First known fire scar on a fossil tree trunk provides evidence of Late Triassic wildfire

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ABSTRACT

Fire scars are well known to fire ecologists and dendrochronologists worldwide, and are used in dating fires and reconstructing the fire histories of modern forests. Evidence of fires in ancient forests, such as fossil charcoal (fusain), is well known to paleontologists and has been reported in geologic formations dating back to the Late Devonian. We describe what we conclude is a fire scar on a fossil tree trunk from the Late Triassic Chinle Formation of southeastern Utah (~200–225 Ma). The external features of the prehistoric scar match those of modern fire scars better than those of scars created by other kinds of wounding events. The fossil specimen also exhibits a number of changes in wood anatomy similar to those reported in modern fire-scarred trees, including a band of very small tracheids that indicate growth suppression immediately associated with the scarring event; an area with a tangential row of probable traumatic resin ducts; and a significant increase in tracheid size following the scarring event that indicates a growth release. No fire scar resembling those in modern trees has previously been described in petrified wood as far as we can determine. The presence of a fire scar not only provides further evidence of ancient fires, but also shows that at least some individual trees survived them, indicating that fire could have been an ecological and evolutionary force in forests at least as early as the Late Triassic.

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1. Introduction

Evidence of fires in ancient forests, such as fossil charcoal (fusain), is well known to paleontologists and has been reported back to the Late Devonian (Scott, 2000). Dechamps (1984) examined fossil wood from early Pliocene and Plio–Pleistocene deposits (3.1 to 1.0 Ma) from North African sites associated with primate fossils, which he claimed gave evidence that the trees had experienced fires based on anatomical features he called "traumatic rings". He stated that these rings were similar to those caused by modern fires but provided no supporting evidence, and did not use the term "fire scar" or describe anything resembling a fire scar on a modern tree.

Putz and Taylor (1996) described what are clearly scars in fossil Triassic wood from Antarctica and concluded that they were probably caused by mechanical wounding, such as flood-scouring. They looked for distinctive anatomical features in the fossil wood associated with the scarring event but did not find them, and reported that fossil charcoal (fusain) was not found on, or associated with, these fossils.

Charcoal and charcoal-like plant fossils preserved in the Petrified Forest National Park provide evidence for Late Triassic wildfires (Jones et al., 2002; Jones and Ash, 2006). Ziegler (2003) described a fossil vertebrate assemblage and charcoal from the Upper Triassic Chinle Formation in north-central New Mexico that she interprets as the site of a forest fire. Uhl and Montenari (2011) reported the presence of ancient charcoal in Late Triassic sandstones from southwestern Germany, which they interpret as evidence of wildfires.

Our objectives are to describe the macro- and microscopic features of a scar preserved on a short length of a fossil tree trunk from the Late Triassic Chinle Formation of southeastern Utah, and to compare them with the characteristics of scars on modern trees resulting from fire and other causes.

2. Materials and methods

2.1. General description of fossil tree trunk

The section of fossil tree trunk with the scar consists only of secondary xylem surrounding a small, poorly preserved pith. It is oval in cross section, about 200 × 140 mm (the slightly oval cross section is probably due to crushing during the burial and fossilization process). Before sectioning for study it was from 100 to 150 mm long (Fig. 1A, B). There is no discernable insect damage in the fossil wood. The structure of the wood is well-preserved in most areas of the cross section and is homozylous,

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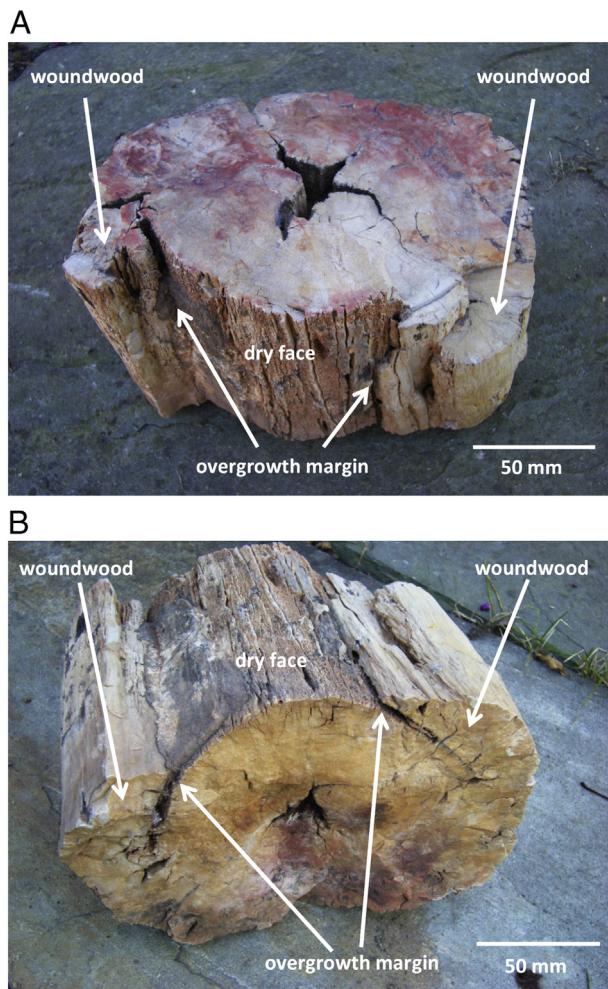E-mail address: bruce.byers@verizon.net (B.A. Byers).

A

B

Fig. 1. (A) (top) Upper side of specimen showing the dry face of the scar and overgrowth of woundwood from both sides. (B) (bottom) Lower side of the specimen.

with no discernable annual rings. The fossil trunk was cross-sectioned and polished for examination (Fig. 2).

The fossil probably represents the dominant petrified pycnoxylic wood found in the Chinle Formation, which has been called *Araucarioxylon arizonicum* for more than a hundred years (Knowlton, 1888), although it should be referred to *Agathoxylon arizonicum* as recommended by Philippe (2011) and advocated by other paleobotanists.
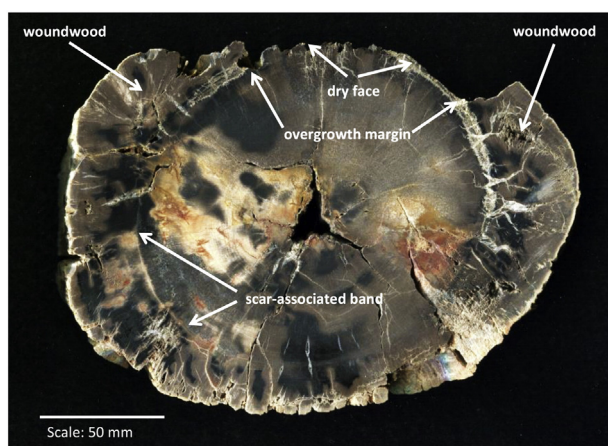

Fig. 2. Cross-section of the specimen showing healing curls of woundwood and dry face of the scar at same radius as scarring event.

Similar petrified wood occurs in the Chinle Formation almost everywhere the unit is exposed, and is especially common in southern Utah (Scott, 1961; Stokes, 1986; Ash, 2003). This formation is widely exposed in the area where this fossil was found.

Specimen: a portion of the scarred fossil tree trunk, USNM 559975, has been deposited in the paleobotanical collections at the National Museum of Natural History, Washington, D.C.

Locality: USNM 43696 (southwest of Bears Ears, UT, Fig. 3A — exact locality data are on record at the museum).

2.2. Geological setting

The Chinle Formation (Late Triassic, Norian–Rhaetian stages) was deposited by a large, low gradient, meandering river system in a large back-arc basin located about 5°–10° north of the paleo-equator, which extended from what is now west Texas to the western Pangean shoreline in Nevada (Fig. 4A) (Dickinson and Gehrels, 2008). The Chinle Formation is composed mainly of colorful mudrock as well as smaller quantities of reddish siltstone, sandstone, conglomerate and limestone (Irmis et al., 2011). They were deposited primarily in fluvial and overbank environments; paludal, lacustrine, and eolian deposits are also present. In the Bears Ears area the Chinle Formation is about 260 m thick and includes six members (Stewart et al., 1972): (oldest to youngest) Shinarump, Monitor Butte, Moss Back, Petrified Forest, Owl Rock, and Church Rock (Fig. 3B). Ramezani et al. (2011) have dated the lower members of the Chinle Formation, through the Petrified Forest Member; the dates range from 213.1 Ma to 209 Ma.

It is not possible to determine the specific member of the formation that was the source of USNM 55995 (this specimen), but most probably it came from the Petrified Forest Member because the fossil was lying in soil of that unit when it was found.

2.3. Wood anatomical analysis

In order to analyze the anatomical features of the fossil wood, photomicrographs (RGB, color 24 bit) of a 25 mm transect of the scar-associated, light-colored band in the petrified wood (Fig. 4) were taken using an Olympus SZX16 microscope with SDF PLAPO 1X PF lens and recorded using an Olympus DP21 camera with an image scale of 0.78 μm/pixel.

Wood anatomical features were measured on both sides of the scar-associated band (Fig. 5). One-hundred-forty-six radial tracheid files, 69 pre- and 77 post-scarring, were plotted using the image analysis program Image J (version 1.48, Abramoff et al. 2004). Tracheid cell walls and lumen diameters were discriminated based on grey values along a radial line passing through the tracheid files (DeSoto et al., 2011). To attain uniform measurements, only the tangentially largest cells in clearly-focused radial tracheid files were measured, and unfocused or deformed cells were not included (Fig.5). The radial lumen diameter (LD), the radial cell wall thickness (CWT), the radial tracheid diameter (TD), and the ratio of radial lumen diameter to radial cell wall thickness (LD/CWT) were calculated with the "tgram" R package, (available from CRAN; http://cran.r-project.org; DeSoto et al., 2011).

Generalized estimating equations (Quinn and Keough, 2002) were used to test the differences in wood anatomical features before and after scarring. Generalized estimating equations allow the modeling of autocorrelations that could arise from the sampling of multiple tracheids in the same radial file. Our model treated the pre- or post-scarring sides of the scar-associated band as a fixed factor, with the tracheid radial file as the subject effect. We assumed a normal error distribution with an identity link function for mean LD, TD and CWT and LD/CWT ratio. Least-square means were obtained for pre- and post-scarring sides, and the differences between them were tested pairwise, by using the DIFF option in the LSMEANS statement. We fitted generalized estimating equations via restricted maximum-likelihood (REML) using the GEMMOD procedure of SAS (SAS Statistical package 9.2).
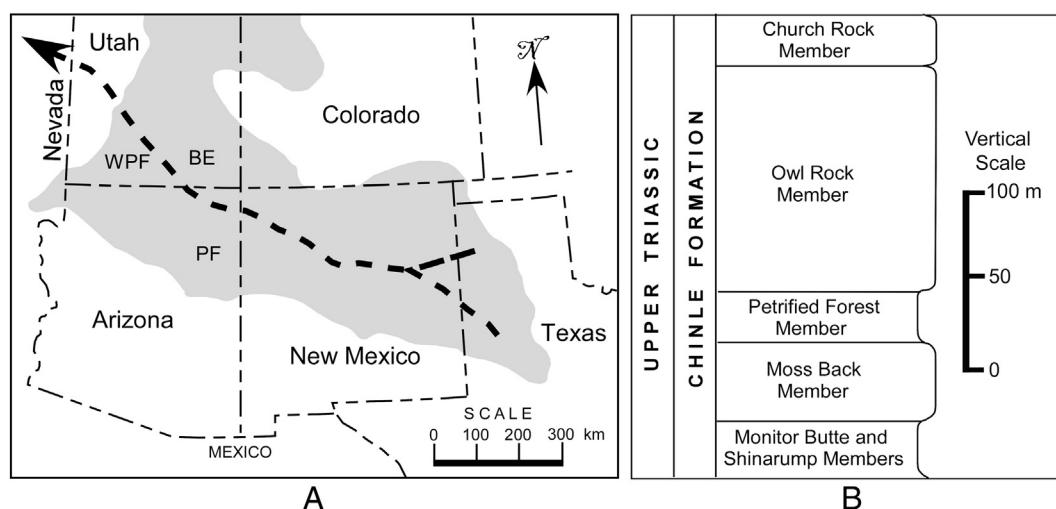
Fig. 3. (A) Index map of a part of the American Southwest showing the location of the Bears Ears (BE), Wolverine Petrified Forest (WPF) and Petrified Forest National Park (PF). The irregular shaded area shows the general distribution of Triassic strata in the region and by inference, the boundaries of the Chinle–Dockum basin. The dashed line extending from Texas to Nevada represents the approximate course of the Chinle–Dockum river system. Adapted from Dickinson and Gehrels (2008) and Riggs et al. (1996). Adapted from Dickinson and Gehrels (2008) and Riggs et al. (1996). (B) Simplified stratigraphic chart showing the members of the Chinle Formation exposed in the vicinity of the Bears Ears and their relative thicknesses. Petrified wood is known to occur in the Petrified Forest Member and all the underlying members of the Chinle Formation at many places in the American Southwest. Based on stratigraphic section U–25 measured in the vicinity of the Bears Ears by J. H. Stewart and G A. Williams (in Stewart et al., 1972).

3. Results

3.1. Macroscopic features of the scar

The scar extends vertically along one side of the trunk and the overgrowth of wood has occurred along both edges of the dry face of the scar (Fig. 1A, B). The two healing curls are vertical, straight, and nearly parallel, slightly converging upward — their edges are about 92 mm apart at what we assume is the bottom of the tree, narrowing to 85 mm apart at upper end. The scar must have been much longer than the preserved length on the specimen described here.

The orientation of wood rays that created the overgrowth of xylem and the healing curl of woundwood can be clearly seen in the polished cross section under low magnification (Fig. 6). In the transverse section the dry face of the scar is about 90 mm wide and the locations of the origins of the scars, overgrown by woundwood, can be pinpointed by the change in direction of growth of the wood rays. About 50 mm of the original scar area has been overgrown by woundwood in the upper left portion of the scar face (Fig. 7A) and about 40 mm on the upper right (Fig. 7B). Thus, the scar was originally about 180 mm wide, and when it was formed the tree had a circumference measured at about 400 mm. Approximately 60 mm of growth was added to the tree diameter after the scarring event.

3.2. Microscopic features associated with the scar

A whitish band in the fossil wood at the same radius as the dry face of the scar and the edges of the healing curls is visible in the lower left quadrant of the bottom face of the cross section, apparently caused by the scarring event (Figs. 2, 4). Microscopic examination of wood anatomy along this band shows several distinctive features. First, the scar-associated band is composed of approximately six to eight concentric rows of tracheids that are significantly smaller than those before or
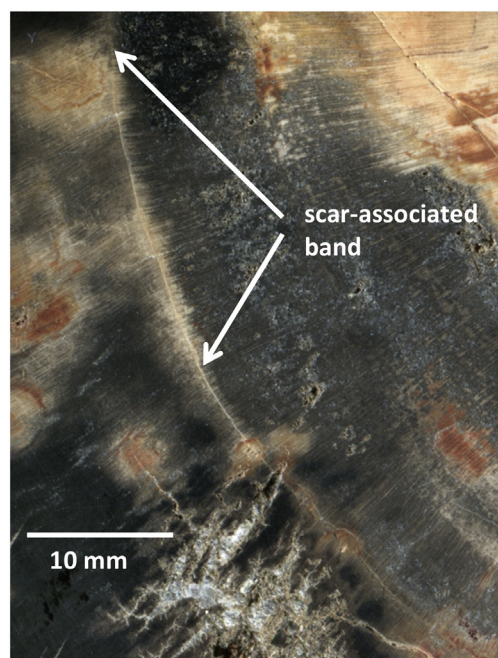

Fig. 4. Enlargement of scar-associated band; arrows mark ends of the 25 mm section from which photomicrographs were taken for tracheid analysis.
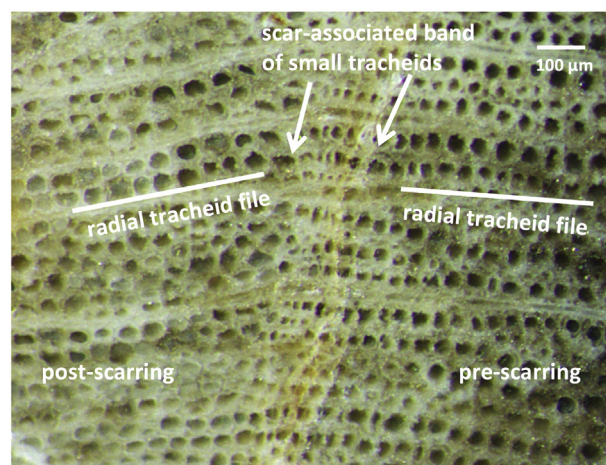

Fig. 5. Photomicrograph of scar-associated band; arrows point to edges of visible band composed of small tracheids; pre- and post-scarring radial tracheid files marked to illustrate tracheid sampling methodology.
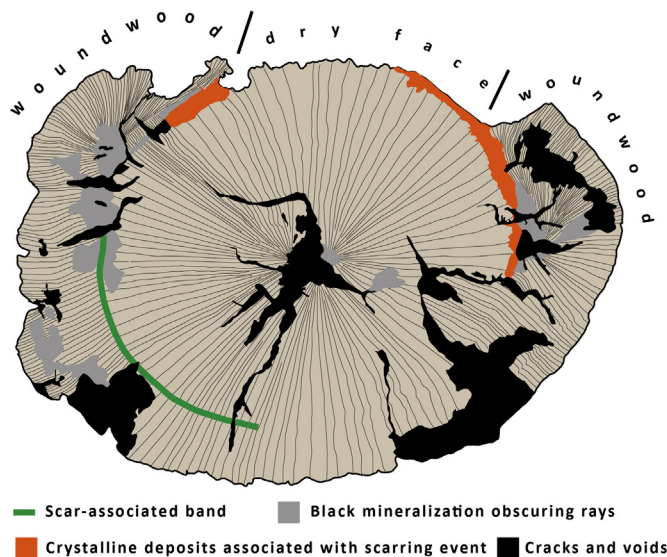
Fig. 6. Drawing based on Fig. 2 cross section showing orientation of wood rays, reorientation of ray growth in woundwood, and position of scar-associated band.
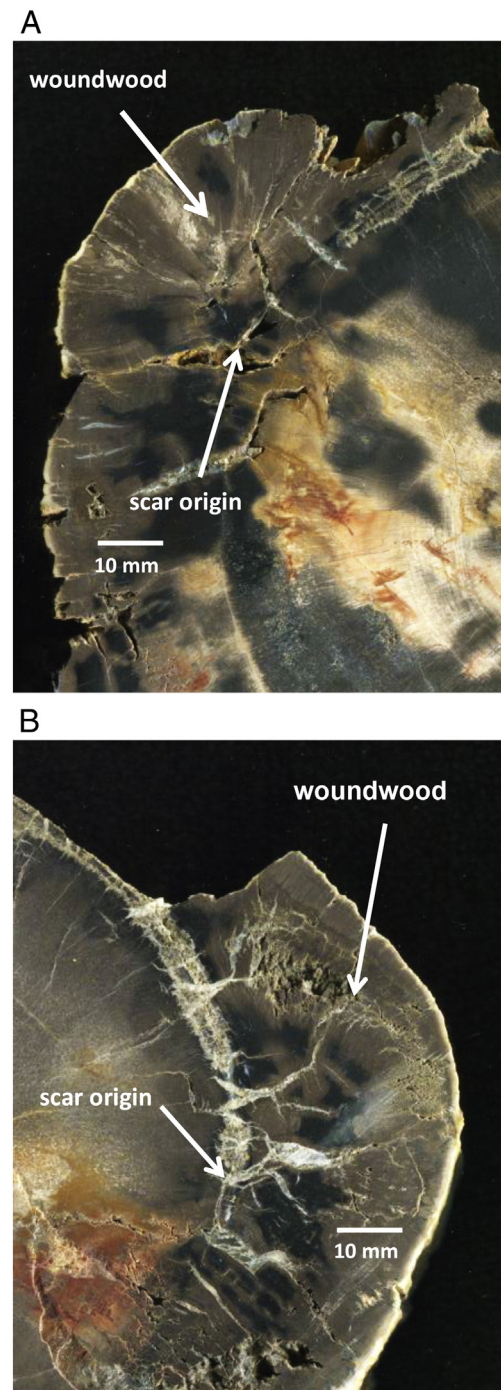

Fig. 7. (A) (left) Woundwood and healing curl, left side, showing scar origin where ray growth direction changes to form woundwood. (b) Woundwood and healing curl, right side.

after the band (Fig. 5). Second, in some places along the visible band there are cracks or gaps between the compressed rows of tracheids and those that grew after them, probably representing a tangential row of traumatic resin ducts (Fig. 8). Finally, we found statistically-significant differences in wood anatomy before and after the scarring event (Table 1). The mean tracheid diameter (TD) and mean lumen diameter (LD) were larger after scarring, whereas the mean cell wall thickness (CWT) was larger before the scarring event. Consequently, the mean LD/CWT ratio was higher after the event.

4. Discussion

We compared the macro- and microscopic characteristics observed in modern trees scarred by fires and other events with those of the fossil specimen (Table 2).

4.1. Scar morphology

The shapes and other macroscopic features of tree scars depend upon the mode of scar formation (Long, 2003). The characteristic shape of a fire scar is the result of heat from a ground fire that kills part of the vascular cambium on one side of the tree only and does not kill the tree (Gutsell and Johnson, 1996; Smith and Sutherland, 2001). Fire scars are generally triangular or elongate and oriented vertically starting from the base of the tree. The healing curls of woundwood at the scar margins are generally straight, smooth, and roughly parallel, converging toward the scar apex. The scar described here has smooth, straight, and almost parallel edges similar to modern fire scars.

Mechanical wounding from logs and other debris carried by floods, or from rockfalls, produces morphologically different scars, which are often oval, round, or irregular in shape, and are typically located above the base of the tree (Yanofsky and Jarrett, 2002; Stoffel and Bollschweiler, 2008; Schneuwly et al., 2009; Ballesteros et al., 2010a,b, 2011; Chiroiu, 2013; Trappmann and Stoffel, 2013; Stoffel and Klinkmüller, 2013).

We found no published studies describing the characteristics of lightning scars, another possible cause of wounding. Discussions with several experienced pyrodendrochronologists suggest that lightning scars usually affect only a narrow portion of the circumference of the trunk (less than 10%), sometimes have ragged edges, and often do not create a strong overgrowth of woundwood as generally seen in fire

scars (E. Bigio, P. Brown, H. Grissino-Mayer, L. Huckaby, personal communications).

Because fire scars result from fast-moving ground fires that kill the vascular cambium under the bark, there is generally not sufficient heat or time to dry and burn the underlying secondary xylem (Gutsell and Johnson, 1996; Smith and Sutherland, 2001), and thus there are no missing rings or loss of secondary xylem at the face of the scar (i.e., the scar face is at the radius of the tree when the fire occurred). If a fire scarred tree is scarred a second time, some xylem may be burned at the dry face of the scar. Although mechanical wounding, such as floods, rock falls, debris flows, and avalanches frequently does not
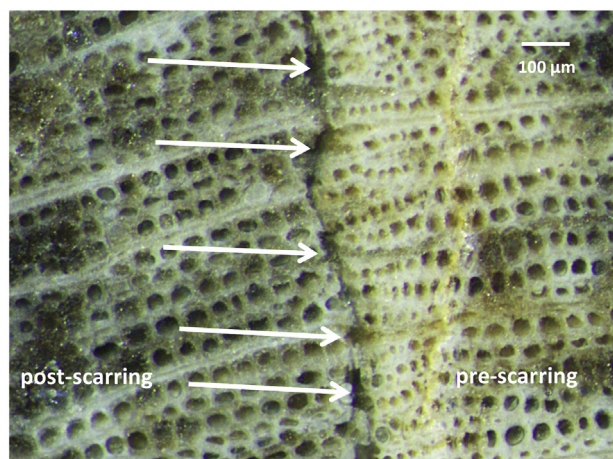
Fig. 8. Photomicrograph of scar-associated band; arrows point to a tangential row of traumatic resin ducts.

damage the xylem (M. Stoffel, personal communication) it can sometimes do so, resulting in missing rings at the scar face (Schneuwly et al., 2009; Chiroiu, 2013; Stoffel and Klinkmüller, 2013). The specimen described here appears to have intact secondary xylem that extends continuously across the dry face of the scar, as is typical of modern fire scars.

Charcoal is not necessarily found in or with a fire scar in modern trees, especially if the tree has been scarred only once. Any charred bark over the area where the cambium was killed generally sloughs or is eroded off later, leaving exposed secondary xylem with no charring. Fossilized bark is very rare, and was not found on this specimen. The specimen contains no visibly-apparent ancient charcoal.

After a portion of the vascular cambium is killed by fire or other wounding event, the orientation of the growth of wood rays in the living cambium on either side of the scar changes, and overgrowth of woundwood begins to contain and cover the scar face. Such reorientation of the wood rays in the healing curls is clearly seen in this fossil specimen, exactly as observed in modern scarred trees.

4.2. Scar-associated changes in wood anatomy

Distinctive visible and measurable changes in the anatomy of wood that grows after a fire have been described in gymnosperms (Brown and Swetnam, 1994; Lageard et al., 2000; Lombardo et al., 2009; Swetnam et al., 2009) and angiosperms (Bigio et al., 2010; Kames et al., 2011). Fire-associated anatomical changes have been described in the wood of both scarred and unscarred trees that survived wildfires. These are attributed to physiological responses to heat-stress of the cambium and/or damage to the foliage of the tree. Immediate and generally short-term fire-associated changes reported in conifers include suppression of growth (Brown and Swetnam, 1994; Sherriff and Veblen, 2006; Lombardo et al., 2009; Swetnam et al., 2009), and sometimes the presence of traumatic resin ducts or ring separations (Brown and Swetnam, 1994; Swetnam et al., 2009).

Table 1
Least-square means and standard error (Mean $\pm$ SE) of wood anatomical features, radial lumen diameter (LD), radial cell wall thickness (CWT), radial tracheid diameter (TD) and ratio of radial lumen diameter to radial cell wall thickness (LD/CWT), and Type III test conducted on the generalized linear model to test the effect of the fire on wood anatomy features (total number of tracheids = 889).

Wood features (µm)	Pre-fire		Post-fire		df	χ^2	P
TD	45.94	± 0.51	50.97	± 0.52	1	32.98	<0.001
LD	26.55	± 0.42	33.66	± 0.48	1	50.64	<0.001
CWT	9.74	± 0.18	8.58	± 0.16	1	15.88	<0.001
LD/CWT ratio	2.87	± 0.08	4.13	± 0.10	1	41.37	<0.001

The fossil specimen exhibits a visible band, lateral to the scar at exactly the same radius, which we call the scar-associated band. Such visible bands are not uncommon in cross sections of modern fire-scarred conifers (P. Brown, H. Grissino-Mayer, L. Huckaby, personal communications). In the fossil specimen, microscopic examination of the visible band shows it to consist of approximately six to eight rows of very small tracheids. We interpret these very small tracheids as evidence of suppressed wood growth caused by environmental stress from a fire. This specimen has no annual rings, as is typical for fossil trees of the Late Triassic Chinle Formation (Ash and Creber, 1992), but the band of small tracheids is probably comparable to the narrow rings of suppressed growth sometimes seen in modern conifers following a fire, which Brown and Swetnam (1994) call "fire rings." Arbellay et al. (in press) report significantly smaller tracheids immediately following fires in two North American conifer species.

Some areas along the scar-associated band of the fossil trunk show cracks or gaps between the rows of very small tracheids and those that grew after the scaring event (Fig. 8). This feature appears to be a tangential row of traumatic resin ducts similar to those seen in modern conifers following fire (Brown and Swetnam, 1994; Swetnam et al., 2009) or other wounding events (Bollschweiler et al., 2008; Stoffel, 2008; Stoffel and Bollschweiler, 2008; Schneuwly et al., 2009; Chiroiu, 2013).

4.3. Post-fire growth response

Fire-scarred conifers often exhibit an increase in growth rate, known as "growth release," after they have recovered from the fire (Brown and Swetnam, 1994; Caprio et al., 1994; Mutch and Swetnam, 1995; Lageard et al., 2000; Lombardo et al., 2009; Swetnam et al., 2009). Growth release is generally attributed to two factors: 1) a reduction of competition for light, nutrients, and/or water caused by the mortality of nearby trees or other vegetation; and/or 2) an increase in available nutrients caused by the burning of live vegetation or litter (Caprio et al., 1994; Mutch and Swetnam, 1995; Lombardo et al., 2009). Swetnam et al. (2009) call growth release a "fire indicator" in giant sequoias, *Sequoiadendron giganteum*.

Studies of fire-associated growth release in modern conifers have used ring widths as a measure of growth rate, and growth release implies an increase in the width of rings growing after a fire compared to those growing before it occurred (Nowacki and Abrams, 1997). In gymnosperms, wood is mainly composed of tracheids, so wide rings are caused by an increase in tracheid size or tracheid number (DeSoto et al., 2011; Olano et al., 2012; Scott and Vahey, 2012; Martin-Benito et al., 2013). The fossil specimen described here has no apparent rings. However, our analysis showed that the fossil tree produced larger tracheids with larger lumen diameters after the scarring event than before, indicating a growth release (Table 1). We found no studies that analyzed tracheid size or number per se, rather than ring width, as a measure of growth release in modern trees following fire.

Analysis of the fossil tracheids also showed that while the lumen diameter increased after the scarring event, the cell-wall thickness decreased. Increasing water availability has been shown to increase tracheid lumen diameter but reduce cell wall thickness in a modern conifer, *Cryptomeria japonica* (Abe and Nakai, 1999), so this change in wood anatomy observed in the fossil tree is consistent with the hypothesis that it experienced less competition for water because the fire killed other nearby vegetation.

To our knowledge this study is the first to use tracheid anatomy, rather than ring width, to detect growth release following fires in fossil or modern trees.

We conclude that this is most probably an ancient fire scar based on the similarities between macro- and microscopic characteristics observed in modern fire-scarred trees and those of the fossil specimen (Table 2).

Table 2
Comparison of macroscopic and microscopic characteristics of modern tree scars with the fossil specimen.

Characteristic	Modern fire scars	Modern scars caused by floods or corrasion	Fossil specimen
Macroscopic			
Woundwood; healing curl and change in direction of growth of rays	Present	Present	Present (Figs. 1, 2, 6, 7)
Shape of scar	Elongate with arch at top, or triangular, starting from base of tree	Oval, round, or irregular often located above base of tree	Elongate, with slight upward taper (Fig. 1A, B)
Orientation of healing curl(s) and scar borders	Healing curls vertical, parallel, or converging at scar apex (Gutsell and Johnson, 1996; Smith and Sutherland, 2001)	Woundwood overgrowing oval, round, or irregular scars from all directions; borders can be curved, irregular (Ballesteros et al., 2010a,b; Chiroiu, 2013; Schneuwly et al., 2009; Stoffel and Klinkmüller, 2013; Trappmann and Stoffel, 2013; Yanofsky and Jarrett, 2002)	Vertical, straight, slightly converging upward (Figs. 1A, B)
Condition of secondary xylem at face of scar	Typically no missing rings or loss of secondary xylem in single scars; dry face at radius equal to scarring event; burned/missing xylem sometimes present after multiple fire scarring events	Typically no missing rings or loss of secondary xylem, but xylem sometimes crushed or gouged at face of scar from rockfalls (Schneuwly et al., 2009; Chiroiu, 2013; Stoffel and Klinkmüller, 2013)	Scar face at radius equal to scarring event; no apparent missing secondary xylem (Fig. 2)
Microscopic			
Growth suppression associated with scarring event indicated by ring width and/or other features of wood anatomy	Reported for fire events in conifers (Brown and Swetnam, 1994; Lombardo et al., 2009; Bigio et al., 2010; Arbellay et al., in press)	Reported for floods, debris flows, and snow avalanches in conifers (Ballesteros et al., 2010b; Kogelnig-Mayer et al., 2013; Stoffel et al., 2008; Stoffel and Hitz, 2008)	Present in a band at radius of scarring event, with approximately six to eight rows of very small tracheids (Figs. 5, 8)
Growth release following scarring event indicated by ring width and/or other features of wood anatomy	Commonly reported in conifers (Brown and Swetnam, 1994; Caprio et al., 1994; Mutch and Swetnam, 1995; Lageard et al., 2000; Lombardo et al., 2009; Swetnam et al., 2009)	Reported in conifers following debris flows (Mayer et al., 2010; Stoffel et al., 2005)	Significant increase in tracheid diameter and lumen size after the scarring event indicating growth release (Fig. 5)
Tangential rows of traumatic resin ducts associated with scarring event	Reported in conifers (Brown and Swetnam, 1994; Swetnam et al., 2009)	Reported in conifers (Bollschweiler et al., 2008; Chiroiu, 2013; Schneuwly et al., 2009; Stoffel, 2008; Stoffel and Bollschweiler, 2008)	Present in one area of scar-associated band (Fig. 8)
Ring separation associated with scarring event	Reported in conifers (Brown and Swetnam, 1994)	Reported from rockfalls, debris flows (Stoffel, personal communication)	No annual rings present in fossil specimen

4.4. Fire ecology of Chinle Formation forests

Fires of varying intensities and frequencies occur in modern forest ecosystems. At a minimum, a fire scar indicates that there is sufficient understory vegetation or litter to carry a ground fire and create a scar without killing the tree. With only one specimen with a fire scar, it is not possible to say much about the fire regime of the Late Triassic forest in which the tree grew. In modern forests, a single fire-scarred tree could come from forests that span the entire spectrum of fire regimes, from frequent, low-intensity fires to less frequent fires of higher intensity.

The fossil trees of the Late Triassic Chinle Formation typically do not show annual tree rings or other evidence of a seasonal climate, although their wood often has irregular growth interruptions similar to those found in some modern trees of the humid tropics (Ash and Creber, 1992). Even if the climate in which the specimen described here grew was generally uniform, the prehistoric fire scar nevertheless indicates that enough dry fuel was present at some point in time to allow an ignition source – probably lightening – to cause a fire (Scott, 2000). Fire in modern forests is strongly correlated with climatic variability and periodic droughts, which cause decreased growth rates that are reflected in annual rings (Kitzberger et al, 1997; González et al., 2005; Swetnam et al., 2009; Mundo et al., 2012a,b).

The presence of a fire scar not only confirms the presence of fire in the ecosystem where the specimen described here grew, but also shows that at least some individual trees survived those fires. Differential survival of fires by individual trees means that fire would have been an ecological and evolutionary force in the forests of the Late Triassic in the area where the Chinle Formation was deposited. In modern forests, trees show adaptations to fire, such as fire-resistant bark, self-pruning growth forms, the ability to resprout from trunks and roots, and serotiny (Schwilk and Ackerly, 2001; Climent et al., 2004). Some modern members of the family Araucariaceae, such as *Araucaria araucana*, found in the southern Andes, are highly fire-adapted, with thick, fire-resistant bark and an extreme self-pruning growth form that creates umbrella-shaped crowns of branches on older trees. Such adaptations may already have been present in Late Triassic forests. Looy (2013) reported fossil evidence for self-pruning in Permian conifers and discussed the implications of this trait for the fire ecology of the forests in which they grew. Fire-adapted traits may have been present in Cretaceous conifers (He et al., 2012).

Ash and Creber (2000) used fossil evidence to reconstruct tree morphology of *Agathoxylon arizonicum*, the predominant tree species of the Petrified Forest, and proposed that this species probably had thin bark, and branches arrayed from the base to the crown — thus not necessarily a self-pruning growth form as in some modern fire-adapted species. The only known fossil bark of a Late Triassic tree was described by Ash and Savidge (2004). The preserved bark, from a branch, ranges from 2 to 11 mm thick; this thin bark may not reflect the characteristics of bark at the base of the trunk, where thick bark would be expected in fire-adapted species.

4.5. New applications for analysis of microscopic wood anatomy

We were surprised to find only one study that analyzed tracheid anatomy before and after fires in modern trees (Arbellay et al., in press). Information obtained from tracheid analysis could perhaps expand our knowledge about the relationship between climate and fire beyond that already available from dendrochronological studies of tree rings.

To our knowledge this is the first study of tracheid anatomy before and after fires in fossil trees, and the first use of tracheid analysis in fossil or modern trees to detect growth release. Tracheid analysis is bringing new information to questions of modern ecology and climatology, and also may prove to be informative when applied to paleoecological and paleoclimatological questions using fossil wood.

We also found no studies characterizing the growth rates and other aspects of wood anatomy in trees scarred by lightning. Studies of lightning-scarred trees are needed to determine which features of other types of scarring events may be found in them, such as short-term growth suppression, rings of traumatic resin ducts, ring separation, or growth release.

4.6. Prehistoric tree scar research agenda

The fact that paleobotanists have never previously described a prehistoric fire scar is interesting and instructive. Perhaps because of disciplinary specialization, paleobotanists did not previously have a "search image" for fire scars, or tree scars in general. We imagine that although fire scars on fossil tree trunks may be rare, many more examples probably could be found. Systematic research on prehistoric tree scars could provide evidence of ancient disturbance events (e.g., fires, floods, landslides, lahars) exactly as do recent tree scars.

Acknowledgments

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