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Short- and long-term effects of fire on stem hydraulics in *Pinus ponderosa* saplings

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Abstract

Understanding tree physiological responses to fire is needed to accurately model post-fire carbon processes and inform management decisions. Given trees can die immediately or at extended time periods after fire, we combined two experiments to assess the short- (one-day) and long-term (21-months) fire effects on *Pinus ponderosa* sapling water transport. Native percentage loss of conductivity (*n*PLC), vulnerability to cavitation and xylem anatomy were assessed in unburned and burned saplings at lethal and non-lethal fire intensities. Fire did not cause any impact on *n*PLC and xylem cell wall structure in either experiment. However, surviving saplings evaluated 21-months post-fire were more vulnerable to cavitation. Our anatomical analysis in the long-term experiment showed that new xylem growth adjacent to fire scars had irregular-shaped tracheids and many parenchyma cells. Given conduit cell wall deformation was not observed in the long-term experiment, we suggest that the irregularity of newly grown xylem cells nearby fire wounds may be responsible for decreasing resistance to embolism in burned plants. Our findings suggest that hydraulic failure is not the main short-term physiological driver of mortality for *Pinus ponderosa* saplings. However, the decrease in embolism resistance in fire-wounded saplings could contribute to sapling mortality in the years following fire.

KEYWORDS
cambium, cavitation, sapling mortality, wound closure, xylem

1 | INTRODUCTION

By the end of the 21st century, fire seasons worldwide are predicted to be longer with greater associated ecosystem and community impacts due to anthropogenic climate change (Bowman et al., 2017; Flannigan et al., 2013). Regional studies have already shown increases in fire activity over the past 30 years (Abatzoglou & Williams, 2016; Pausas, 2004). Increasing fire activity coupled with more extreme and frequent drought events (Allen, Breshears, & McDowell, 2015; Sheffield & Wood, 2008) and fuel buildup associated with fire exclusion (Naficy, Sala, Keeling, Graham, & DeLuca, 2010) can increase potential post-fire impacts, even for fire-adapted ecosystems (Sparks et al., 2018). Accurate forecasts of post-fire impacts under

changing and novel conditions will require that process-based models better incorporate how fires impact plant physiological processes (Jolly & Johnson, 2018; O'Brien et al., 2018; Smith et al., 2016; Smith, Arbellay, Falk, & Sutherland, 2016). However, considerable uncertainties remain on how fires impact tree physiology and mortality (Bär, Michaeltz, & Mayr, 2019; Hood, Varner, Mantgem, & Cansler, 2018). Improving this understanding is essential to accurately parameterize Earth system models to predict the immediate and extended impacts on terrestrial biogeochemical cycles and, ecosystem services, and to better inform post-fire land management decisions (Krieger, 2001; Smith et al., 2014; Smith, Arbellay, et al., 2016; Smith, Sparks, et al., 2016; Stenzel et al., 2019).

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Given trees can die many years post-fire (McHugh & Kolb, 2003; Ryan, Peterson, & Reinhardt, 1988) and due to their potential exposure to droughts and other stressors in the years after a fire, knowing the persistence of fire effects on tree water transport is crucial to improve long-term post-fire tree mortality estimates. Trees that are not killed immediately by fire are usually left with injuries in the crown and vascular cambium that can potentially lead to mortality (Dickinson & Johnson, 2004; Ryan, 2000; Ryan & Frandsen, 1991). Recently, it has been proposed that dysfunction of the plant hydraulic system is an important mechanism of post-fire tree mortality (Bär, Nardini, & Mayr, 2018; Kavanagh, Dickinson, & Bova, 2010; Michaletz, Johnson, & Tyree, 2012; West, Nel, Bond, & Midgley, 2016). The impairment of the tree hydraulic system caused by fire has been proposed to occur through heat-induced embolism in the xylem conduits and/or deformation of the conduit cell walls. Shifts in atmospheric conditions (high temperature and low relative humidity) caused by the convective heat (i.e., fire plume) may result in increased tension in the xylem water column (Kavanagh et al., 2010) and spread of air bubbles through air-seeding (Delzon, Douthe, Sala, & Cochard, 2010; Sperry & Tyree, 1988) thus causing the disruption of water transport. Tree death is then considered highly likely if embolized xylem conduits reach critical thresholds where the embolism is not reversible (Brodribb & Cochard, 2009; Hammond et al., 2019; Urli et al., 2013). Furthermore, it has been proposed that conductive heat transfer through the bark during fire may cause permanent deformation of xylem conduits (Bär et al., 2018; Michaletz et al., 2012; West et al., 2016) preventing the water transport by the damaged conduits. This deformation is thought to occur because conduit cell walls are formed of polymers that, when exposed to specific temperatures, undergo thermal softening (Irvine, 1985; Olsson & Salmén, 1997) and after cooling, the cell walls may stay permanently deformed. It has been further suggested that damaged xylem may result in decreased water conductivity and increased xylem vulnerability to embolism (Michaletz et al., 2012).

If decreased hydraulic conductivity caused by fire persists over extended time periods, other physiological processes may be affected and potentially contribute to post-fire tree mortality. Prior studies have found that stomatal conductance and photosynthesis declined with decreasing hydraulic conductivity (Hubbard, Ryan, Stiller, & Sperry, 2001). Furthermore, it has been reported that if photosynthesis is reduced for significantly long periods, carbon stores can be depleted due to usage for maintenance of metabolism (Li et al., 2018; McDowell, 2011; Weber et al., 2018). Such reductions in photosynthesis in burned plants have been shown to depend on the intensity of the fire (Smith et al., 2017). In this case, higher usage of stored carbon is expected for tree recovery from the fire damage and to maintain metabolism even if plants are not under water stress post-fire.

Limited studies have assessed the effects of actual fires (as opposed to the use of fire proxies such as radiant heaters, convection ovens or water baths) on the living tree hydraulic system. Experiments conducted with species of *Pinus* exposed to actual fires in the field have found different results in vulnerability to embolism (Battipaglia et al., 2016; Bär et al., 2018). As these experiments were conducted at different time scales, one- and 12-months post-fire respectively, it is possible that the effects of fire on the tree hydraulic system differ between immediate short-term "shock" impacts and extended "recovery" time periods (>6 months) after the trees have had time to regrow new xylem. Studies using water baths as proxies for fire have also suggested that heat-induced impairment of tree water transport can potentially lead to mortality (Bär et al., 2018; Michaletz et al., 2012; West et al., 2016). However, to our knowledge, no prior studies have evaluated the impacts of lethal intensities from actual fires on tree water transport.

In this study, we combined two experiments that allowed us to evaluate the short- (one-day) and long-term (21-months) post-fire impacts on the water transport of well-watered *Pinus ponderosa* saplings. Hydraulic conductivity was assessed in saplings exposed to known lethal and non-lethal fire intensities (Steady et al., 2019) in the short- and long-term experiment, respectively. We also investigated the potential heat-induced damage in the xylem cell walls in both experiments. Although *P. ponderosa* is a fire-resistant species (Miller, 2000), small saplings are easily killed by surface fires (Battaglia, Smith, & Sheppard, 2009; Gartner & Thompson, 1972). Therefore, if the heat generated during fire can cause impairment of the tree hydraulic system, we would expect to observe a substantial decrease in hydraulic conductivity in saplings exposed to lethal fire intensities, given these younger trees have not developed fire-resistant traits, such as thick bark. We hypothesized that sapling hydraulic conductivity and vulnerability to embolism would be impacted negatively by fire in both the short-and long-term experiments as a result of heat-induced deformation of xylem cell walls.

2 | MATERIAL AND METHODS

2.1 | Plant material

In this study, we combined two experiments conducted with well-watered *P. ponderosa* saplings. Following the nomenclature described in Brodersen et al. (2019), we describe these plants as saplings, as opposed to seedlings, given the plants were not in the emergent or established stage and were not producing seeds. For both experiments, 1-year-old saplings were obtained and grown at the University of Idaho's Center for Forest Nursery and Sapling Research facility in Moscow, ID, USA. A total of 54 and 12 saplings were potted in 3.8-L pots with Sungro® Professional Growing mix media beginning of spring 2017 and 2018, respectively, and periodically watered and fertilized. The 12 saplings obtained in 2018 were used in the experiment to evaluate the fire impact on xylem function 1-day post-fire (short-term experiment) and the 54 saplings obtained in 2017 were used to assess the 21-months post-fire treatment impact (long-term experiment). On the day saplings were subjected to the fire treatments, predawn leaf water potential was measured in 6 and 18 saplings for the short- and long-term experiment, respectively, using a pressure chamber (PMS Instruments Co., Albany, OR). Mean predawn leaf water potential (Ψ_{pl}; − MPa) in the short-term

experiment was −0.39 ± 0.04 MPa and − 0.59 ± 0.02 MPa in the long-term experiment.

2.2 | Fire experiments

In fall 2017, the saplings obtained for the long-term experiment were randomly divided into an unburned control (N = 18) and two burned (N = 18 each) treatments. Unburned saplings were not exposed to the fire. The 18 plants per burned treatment were subjected to two fire intensities as described by fire radiative energy (FRE) dosage levels of 0.7 and 1.4 MJ m^{-2}. Mean root collar diameter (RCD) was 1.43 ± 0.30 cm and height were 0.58 ± 0.01 m at the time saplings were subjected to the fire treatments. Following Smith et al. (2013), a linear regression between FRE and fuel load of *P. ponderosa* needles (kg m^{-2}) was calculated using 10 burned pure fuel beds at ~0% moisture content, where FRE = 4.6 × fuel load (kg). FRE data for this regression were obtained via dual-band thermometry using standard methods (Kremens, Smith, & Dickinson, 2010; Smith et al., 2013). To then generate FRE dosage levels of 0.7 and 1.4 MJ m^{-2}, fuel loads of 0.152 and 0.304 kg m^{-2} of oven dried *P. ponderosa* needles were used, respectively. Fuel was oven dried at ~95-105° C for at least 48 hours to obtain moisture content ~0% (Steady et al., 2019).

Following standard methods (Smith et al., 2017; Smith, Arbellay, et al., 2016; Smith, Sparks, et al., 2016; Sparks et al., 2016), saplings were individually placed in a custom cut concrete board, such that the soil surface of the pot was level with the board, and needles were evenly spread in a 1 m^2 circular area surrounding the saplings. Fuel beds were ignited using ~2 g of ethanol on the edge of the circular area (see Steady et al., 2019 for further details). Saplings' bark surface mean temperature after plants were subjected at 0.7 and 1.4 MJ m^{-2} was 32.5 ± 4°C and 53.6 ± 6°C, respectively. Although we did not quantify the percentage of foliage scorched and consumed, saplings burned at 1.4 MJ m^{-2} appeared to have much more foliage scorched/consumed than saplings exposed to 0.7 MJ m^{-2}. After each fire treatment, all plants were transported and kept in the greenhouse at the forest nursery facility for 17 months where they were watered at least twice a week. Then saplings were moved outside in April and irrigated until saplings were harvested for this experiment. Because all plants exposed to the 1.4 MJ m^{-2} dosage were dead at 17 months post-fire, we only used unburned and burned saplings exposed to 0.7 MJ m^{-2} in the long-term experiment.

The 12 saplings obtained in 2018 for the short-term experiment were divided into two fire treatments: an unburned (N = 6) and burned (N = 6) with a lethal fire intensity of 1.4 MJ m^{-2}. Saplings were subjected to the fire treatment during fall 2018 and mean RCD and height were 1.46 ± 0.15 cm and 0.49 ± 0.01 m, respectively, at the time saplings were subjected to the fire treatments. Saplings were burnt following the same procedure as described above. After exposure to the fire, all saplings were transported to the laboratory at the University of Idaho to evaluate the short-term fire impact on sapling xylem. RCD and height average of saplings in both experiments were similar (p > .05) at the time they were subjected to the fire treatment.

2.3 | Stem hydraulics

In the laboratory, the unburned and burned saplings used to assess the short-term impact on xylem were watered and bagged with a black plastic bag overnight. Ψ_{pl} was measured in all saplings the next morning. Because most of the saplings' foliage was fire scorched, we selected the least damaged needles. We recognize that even partially damaged needles may have had slightly altered water potentials (e.g., potential osmotic effects due to cell death). Saplings were then cut at the base of the stem and submerged in a perfusion solution containing 0.02 M KCl and 0.012 M HCl. Foliage was removed under the perfusion solution. The segment of the main stem selected to assess hydraulic conductivity was determined based on a companion fire experiment conducted with saplings of *Populus tremuloides*, *Quercus macrocarpa* and *Pinus monticola*. Specifically, a total 18 plants were burned at 1.4 MJ m^{-2} and immediately after the fire, the highest temperature at the bark surface was measured with an infrared thermometer (Etekcity Co, Anahein, CA) and marked in the sapling stem. Then we measured the height from the pot soil surface to the highest temperature at the bark surface. The bark surface temperature ranged between 33.2 and 77°C and mean height where the maximum temperature occurred at the saplings' bark surface was 9.16 ± 0.68 cm above the soil surface of the pot. To cut the stem segments, we measured 9 cm from pot soil surface, marked that point, and cut the sapling at the base of the stem. Stem segments of approximately 30 cm long were submerged in water and the distal ends were re-cut under water until approximately 14 cm long. All the stems used to measure hydraulic conductivity and vulnerability included the part where the highest temperature at the bark surface occurred. A fresh razor blade was used to cut the distal ends in order to remove any potential emboli caused during the stem segment sampling. To perform the hydraulic measurements, approximately 2 cm of the bark was removed in each distal end of the stem segments.

From the 54 saplings in the long-term experiment, a total of 10 saplings (five unburned and five burned at 0.7 MJ m^{-2}) were randomly chosen to evaluate the long-term impacts on stem hydraulics. In the morning before saplings were harvested Ψ_{pl} was measured in all five unburned (−0.38 ± 0.07 MPa) and five burned (−0.37 ± 0.04 MPa) saplings. Stem segments of ~30 cm from the top of the pot soil were cut, wrapped in a wet paper towel and placed inside an airtight bag and immediately transported to the laboratory. Stem segments were debarked and submerged in the perfusion solution. If the stem had a fire scar formed due to the heat-induced death of cambial cells at temperatures of 60°C or higher (Dickinson & Johnson, 2004), it was included in the stem segment, otherwise we followed the same procedure previously described. In both experiments stem hydraulic measurements were performed in the main stem of the saplings.

After stem segments were re-cut under the perfusion solution, native xylem hydraulic conductivity (k_n; kg s^{-1} m^{-1} MPa^{-1}) was measured using a degassed perfusion solution. To measure stem hydraulic conductivity, we followed the standard method described in Sperry, Donnelly, and Tyree (1988). After measuring k_n, stems were placed in

a vacuum chamber with perfusion solution overnight at ~4°C to remove all xylem emboli. The next morning samples were placed in a container with the perfusion solution at room temperature and left for about 1 h to thermally equilibrate. After equilibration, both stem ends were recut under the perfusion solution and maximum xylem hydraulic conductivity (k_{max}) was measured. All conductivity measurements were corrected for the length of each stem segment and cross-sectional area and native percentage loss of xylem conductivity (nPLC) was calculated using the following equation:

$$nPLC = 100 * [1 - (k_n/k_{max})] \quad (1)$$

After k_{max} was measured, the stems were used to construct vulnerability curves using the centrifugation technique (Alder, Pockman, Sperry, & Nuismer, 1997; Cochard et al., 2013). Stem segments were spun in a centrifuge to induce negative pressures of −0.5 and −1 to −4 (in increments of −1 MPa) in the xylem. After being spun at each pressure, stems were submerged in the perfusion solution and the stem ends were recut. Xylem conductivity (k') was measured at each applied pressure and corrected for the length of each stem and the cross-sectional area. At each given applied pressure, we calculated percentage loss of stem hydraulic conductivity (PLC) using the following equation:

$$PLC = 100 * [1 - (k'/k_{max})] \quad (2)$$

If k' is greater than k_{max} the calculated PLC will be negative. Negative PLC values have been reported, particularly in *P. ponderosa* (Sapes et al., 2019).

2.4 | Xylem microscopy

Sections of ~5 cm long were cut from each stem used to measure hydraulic conductivity in both experiments. Sections were placed in a solution of 1:1:1 of glycerol, ethanol and deionized water (Bär et al., 2018) until being processed. Stem cross sections of 40 μm thickness were cut with a microtome (America Optical Company, Buffalo, NY), stained with 6% safranin solution for 2 min, and washed with distilled water and ethanol until excess safranin was removed. Xylem water conduits, that is, tracheids, were examined for physical cell wall deformation using an Olympus BX51 confocal microscope equipped with an Olympus DP70 digital camera. In the long-term experiment, xylem anatomy analysis was conducted in the ring that was potentially exposed to the heat, that here we call pre-fire xylem, and the new xylem growth or traumatic xylem in the vicinity of the fire scar. Cross-sections with fire scars were stained with safranin and alcian blue to better differentiate between tracheids and parenchyma in the post-fire xylem near the fire scar.

2.5 | Statistical analyses

Statistical analyses were performed using R version 3.6.0 (R Core Team, 2017). nPLC, k_{max} and RCD were tested for normality and homogeneity using Shapiro–Wilk and Levene's test. We performed a *t*-test or Wilcoxon test to determine whether unburned and burned nPLC and k_{max} were significantly different. In the long-term experiment, we excluded one point, based on Cook's distance outlier test, in the unburned treatment due to measurement error ($N = 4$). A *t*-test was also conducted to confirm that saplings had similar RCD and height at the time they were subjected to the fire in the short- and long-term experiment. Means and ± SE were reported for Ψ_{leaf}, nPLC, k_{max}, RCD and height. In both experiments, fitplc package in R (Duursma & Choat, 2017) was used to fit the hydraulic vulnerability curves and estimate the xylem water potential (P_x; x = PLC) needed to cause 12 (P_{12}), 25 (P_{25}), 50 (P_{50}) and 88 (P_{88}) PLC in each treatment. 95% Confidence intervals were used to compare unburned and burned P_{12}, P_{25}, P_{50} and P_{88} to determine if saplings exposed to fire were more vulnerable to cavitation.

3 | RESULTS

3.1 | Stem hydraulics

In the short-term experiment, k_{max} was not significantly different (*t*-test, $p = .06$) in burned (0.33 ± 0.03 kg s^{-1} m^{-1} MPa^{-1}) versus unburned plants (0.25 ± 0.03 kg s^{-1} m^{-1} MPa^{-1}). Mean nPLC also did not differ significantly (Wilcoxon, $p = .69$) in unburned (10.81 ± 5.38%) and burned (7.17 ± 3.03%) saplings (Figure 1a). In addition, burned saplings 1 day after the fire were not more vulnerable to cavitation than unburned plants (Figure 2a). Unburned and burned 95% confidence intervals of each P_{12}, P_{25}, P_{50} and P_{88} overlapped (Table 1).

Similar to the results found in the short-term experiment, k_{max} was not significantly different in the long-term experiment (*t*-test, $p = .52$) in unburned (0.50 ± 0.09 kg s^{-1} m^{-1} MPa^{-1}) and burned plants (0.43 ± 0.07 kg s^{-1} m^{-1} MPa^{-1}). Mean nPLC also did not differ (*t*-test, $p = .51$) between unburned (0.56 ± 1.38%) and burned (−4.62 ± 1.13%) treatments (Figure 1b). However, plants exposed to fire were more vulnerable to embolism than plants not subjected to fire (Figure 2b). Xylem pressures causing 12, 25 and 50% loss of hydraulic conductivity were less negative than in unburned plants (Table 1).

3.2 | Xylem microscopy

In both experiments, no visible damage was observed in the xylem of burned saplings (Figure 3). Burned saplings' xylem conduits did not show any discernable cell wall damage and their appearance was similar to unburned saplings in both experiments. Three of the five sapling stems evaluated 21-months post-fire had vascular cambium damage and had formed a fire scar. A dark brownish colouring was observed in the pre-fire xylem where the fire scar was formed (Figure 4a, Figure S1). We observed irregular xylem tissue formation in the new xylem growth formed in the area of the fire scar (Figure 4b). A more
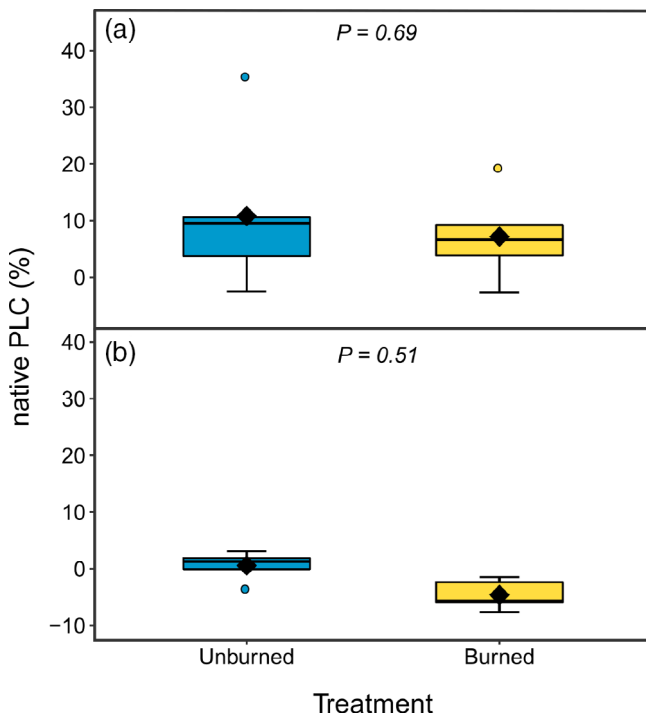
FIGURE 1 Native percentage loss of hydraulic conductivity (*n*PLC) in unburned and burned *Pinus ponderosa* (a) 1-day and (b) 21 months post-fire. Diamond point indicates mean values. Box plots show the median (horizontal line), first and third quartile (box edges), 1.5 × interquartile (whiskers), and outliers (points) [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 2 Percentage loss of stem hydraulic conductivity in *Pinus ponderosa* saplings (a) 1-day and (b) 21-months post-fire. Filled circles indicate the value of hydraulic conductivity measured in each stem at each xylem pressure. Sample sizes are six in experiment 1 (a) and five in experiment 2 (b) for each treatment [Colour figure can be viewed at wileyonlinelibrary.com]

detailed analysis of the new xylem formed in the healing tissue showed a formation of traumatic xylem composed of irregular shaped tracheid and parenchymatous cells (Figure 4c,d, Figure S2). In one stem, the xylem adjacent to the fire scar that formed after the fire showed regular tracheids but with deformed cell walls (Figure S3).

4 | DISCUSSION

A previous study conducted in the field with mature trees exposed to a non-lethal fire intensity (i.e., trees survived) showed that *n*PLC in conifers and deciduous trees was not affected in branches damaged during fire (Bär et al., 2018). We know of no studies to date that have investigated the short-term response of hydraulic conductivity in plants exposed to actual fires at a lethal intensity. However, similar to Bär et al. (2018), we found that *n*PLC in *P. ponderosa* saplings was not affected by fire. Although *n*PLC was not affected by a lethal fire intensity one-day post-fire in our experiment, our data suggest that if an increase in *n*PLC during the fire through the mechanism previously described in Kavanagh et al. (2010) and tested in West et al. (2016) did occur during our fire experiments, saplings were able to repair the hydraulic pathway overnight (Nardini, Gullo, & Salleo, 2011; Tyree, Salleo, Nardini, Gullo, & Mosca, 1999). In addition, since the saplings were rewatered after exposure to the fire this could have potentially favoured the refilling of xylem conduits. However, this is unlikely
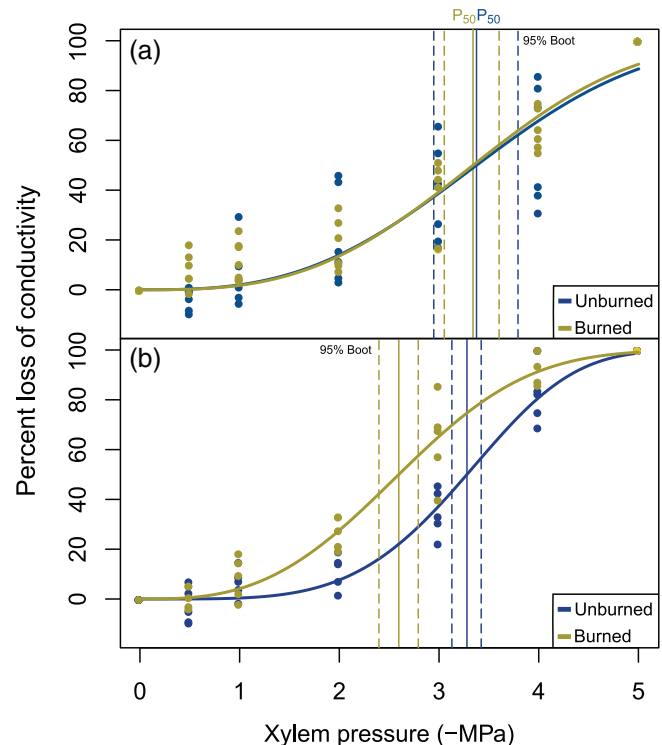
because all saplings were well watered before the fire treatment. Our data suggest that sapling post-fire mortality is not primarily driven by impairment of water transport.

Furthermore, an open question that remains is what extent of embolized xylem is necessary to cause tree mortality? A recent study has shown that a large proportion of the xylem conduits have to be embolized to lead to conifer sapling mortality (Hammond et al., 2019). For instance, at least 80% PLC was necessary to cause mortality in *Pinus taeda* and this PLC was reflected in the amount of functional and non-functional xylem (Hammond et al., 2019). If a similar proportion of xylem has to be embolized or damaged in plants exposed to fire to cause mortality through hydraulic failure, our data suggest that the fires have to be more intense and/or of longer duration than what was used in our experiments. Furthermore, if such a catastrophic embolism formation happened during the fire, we would expect saplings to die rapidly after the fire. Although we did not evaluate time to mortality in this study, we have observed that similarly sized *P. ponderosa* saplings burned at lethal doses generally die between 20 and 35 days post-fire (Steady et al., 2019), which is similar to observations of sapling mortality in other conifer species exposed to lethal fire doses (Smith et al., 2017).
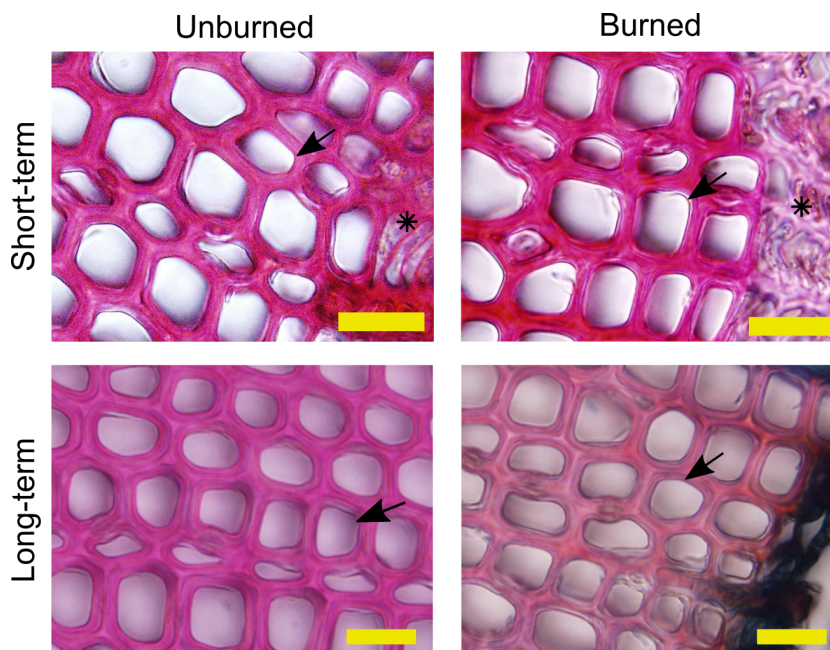
Given that we did not find conduit cell wall deformation in saplings exposed to lethal fire intensity (Figure 3 short-term/burned) other physiological mechanisms may be responsible for explaining

TABLE 1 Predawn water potential resulting in 12, 25, 50, 88% loss of stem conductivity (P_{12}, P_{25}, P_{50}, P_{88}; MPa) in *Pinus ponderosa* saplings 1-day (short-term) and 21-months (long-term) post-fire

Experiment	Water potential	Treatments	
		Unburned	**Burned**
Short-term	P_{12}	−1.88 (−1.33, −2.57)	−1.91 (−1.42, −2.39)
	P_{25}	−2.49 (−1.99, −3.09)	−2.50 (−2.05, −2.90)
	P_{50}	−3.37 (−2.97, −3.81)	−3.34 (−3.04, −3.58)
	P_{88}	−4.95 (−4.41, NA)	−4.82 (−4.55, NA)
Long-term	P_{12}	−2.23 (−1.95, −2.53)	−1.46 (−1.25, −1.69)*
	P_{25}	−2.68 (−2.46, −2.90)	−1.92 (−1.72, −2.16)*
	P_{50}	−3.28 (−3.11, −3.42)	−2.60 (−2.38, −2.81)*
	P_{88}	−4.23 (−3.93, −4.51)	−3.80 (−3.36, −4.12)

Note: Reported values are means and units are MPa. 95% Confidence intervals are given between parentheses. Significant differences between unburned and burned means are indicated with asterisks. Upper Confidence intervals for P_{88} were not available when these values fell outside of the data range.

FIGURE 3 Stem xylem water conduits in unburned and burned *Pinus ponderosa* saplings 1-day (short-term) and 21-months (long-term) post-fire. Asterisk indicates the phloem tissue and arrows the xylem conduits. The picture in the lower row in the burned treatment shows the xylem conduits where cambium cells were killed by heat. Bars, 20 μm [Colour figure can be viewed at wileyonlinelibrary.com]

sapling mortality. Furthermore, if xylem conduit deformation did occur, we would expect the phloem and vascular cambium to exhibit heat induced damage because the heat would have to pass through the phloem and vascular cambium to reach the xylem. And if the fire causes high cambial cell mortality, for example 80% or more in *Pinus halepensis* (Ducrey, Duhoux, Huc, & Rigolot, 1996) and *P. ponderosa* (Ryan, 2000), it is likely that the trees will die due to cambial damage. Thus, an alternative mortality mechanism could be associated with damage to the phloem and cambium cells resulting in dysfunction in carbohydrate transport and/or depletion of carbon reserves (Sevanto, McDowell, Dickman, Pangle, & Pockman, 2014). Prior studies also have shown that similar aged saplings exposed to lethal fire intensities exhibited high foliage damage and impacts to chlorophyll florescence (Smith et al., 2017; Steady et al., 2019), which suggests that the fire damage in meristematic tissues may also be related to sapling mortality.

Decreased resistance to embolism in trees exposed to fire has been attributed to heat-induced damage to the xylem conduits (Bär et al., 2018;Michaletz et al., 2012; West et al., 2016). Our analysis of xylem in both experiments did not provide any evidence of conduit wall deformation (Figure 3). In contrast to our results, a recent study found that xylem wall conduits were deformed in branch segments of *Pinus sylvestris* subjected to water bath at 90°C for 1 h (Bär et al., 2018). Other studies also reported deformation of xylem cell walls in branches of angiosperm species subjected to water bath treatments (Michaletz et al., 2012; West et al., 2016). One explanation is that using a water bath to simulate the effects of fire on trees, and/or the time of exposure used in these experiments results in greater heating of the xylem as compared to fire. Equally, differences could arise from assessing impacts of heat on branch segments as compared to the main plant stem as conducted in our experiment (Johnson et al., 2016; McCulloh, Domec, Johnson, Smith, &
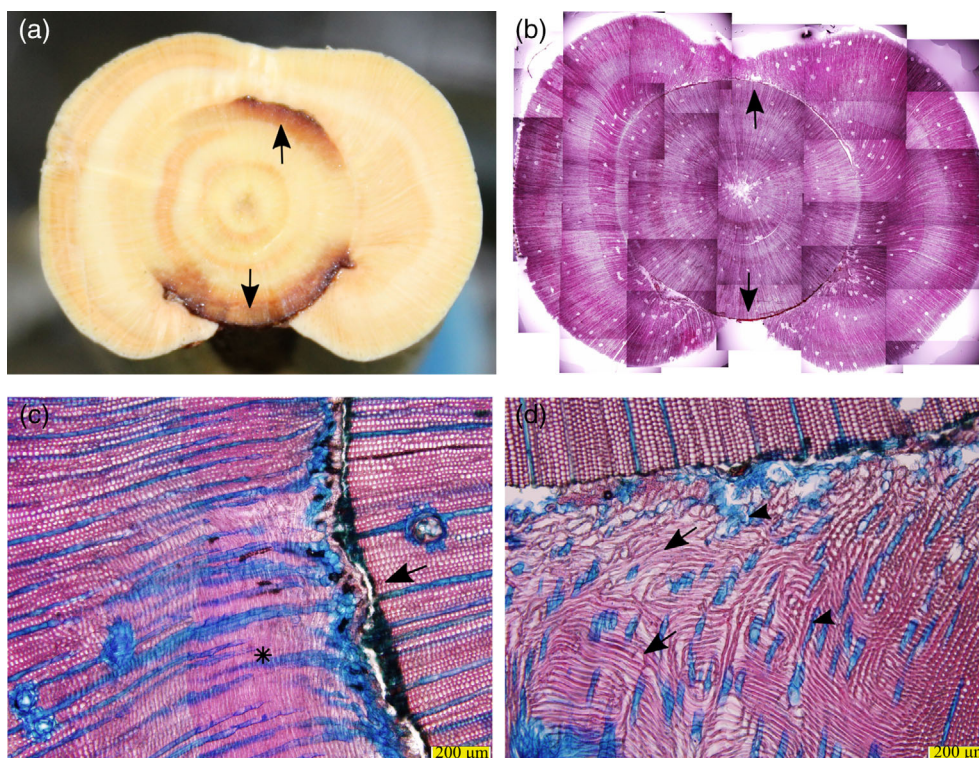
FIGURE 4 Stem cross section of burned *Pinus ponderosa* saplings. (a) Stem cross section show the fire scar (arrows) and dark brownish colouring that indicates the deposition of resin in the fire scar vicinity in the pre-fire xylem. (b) Anatomical cross section of (a) generated with combined images of magnification ×4 of the entire cross section. Arrows indicate where vascular cambium was heat injured. (c) Stem cross section stained with safranin and alcian blue shows the newly traumatic xylem tissue (asterisk) formed after the fire to close the wound. Fire scar is indicated by arrow. (d) Traumatic xylem tissue with irregular shaped tracheid (arrows) and parenchymatous cells (arrowhead). Bars, 200 μm

Meinzer, 2019). Similar to our results, no post-fire conduit damage was observed in stems of *Pinus pinea* during a fire in the field (Battipaglia et al., 2016). Although our data support the hypothesis that at extended time periods after fire, the burned saplings may be more vulnerable to cavitation, they do not support the hypothesis that it is caused by heat-induced deformation of xylem. Furthermore, our results support the hypothesis that the effect of fire on water transport is only observed in the long term. For instance, our hydraulic vulnerability analysis of the saplings burned with a lethal fire intensity and harvested 1-day post-fire showed that stem vulnerability to embolism was not impacted (Figure 2a, Table 1). A similar result was observed in live mature *P. pinea* stems 1-month after a prescribed fire (Battipaglia et al., 2016). However, the vulnerability analyses of living plants 21-months post-fire revealed that saplings exposed to fire were less resistant to embolism. This agrees with a prior study that found similar results in branches of *P. sylvestris* 1 year after a forest fire (Bär et al., 2018).

A potential explanation for the post-fire increase in vulnerability to cavitation observed in the long-term experiment is the development of traumatic xylem, that is, new xylem growth, formed in the vicinity of the fire scar. Similar to our results, hydraulic conductivity was not affected in stems of *P. pinea* 1-month after a prescribed fire (Battipaglia et al., 2016) but it was affected in branches of *P. sylvestris* 1-year after a forest fire (Bär et al., 2018). According to other previous studies, xylem conduit deformation is expected in the xylem conduits present during the fire (Bär et al., 2018; Michaletz et al., 2012; West et al., 2016) not in the xylem formed post-fire. Our anatomical analysis of the fire wound xylem showed that the newly formed xylem at the wound edges was disorganized and composed of irregularly

shaped tracheid and abundant parenchymatous cells (Figure 4c,d). The irregularity of the traumatic xylem can be observed in the stem cross-sections of previous studies with mature *P. halepensis* (Micco, Zalloni, Balzano, & Battipaglia, 2013) and *P. ponderosa* (Smith, Arbellay, et al., 2016; Smith, Sparks, et al., 2016) in the vicinity of fire scars. Smaller conduits adjacent to the fire scar were also reported in the new xylem formed after a fire in different conifers (Arbellay, Stoffel, Sutherland, Smith, & Falk, 2014). Other studies with conifers also found irregularly shaped tracheids in the traumatic xylem tissue (Chano, López, Pita, Collada, & Soto, 2015; Kuroda & Shimaji, 1984; Zajączkowska, 2014). Although our research was conducted with the main stem of saplings whilst previous studies used branches (Bär et al., 2018; Michaletz et al., 2012) and stems of mature trees (Battipaglia et al., 2016), we expect mature trees to show similar new irregular xylem formed if the tree is injured by fire. Thus, mature trees may also have decreased vulnerability to drought-induced embolism. The traumatic xylem observed in this study (Figure S4) was restricted to short distances from the fire scar and it is likely the vulnerability to embolism associated with traumatic xylem may be overcome with time. It is also important to note that in Bär et al. (2018), the decrease in resistance to cavitation was observed in damaged compared with undamaged branches from the same individual tree and not from using an unburned control. It is likely that the "undamaged" branches were still exposed to heat during the forest fire, but the amount of heat that reached those branches was not enough to cause cambial cell damage. Therefore, given the lack of evidence in sapling xylem conduit wall deformation in this study, we suggest that the irregular traumatic xylem tissue formed in the vicinity of the fire scar contributes to increased vulnerability to drought-induced embolism.

We observed a small but not significant k_{max} decrease in burned plants 21-months post-fire. Because we did not observe any physical damage to the tracheid cell walls (Figure 3 burn/long-term) this small difference in stem k_{max} may be related to the deposition of resin in the xylem. Although we did not evaluate the impregnation of xylem conduits with resin in this study, we observed a dark colouration in the pre-fire xylem around the area where the wound was formed (Figure 4a, Figure S1). We also observed that the pre-fire xylem in the vicinity of the fire scar was not conducting water (Figure S5). Because we did not observe conduit deformation it is possible that clogging of the xylem conduits/pits was responsible for the non-functioning pre-fire xylem near the fire scar. Clogging of the xylem conduits and/or pits can possibly occur through the rupture of resin canals. The resin canal is a cavity surrounded by epithelial cells that are responsible for the resin production and excretion (Panshin & Zeeuw, 1980). Because the resin is under pressure inside of the resin canal, if the epithelial cells rupture the resin is forced to flow into the xylem (Hillis, 1987; Loewus & Runeckles, 1977) and can potentially clog the conduits and prevent water flow. It is also possible that there was increased pressure in the resin canals due to enhanced resin production in response to wounding (Hood & Sala, 2015; Lombardero, Ayres, & Ayres, 2006) which could potentially increase the chance of resin canal rupture. However, studies evaluating the resin blockage of water in the pre-fire xylem after fires are needed.

Our findings provide considerable improvements in the understanding of both the short- and long-term hydraulic responses in conifer saplings exposed to fire. The lack of substantial impacts on water conductivity (nPLC) after the fire, particularly in saplings subjected to a lethal fire intensity, suggests that hydraulic failure is not the main physiological driver of mortality in the near-term for conifer saplings exposed to fire. We acknowledge that non-conifer species may respond differently and that the impact of fire on the main stems of saplings may be different than effects of fire on the trunk and branches of mature trees. However, we contend that research using lethal fire intensities from actual fires is needed to definitively confirm past studies using non-fire proxies of heat. We postulate that it is more likely that other physiological mechanisms, such as carbon depletion or destruction of meristematic tissues may be the primary mechanism for fire-induced tree mortality. Although fire did impact the hydraulics of the surviving saplings, the increase in vulnerability to drought-induced embolism was not caused by thermal softening of conduits cell wall as previous studies suggested. Therefore, we suggest that increases in vulnerability to cavitation can occur because of the new irregular xylem growth and the pre-fire xylem dysfunction caused by clogging of xylem cells with resin in the vicinity of fire scars. The decrease in vulnerability caused by fire in the newly grown xylem will likely have a significant impact on post-fire sapling mortality for several years post-fire and therefore research should focus on incorporating these and other post-fire dynamics into ecosystem modelling systems.

CONFLICT OF INTEREST
The authors declare no potential conflict of interest.

AUTHOR CONTRIBUTIONS
R.P.F., A.M.S.S. and D.M.J designed the research. R.P.F. performed data collection and analyses. R.P.F., A.M.S.S., H.D.A., C.A.K. and D.M.J interpreted the data and prepared the manuscript.

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