Research

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Death from hunger or thirst? Phloem death, rather than xylem hydraulic failure, as a driver of fire-induced conifer mortality

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Summary

Disruption of photosynthesis and carbon transport due to damage to the tree crown and stem cambial cells, respectively, can cause tree mortality. It has recently been proposed that fire-induced dysfunction of xylem plays an important role in tree mortality. Here, we simultaneously tested the impact of a lethal fire dose on nonstructural carbohydrates (NSCs) and xylem hydraulics in *Pinus ponderosa* saplings.

Saplings were burned with a known lethal fire dose. Nonstructural carbohydrates were assessed in needles, main stems, roots and whole plants, and xylem hydraulic conductivity was measured in the main stems up to 29 d postfire.

Photosynthesis and whole plant NSCs declined postfire. Additionally, all burned saplings showed 100% phloem/cambium necrosis, and roots of burned saplings had reduced NSCs compared to unburned and defoliated saplings. We further show that, contrary to patterns observed with NSCs, water transport was unchanged by fire and there was no evidence of xylem deformation in saplings that experienced a lethal dose of heat from fire.

We conclude that phloem and cambium mortality, and not hydraulic failure, were probably the causes of death in these saplings. These findings advance our understanding of the physiological response to fire-induced injuries in conifer trees.

Introduction

Millions of hectares of forest are burned every year by wildfires (Van Lierop *et al.*, 2015; Artés *et al.*, 2019), leaving many trees with injuries that can lead to tree death. Disruption of photosynthesis and carbon transport via phloem caused by damage to the crown (buds and leaves) and stem cambial cells, respectively, are well known fire injuries that have been proposed to lead to tree mortality (Ryan, 2000; Hood *et al.*, 2018; O'Brien *et al.*, 2018; Bär *et al.*, 2019). It has also been widely proposed that fire may potentially affect tree water transport after exposure to heat. Previous studies concluded that fire or fire proxies resulted in damage to the water conduit cell walls and induced formation of air bubbles (Michaletz *et al.*, 2012; West *et al.*, 2016; Bär *et al.*, 2018), increased water tension in the xylem (Kavanagh *et al.*, 2010) and increased the vulnerability to drought by formation of new xylem that is more vulnerable to embolism in the vicinity of fire scars (Partelli-Feltrin *et al.*, 2021). Although cessation of photosynthesis and impaired carbon transport have been long proposed as primary causes of postfire tree mortality (Levitt, 1972), most studies since 2000 have assessed plant morphological measures of tree injury (e.g. crown scorch, bark char) and the correlation with postfire tree mortality (Ryan, 2000; Dickinson *et al.*, 2004; Hood & Lutes, 2017). The impacts on tree physiology are predominately only implicit in these studies, whereas studies that have assessed the postfire physiological responses of whole plants that ultimately die are rare (Varner *et al.*, 2021). Indeed, the impact of fires on plant physiological processes is poorly understood but is critically needed to better understand how individual plants and entire ecosystems will respond to novel and changing climate conditions (Smith *et al.*, 2016). The majority of the research conducted with saplings has aimed to use smaller trees to understand the impact of natural disturbances, such as drought and fire, on mature trees (McDowell *et al.*, 2013). However, it is important to point out that forest health and regeneration depend on sapling responses to different disturbances and competition. Considering future drier conditions (IPCC, 2021) favoring more frequent occurrence of fires and a need for more controlled fire to prevent catastrophic wildfires (Vaillant *et al.*, 2016), understanding the impact of fire on sapling physiology is also critical to maintain forest health and resilience (Smith *et al.*, 2017).

Tree nonstructural carbohydrates (NSCs) can potentially be affected by fire and play an important role in postfire tree survival (Bär *et al.*, 2019). During fire, tree tissues directly related to carbohydrate production (leaves) and transport (phloem) can be damaged (Hood *et al.*, 2018) leaving trees partially or completely reliant on their carbon reserves for recovery. Phloem is the vascular tissue responsible for transport of photosynthates from the leaves to the roots (Zimmermann & Milburn, 1975), and phloem dysfunction, such as through irreparable damage to sieve cells, can disrupt carbohydrate transport (Knoblauch & van Bel, 1998; Knoblauch *et al.*, 2014). Vascular cambium cells, responsible for producing both secondary xylem and phloem, are situated between these tissues (Esau, 1965; Larson, 1994). If cambial cells are killed around the entire circumference of the tree bole (i.e. girdling), trees are not able to regrow new phloem and xylem (Goren *et al.*, 2004). Since cambial cells are surrounded by phloem on the outside (towards the bark), any mortality of cambial cells would be accompanied by mortality in phloem cells. Consequently, the transport of photosynthates from the leaves to the roots would be completely disrupted (Rademacher *et al.*, 2019). Trees can still survive for years after complete cambium and phloem damage (Noel, 1970; Ryan, 2000) using carbohydrates stored in their roots (Mei *et al.*, 2015; Aubrey & Teskey, 2018). However, after depletion of the root's reserves, roots die, terminating water and nutrient transport to the rest of the tree and leading to eventual tree mortality. However, if cambial cells are only partially damaged, the phloem and xylem can be restored from undamaged areas (Słupianek *et al.*, 2021). Trees probably depend, in part, on stored carbohydrates to recover from heat injuries to crown, stem and roots caused during fire. In wildland fires, examples of significant (i.e. $\leq$ 80%) but partial damage to cambium cells are commonplace as highlighted by the formation of fire scars, which can appear drastic, but where several studies have observed no significant long-term reduction to growth in surviving trees (Mitchell *et al.*, 1983; Furnis *et al.*, 2020).

Reductions in carbohydrate reserves can also occur by heat-induced necrosis of the crown foliage. When leaves are damaged during a fire, photosynthesis can be significantly affected (Smith *et al.*, 2017; Sparks *et al.*, 2018; Partelli-Feltrin *et al.*, 2020) and may cause decreases in NSC reserves, particularly when photosynthesis is halted for long periods of time (Li *et al.*, 2018; Weber *et al.*, 2018). Experiments conducted under controlled environments have shown that conifer saplings exposed to high doses of heat from fires had significant decreases in photosynthesis as well as high rates of mortality (Sparks *et al.*, 2016; Smith *et al.*, 2017). Other studies have also shown that the probability of postfire tree mortality increases with an increase in the volume of crown foliage necrosis (Peterson & Ryan, 1986; Cansler *et al.*, 2020). Although these studies evaluated the tree physiological response that was related to carbohydrate production (i.e. photosynthesis), it is known that depletion of NSCs can occur when leaves are damaged or removed, such as has been reported in defoliated trees (Gregory & Wargo, 1986; Anderegg & Callaway, 2012; Wiley *et al.*, 2013). Studies have posited that fire-induced tree mortality may be the result of the reduced transport and depletion of carbohydrates (O'Brien *et al.*, 2010; Smith *et al.*, 2017; Partelli-Feltrin *et al.*, 2020). Other than one previous study that assessed the decline of NSC reserves in roots of *Pinus palustris* postfire (Varner *et al.*, 2009), there is as yet no direct evidence of depletion of NSC reserves in a whole plant exposed to fire.

In this paper, for the first time, we examine the simultaneous impact of fire on NSC pools and water transport in 1.5-yr-old *Pinus ponderosa* saplings exposed to a lethal fire dose. Our objectives were to evaluate the impact of fire on needle, stem, root and whole-plant NSCs (starch and sugars) and on saplings' stem hydraulic conductivity. We hypothesized that saplings exposed to lethal fire have lower NSC content in all organs and at the whole-plant scale compared to plants not exposed to fire, and saplings exposed to fire are more vulnerable to embolism and show a decrease in hydraulic conductivity over time. In addition, we tested the hypothesis that burned saplings would have lower NSC content than defoliated plants (a control for needle loss but no stem heating from fire) due to fire damage caused in sapling stems whereas defoliated plants had only foliage loss.

Materials and Methods

Plant material

Two sets of plants were used to conduct this study. For the first experiment, hereafter named 'Experiment 1', a total of 100 2-yr-old *P. ponderosa* Douglas ex P. Lawson & C. Lawson saplings potted in 3.8 l pots with Sungro® Sunshine Mix #3 (Sungro Horticulture, Agawam, MA, USA) were purchased from Western Forest Systems Inc. (Lewiston, ID, USA) in spring 2018. Saplings were kept in a climate-controlled glasshouse at the University of Idaho with maximum and minimum temperatures of 25°C and 15°C, respectively. Plants were watered every other day and fertilized with 20 : 20 : 20 Technigro® fertilizer (Sungro Horticulture) monthly. Sapling mean root collar diameter (RCD) and mean height (SE) were 1.42 0.03 and 55.0 9.0 cm, respectively, at the time of the fire and defoliation treatments. For 'Experiment 2', an additional 40 *P. ponderosa* saplings with RCD average of 0.90 0.01 cm and height of 0.41 0.09 m were purchased from the same nursery in summer 2020 to evaluate the potential cambium necrosis caused by heat generated during fire treatment. Saplings were kept in the same controlled glasshouse and received the same watering and fertilizer as those in Experiment 1.

Treatments

Fire treatments were conducted under a controlled environment at the University of Idaho Fire Initiative for Research and Education (IFIRE) combustion laboratory, Moscow, Idaho, following established methods (Sparks *et al.*, 2018; Steady *et al.*, 2019; Partelli-Feltrin *et al.*, 2021). Thirty well-watered *P. ponderosa* saplings (15 each for Experiments 1 and 2) were randomly chosen and subjected to a surface fire with an intensity of 1.4 MJ m^{-2}, a known lethal (i.e. 100% probability of mortality)

fire intensity for well-watered *P. ponderosa* saplings of this age and size (Steady *et al.*, 2019; Partelli-Feltrin *et al.*, 2021). All saplings were watered to pot capacity 1 d before the burn. A fuel load of 0.304 kg m^{-2} of oven-dried *P. ponderosa* needles was used as fuel bed (Partelli-Feltrin *et al.*, 2020). Needles were oven dried for 48 h at 105°C following the methodology of Matthews (2010) and kept in the oven until immediately before each burn. A 1 m^2 circular concrete board with an opening in the middle was used to align the top of the soil with the surface fire. Saplings were placed in the center opening and the pot soil was leveled with the top surface of the concrete board (Supporting Information Fig. S1). Any pot material above the soil surface was removed to allow for an obstruction-free transition from the cement board surface to the soil around the sapling. Any gaps between the pot and board were sealed from below to ensure air flow did not affect fire behavior. Dried needles were evenly spread around the saplings in the circular area and ignited using *c.* 2 g of ethanol spread on one-quarter of the circumference edge. Each burn lasted *c.* 5 min from ignition to extinction. After fire exposure, burned plants were returned to the glasshouse and watered.

Exposure of saplings to fire in Experiments 1 and 2 was conducted in July 2018 and August 2020. Fire experiments were conducted at this period due to higher fire risk during this time of the year in the western USA (Westerling *et al.*, 2003). On the same day of the burning in Experiment 1, 15 unburned saplings were randomly chosen and manually defoliated. All of the needles were removed from each sapling. A defoliation of 100% was chosen based on a previous study in which *P. ponderosa* saplings of similar size exposed to the same fire intensity (1.4 MJ m^{-2}) had photosynthesis significantly decreased to approximately zero 1-d postfire and did not show any photosynthetic recovery 27 d after the fire treatment (Partelli-Feltrin *et al.*, 2020). From the remaining saplings in Experiments 1 and 2, respectively, 40 and 18 plants were used as unburned and nondefoliated controls, respectively.

Stem hydraulic conductivity

Native percentage loss of xylem hydraulic conductivity (*n*PLC) was measured in five unburned plants before fire treatment and in five unburned and five burned plants on days 6, 14 and 28 postfire in Experiment 1. In addition, *n*PLC was measured in six unburned plants on the day of the fire but before plants were exposed to the fire (day 0) and in six unburned and six burned plants 6 d postfire in Experiment 2. One day before native hydraulic conductivity (k_n) was measured, all saplings were watered, and plants were randomly chosen from each treatment and transported to the laboratory at the University of Idaho Research Building. Saplings were covered with black plastic bags overnight and the next morning predawn leaf water potential (Ψ_p; MPa) was measured using a pressure chamber (PMS Instruments Co., Albany, OR, USA). The main stem was excised at the RCD of each sapling and segments of *c.* 20 cm in length were cut under deionized water at ambient temperature (*c.* 22°C). About 2 cm of the distal ends of each stem were cut with a sharp razor blade to remove any potential embolism caused when stems were harvested.

Stem xylem hydraulic conductivity (k_s, kg m^{-1} MPa^{-1} s^{-1}) was measured using a Sperry apparatus (Sperry *et al.*, 1988). A filtering flask filled with deionized water was connected to a vacuum pump for 48 h for water degassing. k_n was measured just after stem segments were excised. After k_n was measured, stems were placed in a vacuum chamber with deionized water overnight to clear any air emboli. The following morning, stems were placed in another container with deionized water at ambient temperature, both ends were shaved using a fresh razor blade and maximum hydraulic conductivity (k_{max}) was measured. All hydraulic conductivity was corrected by the length of each stem segment and *n*PLC was calculated using the following equation:

$$nPLC = 100\left[1 \quad \left(\frac{k_n}{k_{max}}\right)\right] \qquad \text{Eqn 1}$$

Photosynthesis and NSC analysis

Predawn (Ψ_p) and midday (Ψ_m) leaf water potential and photosynthesis were measured 2 d before fire and defoliation treatments in Experiment 1 in five unburned plants. After plants were exposed to the treatments, measurements were performed on five plants in the unburned and burned groups on days 6, 13 and 27. Photosynthesis (A; μmol CO_2 m^{-2} s^{-1}) measurements were performed in three needles of each sapling between 09:00 and 11:00 h using a Li-Cor 6400XT device (Li-Cor, Lincoln, NE, USA) with constant photosynthetic flux of 1400 μmol m^{-2} s^{-1} and CO_2 set to 400 ppm. During measurements, average leaf temperature, relative humidity and vapor pressure deficit were 30.5 0.43°C, 43.4 0.65% and 2.56 0.1 kPa, respectively. A and stomatal conductance as a function of time were observed in real time; when stability was reached (i.e. no change in A and the conductance trend for at least 1 min), A was recorded. A fascicle of three needles was maintained inside the cuvette until photosynthesis and conductance were stable. The portion of the needles used to measure A were scanned using a Li-3100C area meter (Li-Cor) to correct for leaf area.

Nonstructural carbohydrate analysis was performed in five saplings randomly chosen from each treatment (unburned, burned and defoliated) on days 7, 15 and 29 postburning and defoliation. One day preburning and defoliation, NSC analysis was performed in five randomly chosen unburned saplings. Total soluble sugars and starch content in needles, stem (bark + wood) and roots were analyzed. Each organ was harvested, weighed, microwaved for 90 s to stop enzymatic activity, placed in a paper bag, oven dried for 2 d at 90°C and stored inside an oven at 30°C until samples were ground. One day before samples were ground, they were placed in an oven at *c.* 60°C overnight and weighed the next day to obtain plant dry mass. Samples were ground in a Wiley Mill (Arthur H. Thomas Type) and sieved to pass a number 60 mesh. The fine powder was placed in a vial and stored in the dark. Nonstructural carbohydrate analysis was conducted in the Environmental Ecology Laboratory at Oklahoma State

University, Stillwater, OK, USA. To determine the sugar and starch content, 25 mg of ground plant material was used following the extraction and enzymatic digestion procedure described in Landhäusser *et al.* (2018). Total sugar and starch content in each organ were calculated by multiplying NSC content by the dry mass of each organ and dividing by whole-plant dry mass. Total NSC content in each organ was calculated as the sum of sugar and starch content in each respective organ and whole plant NSCs were the sum of needle, stem and root NSC content.

Xylem anatomy and cambium/phloem analysis

The potential heat damage caused in the xylem conduit cell walls was investigated in the stems used to measure k in Experiment 1. Three sections of the stem of *c.* 5 cm were cut and cross-sections of 40 μm were cut using a microtome (American Optical Co., Buffalo, NY, USA). Samples were stained with safranin 6% and/or alcian blue. Cross-sections were imaged using a confocal microscope (Olympus BX51; Olympus Corp., Tokyo, Japan) equipped with a digital camera (Olympus DP70). Heat-induced phloem cell necrosis of the stems was determined visually. To assess cambial cell necrosis, in Experiment 2, on days 1 and 6 postfire four unburned and four burned plants on each day were randomly chosen. In previous studies, to verify if conifer saplings were still alive after exposure to fire a scratch test was performed (Steady *et al.*, 2019; Partelli-Feltrin *et al.*, 2020). This test consists of visually verifying the change in phloem coloration. Living plants usually show a greenish color when phloem is alive while dead phloem has a brownish color (Fig. S2). Here, to assess phloem viability, we cut the sapling at the root collar and 1 cm increment sections were made in the main stem to observe changes in phloem color.

Statistical analysis

Statistical analysis was conducted using R v.3.5.3 (R Core Team, 2019). We used a linear model to compare the effect of treatment on Ψ_p, Ψ_m, k_{max}, *n*PLC and NSCs. Pairwise comparisons were conducted to evaluate the interacting effect of time and treatment on each response variable, using the R package EMMEANS (Lenth *et al.*, 2020). Heat-induced damage to needles can cause potential errors in water potential measurement using a pressure chamber. Therefore, on days 13 and 27 we were not able to make Ψ_p and Ψ_m measurements for at least three plants. Thus, those days were not included in the analysis to determine the difference in Ψ_p and Ψ_m. Linear regressions between wet and dry mass of a particular tree organ and treatment were fitted to estimate the dry mass of the plants' organs that were missing (Tables S1, S2). Means SE are reported for all parameters.

Results

Stem hydraulic conductivity

In Experiment 1, mean predawn water potential (Ψ_p) measured before native hydraulic conductivity (k_n) measurements in unburned saplings ranged from −0.25 to −0.34 MPa with no significant difference ($P > 0.05$) among unburned plants over time. Average maximum hydraulic conductivity (k_{max}) ranged from 0.402 to 0.494 kg m^{-1} MPa^{-1} s^{-1} in unburned and from 0.328 to 0.413 kg m^{-1} MPa^{-1} s^{-1} in burned saplings over time. Unburned and burned sapling k_{max} did not differ significantly ($P > 0.05$) on each day postfire (Fig. 1), nor when k_{max} was compared over time within each treatment. Average *n*PLC ranged from 8.0% to 16.7% in unburned and from 2.9% to 23.9% in burned plants. Over time, *n*PLC differed between days 14 and 28 postfire in the burned treatment ($P = 0.04$), but no significant difference ($P > 0.05$) between treatments (Fig. 1) on each sampling day was found.

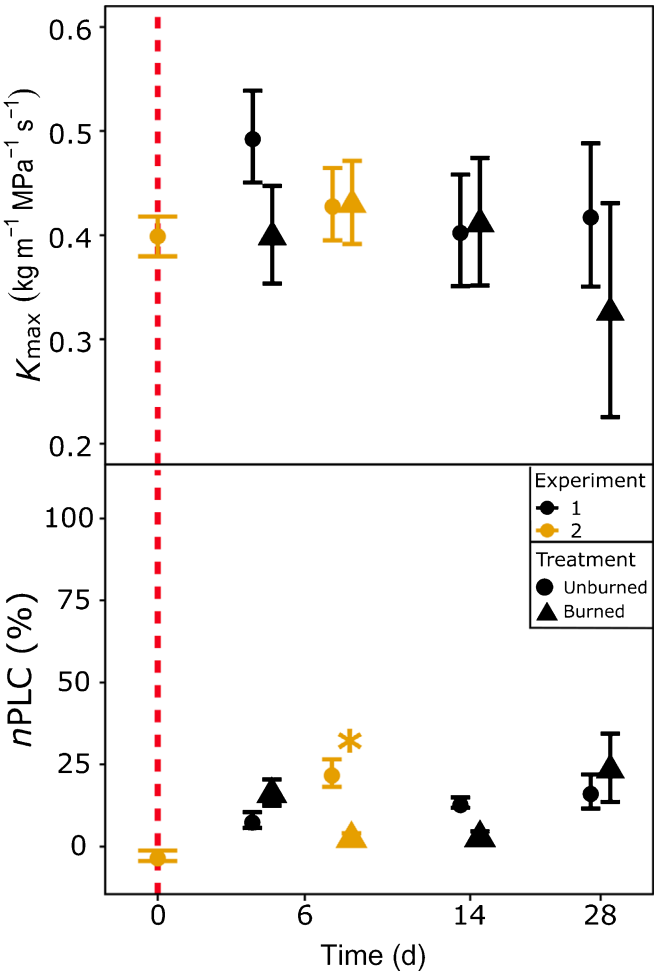

Fig. 1 Maximum hydraulic conductivity (k_{max}) and native percentage loss of hydraulic conductivity (*n*PLC) in stems of *Pinus ponderosa* saplings from 0 to 28 d relative to the fire day (indicated by dashed red vertical line) in Experiments 1 and 2. A pairwise *t*-test was used to determine significant differences ($P < 0.05$) between treatments on the same day. Significant differences are indicated by asterisks. Error bars are SE.

In the second experiment, mean Ψ_p on day 0 (the day saplings were subjected to fire) in unburned plants was −0.26 0.04 MPa. On day 6 postfire, Ψ_p (−0.22 0.02 MPa) and k_{max} (0.430 0.03 kg m^{-1} MPa^{-1} s^{-1}) in unburned plants were similar to those in burned plants (−0.32 0.1 MPa and 0.431 0.04 kg m^{-1} MPa^{-1} s^{-1}). Although *n*PLC differed

significantly ($P = 0.0002$) between unburned and burned plants at 6 d postfire, unburned plants had higher *n*PLC (22.39 4.18%) compared to burned saplings (2.83 1.19%) (Fig. 1).

Photosynthesis and NSCs

Photosynthesis (A) in burned saplings was reduced significantly for all days postfire when compared with unburned plants on the same day. During the period of Experiment 1, burned plant A ranged from 0.9 to 1.8 μmol CO_2 m^{-2} s^{-1} from day 6 to day 27 postfire and A did not recover to prefire values (11.08 2.27 μmol CO_2 m^{-2} s^{-1}; Fig. 2). Ψ_p and Ψ_m were significantly less negative ($P < 0.05$) in burned saplings when compared to unburned saplings 6 d postfire (Fig. 2).

Our NSC analysis showed that total NSCs (sugar + starch) in needles of burned plants were lower but not significantly different than in unburned plants for all days after saplings were exposed to fire (Fig. 3). Stem NSCs in burned plants were 58% lower ($P< 0.05$) 7 and 15 d postfire than NSCs in stems of unburned plants. No significant difference was found between unburned, burned and defoliated stem NSCs at 29 d postfire. Root NSCs of burned plants were significantly lower ($P < 0.05$) than in unburned and defoliated plants on all days postfire. Roots NSCs in burned plants were 37–64% and 36–44% lower than unburned and defoliated plants, respectively, from 7 to 29 d posttreatments. Defoliated plants had 36% lower root NSCs than unburned plants at 29 d post-defoliation (P-value = 0.014). Over time, root NSC content increased about 47% in unburned plants from 1 d prefire to 29 d after, but this change was only significant between 1 d prefire and 29 d postfire ($P = 0.03$). Root NSC content in burned and defoliated plants was similar over time.

Burned plants showed a reduction of 26%, 35% and 32% ($P < 0.05$) in whole-plant NSC content compared to unburned plants at 7, 15 and 29 d postfire, respectively (Fig. 4). Over time, whole-plant NSCs increased in unburned plants with greater NSC content at 29 d posttreatments (13.40 0.26%; $P = 0.009$) compared to pretreatments (7.95 1.38%). Mean total NSCs of burned plants were similar ($P > 0.05$) over time. When leaves were not included in the analysis (stem + root), burned plants had 54% and 49% ($P < 0.05$) lower whole-plant NSC content compared to unburned and 45% ($P < 0.05$) lower than defoliated plants at 7 and 15 d postfire, respectively (Fig. 4). At 29 d postfire, mean total NSC content was significantly lower in burned plants (2.46 0.37%; $P = 0.001$) compared to unburned plants (5.13 0.43%), but similar to defoliated plants (3.91 0.37%). Mean total NSC content in unburned and defoliated plants was similar on all days posttreatment (Fig. 4).

Xylem anatomy and cambium/phloem damage

Our anatomical analysis did not show any potential heat-induced physical damage to the tracheid cells walls in Experiment 1 with no visual difference observed between unburned and burned tracheid cell walls (Fig. 5a,b). The change in phloem/cambium from greenish in unburned plants to a brown coloration was observed in the entire circumference of all burned plant stems in Experiments 1 and 2 (Figs 5c–f, S3). Thus, we concluded that 100% of the cambium and phloem were damaged in these saplings (i.e. was girdled). We also observed an effect of fire-induced heat on the xylem in the stems used to measure water

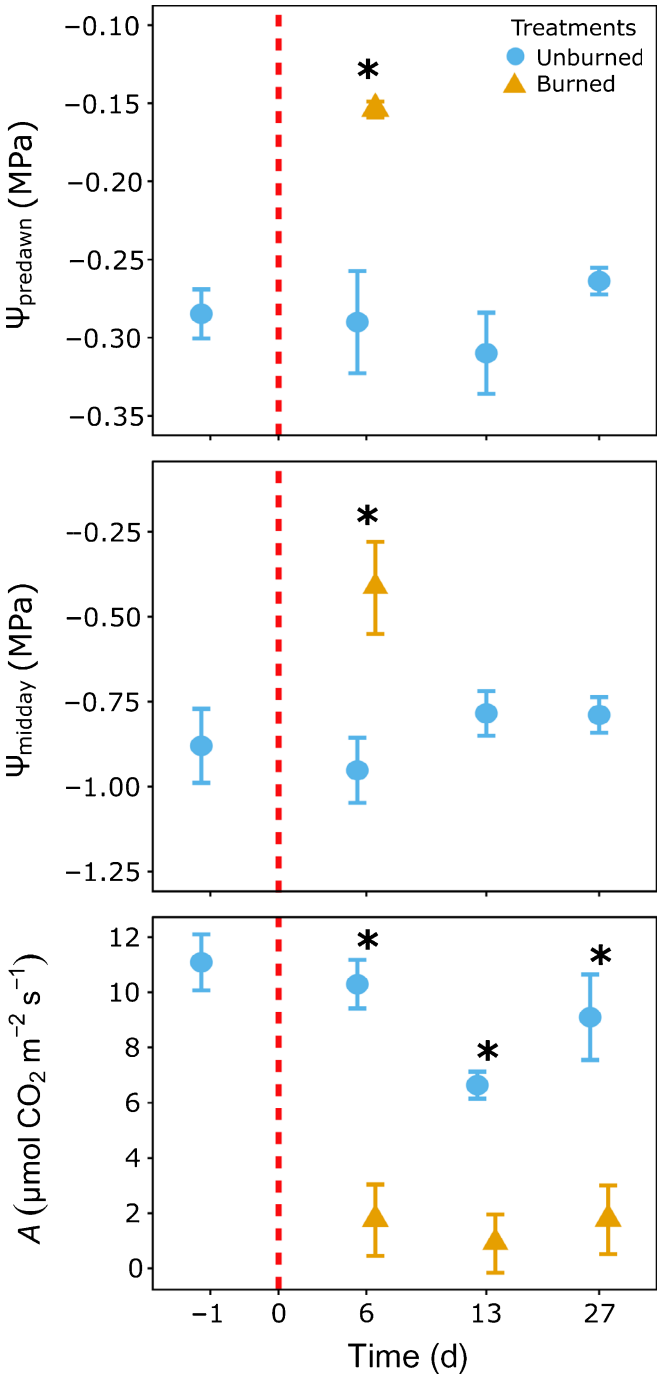

Fig. 2 Mean predawn and midday leaf water potential (Ψ) and photosynthesis (A) in *Pinus ponderosa* saplings from −1 to 28 d relative to the fire day (indicated by dashed red vertical line). A pairwise t-test with Tukey's method of adjustment was used to determine significant differences ($P < 0.05$) between treatments on the same day. Asterisks indicate significant differences between treatments. Error bars are SE.

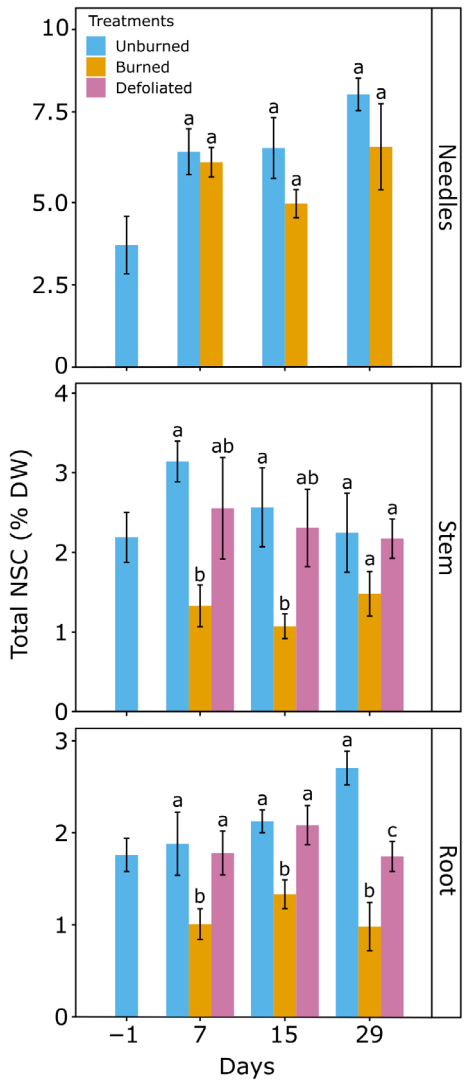

Fig. 3 Mean total nonstructural carbohydrate (NSC) content (%) in needles, stems and roots of *Pinus ponderosa* saplings relative to the fire day. Different bar colors represent the unburned, burned and defoliated treatments. A pairwise *t*-test with Tukey's method of adjustment was used to determine significant differences among unburned, burned and defoliated treatments on the same day. Significant differences among treatments are shown with different letters ($P < 0.05$). Bars are SE.

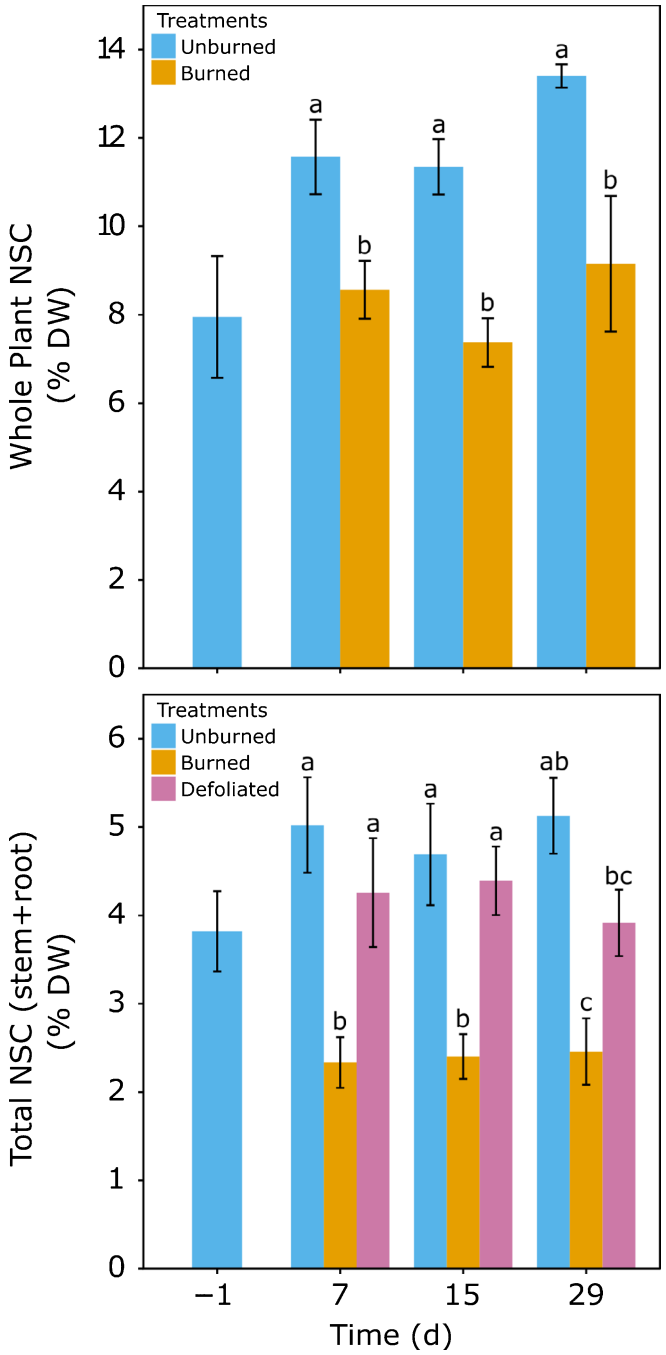

Fig. 4 Mean total nonstructural carbohydrate (NSC) content (%) in whole *Pinus ponderosa* saplings (leaf + stem + root) and stem + root (excluding leaves, to allow for comparison with the defoliated treatment) relative to the fire day. Different bar colors represent the unburned, burned and defoliated treatments. A pairwise *t*-test with Tukey's method of adjustment was used to determine the differences among unburned, burned and defoliated treatments on the same day postfire. Significant differences among treatments are shown with different letters ($P < 0.05$). Bars are SE.

conductivity. This was clearly distinct based on the change in color from light to dark brown on portions of the stem that received heat during fire. For instance, a light brown color was observed in a small portion (stem height closer to the soil surface, Fig. S4) of the stem while the rest of the stem showed a dark coloration.

Discussion

We assessed the impacts of a lethal fire dose on NSCs and stem hydraulic conductivity in *P. ponderosa* saplings over 29 d after exposure to fire. Our results showed that neither the main stem hydraulic conductivity (*n*PLC) nor xylem conduit structure were affected by the lethal fire dose (Figs 1, 5c–f). We found that fire caused a significant decrease in total whole-plant NSCs. Although foliage was injured by fire and photosynthesis was significantly reduced in burned saplings, we did not observe a significant reduction in total NSCs in foliage of burned saplings.

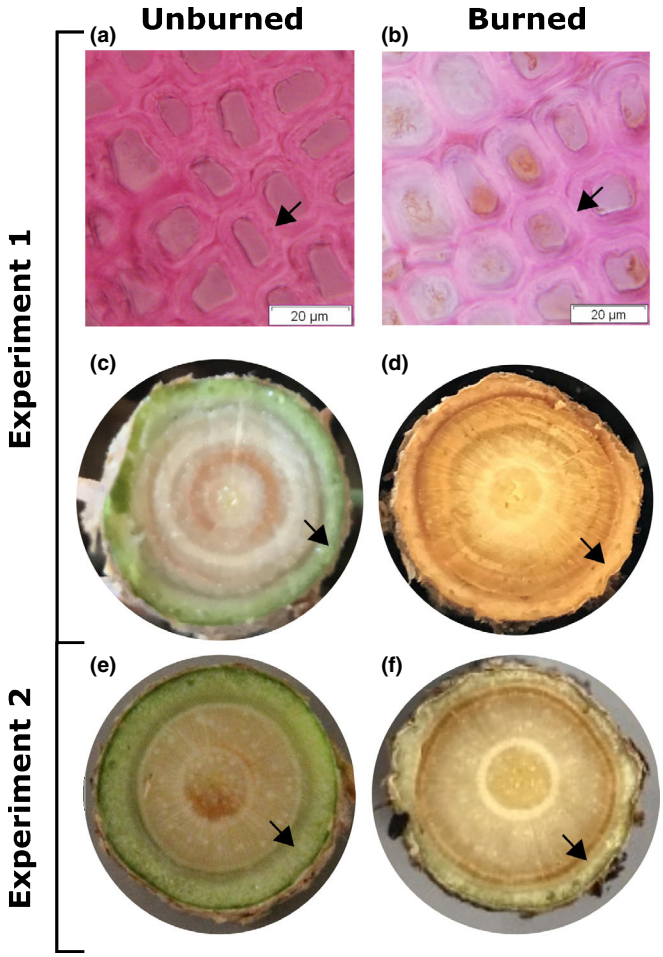

Fig. 5 Phloem and xylem cross-sections of *Pinus ponderosa* saplings exposed to lethal fire intensity. Cross-sections of unburned (a) and burned (b) plants in Experiment 1 show similar nonheat-induced damaged xylem cell walls (arrows). Cross-sections of unburned (c, e) and burned (d, f) plants in Experiments 1 and 2, respectively. Arrows show phloem tissue in unburned plants with a greenish color while in burned plants the arrows show phloem with a brownish coloration around the entire circumference of the sapling stem.

However, total NSCs in stems and roots of burned plants was significantly lower than in unburned plants. Notably, this was driven by lower sugar and starch concentration in these organs of burned plants (Fig. S5). Thus, the NSC depletion in stem and roots contributed the most to reductions in total NSCs in the whole plant. The observed depletions in stem and root NSCs combined with observed phloem and cambium color changes suggest that phloem death had occurred (i.e. inhibited NSC transport) in burned saplings, and the cause of sapling mortality was probably cambial death and/or disruption of carbohydrate transport in the phloem.

Here we provide evidence that NSCs are depleted in *P. ponderosa* saplings after exposure to a lethal fire. We observed a significant reduction in whole burned plant NSCs particularly compared to unburned plants. This reduction was mostly driven by depletion of carbohydrates in stems and roots. Because burned plants suffered 100% cambial cell death, it was expected that depletion of NSCs in roots would occur, consistent with findings that girdled trees have depleted root NSCs (Mei *et al.*, 2015; Aubrey & Teskey, 2018). However, compared to defoliated plants, we found that burned saplings had lower total NSC content. Given that saplings exposed to fire had low rates of photosynthesis and that saplings manually defoliated did not produce new photosynthate (i.e. no photosynthesis), our results suggest that the additional damage caused by fire in the stem contributed to increase the demand of NSCs for recovery and for maintenance of metabolism. In addition, extra demand for NSCs in trees injured by fire can potentially be directed to secondary metabolism, such as resin production (Hermes & Mattson, 1992; Du *et al.*, 2022). Thus, it is possible that plants with larger NSC reserves are more likely to survive as fire can cause injuries in multiple organs and more energy may be required for tree survival. Also, because of the potential higher demand for NSCs to recover from fire injuries, trees that were previously exposed to other disturbances that can impact the NSC pools (Adams *et al.*, 2013; Rosas *et al.*, 2013), such as long periods of antecedent drought or competition, are more likely to die. Although a recent study showed that conifer saplings under drought exposed to fire had higher sapling mortality (Partelli-Feltrin *et al.*, 2021), how fire impacts sapling NSC pools is unknown, particularly when cambial/phloem tissues are only partially damaged. Therefore, more studies assessing the interactions between drought and fire and the impact on physiological mechanisms are needed for a better understanding of how trees and forests will respond to changes in future climates (IPCC, 2021; United Nations Environment Programme, 2022).

Other characteristics previously observed in girdled plants were an increase in NSC accumulation above girdle in stems and foliage and a decrease in photosynthesis due to carbohydrate accumulation (Goren *et al.*, 2004). In the present study, the pattern of NSC accumulation in organs above ground in burned plants was not observed over time. One possible explanation for this is that consumption of carbohydrates for metabolism and repair of fire injuries was potentially greater than production of carbohydrates, which was reduced (Fig. 2) by heat-induced damage to the photosynthetic machinery in needles. This also supports the idea that saplings exposed to fire required higher NSC content when compared to defoliated plants (Fig. 4) to repair the damage caused by fire in the stem.

Plant NSC pools change during the year (Martínez-Vilalta *et al.*, 2016; Furze *et al.*, 2019) and if low NSC reserves contribute to postfire tree mortality, the time of the year and phenological state that plants are experiencing when exposed to fire might increase or decrease the chances of tree mortality. For example, a study with two broadleaf evergreen trees with distinct leaf phenology showed that defoliation at the same period had a significant impact, such as lower NSC content and high mortality rates, in the species that regenerated leaves before defoliation (Chen *et al.*, 2017). It is possible that if saplings were burned when NSC pools were lower (e.g. winter or beginning of spring; Furze *et al.*, 2019), mortality could occur faster. Although plant phenological state coupled with fire behavior can impact the magnitude of heat-induced injuries (Bison *et al.*, 2022), it is still unclear how tree physiological processes will be affected when

plants are exposed to fire in different phenological states. Studies investigating the impacts of fire on plants at different phenological states is extremely important, particularly due to shifts caused by early snowmelt and consequently the greater chances of early fire occurrence (Westerling *et al.*, 2003).

Although we observed differences in NSCs in burned vs unburned plants, sapling hydraulic parameters were not affected by fire. Consistent with previous findings (Partelli-Feltrin *et al.*, 2021), exposure of *P. ponderosa* saplings to a lethal fire dose did not impact *n*PLC in this study. Despite the fact that in Experiment 1 burned plant *n*PLC increased from 3% to 24% between 14 and 28 d after fire, the burned plants did not differ from the unburned plants on those days (Fig. 1). *n*PLC values in our study were similar to those reported in conifer species not under drought stress grown in a controlled environment (Hammond *et al.*, 2019) and mature trees in the field (McCulloh *et al.*, 2011). Moreover, these values did not even approach the critical thresholds of 60–80% observed to result in mortality (Brodribb & Cochard, 2009; Hammond *et al.*, 2019). Thus, the hypothesis that the impacts of fire on xylem function result in sapling mortality was not supported in our study. In addition, the saplings used in this study were short (*c.* 0.5 m), which increased the chances of foliage and bud necrosis. Notre also that saplings of this size lack the thick bark found in mature *Ponderosa* pine trees. Since bark thickness increases with tree age and size (Sonmez *et al.*, 2007; Berrill *et al.*, 2020) and we found no evidence of xylem dysfunction in saplings, which should have the thinnest of bark, we suggest that it is becomes increasingly unlikely that larger tree hydraulics in species with thick bark will be affected by fire. However, the exact age at which bark thickness confers increased fire protection is probably dependent on the tree species and fire behavior (e.g. intensity). For mature tree species with very thin bark (< 1 cm), such as *Populus tremuloides* or *Betula papyrifera*, we acknowledge that damage to the xylem through heat exposure could remain an important process in fire-induced tree mortality.

Studies using water baths have observed heat-deformed conduit cell walls that could potentially increase PLC content (Michaletz *et al.*, 2012; West *et al.*, 2016; Bär *et al.*, 2018). However, our stem anatomical analysis showed that the heat generated by the lethal fire dose did not deform the tracheid cell walls. Although we did not quantify the total heat reaching the xylem, we visually observed changes in xylem coloration, suggesting that heat generated during fire reached the xylem cells (Figs 5c–f, S2, S3). Our findings agree with previous results showing no effect of fire on *n*PLC for saplings of ponderosa pine exposed to nonlethal and lethal fire doses (Partelli-Feltrin *et al.*, 2021). Despite no evidence of tracheid deformation in burned saplings, we did observe a slight decrease in maximum water conductivity from 6 to 28 d postfire in burned plants. Such a decrease in maximum water conductivity could be related to clogging of xylem pits (small pores that link the water conduits) by resin and/or physical deformation of the pits. Another previous study suggested that the prefire xylem conduits in the vicinity of fire scars could have pits clogged by resin (Partelli-Feltrin *et al.*, 2021). However, there is as yet no direct evidence of this or heat-induced deformation of pits. These are interesting possible mechanisms of reduced maximum conductivity, and future investigations of these possibilities are needed.

In addition to the stem anatomical analysis, we visually observed changes in the coloration of phloem/vascular cambium, indicating phloem mortality in the entire circumference of the plant stems. Therefore, our results suggest that the cause of sapling mortality here was cambial death and/or disruption of carbohydrate transport by heat-induced death of phloem. Although xylem hydraulic failure was not observed during our study (29 d postfire) and it was not the cause of mortality, we could have potentially observed an increase in *n*PLC after the onset of root mortality caused by depletion of root NSC reserves due to stem heat-induced girdling. Thus, further research is needed into more diverse factors such as the long term-impact of fire on water transport and the interaction of partial cambium/phloem dysfunction (Partelli-Feltrin *et al.*, 2021) in different tree species.

Depletion of carbohydrates and loss of hydraulic function can cooccur (Sevanto *et al.*, 2014; McDowell *et al.*, 2022), but in this study fire only induced depletion of NSCs in the roots due to heat-induced girdling. Our results implicate phloem dysfunction and cambial death (but not hydraulic failure) as a potential mechanism of postfire tree mortality in ponderosa pine saplings. Although we did not observe changes in *n*PLC, it is likely that when roots reach a maximum depletion of NSCs, thus supplying less water due to root mortality, an increase in *n*PLC can occur. In addition, because fire can potentially have a greater effect on tree NSCs than water transport, our results suggest that trees which do not suffer complete cambial tissue necrosis and have higher NSC content are more likely to survive fire.

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Competing interests

None declared.

Author contributions

RP-F, AMSS, HDA and DMJ designed the research. RP-F and RAT performed data collection and analyses. RP-F, AMSS, RAT, HDA, CAK, KMY and DMJ interpreted the data and prepared the manuscript.

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Data availability

The data that support the findings of this study are available from the corresponding author upon reasonable request.

References

Adams HD, Germino MJ, Breshears DD, Barron-Gafford GA, Guardiola-Claramonte M, Zou CB, Huxman TE. 2013. Nonstructural leaf carbohydrate dynamics of *Pinus edulis* during drought-induced tree mortality reveal role for carbon metabolism in mortality mechanism. *New Phytologist* **197**: 1142–1151.

Anderegg WRL, Callaway ES. 2012. Infestation and hydraulic consequences of induced carbon starvation. *Plant Physiology* **159**: 1866–1874.

Artés T, Oom D, De Rigo D, Durrant TH, Maianti P, Libertà G, San-Miguel-Ayanz J. 2019. A global wildfire dataset for the analysis of fire regimes and fire behaviour. *Scientific Data* **6**: 1–11.

Aubrey DP, Teskey RO. 2018. Stored root carbohydrates can maintain root respiration for extended periods. *New Phytologist* **218**: 142–152.

Berrill JP, O'Hara KL, Kichas NE. 2020. Bark thickness in coast redwood (*Sequoia sempervirens* (D. Don) Endl.) varies according to tree- and crown size, stand structure, latitude and genotype. *Forests* **11**: 637.

Bison NN, Partelli-Feltrin R, Michaletz ST. 2022. Trait phenology and fire seasonality co-drive seasonal variation in fire effects on tree crowns. *New Phytologist* **234**: 1654–1663.

Brodribb TJ, Cochard H. 2009. Hydraulic failure defines the recovery and point of death in water-stressed conifers. *Plant Physiology* **149**: 575–584.

Bär A, Michaeltz ST, Mayr S. 2019. Fire effects on tree physiology. *New Phytologist* **223**: 1728–1741.

Bär A, Nardini A, Mayr S. 2018. Post-fire effects in xylem hydraulics of *Picea abies*, *Pinus sylvestris* and *Fagus sylvatica*. *New Phytologist* **217**: 1484–1493.

Cansler CA, Hood SM, van Mantgem PJ, Varner JM. 2020. A large database supports the use of simple models of postfire tree mortality for thick-barked conifers, with less support for other species. *Fire Ecology* **16**: 25.

Chen Z, Wang L, Dai Y, Wan X, Liu S. 2017. Phenology-dependent variation in the non-structural carbohydrates of broadleaf evergreen species plays an important role in determining tolerance to defoliation (or herbivory). *Scientific Reports* **7**: 10125.

Dickinson MB, Jolliff J, Bova AS. 2004. Vascular cambium necrosis in forest fires: using hyperbolic temperature regimes to estimate parameters of a tissue-response model. *Australian Journal of Botany* **52**: 757–763.

Du B, Luan Q, Ni Z, Sun H, Jiang J. 2022. Radial growth and non-structural carbohydrate partitioning response to resin tapping of slash pine (*Pinus elliottii* Engelm. var. *elliottii*). *Journal of Forestry Research* **33**: 423–433.

Esau K. 1965. *Plant anatomy, 2nd edn.* New York, NY, USA: John Wiley & Sons.

Furnis TJ, Larson AJ, Kane VR, Lutz JA. 2020. Wildfire and drought moderate the spatial elements of tree mortality. *Ecosphere* **11**: e03214.

Furze ME, Huggett BA, Aubrecht DM, Stolz CD, Carbone MS, Richardson AD. 2019. Whole-tree nonstructural carbohydrate storage and seasonal dynamics in five temperate species. *New Phytologist* **221**: 1466–1477.

Goren R, Huberman M, Goldschmidt EE. 2004. Girdling: physiological and horticultural aspects. In: Janick J, ed. *Horticultural reviews, vol. 30*. Hoboken, NJ, USA: John Wiley & Sons, 12–16.

Gregory RA, Wargo PM. 1986. Timing of defoliation and its effect on bud development, starch reserves, and sap concentration in sugar maple. *Canadian Journal of Forest Research* **16**: 10–17.

Hammond WM, Yu KL, Wilson LA, Will RE, Anderegg WRL, Adams HD. 2019. Dead or dying? Quantifying the point of no return from hydraulic failure in drought-induced tree mortality. *New Phytologist* **223**: 1834–1843.

Hermes DA, Mattson WJ. 1992. The dilemma of plants: to grow or defend. *The Quarterly Review of Biology* **67**: 283–335.

Hood SM, Lutes D. 2017. Predicting postfire tree mortality for 12 western US conifers using the first order fire effects model (FOFEM). *Fire Ecology* **13**: 66–84.

Hood SM, Varner JM, van Mantgem F, Cansler C. 2018. Fire and tree death: understanding and improving modeling of fire induced tree mortality. *Environmental Research Letters* **13**: 113004.

IPCC. 2021. Climate change 2021: the physical science basis. In: Masson-Delmotte V, Zhai P, Pirani A, Connors SL, Péan C, Berger S, Caud N, Chen Y, Goldfarb L, Gomis MI *et al.*, eds. *Contribution of working group I to the sixth assessment report of the Intergovernmental Panel on Climate Change*. Cambridge, UK; New York, NY, USA: Cambridge University Press.

Kavanagh KL, Dickinson MB, Bova AS. 2010. A way forward for fire-caused tree mortality prediction: modeling a physiological consequence of fire. *Fire Ecology* **6**: 80–94.

Knoblauch M, Froelich DR, Pickard WF, Peters WS. 2014. SEORious business: structural proteins in sieve tubes and their involvement in sieve element occlusion. *Journal of Experimental Botany* **65**: 1879–1893.

Knoblauch M, van Bel AJE. 1998. Sieve tubes in action. *Plant Cell* **10**: 35–50.

Landhäusser SM, Chow PS, Dickman LT, Furze ME, Kuhlman I, Schmid S, Wiesenbauer J, Wild B, Gleixner G, Hartmann H *et al.* 2018. Standardized protocols and procedures can precisely and accurately quantify non-structural carbohydrates. *Tree Physiology* **38**: 1764–1778.

Larson PR. 1994. *The vascular cambium: development and structure*. Berlin, Germany: Springer.

Lenth RV, Buerkner P, Herve M, Love J, Riebl MFH, Singmann H. 2020. *EMMEANS: estimated marginal means, aka least-squares means.* R package v.1.7.2. [WWW document] URL http://cran.r-project.org/web/packages/emmeans [accessed 25 January 2021].

Levitt J. 1972. *Responses of plants to environmental stress*. New York, NY, USA: Academic Press.

Li W, Hartmann H, Adams HD, Zhang H, Jin C, Zhao C, Guan D, Wang A, Yuan F, Wu J. 2018. The sweet side of global change-dynamic responses of non-structural carbohydrates to drought, elevated CO_2 and nitrogen fertilization in tree species. *Tree Physiology* **38**: 1706–1723.

Martínez-Vilalta J, Sala A, Asensio D, Galiano L, Hoch G, Palacio S, Piper FI, Lloret F. 2016. Dynamics of non-structural carbohydrates in terrestrial plants: a global synthesis. *Ecological Monographs* **86**: 495–516.

Matthews S. 2010. Effect of drying temperature on fuel moisture content measurements. *International Journal of Wildland Fire* **19**: 800–802.

McCulloh KA, Johnson DM, Meinzer FC, Lachenbruch B. 2011. An annual pattern of native embolism in upper branches of four tall conifer species. *American Journal of Botany* **98**: 1007–1015.

McDowell NG, Ryan MG, Zeppel MJB, Tissue DT. 2013. Improving our knowledge of drought-induced forest mortality through experiments, observations, and modeling. *New Phytologist* **200**: 289–293.

McDowell NG, Sapes G, Pivovaroff A, Adams HD, Allen CD, Anderegg WR, Arend M, Breshears DD, Brodribb T, Choat B *et al.* 2022. Mechanisms of woody-plant mortality under rising drought, CO_2 and vapour pressure deficit. *Nature Reviews Earth & Environment* **3**: 294–308.

Mei L, Xiong Y, Gu J, Wang Z. 2015. Whole-tree dynamics of non-structural carbohydrate and nitrogen pools across different seasons and in response to girdling in two temperate trees. *Oecologia* **177**: 333–344.

Michaletz ST, Johnson EA, Tyree MT. 2012. Moving beyond the cambium necrosis hypothesis of postfire tree mortality: cavitation and deformation of xylem in forest fires. *New Phytologist* **194**: 254–263.

Mitchell RG, Martin RE, Stuart J. 1983. Catfaces on lodgepole pine–fire scars or strip kills by the mountain pine beetle? *Journal of Forestry* **81**: 598–613.

Noel ARA. 1970. The girdled tree. *The Botanical Review* **36**: 162–195.

O'Brien JJ, Hiers JK, Mitchell RJ, Varner JM, Mordecai K. 2010. Acute physiological stress and mortality following fire in a long-unburned longleaf pine ecosystem. *Fire Ecology* **6**: 1–12.

O'Brien JJ, Hiers JK, Varner JM, Hoffman CM, Dickinson MB, Michaletz ST, Loudermilk EL, Butler BW. 2018. Advances in mechanistic approaches to quantifying biophysical fire effects. *Current Forestry Reports* **4**: 161–177.

Partelli-Feltrin R, Johnson DM, Sparks AM, Adams HD, Kolden CA, Nelson AS, Smith AMS. 2020. Drought increases vulnerability of *Pinus ponderosa* saplings to fire-induced mortality. *Fire* **3**: 56.

Partelli-Feltrin R, Smith AMS, Adams HD, Kolden CA, Johnson DM. 2021. Short- and long-term effects of fire on stem hydraulics in *Pinus ponderosa* saplings. *Plant, Cell & Environment* **44**: 696–705.

Peterson DL, Ryan KC. 1986. Modeling postfire conifer mortality for long-range planning. *Environmental Management* **10**: 797–808.

R Core Team. 2019. *R: a language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing. [WWW document] URL https://www.R-project.org/ [accessed 15 September 2022].

Rademacher TT, Basler D, Eckes-Shephard AH, Fonti P, Friend AD, Moine JL, Richardson AD. 2019. Using direct phloem transport manipulation to advance understanding of carbon dynamics in forest trees. *Frontiers in Forests and Global Change* **2**: 11.

Rosas T, Galiano L, Ogaya R, Peñuelas J, Martínez-Vilalta J. 2013. Dynamics of non-structural carbohydrates in three Mediterranean woody species following long-term experimental drought. *Frontiers in Plant Science* **4**: 1–16.

Ryan KC. 2000. Effects of fire injury on water relations of ponderosa pine. In: Moser WK, Moser CF, eds. *Fire and forest ecology: innovative silviculture and vegetation management.* Tall timbers ecology conference proceedings no. 21. Tallahassee, FL, USA: Tall Timbers Research Station, 58–66.

Sevanto S, McDowell NG, Dickman T, Pangle R, Pockman WT. 2014. How do trees die? A test of hydraulic failure and carbon starvation hypothesis. *Plant, Cell & Environment* **37**: 153–161.

Smith AMS, Sparks AM, Kolden CA, Abatzoglou JT, Talhelm AF, Johnson DM, Boschetti L, Lutz JA, Apostol KG, Yedinak KM *et al.* 2016. Towards a new paradigm in fire severity research using dose–response experiments. *International Journal of Wildland Fire* **25**: 158–166.

Smith AMS, Talhelm AF, Johnson DM, Sparks AM, Yedinak KM, Apostol KG, Tinkham WT, Kolden CA, Abatzoglou JT, Lutz JA *et al.* 2017. Effects of fire radiative energy density dose on *Pinus contorta* and *Larix occidentalis* seedling physiology and mortality. *International Journal of Wildland Fire* **26**: 82–94.

Sonmez T, Keles S, Tilki F. 2007. Effect of aspect, tree age and tree diameter on bark thickness of *Picea orientalis*. *Scandinavian Journal of Forest Research* **22**: 193–197.

Sparks AM, Kolden CA, Talhelm AF, Smith AMS, Apostol KG, Johnson DM, Boschetti L. 2016. Spectral indices accurately quantify changes in seedling physiology following fire: towards mechanistic assessments of postfire carbon cycling. *Remote Sensing* **8**: 572.

Sparks AM, Talhelm AF, Partelli-Feltrin R, Smith AMS, Johnson DM, Kolden CA, Boschelli L. 2018. An experimental assessment of fire impact of drought and fire on western larch injury, mortality and recovery. *International Journal of Wildland Fire* **27**: 490–497.

Sperry JS, Donnelly JR, Tyree MT. 1988. A method for measuring hydraulic conductivity and embolism in xylem. *Plant, Cell & Environment* **11**: 35–40.

Steady WD, Partelli-Feltrin R, Johnson DM, Sparks AM, Kolden CA, Talhelm AF, Lutz JA, Boschelli L, Hudak AT, Nelson AS *et al.* 2019. The survival of *Pinus ponderosa* saplings subjected to increasing levels of fire behavior and impacts on postfire growth. *Fire* **2**: 1–13.

Słupianek A, Dolzblasz A, Sokołowska K. 2021. Xylem parenchyma – role and relevance in wood functioning in trees. *Plants* **10**: 1247.

United Nations Environment Programme. Sullivan A, Kurvits T, Baker E, eds. 2022. *Spreading like wildfire – the rising threat of extraordinary landscape fires. A UNEP rapid response assessment.* Nairobi, Kenya: United Nations Environment Programme.

Vaillant NM, Kolden CA, Smith AMS. 2016. Assessing landscape vulnerability to wildfire in the USA. *Current Forestry Reports* **2**: 201–213.

Van Lierop P, Linquist E, Sathyapala S, Franceschini G. 2015. Global forest area disturbance from fire, insect pests, diseases and severe weather events. *Forest Ecology and Management* **352**: 78–88.

Varner JM, Hood SM, Aubrey DP, Yedinak K, Hiers JK, Jolly WM, Shearman TM, McDaniel JK, O'Brien JJ, Rowell EM. 2021. Tree crown injury from wildland fires: causes, measurement and ecological and physiological consequences. *New Phytologist* **231**: 1676–1685.

Varner JM, Putz FE, O'Brien JJ, Hiers JK, Mitchell RJ, Gordon DR. 2009. Post-fire tree stress and growth following smoldering duff fires. *Forest Ecology and Management* **258**: 2467–2474.

Weber R, Schwendener A, Schmid S, Lambert S, Wiley E, Landhäysser SM, Hartmann H, Hoch G. 2018. Living on next to nothing: tree seedlings can survive weeks with very low carbohydrate concentrations. *New Phytologist* **218**: 107–118.

West AG, Nel JA, Bond WJ, Midgley JJ. 2016. Experimental evidence for heat plume-induced cavitation and xylem deformation as a mechanism of rapid postfire tree mortality. *New Phytologist* **211**: 828–838.

Westerling AL, Gershunov A, Brown TJ, Cayan DR, Dettinger DMD. 2003. Climate and wildfire in western of United States. *Bulletin of the American Meteorological Society* **84**: 595–604.

Wiley E, Huepenbecker S, Casper BB, Helliker BR. 2013. The effects of defoliation on carbon allocation: can carbon limitation reduce growth in favour of storage? *Tree Physiology* **33**: 1216–1228.

Zimmermann MH, Milburn JA. 1975. *Transport in plants I. Phloem transport.* Berlin & Heidelberg, Germany; New York, NY, USA: Springer-Verlag.

Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Fire experiment setup.

Fig. S2 Undamaged, partially damaged and completely damaged *Pinus ponderosa* saplings phloem/cambium cross-sections.

Fig. S3 Vascular cambium/phloem heat-induced necrosis in *Pinus ponderosa* saplings in Experiment 1.

Fig. S4 Unburned and burned main stem xylem of *Pinus ponderosa* saplings.

Fig. S5 Sugar and starch content in needles, stem and roots in *Pinus ponderosa* saplings.

Table S1 Sample and organ dry mass estimation.

Table S2 Model parameters and statistics used to estimate organ dry mass of spalings.

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