ARTICLE

Macroanatomy and compartmentalization of recent fire scars in three North American conifers

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Abstract: Fire scars are initiated by cambial necrosis caused by localized lethal heating of the tree stem. Scars develop as part of the linked survival processes of compartmentalization and wound closure. The position of scars within dated tree ring series is the basis for dendrochronological reconstruction of fire history. Macroanatomical features were described for western larch (*Larix occidentalis* Nutt.), ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson), and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) injured by fire in 2003 and harvested in 2011 at the Lolo National Forest near Missoula, Montana, USA. Bark scorch did not necessarily indicate the formation of a scar. Wound-initiated discoloration inward from the scar face was bounded tangentially by reaction zones. In western larch, the transition between earlywood and latewood was much less abrupt in woundwood rings than in rings formed the same year but not associated with a scar. Wood formed the year after injury contained tangential rows of resin ducts in the earlywood. Compartmentalization plays a key role in resisting the spread of infection and the loss of healthy sapwood and heartwood. Wound closure restores some degree of circumferential continuity of the vascular cambium and reinforces stem structure. The terminology presented here should facilitate communication among tree pathologists, wound anatomists, and dendrochronologists.

Key words: fire injury, fire history, dendrochronology, wound pathology, reaction zone, barrier zone, bluestain, conifer defense.

Résumé : Les cicatrices de feu résultent de la nécrose du cambium causée par une chaleur létale localisée sur le tronc des arbres. Elles font partie des processus de survie inter-reliés que sont le compartimentage et la fermeture de la blessure. La position des cicatrices dans les séries dendrochronologiques datées constitue les fondements de la reconstitution dendrochronologique de l'historique des feux. Les caractéristiques macroanatomiques ont été décrites chez le mélèze occidental (*Larix occidentalis* Nutt.), le pin ponderosa (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) et le douglas de Menzies bleu (*Pseudotsuga menziesii* (Mirb.) Franco) endommagés par le feu en 2003 et récoltés en 2011 à la forêt nationale de Lolo près de Missoula dans l'État du Montana, aux États-Unis. De façon générale nous avons observé que la présence d'une roussissure de l'écorce n'entraînait pas nécessairement la formation d'une cicatrice. La coloration du bois causée par la blessure derrière la cicatrice était limitée tangentiellement par les zones de réaction. Chez le mélèze occidental, la transition entre le bois initial et le bois final était beaucoup moins abrupte dans les cernes annuels associés à la blessure que dans les cernes annuels formés la même année mais distants de la blessure. Le bois formé l'année suivant la blessure contenait des rangées tangentielles de canaux résinifères dans le bois initial. Le pin ponderosa complétait la différenciation du xylème plus tard que le mélèze occidental et que le douglas de Menzies bleu. Le compartimentage joue un rôle clé dans la résistance à la propagation de l'infection et la perte de bois d'aubier et de bois de cœur sains et fonctionnels. La fermeture de la blessure restaure un certain degré de continuité circonférentielle du cambium vasculaire et assure le renforcement structural du tronc endommagé. La terminologie cohérente présentée dans cet article devrait faciliter la communication entre les phytopathologistes, les anatomistes du bois et les dendrochronologistes. [Traduit par la Rédaction]

Mots-clés : blessure causée par le feu, historique des feux, dendrochronologie, pathologie des blessures, zone de réaction, zone barrière, bleuissement, mécanismes de défense des conifères.

Introduction

The dendrochronological record of fire scars provides the primary evidence of the timing, geographic extent, and other properties of forest fire regimes across scales of space and time (Swetnam et al. 2009; Falk et al. 2011). Derived fire histories can then be related to observed or reconstructed climatic patterns to infer predisposing environmental relationships associated with periods of high or low fire frequency, size, and severity (Kitzberger et al. 2007; Swetnam and Brown 2010; O'Connor et al. 2014; Rother and Grissino-Mayer 2014).

Dendroecological reconstruction of fire occurrence rests on the ability to date fire-related injuries with high temporal (<1 year) precision. Fire scars provide such a high-resolution record, typically for time scales of 10^1–10^3 years. However, not every tree exposed to fire forms a scar. Once formed, scars can decay or be destroyed by subsequent mechanical damage over decades and centuries. Thus, identifying additional anatomical markers of heat exposure would add to the potential proxies for fire occurrence in the tree ring record (Arbellay et al. 2014a, 2014b).

This study describes active responses of compartmentalization and wound closure rather than immediate or delayed mortality associated with lethal heating. Alternative mechanisms of tree mortality from fire include the heat-induced cavitation of conducting xylem (Michaletz et al. 2012), crown injury, and damage to

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fine root systems near the soil surface (Swezy and Agee 1991; Hood et al. 2007, 2010).

Trees killed outright by combustion or lethal heating do not produce fire scars. Far from being passive "data loggers", surviving trees injured by fire undergo profound physiological shifts from primary metabolism to stress metabolism (Smith 2015). The physiological and associated anatomical responses to fire enable tree survival in ecosystems where fire is a recurring disturbance process. These factors that confer individual tree survival provide the organismal context for dendrochronology (Smith 2008) and reconstructions of fire history.

Localized lethality or necrosis of the vascular cambium results from the physical transfer of heat greater than the tolerance threshold interaction of temperature and duration of exposure (Johnson and Miyanishi 1995; Dickinson and Johnson 2004; Jones et al. 2006). After cambial cell death, two dynamic processes result in scar formation: compartmentalization and wound closure. Compartmentalization is the set of constitutive and induced anatomical and physiological boundaries in wood and bark that resist the loss of normal function and the spread of infection after physical injury (Shigo 1984; Shortle and Dudzik 2012). The decay resistance of the fire scar record depends on effective compartmentalization. Wound closure is the reactive formation of wood after injury that tends to grow over and attempt to close the wound surface (termed "wound healing" in Fink (1999) and "wound closure" in Mattheck et al. (2015)). Successful wound closure re-establishes a continuous vascular cambium along the stem axis and around the stem circumference.

Previous research on oak scars produced in response to prescribed fire described the loss of normal function and development of wood decay within compartmentalization boundaries (Smith and Sutherland 1999). The application of established terms and concepts from forest pathology provided a framework to understand processes of fire scar formation in oak and associated eastern broadleaved trees (Smith and Sutherland 2001).

In the intact stem of a mature North American conifer, a band of living sapwood surrounds a core of nonliving heartwood (Wiedenhoeft 2013). The sapwood apoplast of cell walls and open lumina conducts water and provides structural support (Kozlowski and Pallardy 1997). The symplast of interconnected sapwood cytoplasm found in axial and radial parenchyma stores starch as a local reserve stock of energy and biosynthetic feedstocks for primary and stress metabolites (Kolosova and Bohlman 2012). As part of normal ageing and maturation, living conifer sapwood is converted to nonliving heartwood through consumption of locally stored starch and biosynthesis of chemical protectants, tracheid aspiration accompanied by decreased moisture content and, ultimately, necrosis of the symplast (Kampe and Magel 2013).

Wounding and the xylem wound response interrupt the orderly transformation of sapwood into heartwood. The most visible feature of this disruption is the wound-initiated transformation of sapwood tangential to the wound into discolored wood. This discoloration of the former sapwood reflects a series of processes performed by living sapwood cells to compartmentalize the injury (Shigo and Hillis 1973; Shortle and Dudzik 2012). Although discolored wood in the sapwood band may resemble heartwood in color, it lacks the comparatively greater decay resistance of heartwood and is more vulnerable to the spread of infection. The discolored wood is separated from sapwood by reaction zones, necrotic tissue enriched with waterproofing, and inhibitory extractives that resist the expansion of discolored wood into healthy sapwood present at the time of wounding (Shain 1979; Schwarze et al. 2000). By definition, reaction zones are formed through shifts in metabolism that deposit protective chemicals in sapwood present at the time of injury (Shortle 1979). Plugging and aspiration of the tracheids isolate the discolored wood from the hydraulic flow of normal sapwood. In the first annual ring formed after injury, there is frequently an anatomically distinct barrier zone that resists the outward spread of infection towards the vascular cambium and into more recently formed sapwood (Shigo 1984; Shortle and Dudzik 2012).

The objective of this paper is to describe and interpret compartmentalization and wound closure processes in recent (<10 years after wounding) fire scars of three common species of Pinaceae from western North America: western larch (*Larix occidentalis* Nutt.), ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson), and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Scars formed in these three species after a documented recent fire provides a comparatively simple system to qualitatively investigate tree wound response. Dated fire scars of both *P. ponderosa* and *P. menziesii* are widely used for fire history reconstruction (Schweingruber 1993; Falk et al. 2011), whereas scars of *L. occidentalis* has been used only occasionally (Barrett et al. 1991; Marcoux et al. 2015). In this report, observations were centered at the macroanatomical level, which is the visual scale most used by dendrochronologists to date fire scars.

Methods

As part of a larger integrated study on the relationship of forest ecology to wildland fire in western conifer forests of North America, we investigated the macroanatomy of fire scars in the Dry Gulch (46.51.6°N, 114.14.3°W) and Iris Point areas (46.42.437°N, 113.44.054°W; 1800–1900 m above sea level (a.s.l.)) of the Lolo National Forest (LNF) near Missoula, Montana, USA. Sample trees described here were injured in 2003 by the following fires in the LNF: Dry Gulch burned in the Black Mountain fire (2–16 August 2003; 2961 ha in extent) and Iris Point burned in the Cooney Ridge Complex fires (8 August to 15 October 2003; 9600 ha in extent). At the time of sampling in late August through September 2011, surviving trees with charred bark and occasionally prominent fire scars were apparent (Fig. 1).

For the larger integrated study, we established the centers of circular plots at 50 m intervals at each location. Up to three each of the nearest three living western larch, ponderosa pine, and Douglas-fir trees 10–25 cm diameter at breast height (dbh, 1.3 m) with charred bark above the root flare were selected for sampling and felled. We measured total tree height from the felled stem and cut 5 cm thick sample disks at the root flare and at 25 cm, 50 cm, 75 cm, 1 m, and then at 50 cm increments along the stem to 50 cm above the top of the bark char. A total of 59 trees were sampled for the larger study. We visually assessed the disks for patterns of compartmentalization and wound closure as identified previously for oak (Smith and Sutherland 1999, 2001). We selected a subsample of 37 disks for further macroanatomical investigation that represented the range of visible wound responses (Table 1). Macroanatomical studies describe the anatomy and appearance of plant tissues under relatively low magnification and reflected light. The level of visual detail is that of a dissecting microscope (7–15×) or camera fitted with a macro lens. Macroanatomical investigations enable a wider field of view with less intensive sample preparation than for histological analysis of microtomed sections at the cost of reduced structural and histological detail.

The microanatomy of living xylem associated with fire scars from these collections at the LNF includes the structural relationships of tracheids, rays, and resin ducts (Arbellay et al. 2014*a*, 2014*b*). In the current study, samples were sawn through the scar or necrotic cambium. In addition to transverse stem sections, longitudinal sections through fire scars were also collected and processed for macroanatomical comparison.

Sawn surfaces of sample disks and sections were smoothed with a graded series of sandpaper through 600 grit mounted on a drill press. Sanded surfaces were polished with a fine cotton sheet backed by a lamb's-wool buffing pad also mounted on a drill press. Macro photographs (components A–C in Figs. 2–5) were taken

Fig. 1. Open fire scar on ponderosa pine in 2011, injured in the Black Mountain fire of 2003 at the study area in the Lolo National Forest of western Montana, USA.

Table 1. Sample trees dissected for characterization of fire scars in transverse section at Lolo National Forest, Montana, USA.

Species	No. of trees	Mean DBH (and range), cm	No. of stem disks
Larix occidentalis	6	19 (15–24)	13
Pinus ponderosa	3	21 (19–23)	10
Pseudotsuga menziesii	6	16 (12–23)	14

with a Canon EOS 7D digital camera fitted with a macro lens and mounted on a copy stand equipped with four daylight bulbs. To produce a focused image across the field of view, vertical montages of photomicrographs (component D in Figs. 2–5) were constructed using the Leica Application Suite. Each montage was flattened from about 10 images captured at successive focal planes using a Leica M165C microscope fitted with a Leica DFC420 camera and with reflected fiber optic illumination.

Table 2 is a list of terms and concepts drawn from established terms from tree biology and forest pathology (Shigo 1984; Fink 1999) and applied to the macroanatomy of fire scars. The table is consistent with terms previously applied to the macroanatomy of fire scars in oak and other hardwood species (Smith and Sutherland 2001). Signs of insect borers were evaluated using the field guide of Hagle et al. (2003).

Results

General observations

At the 2011 sampling, prominent fire scars were identified by the robust rolls or ribs of woundwood that tended to close over the exposed necrotic wood surface from the tangential and axial margins of the wound (Fig. 1). Scars were attributed to the 2003 fire based on the position of the wound in the annual ring series. For all three tree species, many scars from the 2003 fire were still covered by adhering bark in 2011 and not readily apparent without tree dissection. Beneath the adhering bark, woundwood partially or completely closed the wound face in all three tree species. Frequently, but not uniformly, the rings of woundwood adjacent to and growing over the wound surface were wider than rings along the same radius formed prior to injury, and also wider than the same ring formed at a greater circumferential distance from the wound margin.

Sapwood dieback and discolored wood extended beyond the arc and height of cambial necrosis and the original injury, particularly in Douglas-fir and western larch. Due to the axial orientation of xylem tracheids and to compartmentalization boundaries, discolored wood occurred as a column, with tapered ends at the top and at the bottom. The discolored wood was bounded tangentially by reaction zones and extended radially to the heartwood.

Woundwood rings narrowed abruptly with increasing tangential distance away from the wound margin. Sample disks collected in 2011 frequently contained more than one region of cambial scarring associated with the 2003 fire, resulting in a discontinuous or "patchy" necrosis of the vascular cambium around the stem circumference. The periderm and phloem on the woundwood ribs were thin and lacked a well-developed outer bark or rhytidome.

All three conifer species contained wood borer galleries in discolored wood with infrequent incursions into heartwood. The galleries were packed with fine sawdust in an arced or fingerprint tip print pattern.

Western larch

For each scar, a column of wound-initiated discolored wood extended radially across the narrow sapwood band and inward to the heartwood (Figs. 2A and 2B). The tangential extent of the discolored wood extended beyond the circumferential extent of the necrotic vascular cambium. Two or more successive reaction zones were frequently formed at the sapwood – discolored wood interface (Figs. 2B and 2C). Insect bore holes packed with sawdust occurred in discolored wood but were absent from sapwood and heartwood. Heavy resin soaking was evident in tracheids to the inside of the exposed wood surface. This resin soaking did not appear to be associated with resin ducts (Figs. 2B and 2C).

Constitutive resin ducts were infrequent, usually occurring singly in latewood of rings formed prior to fire injury. Cambial growth was complete in the fire-year ring in the sections we examined. Tangential rows of numerous traumatic resin ducts occurred in the earlywood of the 2004 growth ring, particularly in the woundwood and the transition between woundwood and normal wood (Figs. 2B and 2D). Normal rings formed in 2003–2005 located away from the scar contained an apparently abrupt shift between relatively thin-walled earlywood and thick-walled latewood tracheids. At the transition between woundwood and normal wood, the earlywood to latewood shift was less abrupt in the 2004 growth ring than in the 2003 and 2005 rings (Fig. 2D).

Ponderosa pine

Most scars of ponderosa pine were associated with bark furrows and concealed by attached bark (Figs. 3A and 3B). In both exposed and concealed fire scars, ribs of woundwood tended to close over the exposed wound surface. Ray formation in woundwood maintained a perpendicular orientation to the vascular cambium and an oblique, curved angle to the previously formed wood (Fig. 3B). Constitutive axial resin ducts contained thin-walled epithelial parenchyma and frequently occurred in the latewood portion of annual rings (Fig. 3C). Traumatic resin ducts appeared smaller and more frequent both in the earlywood and latewood in rings

Fig. 2. Transverse stem section of western larch containing (A) closed (upper) and open (lower) fire scars and two detail areas (white boxes). (B) Detail from A (upper) with discolored wood (DW), an arc of necrotic vascular cambium (white arrows), heartwood (HW), sapwood (SW), reaction zones (numbered black arrows), resin soaking (triangle), beetle bore holes (open arrows), and detail area (white box). (C) Detail from A (lower right) with woundwood (WW) closing the necrotic wound face beneath killed, adhering bark (stars). (D) Detail from B with a tangential row of resin ducts (arrows) in latewood formed the year after fire injury. In the image, the 2003 ring is located beneath the 2004 ring and cropped.
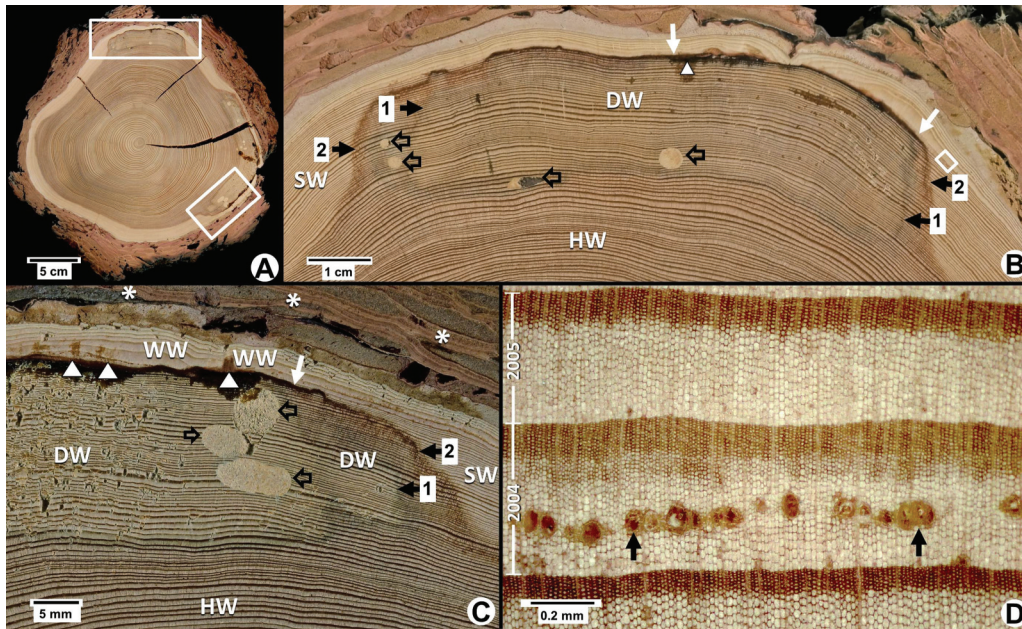

Fig. 3. Transverse stem section through three fire scars of ponderosa pine containing (A) woundwood (WW), discolored wood (DW), reaction zones (open arrows), resin soaking (triangles), and three detail areas (white boxes). (B) Detail from A (left) with WW covering a remnant of killed phloem (open arrows) retained on the wound surface and killed, adhering bark (stars). (C) Detail from A (center) with constitutive resin canals in latewood (arrows). (D) Detail from A (right) with a callus pad (CP) and traumatic resin ducts (arrow).
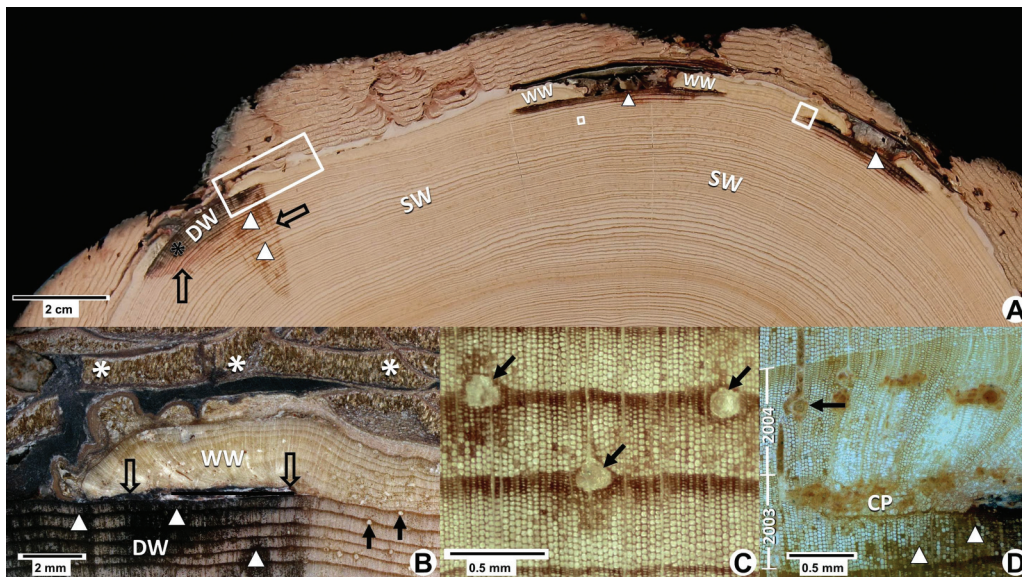
formed after injury, extending beyond the arc of the exposed wood.

Two patterns of resin soaking frequently occurred, namely (*i*) a thin deposit immediately beneath the killed wood surface (Fig. 3B) and (*ii*) a wedge of discolored wood extending towards the pith (Fig. 3A). The most prominent resin soaking extended radially towards the pith from the living phloem at the tangential edge of the wound.

Ray cells along the tangential edge of the wound and contiguous normal wood supported the production of a pad of callus (Fig. 3D), identified by the jumbled arrangement of relatively thin-walled, large, parenchyma cells that later extended into organized radial files of tracheids. The position of the callus pad prior to the completion of the 2003 growth ring (Fig. 3D) indicated that annual ring formation had not yet concluded at the time of the fire.

Fig. 4. Transverse stem section of Douglas-fir containing (A) a large open fire scar (upper half of section), a closed fire scar (lower left), and two detail areas (white boxes). (B) Detail from A (right) with extensive discolored wood (DW), bluestain (BS), heartwood (HW), resin soaking (triangles), the edge of the necrotic vascular cambium (white arrow), and thin bark and narrow phloem (open arrow). (C) Detail from A (left) with the arc of necrotic cambium (between the white arrows), woundwood (WW), necrotic cambium associated with a later injury (black arrows), and a detail area (box). (D) Detail from C with isolated constitutive resin ducts (black arrows), a callus pad (CP), radially flattened tracheids, and successive tangential rows of traumatic resin ducts that occur in the 2006 and 2008 growth rings (open black arrows).
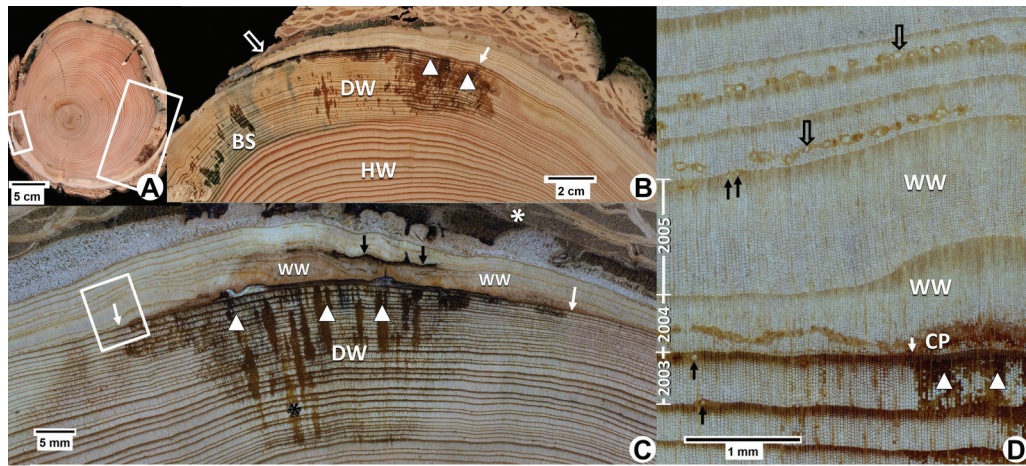

Fig. 5. Longitudinal stem section through a fire scar of Douglas-fir. (A) Resin soaking (triangles) above the lower limit of killed vascular cambium (white arrow), discolored wood (DW), and heartwood (HW), and three detail areas (white boxes). (B) Detail from A (center left) with adhering killed bark (stars) located to the outside of new phloem and thin periderm (collectively labelled P). Sapwood (SW) frequently contained wavy grain and occasional inclusions (arrow). (C) Detail from A (lower left), with a barrier zone (arrows) and beetle bore holes in DW. (D) Detail from the uninjured face of A (right), showing the narrow band of healthy SW to the outside of heartwood (HW), as well as the thick phloem (#) and the well-developed outer bark (stars).
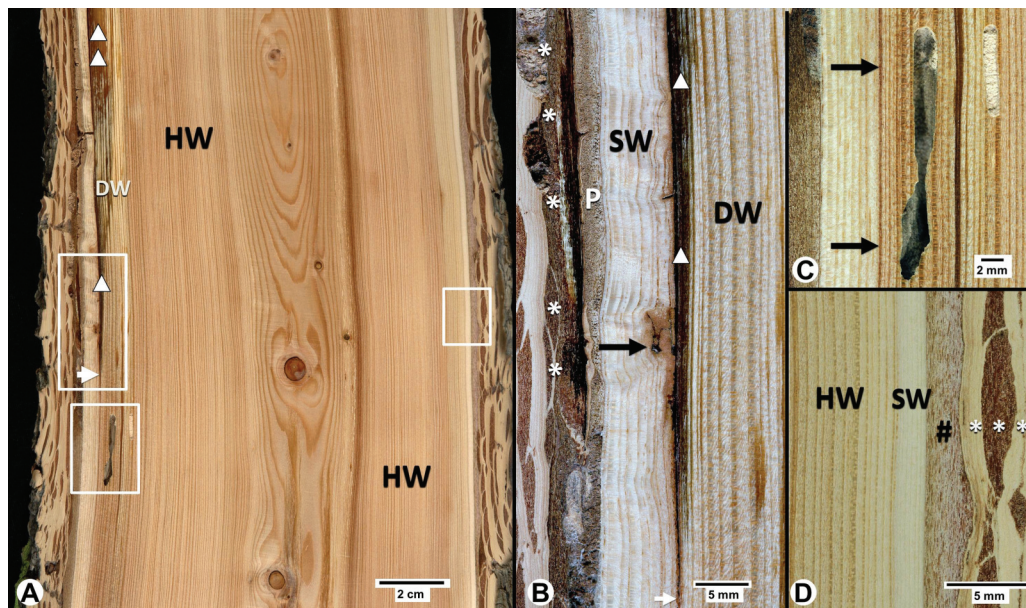
Douglas-fir

Fire killed the vascular cambium in both long and short arcs of the stem circumference (Fig. 4A). Discolored wood and bluestain infection frequently occurred between heartwood and the necrotic vascular cambium (Fig. 4B). Decay and staining were extensive in the discolored wood of Douglas-fir (Fig. 4B). Resin soaking was most apparent in wood formed prior to the fire and near the tangential limits of the wound (Fig. 4B).

Rings of woundwood tended to partially or fully close over the fire scar. In some cases, the vascular cambium of the woundwood ribs was killed, causing a new round of resin duct formation and woundwood production and closure (Fig. 4C). Sparse, constitutive resin ducts occurred in Douglas-fir latewood (Fig. 4D). Adjacent to the arc of killed vascular cambium, radial files of relatively thick-walled latewood tracheids in the 2003 growth ring appeared to terminate normally, indicating that cambial growth was complete before trees were injured. Early in the 2004 ring, three to five apparently thin-walled and radially flattened tracheids were produced (Fig. 4D). This anomaly is restricted to close proximity to the wound margin. A callus pad, probably originating from sapwood rays, remained visible outside of the arc of necrotic vascular cambium (Fig. 4D). In rings formed after injury and near the wound, traumatic resin ducts were produced consistently in tangential

Table 2. Glossary of preferred macroanatomical terms and their sources used to describe fire scars in *Pinus ponderosa*, *Larix decidua*, and *Pseudotsuga menziesii*.

Term	Characteristics	Sources
Barrier zone	A compartmentalization boundary of anatomically and chemically distinct xylem formed after wounding.	Fink 1999 Shigo 1984
Callus or callus pad	Mass of undifferentiated, roughly spherical, dividing cells forming at the wound margin or from outgrowths of xylem rays.	Fink 1999 Shigo 1984
Compartmentalization	After live sapwood is wounded, compartmentalization is the boundary-setting process that resists the loss of function and spread of infection. Compartmentalization includes both constitutive and inducible features of tree anatomy and physiology.	Fink 1999 Shigo 1984
Discolored wood	Former sapwood that has been infected by microorganisms introduced by wounding and which no longer contains living tree cells. Discolored wood is typically enclosed by reaction zones in sapwood present at the time of injury and by a barrier zone in wood formed after injury.	Shigo and Hillis 1973
Heartwood	Wood in the core of the living tree that through age or maturation lacks living tree cells and that may contain wood extractives that tend to confer decay resistance.	Shigo and Hillis 1973
Reaction zone	A compartmentalization boundary formed by shifts in metabolism to produce protective chemicals in wood present at the time of wounding.	Shain 1979
Sapwood	Wood that contains the living symplast involved in water conduction, stores starch or other energy reserves, and dynamically responds to injury and infection.	Shigo and Hillis 1973
Woundwood	Wood produced at the margin of a wound, tending to close over the wound surface.	Fink 1999 Shigo 1984

Note: Sources are commonly available reference texts or articles that may not be the original source of the terms as used here.

rows in earlywood. Although resin-soaked, anatomically distinct resin ducts were not observed within the callus pad.

The extent of woundwood production and wound closure in Douglas-fir was also evident in longitudinal section. Frequently, wide woundwood rings produced a wide band of sapwood following wound closure (Fig. 5A). Interior to the wound surface, discolored wood occupied the radial width of tissues to the heartwood. The grain of the woundwood was wavy compared with the straight grain of normal wood produced prior to fire injury (Fig. 5B). The woundwood was protected by only a thin periderm and showed growth responses to additional injury or inclusions during closure. Insect boreholes were restricted to discolored wood which had been sapwood at the time of the 2003 fire (Fig. 5C). Most boreholes were tightly packed with fine wood dust. Narrow growth rings after injury resulted in a more narrow sapwood band in the uninjured face of the stem. (Fig. 5D).

Discussion

Macroanatomical analysis helps to link large-scale environmental and landscape events such as forest fire to the dynamic processes in living tissues that confer tree survival and that form the tree-ring record. This biological linkage or organismal context (Smith 2008) of scars and related wound responses is the basis of dendrochronological reconstructions of disturbance history.

This current research examined components of tree defense and survival in three species of North American conifers that are regularly exposed to fire. Both open and closed fire scars were frequently covered by adhering bark and not readily evident from simple observation of scorched stems. The adhering bark would likely be sloughed off over time through weathering or mechanical disturbance or burned in a subsequent fire. For these recent scars from single fires, the fire scar is visually defined in the intact stem both by the curved face of killed wood if exposed and by the ribs of woundwood that tend to close over the exposed cambial necrosis and wound surface. As with eastern oaks (Smith and Sutherland 1999), (*i*) the presence of scorched bark did not neces-

sarily indicate cambial necrosis and a fire scar, (*ii*) open and closed fire scars may be covered by adhering bark and not visible on the intact stem, and (*iii*) the necrotic surface of exposed fire scars was frequently but not consistently scorched. Consequently, the absence of scorch on the exposed wood face did not exclude fire as the cause of injury.

Sapwood formed after injury in woundwood ribs and at greater distances away from the wound margin appeared healthy with a light color and absence of bluestain infection. The localization of discolored wood to rings present at the time of injury is consistent with the compartmentalization concept (Shigo 1984; Shortle and Dudzik 2012).

Compartmentalization

Western larch produced the most visually distinct reaction zones of the three sampled species, similar in appearance to reaction zones associated with recent fire scars in eastern oak (Smith and Sutherland 1999). The two reaction zones on each tangential edge of discolored wood in western larch indicated that the column of discolored wood had expanded from its initial position and induced formation of a secondary reaction zone. Reaction zone formation does not always successfully resist the spread of aggressive infections (Schwarze et al. 2000) and the zone may be breached by boring insects (Shortle and Smith 1990). In a comparative analysis of host response to wounding and infection in conifer and broadleaved species, Deflorio et al. (2009) attributed the comparatively less pronounced reaction zones formed in Douglas-fir to a naturally low frequency of radial parenchyma and absent axial parenchyma.

The terms wound-initiated discoloration and discolored wood refer to former sapwood that has responded to injury and infection, resulting in the loss or withdrawal of the symplast and death of living sapwood cells (Shigo and Hillis 1973). Discolored wood associated with these 8-year-old fire scars varied in radial depth or thickness, sometimes extending into the heartwood. Due to the injury and death of living cells, the compartments of discolored

wood do not mature into heartwood normally present in these conifer species. Discolored wood compartments may become surrounded by heartwood through the progressive maturation of sapwood tangential to and to the outside of discolored wood (Shortle et al. 2010).

The alternative term "pathological heartwood" (Jorgensen 1962) for discolored wood is misleading in that the wound-associated tissue does not have the functional characteristic of enhanced decay resistance associated with heartwood nor the similar developmental origin from ageing or maturation (Shigo and Hillis 1973). The alternative term "included sapwood" was applied to injured sapwood that was spatially incorporated into the tree core as radial growth continued but without the preservative properties of heartwood (Bamber 1976; Fink 1999). However, "included sapwood" is misleading as discolored wood has none of the properties of cellular vitality, active water conduction, or the capacity for dynamic response to further injury.

Wound closure

The ribs of proliferating woody tissue at the margins of the scar that tend to close over the exposed, killed wood surface are properly termed woundwood (Fink 1999). The misapplication of the term callus for woundwood confuses two distinct tissues. Callus refers to a mass or pad of thin-walled, undifferentiated, dividing cells containing relatively little lignin. Callus cells are roughly isodiametric, with each cell having equivalent lengths in all dimensions (Kozlowski and Pallardy 1997). Callus associated with fire scars is initiated by dedifferentiation of vascular cambial cells or sapwood parenchyma, usually associated with rays. The dedifferentiated cells divide to form an undifferentiated callus mass. Physical pressure within the callus mass can induce differentiation of a new vascular cambium (Fink 1999). Remnants of callus pads or masses of roughly spherical and undifferentiated cells form at the wound margins and are visible in some of the samples. In contrast, the ribs of woundwood produced by the vascular cambium newly produced in callus or by the surviving vascular cambium at the wound margin contain well-lignified, differentiated, thick-walled xylem cells normally incapable of division (Fink 1999).

The frequently wide rings of woundwood tend to hasten scar closure. Successful closure reduces exposure of tissue to new infection and reduces the aeration and aerobic respiration of established infections. Although the term "healing" will likely remain in use (Baker and Dugan 2013), wound closure is distinct from healing of animal systems in that functionality in injured trees is restored by new tissue in new spatial positions (Shigo 1984) rather than by regeneration in place. Even in the absence of complete wound closure and in the presence of a central void or decay column, woundwood ribs reinforce stem structure and compensates for weakness or "notch stress" at the scar (Mattheck 1998; Mattheck et al. 2015).

In the recent fire scars investigated here, the ring formed after fire injury contained a tangential row of traumatic resin ducts in western larch and Douglas-fir that extended beyond the edge of the cambial necrosis (Arbellay et al. 2014b). The vascular cambium beneath the thin outer bark on the woundwood ribs was subject to further injury and subsequent closure processes. Additional small injuries to the woundwood during closure resulted in similar tangential bands of traumatic resin ducts, as was also reported for mechanical wounding of *Larix decidua* Mill. (European larch) (Stoffel and Klinkmüller 2013). Our observations support the conceptual model of fire-induced resin duct-related defense in western conifers developed by Hood et al. (2015). The model describes the effect of fire suppression on increased mortality of *P. ponderosa* by bark beetles. In brief, the model describes increased vulnerability to trees through fire suppression and associated decreased investment in resin-based defenses. We suggest that the stimulation of resin duct formation may also contribute to resistance of

the spread of infection. Further research is needed to determine whether this relationship can be considered an example of systemic induced resistance (Eyles et al. 2010).

The borer tunnels observed were presumed to be produced by metallic wood borers (family Buprestidae) due to the arced or whorled packing of degraded wood and frass (Hagle et al. 2003). Tunnels occurred in sapwood and discolored wood, with the discolored wood occasionally occupying rings that would otherwise have been heartwood in the absence of injury. Discolored wood in the position of the heartwood core may provide an additional resource for borers intolerant of chemical protectants in heartwood.

We expect that bark thickness and texture would affect the extent of cambial necrosis initiated by a given set of fire conditions. The degree of fire injury to the root system and to the crown will affect the compartmentalization and closure of stem injury through effects on the interrelated factors of tree vigor and stored energy resources.

The consistent application of terms to describe fire scars and wound-altered tissues should facilitate communication within the fire history research community. Uniform terminology will also expedite synthesis across disciplines including tree pathologists and entomologists investigating tree survival and forest ecologists exploring the effect of environmental disturbance on biological communities. Our work underscores the need to recognize that fire scar formation is an adaptive process essential to tree survival and not just a passive epiphenomenon or consequence of fire.

The tree physiological and anatomical responses documented here may provide the basis to develop an additional potential proxy for tree exposure to fire, supplementing fire scars, tree establishment dates, and other lines of evidence. As with currently available proxies, the consistency and reliability of the anatomical record that responds to fire disturbance will require rigorous quantitative statistical analysis. The convergence of multiple proxies into single disturbance chronologies improves accuracy and reduces uncertainty in fire history reconstruction (Margolis et al. 2007). Fire regimes of today's forests may be substantially altered from their historical precedents, and so any additional evidence of past fire regimes prior to Euro–American settlement will add to our understanding of this key ecosystem process.

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