



Nonstructural carbohydrates explain post-fire tree mortality and recovery patterns

Charlotte C. Reed^{1,2,*}  and Sharon M. Hood¹

¹USDA Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, 5775 US Highway 10 W, Missoula, MT 59808, USA

²Division of Biological Sciences, University of Montana, 32 Campus Drive, Missoula, MT 59812, USA

*Corresponding author (reed@usda.gov)

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Trees use nonstructural carbohydrates (NSCs) to support many functions, including recovery from disturbances. However, NSC's importance for recovery following fire and whether NSC depletion contributes to post-fire delayed mortality are largely unknown. We investigated how fire affects NSCs based on fire-caused injury from a prescribed fire in a young *Pinus ponderosa* (Lawson & C. Lawson) stand. We assessed crown injury (needle scorch and bud kill) and measured NSCs of needles and inner bark (i.e., secondary phloem) of branches and main stems of trees subject to fire and at an adjacent unburned site. We measured NSCs pre-fire and at six timesteps post-fire (4 days–16 months). While all trees initially survived the fire, NSC concentrations declined quickly in burned trees relative to unburned controls over the same post-fire period. This decline was strongest for trees that eventually died, but those that survived recovered to unburned levels within 14 months post-fire. Two months post-fire, the relationship between crown scorch and NSCs of the main stem inner bark was strongly negative ($\text{Adj-}R^2 = 0.83$). Our results support the importance of NSCs for tree survival and recovery post-fire and suggest that post-fire NSC depletion is in part related to reduced photosynthetic leaf area that subsequently limits carbohydrate availability for maintaining tree function. Crown scorch is a commonly measured metric of tree-level fire severity and is often linked to post-fire tree outcome (i.e., recovery or mortality). Thus, our finding that NSC depletion may be the mechanistic link between the fire-caused injury and tree outcome will help improve models of post-fire tree mortality and forest recovery.

Keywords: fire-caused injury, inner bark, phloem, *Pinus ponderosa*, *Ponderosa pine*, prescribed fire.

Introduction

Wildfire dynamics are changing globally due to past land use and ongoing climate change (Abatzoglou and Williams 2016, Jones et al. 2022). Longer fire seasons and more extreme fire weather are resulting in increasing area burned in some regions (Jolly et al. 2015, Goss et al. 2020, Jain et al. 2022, Jones et al. 2022), inciting interest in understanding the consequences of these changes on forested systems (Dickman et al. 2023). Fire causes heat transfer to tree tissues that can result in crown injuries (e.g., crown scorch and bud kill), effectively defoliating trees without causing immediate tree mortality (Varner et al. 2021). Crown scorch is an immediate effect of fire and occurs when the tree foliage is killed or consumed by heating during fire. In many non-resprouting tree species, the portion of the tree crown that is scorched also experiences bud kill, which kills the meristematic tissue and prevents further development of foliage, flowers or branches (Varner et al. 2021). Thus, crown injury, in total, determines the degree to which carbon acquisition is decreased by fire and the potential for recovery of foliage from surviving buds.

Trees use carbohydrates produced from photosynthesis to support many vital functions, including growth, metabolism, osmoregulation, defense and recovery from abiotic and biotic disturbances (Dietze et al. 2014, Hartmann and Trumbore 2016). Soluble sugars and starch, termed nonstructural carbohydrates (NSCs), are stored for use during periods when carbon gain is reduced or demand is high and thus serve a critical role not only in maintaining normal tree function

during these periods but also in maintaining resilience to and recovery from stressors like herbivory, drought and fire (Hartmann and Trumbore 2016, Adams et al. 2017, Piper and Paula 2020, Barker Plotkin et al. 2021). When stressors cause NSC depletion below critical thresholds, the potential for recovery is diminished, and carbon may be insufficient to support tree function, leading to death (McDowell et al. 2008, Martínez-Vilalta et al. 2016, Weber et al. 2018, Piper et al. 2022). While evidence for this 'carbon starvation' without concurrent hydraulic failure is mixed in the context of drought (Adams et al. 2017), it may occur as a consequence of severe defoliation (Jacquet et al. 2014, Barker Plotkin et al. 2021), at least for non-resprouting species (Anderegg and Callaway 2012). Similarly, recovery of resprouting species after drought (Zeppel et al. 2015) and fire (Schutz et al. 2009, Peltier et al. 2023) relies on stored NSCs. However, little is known about the role of NSCs for non-resprouting trees that survive fire but sustain some level of fire-caused crown injury and whether there is a critical NSC threshold below which trees cannot recover.

Importantly, crown injury likely informs the degree to which NSCs are depleted post-fire, although this has not been explicitly explored. The few existing studies examining NSC dynamics and plant survival after wildland or prescribed fire (i.e., non-experimental fires) in mature plants focus on resprouting species (Piper and Paula 2020, Peltier et al. 2023), or do not examine the relationships between post-fire changes in NSCs, crown injury and mortality. The only two studies

to examine in situ post-fire NSC dynamics in trees followed longleaf pine (*Pinus palustris* Mill.) after prescribed fires. Varner et al. (2009) found that NSCs in coarse roots exposed to smoldering duff fires (i.e., no crown injury) declined after burning, suggesting that basal heating may lead to reductions in NSC stores, perhaps due to the impairment of carbon transport tissues (i.e., phloem) in roots, preventing accumulation of new photosynthates, or due to increased carbon demand to repair or regrow damaged tissues. Similarly, Sayer et al. (2020) found that fall prescribed burning of longleaf pine saplings reduced shoot starch concentrations for several months, but they did not assess changes in the soluble sugars or relate starch reductions to tree mortality. Recent work in laboratory-burned Ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) seedlings also found that the NSCs of stems and roots of burned seedlings were lower than the unburned controls as soon as 1 week post-burning (Partelli-Feltrin et al. 2023). While the degree of crown injury was not reported in this study, it was likely high as the fire dose applied was intended to be lethal (Partelli-Feltrin et al. 2023). The same study found that manual defoliation did not reduce NSCs to the same magnitude or as quickly as burning, which the authors attributed to fire-induced phloem death restricting post-fire mobilization of carbon stores. However, the degree to which crown injury from non-lethal fire causes NSC depletion and whether such depletion crosses irreversible thresholds that lead to death is unknown, as no existing studies have measured NSC dynamics in non-resprouting species with varying levels of crown injury.

Understanding the mechanistic link between the level of crown injury a tree sustains from fire and the outcome (i.e., mortality or recovery) is necessary for accurately predicting the probability of post-fire mortality or recovery, particularly for non-resprouting species, and for understanding interactions with other post-fire stressors like insects or drought (Hood et al. 2018). Models of post-fire mortality most commonly use crown scorch, combined with species-specific tree characteristics (e.g., bark thickness and diameter) to predict the probability of mortality after fire (Cansler et al. 2020). A mechanistic link between crown scorch and mortality probability would help to improve the predictive capacity of these models, particularly in the context of novel climate and disturbance regimes (Hood et al. 2018, Dickman et al. 2023). For example, post-fire mortality may be exacerbated by other stressors like drought, insect attack or fungal pathogens (Parker et al. 2006, Barker et al. 2022, Fettig et al. 2022), which may interact with fire-induced reductions in NSCs, increasing the susceptibility of trees to mortality (Bär et al. 2019). This is particularly true because NSCs play an important role in both the biosynthesis of defense metabolites during insect attack (Huang et al. 2020) and in drought tolerance (Adams et al. 2017) via the role of soluble sugars in osmoregulation and the maintenance of turgor when water availability is low (Sapes et al. 2021).

We leveraged a spring prescribed fire in a northern Rocky Mountain Ponderosa pine forest to investigate how fire affects NSCs based on the level of fire-caused injury a tree sustains. Ponderosa pine is adapted to survive the frequent, low-intensity surface fires through thick bark that develops at an early age, which prevents cambium damage (Hood et al. 2008, Rodman et al. 2021), large diameter branches and buds protected by needles that can survive even if the foliage is scorched and killed (Fowler et al. 2010, Hood et al. 2010). This ability

for bud survival even when foliage is killed during fire allows for new needle growth within the first growing season post-fire and recovery in the years following fire (Dieterich 1979). We hypothesized that (i) NSCs would decrease post-fire as a result of crown injury due to heat damage to needles and branches and that this NSC decrease would be proportional to crown scorch and bud kill, and (ii) that a reduction in post-fire carbon acquisition and stores coupled with equal or possibly greater carbon demand during post-fire recovery would lead to NSC decline below some threshold for tree survival. We tested these hypotheses by assessing the crown injury and measuring the NSCs of needles and inner bark (i.e., secondary phloem) of small branches and the main stems of trees subject to a spring prescribed fire as well as for trees in an adjacent unburned site. We measured NSCs pre-fire and at six timesteps post-fire (4 days–16 months). We chose to sample the inner bark as it contains the secondary phloem and is an important contributor to NSC storage in woody plants and because soluble sugar concentrations are often higher in the phloem than in the secondary xylem (i.e., wood) (Zhang et al. 2014, Rosell et al. 2021). It is also likely that NSCs in the inner bark are preferentially remobilized during periods of reduced carbon supply (Wiley et al. 2019), and thus this tissue likely contains an important post-fire NSC pool when the carbon supply is reduced due to a reduction in the photosynthetically active leaf area from crown scorch.

Materials and methods

Study site, species and sampling approach

The study was conducted at a site in western Montana, USA, on the Blackfoot-Clearwater Wildlife Management Area and University of Montana's Experimental Bandy Ranch (47.067389, -113.271008; elevation: 1250 m). The site is a mixture of mixed-age Ponderosa pine and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forest with interspersed grasslands and seasonal wetlands. The average growing season temperature (May–September) is 15.2 °C with an average of 162 mm of precipitation over the same time period, with the majority of precipitation falling in May and June (Table S1 available as Supplementary data at *Tree Physiology* Online). We selected sapling-size (2–15 cm diameter at 1.37 m above ground) Ponderosa pines at the transition between forest and grassland. We chose sapling-size trees to increase the likelihood that crown scorch would occur during a low-intensity surface fire. In the fall of 2020, we selected all trees that appeared visually healthy (e.g., no signs of insect activity and dead foliage) at the forest–grassland interface. We chose the location of the site within the burn unit based on a larger number of sapling-size Ponderosa pines at the forest–grassland interface than within the forested burn unit and to have greater control over the ignition pattern to ensure that the fire caused some crown scorch. The site was ~0.1 ha and was within the perimeter of a 44-ha unit in which a prescribed fire was planned for Spring 2021. We identified 21 trees that met these criteria. We additionally selected nine similarly sized trees at an adjacent site outside the planned burned perimeter to serve as a control. The control site was located 1.9 km from the burned site at the same elevation and also at the forest–grassland interface. Both sites had similarly low sapling-size tree density (~200 trees ha⁻¹), with no overstory trees present in the sampling area. The proximity of the two

sites is such that they can be expected to experience very similar climatic conditions. The understory of each site was composed primarily of perennial grasses and forbs. Study trees within both units had not experienced prior fire.

Burn day environmental and weather conditions

On the day of the burn, 17 April 2021, we measured the pre-dawn water potential of Ponderosa pine needles using a Scholander pressure chamber (PMS Instruments, Albany, OR, USA) and the fuel moisture of live needles and dead grasses at the burn site. To assess general site soil water availability on the morning of the burn, we measured the pre-dawn xylem water potential (ψ_{pd}) on needles of a study tree at the burn site and found it to be < -0.1 MPa. We confirmed this measurement on the needles of a second tree outside of the burn unit. At the time of measurement, the air temperature was -7 °C and the relative humidity was 93%; soils were visibly saturated due to recent snowmelt. Thus, we expect that study trees were experiencing their seasonal maximum potential water availability at the time of the burn.

At the time of the prescribed burn, the surface fuels were continuous and consisted primarily of dead grasses, with very little fine woody debris and no coarse woody debris present. To measure the fuel moisture, samples were collected ~ 1 h before the site was burned and were kept sealed in plastic bags in the shade until measurement of wet weight 5 h later. Samples were then dried at 50 °C for 90 h before the dry weight was measured, and the fuel moisture was calculated. Fuel moisture was determined by dividing the difference of the wet and dry weights by the dry weight and multiplying by 100. Fuel moisture 1 h prior to burning was 114.1% (± 5.7) for live needles from six study trees and 3.9% (± 0.7) for dead grasses, collected at five points throughout the site.

After the majority of ignitions had taken place within the larger burn unit, the prescribed fire in the area of our sample trees was lit using hand-held drip torches as a head fire (i.e., aligned with wind) at 16:05 h, with the flaming front moving quickly as a surface fire through the area and consuming understory fuels, primarily dead grasses and forbs. Flame lengths were low (< 1 m), and the flaming was complete by 16:10. Weather data were recorded using a Vaisala WXT520 weather transmitter (Vaisala Oyj, Vantaa, Finland) adjacent to the burn site. During the burn, air temperature was 18 °C, relative humidity was 18% and windspeeds were 3–11 km h⁻¹, with gusts to 21 km h⁻¹.

Tree measurements, sampling timeline and phenology

One day prior to the prescribed fire, we collected data on the size and bark thickness of each study tree at both burn and control sites. We recorded the diameter at breast height (DBH; 1.37 m above ground); groundline diameter (GLD; 0 m above ground); the height, bark thickness at both DBH and GLD and took photos of each tree from each of the cardinal directions. We also sampled for NSCs at this time (see details below). At the time of pre-burn sampling (T0), bud swell or elongation had not begun. Post-fire, we sampled for NSCs at six timesteps: 4 days (T1), 23 days (T2), 61 days (T3), 128 days (T4), 14 months (T5) and 16 months post-fire (T6). We selected the timesteps to capture both immediate, short-term effects of fire (T1 and T2) and longer-term impacts,

corresponding to periods of rapid growth at the start of the growing season (June; T3 and T5), and at the end of the summer drought period, toward the end of the growing season (T4 and T6). At T2, we visually estimated the crown volume needle scorch and crown volume bud kill, as crown scorch had not fully developed at T1 (Figure S1 available as Supplementary data at *Tree Physiology Online*). Scorch was estimated visually based on the percentage of the pre-fire live crown that was either scorched or consumed (i.e., had pale green, brown or blackened needles). Bud kill estimates were made from the percentage of the pre-fire live branches whose buds were not swelling or elongating. Crown scorch and bud kill estimates assessed at T2 were used in all further analyses. We re-took photos at T2, T4 and T5 and recorded the tree status (live or dead) at each of the six timesteps (Figure 1). We considered a tree dead when no green needles remained and confirmed each tree's death at all subsequent sampling times. Bud elongation had begun by T2 (10 May 2021), but no new needle growth had occurred. Needle growth had begun by T3 (17 June 2021) and was complete by T4 (23 August 2021). Tree phenology was similar the second year of sampling (T5—9 June 2022; T6—2 September 2022). At the end of the study, we cut the dead trees at root collar to determine whether radial growth occurred between the time of the fire and when the tree died, as evidenced by an incomplete outermost growth ring.

Nonstructural carbohydrates

We collected samples for NSC analyses from needles, the inner bark of the main tree stem and the inner and outer barks of a lateral branch. Prior to the complete development of new needles (T0 and T1), we collected needles from the previous year (2020). From T4 to T6, we collected needles from 2021. Needles were sampled from branches ~ 1 –2 m off the ground. Needle scorch does not develop immediately post-fire; thus, it was difficult to determine the level of scorch on needles at T1, 4 days post-fire. Therefore, we did sample needles at T1, but not at T2 or T3, once the scorch had developed, so as to avoid sampling scorched needles. While we could have collected unscorched needles from the tops of some trees (some trees had no unscorched needles), we wanted to keep sampling height similar across timesteps and thus did not sample needles at T2 and T3 before new needles had flushed. Inner bark was sampled from the main stem at ~ 1 –1.5 m height. Two phloem punches (diameter = 15 mm) were taken per tree per timestep around the circumference of the bole. Punches were taken randomly within the specified height range, with care not to place two punches directly adjacent to each other to avoid girdling. We removed the outer bark in the field with a razor blade. The inner bark is primarily composed of secondary phloem, and thus we refer to these samples as main stem phloem. All phloem punches collected at T1–T3 were moist and pliable, with no visible signs of any necrosis. Because the bark on branches was thinner and more difficult to separate into inner and outer bark, we sampled both inner and outer barks together from live lateral branches at ~ 1 –2 m height. We chose branch segments that had developed in 2019 (T0–T3) and 2020 (T4–T6), as the most recent year of growth often did not contain sufficient tissue for sampling. Branches were not sampled from any particular cardinal direction; sampling location was based on the presence of live lateral branches. Henceforth, we refer to these samples as the branch phloem. At T0–T2, we sampled lateral branches from the same primary branch, but

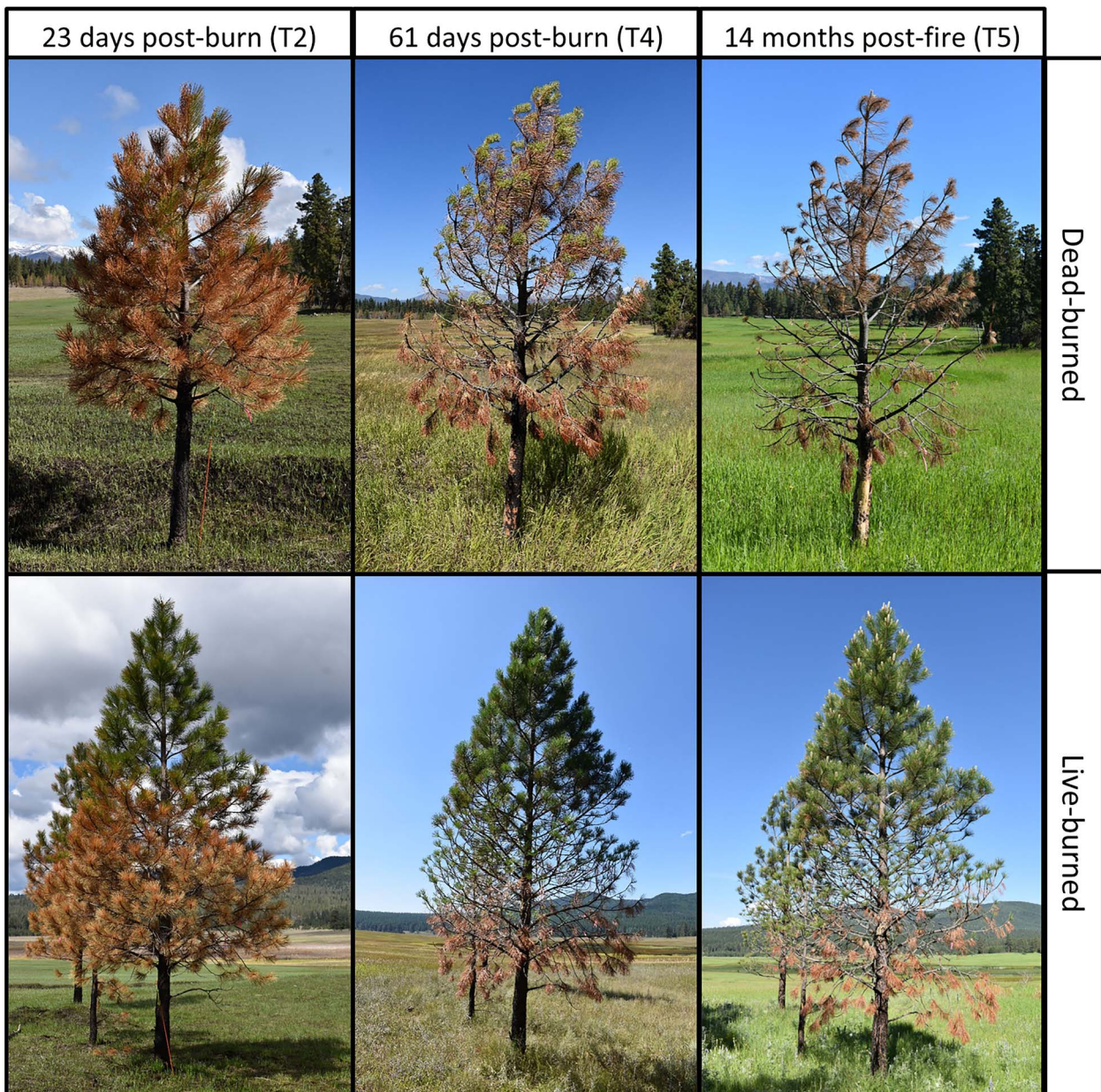


Figure 1. Time series of recovery (live-burned) or death (dead-burned) for trees at the burn site. Photos were taken from the same location at three timesteps (T2, T4 and T5) after a prescribed fire on 17 April 2021.

at later timesteps, we selected lateral branches exclusively with live buds or needles, which necessitated being less selective of the lateral branches we sampled, although branches were still sampled within 1–2 m in height from the ground. Only one branch was sampled per timestep, and all needle and branch phloem samples were collected from the same lateral branch. All branch phloem samples had mostly live (green) phloem tissue, although we noted some samples with partial phloem necrosis (Figure S6 available as Supplementary data at *Tree Physiology Online*). Samples were stored in a cooler on ice for transportation and were immediately microwaved for three 30-s intervals upon return to the laboratory and within 4 h of collection. Microwaving denatures enzymes and stops respiration and hydrolysis (Landhäusser et al. 2018, Piper and Reyes 2020), and 30-s intervals prevented samples from

burning. Samples were then stored in a freezer until further processing.

Samples were dried at 60 °C for 48–72 h before grinding. Samples were first coarsely ground with a Wiley mill (Thomas Scientific, Swedesboro, NJ, USA). We then further homogenized and ground samples to a powder with a mixer mill (Retsch, Hann, Germany). Prior to weighing samples for NSC analyses, samples were again dried overnight at 60 °C. We followed the protocol by Landhäusser et al. (2018) for NSC quantification. Briefly, soluble sugars were extracted from ground samples via ethanol at 90 °C. Total free sugars (glucose, fructose and sucrose) were then determined by Nicotinamide-adenine dinucleotide (NAD)-linked enzymatic assays where invertase breaks down the glucose and fructose for sucrose quantification, and fructose is converted to glu-

cose by isomerase. After conversion of glucose to gluconate using hexokinase (glucose assay reagent, Sigma Aldrich), total sugars were determined photometrically at 340 nm. From the remaining pellet, starch was converted to glucose via α -amylase, followed by amyloglucosidase. Glucose hydrolysate was then measured photometrically at 340 nm to determine the starch content. We used serial dilutions of a glucose standard stock solution (1 mg mL^{-1}) for glucose quantification and fructose and sucrose standards to ensure the efficacy of enzyme activities (Landhäusser et al. 2018). All chemicals were from Sigma Aldrich. We also used a synthetic standard described by Landhäusser et al. (2018) as well as a laboratory standard from Ponderosa pine needles to ensure the reproducibility. Tissue concentrations in needles, main stem phloem and branch phloem were expressed on a dry matter basis.

Data analysis

We compared tree characteristics between the burned and control trees and between the trees at the burn site that survived the fire and those that did not via Student's *t*-tests. We compared the soluble sugars, starch and total NSC between treatment (burned and control) and tree outcomes (live-unburned, live-burned and dead-burned) across timesteps using generalized linear mixed models (GLMMs) with a Gamma response distribution and using a natural log-link function. We modeled response variables (sugars, starch or total NSC concentration) as a function of time, treatment or tree outcome, and their interaction. Tree outcomes included trees that were burned but were still alive 16 months post-fire when the study ended (live-burned), those that were burned and eventually died (dead-burned) and live-unburned trees (control). Standard errors of the parameters were adjusted for temporal correlation due to remeasures of the same tree by incorporating an unstructured off-diagonal covariance in the model. We then performed simple main-effect comparisons, which compare levels of one factor while holding the others fixed, to determine the differences between treatments or mortality outcomes at each timestep using the 'emmeans' package, which also accounts for the imbalance in numbers across the tree outcomes (Lenth 2022). All analyses were conducted in R version 4.2.2 (R Core Team 2022). We used the package 'glmmTMB' for building GLMMs (Brooks et al. 2017). We tested for overdispersion using simulation-based tests from the 'DHARMA' package (Hartig 2022) and examined the residuals via quantile–quantile plots.

In order to determine the degree to which NSCs were related to the tree size or fire-caused injury, we built generalized additive models. First, we explored whether NSCs were related to tree size prior to burning, at T0. Because we found no clear relationships between the tree size and pre-burn NSCs that would explain post-burn NSC patterns (Figure S2 available as Supplementary data at *Tree Physiology* Online), we proceeded with exploring the relationships between post-burn NSCs and crown injury (crown scorch and bud kill) and did not consider the tree size in further analyses. To determine whether the changes in NSCs post-burn were a product of crown injury, we analyzed the relationships between NSCs and crown scorch/bud kill at each post-burn timestep. We also examined the relationships between the degree to which NSCs declined post-fire and crown scorch/bud kill. To analyze the relationships between NSCs and crown injury, we modeled soluble sugars, starch and total NSC concentrations at each timestep as a function of percent crown scorch or

bud kill using the 'mgcv' package (Wood 2011). Relationships between NSCs and crown scorch were stronger than between NSCs and bud kill, and crown scorch and bud kill are highly colinear, thus we just report results for those models. To model relationships between the NSC decline and crown injury, we modeled the change in total NSC concentrations between T0, prior to burning and T3, the last timestep at which all trees were alive and when the NSC differences between tree outcomes were most apparent. Needles were not sampled at T3, and thus we used values from T4 for these analyses instead. We performed model diagnostics and examined residuals using the gam.check function in the 'mgcv' package. Some of the relationships between NSCs and crown scorch were clearly linear, and thus we modeled those relationships with linear models and examined the residuals via quantile–quantile plots.

Results

Tree characteristics and mortality outcomes

Trees at both the burn and control sites had similar diameters, bark thickness and height, although the bark thickness at breast height was greater for trees at the burn site (Table 1). By T6 (16 months post-fire), eight trees had died at the burned site (Table 2). Two trees died between T3 and T4, and six died between T4 and T5. No trees died after T5, and no trees died at the control site throughout the study period. Burned trees that survived and those that died differed significantly in size (Table 2). Trees that died had smaller diameters, thinner bark and were shorter. As expected, trees that died also had higher crown volume scorched and higher bud kill (Table 2; Figure 1). No trees had 100% bud kill post-fire, and all trees had begun to flush new needles by T3 on branches that survived the fire. By T4, at the end of the first growing season post-fire, many of the needles that flushed had died, and this was particularly true for the two trees that died between T3 and T4 and the six that would die between T4 and T5 (Figure 1). Out of the eight trees that died, four showed radial growth in the period between when the fire occurred and when they died, evidenced by an incomplete outermost growth ring. We neither found evidence of heat-killed cambium in the main stems of trees during NSC sampling at the first three timesteps post-fire nor were there any visible signs of heat-killed cambium when the dead trees were cut, which suggests that the fire did not cause an immediate cambial necrosis of the main stem.

Nonstructural carbohydrates

Soluble sugars and total NSC concentrations for all measured tissues of trees at the burn and control sites were similar at T0 before the prescribed fire occurred, while the pre-fire (T0) starch concentrations were higher in trees at the burn site compared with trees at the control site (Table S2 available as Supplementary data at *Tree Physiology* Online). In general, clear differences in NSCs emerged when we compared trees that eventually died post-fire (dead-burned), those that were burned but survived (live-burned) and unburned control trees at each of the seven timesteps (Figure 2, Table S3 available as Supplementary data at *Tree Physiology* Online). Differences across tree outcomes were generally small at T0 and T1, although some were significant. For example, starch was higher for live-burned than control trees for all

Table 1. Mean values of tree characteristics for both treatments with ranges in parentheses.

	<i>n</i>	DBH (cm)	GLD (cm)	BT at DBH (mm)	BT at GLD (mm)	Height (m)
Control	9	8.0 (3.1–15.0)	13.4 (7.4–21.8)	3.2 (1.3–7.6) a	10.4 (5.1–17.8)	3.7 (2.1–6.7)
Burned	21	10.0 (2.0–16.8)	15.3 (6.4–23.9)	5.5 (1.3–10.2) b	10.9 (2.5–17.8)	4.3 (1.8–6.6)

DBH = stem diameter 1.37 m above ground; GLD = groundline stem diameter; BT = bark thickness. Significant differences between treatments are denoted by letters ($P < 0.05$).

Table 2. Mean values characteristics for trees at the burn site that survived (live-burned) and those that died (dead-burned) after a prescribed fire.

	<i>n</i>	DBH (cm)	GLD (cm)	BT at DBH (mm)	BT at GLD (mm)	Height (m)	Crown scorch (%)	Bud kill (%)
Live-burned	13	12.3 (8.9–16.8) a	18.1 (11.9–23.9) a	7.1 (5.1–10.2) a	12.7 (8.9–17.8) a	5.1 (4.0–6.6) a	56.5 (0–100) a	11.5 (0–40) a
Dead-burned	8	6.3 (2.0–11.9) b	10.7 (6.4–18.0) b	2.9 (1.3–7.6) b	8.1 (2.5–17.8) b	3.0 (1.8–5.7) b	94.8 (80–100) b	39.4 (15–80) b

Minimum and maximum values are in parenthesis. Significant differences between mortality outcomes are denoted by letters ($P < 0.05$).

tissues at T0. This was also true for soluble sugars in the main stem phloem as well as for total NSC of the branch phloem. At T1, burned trees that later died had lower concentrations of soluble sugars and total NSC than controls in branch phloem, and live-burned trees had lower soluble sugars than controls in the main stem phloem (Figure 2, Table S3 available as Supplementary data at *Tree Physiology* Online).

Differences started to emerge more clearly by T2 and were most apparent by T3 when new needle growth had been initiated (Figure 2, Table S3 available as Supplementary data at *Tree Physiology* Online). At T2, all burned trees had lower soluble sugars in the branch and stem phloem than controls as well as total NSC in branch phloem. Starch was also lower in stem phloem, but this was only for dead-burned trees. Total NSC was lowest in the dead-burned and was highest in controls for stem phloem, and the differences were significant between each mortality outcome. At T3, dead-burned trees had the lowest soluble sugars, starch and total NSC, while controls had the highest concentrations in both main stem and branch phloem. Differences between each of the tree outcomes were significant, except for between live-burned and dead-burned soluble sugars in the branch phloem. Differences between each of the mortality outcomes began to lessen by T4, although patterns remained similar, with dead-burned trees generally having the lowest NSC concentrations across tissues. However, a slight increase in branch phloem soluble sugars between T3 and T4 suggests that even trees that eventually died initially accumulated some NSCs in the branches where needles had flushed during the first spring after the burn. Interestingly, new needles of dead-burned trees also had lower NSC concentrations than live-burned and controls at T4 when we resumed needle collection. Few differences were apparent between the surviving burned trees (live-burned) and controls by T5, 14 months post-fire and at the start of the second growing season. Similarly, by the end of the growing season, 16 months post-fire, NSCs were mostly similar between live-burned and control trees. However, needles from live-burned trees had a slightly lower starch and total NSC, and phloem from the main stem had slightly lower total NSC concentrations at T6, although the magnitude of these differences was small compared with differences observed the season immediately post-fire (Figure 2, Table S3 available as Supplementary data at *Tree Physiology* Online).

Relationships between NSCs and crown scorch

No relationship between crown scorch and NSCs existed at T1, 4 days post-fire (Figures S3–S5 available as Supplementary data at *Tree Physiology* Online). Relationships between crown volume scorched and NSC concentrations began to emerge at T2 and were most apparent at T3 when new needle growth was actively occurring and before any trees died (Figure 3, Figures S3–S5 available as Supplementary data at *Tree Physiology* Online). In general, NSCs declined as crown scorch increased, although the shape of the curve differed across tissues and the measured NSC component. At T3, NSCs declined more quickly with increasing crown scorch in the branch phloem than the stem phloem, and the relationships between soluble sugar concentrations and crown scorch were not as strong as for starch and total NSC (Figure 3). Total NSCs in main stem phloem began to decline more sharply around 60% crown scorch. In general, trees that died by the end of the study had both high crown scorch and low NSC concentrations at T3, 61 days post-fire, which was the final time step before any mortality occurred (Figure 3). Relationships between crown scorch and NSCs were less clear by T4, once new needle growth was complete, except in the phloem of the main stem, which continued to show a negative relationship, and a weak negative relationship was also still apparent at T5 for starch and total NSCs in the branch phloem (Figures S3–S5 available as Supplementary data at *Tree Physiology* Online).

All trees that died had lower total NSC concentrations in the main stem phloem at T3 than pre-fire, with a strong negative relationship between the declines in NSCs and crown scorch (Figure 4; $\text{Adj-}R^2 = 0.81$). Only one tree that survived experienced a decline in main stem phloem NSCs, and it was a tree that experienced 90% crown scorch and 40% bud kill. The relationship between NSC change and bud kill was less strong, but this was still significant for the main stem phloem ($\text{Adj-}R^2 = 0.47$), with higher bud kill corresponding to larger declines in NSCs. The NSC concentrations for branch phloem also tended to decline for trees that died, and the relationship between NSC change and crown scorch was also strong ($\text{Adj-}R^2 = 0.79$). No relationships existed between the crown injury and NSC changes in the needles. In general, crown scorch was a better predictor of NSC change than bud kill, although there was still a clear negative relationship between the bud kill and NSC change for main stem phloem (Figure 4; $\text{Adj-}R^2 = 0.47$).

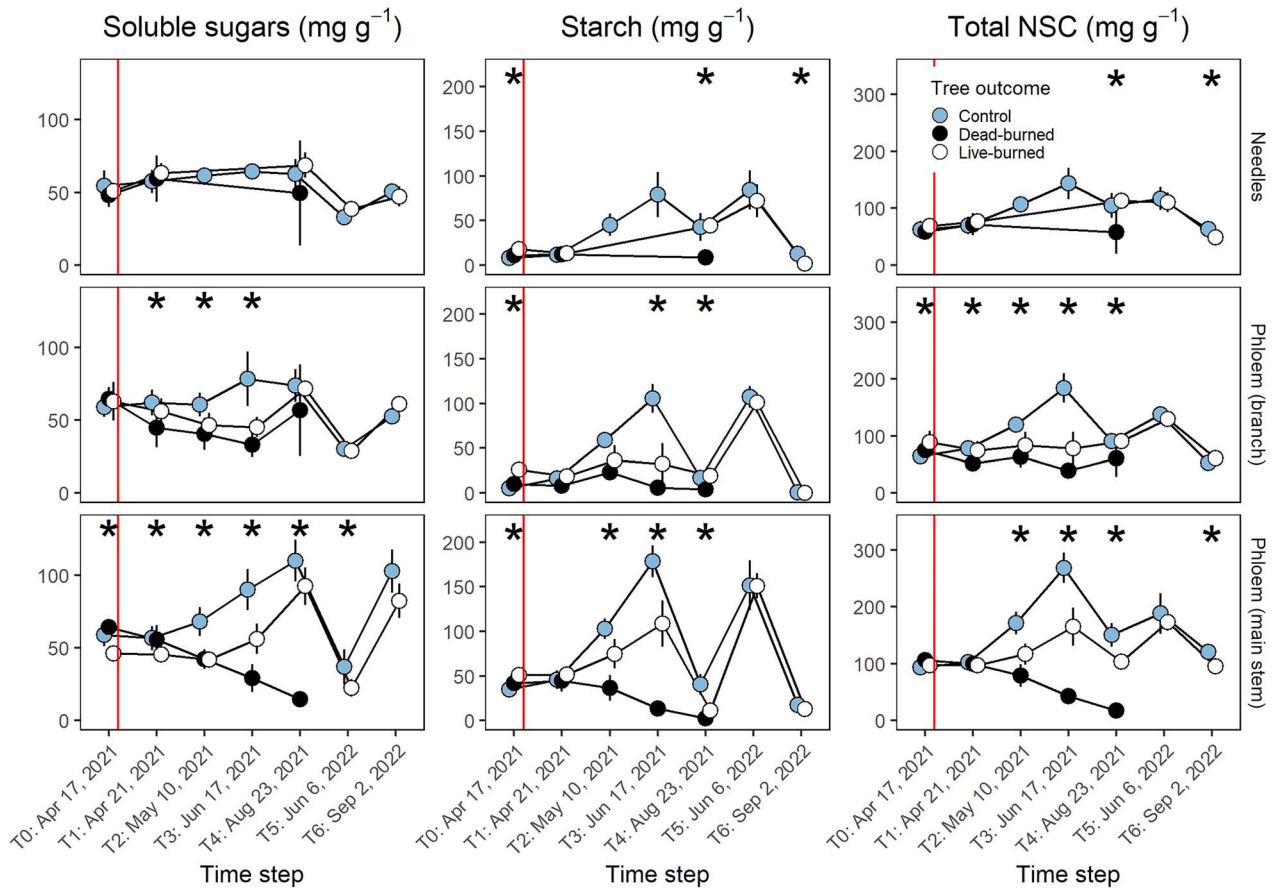


Figure 2. Soluble sugars, starch and total NSCs at seven timesteps in three tissue types for *Ponderosa* pine. The T0 samples were collected before a prescribed fire occurred (vertical red line). Tree outcome describes the status of a tree (control, live-burned and dead-burned) at the end of the study, 16 months post-fire. Once a tree died, it was no longer sampled, and no new trees died after T5. Asterisks indicate at least one significant difference ($P < 0.05$) between mortality outcomes at a timestep (see Table S3 available as Supplementary data at *Tree Physiology* Online for all statistical comparisons). Error bars are 95% confidence intervals. Note variable y-axes across NSC components.

Discussion

Our results support the importance of NSCs for tree survival and recovery post-fire. We show that, in general, after a low-intensity fire in which all trees initially survived, NSC concentrations declined quickly in burned trees relative to unburned trees over the same post-fire period. This decline was most pronounced for trees that eventually died in the months after a spring prescribed fire (Figure 2), providing some support for our second hypothesis that when carbon stores and acquisition are lower than carbon demand post-fire, NSCs decline below some threshold for tree survival. Although we do not identify an explicit threshold of NSC concentration at which trees die, we find that any total NSC decline in the main stem phloem between T0 to T3 portends death (eight of nine trees; Figure 4), and further study to identify a threshold is warranted, particularly for trees that have high crown scorch. Interestingly, our results align well with post-fire mortality models for *Ponderosa* pine in the Intermountain West of the USA, which predict tree death at 70% and greater crown scorch when foliage consumption, which causes bud kill, is low (Sieg et al. 2006). We found that trees that died in our study had at least 75% crown scorch and that considering NSC declines in the main stem phloem further separated trees that died from those that survived (Figure 4). Our results are also consistent with

Jacquet et al. (2014), where 100% defoliated *P. pinaster* trees had reduced NSCs relative to control trees, but NSCs were not reduced in 50% defoliated trees. The NSCs in the main stem also did not decline until crown scorch levels exceeded 50% in our study (Figure 3).

The NSC concentrations of the main stem phloem likely better integrate the whole-tree status than the branch phloem. Branch NSCs are often more dynamic than the NSCs of stems as they are close to the source of carbon acquisition (Landhäusser and Lieffers 2012, Blumstein et al. 2022). Similarly, the patterns of needle NSCs were less clear, although newly flushed needles of trees that eventually died did have generally lower NSC concentrations (Figure 2). We also show that NSCs, particularly of the inner bark of the main stem at the timestep when new needle growth was occurring (T3), were negatively related to crown scorch (Figure 3), confirming our first hypothesis that NSCs would decline proportionally to crown injury. However, relationships between NSCs and bud kill were not as clear as for crown scorch, possibly because there was much less range of variation in bud kill among the burned trees compared with crown scorch (Table 2).

Although NSCs have been found to decline immediately post-fire in other conifers (Varner et al. 2009, Sayer et al. 2020, Partelli-Feltrin et al. 2023) and for resprouting tree species (Schutz et al. 2009), we show that these declines are

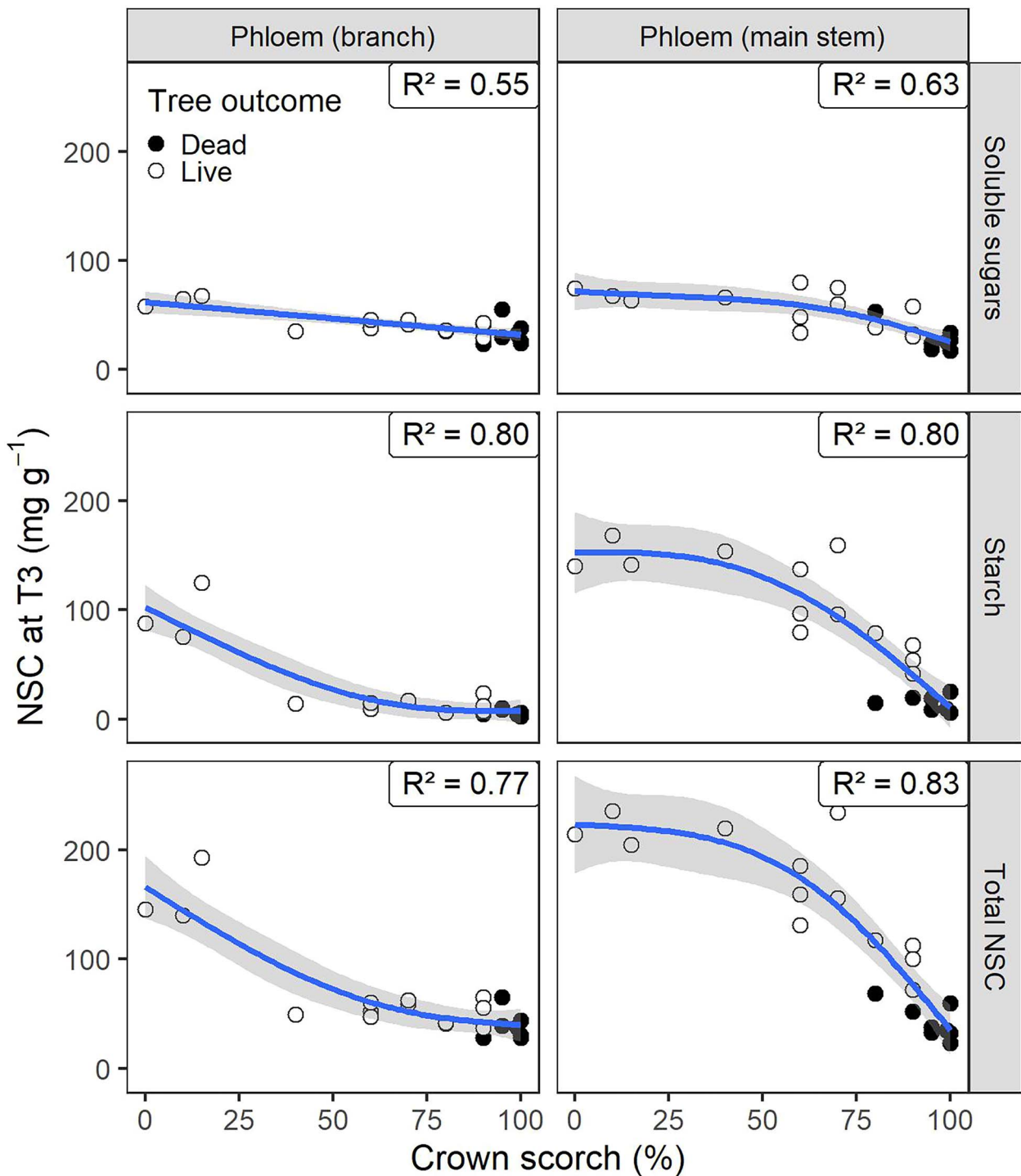


Figure 3. Relationships between NSC concentrations in the branch phloem and main stem phloem and crown volume scorched at T3, 61 days post-fire. Relationships were modeled using generalized additive models, except for soluble sugars of the branch phloem, which was modeled as a linear relationship. Trees that died during the study period are distinguished from those that survived by fill. Shading is 95% confidence interval. Adjusted R^2 values are shown. Predictors were significant in all models shown ($P < 0.05$).

clearly related to the crown injury for trees burned in a field setting during a spring prescribed fire. No prior work has linked fire-caused injury to NSC declines, nor has any work demonstrated a relationship between post-fire NSC declines and mortality in a field setting. Together, our results suggest a mechanistic link between the crown scorch and tree mortality: high crown scorch leads to a negative carbon balance and

subsequent depletion of NSC reserves below critical thresholds for survival. However, whether this carbon imbalance is entirely due to crown scorch or whether higher crown scorch is linked to greater phloem and cambium damage in small branches preventing carbon translocation throughout a tree deserves further study. Still, either mechanism provides a link between crown scorch, NSC depletion and mortality.

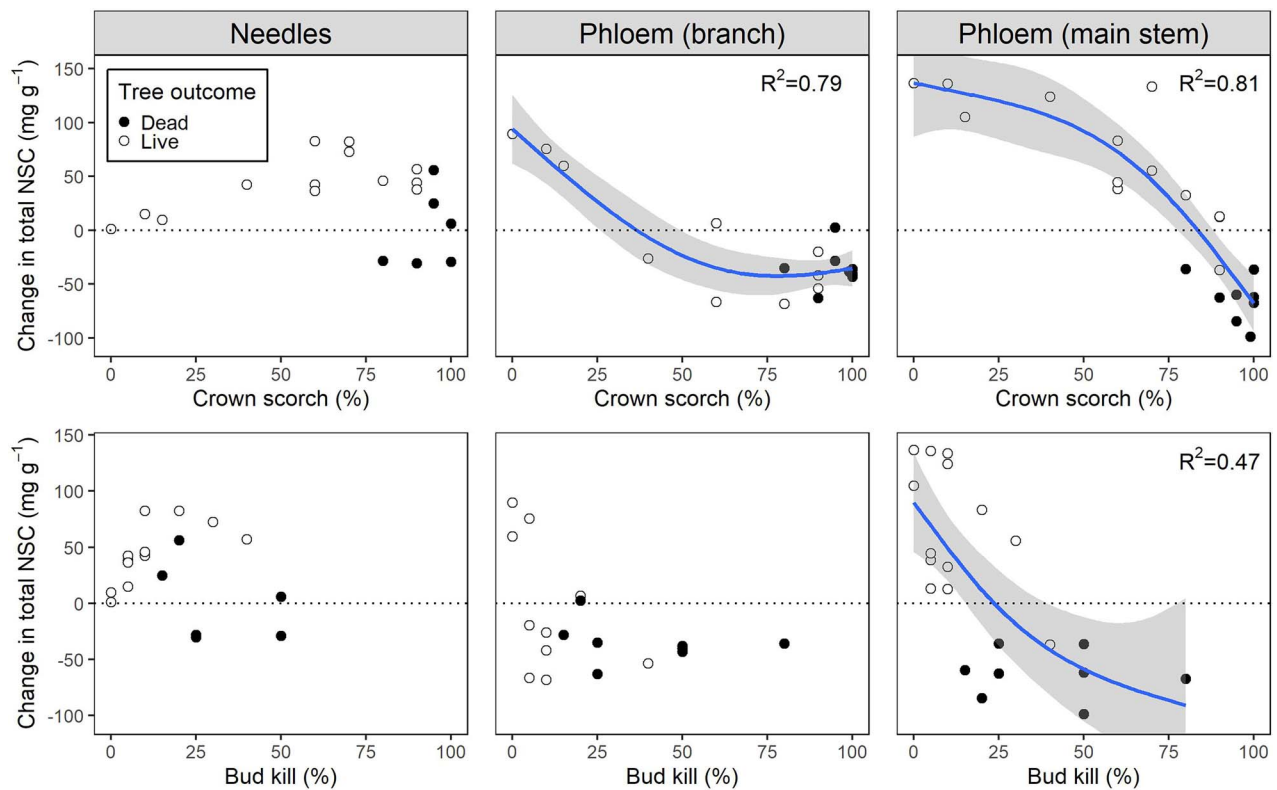


Figure 4. Change in total NSC between T0 and T3 (phloem) or T0 and T4 (needles) as a function of crown injury (crown scorch and bud kill). Relationships were modeled using generalized additive models. Trees that died during the study period are distinguished from those that survived by fill. Adjusted R^2 values are shown. Shading is 95% confidence interval. Predictors were significant for models with R^2 values shown ($P < 0.05$).

Evidence for true ‘carbon starvation’ is mixed in the context of defoliation (Anderegg and Callaway 2012, Barker Plotkin et al. 2021). However, mortality may occur when defoliation is severe enough to cause NSC declines below a threshold at which trees can survive (Webb 1981, Barker Plotkin et al. 2021) unless the NSC storage is sufficient to support foliage regrowth (Anderegg and Callaway 2012, Palacio et al. 2012). Similarly, we show that carbon starvation, defined here as unsustainable negative carbon balance, may also contribute to delayed post-fire mortality when trees sustain high levels of crown injury. There are two interacting mechanisms by which this may occur. First, reduced live leaf area, in the absence of any heat damage to the phloem, may lead to a reliance on stored NSCs to maintain tree metabolism and to flush new leaves, assuming some level of bud survival. Importantly, all of the trees that were burned in our study had surviving buds and flushed new needles 2 months post-fire. It is likely then, that the observed declines in burned trees’ main stem and branch phloem NSCs reflect, to some degree, a decrease in carbon acquisition due to lower live leaf area, as evidenced by decreasing soluble sugars, as well as a drawdown of stored NSCs, as shown by decreasing starch concentrations (Figure 2). Indeed, NSCs of the inner bark tend to be higher than in sapwood for Ponderosa pine and appear to be important for supporting metabolism (Pruyn et al. 2005). In contrast to burned trees, NSCs in unburned trees tended to increase over the same period.

Second, it is possible that high levels of crown scorch also correspond to higher levels of heat damage to the phloem and cambium in tree branches. Phloem damage was the

hypothesized mechanism of NSC decline in lethal laboratory-burned Ponderosa pine seedlings (Partelli-Feltrin et al. 2023) and may have contributed to the observed declines in NSCs in our study as well. We did see some evidence for this, as some branches from which we collected phloem had clear portions of live (green) and dead (brown) tissue (Figure S6 available as Supplementary data at *Tree Physiology* Online), and these samples were more common in branches of trees that eventually died (e.g., five out of eight samples had some dead phloem tissue at T3). However, the main stem phloem was healthy in appearance when sampled at the first three timesteps post-fire, suggesting no immediate fire-caused cambium necrosis or phloem death in the main stem. In addition, the observed increase in soluble sugar concentrations in branch phloem over the first growing season post-fire for trees that eventually died, but not for stem phloem, could also support this mechanism if damage to branch phloem prevented translocation of newly assimilated carbon to other sinks within the tree. If phloem in tree branches sustains enough heat damage that it cannot translocate sugars from newly flushed leaves, then this could also lead to the depletion of carbon reserves and delayed post-fire mortality. Phloem damage may also occur without heat, as manual defoliation has been shown to alter phloem anatomy and possibly impede the transport of photosynthates (Hillabrand et al. 2019). Importantly, these two mechanisms are not mutually exclusive, and both likely occurred in our study, contributing to the correlation between crown scorch and mortality. Future work should aim to identify the relative contribution of reduced leaf area versus phloem and cambium damage to small branches to post-fire NSC depletion under

initially non-lethal doses of fire. Importantly, both mechanisms could lead to a whole-tree carbon imbalance and link crown injury to post-fire mortality.

Patterns of NSCs for trees that were burned but were still alive at the end of the study period were different from both unburned control trees and burned trees that died. Interestingly, although live-burned trees also experienced NSC reductions over the first few months post-fire, once new needle growth occurred, their NSC stores recovered quickly (Figure 2). By the beginning of the second growing season post-fire, the total NSCs of live-burned trees had recovered to match the levels of unburned trees across all tissue types sampled. However, in some tissues, live-burned trees still had slightly lower NSCs at the end of the second growing season post-fire, although these differences were minimal. This suggests that impacts of crown scorch and subsequent reduction in photosynthetically active leaf area are short-lived and that the recovery of NSC stores, at least in the inner bark and new needles, is swift if minimal bud kill occurs and if the crown scorch is not high. This finding aligns with studies that have measured changes in the photosynthetic capacity of live needles post-fire, which sometimes find higher photosynthetic rates after fire (Wallin et al. 2003, Renninger et al. 2013), particularly for trees that sustain moderate levels of crown injury but that survive, possibly to compensate for the lost leaf area (Bryant et al. 2022). However, even with increased photosynthetic rates, large reductions in leaf area due to high crown scorch could likely lead to whole-tree imbalances for NSCs and the inability to meet metabolic demands. We did not assess NSCs in longer-term storage tissues like roots and sapwood, which may play a larger role in a tree's ability to survive beyond the initial season after fire, as these tissues can be large NSCs storage pools (Landhäusser and Liefers 2012). Further study of post-fire NSC dynamics in long-term storage tissues is necessary to confirm this result. Additionally, we caution that our findings may not hold for conifer species with smaller buds that are less resistant to heating than *Ponderosa* pine, and further research is needed.

Phenological changes in NSCs are common across tree species (Martínez-Vilalta et al. 2016, Tixier et al. 2020). Thus, the seasonal timing of fire likely has an impact on the relationship between the crown injury and post-fire NSCs, and climatic seasonality may also influence this relationship. We find that soluble sugars tend to be highest in the late summer and starch tends to be highest at the start of the growing season in June (Figure 2), which is the same pattern observed for NSCs in the bark of two boreal conifers (Schoonmaker et al. 2021), and this is similar to the observations of seasonal fluctuations in the leaves and stems of temperate species more broadly (Martínez-Vilalta et al. 2016). Fires that occur toward the end of the growing season or in the fall, as is common in western North America, when NSC stores are seasonally lowest, may require less crown scorch to kill trees. Indeed, the interaction of tree phenology and insect defoliation timing led to differing impacts of defoliation-induced NSC reductions on the growth and mortality of two broadleaf evergreen species in southern China, suggesting that phenology can influence the tolerance of trees to defoliation (Chen et al. 2017). However, bud phenology may also impact the tolerance of trees to crown scorch (Bison et al. 2022), with fires that occur in the fall after bud set having lower mortality than spring and summer fires, regardless of the level of crown scorch (Harrington 1987). Additionally, the occurrence of

other stressors, such as drought in the first season after fire, may portend lower tolerance of trees to crown scorch since drought typically further reduces NSC stores, particularly in conifers (Adams et al. 2017), and because of the role that NSCs play in osmoregulation and turgor maintenance (Sapes et al. 2021). We did not assess how seasonal drought may have exacerbated post-fire NSC reductions and contributed to mortality, which deserves additional study. It is also possible that the fire-induced reductions of NSCs, and soluble sugars in particular, in the six trees that died between August 2021 and June 2022 led to greater vulnerability to cold temperatures, as soluble sugars are important for frost resistance (Villar-Salvador et al. 2015, Blumstein et al. 2022). Further understanding how phenology impacts the way in which fire affects NSC stores and subsequent mortality, and the role of fire-induced NSC reductions in drought and cold tolerance, could provide additional valuable information for a better understanding of the mechanisms of post-fire mortality and for post-fire mortality modeling.

Conclusions

Fire impacts on tree physiological function are only beginning to be understood, and understanding these impacts is important for fire effects modeling and for predicting the potential for forest recovery post-fire (Hood et al. 2018). Together, our results suggest a mechanistic link between crown scorch, which is a commonly assessed metric of fire effects and used in post-fire mortality models, and post-fire tree outcome. Our results align with the few studies that quantify NSCs in fire-exposed trees, which show a decline in NSCs post-fire, but our research expands the scope of previous research to link fire-caused injury to NSC reductions to tree mortality or recovery. More data from other species in field-based studies are needed to confirm this link and establish a fire-related NSC depletion-mortality threshold before building NSC dynamics into mortality models, but our results demonstrate the usefulness of doing so. While our study focused on small trees, fires routinely cause crown scorch in overstory trees, and thus our results are likely relevant for larger trees, but more research is needed to confirm this. Importantly, the link between crown scorch and NSCs (Figure 3) may explain why crown scorch is such an important predictor of post-fire mortality (Sieg et al. 2006). Further study of the interaction between NSC dynamics and phenology and other post-fire disturbances like drought is needed to determine whether the patterns we observed hold more broadly (Nolan et al. 2021). We do not quantify potential fire impacts on tree hydraulic systems in this study, although support for fire-caused damage to xylem function in studies that use fire, and not fire-proxies like water baths, is minimal in the first year post-fire (Bär et al. 2019, Hood 2021). However, longer-term impacts may occur due to xylem deformities around newly formed fire scars (Partelli-Feltrin et al. 2021). Hydraulic dysfunction unlikely contributed to mortality in our study, as all trees that died did so within the first year post-fire, and fire that is intense enough to cause immediate damage to the xylem would likely cause widespread phloem and cambium death as well. Additionally, species-specific differences in bud characteristics may change the relationships between crown scorch and NSCs that we observe, particularly when species do not have large or protected buds with a high likelihood of

re-growing needles post-fire. Further research that considers other species and accounts for the compounding impacts of fire and other disturbances on post-fire changes to NSCs is needed. Our findings that NSC dynamics may explain the link between crown injury and the likelihood of post-fire mortality or recovery are highly novel and important for improving our understanding of the mechanisms of fire-induced mortality and the potential for forest recovery post-fire.

Supplementary data

Supplementary data for this article are available at *Tree Physiology* Online.

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Conflict of interest

None declared.

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Data availability statement

Data are available in the USDA Forest Service Research Data Archive in the following data set: Reed and Hood (2024), <https://doi.org/10.2737/RDS-2024-0003>.

Authors' contributions

C.C.R. led the NSC quantification, data analysis and the writing of the manuscript. S.M.H. conceptualized the study design, obtained funding, and edited and wrote portions of the final version. Both authors equally contributed to collecting data and interpretation of results.

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