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Research

Fire directly affects tree carbon balance and indirectly affects hydraulic function: consequences for post-fire mortality in two conifers

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Summary

- The mechanistic links between fire-caused injuries and post-fire tree mortality are poorly understood. Current hypotheses differentiate effects of fire on tree carbon balance and hydraulic function, yet critical uncertainties remain about the relative importance of each and how they interact.
- We utilize two prescribed burns with Douglas-fir and ponderosa pine to examine: the relative evidence for fire-caused changes in hydraulic function and carbon dynamics, and how such impacts relate to fire injuries; which impacts most likely lead to post-fire mortality; and how these impacts vary by species and burn timing (fall vs spring).
- We find that fire-caused impacts to non-structural carbohydrates (NSC) are immediate, persistent, correlated with crown injury severity, and strongly related to post-fire mortality. By contrast, hydraulic impacts are delayed and not directly attributable to fire-caused injuries, although some burned trees do exhibit signs of increased hydraulic dysfunction and water stress before death. This suggests that fire may indirectly affect tree water relations, possibly through an interaction with direct fire impacts on NSC.
- These findings offer a more nuanced understanding of fire's effect on post-fire tree function and mortality and are important in the context of increased fire activity in forests globally.

Introduction

Fire affects millions of hectares of forests annually, resulting in widespread fire-caused tree death (Jones *et al.*, 2022), with many more trees dying in the following years due in part to fire-caused injuries (Busby *et al.*, 2024). For trees that initially survive fire, the severity of the fire injuries they sustain can be predictive of whether they will survive or die in the months or years post-fire, yet the mechanistic link between these injuries and post-fire tree mortality as well as the lasting impacts of these injuries on tree function for surviving trees is poorly understood (Hood *et al.*, 2018b; Nolan *et al.*, 2024). Understanding how fire impacts tree function and subsequent vulnerability to mortality is important for modeling fire effects on vegetation and carbon emissions, understanding the potential for other disturbances to interact with fire impacts, as well as for planning forest management activities like prescribed fire (Hood *et al.*, 2018b). As forest disturbance dynamics adjust to climate change (Seidl *et al.*, 2017; Jones *et al.*, 2022), and as intentional fire is increasingly used as a management tool (Kolden, 2019; Morgan *et al.*, 2020), a deeper understanding of the fundamental impacts of fire on tree function is needed.

The impacts of fire on tree physiological function are generally separated into two categories: impacts to tree carbon balance (via disruption of carbohydrate acquisition/transport due to phloem and foliage necrosis), and impacts to hydraulic function (via heat-caused embolism formation or xylem cell deformities/-blockages) (Nolan *et al.*, 2024). These impacts likely also interact (Bär *et al.*, 2019). Impacts to carbon balance are directly linked to the ability to access and use stored non-structural carbohydrates (NSC; soluble sugars and starch) and acquire new NSC, both of which are necessary for post-fire maintenance of tree metabolism and growth of new tissues (e.g. leaves, xylem) that allow a tree to recover from injuries (Dietze *et al.*, 2014; Nolan *et al.*, 2021). Fire impacts on hydraulic function, on the other hand, may affect a tree's ability to transport water and nutrients and maintain turgor. This may lead to hydraulic failure in extreme cases, a reduced ability to withstand future water stress, or generally impaired physiological performance, which may lead to lower photosynthetic rates that further exacerbate carbon deficits.

Fire-caused cambium and phloem necrosis and resultant heat-girdling of stems have long been understood to contribute to post-fire mortality (reviewed in Michaletz & Johnson, 2007).

Similarly, there is a well-understood relationship between high levels of foliage loss and an increased probability of post-fire mortality (Woolley *et al.*, 2012), although the physiological basis for this has only recently begun to be explored (Reed & Hood, 2024). However, some trees decline more rapidly (e.g. within weeks) post-fire than is expected from girdling or foliage loss alone (Michaletz *et al.*, 2012). Mechanisms that have been proposed to explain more rapid patterns of death tend to focus on how fire affects a tree's hydraulic system. For example, the heat plume hypothesis states that superheated, dry air during a fire leads to rapid water loss from leaves, resulting in extensive embolisms within the distal regions of the hydraulic apparatus, potentially leading to whole plant hydraulic failure (Kavanagh *et al.*, 2010; Bär *et al.*, 2018; Lodge *et al.*, 2018; Salladay & Pittermann, 2023). Likewise, reduced surface tension of water at high temperatures could lead to a similar outcome (Michaletz *et al.*, 2012). Additionally, heating of tree branches and stems is hypothesized to result in deformation of existing and/or subsequent years' xylem cell walls, making the xylem more vulnerable to cavitation and thus rapid hydraulic failure (Michaletz *et al.*, 2012; West *et al.*, 2016; Bär *et al.*, 2018; Partelli-Feltrin *et al.*, 2021). Recent experimental work has also postulated that heat-caused hydraulic dysfunction could result from physical xylem occlusions (e.g. from resins or tyloses), which may also increase the risk of hydraulic failure (Hoffmann *et al.*, 2024). All of the proposed impacts of fire on a tree's hydraulic system have the potential to lead to rapid post-fire hydraulic failure, but if impacts are not extensive, they may also drive more slowly realized effects and contribute to delayed patterns of mortality, especially through interactions with other fire effects like those affecting tree carbon balance.

Importantly, most evidence for fire-caused hydraulic dysfunction has come from laboratory studies often using fire proxies (Smith *et al.*, 2025), such as water baths, which have shown evidence of immediate fire-caused xylem deformation (Michaletz *et al.*, 2012; West *et al.*, 2016; Bär *et al.*, 2018). However, studies that utilize fire or other fire proxies at non-lethal doses have not shown immediate deformation (Bär *et al.*, 2018; Partelli-Feltrin *et al.*, 2021; Hoffmann *et al.*, 2024). Salladay & Pittermann (2023) further demonstrated that the 'dose' of heat necessary to cause xylem deformation was greater than that needed to cause phloem and cambium necrosis, suggesting that heat-caused xylem deformation is potentially less important if the more exterior cambium and phloem are killed first. These findings highlight the need for further testing of hydraulic impacts with studies utilizing realistic, sub-lethal fire intensities, rather than fire proxies.

The relatively limited evidence for heat-caused xylem dysfunction, combined with the reality that temperatures needed to cause xylem deformities will first cause phloem necrosis, has generated renewed interest in whether post-fire mortality may be more directly linked to effects on carbon balance (Dickman, 2024; Reed & Hood, 2024). Fire can cause partial or complete heat-girdling of the stem and branch phloem and cambium (Michaletz & Johnson, 2007; Bär *et al.*, 2019), disrupting the transport of NSC within a tree and leading to a drawdown of NSC in impacted areas (Partelli-Feltrin *et al.*, 2023). At the same time, fire often partially or completely defoliates trees via leaf necrosis caused by crown scorch and consumption (Varner *et al.*, 2021). While some species have buds capable of surviving some fire intensities and/or the ability to resprout, others do not. Even for trees with surviving buds and/or resprouting abilities, fire-caused defoliation may still reduce stored NSC (Nolan *et al.*, 2021; Reed & Hood, 2024). Further, areas of phloem death throughout a tree and simultaneous partial defoliation may have compounding impacts on carbon balance and lead to more rapid death than stem girdling or defoliation alone. It is also possible that NSC declines may increase vulnerability to water stress due to the importance of NSC for new xylem growth, turgor maintenance and osmoregulation (Sapes *et al.*, 2021), and fine root production (Sword & Haywood, 1995). Even for trees that do not die in the first few years post-fire, impacts on carbon balance may have long-lasting effects on growth or susceptibility to insects, disease, or drought (Bär *et al.*, 2019).

While the evidence for direct fire impacts on NSC may be more straightforward than hydraulic impacts, fire-caused NSC impacts have also received less recent attention. For example, the degree to which fire and species' characteristics, such as heat tolerance of buds and branches, interact to impact post-fire NSC dynamics has not been tested. Only a few studies have measured NSC (both soluble sugars and starch) of non-resprouting species after sub-lethal fire, and these were all from species with large buds that can withstand some heating, necessitating a better understanding of how fire-caused NSC impacts differ between species with differing fire resistance (Varner *et al.*, 2009; Reed & Hood, 2024). Further, the seasonal timing of fire may also lead to differential levels of fire injury in tree crowns due to differences in heat tolerance associated with bud phenology (Bär *et al.*, 2021; Bison *et al.*, 2022) and seasonal fluctuations in NSC (Martínez-Vilalta *et al.*, 2016). These differences are particularly important in the context of lengthening fire seasons and prescribed fire use (Knapp *et al.*, 2009; Miller *et al.*, 2019; Senande-Rivera *et al.*, 2022). Understanding how tree phenology and seasonal NSC fluctuations influence these carbon-related fire effects is therefore needed.

Nearly all studies that have tested post-fire mortality hypotheses have focused on impacts to hydraulic function or carbon balance separately (but see Partelli-Feltrin *et al.*, 2023), yet if these impacts occur simultaneously, they likely interact (Sala *et al.*, 2012; Sevanto *et al.*, 2014). Prescribed burns offer good opportunities for testing these hypotheses on trees in the field and over multiple phases of phenology. Prescribed fires often occur during the dormant season or in the spring or fall when trees are going into or coming out of dormancy, offering the chance to study fire effects during a variety of phenological stages. Examining impacts on both carbon balance and hydraulic function simultaneously allows us to address questions about the relative importance of each for post-fire tree mortality, how their impacts interact, and the duration over which non-lethal physiological impacts persist.

We utilized a fall and spring prescribed burn to examine: (1) the relative contribution of fire-caused hydraulic and carbon-related impacts on two conifer species and whether

impacts relate to levels of fire injury; (2) which physiological impacts relate most strongly to post-fire mortality; and (3) the degree to which these impacts vary by species and burn season. We assessed fire-caused physiological carbon (NSC) and hydraulic impacts to Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) pre-fire and over multiple timesteps through 22 months post-fire (Fig. 1) and related physiological variables to the degree of fire-caused injuries. Each burn site was paired with a nearby unburned 'control' site. By the end of the study, 27 of 80 burned trees that initially survived fire had died, allowing us to model the probability of mortality as a function of tree characteristics and physiology to determine the relative importance of each on tree death. We hypothesized that: (1) fire would have greater impacts on NSC than hydraulic function, due to the higher heating necessary to deform xylem than to kill phloem combined with concurrent reductions in photosynthetic leaf area; (2) post-fire tree mortality would be most attributable to fire-caused drawdowns of NSC, a proxy for impacts to carbohydrate transport and acquisition, and important for recovery from fire injuries; and (3) tree species and burn season would affect the direction and/or magnitude of physiological fire impacts due to differences in bud morphology and phenological stage, respectively, with more negative impacts on Douglas-fir and spring-burned trees. Our work contributes to the growing understanding of how fire that is not immediately lethal can impact tree physiology in the short- and mid-term and helps elucidate the mechanistic link between fire injuries and post-fire mortality. This information can inform post-fire mortality models and our understanding of how fire impacts on surviving trees might interact with other disturbances post-fire.

Materials and Methods

Study sites, species, sampling approach, and prescribed fire information

We selected two sites in western Montana, USA, that were scheduled for prescribed burning within the following year, had no recent fire activity, and were dominated by mature ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) with patches of regenerating trees in the understory. Both species are considered resistant to low-intensity fires due to thick bark, although ponderosa pine is relatively more resistant due to large buds that can withstand some heating, its tendency to self-prune lower branches minimizing crown scorch, and quick-developing thick bark (Hood *et al.*, 2018a; Rodman *et al.*, 2021). One site was burned on 10 October 2022 (henceforth, fall burn), and another on 3 May 2023 (spring burn). Each burned site was paired with a nearby unburned site (control) with a similar aspect, forest structure, and species composition (Supporting Information Fig. S1). Paired sites were no > 800 m apart at similar elevations, and the two burn sites were 8.5 km apart. Site coordinates and climate information are included in Methods S1.

Approximately 1 month before each burn, we tagged 20 ponderosa pine and 20 Douglas-fir trees at each of the four sites (fall-burn, fall-control, spring-burn, and spring-control), for a total of 160 trees. We selected trees 7–16 cm diameter at breast height (DBH) to increase their likelihood of experiencing crown scorch, as the prescribed burns were planned to be low-intensity surface fires. All trees appeared visually healthy pre-fire. During tagging, we took initial measurements of tree size (DBH, height), compacted crown ratio (accounts for gaps in foliage), and bark thickness.

The fall burn occurred when buds were set on both species, and the spring burn occurred when bud swell had begun on ponderosa pine but not Douglas-fir. Information on weather conditions, fuel moisture, and fire intensity on burn days is included in Methods S1. Fire intensity was greater for the fall prescribed burn than the spring (Fig. S2), consistent with patterns in dry conifer forests (Knapp *et al.*, 2009), although the extent of crown injuries on focal trees was similar across sites (Table 1). The fall burn was higher intensity than expected, and 28 of the 40 tagged trees (14 ponderosa pine, 14 Douglas-fir) died during the fire (i.e. 100% crown consumption or 100% needle scorch and bud kill). These trees were replaced immediately post-fire with nearby trees of the same species and size that were still alive (i.e. some green foliage),

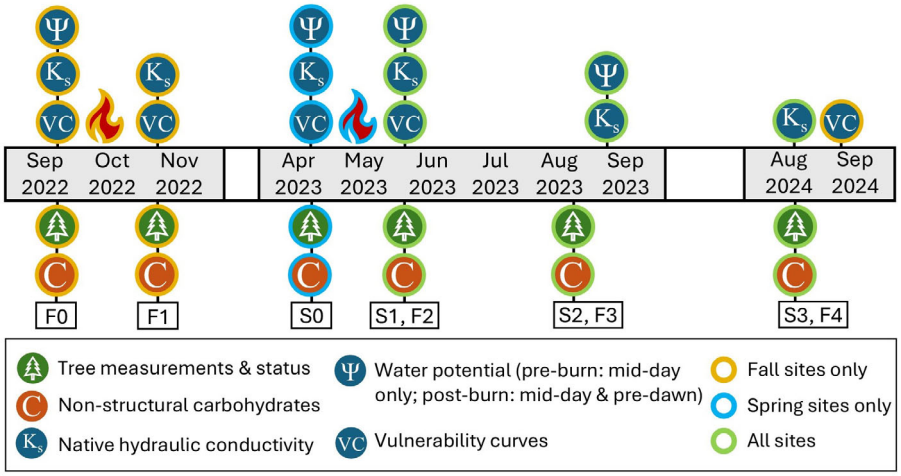

Fig. 1 Sampling timeline with respect to each prescribed burn and associated sites. Symbols and colors denote specific variables sampled and which sites were sampled at that timestep. Timestep abbreviations (e.g. F0, S0) denote sampling timesteps for fall (F) and spring (S) sites. Sampling of each variable occurred within 1 wk at paired burn and control sites. Specific sampling dates for each variable and site are listed in Supporting Information Table S2.

Table 1 Attributes of burned ponderosa pine and Doulglas-fir that survived and those that died by the end of the study.

Season	Outcome	Species	*n*	DBH (cm)	Height (m)	Bark thick. (cm)	Crown scorch (%)	Bud kill (%)
Fall	Dead	Ponderosa pine	3	9.8 (0.2)	6.5 (0.0)	0.68 (0.1)	59 (20–98)	38 (10–75)
Fall	Live	Ponderosa pine	17	10.8 (0.4)	7.2 (0.3)	0.78 (0.1)	55 (25–98)	39 (5–90)
Fall	Dead	Douglas-fir	7	10.5 (0.4)	7.1 (0.4)	0.47 (0.1)	62 (10–98)	na
Fall	Live	Douglas-fir	13	10.9 (0.3)	8.0 (0.3)	0.57 (0.1)	42 (10–90)	na
Spring	Dead	Ponderosa pine	10	10.4 (0.3)	5.9 (0.2)	0.87 (0.1)	66 (15–100) a	22 (2–90)
Spring	Live	Ponderosa pine	10	10.4 (0.3)	6.0 (0.4)	0.84 (0.1)	31 (2–70) b	16 (0–60)
Spring	Dead	Douglas-fir	7	8.6 (0.1) a	6.1 (0.2)	0.69 (0.1)	61 (15–95) a	na
Spring	Live	Douglas-fir	13	11.0 (0.3) b	6.6 (0.2)	0.80 (0.1)	29 (2–75) b	na

Values are means with SE (diameter at breast height (DBH), height, bark thickness) or range (crown scorch, bud kill) in parentheses. *n*, number of individuals. Letters indicate significant ($P < 0.05$) differences between live and dead trees (*t*-tests). na, not applicable.

as we were interested in sublethal fire effects. The spring burn was patchier than the fall burn, and 6 of the 40 trees (2 ponderosa pine, 4 Douglas-fir) did not experience fire (i.e. no crown scorch); those trees were similarly replaced. There were no differences in tree characteristics between originally tagged trees and their replacements (Table S1). The pre-fire timestep, therefore, includes data collected on originally tagged trees, while post-fire timesteps include a mix of original trees and replacements. For analyses that required us to calculate percent changes in physiological variables from pre-burn to post-burn, we calculated within-species means from the original trees at the pre-burn timestep and used those values as the baseline to calculate percent change for replacement trees.

Sampling timeline and tree measurements

We sampled tree physiology (NSC, hydraulic function) *c.* 1–2 wk pre-burn (F0, S0; see Fig. 1 for timestep abbreviations) and 3 wk post-burn (F1, S1) at both burn and paired control sites (Fig. 1). We resampled the fall-burn and fall-control sites again at the end of the first spring post-fire (7 months post-fire; late May 2023; F2). We resampled all sites again at the end of the first summer post-fire (Aug–Sep 2023; S2, F3) and at the end of the second summer post-fire (Aug–Sep 2024; S3, F4) (Fig. 1; Table S2). To assess the general pre-fire water stress of study trees, we measured midday water potential (12:00 h–14:00 h; Ψ_{md}) of needles using a Scholander pressure chamber (PMS Instruments, Albany, OR, USA) 1 wk pre-fire. Site accessibility issues due to snow prevented measurement of pre-dawn water potential (Ψ_{pd}) at the spring sites, and thus, we do not report pre-burn Ψ_{pd} at either site. We additionally measured both Ψ_{md} and Ψ_{pd} the first spring post-fire (S1, F2) and in September 2023 (S2, F3) to determine whether tree water status related to post-fire mortality. Water potential samples were collected from the upper half of tree crowns and stored in humidified bags until sampling *c.* 30 min later. We noted new mortality (i.e. no green needles or live buds) at each timestep. We assessed percent crown volume scorched (including consumption) for both species and percent of buds killed for ponderosa pine 3 wk post-burn. We assumed 100% bud death on scorched Douglas-fir branches. In 2024 (S3, F4), we calculated cambium kill rating (CKR) on all surviving trees and cut sections from the base of dead trees for retrospective CKR assessment. Cambium kill rating is a measure of the number of quadrants (0–4) with dead cambium post-fire (Hood *et al.*, 2010). Only 7 out of 80 trees had a CKR of 3 or 4, so we grouped CKR into low (0–1 quadrant affected) and high (2–4 quadrants affected) ratings for analyses. We also cut sections from the base of dead trees and took increment cores from live trees to estimate tree age. Our complete sampling timeline is described in Table S2.

Hydraulic function

Detailed information on hydraulic sampling is included in the Methods S1. Briefly, we measured native specific hydraulic conductivity (K_s) from live branches at all timesteps (Fig. 1) using the gravimetric method (Sperry *et al.*, 1988) with a modified hydraulic apparatus using a micro-flow sensor (Sensirion SLI-0439, Sensirion, Inc., Staefa ZH, Switzerland) as described in Sapes *et al.* (2019). One live terminal branch was sampled from the top half of the tree crown for each measurement. We sampled green branches with no or very minimal scorch because we were interested in branches likely to survive post-fire. At the first post-burn timestep, we additionally collected samples from visibly scorched branches with live buds on a subset of 10 ponderosa pine to compare the hydraulic function (K_s and vulnerability to embolism formation) of scorched and green branches on the same tree. We did not do this for Douglas-fir, as branches with needle scorch typically have little chance of surviving post-fire (Hood *et al.*, 2021).

We constructed vulnerability curves (VCs) and calculated P_{12}, P_{50}, and P_{88} using the 'fitplc' package (Duursma & Choat, 2017) to assess changes in post-fire branch vulnerability to embolism formation, which is expected if heating causes xylem cell wall deformation. We used a subset of hydraulic samples to construct VCs for both species pre-fire (timestep F0, S0) and 3 wk post-fire (F1, S1), as xylem deformation caused by heating should have immediate effects. We also sampled fall-burned and unburned ponderosa pine at the final timestep 23 months post-fire (F4), to test for consequences of fire scar formation on surviving burned branches (additional detail in Methods S1). We used the air injection method for VCs. Each branch was placed inside a pressure sleeve (PMS Instruments, Albany, OR, USA) with both ends protruding. Bark was removed and the stem notched with a razor

blade to ensure air entry into the stem (Sperry & Saliendra, 1994; Ennajeh *et al.*, 2011). After overnight vacuum infiltration to remove embolisms and measurement of K_{max}, samples were pressurized for 3 min at −0.5, −1.5, −3, −4.5, −6, and −7.5 MPa. After each air injection step, samples were relaxed in deionized water until bubbles were no longer coming out of the ends before K_s was measured as described above.

Non-structural carbohydrates

We measured concentrations of NSC in tree stems to quantify changes in carbon stores post-fire, likely due to changes in carbon acquisition and transport. We took a tissue sample for NSC analyses from the stem xylem and phloem of each focal tree at *c.* 1–1.5 m height using a 20-mm-diameter punch at each timestep (Fig. 1). Samples were collected haphazardly around the circumference of the bole, with care to not accidentally girdle a tree. All samples had visually live phloem. Outer bark was discarded, and phloem and xylem were separated. We additionally collected samples from coarse roots (xylem only), the first spring (S1, F2), and at the end of the first summer post-burn (S2, F3). We did not collect root samples pre-fire to not disturb the litter and duff around the base of trees, which could affect fire intensity. We did not sample needles as previous analyses found minimal effects of fire on needle NSC (Reed & Hood, 2024). Samples were transported to the lab on ice, where samples were immediately microwaved for three 30-s intervals in order to denature enzymes and stop respiration and hydrolysis (Landhäusser *et al.*, 2018; Piper & Reyes, 2020). The time between collection and microwaving was *c.* 4–6 h. Samples were frozen until further processing. Before grinding, samples were dried at 60°C for 48–72 h. We coarsely ground samples with a Wiley mill (Thomas Scientific, Swedesboro, NJ, USA) and then homogenized and ground them to a powder using a mixer mill (Retsch, Hann, Germany). Samples were dried again overnight before weighing for NSC analysis. Samples were measured for NSC (soluble sugars, starch) as described in Reed & Hood (2024). Briefly, we used the Landhäusser *et al.* (2018) protocol for NSC quantification and followed the enzyme method for quantification of sugars (glucose, fructose, and sucrose). We used a synthetic standard as described by Landhäusser *et al.* (2018) and two laboratory standards from ponderosa pine needles to ensure the reproducibility of results. Tissue concentrations are expressed on a dry matter basis (mg g^{-1}).

Data analyses

We tested for pre-burn differences in tree attributes (DBH, height, bark thickness, crown ratio, Ψ_{md}, estimated age) across sites (fall-burn, fall-control, spring-burn, spring-control) and between species using 2-way ANOVAs with site, species, and their interaction as predictor variables. We used Tukey's HSD for multiple pairwise comparisons. Within each combination of species and burn season, we used Welch's two-sample *t*-tests to compare DBH, height, bark thickness, crown scorch, and bud kill for trees that died by the end of the study and those that survived. We also examined pre-burn relationships between tree size (DBH, height) and physiological variables (NSC, K_s) and fire injuries, and found no significant relationships (data not shown). All statistical analyses were conducted in R v.4.4.1 (R Core Team, 2024).

We tested for differences in K_s between live-green branches from burned trees and unburned controls across timesteps using generalized linear mixed-effects models (GLMMs) and a difference-in-differences approach (Donald & Lang, 2007; Butsic *et al.*, 2017) to account for pre-burn differences between trees at burn and control sites. Briefly, the difference-in-differences approach calculates the treatment effect as the difference between the differences of burned and control observations before and at each timestep after the burns. We used the same approach to test for differences in NSC variables between burned and control trees. Root NSC was excluded from these analyses as we did not collect pre-burn samples. Using GLMMs with a lognormal distribution and log-link, we modeled K_s or NSC variables as a function of the fixed effect variables site treatment (burned, control), timestep, and their interaction. We built separate models for each species and site combination as we were interested in temporal fire effects specific to each species and site; therefore, sites are not intended to act as replicates. We included timestep within tree as a random effect. We adjusted SE of the parameters to account for temporal correlation due to remeasures of the same trees at the post-burn timesteps by incorporating a heterogenous compound symmetry covariance structure. We then built custom contrasts using the 'emmeans' package (Lenth, 2022) to compare differences between the burned and control trees from pre-burn to each timestep post-burn using the difference-in-differences approach. We tested for normality and overdispersion using simulation-based tests from the DHARMA package (Hartig, 2022). We used the GLMMTMB package for building GLMMs (Brooks *et al.*, 2017). In addition to comparisons between burned and control trees, we examined differences in K_s between scorched ponderosa pine branches with live buds (scorched) and non-scorched branches (green) on the same tree at the first post-burn timestep (3 wk) via paired *t*-tests.

At each timestep, we tested for relationships between physiological variables (K_s, total NSC in phloem, xylem, and roots) and crown scorch via generalized additive models (GAMs), as we expected nonlinear relationships (Reed & Hood, 2024). We found no pre-treatment relationships. We used the gam.check function in the MGCV package (Wood, 2017) to examine residuals via quantile-quantile plots and determine whether our selection of *k* fit the predictor.

To determine whether physiological changes preceded tree death or persisted in surviving burned trees, we examined differences in the magnitude of changes in K_s and NSC between tree outcomes (dead-burned, live-burned, live-control). We assessed both short-term (pre-burn to 3 wk post-burn) and mid-term changes (pre-burn to the end of the first summer post-burn (S2, F3)). If a tree died before the end of the first summer post-burn, we used values from its last live timestep. We modeled the percent change in K_s or NSC (from xylem, phloem) as a function of tree outcome using linear models with a dispersion formula to

account for differences in variances across tree outcomes. We built separate models for each species-site combination, although we pooled both species for fallsite models, allowing us to statistically analyze differences between tree outcomes, as only three ponderosa pine died by the study end at this site. We used percent change to account for both expected seasonal differences in NSC and pre-burn differences in variables between burned and control sites. We calculated simple changes (rather than percent change) in root NSC over the first summer post-burn because we did not have pre-burn data. We assessed model assumptions of normality via quantile-quantile plots. We used pairwise comparisons to determine whether short- or mid-term changes in physiological variables varied between tree outcome groups.

To assess burning effects on vulnerability to embolism formation, we compared P_{12}, P_{50}, and P_{88} from samples collected pre-burn (F0, S0) at both burn and control sites, and those collected 3 wk post-burn (F1, S1) at the burn site. Using linear mixed effects models, we modeled P_{12}, P_{50}, or P_{88} as a function of time-treatment category (control, pre-burn, post-burn), and included tree-tag number nested within site treatment as a random effect. We assessed normality via quantile-quantile plots. Pairwise comparisons were made to determine differences in vulnerability between controls, pre-burn, and post-burn samples. To determine whether needle scorch might indicate greater damage to xylem, we compared – via paired *t*-tests – P_{12}, P_{50}, or P_{88} of scorched ponderosa pine branches with live buds (i.e. scorched branches) to green branches from the same trees 3 wk post-fire. Finally, we examined vulnerability to embolism formation in ponderosa pine 23 months post-fire at the fall sites (F4). We compared values from branches of unburned controls and two branches from burned trees, one that clearly experienced scorch but survived (i.e. scorched), and one with minimal scorch (i.e. green). Means of these three categories were compared as described above, but with branch category (unburned control, burned-scorched, burned-green) as the predictor variable.

Lastly, we modeled tree mortality probability (burned sites) as a function of physiological and fire injury variables using binomial GLMMs with site (fall or spring) as a random effect. We did not intend this model to be predictive of tree mortality; rather, we aimed to identify the physiological variables that are most strongly linked to post-fire tree mortality. All predictors were scaled and centered to allow for effect size comparisons. We first used univariate models to explore relationships between tree mortality and the following variables: DBH, bark thickness, tree age estimate, CKR, crown scorch, Ψ_{pd}, Ψ_{md}, K_s, phloem sugars, phloem starch, phloem total NSC, xylem sugars, xylem starch, and xylem total NSC. For physiological variables, we used values from the end of the first summer post-burn (S2, F3) since most trees were still alive and physiological impacts were clear at this timestep (see Results). However, for trees that died before this timestep, we used values from their last live timestep. For NSC variables, we calculated the percent change from pre-burn to the S2/F3 timestep (11 months post-fire for fallsites, 4 months post-fire for spring sites) since we expected seasonal differences in NSC to be greater than differences between surviving and dying trees. We explored interactions between physiological variables and species, although none were significant ($P > 0.05$), so they were not included; thus, we proceeded with one model including both species. Of the univariate models, NSC variables (except xylem starch), K_s, tree age estimate, Ψ_{pd}, CKR, and crown scorch were included in the full model. We examined residuals for normality via quantile-quantile plots. Due to high collinearity between NSC variables, we built models with each variable separately and chose the variable that resulted in the lowest AIC (phloem sugars) for the final model (Table S3). Because our model is not predictive, we report one model that includes each variable identified as significant in the univariate models.

Results

Tree attributes

We observed no differences in DBH, height, and crown ratio between trees of the same species across the four season-site treatment combinations before the prescribed burns (Table S4). Despite similar tree sizes across the four sites, there was considerable variability in tree age, with a mean of 45.4 yr and a range from 23 to 154 yr (Table S4). Bark thickness was similar between trees of the same species across sites, although it was generally greater for ponderosa pine than for Douglas-fir (Table S4). Pre-burn water status was similar across species and sites, although ponderosa pine at the spring-burn site had slightly less negative (-0.86 ± 0.02), yet significantly different, mid-day water potential than the spring-control (-1.07 ± 0.03) (Fig. S3).

A total of 10 of 40 trees (15% ponderosa pine; 35% Douglas-fir) died by 22 months post-fire at the fall-burned site, whereas 17 of 40 (50% ponderosa pine, 35% Douglas-fir) died by 15 months post-fire at the spring-burned site (Table 1). We generally observed no differences in DBH and height between trees that died and those that survived within each species-site combination (Table 1). However, at the spring-burned site, Douglas-fir trees that died were smaller than those that survived, and both ponderosa pine and Douglas-fir that died had higher crown scorch. Trends were similar but not significant at the fall-burned site (Table 1). No trees died at either of the unburned control sites.

Impacts of fire on hydraulic conductivity and relationships with crown injury

After accounting for pre-burn differences between trees at the burn and control sites, differences in K_s between burned and control trees were not significant at any timestep or any site (Fig. 2). Similarly, K_s of scorched ponderosa pine branches at the fall-burn site ($M = 0.37$, SD = 0.11) did not differ from green branches ($M = 0.36$, SD = 0.17) on the same tree at the first timestep (F1, S1) post-fire ($t(9) = -1.92$, $P = 0.85$). However, K_s for scorched branches ($M = 0.33$, SD = 0.15) were lower compared to green branches ($M = 0.45$, SD = 0.1) at the spring-burned site 3 wk (S1) post-burn ($t(9) = 2.86$, $P = 0.02$). Native K_s and crown scorch were unrelated at any of the timesteps for either species (Fig. S4).

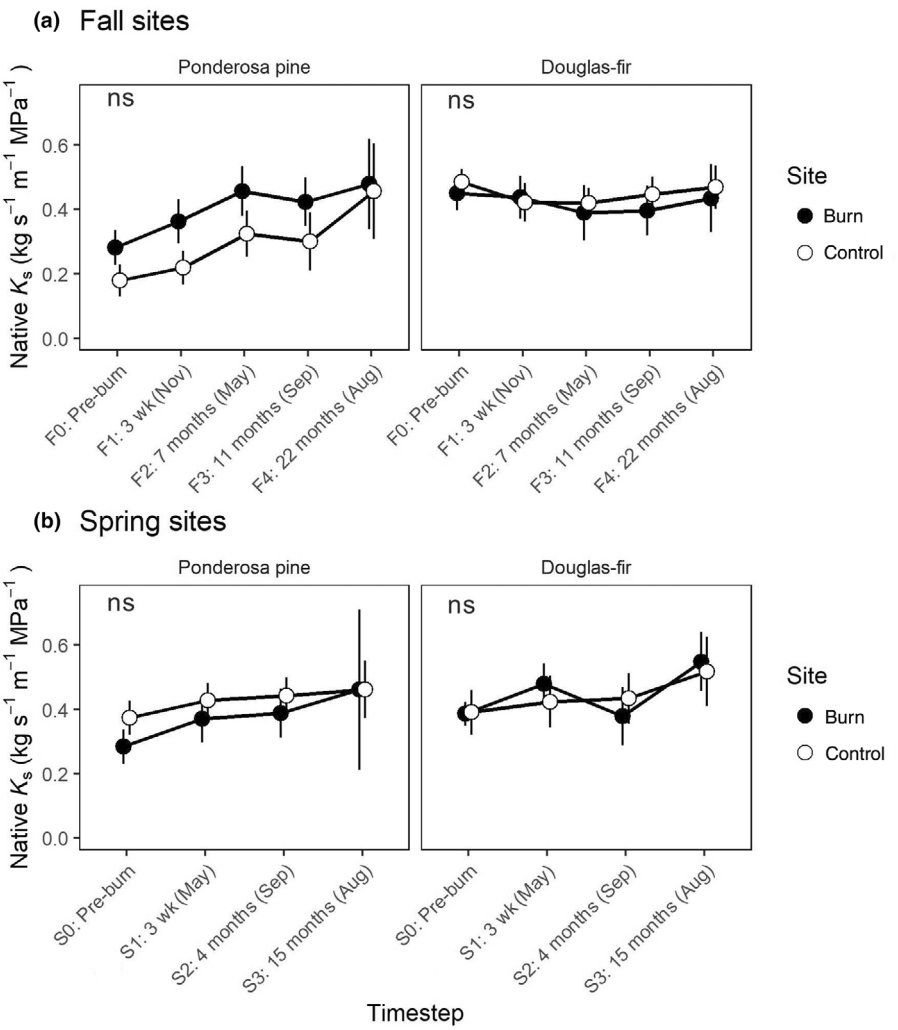

Fig. 2 Native hydraulic conductivity (K_s) from branches of live-burned (closed circles) and unburned control (open circles) ponderosa pine and Douglas-fir pre-burn and at each timestep post-burn. Samples were collected from fall (a) and spring (b) prescribed burn sites and their paired unburned control sites. Values are means, and error bars are 95% confidence intervals. We used GLMMs with a difference-in-differences approach to assess the significance of the treatment effect at each timestep after accounting for pre-burn differences between burn and control sites. No significant treatment effect (ns) was found for either species or either site at any timestep.

While changes in K_s from pre-burn (F0, S0) to 3 wk post-burn (F1, S1) did not differ between trees that eventually died (dead-burned), those that survived (live-burned), and unburned controls (live-control), some differences emerged by the end of the first summer (S2, F3) post-fire (Fig. 3). Fall-burned trees that died generally had no change or a decrease in K_s in comparison to live-burned and live-control trees, which tended to increase over the same duration (Fig. 3a). This was particularly true for Douglas-fir, which comprised the majority of dying trees at the fall-burned site and showed the strongest differences between dying and surviving trees at the spring-burned site (Fig. 3b).

Impacts of fire on vulnerability to embolism formation

Vulnerability to embolism formation (P_{12}, P_{50}, P_{88}) generally did not differ between unburned branches (control), branches from burn site trees before burning (pre-burn; F0, S0), and live branches from burned trees 3 wk post-burn (post-burn; F1, S1) (Table S5). P_{50} of Douglas-fir at the fall site did increase significantly from pre-burn to post-burn, but this increase was small and not in the direction of expected effects of burning on vulnerability. Similarly, vulnerability did not differ between scorched and green branches sampled from the same tree at the first post-burn timestep for either species, nor at 23 months post-burn (F4) when only ponderosa pine was assessed (Tables S6, S7). Because we did not see changes in vulnerability to embolism formation post-fire, we did not look further for xylem deformities in these samples.

Impacts of fire on NSC

In general, NSC declined for burned trees relative to unburned controls at both spring and fall sites, and for both species (Figs 4, S5). The magnitude of the impact of burning on NSC was generally greater in the phloem tissue than in the xylem for both fall- and spring-burned sites (Fig. 4). Declines in phloem NSC at the fall site were attributable mostly to strong initial declines in starch, whereas at the spring site, NSC declines were due to changes in both sugars and starch (Fig. S5). By the end of the second summer post-fire (S3, F4), NSC had not completely recovered to the levels of unburned control trees, although Douglas-fir NSC appeared to be getting closer to recovery than ponderosa pine (Figs 4, S5).

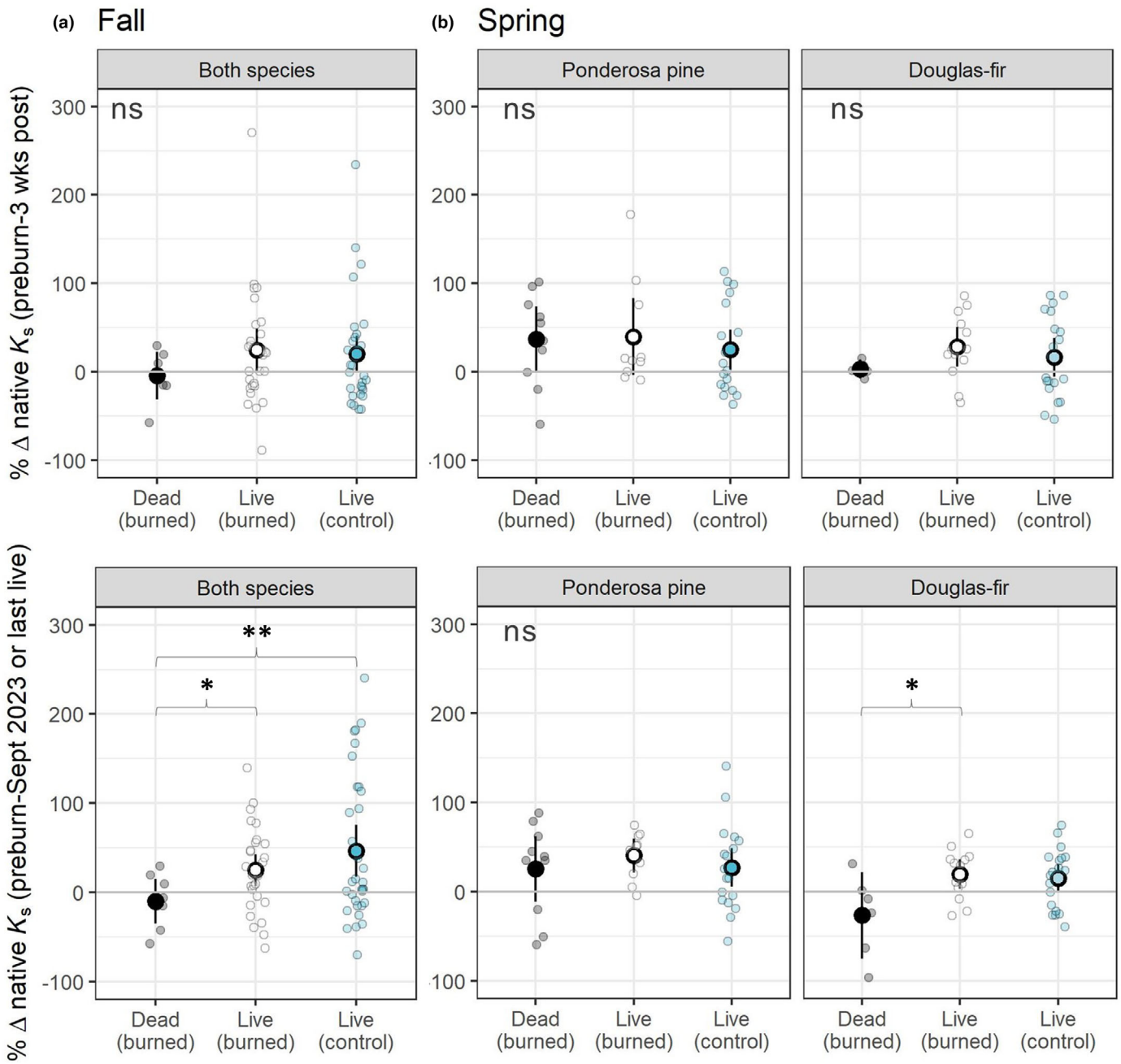

Fig. 3 Percent changes in native hydraulic conductivity (K_s) for trees that eventually died but were alive at the measurement timestep (dead-burned), those that survived but were burned (live-burned) and unburned controls (live-control) at the fall sites (a) and spring sites (b). Species (ponderosa pine, Douglas-fir) were combined at the fall site because only three ponderosa pine had died by the end of the study. Changes are from pre-burn (F0, S0) to 3 wk post-burn (F1, S1) (upper panel) or to the end of the first summer post-burn (S2, F3) (lower panel). We included trees that died before September 2023 by using their values at the last timestep at which they were alive. Significant differences determined from linear models with pairwise comparisons between tree outcomes are noted with asterisks. Non-significant differences noted with ns. Values are means, and error bars are 95% confidence intervals. *, $P < 0.05$; **, $P < 0.01$.

Relationships between NSC and crown injury

Phloem and xylem NSC tended to be lower in trees with higher levels of crown scorch (Fig. 5). Clear negative relationships emerged in the first spring post-fire for both fall-burn (F2; 7 months post-fire) and spring-burn (S1; 3 wk post-fire) sites (Fig. 5). Although there were no clear relationships between total NSC and crown scorch at the first post-burn timestep (F1) at the fall-burn site, significant negative relationships emerged 7 months post-burn (F2) in xylem and phloem tissues but not roots (Figs S6, S7). Dying ponderosa pine tended to have high crown scorch and low NSC at the spring-burn site, but this

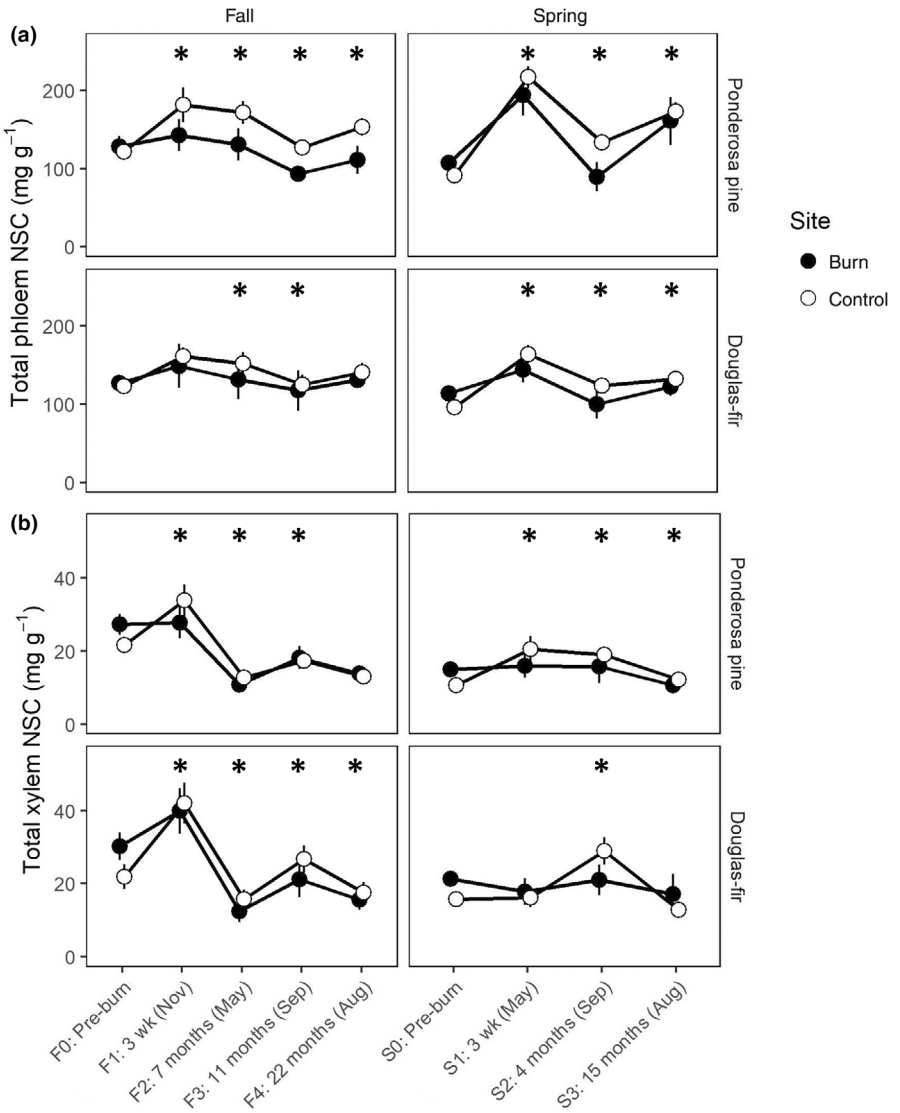

Fig. 4 Total non-structural carbohydrates (NSC) from phloem (a) and xylem (b) of live-burned (closed circles) and unburned control (open circles) ponderosa pine and Douglas-fir pre-burn and at each timestep post-burn. Values are means, and error bars are 95% confidence intervals. Data for starch and soluble sugars are shown separately in Supporting Information Fig. S5. We used GLMMs with a difference-in-differences approach to assess the significance of the treatment effect at each timestep after accounting for pre-burn differences between burn and control sites. Significant difference ($P < 0.05$) between burned and control samples in comparison to pre-burn differences is indicated with an asterisk.

pattern did not always hold for Douglas-fir or the fall-burn site. By the end of the first summer post-burn (F3), negative NSC-crown scorch relationships were only significant for Douglas-fir at the fall-burn site. At the spring-burn site, these negative relationships did not persist beyond the end of the first summer post-burn for either species (Fig. S8). Interestingly, by the end of the second summer post-burn (S3), the relationship between xylem NSC and crown scorch reversed from negative to positive at the spring-burn site for both species (Fig. S8).

Changes in NSC post-fire and tree mortality

Unlike hydraulic conductivity, xylem and phloem NSC of trees that eventually died clearly decreased or increased to a smaller degree, relative to surviving burned trees (live-burned) or unburned control trees (live-control), from pre-burn (F0, S0) to 3 wk post-burn (F1, S1) (Fig. 6). The NSC decline for trees that eventually died, relative to live-burned and live-control, generally held true when comparing pre-burn to the end of the first summer post-burn (S2, F3) as well (Fig. 6). Root NSC patterns were somewhat consistent with xylem and phloem NSC, with NSC declining more over the first summer post-fire for trees that died in the fall burn and Douglas-fir that died in the spring (Fig. S9). We did not sample root NSC pre-fire, so we would not expect the magnitude of these changes to be as pronounced.

Mortality model

Trees that died tended to have declining phloem sugars and signs of hydraulic stress before death (Table 2; Fig. 7). Tree mortality after fire was influenced most strongly by the change in phloem sugars from pre-burn to the end of the first summer post-burn, followed by CKR, pre-dawn water potential at the end of the first summer post-fire (S2, F3), and K_s, respectively (Table 2). Tree age and crown scorch were not significant

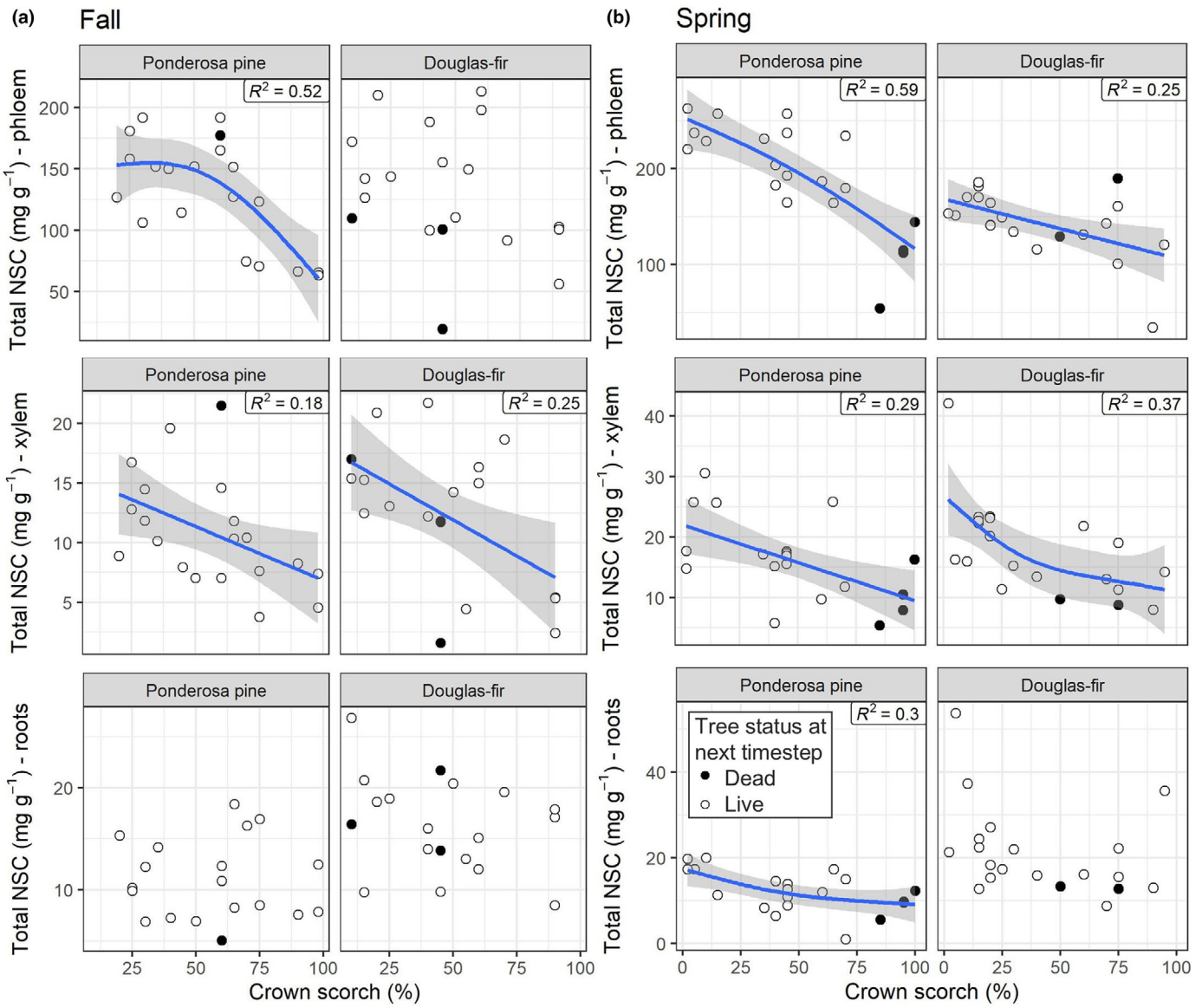

Fig. 5 Relationships between non-structural carbohydrates (NSC) in the phloem, xylem, and roots and percent crown scorch sustained by ponderosa pine and Douglas-fir during a spring (a) and spring (b) prescribed fire. Relationships assessed in the first spring (May) post-fire (S1, F2). Point color indicates whether the tree was alive or dead at the following timestep. Significant ($P < 0.05$) relationships from GAMs with 95% confidence intervals and adjusted-R^2 values are shown.

predictors of tree death (Table 2). Although tree size and bark thickness are typically important variables in post-fire tree mortality models (Cansler *et al.*, 2020), it is unsurprising that they were not included in ours, as we specifically selected similarly sized trees for our study. When we visualized the relationship between the percent change in phloem sugars and each of the two water-related predictors (K_s and pre-dawn water potential), it is clear that the strongest separator of surviving and dying trees is the change in sugars (Fig. 7). Nearly all trees that died had a decrease or negligible increase in phloem sugars over the time period assessed, and dying trees had, on average, lower K_s as well as lower and more variable pre-dawn water potential (Fig. 7).

Discussion

We used two prescribed burns to address hypotheses about the relative impacts of fire on tree hydraulic function and carbon balance and their contributions to post-fire tree function and mortality. We find that fire-caused impacts to NSC are immediate, persistent, strongly related to post-fire mortality, and consistently correlated with the degree of crown injury, whereas hydraulic impacts are indirect, delayed, and not directly attributable to fire-caused injuries. However, hydraulic impacts are likely still important in explaining post-fire mortality, as we find that some trees that go on to die exhibit signs of hydraulic stress (reduced hydraulic efficiency and increased tissue water stress) before

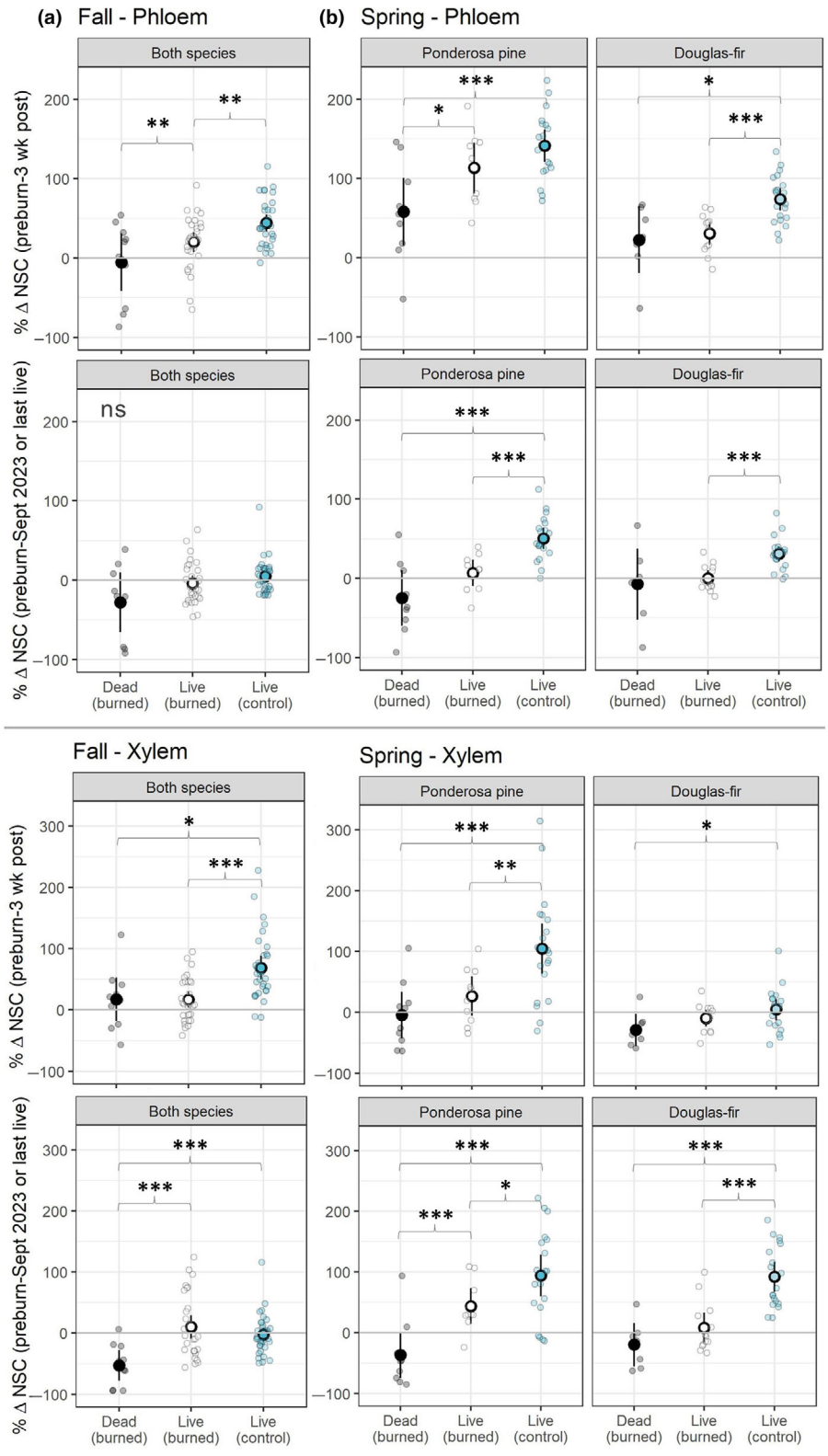

Fig. 6 Percent changes in phloem (upper panels) and xylem (lower panels) total non-structural carbohydrates (NSC) for ponderosa pine and Douglas-fir that eventually died but were alive at the measurement timestep (dead-burned), those that survived but were burned (live-burned), and unburned controls (live-control) at the fall sites (a) and spring sites (b). Changes are short-term (upper panels) and longer-term (lower panels). We included trees that died before September 2023 (S2, F3) by including their values at the last timestep at which they were alive. Significant differences determined from linear models with pairwise comparisons between tree outcomes are noted with asterisks. Non-significant differences noted with ns. Values are means, and error bars are 95% confidence intervals. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

death. This suggests that fire may have an indirect effect on hydraulic function and water relations, possibly due to changes in tree-level carbon balance (Sala *et al.*, 2012). While past research on fire-caused impacts to tree physiology has acknowledged the potential for interactions between tree-level carbon balance and hydraulic function, most research has examined these mechanisms independently (Bär *et al.*, 2019). Our results suggest that these effects may indeed be interrelated, with direct impacts on

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Table 2 Coefficients for tree mortality model.

Intercept	CKR = high	Crown scorch	Native K_s	Pre-dawn water potential	% change in phloem sugars	Age estimate
−3.147	**3.157**	−0.076	**−2.025**	**−2.216**	**−5.249**	1.666

Bold indicates significance ($P < 0.05$) of the predictor in best-fit binomial GLMM. CKR, cambium kill rating. Native hydraulic conductivity (K_s) and pre-dawn water potential were measured at the end of the first growing season post-burn or at the last live timestep if the tree died before then. The percent change in phloem sugars was calculated from pre-burn to that same timestep. The model includes both ponderosa pine and Douglas-fir and both spring- and fall-burned sites. All variables were scaled before inclusion in the model.

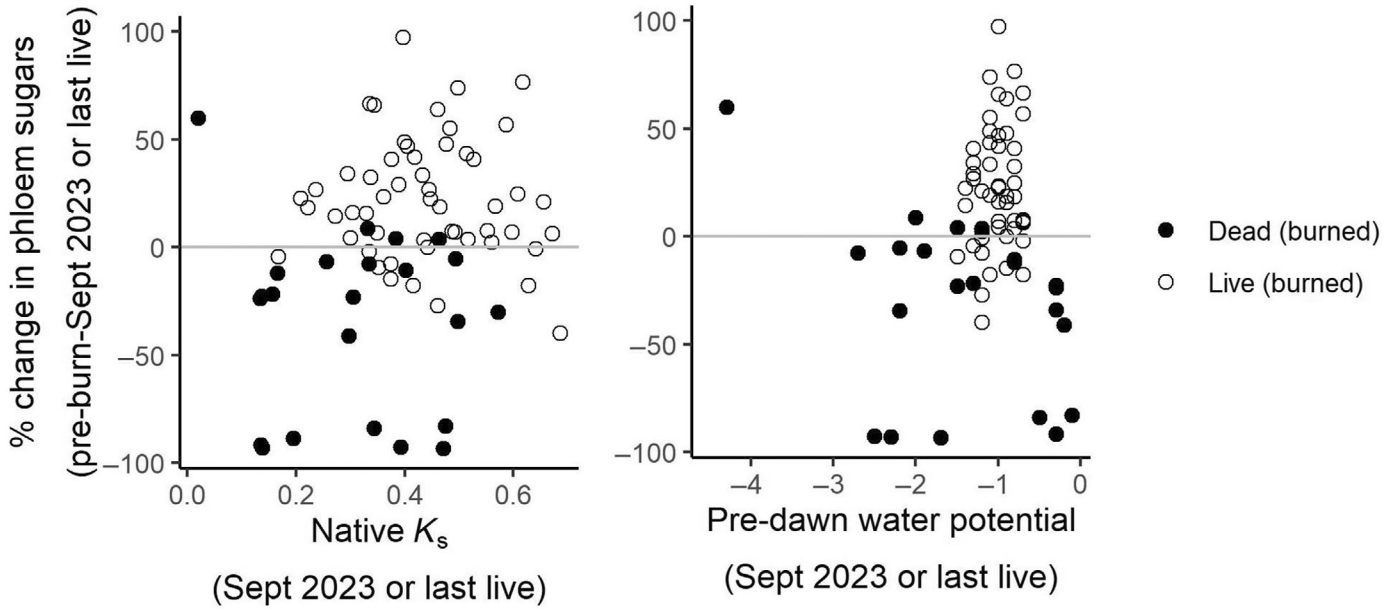

Fig. 7 Relationships between the percent change in phloem sugars from pre-burn to the end of the first summer post-burn (or last live timestep for trees that died prior) and native hydraulic conductivity (K_s) at the same post-burn timestep (left) or pre-dawn water potential (right). Includes both ponderosa pine and Douglas-fir and both spring- and fall-burned sites. Trees that went on to die are noted with closed circles.

NSC dynamics acting as a precipitating agent for indirect effects on tree hydraulics and water balance that work in tandem to drive post-fire mortality.

We saw immediate and lasting impacts of fire on NSC (Fig. 4), with declines strongly linked to post-fire mortality (Table 2; Fig. 6). Changes in phloem soluble sugars in particular were the strongest predictor of mortality, with nearly all trees that died either experiencing declines or no change in sugars from pre-burn to the end of the first growing season post-burn (Table 2; Fig. 7). Post-fire NSC dynamics also appear to be directly attributable to the magnitude of fire-caused injuries (Fig. 5), which affect both carbon acquisition and transport. Trees with more severe injuries may also have higher carbon demands for tissue regrowth and wound compartmentalization. Consistent with prior work, negative relationships between post-fire NSC and crown scorch for both study species (Fig. 5) suggest that direct impacts of fire on NSC are likely due to the combination of fire injuries to foliage and phloem tissues (Partelli-Feltrin *et al.*, 2023; Reed & Hood, 2024). However, our study did not allow us to determine the degree to which these relationships were due to reduced acquisition of carbohydrates or greater phloem necrosis in branches and/or stems of trees with higher crown scorch. Parsing out the relative contribution of each will require a controlled laboratory study. While some recent work has suggested that post-fire photosynthetic capacity may increase in ponderosa pine with high levels of crown scorch (Bryant *et al.*, 2022), our results suggest that if this does occur, it may not be sufficient to override the effects of reduced leaf area. Interestingly, fall-burned trees experienced immediate effects (3 wk post-burn; F1) on NSC, yet no immediately clear relationships between NSC and crown scorch (Fig. S6). This suggests that areas of phloem necrosis may have hindered NSC transport to the main stem, where samples were collected. However, negative relationships between NSC and crown scorch the following spring (F2) suggest that reduced leaf area may affect NSC acquisition more during the growing season (Figs 5, S6). Our mortality model provided further evidence that crown scorch may not be the only link between fire injury and post-fire NSC declines, as it showed that the level of cambium kill a tree sustained was a better predictor of post-fire mortality than crown scorch (Table 2). This suggests that disruption of phloem transport, as expected with high cambium kill, is likely also contributing to

observed NSC declines. This result is somewhat surprising given the preferential inclusion of crown scorch over cambium kill in most post-fire mortality models for mature thick-barked trees (Cansler *et al.*, 2020), yet it may be explained by the relatively small size of our trees, and thus thinner bark, which may have led to greater cambium kill. Still, irrespective of what type of fire injury causes NSC declines, it is clear that NSC reduction is related to post-fire mortality and may have lasting impacts even in surviving trees.

Recent work on the mechanisms of post-fire tree mortality has primarily focused on impacts to hydraulic function (Salladay & Pittermann, 2023; West *et al.*, 2023; Hoffmann *et al.*, 2024) in response to observations of rapid post-fire tree decline, which is not expected from heat girdling or foliage necrosis alone (Michaletz *et al.*, 2012). However, work using fire rather than fire proxies to examine hydraulic impacts has found little evidence that non-lethal fire directly and immediately affects hydraulic function (Battipaglia *et al.*, 2016; Partelli-Feltrin *et al.*, 2021). Similarly, we see little evidence for direct effects of fire on hydraulic function in two thick-barked conifer species. After accounting for pre-burn differences between sites (burn, control), K_s of green branches on fire-injured trees were unaffected by burning across all timesteps (Fig. 2). However, for spring-burned ponderosa pine, we did see moderately lower K_s in scorched branches with live buds in comparison to green branches on the same tree 3 wk post-fire, suggesting potential support for the heat plume hypothesis for branches experiencing temperatures hot enough to cause scorch. We did not see these patterns for fall-burned trees, possibly due to differing phenological stages during the burns, with fall-burned trees nearing dormancy. Indeed, recent work has shown greater heat tolerance of buds in the dormant season (Bär *et al.*, 2021; Bison *et al.*, 2022). Even if the difference in K_s between scorched and green branches on spring-burned ponderosa pine was caused by heat-induced embolism formation, the magnitude of this effect was small (mean difference of 0.12 kg s^{-1} m^{-1} MPa^{-1}) and did not spread beyond scorched branches, so it is unlikely to play a significant role in post-fire mortality for trees that initially survive unless crown scorch is very high. However, it is still possible that this type of heat-induced cavitation plays a role in branch and needle necrosis that occurs during fire or that hydraulic segmentation in our study species prevented the spread of embolisms beyond affected branches (West *et al.*, 2023).

We similarly saw no evidence for greater vulnerability to embolism formation in live branches from burned trees relative to controls, or when comparing scorched and green branches on the same tree, as would be expected if fire causes xylem deformation (Tables S5, S6). Likewise, there were no long-term (23 months post-fire; F4) differences in vulnerability in ponderosa pine branches, despite clear formation of fire scars on some of our sampled branches (Table S7). These results contrast with those of Partelli-Feltrin *et al.* (2021) who found that deformities in newly formed xylem around fire scars on the stems of ponderosa pine seedlings led to greater vulnerability to embolisms. These differences could be due to greater resistance to embolism formation in branches than stems (Johnson *et al.*, 2016) or differences in physiological fire effects between seedlings and larger trees, although this has not been explored. Still, the lack of any evidence for this in surviving branches suggests it may not be common or important to post-fire survival. Indeed, a study that followed mature *Pinus pinea* L. after prescribed burning found no impacts to xylem vulnerability in main tree stems (Battipaglia *et al.*, 2016). Additionally, we did not see any evidence of necrosis extending into the xylem when we cut sections from the base of trees that had died. Our results add support to the notion that heating intense enough to cause extensive xylem deformation is likely to result in immediate branch death and widespread necrosis of the cambium and phloem, and thus, xylem deformities are not likely a key physiological impact of fire in surviving stems or branches on their own (Partelli-Feltrin *et al.*, 2023; Salladay & Pittermann, 2023).

While our results generally support our first and second hypotheses that fire-caused impacts to NSC are stronger than hydraulic effects and more clearly related to post-fire mortality, we also found indications that water stress was greater in some trees that eventually died post-fire. Within 3 wk post-fire, impacts to NSC were evident, particularly for trees that eventually died (Fig. 6), yet hydraulic impacts were not apparent within this same timeframe (Fig. 3). However, hydraulic effects became apparent by the end of the first summer post-fire (S2, F3), particularly for Douglas-fir, when, on average, K_s of trees that eventually died declined relative to surviving burned trees or controls (Fig. 3). Stronger impacts on Douglas-fir could possibly be explained by its generally higher hydraulic burden relative to ponderosa pine, due to its higher leaf area to sapwood ratio (Piñol & Sala, 2000). Interestingly, unlike for NSC, there were no differences between surviving burned and control trees. This, in conjunction with the lack of initial differences in K_s between dying and surviving trees and no clear relationships with fire injury, suggests that the delayed decline in K_s for dying trees may be a symptom of tree decline rather than a cause directly attributable to impacts from fire. Further supporting this is the lack of difference in vulnerability to embolism formation (P_{12}, P_{50}, P_{88}) we observed between burned and unburned trees both 3 wk and 23 months post-fire (Table S7). Because we assessed long-term changes in vulnerability in only ponderosa pine, it is possible that wound responses in Douglas-fir led to greater vulnerability in the longer term (Partelli-Feltrin *et al.*, 2021). However, the fact that we did not see any evidence for this even in scorched branches of ponderosa pine suggests it is unlikely a widespread occurrence. Even if hydraulic impacts are not directly related to fire injuries, they are still clearly important for post-fire tree mortality as our mortality model indicated that dying trees exhibited both tissue water stress and lower hydraulic efficiency before death (Table 2).

There are a few possible explanations for the observed declines in K_s of dying trees. First, fine root die-off due to lack of NSC could decrease water availability, leading to increases in xylem tensions and formation of embolisms throughout the tree, thus reducing K_s (McDowell, 2011; Wiley *et al.*, 2017). Indeed, we saw that pre-dawn water potential was a significant predictor in our model, with dying trees having generally lower pre-dawn water potential before death (Fig. 7; Table 2), suggesting that

trees that die may be struggling to access soil water. This somewhat contrasts with work suggesting that high levels of crown scorch may reduce water stress of surviving needles in mature ponderosa pine (Wallin *et al.*, 2003; Bryant *et al.*, 2022), although this may only be true for larger trees with thicker bark and therefore fewer areas of phloem necrosis inhibiting transport of NSC to fine roots. Larger trees with high levels of fire injury may also persist longer post-fire than the smaller trees in our study if NSC stores are greater in larger trees (Woodruff & Meinzer, 2011). Second, the relationship between declining phloem sugars and post-fire mortality could suggest that reduced availability of soluble sugars, which are important for osmoregulation and turgor maintenance (Sapes *et al.*, 2021; Natale *et al.*, 2023), increased the likelihood of hydraulic dysfunction. While impaired osmoregulation and a resulting increase in xylem vulnerability to embolism have been linked to reductions of NSC in angiosperms, this has not been tested in gymnosperms (Tomasella *et al.*, 2021; Natale *et al.*, 2023). If the drawdown we see in phloem sugars of the main stem is linked to the decline in hydraulic conductivity of branches, it is likely only happening in a subset of trees since not all dying trees with decreases in phloem sugars had low K_s (Fig. 7). However, it is also possible that we did not always capture the decline in K_s before death since this may be a late-stage symptom of the death spiral that is difficult to capture when mortality occurs progressively over many months, as was the case in our study.

Overall, species and burn season differences were relatively small, providing only partial support for our third hypothesis. We saw some evidence that ponderosa pine may recover from crown impacts more quickly than Douglas-fir, particularly at our fall-burn site where negative relationships between NSC and crown scorch had become neutral by 11 months post-fire (F3) while they persisted for Douglas-fir (Figs S6, S7). This is likely attributable to the relatively heat-resistant buds of ponderosa pine and thus the ability to regrow needles more quickly post-fire (Hood *et al.*, 2018a). While there is a paucity of research comparing physiological effects of fire across burn seasons, spring burns have been found to result in greater mortality than fall burns after accounting for differences in crown scorch due to varying fire intensity (Valor *et al.*, 2017). Our work suggests that these differences in mortality across burn seasons could be partially due to differences in the timing of impacts from crown injuries, with spring-burned trees emerging from dormancy experiencing immediate impacts from crown scorch on NSC (Figs 5, S6). However, additional data from other species and sites are needed to more fully understand how species traits and fire seasonality influence tree physiology and survival after fire.

Although negative relationships between crown scorch and NSC had mostly become neutral by the end of the study period, some differences did remain between the NSC of burned and control trees (Fig. 4), suggesting that recovery was not complete by 15 months (spring sites; S3) and 22 months (autunsites; F4) post-burn. Interestingly, the negative relationship between xylem NSC and crown scorch had switched to a positive relationship by 15 months post-burn for both species at the spring-burned site (Fig. S8). Because this pattern occurred only for xylem NSC, which is considered a longer-term storage pool than phloem (Furze *et al.*, 2018), we postulate that trees with more severe fire injuries may be prioritizing NSC storage during the post-fire period of carbon imbalance (Huang *et al.*, 2021). We see further evidence of this with weaker impacts of burning on starch than sugars in both xylem and phloem (Fig. S5). This is perhaps not surprising, since some trees that experience drought stress or defoliation also increase NSC storage during stress, often at the expense of growth (Wiley & Helliker, 2012; Adams *et al.*, 2013; Wiley *et al.*, 2013).

Trees that survive the first year or two post-fire and begin to recover may also be affected by persistent impacts to carbon acquisition and transport. Growth is often reduced in the first few years post-fire (Peterson *et al.*, 1991; Willson *et al.*, 2024), yet how the length of the post-fire growth recovery period relates to NSC impacts has not been explored. Slow growth is linked to greater post-fire mortality (van Mantgem *et al.*, 2020), and also to mortality from drought (Cailleret *et al.*, 2017), which combined with potential impacts of reduced NSC on hydraulic function, may mean greater tree susceptibility to post-fire drought or future fires. Similarly, reduced NSC may affect susceptibility to insects (Huang *et al.*, 2020). While our study trees were not large enough to host primary bark beetles, future studies could further integrate fire impacts to tree defense and NSC with susceptibility to bark beetles post-fire. As drought frequency and intensity increase and interact with insect outbreaks (Robbins *et al.*, 2022), particularly in parts of the world where wildfires are common, an understanding of how fire-caused NSC reductions interact with these disturbances is needed.

Our results suggest that fire impacts to NSC transport and acquisition are likely more important than immediate hydraulic impacts for both post-fire mortality and mid- to long-term impacts on tree physiological function in thick-barked conifers. This is perhaps not surprising as NSC stores are important for many functions that are critical in the post-fire period, including compartmentalization of fire-caused wounds, growth of new tissues, and basic maintenance of tree metabolism (Hartmann & Trumbore, 2016). We also find that branch hydraulic efficiency and tissue water status of some trees that die post-fire decrease before death and that these reductions are likely a late-stage symptom of tree decline rather than its cause. We posit that pre-death declines in hydraulic function may be linked to fire-related impacts to soluble sugar acquisition and transport that affect osmoregulation and turgor maintenance and/or lead to fine root die-off. However, we cannot rule out the possibility that fire-caused damage to the hydraulic system within the main stem (rather than branches) also contributed to delayed hydraulic stress. Still, fire impacts to NSC pools are direct, immediate, and clearly associated with post-fire mortality. Nonstructural carbohydrate declines are also likely to have consequences for the maintenance of tree water status, the length of time needed for recovery post-fire, vulnerability to other disturbances (e.g. pests and pathogens), and post-fire growth and reproduction. All of these consequences are particularly important in the context of increased fire occurrence and fire use as a management tool as well as the changing dynamics of other disturbances such

as drought or insect outbreaks which likely interact with these fire-caused physiological effects.

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Competing interests

None declared.

Author contributions

CCR and AS designed the research and conceptualized the project. CCR led data collection, analysis, and interpretation, and writing of the manuscript. AS, SMH and ARR contributed to the interpretation of the data and the writing and editing of the manuscript.

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Data availability

Data are archived and available on Dryad: DOI 10.5061/dryad.qv9s4mws1.

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.

Bär A, Michaletz 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.

Bär A, Schröter DM, Mayr S. 2021. When the heat is on: high temperature resistance of buds from European tree species. *Plant, Cell & Environment* **44**: 2593–2603.

Battipaglia G, Savi T, Ascoli D, Castagneri D, Esposito A, Mayr S, Nardini A. 2016. Effects of prescribed burning on ecophysiological, anatomical and stem hydraulic properties in *Pinus pinea* L. *Tree Physiology* **36**: 1019–1031.

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.

Brooks ME, Kristensen K, Van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Machler M, Bolker BM. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal* **9**: 378–400.

Bryant KN, Stenzel J, Mathias J, Kwon H, Kolden CA, Lynch L, Hudiburg T. 2022. Boosts in leaf-level photosynthetic capacity aid *Pinus ponderosa* recovery from wildfire. *Environmental Research Letters* **17**: 114034.

Busby S, Evers C, Holz A. 2024. Patterns, drivers, and implications of postfire delayed tree mortality in temperate conifer forests of the western United States. *Ecosphere* **15**: e4805.

Butsic V, Lewis DJ, Radeloff VC, Baumann M, Kuemmerle T. 2017. Quasi-experimental methods enable stronger inferences from observational data in ecology. *Basic and Applied Ecology* **19**: 1–10.

Cailleret M, Jansen S, Robert EM, Desoto L, Aakala T, Antos JA, Beikircher B, Bigler C, Bugmann H, Caccianiga M. 2017. A synthesis of radial growth patterns preceding tree mortality. *Global Change Biology* **23**: 1675–1690.

Cansler CA, Hood SM, Van Mantgem PJ, Varner JM. 2020. A large database supports the use of simple models of post-fire tree mortality for thick-barked conifers, with less support for other species. *Fire Ecology* **16**: 1–37.

Dickman LT. 2024. Tree mortality after a spring fire: the role of reduced live leaf area in depletion of early growing season bole NSC. *Tree Physiology* **44**: tpae063.

Dietze MC, Sala A, Carbone MS, Czimczik CI, Mantooth JA, Richardson AD, Vargas R. 2014. Nonstructural carbon in woody plants. *Annual Review of Plant Biology* **65**: 667–687.

Donald SG, Lang K. 2007. Inference with difference-in-differences and other panel data. *The Review of Economics and Statistics* **89**: 221–233.

Duursma R, Choat B. 2017. FITPLC – an R package to fit hydraulic vulnerability curves. *Journal of Plan Hydraulics* **4**: e002.

Ennajeh M, Simões F, Khemira H, Cochard H. 2011. How reliable is the double-ended pressure sleeve technique for assessing xylem vulnerability to cavitation in woody angiosperms? *Physiologia Plantarum* **142**: 205–210.

Furze ME, Trumbore S, Hartmann H. 2018. Detours on the phloem sugar highway: stem carbon storage and remobilization. *Current Opinion in Plant Biology* **43**: 89–95.

Hartig F. 2022. DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R Package v.0.4.6. [WWW document] URL https://CRAN.R-project.org/package=DHARMa.

Hartmann H, Trumbore S. 2016. Understanding the roles of nonstructural carbohydrates in forest trees–from what we can measure to what we want to know. *New Phytologist* **211**: 386–403.

Hoffmann WA, Sherry CD, Donnelly TM. 2024. Stem heating results in hydraulic dysfunction in *Symplocos tinctoria*: implications for post-fire tree death. *Tree Physiology* **44**: tpae023.

Hood SM, Abrahamson I, Cansler CA. 2018a. *Fire resistance and regeneration characteristics of Northern Rockies tree species.* Fire Effects Information System. USDA Forest Service, Rocky Mountain Research Station, Missoula Fire Sciences Laboratory (Producer). [WWW document] URL https://www.feis-crs.org/feis/ [accessed 1 November 2024].

Hood SM, Harvey BJ, Fornwalt PJ, Naficy CE, Hansen WD, Davis KT, Battaglia MA, Stevens-Rumann C, Saab V. 2021. Fire ecology of Rocky Mountain forests. In: Collins B, Greenberg CH, eds. *Fire ecology and management: past, present, and future of US forested ecosystems.* Berlin, Germany: SpringerNature.

Hood SM, Smith S, Cluck D. 2010. Predicting tree mortality for five California conifers following wildfire. *Forest Ecology and Management* **260**: 750–762.

Hood SM, Varner JM, VAN Mantgem P, Cansler CA. 2018b. Fire and tree death: understanding and improving modeling of fire-induced tree mortality. *Environmental Research Letters* **13**: 113004.

Huang J, Hammerbacher A, Gershenzon J, Van Dam NM, Sala A, Mcdowell NG, Chowdhury S, Gleixner G, Trumbore SAND, Hartmann H. 2021.

Storage of carbon reserves in spruce trees is prioritized over growth in the face of carbon limitation. *Proceedings of the National Academy of Sciences, USA* **118**: e2023297118.

Huang J, Kautz M, Trowbridge AM, Hammerbacher A, Raffa KF, Adams HD, Goodsman DW, Xu C, Meddens AJ, Kandasamy D. 2020. Tree defence and bark beetles in a drying world: carbon partitioning, functioning and modelling. *New Phytologist* **225**: 26–36.

Johnson DM, Wortemann R, Mcculloh KA, Jordan-Meille L, Ward E, Warren JM, Palmroth S, Domec J-C. 2016. A test of the hydraulic vulnerability segmentation hypothesis in angiosperm and conifer tree species. *Tree Physiology* **36**: 983–993.

Jones MW, Abatzoglou JT, Veraverbeke S, Andela N, Lasslop G, Forkel M, Smith AJ, Burton C, Betts RA, Van Der Werf GR. 2022. Global and regional trends and drivers of fire under climate change. *Reviews of Geophysics* **60**: e2020RG000726.

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.

Knapp EE, Estes BL, Skinner CN. 2009. *Ecological effects of prescribed fire season: a literature review and synthesis for managers*. Washington, DC, USA: USDA Forest Service General Technical Report PSW-GTR-224.

Kolden CA. 2019. We're not doing enough prescribed fire in the Western United States to mitigate wildfire risk. *Firehouse* **2**: 30.

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

Lenth RV. 2022. Emmeans: estimated marginal means, aka least-squares means, v.1.8.

Lodge AG, Dickinson MB, Kavanagh KL. 2018. Xylem heating increases vulnerability to cavitation in longleaf pine. *Environmental Research Letters* **13**: 055007.

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.

Mcdowell NG. 2011. Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality. *Plant Physiology* **155**: 1051–1059.

Michaletz ST, Johnson EA. 2007. How forest fires kill trees: a review of the fundamental biophysical processes. *Scandinavian Journal of Forest Research* **22**: 500–515.

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

Miller RG, Tangney R, Enright NJ, Fontaine JB, Merritt DJ, Ooi MK, Ruthrof KX, Miller BP. 2019. Mechanisms of fire seasonality effects on plant populations. *Trends in Ecology & Evolution* **34**: 1104–1117.

Morgan G, Tolhurst KG, Poynter M, Cooper N, Mcguffog T, Ryan R, Wouters M, Stephens N, Black P, Sheehan D. 2020. Prescribed burning in south-eastern Australia: history and future directions. *Australian Forestry* **83**: 4–28.

Natale S, Tomasella M, Gargiulo S, Petruzzellis F, Tromba G, Boccato E, Casolo V, Nardini A. 2023. Stem photosynthesis contributes to non-structural carbohydrate pool and modulates xylem vulnerability to embolism in *Fraxinus ornus* L. *Environmental and Experimental Botany* **210**: 105315.

Nolan RH, Collins L, Leigh A, Ooi MK, Curran TJ, Fairman TA, De Resco Dios V, Bradstock R. 2021. Limits to post-fire vegetation recovery under climate change. *Plant, Cell & Environment* **44**: 3471–3489.

Nolan RH, Reed CC, Hood SM. 2024. Mechanisms of fire-caused tree death are far from resolved. *Tree Physiology* **44**: tpae073.

Partelli-Feltrin R, Smith AM, 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.

Partelli-Feltrin R, Smith AM, Adams HD, Thompson RA, Kolden CA, Yedinak KM, Johnson DM. 2023. Death from hunger or thirst? Phloem death, rather than xylem hydraulic failure, as a driver of fire-induced conifer mortality. *New Phytologist* **237**: 1154–1163.

Peterson DL, Arbaugh MJ, Pollock GH, Robinson LJ. 1991. Postfire growth of Pseudotsuga menziesii and *Pinus contorta* in the Northern Rocky Mountains, USA. *International Journal of Wildland Fire* **1**: 63–71.

Piñol J, Sala A. 2000. Ecological implications of xylem cavitation for several Pinaceae in the Pacific Northern USA. *Functional Ecology* **14**: 538–545.

Piper FI, Reyes A. 2020. Does microwaving or freezing reduce the losses of non-structural carbohydrates during plant sample processing? *Annals of Forest Science* **77**: 1–9.

R Core Team. 2024. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Reed CC, Hood SM. 2024. Nonstructural carbohydrates explain post-fire tree mortality and recovery patterns. *Tree Physiology* **44**: tpad155.

Robbins ZJ, Xu C, Aukema BH, Buotte PC, Chitra-Tarak R, Fettig CJ, Goulden ML, Goodsman DW, Hall AD, Koven CD. 2022. Warming increased bark beetle-induced tree mortality by 30% during an extreme drought in California. *Global Change Biology* **28**: 509–523.

Rodman KC, Veblen TT, Andrus RA, Enright NJ, Fontaine JB, Gonzalez AD, Redmond MD, Wion AP. 2021. A trait-based approach to assessing resistance and resilience to wildfire in two iconic North American conifers. *Journal of Ecology* **109**: 313–326.

Sala A, Woodruff DR, Meinzer FC. 2012. Carbon dynamics in trees: feast or famine? *Tree Physiology* **32**: 764–775.

Salladay RA, Pittermann J. 2023. Using heat plumes to simulate post-fire effects on cambial viability and hydraulic performance in Sequoia sempervirens stems. *Tree Physiology* **43**: 769–780.

Sapes G, Demaree P, Lekberg Y, Sala A. 2021. Plant carbohydrate depletion impairs water relations and spreads via ectomycorrhizal networks. *New Phytologist* **229**: 3172–3183.

Sapes G, Roskilly B, Dobrowski S, Maneta M, Anderegg WR, Martinez-Vilalta J, Sala A. 2019. Plant water content integrates hydraulics and carbon depletion to predict drought-induced seedling mortality. *Tree Physiology* **39**: 1300–1312.

Seidl R, Thom D, Kautz M, Martin-Benito D, Peltoniemi M, Vacchiano G, Wild J, Ascoli D, Petr M, Honkaniemi J. 2017. Forest disturbances under climate change. *Nature Climate Change* **7**: 395–402.

Senande-Rivera M, Insua-Costa D, Miguez-Macho G. 2022. Spatial and temporal expansion of global wildland fire activity in response to climate change. *Nature Communications* **13**: 1208.

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

Smith AM, Partelli-Feltrin R, Sparks AM, Moberly JG, Adams HD, Schwilk DW, Tinkham WT, Kok JR, Wilson DR, Thompson A. 2025. Methods to assess fire-induced tree mortality: review of fire behaviour proxy and real fire experiments. *International Journal of Wildland Fire* **34**: 2546.

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

Sperry J, Saliendra N. 1994. Intra-and inter-plant variation in xylem cavitation in Betula occidentalis. *Plant, Cell & Environment* **17**: 1233–1241.

Sword MA, Haywood JD. 1995. Effects of crown scorch on longleaf pine fine roots. *General Technical Report Southern Research Station* **1**: 223.

Tomasella M, Casolo V, Natale S, Petruzzellis F, Kofler W, Beikircher B, Mayr S, Nardini A. 2021. Shade-induced reduction of stem nonstructural carbohydrates increases xylem vulnerability to embolism and impedes hydraulic recovery in *Populus nigra*. *New Phytologist* **231**: 108–121.

Valor T, González-Olabarria JR, Piqué M, Casals P. 2017. The effects of burning season and severity on the mortality over time of *Pinus nigra* spp. salzmannii (Dunal) Franco and *P. sylvestris* L. *Forest Ecology and Management* **406**: 172–183.

Van Mantgem PJ, Falk DA, Williams EC, Das AJ, Stephenson NL. 2020. The influence of pre-fire growth patterns on post-fire tree mortality for common conifers in western US parks. *International Journal of Wildland Fire* **29**: 513–518.

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

Wallin KF, Kolb TE, Skov KR, Wagner MR. 2003. Effects of crown scorch on ponderosa pine resistance to bark beetles in northern Arizona. *Environmental Entomology* **32**: 652–661.

West AG, Bloy ST, Skelton RP, Midgley JJ. 2023. Hydraulic segmentation explains differences in loss of branch conductance caused by fire. *Tree Physiology* **43**: 2121–2130.

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

Wiley E, Helliker B. 2012. A re-evaluation of carbon storage in trees lends greater support for carbon limitation to growth. *New Phytologist* **195**: 285–289.

Wiley E, Hoch G, Landhäusser SM. 2017. Dying piece by piece: carbohydrate dynamics in aspen (*Populus tremuloides*) seedlings under severe carbon stress. *Journal of Experimental Botany* **68**: 5221–5232.

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.

Willson KG, Margolis EQ, Hurteau MD. 2024. Trees have similar growth responses to first-entry fires and reburns following long-term fire exclusion. *Forest Ecology and Management* **571**: 122226.

Wood SN. 2017. *Generalized additive models: an introduction with R.* London, UK: Chapman and Hall/CRC.

Woodruff DR, Meinzer FC. 2011. Water stress, shoot growth and storage of non-structural carbohydrates along a tree height gradient in a tall conifer. *Plant, Cell & Environment* **34**: 1920–1930.

Woolley T, Shaw DC, Ganio LM, Fitzgerald SA. 2012. A review of logistic regression models used to predict post-fire tree mortality of western North American conifers. *International Journal of Wildland Fire* **21**: 1–35.

Supporting Information

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

Fig. S1 Representative site photos of all four study sites pre-burning.

Fig. S2 Crown scorch heights on original study trees at both the fall-burned and spring-burned sites.

Fig. S3 Mid-day water potential *c.* 3 wk before burning at each of the four sites, separated by species.

Fig. S4 Relationships between native hydraulic conductivity (K_s) and crown scorch for ponderosa pine and Douglas-fir at the fall-burn and spring-burn sites.

Fig. S5 Sugars and starch from phloem and xylem of live burned and unburned control trees pre-burn and at each timestep post-burn.

Fig. S6 Relationships between nonstructural carbohydrates (NSC) in the phloem and xylem and percent crown scorch sustained by ponderosa pine and Douglas-fir during a fall prescribed fire.

Fig. S7 Relationships between nonstructural carbohydrates (NSC) in the roots and percent crown scorch sustained by ponderosa pine and Douglas-fir during a fall and spring prescribed fire.

Fig. S8 Relationships between nonstructural carbohydrates (NSC) in the phloem and xylem and percent crown scorch sustained by ponderosa pine and Douglas-fir during a spring prescribed fire.

Fig. S9 Changes in roots total NSC for trees that eventually died but were alive at the measurement timestep (dead-burned), those that survived but were burned (live-burned), and unburned controls (live-control) at the fall sites and spring sites.

Methods S1 Additional site, fuel moisture, fire behavior, and hydraulics methods.

Table S1 Means of diameter at breast height and height for original and replacement trees.

Table S2 Full sampling timeline.

Table S3 Model selection table for GLMMs of mortality probability using different NSC variables.

Table S4 Pre-burn tree attributes.

Table S5 P_{12}, P_{50}, and P_{88} values for ponderosa pine and Douglas-fir at all four study sites.

Table S6 P_{12}, P_{50}, and P_{88} values for burned ponderosa pine *c.* 3 wk post-burn.

Table S7 P_{12}, P_{50}, and P_{88} values for ponderosa pine at the fall-burned site *c.* 23 months post-burn.

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