Fire-scar formation and compartmentalization in oak

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Abstract: Fire scars result from the death of the vascular cambium resulting from excessive heating, which exposes sapwood to infection and initiates the wood decay process. In southeastern Ohio, prescribed fires in April 1995 and 1997 scarred *Quercus prinus* L. and *Q. velutina* Lam. Low-intensity fires scorched bark and produced scars, primarily on the downslope side of the stem. Eighteen scorched trees (4–23 cm at DBH) were dissected in November 1997, 14 of which had fire scars. The vascular cambium beneath natural bark fissures was most vulnerable to injury. No charred or scorched wood was associated with scars of trees exposed to single fires; wood exposed by scars from the 1995 fire was charred by the 1997 fire. Consistent with the compartmentalization process, discoloration and whiterot occurred within compartment boundaries of wood present at the time of wounding. Scars from the prescribed fires were consistent in size and shape with scars in nearby oak trees previously hypothesized to have been burned prior to 1950.

Résumé : Les blessures dues au feu résultent de la mort du cambium vasculaire causée par la chaleur excessive qui expose le bois d'aubier à l'infection et initie le processus de carie du bois. Dans le sud-est de l'Ohio, des brûlages dirigés effectués en avril 1995 et 1997 ont endommagé le *Quercus prinus* L. et le *Q. velutina* Lam. Des feux de faible intensité ont brûlé légèrement l'écorce et produit des blessures au tronc, principalement du côté situé vers le bas de la pente. Dix-huit arbres brûlés légèrement (4–23 cm au dhp), dont 14 avaient des blessures dues au feu, ont été disséqués en novembre 1997. Le cambium vasculaire situé sous des fissures naturelles dans l'écorce était le plus vulnérable aux dommages. Le bois associé aux blessures des arbres exposés à un seul feu était ni carbonisé ni brûlé légèrement. Le bois exposé par les blessures dues au feu de 1995 a été carbonisé par le feu de 1997. Conformément au processus de compartimentage, la coloration et la carie blanche se sont développées à l'intérieur des limites du bois présent au moment de la blessure. Les blessures causées par les brûlages dirigés avaient une forme et une dimension qui correspondaient aux blessures des chênes situés à proximité et qui auraient été endommagés par le feu avant 1950.

[Traduit par la rédaction]

Introduction

Fire is a significant component of the disturbance regime of eastern North America's oak-dominated forests (Abrams 1992). Fire scar analysis is an important tool in understanding the dynamics of these forests, as fire scars record the timing, frequency, and spatial extent of fire within a forest stand. Historical fire regimes in oak-dominated forests have been inferred from patterns of scarring (e.g., Guyette and Cutter 1991; Guyette and Dey 1995; Sutherland 1997). The stands in these studies experienced high-frequency (3- to 5-year return interval) fire regimes.

Scars result when excessive heat due to fire kills the vascular cambium of trees and are most frequently identified by the resulting strips or ribs of woundwood that partially or completely cover the killed area (Guyette and Cutter 1991). Although woundwood is frequently referred to as "callus," the latter term properly refers to meristematic masses of roughly isodiametric cells that contain only small amounts of lignin. Callus does form from dedifferentiated sapwood parenchyma shortly after wounding. However, as the cells become differentiated and lignified, they are more properly referred to as woundwood (Shigo 1991, 1995). Woundwood ribs are the thickened rings produced by the vascular cambium that eventually close the wound face at wound margins. The orientation of wood cells within woundwood is frequently distorted compared with the cellular arrangement in normal wood.

Fire scars, as with all wounds, provide opportunities for infection by wood-inhabiting microorganisms including decay fungi. The thick bark of many oak (*Quercus*) species in the forests of North America insulates the vascular cambium and minimizes fire-caused wounding (Lorimer 1985). In service, oak heartwood varies from being decay resistant (e.g., *Quercus prinus* L., chestnut oak) to nonresistant (e.g., *Quercus velutina* Lam., black oak) (USDA Forest Products Laboratory 1987). In living oaks, resistance to the spread of the decay process and loss of normal wood function and the reestablishment of a continuous vascular cambium is accomplished by compartmentalization following scarring (Shigo 1984). In a high-frequency fire regime, the limited spread of decay in eastern oaks following fire (Abrams 1996) is likely due to effective compartmentalization.

Trees are scarred by numerous biotic and abiotic agents. Thus, accurate estimates of natural fire frequency requires the determination of fire as the cause of scarring. Prescribed

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Table 1. Oak trees (*Quercus*) burned by prescribed fires in southeastern Ohio.

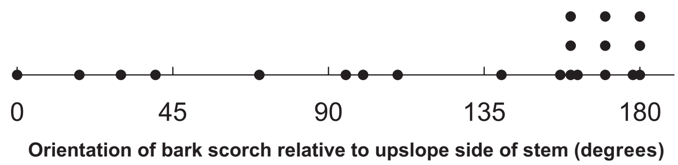
Tree No.	Species	DBH (cm)	Scorch height (cm)	Discoloration height (cm)[a]
1	Q. velutina	6.0	17	14
2	Q. prinus	4.0	15	4
3	Q. prinus	6.4	15	none
4	Q. velutina	5.3	28	22
5	Q. velutina	16.3	38	15
6	Q. velutina	15.6	23	12
7	Q. velutina	11.6	26	None
8	Q. coccinea	6.2	30	20
9	Q. prinus	21.2	17	None
10	Q. prinus	23.2	69	15
11	Q. prinus	7.1	43	9
12	Q. prinus	8.9	37	7
13	Q. prinus	20.2	73	13
14	Q. prinus	15.7	73	None
15	Q. prinus	22.0	94	39, 20[b]
16	Q. prinus	9.4	72	None
17	Q. prinus	12.5	40	19
18	Q. prinus	16.3	72	22

Note: All trees were burned prior to the 1995 growing season. Trees 9–18 were also burned prior to the 1997 growing season.

[a]Height of column of wound-initiated discoloration associated with scorched bark and fire scars. None indicates that no fire scar or column of discoloration was associated with the bark scorch.

[b]Two columns of discoloration were recorded for the 1995 and 1997 fires, respectively.

Fig. 1. Relationship of bark scorch to upward-sloping terrain. Scorch on the upslope side of the stem was oriented at 0°, scorch at right angles to the ground slope and on either side of the tree was oriented at 90°, and scorch on the downslope side of the stem was oriented at 180°.



fires, which are set intentionally for management or research purposes, provide an opportunity to investigate the response of trees to fire injury and to identify characteristics of fire scars. The objectives of this study were to determine whether prescribed fires of low-intensity initiated fire scars in oak, how fire scars related to the compartmentalization response of trees to injury, and whether the fire scars from the prescribed fires were consistent with scars described in fire-history studies from similar, nearby forests.

Materials and methods

We investigated the response of oak trees to fire in a stand located in the unglaciated Allegheny Plateau of Vinton County in southeastern Ohio (the "Hill Country" of Braun (1950)). The stand is part of the Raccoon Ecological Management Area (REMA) owned by Mead Paper Corporation. The REMA is hilly and densely forested, with oak species dominating the overstory. The forests are second growth, and dominant trees in the canopy are about 100 years old. Until the prescribed burns of 1995 and 1997, no fires had occurred since at least 1952, when the area was set aside for research.

We collected specimens from a prescribed burning demonstration area on the REMA. This 3.5-ha upland tract was dominantly south facing, with 25–35% slopes. The area was first burned on April 5, 1995. One half of the area was burned a second time on April 3, 1997. Both fires occurred nearly a month before leafout and likely prior to the initiation of the 1995 and 1997 growth increments (Shigo 1995). Fuel consisted largely of hardwood litter, described by Fire Behavior Fuel Model 9 (Anderson 1982). The weather for the 1995 fire was clear and cool, with temperature at the time of ignition of 2°C and 30% relative humidity. The area was ignited using strip headfires at 11:30 EST, and the area was completely burned by 12:30 EST. The fire was generally of low intensity, with flame lengths about 30–50 cm. More intense fires burned in microsites with steep topography or with a heavier fuel load. Fuels burned uniformly, blackening about 80% of the area. The top surface litter was burned, but little or no duff was consumed. In some microsites, heavier fuels continued to burn for 24–48 h. The behavior and litter consumption of the 1997 fire were similar to the 1995 fire. The weather was clear and warm, with temperature at the time of ignition of 20°C and 11% relative humidity. The fire was ignited at 17:15 EST and burning was complete by 18:30 EST.

Living oak trees from the once- and twice-burned locations were dissected in November 1997 to observe patterns of tree response to fire injury. Trees selected for dissection had scorched bark and were representative of the stand with respect to size and canopy position. Stem diameter and the compass orientation of both the upward sloping terrain and the bark scorch on the standing tree were recorded. The stem was notched and sawn through at approximately 1.5 m aboveground. The butt section containing the fire scar was felled with a single sawcut at groundline.

A stem disk (ca. 2–4 cm in thickness) was sawn from the base. Successive short bolts (ca. 10–12 cm in length) alternating with stem disks were sawn through the scarred stem. An additional disk was sawn at the position corresponding to 1.4 m aboveground in the intact stem. Short bolts were split radially through the wound surface. The vertical extent of wood discoloration, boundary formation around the columns of wound-initiated discoloration, and ribs of woundwood were recorded. Selected disks and split bolts were smoothed with sandpaper to enhance the appearance of wood features.

The orientation of the scorch relative to the slope of the terrain was plotted. The hypothesis of random distribution of scorch with respect to terrain slope was tested using a single classification goodness of fit test (Sokal and Rohlf 1981). Three slope categories of equal area were defined: upslope (≤60° of upslope direction), downslope (≥120° of upslope direction), and sideslope (>60° and <120° on either side of the upslope direction).

Transverse sections through historical wounds (1850s–1950s) of oaks grown outside of the prescribed burn area (Sutherland 1997; E.K. Sutherland, unpublished data) were compared with those taken from trees within the burn area.

Results

Oak stems in the study area had scorched bark from 0 to 75% of the basal circumference. Bark scorch was roughly triangular with the apex of the scorch extending from 17 to 94 cm aboveground (Table 1). Scorch was not randomly distributed with respect to slope orientation (goodness of fit statistic, G = 7.14, P < 0.05, df = 2). In 21 instances of scorch on 18 trees (three trees in the twice-burned area were scorched twice), 4 occurred in the upslope direction, 4 in the side slope, and 13 in the downslope direction (Fig. 1).

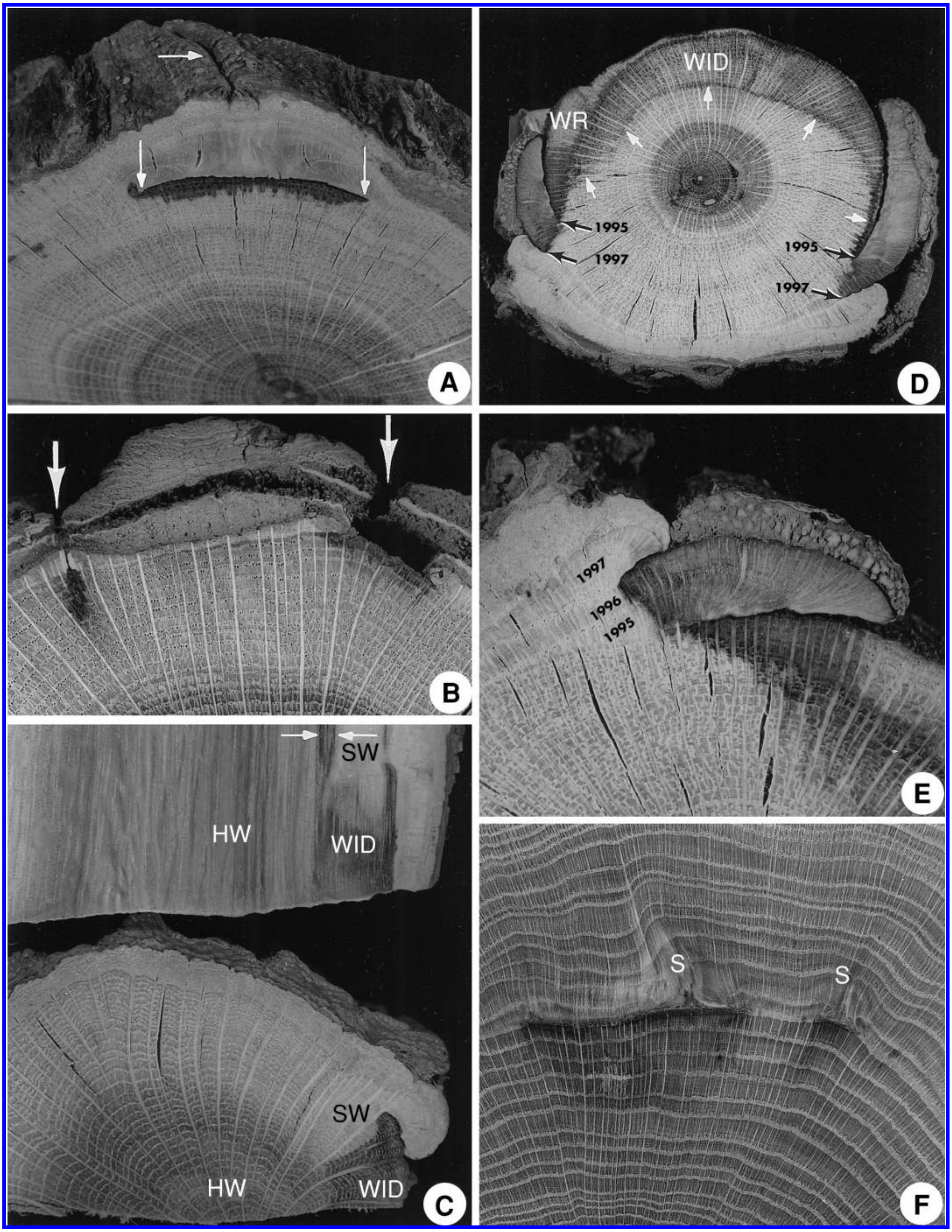

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Fig. 2. Dissections of oak fire scars harvested in November 1997. (A) Fire scar of *Q. prinus* wounded prior to 1995 growing season. Death of the vascular cambium was localized (between vertical arrows). A seam in the bark (horizontal arrow) formed from the meeting of thickened woundwood ribs that closed over the killed vascular cambium. Wound-initiated discoloration was located from the wound surface inward toward the pith. A small arc of discoloration (left of left arrow) was initiated by a crack in the woundwood formed in 1995. (B) *Quercus prinus* wounded prior to the 1997 growing season. The small closed or partially closed fire wounds were associated with bark fissures (arrows). (C) Fire scar of *Q. velutina* wounded prior to 1995 growing season. The longitudinal view (above) contained the upper portion of a column of wound-initiated discoloration (WID) formed from sapwood (SW) present at the time of fire injury. The greatest longitudinal extent of the column was along the sapwood : heartwood (HW) interface (white arrows) that extended beyond the edge of the photograph. The adjacent transverse section (below) contained woundwood ribs that incompletely closed the wound. (D) Fire scar of *Q. prinus* wounded prior to both the 1995 and 1997 growing seasons. The stem has a flattened appearance resulting from successive, overlapping ribs of woundwood. The extent of cambial death due to the two injuries are marked (black arrows). The exposed sapwood contains whiterot (WR). The exposed surface of the 1995 wound is charred. Wound-initiated discoloration is separated from healthy sapwood by a column boundary layer (white arrows). (E) Closeup of (D). Boundaries for the 1995–1997 growth rings are evident in the radially thickened woundwood although the ray cells deviate from a strictly radial orientation. Bark killed by the 1997 fire adhered to woundwood formed in 1996 in response to the 1995 fire. (F) Fire scar of *Q. velutina* wounded prior to the the 1930 growing season. The vascular cambium was killed in narrow strips. Although wound closure was complete within two growing seasons, wood from opposing woundwood ribs formed seams (S) and did not regain circuit continuity for several years following closure.

Fourteen of the 18 scorched trees that were dissected (ca. 80%) contained fire scars. Most fire scars were concealed by intact bark. When not covered by bark, a fire scar appeared either as an area of wood exposed by missing bark or as a seam (Fig. 2A). As with the bark scorch, fire scars were roughly triangular in shape. Seams resulted from the meeting of woundwood ribs growing from opposite sides of the wound (Fig. 2A). Cambial death associated with fire scars occurred only at the ring boundaries between the growth rings 1994 and 1995 and between 1996 and 1997. None of the fire scars were accompanied by scorched or charred wood except for wood exposed by the 1995 fire that was subsequently burned by the 1997 fire. Although bark scorch was widest at groundline, the greatest amount of scarring as a proportion of stem circumference ranged from 10 to 20 cm aboveground. Radial growth of woundwood ribs was two to five times greater than the unaltered growth rings on the portion of the stem opposite the wound. Points or short arcs of dead vascular cambium were often associated with deep fissures present in the bark prior to the fires (Fig. 2B).

Columns of wound-initiated discoloration were located in sapwood inward from the killed area of vascular cambium (Fig. 2C). Most columns extended 5–20 cm above the topmost edge of the area of killed vascular cambium. The greatest vertical extent of column development occurred at the transition between sapwood and heartwood and in the outermost sapwood present at the time of wounding. The upper portion of the discoloration columns appeared as three bands, a light brown central core that was bounded by an irregular dark brown edge or layer that was topped by a more diffuse tan zone.

Repeated injury resulted in larger transverse areas of wound-initiated discoloration (Fig. 2D). In some instances, vascular cambium over more than 60% of the stem circumference was killed by the 1995 and 1997 fires. Successive ribs of woundwood resulted in flattened stems due to exaggerated growth at right angles to the wound surface. Discoloration and decay was limited to wood present at the time of wounding.

Transverse sections of oaks harvested at similar locations outside of the area of prescribed burning (Sutherland 1997; E.K. Sutherland, unpublished) contained compartmentalized wounds similar in appearance, size, and rate of closure as for the trees examined from the prescribed burn locations. Included bark in woundwood seams hindered the formation of continuous sapwood across the scar (Fig. 2F) for several years following scar closure.

Discussion

Low-intensity prescribed fires produced fire scars in oak. Prior to dissection, scars were not visible in scorched trees that retained intact bark. No charcoal was associated with scars in trees burned in 1995 and not burned in 1997. The only scars that contained charcoal were those exposed by the 1995 fire and later charred by the 1997 fire (Figs. 2D and 2E).

For these low-intensity fires, neither the presence nor absence of charcoal in fire scars was a reliable indicator of the cause of wounding. The presence of charcoal would not differentiate between fire having caused the scar or whether the fire charred wood exposed by a previous fire or some other mechanical injury. These results as well as those of Hepting (1935), Kayll (1968), Gill (1974), and Guyette and Cutter (1991) show that many fire scars are not associated with charcoal in the wound.

If the bark does not actually ignite and combust, then the xylem is not charred. In this case, heat-killed phloem and xylem tissue beneath the bark may be the only evidence of the fire event. The bark often adheres and persists over the heat-killed tissue for some time after the killing event, sometimes for years. If the bark is still present over the wound, or if the wound completely closes before the next fire, then the killed xylem surface is unlikely to be charred. Alternatively, if the bark does slough off from the killed xylem surface and this surface is exposed, the xylem surface is subject to charring by a subsequent fire. Occasionally, a single fire can ignite the bark, scar the stem, and char the exposed wood. More commonly, charring occurs on stem faces that have been repeatedly burned and not allowed to close because of repeated scarring. In our case, because most scars were rapidly compartmentalized and closed over before the subsequent fires, charring was rare. Charcoal may be more useful to confirm fire as a cause of scarring for other tree species and fire conditions (Abrams 1985).

The seasonal timing of fires and their potential ecological effect may be inferred from the position of fire scar within the annual growth ring. Fires of a given intensity usually cause more injury and mortality when they happen in the growing season compared with the dormant season (Whelan 1995). Most fires in Ohio burn during the dormant season, primarily in the early spring (March and early April) and secondarily in the autumn (October and November) (Haines and Johnson 1975). All scars associated with prescribed fires occurred between complete annual rings, during the dormant season (Baisan and Swetnam 1990, Swetnam and Baisan 1996). This finding supported the hypothesis that dormant season scarring would result from early April fires that burned well before spring leafout (early May) in these forests. Oaks produce most earlywood immediately before leafout. In southern Ohio, this initial period of earlywood growth occurs in mid-April and corresponds with the period of highest fire occurrence in southern Ohio (Sutherland 1997). Sutherland (1997) found that 25% of all historical scars occurred in earlywood, corresponding to the period of highest fire frequency. Latewood scars, which resulted from growing season fires were rare, occurring as only 6% of all scars.

All scorch heights were below 100 cm aboveground, and all columns (but one) of wood discoloration associated with fire scars were below 30 cm (Table 1), similar to Guyette and Cutter's (1991) findings that most fire scars occurred within 30 cm of ground level. Heat produced by the prescribed fires was not evenly distributed, as scorched and unscorched trees were mixed throughout the burned area.

Scorched bark was frequently on the downslope side of standing trees (Fig. 1). This finding differed from the observations following wildfires that scars tended to occur on the upslope side (Gill 1974; Grissino-Mayer and Swetnam 1997). These differences in the orientation of bark scorch may be due to different ecosystem and topographic properties. However, our results were also in contrast to Franklin et al. (1997) who found average higher temperatures on the upslope side compared with the downslope side of large oak trees in a similar prescribed fire in Kentucky, as well as those of Paulsell (1957), who found that 90% of fire scars occurred on the upslope side the boles of *Q. stellata*. The scorch position in our study suggests that either the downslope was leeward with respect to wind direction (Gutsell and Johnson 1996) or that large amounts of fuel were accumulated immediately below most of the scorched stems.

Thick, corky bark completely insulated the vascular cambium from lethal heating in two of the scorched trees. The localized death and compartmentalization of vascular cambium beneath bark fissures (Fig. 2B) illustrated the effectiveness of thick bark as insulation (Hengst and Dawson 1994). Larger areas of vascular cambium were killed in other trees, presumably by locally more intense fire (Figs. 2C and 2D).

The production of wide growth rings in woundwood adjacent to fire scars was a characteristic, localized wound response. Enhanced growth of woundwood hastened wound closure and the re-establisment of continuity of the vascular cambium and sapwood around the stem circumference. Woundwood is also adaptive growth that strengthens injured stems through the redistribution of stress loading (Matthek and Kubler 1995). Repeated fires initiated overlapping ribs that result in the development of a flattened appearance of the stem butt (Fig. 2D).

Dissection of fire scars revealed effective compartmentalization of the effects of fires. Compartmentalization, initiated by wounding, is a dynamic process that resists both the loss of normal function and the spread of infection in sapwood and bark (Shigo 1984; Blanchette and Biggs 1992). Compartmentalization resulted in the formation of attenuated columns of wound-initiated discoloration (Fig. 2C; Shigo 1984). The discoloration was primarily due to the oxidation of constitutive phenolic compounds (Smith 1997). Wound-initiated discoloration was limited to wood present at the time of wounding and did not extend into wood formed after wounding (Figs. 2A–2E).

Historical scars attributed to fire in the late 19th to the mid-20th century (Sutherland 1997) were similar in appearance with fire scars produced by prescribed fires (Fig. 2F). Most scars formed prior to 1950 were not associated with any visible external defect on the stem. Neither consistency of appearance or the presence of charcoal prove that the historical wounds were made by fire. The determination that a particular scar was likely caused by fire may require a more holistic assessment of historical corroboration, scar seasonality, and land-use patterns.

We have demonstrated that rapid and effective compartmentalization of wounding from low-intensity fires occurred in small oak trees growing in southern Ohio. Previous workers (e.g., Crow 1988; Abrams 1992; Van Lear and Watt 1993; Guyette and Dey 1995) have proposed that low-intensity fires promote the occurrence and dominance of oak trees in hardwood forest of the eastern United States. Rapid and effective compartmentalization of fire scars is an important contributor to survival of oak in these forests.

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References

Abrams, M.D. 1985. Fire history of oak gallery forests in a northeast Kansas tallgrass prairie. Am. Midl. Nat. **114**: 188–191

Abrams, M.D. 1992. Fire and the development of oak forests. BioScience, **42**: 346–353.

Abrams, M. 1996. Distribution, historical development, and ecophysiological attributes of oak species in the eastern United States. Ann. Sci. For. **53**: 487–512.

Anderson, H.E. 1982. Aids to determining fuel models for estimating fire behavior. USDA For. Serv. Gen. Tech. Rept. No. INT-122.

Baisan, C.H., and Swetnam, T.W. 1990. Fire history on a desert mountain range: Rincon Mountain wilderness, Arizona, U.S.A. Can. J. For. Res. **20**: 1559–1569.

Blanchette, R.A., and Biggs, A.R. (*Editors*). 1992. Defense mechanisms of woody plants against fungi. Springer, Berlin and New York.
Braun, E.L. 1950. Deciduous forests of eastern North America. Blakiston Co., Philadelphia, Pa.
Crow, T.R. 1988. Reproductive mode and mechanisms for self-replacement of northern red oak (*Quercus rubra*)—a review. For. Sci. **34**: 19–40.
USDA Forest Products Laboratory. 1987. Wood handbook: wood as an engineering material. U.S. Dep. Agric. Agric. Handb. No. 72.
Franklin, S.B., Robertson, P.A., and Fralish, J.S. 1997. Small-scale fire temperature patterns in upland *Quercus* communities. J. Appl. Ecol. **34**: 613–630.
Gill, A.M. 1974. Toward an understanding of fire-scar formation: field observation and laboratory simulation. For. Sci. **20**: 198–205.
Grissino-Mayer, H., and Swetnam, T.W. 1997. Multi-century history of wildfire in the ponderosa pine forests of El Malpais National Monument. Bull. N.M. Bureau Mines Mineral Resour. No. 156. pp. 163–172.
Gutsell, S.L., and Johnson, E.A. 1996. How fire scars are formed: coupling a disturbance process to its ecological effect. Can. J. For. Res. **26**: 166–174.
Guyette, R.P., and Cutter, B.E. 1991. Tree-ring analysis of fire history of a post oak savanna in the Missouri Ozarks. Nat. Areas J. **11**: 93–99.
Guyette, R.P., and Dey, D. 1995. A history of fire, disturbance, and growth in a red oak stand in the Bancroft District, Ontario. Ontario Forest Research Institute, Sault Ste. Marie, For. Res. Inf. Pap. No. 119.
Haines, D.A., and Johnson, V.J. 1975. Wildfire atlas of the northeastern and north central States. USDA For. Serv. Gen. Tech. Rep. No. NC-16.
Hengst, G.E., and Dawson, J.O. 1994. Bark properties and fire resistance of selected tree species from the central hardwood region of North America. Can. J. For. Res. **24**: 688–696.
Hepting, G.H. 1935. Decay following fire in young Mississippi delta hardwoods. U.S. Dep. Agric. Tech. Bull. No. 494.
Kayll, A.J. 1968. Heat tolerance of tree seedlings. Proc. Tall Timbers Fire Ecol. Conf. **8**: 89–105.
Lorimer, C.G. 1985. The role of fire in the perpetuation of oak forests. *In* Challenges in oak management and utilization. *Edited by* J. Johnson. University of Wisconsin Cooperative Extension Service, Madison. pp. 8–25.
Mattheck, C., and Kubler, H. 1995. Wood—the internal optimization of trees. Springer-Verlag, Berlin and New York.
Paulsell, L.K. 1957. Effects of burning an Ozark hardwood timberland. College of Agriculture, University of Missouri, Columbia, Res. Bull. No. 640.
Shigo, A.L. 1984. Compartmentalization: a conceptual framework for understanding how trees grow and defend themselves. Annu. Rev. Phytopathol. **22**: 189–214.
Shigo, A.L. 1991. Modern arboriculture. Shigo & Trees, Associates, Durham, N.H.
Shigo, A.L. 1995. Tree anatomy. Shigo & Trees, Associates, Durham, N.H.
Smith, K.T. 1997. Phenolics and compartmentalization in the sapwood of broad-leaved trees. *In* Methods in plant biochemistry and molecular biology. *Edited by* W.V. Dashek. CRC Press, Boca Raton, Fla. pp. 189–198.
Sokal, R.R., and Rohlf, F.J. 1981. Biometry—the principles and practice of statistics in biological research. 2nd ed. W.H. Freeman, New York.
Sutherland, E.K. 1997. History of fire in a southern Ohio second-growth mixed-oak forest. *In* Proceedings of the 11th Central Hardwood Forest Conference, 23–26 Mar. 1997, Columbia, Mo. *Edited by* S.G. Pallardy, R.A. Cecich, H.E. Garrett, and P.S. Johnson. USDA For. Serv. Gen. Tech. Rep. No. NC-188. pp. 172–183.
Swetnam, T.W., and Baisan, C.H. 1996. Fire histories of montane forests in the Madrean borderlands. USDA For. Serv. Gen. Tech. Rep. No. RM-289.
Van Lear, D.H., and Watt, J.M. 1993. The role of fire in oak regeneration. *In* Proceedings of Oak Regeneration: Serious Problems, Practical Recommendations, 8–10 Sept. 1992, Knoxville, Tenn. *Edited by* D.L. Loftis and C.E. McGee. USDA For. Serv. Gen. Tech Rep. No. SE-84. pp. 66–78.
Whelan, R.J. 1995. The ecology of fire. Cambridge University Press, New York.