

Understanding and Defining Mortality in Western Conifers

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Tree mortality is a complex process that is influenced by plant physiology, the environment, stand succession, tree age and vigor, injuries, diseases, and insects (Shigo 1985, Harcombe 1987, Franklin et al. 1987). Common measures of animal mortality are not useful for trees. For example, tree death is not signified by a cessation of heartbeat; in fact, a tree's "heart" can rot and the tree remain alive for decades or even centuries. Trees die when they cannot acquire or transport sufficient resources to recover from attack by pathogens and insects, environmental stress, and injuries (Waring 1987). Trees die in three basic ways: mechanical disruption, dysfunction, and infection and energy loss (starvation) (Shigo 1985). Death may follow a period of acute stress that kills trees outright, or more frequently, stress predisposes trees to secondary agents such as root disease or bark beetles that kill weakened trees (Gara et al. 1985, Amman and Ryan 1991, Thies et al., in review). Forest fire, insects, and diseases are important historical and contemporary components of tree mortality and forest health in western North America (Wickman 1992, Hessburg et al. 1994, Campbell and Liegel 1996, Edmonds et al. 2000).

The death of a tree can be detrimental or beneficial, depending on viewpoint (Edmonds et al. 2000). A dead tree begins to lose economic value when it dies or shortly thereafter. Bark beetles and other insects introduce stain and decay-causing micro-organisms even before a tree is dead. These organisms deteriorate the sapwood and eventually the heartwood of roots, stems, and branches with the rate of deterioration dependent on many factors such as climate, site, tree species, and tree age. Dead trees are more flammable than live trees (Edmonds et al. 2000) and thus increase wildfire severity more than live trees. Dead trees or their parts generally are more prone to failure because of deterioration and therefore are potentially more hazardous to humans or their property than live trees (Harvey and Hessburg 1992). On the other hand, dead trees (snags) form ideal habitat for many wildlife species while the snags are standing and after they fall to the ground or into streams (Thomas 1979). Dead trees also aid in nutrient cycling as insects, fungi, and other micro-organisms decompose dead foliage, branches, stems, and roots (Waring and Schlesinger 1985). Regardless of viewpoint, economic or ecologic, it often is important to be able to determine if a tree is dead or how long it has to live.

Although many would consider the death of a single tree or small groups of trees as a natural or innocuous event in forest stand dynamics and development, there often is question as to whether injured trees are dead or alive following major disturbances such as wildfire. There are important resource management considerations with western conifers, such as post-fire salvage harvest, where it is necessary to determine whether a tree is alive, dead, or will soon be dead, as accurately and expediently as

possible. There is controversy over labeling injured green trees as “dead” even when it is virtually certain that they will die in a few years (delayed mortality). A tree may incur injury that makes mortality imminent. In some cases, the crown may remain green, however, and non-symptomatic for a few years before actual death. Many such trees eventually exhaust all resources, die, and become snags. Frequently, resource managers need to determine tree survival soon after a catastrophic event such as wildfire. Waiting for trees to show symptoms of mortality can exacerbate forest conditions that promote beetle epidemics that can affect healthy green trees.

Delayed mortality in fire-injured conifers is a second-order fire effect that is gaining greater recognition and study, as evidenced by recent publications in the fire-effects literature (Fowler and Sieg 2004). Many fire-effects studies have focused on plant communities that developed under frequent fire-return intervals and low-severity fire regimes that have missed multiple fire-return cycles over the last century, and then were exposed to an uncharacteristically severe fire event. This may have resulted from a greater than normal fuel load ensuing from an unusually long fire-return interval. It is mostly within these uncharacteristically severe fires that delayed mortality of pre-settlement era ponderosa pines has been reported (Ryan and Frandsen 1991). Delayed mortality also has been observed for other tree species in other plant associations and fire regimes as well (Thomas and Agee 1986, Ryan and Amman 1996, van Mantgem et al. 2003).

In this paper, we discuss and attempt to answer three questions: 1) What are common precursors of conifer mortality? 2) When is tree death imminent? and 3) When is a tree dead?

Basic Tree Physiology and Tree Mortality

Translocation of carbohydrates within trees is necessary to support five different physiological processes. Oliver and Larson (1996) identify the priority order of the allocation of these resources:

- 1) Maintenance of living tissue (respiration)
- 2) Production of fine roots
- 3) Flower and seed production
- 4) Primary growth (elongation of branches and roots).
- 5) Secondary/diameter growth (growth of xylem) and developing active resistance mechanisms to insects and diseases such as increased resin production

Trees eventually die when the amount of carbohydrates used in respiration exceeds that produced in photosynthesis, and termination of respiration is the final stage in the process of tree death. Respiration ceases as the result of depletion of stored carbohydrates following the end of carbohydrate production (photosynthesis) or translocation. Carbohydrate production occurs in the crown and varies substantially with light, temperature, moisture, nutrients, and season (Kramer and Kozlowski 1979, Waring and Schlesinger 1985). Carbohydrates are required by all living cells of the tree, and the transport function of the phloem is required to distribute these products from the crown to the stem and roots. Respiration produces energy through the oxidation of carbohydrates, and this process continues to some degree at all times in a

living tree throughout the year. Net carbohydrate production (photosynthesis) needs to exceed respiration rates for trees to sustain life.

Conifers are highly compartmentalized, having woody (large roots and stems) and non-woody parts (foliage, reproductive cones, and fine absorbing roots) (Shigo 1985). The roots acquire water, minerals, and nutrients through the fine root hairs and mycorrhizae and move them into the root xylem for transport up through the bole xylem to the crown. The phloem transports products of photosynthesis (carbohydrates) downward for storage mainly in the lower bole and roots. Thus, the bole serves to transport water upward and carbohydrates downward. A tree remains alive after injury and infection because of its ability to set firm boundaries around affected tissues. This is in contrast to animal systems where a bacterial infection may attack the whole organism. While forming barrier zones to isolate an injury, insect, or pathogen, the tree sacrifices space used for storing energy reserves. More reserves are deployed in regenerating new tissues. If the volume of new energy-storing tissue formed after injury and infection is equal to or greater than the volume of tissue walled off, the tree can survive (Shigo 1985). Uninjured portions of the tree will remain functioning when other portions die or are destroyed until those parts are impacted by loss of necessary support of carbohydrates and water.

Large trees have potentially larger carbohydrate reserves, stored primarily in the roots (as well as the buds, stem, and cambium), and may draw on those reserves during periods of environmental stress, or when functional portions of the tree are damaged or killed (Waring and Schlesinger 1985). While large trees have potentially large reserves, they also have proportionally higher maintenance costs (respiration to photosynthesis ratio) than smaller trees because of the larger proportion of stem wood per unit of foliage (Waring 1987). Therefore, large trees have proportionally smaller crowns to their total biomass, and are more likely to have deficit carbohydrate production when stressed or damaged.

The resource allocation hierarchy creates a physiological tradeoff between allocating carbohydrates for growth and reproduction, or for the production of defensive compounds. If carbohydrates are allocated primarily for growth, then less is available for the production of defense chemicals such as phenols, tannins, and terpenoids that can interfere with attack by insects and pathogens (Waring and Schlesinger 1985, Herms and Mattson 1992). This has important ramifications for tree health and survival.

Common Precursors of Conifer Mortality: Root Disease, Insects, and Fire

Tree mortality can be a gradual process when tree vigor is impacted due to cumulative site, environmental, or biotic factors including some insects and most diseases. Mortality can be more abrupt when secondary biotic agents, such as bark beetles, respond to declining tree vigor, or it can be immediate when injuries, such as from severe wildfire, significantly disrupt or destroy main functional processes. Most biotic agents such as pathogens or insects attack, damage, or kill a limited portion of a tree. Root pathogens kill roots, bark beetles damage stems, and defoliating insects injure crowns, especially if the tree has been weakened (Edmonds et al. 2000). If any of the main structural components (crown, stem, or roots) are destroyed or sufficiently damaged, that part of the tree will die; the surviving components will continue

functioning until they are impacted by loss of the dead portion. Also, the physiological impact of a localized attack in one part of a tree usually is transmitted to other distant parts, often in a complex manner that eventually affects the whole tree (Kramer and Kozlowski 1979). Girdled trees eventually die because of depleted water and carbohydrates, and injury to the root system as the transport function of the stem phloem is destroyed (Kramer and Kozlowski 1979).

Root diseases, such as laminated root rot caused by the fungus *Phellinus weirii*, cause tree mortality by decaying the root system of their host. When a substantial portion of the root system is destroyed by root disease, the tree often will be attacked by bark beetles (Hadfield 1985; Thies and Sturrock 1995) that destroy the cambium and phloem of the bole and may introduce stain fungi such as *Ceratocystis* spp., *Ophiostoma* spp., and *Leptographium* spp., in pines and Douglas-fir, and *Trichosporium symbioticum* in true firs (Schowalter and Filip 1993). Stain fungi plug the water-conducting xylem, and crown symptoms quickly may become apparent. Spores of decay fungi, such as *Cryptoporus volvatus* and *Fomitopsis pinicola* that decay the sapwood and eventually the heartwood after the tree is dead, are also vectored by bark beetles (Schowalter and Filip 1993).

In the absence of beetle activity, crown symptoms develop when a large portion of the root system has been destroyed by *P. weirii*, probably due to water deficit to the crown. Fading crowns are used as an indicator or symptom of trees having advanced root disease. The time from initial pathogen infection to tree mortality is highly dependent on the size of the root system and the colonization rate of the pathogen. Trees that initially become infected when they are already mature may not be killed quickly or even at all by the pathogen, because the fungus colonizes the roots slowly, perhaps requiring several decades (Hadfield 1985; Thies and Sturrock 1995). As long as a substantial portion of the root system remains functional and the tree is not attacked by other biotic agents such as bark beetles, the bole and crown will remain alive.

The effects of fire on trees are highly variable. Species, size, and stand structure; season of burn; weather; fuel loading; topography; and fire severity are among the important variables that determine the degree of injury to trees and probability of immediate or delayed mortality, or attack by bark beetles or other opportunistic pests in subsequent years (Miller and Patterson 1927, Gara et al. 1985, Ryan and Reinhardt 1988, Amman and Ryan 1991, Agee 1993, Thies et al., in review). Species such as ponderosa pine have adapted to fire-prone ecosystems and can withstand fire damage better than many other associated tree species. Proportion of crown volume scorch (foliage and buds) is probably the most reliable indicator of crown injury and predictor of tree mortality soon after a fire (Wyant et al. 1986). Trees with high proportions of their crowns damaged by fire are unlikely to survive, although light crown damage alone seldom results in tree mortality (Wagener 1961; Ryan and Reinhardt 1988; Borchert and Schreiner 2002; Thies et al., in review; Thies et al., in press). Bole injury and associated cambium damage are highly dependent on bark thickness, which is related to tree species and size (Ryan and Reinhardt 1988; van Mantgem and Schwartz 2004; Thies et al., in review). Even if trees are not killed by bole damage, partial cambial death may result in internal injury and eventual decay and stress (Gara et al. 1985), which can lead to depletion of energy-storing tissue and

possible tree death after many years (Shigo 1985). Similarly, trees with partial root mortality from fire or root disease may survive as long as an adequate portion of the root system remains alive to support the tree, and damage, if any, to the bole and crown is not severe.

Numerous fire-effects studies, as cited above, have produced logistic regression equations or other statistical models to help determine probability of tree survival. Some data are currently available for several conifer species that relate various levels of fire-caused damage to probability of tree survival (Wagener 1961; Furniss 1965; Bevins 1980; Ryan 1990; Ryan and Noste 1985; Ryan and Reinhardt 1988; Ryan and Frandsen 1991; Reinhardt and Ryan 1988; Thies et al., in press; Wyant et al. 1986; Peterson and Arbaugh 1989; Saveland and Neuenschwander 1990; Borchert and Schreiner 2002; van Mantgem and Schwartz 2004). Monitoring survival of fire-damaged trees across a variety of sites in Oregon and Washington is currently underway (Walter Thies, Robert Progar and Chris Niwa, USDA Forest Service, Pacific Northwest Station, Corvallis, OR. Personal communication). Results from these studies will be used to validate and calibrate a recently developed survival rating system (Scott et al. 2002).

When is Tree Death Imminent?

The exact time of tree death due to damage is subjective. The crown and the stem will continue to function until they are affected by lack of water. Mortality is imminent when the majority of the root system is destroyed and the remaining roots can no longer support the remaining live portions of the tree (Thies and Sturrock 1995). We define "imminent" as likely to occur in several months to, possibly, a few years (up to five). Similarly, mortality is imminent in trees with destroyed portions of crowns and thus with greatly diminished ability to supply adequate quantities of carbohydrates to the bole and roots. Imminent mortality occurs when the carbohydrate budget is in deficit; respiration exceeds photosynthesis, and stored carbohydrate reserves become exhausted (Waring 1987).

Trees with roots or the root collar severely damaged or killed by long-duration exposure to heat from a surface fire and often lacking other injuries to the bole or crown will retain green crowns for one to several years before the crowns begin to fade (Amman and Ryan 1991, Thies et al., in press). This is the result of the root systems being immediately killed or having diminished function over a few years due to resin infusion of the root xylem from damaged resin canals (Ryan 2000). As the function of root systems begin to degrade, trees experience moisture stress as their crowns transpire moisture before going into late season dormancy. Stressed trees are further compromised by attack by bark beetles (Amman and Ryan 1991).

As root systems degrade, excessive stress develops, and bark beetles may attack and girdle the inner phloem and cambium, thereby destroying the carbohydrate transport system of the stems (Schowalter and Filip 1993). The stain fungi introduced by attacking beetles plug the xylem, thus rendering the water transport system non-functional. The crowns may remain green until the year following beetle attack, although the trees could be considered dead as soon as the phloem and xylem become

permanently impaired to the point that they no longer support the water requirements of the tree.

Fire injuries to the crown and bole are not independent; trees with crown injury have higher mortality rates when accompanied by cambial damage (Wagener 1961). Thin-barked trees nearly always are killed by fires that completely encircle them, as the cambium is completely killed around their base (Ryan and Reinhardt 1988). Large old ponderosa pines growing on sites that have missed numerous cycles of light ground fires will often have substantial accumulations of sloughed-off bark scales, needles and other debris around their bases. These trees seem to be especially susceptible to imminent mortality following burning since the heat generated by the smoldering accumulation of debris and duff is situated directly against the root collar and over the root system. The probability of cambial survival at the root collar declines in mature ponderosa pines as the depth of duff consumed adjacent to the cambium increases (Ryan 1990; Ryan and Frandsen 1991, Thomas and Agee 1986). Fine roots growing into the thick duff layer are killed by heat, especially in the spring, and the upper portions of large roots are killed (Swezy and Agee 1991, Busse et al. 2000). Also, fall underburns can significantly remove live root biomass to a depth of 10 cm and significantly reduce mycorrhizal species richness compared with spring underburns or non-burned controls in ponderosa pine in eastern Oregon (Smith et al. 2004).

Large pine mortality from smoldering debris usually is not immediate. Rupturing of resin canals, mainly on the upper portions of main roots near the root collar where they are at or near the surface of mineral soil, results in a generalized wound response known as resinosis. Ruptured resin canals allow seepage of resin into the xylem that leads to increased stem resistance (Ryan 2000), and effectively reduces the water transport function. Crowns may remain green for one to five years following a fire as root function declines. Moisture stress develops over subsequent years, and incidence of bark beetle-caused delayed-tree mortality may be very high (Mastrogiuseppe and Mastrogiuseppe undated, Ryan and Amman 1996, Ryan and Frandsen 1991, Agee 2003, Kangas et al. in review).

When is a Tree Dead?

When should a tree be considered dead? The usual and most common conception of a dead conifer is one where the needles have changed from green to red or brown. This is a lay-person's perception of tree death, however, and the result of crown death that is easy for the lay-person to see. Often all three of the main parts of the tree cease to function. However, damage to the root system or stem that destroys their function also is fatal to the tree, although the crown may remain green for one or two years. A tree may be considered "dead" when one of the three functional parts (crown, stem, or roots) ceases to function. The familiar case of the Christmas tree serves as a good example; trees severed from the root system are clearly "dead" but will remain green with the crown continuing to function and the xylem continuing to transport water for over a month if the reservoir on the tree stand is kept full. A crown and bole without a root system is a dead tree, as is a portion of a stem and attached root system of a wind-snapped tree without a crown. Similarly, a tree with the cambium fully mined by bark beetles is dead, despite retaining a green crown. The lay-person does not notice this until the xylem is plugged with stain fungi introduced by the

attacking beetles or the roots die from lack of nutrients and the crown dries and turns red, usually in 6 to 12 months after beetle attack.

Severe fire damage may kill trees outright and is immediately recognizable when the crown is completely consumed. Crown scorch involves heat damage that may or may not result in bud kill (Wagener 1961). Tree mortality occurs when a high proportion of the crown is scorched and buds are killed, particularly with bole and root damage (Dieterich 1979, Peterson and Arbaugh 1986, Ryan and Reinhardt 1988). Less severe scorching, especially when buds remain alive, is less likely to result in immediate tree death, depending on tree species and injury to other parts. A small percentage of trees with completely consumed crowns, however, may survive. In a study of ponderosa pine in eastern Oregon, of 278 trees that had all needles consumed or scorched, 30 (11%) of these trees produced needles one year later (Thies et al., in press). All needle production occurred by the end of the growing season after the burn. Species other than ponderosa pine may behave differently regarding crown damage and foliage production.

A tree can be considered dead when most of the cambium around the root collar is discolored and dead. Wagener (1961) suggests that white pines are able to survive girdling of up to 60% of their circumference while other conifer species have a low chance of survival if more than 25% of the circumference is girdled at the base. Ryan (1990) states that in the absence of significant crown injury, most trees survive up to 25% basal girdling, but few trees survive more than 75% girdling, and between these ranges about 50% of the trees survive. Amman and Ryan (1991) found that bark beetle infestation usually occurred in trees having 50% or more basal girdling by fire. Determining the status of cambium at the root collar is easier than detecting dead roots below the ground or dead crowns before the buds have a chance to grow.

Given the evidence for delayed tree mortality after fire and insect attack, and the supporting published literature cited above, we suggest that a "dead tree" designation is justified when more than 50% of the cambium sampled from four quadrants around the base of the tree at the root collar or from the top surfaces of lateral roots near the root collar are discolored and dead. Depending on tree species, this can be evidenced by sapwood (xylem) infiltration of resin, or by the inner phloem and cambium at those locations having become stained, dehydrated, leathery-like, sticky with resin, or infiltrated with fungal mycelium. Determining discolored and dead cambium can be done by removing bark with an axe or Pulaski. Determining whether the cambium is alive or dead also can be tested visually using ortho-tolidine (Hare 1965, Mohr 1989). Live cambium turns purple or blue when the chemical is applied. This can be done using an increment borer. Ortho-tolidine is a benzene compound and a suspected carcinogen, however, that would require special precautions and documentation if used on federal lands. Cambium condition can be tested non-destructively in June by a Shigometer with a cambial probe that measures cambial electrical resistance (Shigo and Shortle 1985). Healthy conifers have resistance values below 10 K ohms; injured, infected, or insect-attacked trees have readings between 10 and 30 K ohms; and trees with imminent mortality have resistance values above 30 K ohms.

Current USDA Forest Service Direction in the Pacific Northwest

Current direction of the Forest Service regarding the harvesting of live vs. dead trees appears in the *Regional Forester's Eastside Forest Plan Amendment No.2, August 18, 1993*

“All sale activities (including intermediate and regeneration harvest in both even-age and uneven-age systems, and salvage) will maintain snags and green replacement trees of ≥ 21 inches dbh, (or whatever is the representative dbh of the overstory layer if it is less than 21 inches), at 100% potential population levels of primary cavity excavators. This should be determined using the best available science on species requirements as applied through current snag models or other documented procedures.”

and in Appendix B. 6. Interim wildlife standard d. Scenario A 2) a)

“Maintain all remnant late and old-seral and/or structurally live trees ≥ 21 inches dbh that currently exist within stands proposed for harvest activities.”

A direct question and answer regarding tree death appear in *2430/2600 Memo to the Forest Supervisors, Eastside Forests: Screens Review, Colville NF, August 27, 1998 (Clarifies RF's Eastside FP Amendment No. 2)*

“Question: When are (bark) beetle-infested trees considered “dead” and available for salvage?”

“Answer: Rigorous application of Forest Pest Management (Forest Health Protection)-written standard for identifying the level of infestation expected to be fatal, is sufficient to identify trees as dead. The standard should be included or referenced in the project planning documents.”

and in *2430/2600 Memo to the Forest Supervisors, Eastside Forests Screens Review, Winema and Fremont NF's, September 10, 1998 (Clarifies RF's Eastside FP Amendment No. 2)*

“Question: Do trees with dead tops count as snags?”

“Answer: In addition, dying trees can be counted as snags if there is professional determination that the tree will definitely be dead in 5 years. Careful documentation is important. Trees with dead tops that are weakened or defoliated from stress or disease, but which do not meet documented, professional criteria that they will definitely be dead in 5 years cannot be counted as snags. “

These directives supply policy concerning the harvesting of dead and live trees, especially over 21 inches dbh, but they do not provide a definition of tree mortality or give direction on how to determine mortality in the field. We hope that our paper accomplishes this.

Conclusions

Tree mortality is a complex process involving several interrelated factors. Immediate mortality from fire damage may be obvious, but currently there is considerable controversy about labeling green trees as dead that have a probability of experiencing delayed mortality. Basically, trees die when carbohydrates used in respiration exceed those produced in photosynthesis, or water movement is impaired and the tree desiccates. Also, as long as the volume of new energy-storing wood cells formed after injury and infection is equal to or greater than the volume of damaged cells walled off, the tree can survive. Mortality or delayed mortality may be directly due to biotic or abiotic causes, and may be affected by previous damage, current condition and attack by secondary agents such as bark beetles. A particular pathogen or insect usually attack, damage, or kill only one portion of a tree. Trees that are damaged or attacked by pests and expected to have a dead or non-functional root system and/or a non-functional stem within 5 years will be considered either dead or death is imminent. Numerous fire-effects studies have produced logistic regression equations or other statistical models to help determine probability of tree survival. A “dead tree” designation is justified where more than 50% of the cambium sampled from four quadrants from around the base of the tree at the root collar is discolored and dead.

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Glossary of Terms Used

All terms are defined by Helms (1998) unless cited otherwise.

Abiotic – pertaining to the non-living parts of the ecosystem such as soil particles, bedrock, air, water

Bark beetle – an insect in the family Scolytidae (Coleoptera), particularly species in the genera *Dendroctonus*, *Ips*, and *Scolytus* whose adults and larvae tunnel in the cambium region either in the bark only or in the bark and xylem of living, dying, and recently dead or felled trees

Biotic – pertaining to living organisms and their ecological and physiological relations

Cambial electrical resistance – the amount of opposition to a pulsed direct electric current, usually measured in kilo-ohms (K ohms), that is applied to tree cambiums. Cambial electrical resistance is affected by moisture and ion concentrations within the cambium and varies by tree vigor, tree size, and season (Shigo and Shortle 1985).

Cambium – a layer of living cells between the wood (secondary xylem) and the innermost bark (secondary phloem) of a tree

Carbohydrate – a class of organic compounds built of carbon, hydrogen, and oxygen

Dbh – diameter at breast height; the diameter of the stem of a tree measured at breast height (4.5 ft) above the ground

Decay (rot) – the decomposition of wood by fungi and other microorganisms resulting in softening, progressive loss of strength and weight, and often in changes in texture and color

Delayed mortality – caused by physiological processes set in motion by a fire that will result in death of tissues and eventually tree death. These changed processes may expose the trees to secondary causes of mortality, such as bark beetles or other insects (Thies et al. a, in review).

Disease – a harmful deviation from normal functioning of physiological process

Duff – the partially decomposed organic material of the forest floor beneath the litter of freshly fallen twigs, needles, and leaves

Dysfunction – impaired or abnormal function as an organ of a body (Gove 1976)

Eastside forests – all forests east of the crest of the Cascade Mountains in Oregon, Washington, and California (the authors)

Even-age system – a cutting procedure that regenerates and maintains a stand with a single age class

Fuel load – the oven-dry weight of fuel per unit area

Heartwood – the inner, nonliving part of a tree stem that is altered to a protective state as a result of normal, genetically controlled aging process as cells die, and that provides mechanical support

Host – an organism on or within which another organism develops and obtains all or part of its food

Infection – the establishment of a food relationship between a microscopic organism, pathogen, or parasitic plant, and a host

Intermediate harvest – any harvest treatment designed to enhance growth, quality, vigor, and composition of the stand after establishment or regeneration and prior to final harvest

Mycelium plural **mycelia** – the vegetative part of a fungus composed of filamentous elements

Mycorrhizae – the usually symbiotic association between higher plant roots (host) and mycelia of specific fungi that aid plants in the uptake of water and certain nutrients and may offer protection against other soil-borne organisms

Overstory layer – that portion of trees, in a forest of more than one story, forming the upper or upper-most canopy layer

Pathogen – a parasitic organism directly capable of causing disease

Pest – an organism that is undesirable or detrimental to the interest of humans

Phloem – a layer of cells just inside the bark of plants that conducts food from the leaves to stems and roots

Photosynthesis – the manufacture of organic compounds, particularly carbohydrates, in the chlorophyll cells of plants from carbon dioxide, water, and enzymes in the presence of light as the energy source

Plant association – a plant community type based on land management potential, successional patterns, and species composition

Primary cavity (excavators) nesters – wildlife species that excavate cavities in snags (Thomas 1979)

Regeneration harvest – any removal of trees intended to assist regeneration already present or to make regeneration possible

Resin – secretions of certain trees, or of insects feeding on them, which are oxidation or polymerization products of terpenes, consisting of mixtures of aromatic acids and esters insoluble in water but soluble in ether, alcohol, or other organic solvents

Resin canal (duct) – an intercellular space in conifers into which resin is secreted and transported. Traumatic resin canals are caused by wounding (Kramer and Kozlowski, 1979)

Respiration – a process in plants involving the breakdown of carbon-containing compounds (maintenance or growth respiration) or competitive reactions during photosynthesis (photorespiration) resulting in the release of carbon dioxide

Salvage cutting or harvest – the removal of dead trees or trees damaged or dying because of injurious agents other than competition, to recover economic value that would otherwise be lost

Sapwood – the outer layers of a stem, which in a live tree are composed of living cells and conduct water up the tree

Scorch – an injury to bark, foliage, flowers, or fruit from excessive heat from fires

Seral stage – a temporal and intermediate stage in the process of succession

Snag – a standing, generally unmerchantable dead tree from which the leaves and most of the branches have fallen

Stain – a discoloration of wood, usually only the sapwood, in live or recently cut trees (including timber, chips, and pulp) caused by certain fungi

Stand – a contiguous group of trees sufficiently uniform in age-class distribution, composition, and structure, and growing on a site of sufficiently uniform quality, to be a distinguishable unit

Stress – a reversible condition caused by a drain, blockage, disruption, or shunt of energy (Shigo 1985)

Succession – the gradual supplanting of one community of plants by another

Uneven-age system – a cutting procedure that regenerates and maintains a multi-aged structure by removing some trees in all size classes either singly, in small groups, or in strips

Vigor – the genetically controlled capacity or potential to survive after injury or infection (Shigo 1985)

Xylem – the principal water-conducting tissue and the chief supporting system of higher plants

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