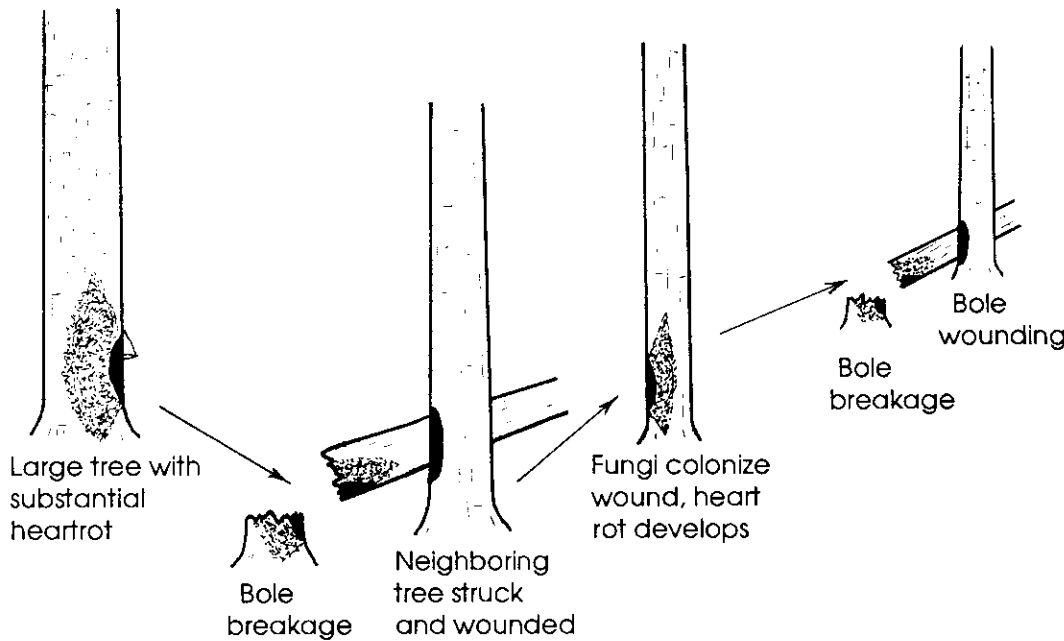


Figure 1. The hypothetical heart rot-bole breakage-wound cycle. Large, old trees frequently contain substantial amounts of heart rot in coastal Alaska. They are predisposed to die by bole breakage and frequently cause bole wounds on adjacent trees. The thin bark and decay-susceptible wood of coastal tree species offers little protection. Heart rot fungi colonize wood in the exposed wound and, long after the wounding event, these trees have developed enough heart rot to also succumb to bole breakage. The time required between bole wounding and the development of substantial heart rot suggests that this process of disturbance would result in small canopy gaps opening and closing in a dispersed spatial pattern.

ment of forest soils (Gilbertson and Ryvardeen 1986) where they may comprise up to 30 per cent of soil volume in the upper layers (McFee and Stone 1966). Nitrogen fixation is performed by various soil microorganisms in brown-rotted wood which leads to an important nutrient source for vegetation and their mycorrhizal symbionts (Larsen et al 1982). Nitrogen fixation has also been demonstrated in heart rot columns of live trees, including several combinations of tree and fungal species that occur in Alaska (Harvey et al. 1989). Thus, higher levels of nitrogen in live trees with heart rot may influence ecological processes after these trees die.

Ugolini and Mann (1979) suggest that old forests in coastal Alaska eventually convert to bogs if they persist for very long periods of time without a disturbance that causes soil mixing. Gradually, trees die as soil layers accumulate that restrict moisture drainage (i.e., paludification) and forest floor organic matter increases, tying up nutrients and oxygen. The mode of tree death (soil mixing from uprooting or without soil mixing from

bole breakage or trees dying upright) may affect the future productivity and direction of succession. Disturbance caused by heart rot fungi may contribute negatively to the long-term productivity of such sites. Whether paludification is occurring region-wide and bogs are the "climax" condition are not known (Harris and Farr 1974).

Heart Rot Fungi and Recent Gap-Phase Studies

Most studies on gaps have investigated the vegetation response to disturbance, but have not thoroughly examined causes of gap formation. Several recent studies, however, have documented different mortality causes of canopy-level trees. In a study of gap-dynamics of *Acer-Fagus* forests in Ohio, for example, Runkle (1990) described that gaps are caused in roughly equal numbers by trees being uprooted, broken off low (<2.5m) or broken off high. The very largest trees tended to die by bole breakage, but no mention of the presence of heart rot was made. Dead standing

trees were the most common gapmakers followed by trees with bole breakage and then uprooting in a subalpine forest in British Columbia (Lertzman and Krebs 1991). Putz et al. (1983) described the frequency of uprooting and bole breakage of trees in gap formation of a rainforest in Panama. Bole breakage accounted for 70% of fallen trees, but only 13% of these had heart rot, thus illustrating that tree boles can break without having heart rot. Bole breakage in this example was associated with tree species with low density, weak wood.

Bole breakage of old-growth overstory trees accounted for 30% and 19% of mortality in Douglas-fir and western hemlock, respectively, in Oregon and Washington (Spies et al. 1990). Associated heart rot was not discussed but, elsewhere, Franklin et al. (1987) described that a large percentage of windthrown old-growth Douglas-fir contain substantial butt rot by the decay fungus *Phaeolus schweinitzii*. Gratkowski (1956) did not distinguish between uprooting and bole breakage when discussing windthrow of old-growth Douglas-fir near cutting boundaries in Oregon, but the author did note that root rots (caused primarily by *Phellinus weirii*) and butt rots (caused primarily by *Phaeolus schweinitzii*) were associated with 34% and 20% of windthrow, respectively. Breakage high on boles accounted for only 5% of windthrown Douglas-fir, but every affected tree had advanced heart rot caused by *P. pini*. Holah et al. (1993) determined that root disease-mortality (caused by *Phellinus weirii*) initiated considerable change in the composition of plant communities in old-growth Douglas-fir forests in Oregon. Several root and butt rot fungi, including *P. weirii*, are likely important disturbance agents in coniferous forests of British Columbia (van der Kamp 1991) where they enhance biological diversity.

In a gap-phase forest in Japan, Kanzaki (1984) found heart rot to be more common in *Abies* spp., where it apparently led to high mortality, compared to *Tsuga diversifolia* (Maxim.) Masters. Kanzaki (1984) concluded that the "life-span" of some species in Japan may be determined by heart rot but the causal fungi or incidence of bole breakage were not reported. In a study on the causes of forest gaps at various elevations in New Hampshire (Worrall and Harrington 1988), diseases were responsible for up to 66% of the gap area with several species of root and butt rot fungi contribut-

ing to this disturbance at low elevations, primarily by bole breakage.

Heart Rot Fungi, Diversity, Stability, and Wildlife Habitat

Decay fungi, as members of the flora present, contribute directly to biological diversity of forests. Basidiocarps (conks) of some heart rot fungi are commonly collected as edibles (e.g., *L. sulphureus*) and at least one has been gathered because of its medicinal use (e.g., *Fomitopsis officinalis* (Vill.:Fr.) Bond. et Sing.). The latter fungus was also collected by Native shamen in coastal Alaska because it was thought to contain supernatural powers. The basidiocarps were carved into figures and, known as "bread of ghosts," were used in rituals and as the guardians of grave sites (Blanchette et al. 1992).

The old-growth phase of forests in coastal Alaska has extreme variation in vertical and horizontal structure (Alaback 1982). Heart rot fungi may contribute to maintaining this diverse phase by aiding in its development and stability. Frequent, small-scale disturbance (e.g., bole breakage gaps) may reduce the likelihood of large-scale pest epidemics because no single age group or stress group is widely represented as would be the case in a more homogenous forest. Along with the other forms of mortality, heart rot fungi contribute to the variety of snags, completely uprooted trees with their resulting associated pit and mound topography, and the stump-like lower bole of broken trees and hollow logs on the forest floor.

By increasing the variability of structure in forests, heart rot fungi indirectly enhance habitat for many wildlife species. Mortality factors of large trees that open the canopy and allow more light to reach the forest floor are beneficial to wildlife species that feed on understory vegetation, such as black-tailed deer in southeast Alaska (Taber and Hanley 1979).

Wood decay fungi initiate a complex succession of organisms in logs and standing boles that range from saprophytic microorganisms (some of which fix nitrogen), invading plants and their mycorrhizal fungi, animal herbivores and fungivores, omnivores, to many predators including vertebrates such as salamanders, bats, and bears (Maser et al. 1988). Heart rot fungi speed access to tree boles because many organisms, large and small, rely on the creation of open, internal spaces

in wood (Maser et al. 1988). Heart rot fungi are critically important for cavity nesting birds. Wood decay in trees is an essential precursor to use by cavity excavators (McClelland and Frissell 1975). Large trees that contain heart rot before they die may be particularly important to cavity-nesting birds because these trees may be used by primary excavators before and long after tree death.

Conclusions

Old hemlock-spruce forests of coastal Alaska have large quantities of heart rot. Many of these forests appear to be functioning by gap development between the long periods of episodic large-scale disturbances. Heartrot fungi may also contribute to large-scale disturbance; Harris (1989) suggested that catastrophic windthrow is more common in stands containing heartrot. Uprooted trees, trees with broken boles, and dead standing trees all appear to be common and seem to be initiating or continuing the development of gaps, perhaps in combination with one another. But until we gather such data, we will not have an understanding of what factors, alone or in combination, drive the gap-dynamic process of these forests.

Ecological studies on gaps should consider the disturbance role of heart rot fungi by determining the incidence of uprooted trees, trees whose boles break, and trees that die standing—all with and without the presence of heart rot. Comparisons should be made with the level of heart rot in

surviving, standing trees. Identifying heart rot fungi to species in these gaps will convey additional information on spatial relationships because we have knowledge of how some of these fungi spread within and among trees. For example, several of the root and butt rot fungi spread along root systems and kill adjacent trees in groups. Comparing the incidence of different gapmakers with site environmental variables may indicate that some sites favor heart rot and bole breakage while on other sites uprooting or standing death may be more common in gap development. Sites with soils that allow deeper rooting and thus greater resistance to uprooting (Putz et al. 1983), for example, may have relatively more bole breakage.

Although there are some apparent differences, the temperate rainforests of coastal Alaska may share a similar pattern of forest development with rainforests in the tropics and subtropics where large-scale disturbance is also infrequent. Perhaps the importance of pathogens, and heart rot fungi in particular, has been overlooked or downplayed in many of these gap-dynamic forests. Working together, ecologists, pathologists, and mycologists can contribute significantly to our understanding of disturbance ecology by investigating the causes as well as the consequences of tree mortality in studies on forest canopy gaps.

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