RESISTANCE OF EASTERN HARDWOOD STEMS TO FIRE INJURY AND DAMAGE

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Abstract.—This paper reviews the protective features and defensive responses of eastern hardwood species exposed to fire. Trees survive fire through protective features such as thick bark and the induced defenses of compartmentalization. Dissection of trees exposed to prescribed fire in an oak forest in southern Ohio highlights the need to distinguish between bark scorch, stem injury, and damage in evaluating the effects of fire on surviving overstory trees.

BACKGROUND

Fires ignited by humans or by lightning are fundamental influences on eastern oak forests. In the absence of suppression efforts, these fires are generally frequent, low in intensity, and patchy in extent resulting in variable exposure of trees to fire (Wendell and Smith 1986; Shumway, Abrams, and Ruffner 2001; Guyette and Spetich 2003). The eastern oak forests of today frequently contain an overstory that is comparatively fire-tolerant and a dense understory of more fire-sensitive and shade-tolerant species (Abrams 1990; Yaussy et al. 2003). In ecological terms, the current overstory is the likely result of regeneration or release of fire-tolerant trees prior to the onset of fire suppression. The current understory is dominated by fire-sensitive species that compete favorably with fire-tolerant species in the absence of fire. Under a scenario of continued fire suppression, the frequency of fire-sensitive species will likely increase in the canopy and remain high in the understory. The lower bole is potentially the most vulnerable part of a tree exposed to surface fires. How do some trees tolerate fire while others are sensitive? This review examines the basic survival mechanisms that reduce injury and damage to trees exposed to fire in eastern oak forests.

ENERGY BUDGETS AND TRADEOFFS

Although difficult to quantify, the concept of competitive advantage in the presence or absence of fire may be readily understood in terms of energy budgets. A budget reconciles outlays among various possible expenditures within the limits of income. An optimal budget strategy meets the needs of necessary expenditure with minimal surplus, leaving more resources available for other categories.

As green plants, trees capture and convert solar energy into chemical energy that is then dynamically allocated to meet the changing needs of the tree, including that of stored energy for future needs. Although strategies for allocation vary among species and settings, all trees need energy for growth, reproduction, protection, defense, and maintenance of the living system. One of the central dilemmas addressed by these strategies is the tradeoff between the allocation of energy to growth or to protection and defense (Loehle 1988; Herms and Mattson 1992). Height growth and a spreading crown architecture promotes energy capture under favorable conditions. Increased stem growth can enhance structural stability and supporter taller, broader crowns. On the other hand, investments such as thick bark and a heartwood that is enriched with wood-preserving chemicals can increase the probability of survival after injury.

One yardstick for describing the strategy for energy allocation is allometrics, the relative biomass distribution among various plant parts such as roots, foliage, wood, etc. Effective strategies promote while less effective strategies reduce the probability of survival. Tree species undergoing competition can have different strategies for energy allocation. These strategies vary among tree species and may also shift as trees increase in size (Jackson, Adams, and Jackson 1999). Trees survive fire

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exposure through the (1) constitutive, inborn allocation of energy for protective features that prevent injury and (2) induced allocation of energy for defense that maintains and restores tree health, particularly the continuity of the vascular cambium.

FIRE BEHAVIOR AND THE POTENTIAL FOR TREE INJURY

Patterns of fire injury reflect patterns of fire behavior. Most descriptions of fire behavior and its consequences have been based on observations of western conifers (Miller 2001) although some work has been done in eastern oak forests (Bova and Dickinson 2005). Although crown involvement of overstory trees may occur, eastern oak forests are most often subjected to surface fires fueled by fine or coarse woody debris and low-growing living plants. The direction and rate of movement of a forest fire depends on fuel quality and quantity, topography, and atmospheric conditions, including the prevailing wind direction.

Following ignition, a downwind-burning fire presents a fast-moving front with flames that typically burn the most readily combustible fuel and leave behind much charred and incompletely burned fuel. The upwind or backing fire is a much more slowly moving front that burns fuel more completely. The severity of tree injury is due to both fire intensity (amount of heat generated per length of front) and the duration of the period in which the flames are close to the stem.

As the flames of the heading fire pass a tree stem, flame height increases on the leeward side of the stem (Gill 1974). This increase in height of the standing leeward flame is accompanied by increased residence time and greater stem heating (Gutsell and Johnson 1996). The same process increases heating on the upslope side of trees on uneven terrain as flames and the air entrained into the flames flows past tree stems.

CONSTITUTIVE PROTECTION

Activity by all of the meristematic tissues (shoot and root tips, vascular cambium, bark or cork cambium) results in compartmentation, the arrangement of tree cells into various tissues and organs (e.g. roots, foliage, branches, sapwood, heartwood) with specific roles in maintaining tree function. The unique characteristic of woody plants is the dominant role of the vascular cambium in tree survival and growth. The vascular cambium is the continuous sheath of small, fragile, thin-walled cells located immediately outside of the most recently formed wood and to the inside of the phloem or inner bark. The vascular cambium is the “new cell generator” for both xylem (that matures into wood) and phloem (sometimes referred to as inner bark, the transport tissue for most of the sugar and other biochemicals essential for tree life). An element of compartmentation is the annual growth layer or increment of wood in the boles, branches, and woody roots of temperate zone trees that appear in cross-section as tree rings. Essentially, a new sheath is formed every year over the core of the tree grown in previous years.

As an integrated system, all parts of the tree are essential for healthy functioning. However, we emphasize the survival of the vascular cambium in that it is more difficult to restore or replace than other plant tissues or organs (e.g. roots, foliage, branches). Also because of its anatomical position, death of the vascular cambium (sometimes referred to as “cambial necrosis”) also indicates the death of the phloem located to the outside and death of the sapwood located to the inside of the vascular cambium. In surviving trees, fire kills the vascular cambium and associated tissues by heat conducted through intact bark, rather than from direct combustion. This heat transfer can be modeled using a variety of approaches (Gutsell and Johnson 1996; Dickinson and Johnson 2001; Jones et al. 2004).

The vascular cambium of oaks is protected by a thick layer of bark. Bark is a poor conductor of heat and serves to insulate the vascular cambium from the heat of forest fire. Bark thickness has been used as the most obvious and readily measured protective feature that varies among tree species (e.g., Nelson, Sims, and Abell 1933; Harmon 1984). However, other bark qualities, such as texture and the effect of developmental stage on bark thickness, also affects the effectiveness of bark in protecting the vascular cambium (Gignoux, Clobert, and Menaut 1997).

Traditionally, 60°C (140°F) has been used as the critical threshold temperature that kills the cells of the vascular cambium. This injury is termed cambial necrosis. However, there may be differences in the rate of cambial cell death at elevated temperatures among tree species and season of exposure (Dickinson and Johnson 2004). Cambial cell death also is affected by the duration of exposure to elevated temperatures and the rate of temperature increase (Dickinson, Joliff, and Bova 2004).

INDUCED DEFENSE

Cambial necrosis provides access for the infection of wood by fungal decay pathogens and associated organisms. Injury and subsequent infection induce a cascade of responses within the constitutively compartmented portions of the tree. This process is collectively termed compartmentalization (Shigo 1984). Compartmentalization resists the spread of infection in wood. Compartmentalization is a boundary-setting process that consists of two parts. The first part of compartmentalization occurs in wood present at the time of injury. As living cells are injured, plugs form in the water-conducting cells that resist the spread of further cell death in the sapwood by aeration and desiccation. The plugging is accomplished both through the triggering of formation of specialized structures (tyloses) to block the axial water-conducting system as well as shifts in metabolism to produce waxes, gums, and resins that also restrict dessication and the entry of air into the xylem (Shigo 1984; Pearce 1996).

These shifts in metabolism of wood cells, as well as subsequent infection by fungi, tend to discolor or darken the affected wood. Because of wood anatomy, the spread of cell death and infection tends to occur in columns within the length of the stem. Boundaries are formed by living wood cells that limit the spread of wood cell death and infection to the smallest possible volume. These boundaries that resist the spread of the columns into healthy wood are referred to as reaction zones or column boundary layers. In oaks and other broadleaved trees, these layers frequently contain waterproofing materials similar to those found in bark and phenolic compounds such those found in heartwood and bark.

The second part of compartmentalization occurs in wood formed after injury. The vascular cambium produces an anatomically distinct barrier zone to both sides and above and below the injury. The barrier zone is frequently visible to the unaided eye as a darkened line within or between annual growth ring(s). The barrier zone is most obvious near the wound, but may extend around the tree circumference at some distance away from the injury. The position of the barrier zone within the growth ring allows the estimation of the timing of the fire within or between the growing seasons. In the absence of additional wounds that breach the barrier zone, wood decay will tend to occur within the compartment described by the barrier zone. The compartmentalization of infection and decay enables the vascular cambium to continue to divide and to move outward and away from the infection.

In an otherwise healthy, vigorous tree, the fire injury stimulates cell divisions of the vascular cambium at the edge of the area of cambial necrosis or fire scar, resulting in locally wide growth rings. This local growth stimulation serves to both hasten wound closure and to provide additional strength to the loadbearing structure of the tree. These thickened woundwood ribs serve to efficiently distribute the mechanical loading of the stem, branch, or root and to reduce the risk of structural failure (Mattheck 1998).

TREE DISSECTIONS AND QUALITATIVE ANALYSIS

We dissected eastern oak and associated trees previously exposed to prescribed fire at the Raccoon Ecological Management Area in southeastern Ohio (Yaussy, Hutchinson, and Sutherland 2003; Hutchinson, Sutherland, and Yaussy 2005). Our qualitative analysis (Smith and Sutherland 1999, 2001; Sutherland and Smith 2000) indicated that trees with scorched bark generally occurred in scattered clusters. Individual trees located near discrete fuel sources, such as snags and logs, were also scorched. Dissections showed that the vascular cambium of some scorched trees, particularly those with thick bark, was not injured by the prescribed fires. Thin-barked red maples were more frequently and severely injured than oaks and hickories. In oaks and hickory

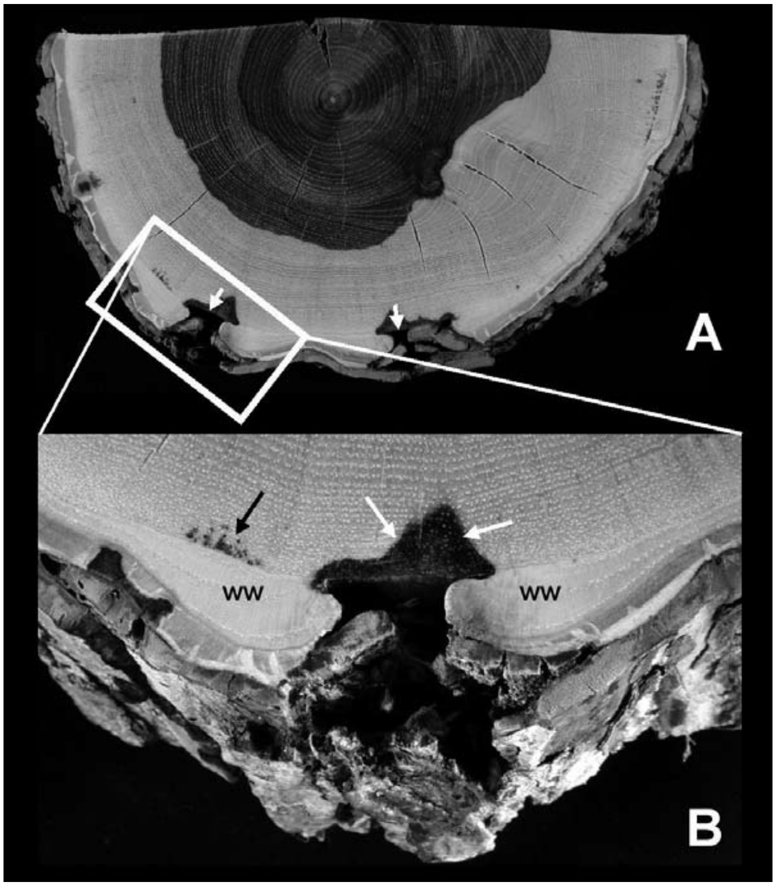

Figure 1.—Cross- section of pignut hickory (*Carya glabra*) with small fire scars covered by intact bark, dissected in the third year after fire injury. A. Cambial necrosis (white arrows) associated with bark furrows. B. The column of wound-initiated discoloration (white arrows) is small and well-defined. Woundwood (ww) appears as locally wide annual rings. The small points of discoloration (black arrow) are likely the ends of small columns of discoloration initiated by a wound several centimeters above or below the plane of the section.

that were slightly injured, cambial necrosis was localized to the areas beneath deep furrows in the bark, where the insulation provided by the bark was least.

Two years after fire injury, few if any overstory trees were killed by the fire. Most fire scars were concealed by intact bark. As with the pattern of bark scorch, these basal fire scars were triangular in shape (Smith and Sutherland 1999). This shape has been attributed to the triangular pattern of heat intensities within and around a flame (Gill 1974). However, basal wounds not caused by fire frequently form triangular scars due to increased dieback of the vascular cambium along the stem axis. Observations of trees exposed to two prescribed fires verify that the scorching or charring of wood in the open wound face resulted from exposure to a later fire and not to the fire that caused the initial scar.

Tree dissections showed that fire scars were often associated with bark fissures, particularly in tree species with thick bark (Fig. 1A, B). The relatively thin bark in the fissure provides less protective insulation to the vascular cambium beneath the fissure (Guyette and Stambaugh 2004; Smith and Sutherland 1999). The surviving vascular cambium adjacent to the fire scar generally produced xylem cells at an accelerated rate, resulting in a fold or rib of woundwood at the scar margin (Fig. 1A, B). This enhanced production of wood was seen as wider growth rings adjacent to the wound. This localized stimulation in growth tends to close over the exposed wood more quickly than at normal growth rates. Successful wound closure reduces the access of exposed wood and associated tissues to infection and allows for the potential restoration of the vascular cambium around the stem circumference.

The formation of woundwood ribs also contributes to the structural stability of the standing tree (Fig. 2A, B). In engineering terms, most of the mass of the above-ground portion of the tree is supported by the outermost portion of the roughly cylindrical stem (Mattheck 1998). Stem growth tends to uniformly distribute the loading

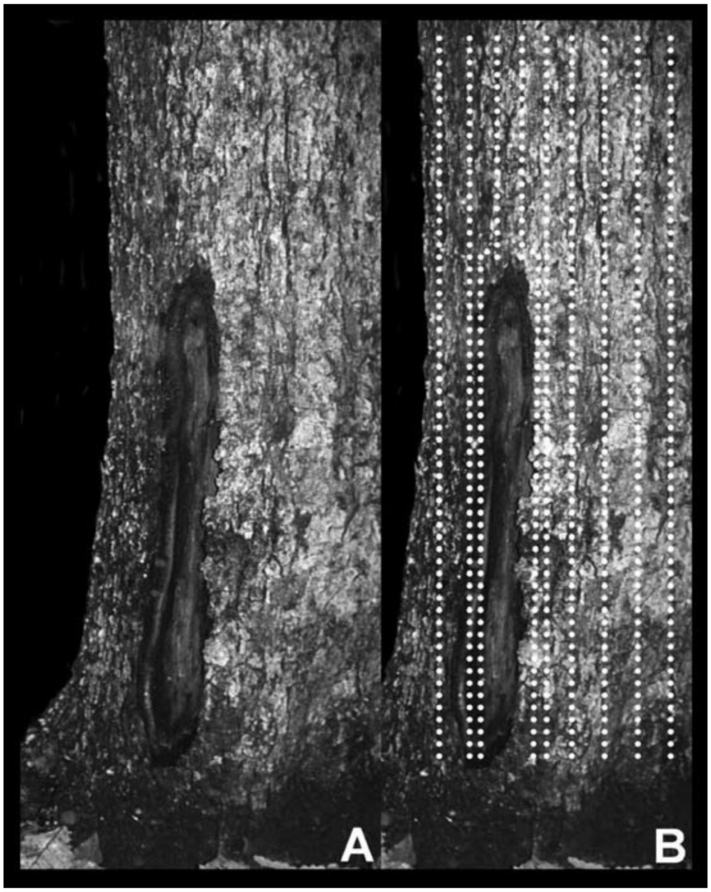

Figure 2..—Oak tree with a 4-year-old fire scar in southeastern Ohio. A. The scar is characterized by the exposed wood face that is almost completely covered by woundwood ribs. B. Simplified overlay diagram showing the mechanical loading of the stem (dotted lines). The decreased spacing of the load lines represents the increased load stress adjacent to the fire scar.

around the stem circumference. Cambial necrosis locally interrupts the formation of the wood annual increment. As the stem continues to increase in girth, the physical loading becomes less uniformly distributed with additional stress applied at the margins of the wound (Fig. 2A, B). The tree woundwood ribs add support where the stress is increased. The curved orientation of wood cells at the inward-facing edge of the woundwood resists shearing stress parallel to the wound surface (Mattheck 1998).

The long-term effect of cambial injury caused by fire illustrates the effectiveness of compartmentalization in resisting the spread of infection and wood decay and contributing to tree survival. From the perspective of compartmentalization, a tree with a well-defined hollow or cavity can indicate a successful outcome (Fig. 3). The cavity is contained within a relatively small volume and surrounded by a continuous band of healthy and structurally sound wood. The vascular cambium is intact and not compromised.

IMPLICATIONS FOR MANAGEMENT

Evaluating the effects of fire on surviving trees, particularly low-intensity prescribed fire, requires an understanding of the distinctions and linkages among signs of a fire (e.g., bark scorch), stem injury (e.g., cambial necrosis, death of associated living phloem and sapwood, and resulting infection), internal discoloration and decay (limited by compartmentalization), and damage (loss of value). The mere presence of bark scorch does not necessarily indicate injury to the vital processes of a tree. Wound-initiated discoloration and decay can, within limits, be contained to small volumes within the living tree. The tree response to extensive injury and infection depends on induced defenses. The effectiveness of compartmentalization to resist the spread of infection depends on the genetic capacity of the tree for compartmentalization and the ability of the tree to use that capacity. That ability rests on the condition of the particular tree at the time of injury (Shigo 1986). The importance of pre-existing tree conditions for survival following fire injury was observed for eastern oaks (Yaussy, Dickinson, and Bova 2004) as was previously seen for northern hardwoods exposed to storm injury (Shortle, Smith, and Dudzik 2003).

The distinction between injury and damage is especially important. "Damage" refers to a loss of value (Shigo 1986). Value is directly related to the specific goal of forest management. If prescribed fire shifts species frequency towards a more desirable stand composition, there may be significant injury to less-desirable species yet little or no damage in the sense of loss of value. Well-compartmentalized infections in the core of desirable tree species may result in a central column of wood decay or a cavity, but have little negative effect on the stem outside of that column, resulting in the potential for high wood quality for products or high habitat quality for wildlife. Depending on the severity of injury and the time required to restore continuity of the vascular cambium, fire can affect the value of overstory trees by decreasing the volume of comparatively more valuable heartwood both by increasing the volume of cull as discolored and decayed wood and by delaying the formation of heartwood (McGinness and Shigo 1975; Phelps and McGinness 1977). The degree of volume loss will depend on the extent of the injury and the effectiveness of compartmentalization.

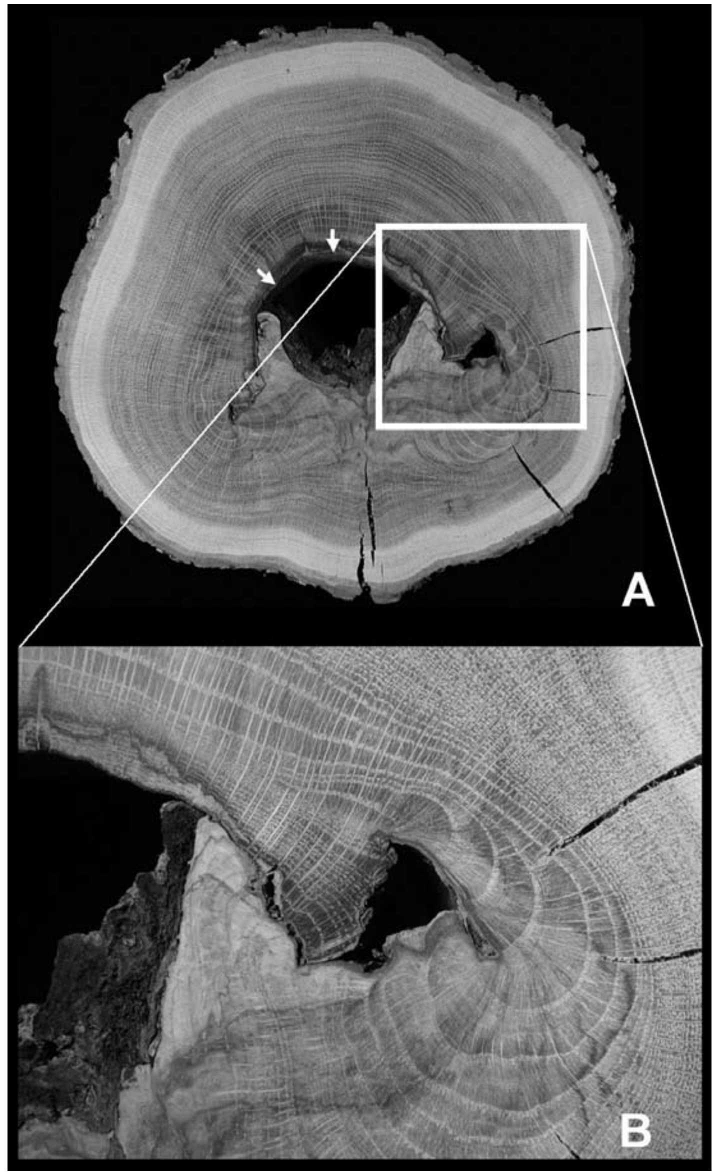

Figure 3.—Cross-section of white oak (*Quercus alba*) illustrating the long-term response to cambial wounding. A. The tree was likely injured at the size and age indicated by the outer edge of the central cavity (small white arrows). Over the next approximately 40 years, woundwood ribs grew on either side of the exposed wound face, eventually restoring the continuity of the vascular cambium. Infection by wood decay fungi and their associates resulted in the complete decay of wood present at the time of injury. However, infection did not spread into wood formed after the injury. B. Changes in orientation of wood cells in woundwood ribs. Bark that lined portions of the inside of the cavity was produced on the outer surface of the ribs as they closed over the wound.

CONCLUSIONS

Fire affects overstory trees in eastern oak forests in both obvious and hidden ways. Trees resist the occurrence of injury through constitutive protection and resist the spread of infection by induced defenses. Recognizing the patterns of fire effects can help guide prescriptions for the use of fire as a silvicultural tool and to understand the effects of wildfire. Bark scorch, tree injury, and damage are not equivalent terms. Useful evaluation of fire effects on and the implications for overstory trees requires an understanding of fire physics and tree physiology. The degree of damage sustained by fire injury depends on the specific goals of forest management.

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