TERMINOLOGY AND BIOLOGY OF FIRE SCARS IN SELECTED CENTRAL HARDWOODS

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ABSTRACT

Dendrochronological analysis of fire scars requires tree survival of fire exposure. Trees survive fire exposure by: (1) avoidance of injury through constitutive protection and (2) induced defense. Induced defenses include (a) compartmentalization processes that resist the spread of injury and infection and (b) closure processes that restore the continuity of the vascular cambium after fire injury. Induced defenses are non-specific and are similar for fire and mechanical injury. Dissection of central hardwood species in a prescribed fire treatment area in southeastern Ohio provided an opportunity to place features seen in dendrochronological samples into their biological context. Terms for these features are proposed and further discussion is solicited.

Keywords: Compartmentalization, tree wound response, fire biology, fire scars, tree injury.

INTRODUCTION

Fire may injure both above- and belowground portions of living trees. Stem injuries, commonly referred to as fire scars, are readily investigated using standard dendrochronological methods and are the subject of this report. The precise dating and understanding of fire scars links wood anatomy, tree allometry and survival strategies, and forest community dynamics. Through fire scar analysis, dendrochronology contributes to the understanding of forest stand development (Anderson et al. 1987; Dey and Guyette 2000; Wills and Stuart 1994), climatic variability (Grissino-Mayer et al. 1997; Swetnam 1993; Swetnam and Betancourt 1998; Grissino-Mayer and Swetnam 2000; Veblen et al. 1999), and forest management and sustain-

ability (Guyette and Cutter 1991; Baisan and Swetnam 1990; Dey and Guyette 2000).

Trees are not passive recorders of fire. The likelihood and severity of stem injury at a given level of fire intensity depends largely on constitutive protection (e.g. bark characteristics and seasonal dormancy). After fire injury, trees survive through induced defensive responses to injury and infection by wood decay pathogens (compartmentalization and wound closure). These responses enable trees to survive and record the occurrence of successive fires over a long period of time.

This paper defines terms and illustrates patterns of fire scars and the tree response to fire injury that were evident in dendrochronological samples from a study of single and multiple prescribed
low-intensity fires at the Raccoon Ecological Management Area (REMA) in Vinton County, Ohio (Boerner et al. 2000; Smith and Sutherland 1999; Sutherland and Hutchinson, in press). These prescribed fires were conducted 1996–1999 during the late dormant season (late March to early April) before leaf-out. (Most wildfires in Ohio burn during this time period [Haines and Johnson 1975]). In one burn treatment, fires were set annually. In the other treatment, fires were set in 1996 and then in 1999. This qualitative survey is supported by cross-sections of the trunk of white, chestnut, and black oak (Quercus alba, Q. prinus, Q. velutina), pignut hickory (Carya glabra), and red maple (Acer rubrum).

DEFINITIONS

The pattern of tree response to fire injury appears similar to response to other mechanical injuries to the stem. In the spirit of enhancing the interpretation and discussion of fire scars, we will use the following definitions, derived from plant anatomy (Fink 1999) and forest pathology (Shigo 1984, 1986) and offer them for consideration and improvement by the dendrochronology and fire ecology communities.

An injury is an impairment or loss of function. A wound is a type of injury characterized by a physical disruption of living tissues. A fire scar is a wound caused by fire and involves the disruption and death of some portion of the vascular cambium. Compartmentalization is the limit-setting process that resists the loss of normal wood function and the spread of microbial infection after wounding. Compartmentalization occurs in both broadleaved hardwood and coniferous softwood species, although the details of the process vary among species groups. Callus is a soft mass or layer of essentially undifferentiated, thin-walled, isodiametric cells that contain little lignin. Callus production is an ephemeral, transient response to injury that may help reestablish the vascular cambium after disruption. Woundwood results from enhanced cell divisions of the vascular cambium and arises from the margins of the fire scar. Woundwood contains well-differentiated and lignified cells. Woundwood production is an ongoing, persistent response to injury. Wound closure, often referred to as healing, is the process of restoring the circumferential continuity of the vascular cambium. Wound closure protects wood from external infection and dehydration and may not be complete for many years, if ever. Healing, strictly speaking, is a term more appropriate for animal systems in which wounded tissues are restored in the same spatial positions where they were injured (“making whole”). Bark scorch is a sign that a tree has been exposed to fire. Bark scorch does not necessarily indicate injury (Smith and Sutherland 1999). Fire may scorch and even char the bark without wounding the vascular cambium. Damage is not a synonym for injury; damage involves a loss of property, value or usefulness. The damage caused by a fire scar may be great in a forest stand managed for veneer production and be essentially zero in a wilderness area. Alternatively, fire injury and subsequent stem decay may enhance the value of trees for wildlife.

FIRE-INDUCED WOUNDING AND TREE RESPONSES

Standing scorched trees were scattered across the burned area and were separated by trees that were unscorched. The inconsistent distribution of bark scorch and stem injury suggests that developing the historical frequency of low-intensity fires requires intensive sampling within as well as across the landscape under investigation.

Bark scorch and fire scars were frequently associated with nearby charred stumps or pieces of coarse woody debris that likely served as a fuel source for locally intensive heating that resulted in wounding (Figure 1). When present, one or more vertical seams in the scorched bark indicated closed fire scars. The seam was formed by the meeting of thickened ribs of woundwood at the edges of the wound (Figure 1). Frequently, scarring occurred without combustion of the vascular cambium or underlying sapwood. Consequently, sampled scars from single fires did not contain scorched wood or charcoal. Killed bark required several years to slough off the stem.

Fire scars in red maple ranged from being broad (greater than one-quarter of the stem circumfer-
Figure 1. Oak tree with fire scar in southeastern Ohio. The edges of the open scar contain thickened ribs of woundwood (arrows). Over the next several years, the woundwood ribs will meet to close the scar and form a vertical seam. The fire scar is oriented towards a charred stump.

ence) to being quite narrow (the width of a single bark furrow, Figure 2A). Fire scars in pignut hickory were also variable in size. Fire scars in oak were usually narrow in lateral extent and were associated with bark fissures in rough-barked species (e.g. chestnut oak).

Locally absent rings were associated with fire scars in red maple. In this red maple section (Figure 2B), the 1996 growth ring (the first ring following the dormant season fire) was essentially missing from along the circumference between two scars. The locally absent rings may reflect a decrease in radial growth to accommodate an increased allocation of energy to defensive processes in existing wood. Sublethal heating may have disrupted the delivery or activity of plant growth regulators as has been suggested for oak after fire injury (Jordan 1966). Alternatively, the cambium may have been killed without injury to the subtending wood.

When heating kills the vascular cambium, living wood parenchyma and phloem cells can dedifferentiate and divide to form a callus pad (Fink 1999). Over a period of days or weeks, a new cambium is formed within the callus. The newly formed cambium then becomes confluent with the surviving cambium and produces new wood and phloem. The enhanced cambial metabolism that produces woundwood is likely induced through a complex mechanism of ethylene production and the potentiation and long-distance transport of plant growth regulators including auxins (Fink 1999; Smith and Shortle 1990).

The locally wide woundwood rings formed adjacent to the scar served two complementary functions: (1) to more rapidly close and reduce the threat to the vascular cambium posed by infection from the open scar and (2) to reduce mechanical notch stresses. Effective wound closure reduces the rate of wood decay through reduced aeration and increased moisture content of infected wood. Wound closure is a necessary step in the restoration of the continuity of the vascular cambium around the stem circumference. From the mechanical perspective, tree growth after scarring resulted in a notch in the outer circumference of the stem as the tree increased in diameter on either side of the scar. This notch increases the localized stress to the stem through mechanical loading. The radially thickened woundwood provides additional support in the compromised portion of the stem (Matthek 1998).

The first wood formed after wounding is anatomically distinct and has been termed a “barrier zone” in that decay initiated by wounding does not spread into wood formed after wounding unless there is additional injury that breaches the barrier zone (Pearce 1996; Rademacher et al. 1984). The vascular cambium forms barrier zones at some distance removed from the actual injury, well beyond the site of woundwood formation (Shigo and Dudzik 1985).

Red maple, unlike oak and hickory species, does not produce colored heartwood as a result of
aging or maturation (Shigo 1986). Large scars in red maple were associated with extensive areas of wound-initiated discoloration (Figure 2A). The color quality varied at least in part due to the breakdown of the condensed phenolic compounds and the bleaching of the wood by fungi as part of the decay process. Columns of wound-initiated discoloration extended vertically beyond the top edge of the scar. In transverse sections taken above the scar, the areas of discoloration appeared to be “floating” in the sapwood, without apparent connection to the fire scars that induced their formation (Figure 2A).

The discoloration process is initiated by the lethal heating of the vascular cambium. Even if the bark continues to adhere over the killed area, the wound causes the water columns under tension in functional sapwood to break, resulting in wood aeration and desiccation. Tyloses, gums, and other plugging materials are produced to resist the loss of moisture. These tyloses and plugging processes comprise the first component of the compartmentalization process. Compartmentalization proceeds through a metabolic shift in sapwood parenchyma from energy storage to enhanced biosynthesis of defensive chemicals. This shift in oxidative metabolism removes readily assimilable carbohydrates from the wood through conversion to phenolic compounds (Smith 1997) that are broadly inhibitory to the development of pests and pathogens. These oxidative processes tend to darken the sapwood in broadleaved tree species (see red ma-
Figure 3. Transverse section of a fire scar in pignut hickory. A. Extensive decay of both sapwood and heartwood beneath the fire scar includes zone lines (black arrows) produced by wood decay fungi. Woundwood ribs (WW) are prominent at the edge of the fire scar. (Scale bar = 1 cm). B. Included phloem (IP) incorporated into the woundwood. (Scale bar = 1 cm).

ple in Figures 2A, B). Although wound-initiated discoloration is initially protective with respect to infection, wood-inhabiting bacteria and fungi infect the discolored wood, degrade the phenolic compounds, and eventually break down the wood substance.

The attack of healthy sapwood by microorganisms that have colonized wound-initiated discoloration can stimulate the production of a distinct column boundary layer (CBL, also referred to as a reaction zone) between discolored wood and healthy sapwood (Pearce 1996; Shortle and Smith 1990). In freshly cut sections from living trees, this thin layer may be highly colored (the “green zone” in maple, for example). When dried, the column boundary layer is still frequently distinct in color from the rest of the wound-initiated discoloration and is most prominent when in radial alignment with intact phloem. The CBL is enriched with plugging materials, phenols, and mineral elements and resists the spread of desiccation/aeration and wood-invading fungi. The CBL can be overcome and breached by wood decay fungi. When breached, a sufficiently vital tree forms a new CBL at some distance further from the original wound as the column of wound-initiated discoloration expands. Increment cores taken from fire scars can contain these successive boundaries.

Four years after fire injury, broad scars often contained extensive decay in both sapwood and heartwood (for example, pignut hickory in Figure 3A). Zone lines indicated advanced stages of decay, the result of inter-genomic antagonism by wood decay fungi. Woundwood production was
stimulated at the margin of each scar. Notably, remnants of inner bark (nonconducting phloem) were occasionally incorporated in rolls of woundwood (Figure 3B). Such bark inclusions could complicate ring assessments and the dating of fire events.

Two years after fire injury to white oak, wound-initiated discoloration associated with narrow fire scars did not penetrate deeply into sapwood (Figure 4A). However, discoloration and sapwood decay was evident in the few relatively broad fire scars in oak. The transformation of sapwood into colored heartwood is likely to be delayed in trees with fire scars (McGinnes and Shigo 1975). Four years after fire injury, adhering bark continued to cover fire scars in hickory and oak (Figure 4B). Narrow fire scars appeared closed, but the inrolled bark of the woundwood ribs still prevented the restoration of a continuous vascular cambium.

CONCLUSIONS

Typical induced defenses to mechanically injured cambium such as column boundary layers, barrier zones, and woundwood ribs are prominent in samples of fire scars collected for dendrochronology. Interpretation of the tree-ring record for the dating of fire events and their consequences requires an understanding of how these defensive processes contribute to tree survival and how their failure contributes to tree mortality. Here, we offer a common terminology describing how fire injuries and associated defense mechanisms result in the anatomical features known as fire scars. We
hope that this terminology will aid interpretations of fire scars.

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