Resistance is not futile: The response of hardwoods to fire-caused wounding

Elaine Kennedy Sutherland[1] *and Kevin T. Smith*[2]

Abstract

Fires wound trees; but not all of them, and not always. Specific fire behavior and differences among tree species and individual trees produce variable patterns of wounding and wound response. Our work focuses on the relationships between fire behavior and tree biology to better understand how hardwood trees resist injury to the lower stem and either survive or succumb to low-intensity fire. Our objectives here were to 1) define and describe the wounding process, 2) to describe compartmentalization and wound closure and 3) to discuss species-specific differences among several common hardwood trees in the resistance to injury and resilience after wounding. Characteristics of fire scars are summarized.

Introduction

Prescribed fire is a frequently discussed and under-utilized tool to restore upland oak (*Quercus*) communities in Central Hardwoods forests. One barrier to the use of prescribed fire is a lack of understanding of how fire, especially low-intensity prescribed fire, affects individual trees and tree species. Fires wound tree stems (Gustafson 1946, Kaufert 1933, Nelson and others 1933, Wendel and Smith 1986), but not all of them, and not always (Smith and Sutherland 1999). Patchiness of fire behavior and different susceptibilities among individual trees produce variable patterns of wounding. Additionally, tree species differ in their effectiveness to resist injury and the spread of infection after wounding. Knowledge about potential wounding from fire may be an important consideration in forest managers' decision-making processes. For example, some managers may be concerned about loss of economic value through damage to potential high-quality veneer logs. Alternatively, those burning to restore the structure and composition of oak communities undergoing succession to mesic forest types might want to maximize injury to undesirable species (such as maple (*Acer*)). Here, we define and describe the processes of fire-caused wounding, the generalized response of hardwood trees to wounding, and species-specific differences in protection from fire injury and effectiveness in the tree wound response.

How Fires Wound Trees

In hardwood forests, fires typically burn in light fuels (hardwood litter) and are low in intensity (Komarek 1974). Not all trees are wounded by any one low-intensity fire (Smith and Sutherland 1999) because within a fire perimeter there are usually unburned patches; obviously, trees in these patches are unlikely to be injured. The probability that a hardwood tree will be wounded during a fire depends on many factors— primarily weather, fire behavior and bark characteristics. Fire wounds the vascular cambium by lethal heating, which depends on flame length, fire temperature, and duration of heating (Ryan 1998). These fire behaviors are in turn affected by fuel quantity and moisture content, ambient temperature, wind, slope, and in prescribed fires, by ignition pattern (Ryan 1998). Wildfires differ from prescribed fires. By definition and by regulation, prescribed fires should only be ignited when they are judged controllable, under specific parameters of weather and fuel conditions. Thus, the fire manager igniting a prescribed fire has some control over fire behavior and by extension, the probability of tree injury and damage.

By itself, scorch is not an indicator of injury. Fire injury is the result of fire causing a wound, a disruption of living tissues including the vascular cambium that results in an impairment or loss of function. These wounds are typically referred to as fire scars. However, not all scorched trees are injured; scorch is simply a sign or indicator of a fire occurrence. Further, a scorched or even an injured tree is not necessarily damaged: damage involves a loss of desirable wood characteristics, value, or usefulness. The determination of damage is relative to management goals. Damage due to a fire scar may be essentially zero to a tree in a conservation/preservation area, be worth thousands of dollars to an identical tree managed to produce high-quality veneer, or actually be desirable for wildlife management goals (e.g., to promote habitat for animals that dwell or feed under dead bark or in cavities). For timber management, methods to estimate cull as a result of fire wounding were developed by Hepting (1941) and Loomis (1973,1974). Notably, estimated cull is virtually negligible when externally visible wounds are less than 2 inches inches width at 1 foot aboveground (Hepting 1941). Loomis (1974) suggested that oak trees with wounds less than 6 in wide are unlikely to lose quality and no more than 3 board feet in volume, and that pole-sized trees were unlikely to lose any quality. Unpublished data of the authors indicates that most prescribed fire-caused wounds were less than 1 inch in width.

Most fire-caused injuries from low-intensity fires result from heating without combustion. Smith and Sutherland (1999) found that most injury to stems in *Quercus* sp. from two prescribed fires resulted from heat conducted through bark, and not flaming combustion. Heat transfer properties govern resistance to fire-caused injury (Ryan 1998). The single most important biological factor determining resistance to fire injury to stems is bark thickness (Hare 1965, Jackson and others 1999, Ryan 1998, Ryan and Reinhardt 1988, Vines 1968). Bark serves as an insulator that slows heat

[1]Project Leader, USDA Forest Service, Rocky Mountain Research Station, Forestry Sciences Laboratory, PO Box 8089, Missoula, MT 59807

[2]Plant Physiologist, USDA Forest Service, Northeastern Research Station, Forestry Sciences Laboratory, 271 Mast Rd., Durham, NH 03824.

conduction to the vascular cambium (Spalt and Reifsynder 1962). The thicker the bark, the longer the heating period required to injure underlying cambium (Uhl and Kaufman 1990, Vines 1968).

In general, bark thickens as trees grow in diameter, and resistance to fire-caused wounding increases (Harmon 1984, Hengst and Dawson 1994, Pausas 1997, Spalt and Reifsynder 1962). Bark thickness is dependent on diameter, not age (Hengst and Dawson 1994); suppressed trees the same age as dominant trees have relatively thinner bark and hence greater susceptibility to fire injury (Harmon 1984). Consequently, ability to resist fire injury has been attributed to stem diameter and to variability among tree species (Hare 1965, Hengst and Dawson 1994, Pausas 1997, Spalt and Reifsynder 1962).

Some tree species fundamentally have thicker bark than others, and as such have greater resistance to fire injury. Because texture is so variable thickness is difficult to quantify, but general patterns among species have been noted (e.g., Harmon 1984, Hengst and Dawson 1994). For example, upland species generally have thicker bark than bottomland species, perhaps because fire is typically more frequent at upland sites compared to bottomland sites (Hengst and Dawson 1994, Jackson and others 1999). Comparisons of data presented by Harmon (1984), Hengst and Dawson (1994), Jackson and others (1999), and Spalt and Reifsynder (1962) reveal certain patterns. As a group, white oaks (*Quercus* subgenus *Lepidobalanus*) have the thickest barks of the central hardwoods species, followed by the red oaks (*Quercus* subgenus *Erythrobalanus*). Examples of thinner barked species include American beech (*Fagus grandifolia*), maple species (*Acer*), hickory species (*Carya*), flowering dogwood (*Cornus florida*), and black cherry (*Prunus serotina*).

Additionally, the rate of bark thickening on the lower stem varies among species and primarily determines resistance to heat-caused injury; the sooner bark thickens at the base, the earlier in life the stem gains resistance (Hare 1965, Harmon 1984, Hengst and Dawson 1994). For example Hengst and Dawson (1994) showed that tulip poplar (*Liriodendron tulipifera*) has very thin bark when small but has a very rapid rate of bark thickening. Thus, seedling and sapling-sized tulip poplar trees are susceptible to topkilling by fire (Barnes and Van Lear 1998, Brose and Van Lear 1998), but tree-sized tulip poplar has been described as particularly resistant to fire-caused wounding (Gustafson 1946, McCarthy 1933, Nelson and others 1933). By contrast, silver maple (*Acer saccharinum)* also has very thin bark when small but a slow rate of bark thickening, which results in thin bark throughout its life (Hengst and Dawson 1994); silver maple is highly susceptible to fire injury (Auclair and others 1973).

The distribution of bark along and around the stem is also variable among species. Bark texture can vary from smooth to fissured and can vary significantly within as well as among species (Howard 1977). For trees with deeply fissured bark, such as chestnut oak (*Q. prinus*), the cambium directly beneath the fissures is more susceptible to injury, and multiple, discontinuous fire scars may occur around the stem (Smith and Sutherland 1999, Stickel and Marco 1936). Factors that contribute to variability in bark texture include tree vigor and growth rate, age, and height on the tree (Howard 1977). In regimes characterized by low-intensity surface fires, thick bark at tree bases provides protection from heating and a competitive advantage over trees with thin bark at the base, but since fires typically have low flames heights, bark rapidly thins with increasing height (Harmon 1984, Jackson and others 1999). For example, bur oak (*Quercus macrocarpa*) has relatively thick bark near the ground (but thinning with height); it grows in oak savannas that are maintained by frequent fire. By contrast, water oak (*Quercus nigra*) has relatively thin bark near the ground, and typically grows in bottomland forests where fire rarely occurs (Jackson and others 1999).

Heat conduction properties of bark tissue play a role in resistance to heating and injury of the vascular cambium during fires, and these properties vary among species (Hare 1965, Harmon 1984, Hengst and Dawson 1994). For example, for a given bark thickness, red maple (*Acer rubrum*) conducts heat relatively quickly (Hare 1965). Heat conduction properties have been expressed as thermal conductivity (the ability of a material to transfer heat), specific heat (the ability to absorb heat), and thermal diffusivity (ratio of thermal conductivity to the product of specific heat and bark density) (Martin 1963, Harmon 1984). The ratio of outer bark (rhytidome) to inner bark (phloem) increases with tree diameter in many species, and this factor affects heat conduction properties: rhytidome conducts heat more slowly (Hare 1965). Thus, trees with substantial rhytidome such as chestnut oak (*Quercus prinus*) are more heat-resistant than trees with little rhytidome such as American beech (*Fagus grandifolia*) (Stickel 1936). However, bark thickness alone remains the simplest, best predictor of heat conduction (Vines 1968).

How Trees Respond to Fire Injury

Tree survival after mechanical injury, including wounding caused by fire, depends on the internal boundary-setting process known as compartmentalization (Shigo 1984). Compartmentalization in the wood of living trees resists the spread of decay and loss of normal wood function, and minimizes the extent of injury. Tree species vary in ability to compartmentalize injury (Shigo 1984, Shortle and others 1996) and hence in resilience to fire-caused injury. For example, trees in the white oak group (*Quercus* subgenus *Lepidobalanus)* are unusually effective at compartmentalizing decay, which places them at a competitive advantage over other injured trees (Abrams 1996). Understanding the role of compartmentalization effectiveness following fire may be critical to understanding patterns of tree survival and changes in wood quality following fire.

Compartmentalization is a set of processes that integrate tree anatomy, physics, and inducible changes in tree physiology. These processes may be divided into those that occur in wood present at the time of wounding and those that occur in wood formed after wounding. Tree survival depends on maintaining a healthy vascular cambium, the thin layer of generative cells located beneath the bark. As the cells of the vascular cambium divide, wood (xylem) is formed to the inside of the cambium and inner bark (phloem) is formed to the outside. When part of the vascular cambium and associated tissues are overheated and killed by fire, the first changes are physical and immediate: water columns (normally held under tension in functional wood vessels) snap which is dangerous for the tree because drying kills living sapwood cells and provides a favorable environment for the spread of microbial infection. Because of cellular architecture and inducible changes in wood physiology, these abrupt changes in water tension induce the immediate formation of plugs and the eventual formation of chemical boundaries that resist both wood drying and the spread of microorganisms that lead to the breakdown of wood. Some of the physiological changes involve the oxidation and polymerization of phenolic compounds that then discolor or stain the wood (Smith 1997).

After wounding, probably in response to changes in plant growth regulators (Smith and Shortle 1990), the surviving vascular cambium produces an anatomically distinct barrier zone (Shigo 1984) that can appear as a “false ring” in the wood. This barrier is most effective in resisting the outward loss of wood function and the spread of microorganisms. Effective barrier zones limit wood discoloration and decay to wood present at the time of injury. Compartmentalization allows for the continued survival of the vascular cambium and the generation of new wood. These boundaries, although frequently effective at resisting the spread of infection, can and do fail. The effectiveness at compartmentalization depends on the severity of the wound, the tree species involved, and on the individual tree.

For years following the injury, conspicuously wide growth rings may be produced at the wound margins, apparently to both speed closure of the wound and to provide additional mechanical support for the wounded stem. Wound closure, although apparently not essential for tree survival, aids tree functioning by restoring the continuity of the vascular cambium and wood formation around the tree perimeter. Closure also seals off the wound and infected wood from the outside atmosphere, reducing the partial pressure of oxygen and increasing the partial pressure of carbon dioxide. These changes in the internal atmosphere tend to reduce the rate of the anaerobic wood decay process. Research on northern hardwoods indicates compartmentalization is more effective in sugar and red maple and red oak than in paper and yellow birch, following equivalent levels of storm injury (Smith, unpublished data).

Characteristics of Fire Scars

In earlier work (Smith and Sutherland 1999), we characterized fire scars in small, dissected oaks in southern Ohio that had been exposed twice to prescribed fire. We learned that: 1) the prescribed low-intensity fires wounded some trees, but because heat was unevenly distributed, not all trees were scorched, and not all scorched trees were wounded; 2) because flame heights were low, most wounds were small and low to the ground (about 1 foot in height above groundline); 3) wounds resulted in typical defense processes against infection, including compartmentalization and closure; and 4) nearly all wounds were caused by heating through the bark, which often persisted over the heat-killed tissue after wounding, sometimes for years, thus, small wounds that rapidly compartmentalize may only be apparent when the tree is felled and dissected.

Implications

The resistance of any hardwood tree stem to fire-caused wounding is primarily determined by bark thickness. Generally, as stems increase in diameter, bark thickness concomitantly increases along with resistance to fire-caused wounding. Additionally, there are species-specific differences in bark thickness. Thus, there is a gradient of susceptibility: small, thin-barked trees are most susceptible to wounding and large, thick-barked trees are least susceptible.

Many researchers have suggested that fire is an important process in promoting oak dominance in upland oak types, for example Abrams (1992) and Lorimer (1985, 1993). Differences among species in resistance to wounding by fire and the effectiveness of wound response (resilience to wounding) is probably an important determinant of species composition and dominance in forests exposed to fire. Jackson and others (1999) provided evidence for this idea. They pointed out that for any tree, the greatest improvement in survival probability occurs at sapling sizes, and then demonstrated that the rate of overall growth and bark thickening is more rapid in oak species typical of fire-prone habitats than those associated with moist habitats (e.g., bottomlands) that burn infrequently. They showed that resistance is higher in species typical of fire-prone habitats, and suggested that other defenses would probably be quantifiable. We believe that resilience to injury (effective compartmentalization) is one of those defenses, and would likely follow similar patterns of greater resilience in species typical to fire-prone habitats compared to those where fire is rare.

Conclusions

Any fire, whether wild or prescribed, can injure a tree, but not all trees are wounded by fire. Fires in hardwood forests are typically low in intensity and patchy in distribution. Even when scorched, not all trees are wounded. Bark is an insulator from heat and if scorched, the underlying cambium may not be damaged. Most wounds, when they occur, are near the ground, small in size, and rapidly compartmentalized: few are externally visible. In addition, not all wounds are caused by fire: other events also mechanically wound trees, including impacts from treefalls (e.g., windthrows) and management activities, including logging. Because damage is relative to management objectives, not all injuries result in damage. In the development of fire prescriptions and in implementing fires, managers have a degree of control over potential for fire-caused injury based on their desired outcome.

Better understanding of species-specific resistance and resilience to fire injury are essential to improving predictions about the effect of prescribed fire on surviving trees. To this end, the authors are currently conducting research on the characteristics of prescribed fire-caused wounds, resistance to injury, and comparative effectiveness of compartmentalization in central hardwood species.

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