# Compartmentalization of pathogens in fire-injured trees

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*Fire in the landscape*

Wildland fire is an episodic process that greatly influences the composition, structure, and developmental sequence of forests (McKenzie et al. 2011). Most news reports of wildland fire involves blazes fueled by slash, standing dead stems, and snags that reach into tree crowns and burn deeply into the forest floor, causing extensive tree mortality and the eventual replacement of the standing cohort of trees. Fires as part of a silvicultural prescription or that occur at the edges of wildfires are usually less devastating surface fires fueled by surface litter, herbaceous vegetation, and downed woody material. These fires tend to scorch the outer bark for some distance up the stem but generally do not extensively involve the crown or cause severe mortality of roots.

Tree species vary in survival strategies under different fire regimes. Some species allocate resources to reduce injury by insulating stems from excessive heating. Other species rely on sprouting from the base of killed stems or from residual root systems. Still other species store or bank seeds in the forest floor that are ready to germinate after the fire passes. Most western “fire-adapted” species rely on constitutive protection provided by thick bark as wells as by induced defenses to survive fire.

*Mechanisms of fire injury*

Most published research attributes cell death from fire to direct necrosis or lethal heating, although indirect mortality from induced cavitation at elevated temperatures has also been suggested (Michaletz et al. 2011). Whether direct or indirect, tissue mortality occurs at a variable combination of surface temperature and duration of exposure. Killed tissue provides a portal of entry for wood destroying infectections. The most obvious constitutive protection is provided by thick bark that insulates the living phloem, vascular cambium, and xylem parenchyma (van Mantgem and Schwartz 2003). The insulating capacity of bark of a given thickness varies with species and increases with increasing bark density and increasing moisture content (VanderWeide and Hartnett 2011). Although a useful marker for some fire characteristics, the presence of bark scorch does not mean that living tissues were killed or functions disrupted as shown in eastern oak (Smith and Sutherland 1999).

The vascular cambium (VC) is the most critical tissue and characteristic feature of trees. The VC is located to the outside of the annual rings of differentiated xylem or wood. The most recently formed wood is sapwood (SW). SW contains relatively large and thick-walled piping or conducting elements that are devoid of cellular contents at functional maturity. The conducting elements provide much of the pathway for conduction of water and dissolved substances from root tips, through woody roots, stem, and branches, and into the foliage. Intermixed with the conducting elements are several other types of cells including living parenchyma that are small, thin-walled, and very numerous. SW parenchyma store metabolic energy, usually in the form of starch and are capable of forming inducible defensive materials when needed.

In the western conifers described here, healthy SW undergoes maturation through a pre-programmed physiological transformation into heartwood (HW). The SW to HW transformation involves the plugging of the conducting elements or tracheids, the conversion of stored energy into decay-resistant chemicals or “extractives”, and cell death. The width of sapwood with respect to radial distance or number of rings varies according to species, growth rates, and environmental conditions.

The death of cells from fire injury causes a cascade of effects. Loss of living phloem reduces the supply of photosynthate to support metabolism and for storage in the stem and roots. Death of living sapwood by fire injury reduces the capacity of the stem to conduct water. As the capacity in healthy trees usually exceeds the amount of water flow required to support the needs of foliage in the live crown, a greater effect may be on the loss of capacity for energy storage. Death of the VC is especially serious as that tissue provides for the formation of new phloem and sapwood.

*Compartmentalization*

Compartmentalization is the boundary-setting process that resists (1) the loss of normal function and (2) the spread of infection (Smith 2006). Although convenient to describe these separately, they are frequently concurrent processes as in the maintenance of hydraulic integrity. The moisture content of intact, healthy sapwood is generally above the fiber saturation point (about 30% moisture content on a dry weight basis). This level of moisture supports the metabolism of the wood parenchyma and the continuity of the water column through the lumens of the conducting tracheids and vessels. Maintaining the water column is essential to provide hydraulic continuity and to prevent the formation of embolisms along the flowpath from roots to the foliage in the canopy. At the same time, the high moisture content in sapwood also inhibits the development of aerobic infections introduced through small openings such as incompletely suberized lenticels or leaf scars or small wounds such as those made by egg-laying insects. With seasonal exceptions in some diffuse-porous northern hardwoods, water in the conducting lumina is generally under tension. Direct mechanical injury to the conducting sapwood or indirect injury from desiccation following bark injury or charring introduces air into the xylem translocation stream, causing the water columns to snap, compromising hydraulic integrity as providing an aerated environment suitable for the development of infection. Consequently, resisting both the loss of function and the spread of infection are two equally important aspects of the same dynamic process.

*Current research on compartmentalization in western conifers*

Current research by the author and collaborators investigates the links between landscape features, community ecology, surface fire behavior, and tree injury in western conifers. As part of that work, we are identifying patterns of compartmentalization through tree dissection and macroanatomical characterization as previously described for central and northern hardwood species (Smith and Sutherland 1999, 2001).

The analysis is insufficiently complete to rank tree species for effectiveness in compartmentalization under uniform conditions of fire exposure or severity of injury. Some patterns are clear. The column of WID can extend along the arc of the stem circumference beyond the arc of killed vascular cambium. This can occur from tangential spread but more frequently from axial spread from cambial injury below the plane of the sample. In the section from western larch (Figure 1A), rings have woundwood have closed over the killed cambium and the outermost extent of WID on the right-hand side. On the left-hand side, spread of infected WID is also checked by reaction zone formed in the absence of death of the vascular cambium Over the years since the fire, the reaction zone that was first formed (black arrow 1) was overcome and a second reaction zone was formed further from the injury (black arrow 2).

Although adjacent to the heartwood (HW in Figure 1A), the WID was likely sapwood at the time of injury. Following injury, the killed sapwood would not undergo the usual maturation process to become comparatively more decay-resistant heartwood. Over time, additional rings of sapwood are formed by the vascular cambium which eventually mature into comparatively decay-resistant heartwood to the outside of the WID. After several decades, this can result in large pockets or band of decayed wood (DW) with healthy heartwood both to the inside and outside of the DW or the void created by the decay process.

In the section from Ponderosa pine (Figure 1B), two localized arc of killed cambium are separated by a narrow strip of intact vascular cambium. The sapwood shows extensive, constitutive resin canals that are characteristic of the species. The wood immediately beneath the killed vascular cambium is resin-soaked with little associated WID or decay. After several years, the locally wide rings of woundwood (ww) have partially closed the sound.

In the section from Douglas-fir (Figure 1C), extensive WID and decayed wood (DW) has formed beneath the killed arc of vascular cambium. Small pockets of resin occur throughout the WID. Resin-soaking is most prominent along the tangential side of the WID and to the inside of the RZ that separates WID from healthy SW. Within the WID, bluestain infection is visible, further reducing the economic value of the timber for many commercial purposes.

## References

McKenzie, D.; Miller, C.; Falk, D.A. (eds.) 2011. The Landscape Ecology of Fire. Springer, New York and elsewhere. 312 pp.

Michaeletz, S.T.; Johnson, E.A.; Tyree, M.T. 2012. New Phytologist 194: 254-263.

Schwarze, F.W.M.R.; Engels, J., Mattheck, C. 2004. Fungal strategies of wood decay in trees. Springer, New York and elsewhere. 185 pp.

Shortle, W.C; Dudzik, K.R.; Smith, K.T. 2010. Development of wood decay in wound-initiated discolored wood of eastern red cedar. Holzforschung 64: 529-536.

Smith, K.T. 2006. Compartmentalization today. Arboricultural Journal 29: 173-184.

Smith, K.T.; Sutherland, E.K. 1999. Fire scar formation and compartmentalization in oak. Canadian Journal of Forest Research 29: 166-171.

Smith, K.T.; Sutherland, E.K. 2001. Terminology and biology of fires scars in selected central hardwoods. Tree-Ring Research 57: 141-147.

van Mantgem, P.; Schwartz, M. 2003. Bark heat resistance of small trees in Californian mixed conifer forests: testing some model assumptions. Forest Ecology and Management

VanderWeide, B.L.; Hartnett, D.C. 2011. Fire resistance of tree species explains historical gallery forest community composition.

Figure 1. Cross-sections of compartmentalized fire injury showing context (left) and detail (right) for western larch (A), ponderosa pine (B), and douglas-fir (C). Sapwood (SW), heartwood (HW), wound-initiated discoloration (WID), woundwood (WW), reaction zones (black arrows), and bluestain infection (white arrows) are marked. The position of the killed cambium (black dots) and the barrier zone (white dots) are shown.