

Fire scar growth and closure rates in white oak (*Quercus alba*) and the implications for prescribed burning



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ABSTRACT

In burned forestlands, fire scar wounds commonly occur on tree stems as a result of cambial heating. In hardwood forests in particular, wounding can lead to stem decay with the extent of decay being related to scar size and exposure time. Therefore, wound closure rates are important to understand in the context of fire management such that allowing sufficient time for wound closure to occur between fires would enhance wood quality. Conversely, in the context of wildlife management, understanding wound closure rates would improve fire prescriptions needed for creating basal tree cavities as keeping wounds open prior to wound closure could enhance cavity development. The objectives of this study were to quantify growth and wound closure rates of white oaks (*Quercus alba*), one of the most valuable tree species in the central U.S. to both commercial forestry and wildlife. From historically burned, mature, oak-hickory forest site in Missouri, we sampled a wide range of tree sizes, fire scar sizes, and fire scar ages to determine the environmental and tree factors related to closure rates. Dendrochronological techniques were paired with new approaches of digitizing tree rings to capture malformed woundwood areas. The time required for wound closure ranged from 1 to 24 years and was significantly correlated to scar size. Surprisingly, post-fire growth trends were positive following scarring. Growth was positively related to scar and tree size. With this information, we expect that the process of basal wound closure and tree growth can be considered in a quantitative framework and used to guide fire management for wood quality or wildlife tree cavities.

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1. Introduction

The fire ecology and management of oak forests in the eastern United States has undergone significant changes in concept and practice in recent decades (Nowacki and Abrams, 2008; Arthur et al., 2012). In the early 20th century, establishment of public forestlands in the U.S. was, in part, to protect forests from fires and minimize damage through fire suppression (Pyne, 1982). The unforeseen effect of fire suppression has been nation-wide increases in woody vegetation density, particularly trees (USFS, 2014). In the eastern U.S., the extent of changes from less mesic and more fire-tolerant species to more mesic and fire-intolerant tree species is an alarming concern (Brose et al., 2001; Nowacki and Abrams, 2008).

Perspectives of prescribed fire in eastern U.S. forests are complicated by both historical and present day conditions. For example,

due to fire suppression and improved forest management over the last half century, forest growing stock volumes have increased and wood quality has improved (Dey and Schweitzer, 2015). From a tree quality perspective, fire concerns include top-kill, injuries, induced cavity formation, and potentially reduced future merchantable volume and value (Loomis, 1974; Marschall et al., 2014). Nonetheless, other consequences of fire suppression weigh against these concerns such as increased oak regeneration failures (Dey, 2014), shifts in oak forest composition to less desirable mixtures (Brose et al., 2014), and the loss open forest ecosystems (Hanberry et al., 2014; Dey and Kabrick, 2015) among others.

In response to these issues, research and development of science-based management tools have received increased attention. Likely of particular relevance to forest management, are studies documenting long-term fire effects on vegetation (Waldrop et al., 2008; Hutchinson et al., 2012; Knapp et al., 2015) and interactions among fire and silvicultural treatments (Kinkead et al., 2013; Kabrick et al., 2014; Schweitzer et al., 2016). Despite renewed interest in fire ecology and management in the eastern

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U.S., there is great debate and resistance to prescribed fire treatments particularly due to perceived threats to timber value (Dey and Schweitzer, 2015). For forest managers to benefit from fire applications within silvicultural systems, evidence is needed that fire can control oak competitors, enhance oak regeneration and recruitment, and, if desired, be prescribed to minimize economic losses caused by stem injury.

For injured yet surviving trees, cambial necrosis results from the transfer of lethal levels of heat through the bark for a portion of the stem circumference (Dickinson and Johnson, 2001; Jones et al., 2006). Some degree of protection from lethal heating is provided by bark that insulates the vascular cambium and other living tissues. In addition to the relatively thick bark providing enhanced protection, oak apparently is more effective in compartmentalization than thinner-barked species such as maple, which may contribute to a greater degree of fire adaptedness in oak (Smith and Sutherland, 2001; Smith, 2015).

Fire scar development on oaks follows processes of wound closure and compartmentalization of injury and infection (Smith and Sutherland, 1999, 2001). Externally, open fire scars are recognized by the stimulated growth of ribs or curls of woundwood that tend to close over (occlude) the dead face of the tree (i.e., wound). Dissected scars contain the constitutive and induced boundaries that resist the spread of infection and loss of function, the hallmarks of compartmentalization (Shigo, 1984; Smith, 2015). Over time, wood within the compartmentalization boundaries will discolor and eventually decay. For oak forests managed for timber products, wound-initiated discoloration and decay represents a loss of yield and economic value. However, for oak forests managed for wildlife, the same processes of defense and deterioration can increase the value of injured trees for certain wildlife and biodiversity management objectives (Tews et al., 2004; Remm and Löhms, 2011).

Scar closure is an important factor related to managing wood quality and is accomplished by the progressive apposition of woundwood ribs. Closure likely slows the aerobic wood decay process through reduced aeration within compartmentalization boundaries. Further, closure removes a point of fungal entry by covering the wound surface (Rayner and Boddy, 1988). Complete closure involves the restoration of the circumferential continuity of the vascular cambium facilitating the production of clear, straight-grained wood.

Little is known about the fire scar durations, rates of wound closure, and the impact on wood production and quality upon which value depends (Marschall et al., 2014). Therefore, the objectives of this study were to: (1) quantify the time required for wound closure and growth rates for white oak (*Quercus alba*) and (2) identify and model environmental and tree factors related to post-fire growth. We focused on white oak because of the relatively high decay resistance of its heartwood, the ability of individual trees to be long-lived and to have sustained multiple injuries, high economic and wildlife value, broad distribution across the eastern U.S. including areas managed with prescribed fire, and high likelihood of survival following multiple fires. Further, we expect that this information will be generally applicable to understanding processes affecting tree survival, growth, and cavity formation related to fire injury and prescribed fire management.

2. Methods

2.1. Study site

The study site was located at the Rudolf Bennitt Conservation Area (RBCA, 39.25.12°N, 92.43°W), 35 km north of Columbia, MO, USA. The climate is humid-continental with a mean total annual precipitation and temperature of 109.2 cm and 12.5 °C, respec-

tively. Terrain is gentle to rolling with slopes ranging from 0 to 15 degrees. Elevation is 252 m a.s.l. and soils are glacial till in origin and consist of well-drained clay loam. The dominant forest type is oak-hickory and the study area is currently dominated by 80–150 yr-old oaks, especially white oak with inclusions of black oak (*Q. velutina*) and post oak (*Q. stellata*). In the last century, the RBCA has undergone grazing, logging, and burning. Since 2001, the Missouri Department of Conservation has managed about 240 ha of the oak woodland at RBCA with a combination of timber stand improvement, commercial harvesting, and prescribed burning.

2.2. Field and laboratory data collection

Within the RBCA oak woodland management area, we sampled 43 recently cut or naturally dead fire-scarred white oaks ranging from 9.1 to 52.1 cm dbh. Sampling targeted trees with embedded fire scars (wounds that had successfully closed). In an effort to document fire scar closure rates through different tree and climate conditions, we sampled a wide range of tree sizes, scar sizes, and scar ages. For each sample tree, site conditions noted were: slope, aspect, slope position, canopy position, basal area surrounding the tree, and percent ground cover under the canopy. Sample trees were felled and a cross-section was cut at ground level. In the field, locations of fire scars on cross-sections were identified in the tree-ring sequence. Of the fire scars viewed on the cross-section in the field, a primary fire scar was identified within the ring sequence. Primary fire scars were selected as those having a viewable period of scar closure (i.e., little to no wood decay prior to the fire scar year and for all post-fire growth rings) that was unaffected by subsequent scarring. The height of primary fire scars was determined by continued cross-sectional cutting up the bole (Fig. 1). A second cross-section was collected that contained the top of the primary fire scar. If scars were >50 cm in height from the ground, then an additional cross-section was collected half way between ground level and the top of the scar. Heights above ground were measured for the bottom surface of each cross-section to the nearest centimeter. Due to a history of repeated burning in the late 19th to early 20th century, some sample trees contained multiple scars of various sizes and ages. These additional fire scars were not used in fire scar closure and tree growth analysis, but were used to reconstruct the history of fire events at the site.

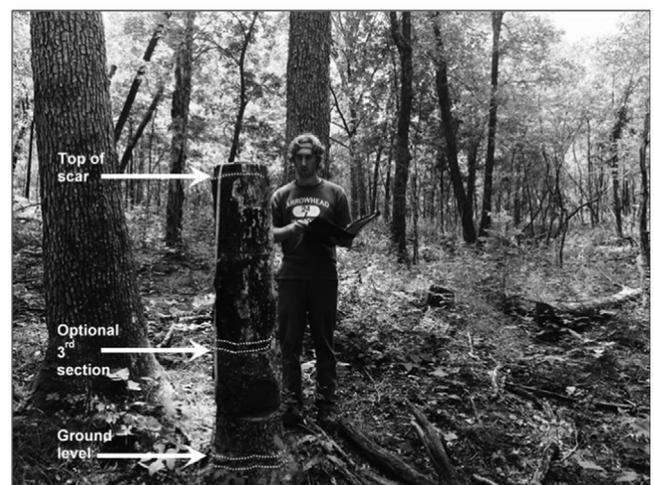


Fig. 1. Site condition, individual sample tree and context at the Rudolf Bennitt Conservation Area, near Columbia, Missouri. Arrows indicate height that cross-sections were collected along the tree bole. Average correlations of growth rates between these different levels was $r = 0.82$.

In the laboratory, cross-sectional surfaces were planed and sanded to a high polish to reveal the cellular detail of tree rings and fire scars. Care was taken to prepare each sample surface as a flat and transverse plane as deviations could affect measurements of stem and woundwood areas. Radial tree-ring width was measured (0.01 mm precision) with a Velmex measuring system (Velmex, Inc., Bloomfield, NY). Ring-width series were cross-dated using standard dendrochronological techniques (Stokes and Smiley, 1968). Crossdating was accomplished through visual comparisons of ring-width plots, identification of signature years, and statistical verification utilizing COFECHA software (Holmes, 1983; Grissino-Mayer, 2001). Once crossdated, the calendar year of cambial injury was assigned to each fire scar. For each sample tree, matching of calendar dates of the primary fire scar was reconfirmed on all cross-sections. The occurrence of fire scars in samples collected at RBCA was plotted along a timeline using FHAES software (Brewer et al., 2016).

Cross-sectional surfaces were scanned at 1200 dpi using a Regent Instruments LA2400 area calibrated scanner with images acquired by Epson SilverFast Ai IT8 v.8 software. Image files (.eps format) were imported to WindDendro software (Regent Instruments Inc.) to measure stem areas. Stem areas were measured by digitizing tree-ring boundaries and, then, annual area increment (AAI, mm²) was derived by differencing subsequent year stem areas (Fig. 2). AAI is unlike the commonly reported basal area increment (BAI; sometimes also referred to as diameter increment) only in that it is not necessarily measured at breast height (1.37 m above ground). Compared to the more customary estimates of stem areas from tree-ring width, this method of direct measurement avoids inaccuracy from eccentric growth and partial rings. AAI was measured for the six years prior to fire scars and all subsequent years until woundwood ribs met. We measured years to wound closure two different ways: (1) when wound wood ribs met and, (2) when circuit continuity of cambium was restored. We chose to conduct analyses for when wound wood ribs met since it was often the same or differed by 1 year or less (partial ring) from when cambium was restored. The number of years to

wound closure were counted from the year of cambial injury to year of woundwood ribs meeting (Fig. 2). For each primary fire scar, scar size was measured as the scar arc length (mm) of the killed cambium. Scar closure rates were calculated as the scar arc length divided by the number of years to wound closure. Tree diameter when scarred was determined as the average length (mm) measured along two radii from pith to the year of scar and multiplied by two. All measurements were made utilizing WinDendro software tools. Three trees were omitted from the analysis due to the potential for compounding problems (i.e., woundwood subsequently affected during wound closure (by insects, decay, fire), anomalous woundwood and fiber orientation, decay, or missing wood).

2.3. Data analysis

Summary statistics described tree sizes when scarred, scar sizes, and wound closure rates. Scatterplots were used to inspect relationships among tree size, scar size, and time to closure. We plotted tree AAI to inspect changes in tree growth rates from pre- to post-fire scarring periods. Linear regression was used to determine whether trends in AAI were positive or negative from pre- to post-scar years. We compared AAI at different heights within individual trees using Pearson correlations.

To understand factors that contribute to scar closure and post-fire growth, we used correlation and regression analysis to identify significant predictors and to develop statistical models. For AAI (dependent variable), we separately considered analyses of the change in AAI from one year prior to the fire scar (lag-1) to the scar year and the absolute AAI of the scar year (Fig. 2). Tree and environmental (independent) variables included: age when scarred, scar arc length, diameter when scarred, and the Palmer Drought Severity Index (PDSI) of the scar year. We included PDSI because in this region of Missouri up to 65% of the variance in white oak annual growth can be explained by summer season (June, July, and August (JJA)) drought conditions (Stambaugh et al., 2011). Drought data represented the mean PDSI value for June, July, and August (data source: MO Climate Division 2, Monthly data; NCDC 2001). Scar arc length and tree diameter when scarred were positively correlated to each other and separately (both positively) with AAI of the scar year. For this reason, we developed an interactive variable 'SCAR_LxD' to represent the combined tree conditions calculated as the product of scar arc length and tree diameter. Final regression model selections were based on model significance, r-square values, and normality of residuals. Variables were removed from models when variance inflation factors ≥ 10 . Models and variables were considered significant when $p < 0.05$. Scar years prior to 1895 were not included in the analysis due to the unavailability of PDSI data. Only one observation per tree was included in the model analysis, despite data from multiple sections of individual trees being available.

3. Results

3.1. Fire scar characteristics

Fire scars at the study site occurred from 1854 to 1967 and were particularly frequent after 1895. In fire years, relatively low percentages of trees were scarred (Fig. 3). Calendar years of primary fire scars ranged from 1887 to 1962. The majority of sample trees had additional fire scars before and/or after the primary fire scar. Mean JJA PDSI values for the primary fire scar years ranged from 2.27 (moderately wet) to -6.6 (extreme drought). Tree ages when scarred ranged from 10 to 70 years. Diameters of trees when

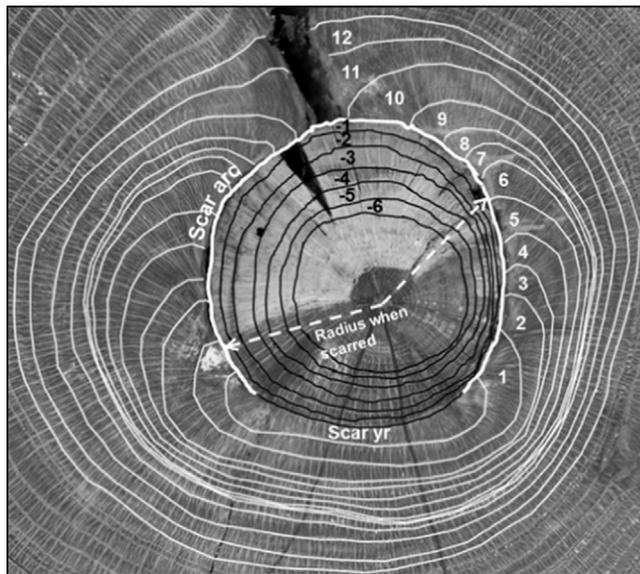


Fig. 2. Cross-sectional (transverse) view of the inner portion of a white oak (*Quercus alba*) tree showing growth rings before and after fire scar injury. The heavy white line denotes the fire scar injury arc or the portion of the tree's circumference killed due to fire. Black and white lines represent annual ring boundaries before and after injury, respectively. Numbers within rings represent the lag year from the year showing initial cambial response to injury. Scar year denotes the first year of cambial response to injury. All fire scars occurred in the dormant season.

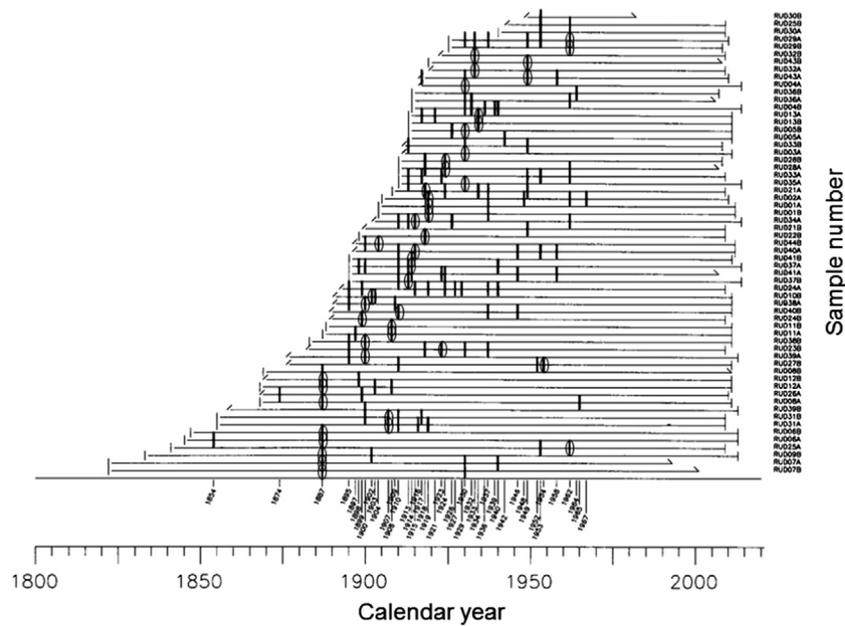


Fig. 3. Chart showing the periods of tree ring records and years of fire scars on 43 white oaks at Rudolf Bennett Conservation Area, Boone County, MO. Horizontal lines represent the periods of tree-ring record for individual trees indicated by the sample numbers along the right margin. Sample number designations ending with “A” and “B” represent ground-level and top-of-scar sections, respectively (see Fig. 1). Bold vertical tick marks indicate all fire scar years on samples and circled ticks are the primary scars included in the analysis of closure rates and tree growth. A composite record of all fire years at the site is given at the bottom of the chart.

scarred ranged from 9.2 to 108.6 mm and scar heights ranged from 17 to 350 cm above the ground level and averaged 71.2 cm (Fig. 4).

3.2. Fire scar closure and tree growth

Fire scar injuries ranged from 2 to 80 percent of tree circumferences being killed. Scar arc lengths ranged from 9 to 233 mm (average = 89 mm). For these arcs, years to wound closure ranged from 1 to 24 years (Fig. 4). Fire scar closure rates ranged from 4.6 to 40.7 mm yr⁻¹ (average = 13.2 mm yr⁻¹). Years to wound closure was positively correlated with scar arc length and a significant model relating scar arc length to years to wound closure was given as (Fig. 5):

$$\text{Years to wound closure} = 0.748 + 0.0756 * \text{scar arc length};$$

$$(r^2 = 0.54, p < 0.001),$$

where

years to wound closure is number of years, and scar arc length is the circumference of the stem killed in millimeters.

AAI ranged from 26 to 3182 mm² (mean = 636 mm²) for the five years prior to injury until the year in which wounds closed (Fig. 6). In the scar year, trees varied in the sign of change of AAI from the previous year (i.e., lag-1). From pre-fire to scar closure, AAI trends

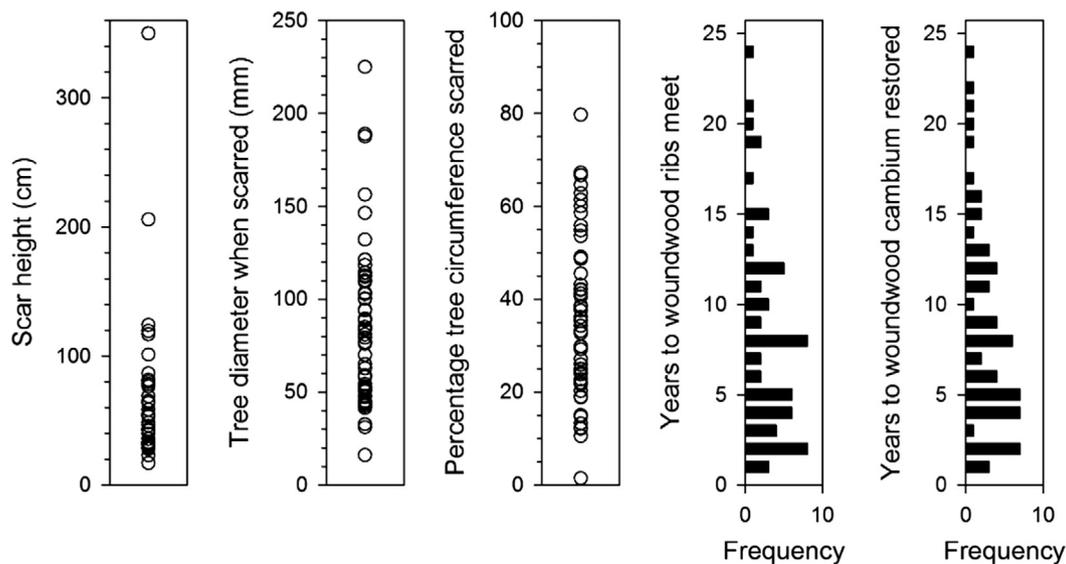


Fig. 4. Scatterplots and histograms illustrating the characteristics of sample trees and primary fire scar data. Primary fire scars were those with clear growth features allowing pre- and post-scarring measurements of tree-rings. Trees with multiple repeated scars, extensive decay, or missing wood were not considered. Data shown are for both ground level and top of scar cross-sections.

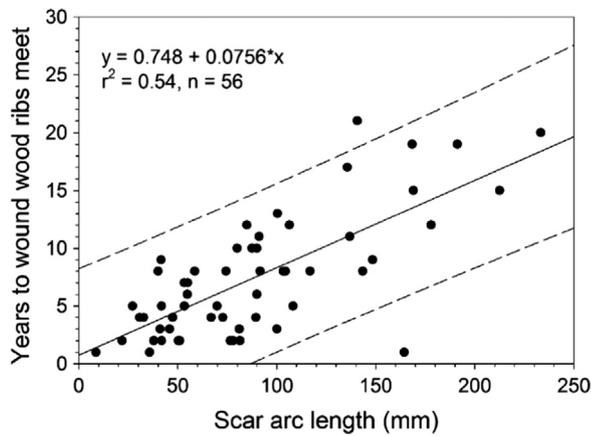


Fig. 5. Relationship between scar arc length and the years to wound closure for white oaks (*Quercus alba*). Dashed lines represent 95% prediction intervals.

were positive for all but one sample tree. Mean (range) AAI prior to injury was 395 mm² (26–1417 mm²) and following injury was 744 mm² (33–3182 mm²). Annual variation in AAI at ground line was significantly correlated with AAI at the top of the scar (average $r = 0.82$). Scar year AAI was significantly related to SCAR_LxD and tree age when scarred. Increased scar arc length was positively related to AAI in the scar year (Fig. 7). The best model predicting AAI in the scar year was Table 1:

$$\text{AAI} = 392.94913 + 0.02523 * \text{SCAR_LxD} - 5.19851 * \text{treeage};$$

$$(r^2 = 0.61, n = 23),$$

where

AAI is the Annual Area Increment (mm²),
 SCAR_LxD is the product of scar arc length (mm) and stem diameter when scarred (cm), and treeage is the age (years) of the tree (determined at ground level).

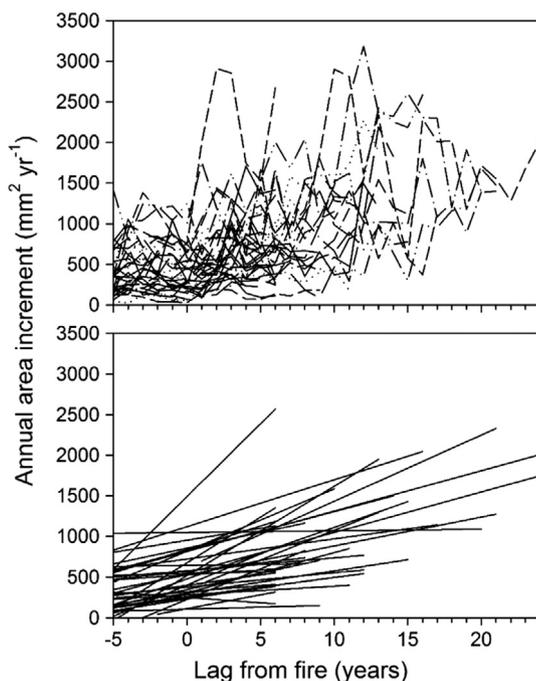


Fig. 6. Top panel: Annual area increment of white oaks (*Quercus alba*) pre- and post-fire scarring. Year 0 represents the scar year or first year of cambial response to injury (see Fig. 2). Bottom panel: growth trends of sample trees from 5 years prior to injury until woundwood ribs meet.

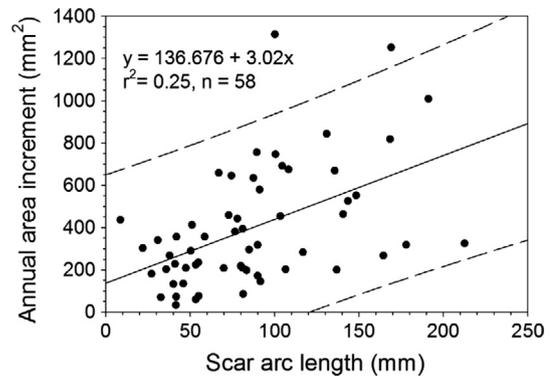


Fig. 7. Relationship between scar arc and annual area increment (AAI) of white oaks (*Quercus alba*). Dashed lines represent 95% prediction intervals.

No significant models resulted for predicting change in AAI from one year prior to the fire scar to the scar year (i.e., lag-1 to scar year, Fig. 2).

4. Discussion

4.1. Fire scar occurrence, size, and closure rate

The size of the wound that initiated fire scar formation indicated the extent of lethal heating of the vascular cambium. The level of heating sufficient to kill vascular cambial cells is an interaction of the duration and degree of temperature elevation (Dickinson and Johnson, 2001). Consequently, lethal heating depends on the interaction of fire conditions at or near the stem surface with constitutive protection provided by bark insulation. Local variation in the fire environment such as the presence of nearby pieces of combustible fuel (Smith and Sutherland, 1999) and bark qualities such as thinner bark in younger, smaller-diameter stems and the presence of bark fissures and ridges could readily account for the tree-to-tree variation in fire scar sizes observed. Our study trees were collected from flat to rolling terrain. Stevenson et al. (2008) showed that fire scar sizes are significantly greater on exposed slopes (i.e., where fire severity is increased) for several tree species, including white oak.

Commonly, the shapes of open external fire scars on oaks are “catface” (i.e., triangular) or oval (Stambaugh and Guyette, 2008). Consequently, years to wound closure on these different shapes varies and is less where the wound wood ribs are closer together (e.g., top of scar for “catface” shapes, top and bottom of scar for oval shapes). Conversely, the wounds are open for a longer period of time at the widest locations which would be at the ground level for “catface” shapes, and some distance off the ground (typically less than 40 cm) for oval shapes.

4.2. Growth of fire-scarred trees

Tree-growth studies utilize ring-area measurements, such as BAI or AAI, because the annual tree growth metric has the effects of stem size removed (Berrill and O'Hara, 2014). Measurements of tree growth rates of fire-scarred trees likely cannot use measurements of tree-ring width applied to BAI equations (sensu Phipps and Field, 1989). Often, studies that report BAI utilize radial growth measurements and geometric equations to calculate stem areas that assume circuit continuity and ring uniformity around the stem. To our knowledge, the present study is the first to report on tree growth by digitizing tree-ring areas. Unlike estimates from increment cores, this technique directly measured annual growth

Table 1

Model and variable multiple regression results for tree annual area increment (AAI) in the scar year. Variable 'SCAR_LxD' is the product of scar arc length and tree diameter when scarred; AGESCARRED is the tree age when scarred.

Source	DF	Sum of squares	Mean square	F value	Pr > F	
<i>Model</i>						
Model	2	1,340,846	670,423	15.59	<0.0001	
Error	20	860,144	43,007			
Corrected Total	22	2,200,990				
	DF	Parameter estimate	SE	t value	Pr > t	Variance inflation
<i>Variables</i>						
Intercept	1	392.94913	90.29	4.35	0.0003	
SCAR_LxD	1	0.02523	0.005	5.27	<0.0001	1.00304
AGESCARRED	1	-5.19851	2.44	-2.13	0.0457	1.00304

increment in trees with killed cambial areas and associated mal-formed stems.

Following fire scarring, stem growth can only proceed from the living portions of the cambium. Results of previous studies reporting white oak growth following burning are mixed; they show growth can be both increased (Anning and McCarthy, 2013) and decreased (Kinkead, 2013). For many oak and pine species, ring-width is commonly increased along the woundwood ribs as compared to the portions of the stem further away from the killed cambium (Smith and Sutherland, 1999; De Micco et al., 2013). Through digitization, measurements captured the increased stem growth along woundwood ribs and we found no decreases in growth rate associated with wounding, even in cases when the majority of the cambial circumference was killed. This surprising result leads us to hypothesize that the growth area that would be allocated to the entire circumference on an uninjured stem, is reapportioned to the area represented by un-killed cambium. Hence, through the measurement utilizing digitized ring areas, no declines in AAI were observed. The process and determination of wood area reapportioning is likely not this simple or predictable, particularly in cases where other major growth limiting factors are affected such as tree foliar area, root capacity, or soil exposure (Butler and Dickinson, 2010). Other causes for sustained growth despite wounding are plausible and warrant investigation including increased nutrient availability, improved leaf physiology, or reduced competition.

Scar year AAI was significantly related to degree of scarring (i.e. variable SCAR_LxD) and tree age when scarred, but not PDSI. Interestingly, SCAR_LxD was positively related to AAI whereby larger scars on larger trees result in larger scar year growth. Based on a few comparisons, it appears that similar SCAR_LxDs on small versus larger trees result in higher immediate growth (i.e., scar year AAI) for larger trees. This observation requires further testing with appropriate sample sizes and experimental design. Similarly, we suggest that the influence of PDSI should be further considered in future studies as it was surprising that PDSI was not significantly related to growth when regional studies over longer time periods suggest its importance (LeBlanc and Terrell, 2009).

4.3. Implications for management

In the last century, forestry professionals have generally considered the intentional burning of commercial hardwood forests as counterproductive and irresponsible. This viewpoint is oversimplified and short-sighted as it overlooks tree species adaptations for survival and competition, the complex scenarios of stand conditions and potential fire timing (Dey and Schweitzer, 2015), broader forest ecosystem function and values, and the long association of oak ecosystems with fire (Arthur et al., 2012; Brose et al., 2014). In recent years, the potential role for fire in eastern U.S. forest management has been revisited and debated (Matlack, 2013; Stambaugh et al., 2015). Prescribed fire as a tool for the management of oak ecosystems is gaining interest not just for promoting

oak, but also for broader ecosystem attributes and services (Hutchinson et al., 2005; Scharenbroch et al., 2012; Harper et al., 2016). In managed forests where commercial timber value is important, critical questions related to fire prescriptions and silvicultural practices remain such as those that further address effects on tree quality and growth, cavity formation, and survival.

Though seemingly reductionist, information specific to wound formation and closure likely has much to bear on developing fire prescriptions for forest management. Managers desiring to minimize cavity formation and protect the value of wood for products may wish to wait for wound closure to occur before conducting subsequent burns. We found the years to wound closure ranged from 1 to 24 years with the majority of wounds closing within 10 years. The duration to delay burning until wound closure occurs can be guided by measurements of scar arc length.

Prescribed burns conducted when wounds are "open" have the potential to enlarge basal cavities and cause further wounding. Bark along woundwood ribs is typically young and thin compared to uninjured portions of the tree. Within open wounds, dry heartwood that would otherwise be enclosed by layers of bark, cambium, and sapwood, is exposed and can ignite and combust for prolonged periods under favorable conditions. In contrast, for managers desiring to maximize wounding and cavity formation, burning during the period preceding wound closure provides an opportunity to manage for wildlife habitat. In Missouri, forest management guidelines require cavity trees and snags be provided for wildlife, recognizing that these features provide escape cover, thermal protection, rearing areas for young, and food storage locations (Jensen et al., 2002).

Currently, historical fire regime data (frequency, seasonality) are considered in fire management, not fire scar and tree conditions. Within the region, historical fire frequencies of oak woodlands fall within the range of wound closure times that we observed; a common historical fire frequency would be 5–10 years throughout the Central Hardwoods region (Guyette et al., 2006; Stambaugh et al., 2006). For fire intervals of 5 years, wounds would expect to be able to close prior to the next burn if scar arc lengths (Fig. 5) are <60 mm. Following repeated burning, the processes related to scarring of trees is likely to change with changes in fuel loading, fuel types, and the resulting fire behavior. Several studies have shown that during periods of very frequent burning, the percentages of trees scarred are reduced compared to periods with longer fire intervals (McEwan et al., 2007; Stambaugh et al., 2014; Knapp et al., in press), an effect likely caused by lowered fuel loading from repeated consumption. Although increases in percentages of trees scarred has not been related to increases in scar sizes, these scarring metrics are likely related when resulting from variable fire intensity. In summary, frequent burning is likely one approach to reduce scarring since fires would potentially be lower intensity and smaller scars would be expected that also require less time for wound closure. In contrast, less frequent burning would be expected to have greater potential to create larger

wounds which require greater time for wound closure. Certainly, other factors are important to consider for determining the timing and frequency of burning such as tree sizes, species composition, time to harvest, and overall management objectives.

Where timber quality is of concern, fire management programs should be cautious on first-entry burns, particularly when followed by repeated frequent burning. Due to 20th century fire suppression, heavy fuel loading and maximum litter accumulation conditions are common conditions. In this case, first entry burns have high potential to result in larger scars compared to areas with lighter fuels. Larger scars on smaller trees are of greater concern since they are expected to close more slowly and have longer time to reach merchantable sizes. A few studies suggest that large scars, if followed by frequent burning, would cause basal cavity formation since heartwood is exposed. For reducing cavity formation and damage, large scars should be followed by longer time periods to allow wound closure to occur. In this situation, timing of subsequent fires should balance timing of wound closure and the reaccumulation of fuels that would lead to increased fire intensities. To this end, future research that attributes tree wounding and wound closure to fire behavior would be beneficial.

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References

- Anning, A.K., McCarthy, B.C., 2013. Long-term effects of prescribed fire and thinning on residual tree growth in mixed-oak forests of southern Ohio. *Ecosystems* 16, 1473–1486.
- Arthur, M.A., Alexander, H., Dey, D.C., Schweitzer, C.J., Loftis, D.L., 2012. Refining the oak-fire hypothesis for management of oak-dominated forests of the eastern United States. *J. Forestry*, 257–266. July/August.
- Berrill, J.-P., O'Hara, K.L., 2014. Estimating site productivity in irregular stand structures by indexing the basal area or volume increment of the dominant species. *Can. J. For. Res.* 44, 92–100.
- Brewer, P.W., Velásquez, M.E., Sutherland, E.K., Falk, D.A., 2016. Fire History Analysis and Exploration System (FHAES) version 2.0.1. [computer software], <<http://www.fhaes.org>>. DOI: <http://dx.doi.org/10.5281/zenodo.34142>.
- Brose, P.H., Schuler, T.M., Van Lear, D.H., Berst, J., 2001. Bringing fire back: the changing regimes of the Appalachian mixed-oak forests. *J. Forestry* 99, 30–35.
- Brose, P.H., Dey, D.C., Waldrop, T.W., 2014. The fire-oak literature of eastern North America: synthesis and guidelines. USDA Forest Service, GTR-NRS-135, Newtown Square, Pennsylvania.
- Butler, B.W., Dickinson, M.B., 2010. Tree injury and mortality in fires: developing process-based models. *Fire Ecol.* 6, 55–79.
- De Micco, V., Zalloni, E., Balzano, A., Battipaglia, G., 2013. Fire influence on *Pinus halapensis*: wood response close and far from the scars. *IAWA J.* 34, 446–458.
- Dey, D.C., 2014. Sustaining oak forests in eastern North America: regeneration and recruitment, the pillars of sustainability. *For. Sci.* 60, 926–942.
- Dey, D.C., Kabrick, J.K., 2015. Restoration of midwestern oak woodlands and savannas. In: Stanturf, J.A. (Ed.), *Restoration of Boreal and Temperate Forests*. second ed. CRC Press, Boca Raton.
- Dey, D.C., Schweitzer, C.J., 2015. Timing fire to minimize damage in managing oak ecosystems. In: Gordon, H.A., Connor, K.F., Haywood, J.D. (Eds.), *Proceedings of the 17th Biennial Southern Silvicultural Research Conference*. e-Gen. Tech. Rep. SRS-203. USDA Forest Service, Southern Research Station. 11 p.
- Dickinson, M.B., Johnson, E.A., 2001. Fire effects on trees. In: Johnson, E.A., Miyanishi, K. (Eds.), *Forest Fires: Behavior and Ecological Effects*. Academic Press, New York.
- Grissino-Mayer, H.D., 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. *Tree-Ring Res.* 57, 205–221.
- Guyette, R.P., Dey, D.C., Stambaugh, M.C., Muzika, R.-M., 2006. Fire scars reveal variability and dynamics of eastern fire regimes. In: Dickinson, M.B. (Ed.), *Fire in Eastern Oak Forests: Delivering Science to Land Managers*, Proceedings of a Conference. Gen. Tech. Rep. NRS-P-1. USDA Forest Service, Northern Research Station, pp. 20–39.
- Hanberry, B.B., Kabrick, J.M., He, H.H., 2014. Densification and state transition across the Missouri Ozarks. *Ecosystems* 17, 66–81.
- Harper, C.A., Ford, W.M., Lashley, M.A., Moorman, C.E., Stambaugh, M.C., 2016. Fire effects on wildlife in the Central Hardwoods and Appalachian Regions. *Fire Ecol.* 12, 127–159.
- Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurements. *Tree-Ring Bull.* 43, 69–78.
- Hutchinson, T.F., Boerner, R.E.J., Sutherland, S., Sutherland, E.K., Ortt, K., Iverson, L.R., 2005. Prescribed fire effects on the herbaceous layer of mixed-oak forests. *Can. J. For. Res.* 35, 877–890.
- Hutchinson, T.F., Long, R.P., Rebbeck, J., Sutherland, E.-K., Yaussy, D.A., 2012. Repeated prescribed fires alter gap-phase regeneration in mixed-oak forests. *Can. J. For. Res.* 42, 303–314.
- Jensen, R.G., Kabrick, J.M., Zenner, E.K., 2002. Tree cavity estimation and verification in the Missouri Ozarks. In: Shifley, S.R., Kabrick, J.M. (Eds.), *Proceedings of the Second Missouri Ozark Forest Ecosystem Project Symposium: Post-treatment Results of the Landscape Experiment*. Gen. Tech. Rep. NC-227. USDA Forest Service, North Central Forest Experiment Station, pp. 114–129.
- Jones, J.L., Webb, B.W., Butler, B.W., Dickinson, M.B., Jimenez, D., Reardon, J., Bova, A.S., 2006. Prediction and measurement of the thermally induced cambial tissue necrosis in tree stems. *Int. J. Wildl. Fire* 15, 3–17.
- Kabrick, J.M., Dey, D.C., Kinkead, C.O., Knapp, B.O., Leahy, M., Olson, M.G., Stambaugh, M.C., Stevenson, A.P., 2014. Silvicultural considerations for managing fire-dependent oak woodland ecosystems. In: Groninger, J.W., Holzmüller, E.J., Nielsen, C.K., Dey, D.C. (Eds.), *Proceedings 19th Central Hardwood Forest Conference, GTR-NRS-P-142*. USDA Forest Service, Northern Research Station, pp. 2–15.
- Kinkead, C.O., 2013. *Thinning and Burning in Oak Woodlands M.S. thesis*. University of Missouri, Columbia, MO. 125 pp.
- Kinkead, C.O., Kabrick, J.M., Stambaugh, M.C., Grabner, K.W., 2013. Changes to oak woodland stand structure and ground flora composition caused by thinning and burning. In: Miller, G., Schuler, T.M., Gottschalk, K.W., Brooks, J.R., Grushecky, S.T., Spong, B.D., Rentch, J.S. (Eds.), *Proceedings, 18th Central Hardwood Forest Conference, GTR-NRS-P-117*. USDA Forest Service, Northern Research Station, pp. 373–383.
- Knapp, B.O., Marschall, J.M., Stambaugh, M.C., 2017. Effects of long-term prescribed burning on timber value in hardwood forests of the Missouri Ozarks. In: Kabrick, J.M., Dey, D.C., Knapp, B.O., Larsen, D., Saunders, M. (Eds.), *Proceedings of the 20th Central Hardwood Forest Conference, GTR-NRS-P-XX*. USDA Forest Service, Northern Research Station, pp. XX–XX (in press).
- Knapp, B.O., Stephan, K., Hubbart, J.A., 2015. Structure and composition of an oak-hickory forest after over 60 years of repeated prescribed burning in Missouri, USA. *For. Ecol. Manage.* 344, 95–109.
- LeBlanc, D.C., Terrell, M.A., 2009. Radial growth response of white oak to climate in eastern North America. *Can. J. For. Res.* 39, 2180–2192.
- Loomis, R.M., 1974. Predicting the losses in sawtimber volume and quality from fire in oak-hickory forests. Res. Pap. NC-104. USDA Forest Service, North Central Research Experiment Station, 6 p.
- Marschall, J.M., Guyette, R.P., Stambaugh, M.C., Stevenson, A.P., 2014. Fire damage effects on red oak timber product value. *For. Ecol. Manage.* 320, 182–189.
- Matlack, G.R., 2013. Reassessment of the use of fire as a management tool in deciduous forests of eastern North America. *Conserv. Biol.* 27, 916–926.
- McEwan, R.W., Hutchinson, T.F., Ford, R.D., McCarthy, B.C., 2007. An experimental evaluation of fire history reconstruction using dendrochronology in white oak (*Quercus alba*). *Can. J. For. Res.* 37, 806–816.
- Nowacki, G.J., Abrams, M.D., 2008. The demise of fire and “mesophication” of forests in the eastern United States. *Bioscience* 58, 123–138.
- Phipps, R.L., Field, M.L., 1989. Computer programs to calculate basal area increment from tree rings. Water-Resources Investigations Report 89-4028, U.S. Geological Survey, 124 pp.
- Pyne, S.J., 1982. *Fire in America: A Cultural History of Wildland and Rural Fire*. Princeton University Press, Princeton, p. 654.
- Rayner, A.D.M., Boddy, L., 1988. *Fungal Decomposition of Wood: Its Biology and Ecology*. Wiley, New York, p. 602.
- Remm, J., Löhmus, A., 2011. Tree cavities in forests – the broad distribution pattern of a keystone structure for biodiversity. *For. Ecol. Manage.* 262, 579–585.
- Scharenbroch, B.C., Nix, B., Jacobs, K.A., Bowles, M.L., 2012. Two decades of low-severity prescribed fire increases soil nutrient availability in a Midwestern, USA oak (*Quercus*) forest. *Geoderma* 183–184, 80–91.
- Schweitzer, C.J., Dey, D.C., Wang, Y., 2016. Hardwood-pine mixedwoods stand dynamics following thinning and prescribed burning. *Fire Ecol.* 12, 85–104.
- Shigo, A.L., 1984. Compartmentalization: a conceptual framework for how trees grow and defend themselves. *Ann. Rev. Phytopath.* 22, 189–214.
- Smith, K.T., 2015. Compartmentalization, resource allocation, and wood quality. *Curr. For. Rep.* 1, 8–15.
- Smith, K.T., Sutherland, E.K., 1999. Fire-scar formation and compartmentalization in oak. *Can. J. For. Res.* 29, 166–171.
- Smith, K.T., Sutherland, E.K., 2001. Terminology and biology of fire scars in selected Central Hardwoods. *Tree-Ring Res.* 57, 141–147.
- Stambaugh, M.C., Guyette, R.P., McMurry, E.R., Cook, E.R., Meko, D.M., Lupo, A.R., 2011. Drought duration and frequency in the U.S. Corn Belt during the last millennium (AD 992–2004). *Agric. For. Meteorol.* 151, 154–162.
- Stambaugh, M.C., Guyette, R.P., McMurry, E.R., Dey, D.C., 2006. Fire history at the eastern Great Plains margin, Missouri River loess hills. *Great Plains Res.* 16, 149–159.
- Stambaugh, M.C., Guyette, R.P., 2008. Prescribed fire effects on the wood quality of three common oaks in the Ozark region, *Q. coccinea*, *Q. velutina*, *Q. alba*. Final

- report prepared for the Missouri Department of Conservation, Jefferson City, Missouri, 23 p.
- Stambaugh, M.C., Marschall, J.M., Guyette, R.P., 2014. Linking fire history to successional changes of xeric oak woodlands. *For. Ecol. Manage.* 320, 83–95.
- Stambaugh, M.C., Varner, J.M., Noss, R.F., Dey, D.C., Christensen, N.L., Baldwin, R.F., Guyette, R.P., Hanberry, B.B., Harper, C.A., Lindblom, S.G., Waldrop, T.A., 2015. Clarifying the role of fire in the deciduous forests of eastern North America: reply to Matlack. *Conserv. Biol.* 29, 942–946.
- Stevenson, A.P., Muzika, R.-M., Guyette, R.P., 2008. Fire scars and tree vigor following prescribed fires in Missouri Ozark upland forests. In: Jacobs, D.F., Michler, C.H. (Eds.), *Proceedings of the 16th Central Hardwood Forest Conference*, Gen. Tech. Rep. NRS-P-24. USDA Forest Service, Northern Research Station, pp. 525–534.
- Stokes, M., Smiley, T., 1968. *Introduction to Tree-Ring Dating*. Univ. of Chicago Press, Chicago, p. 73.
- Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M., Jeltsch, F., 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *J. Biogeogr.* 31, 79–92.
- U.S. Forest Service, 2014. *U.S. forest resource facts and historical trends*. USDA Forest Service, Washington D.C., 63 p.
- Waldrop, T.A., Yaussy, D.A., Phillips, R.J., Hutchinson, T.A., Brudnak, L., Boerner, R.E.J., 2008. Fuel reduction treatments affect stand structure of hardwood forests in western North Carolina and southern Ohio, USA. *For. Ecol. Manage.* 255, 3117–3129.