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Fire-caused injuries to conifers can result in a period of reduced tree growth and elevated drought vulnerability within the first two years after fire

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Abstract

Background Managers of seasonally dry western North American conifer forests are tasked with increasing forest resilience to both wildfire and drought. Wildfire hazard reduction techniques, like prescribed fire, that reduce forest density may also lessen forest vulnerability to drought and enhance growth by reducing competition for water. However, fire may also come with costs, if fire-caused injuries impair growth and the maintenance of tree water balance. We examined whether fire-caused injuries and their physiological impacts limit the degree to which fire-induced reductions of competition improve tree water relations and growth. We monitored two widespread western North American conifer species before and after two prescribed burns in comparison to unburned control sites. Additionally, we implemented a rainfall exclusion treatment to explicitly examine whether fire-caused injuries exacerbate post-fire drought effects. We followed Douglas-fir and ponderosa pine pre-fire and at multiple timesteps up to 22 months post-fire to assess short-term changes in water status and growth as a function of changes in tree carbon balance (non-structural carbohydrates), fire injuries (crown scorch, cambium kill), and changes in competition.

Results We found that, on average, burned trees exhibited higher water stress relative to unburned controls over the first 1–2 years post-fire, despite fire-induced decreases in competition. Experimental post-fire drought exacerbated these differences at one of our two sites. Burning also caused a transient reduction in radial growth which was strongly related to the level of crown scorch a tree sustained. Our results also suggest that tree growth and water status may recover after initial declines, but to different degrees at our two sites.

Conclusions Our results show that, in the short-term, negative effects of fire injuries can complicate positive effects of density reductions. Trees may be more vulnerable to drought or other stressors during this time period, although benefits may be realized once recovery from fire injuries has occurred. Although our results show a fire-induced window of susceptibility to drought and reduced growth, we acknowledge the myriad demonstrated benefits of prescribed burning, and caution that our results should be placed in the context of larger efforts to restore vast areas of fire-prone forests.

Keywords Post-fire recovery, Prescribed burning, Tree mortality, Non-structural carbohydrates, Water dynamics, Fire effects, *Pinus ponderosa*, *Pseudotsuga menziesii*

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Resumen

Antecedentes Los gestores de bosques de coníferas secos estacionales del oeste de los EEUU, están ocupados en lograr un incremento de la resiliencia de los bosques tanto al fuego como a la sequía. Las técnicas de reducción del riesgo de incendios, como las quemas prescriptas, que reducen la densidad del bosque, pueden también disminuir la vulnerabilidad de esos bosques a la sequía y aumentar el crecimiento mediante la reducción de la competencia por agua. Sin embargo, el fuego puede tener algunos costos, si las heridas causadas por el fuego reducen el crecimiento y el mantenimiento del balance hídrico de los árboles. Examinamos si las heridas causadas por fuegos y sus impactos fisiológicos limitan el grado al cual las reducciones en la competencia inducidas por el fuego mejoran las relaciones hídricas y el crecimiento de los árboles. Monitoreamos dos especies de coníferas ampliamente difundidas en el oeste de Norteamérica antes y después de dos quemas prescriptas y su comparación con sitios control no quemados. Adicionalmente, implementamos un tratamiento de exclusión de lluvias para examinar explícitamente si las heridas causadas por el fuego exacerban los efectos de la sequía post fuego. Seguimos a pinos ponderosa y pinos de Oregón en el pre fuego y en múltiples pasos y hasta 22 meses después de las quemas, para determinar los cambios a corto plazo en el estatus hídrico y el crecimiento en función de los cambios en el balance de carbono de los árboles (carbohidratos no estructurales), las heridas causadas por el fuego (chamuscado de copas, muerte del cambium), y cambios en la competencia.

Resultados Encontramos que, en promedio, los árboles quemados exhibieron un estrés hídrico mayor en relación a los no quemados (control), en los primeros 1–2 años post fuego, a pesar de la inducción del fuego en la reducción de la competencia. Las sequías experimentales exacerbaron esas diferencias en uno de nuestros cuatro sitios. La quema también causó una reducción transitoria en el crecimiento radial, lo que fue fuertemente relacionado con el nivel de chamuscado de la copa que cada árbol recibió durante la quema. Nuestros resultados también sugieren que el crecimiento de los árboles y el estatus hídrico se recuperan luego de la declinación inicial, aunque en grados diferentes de acuerdo a dos de los sitios.

Conclusiones Nuestros resultados muestran que, en el corto plazo, los efectos negativos de las heridas por las quemas prescriptas pueden complicar los efectos positivos de la reducción en la densidad. Los árboles pueden ser más vulnerables a la sequía u otros factores estresantes durante este período, aunque los beneficios pueden ser alcanzados cuando ocurra la recuperación de las heridas. Aunque nuestros resultados muestran un ventana de susceptibilidad inducida por el fuego en cuanto a la sequía y la reducción en el crecimiento, estamos de acuerdo de que un gran número de beneficios son demostrados por las quemas prescriptas, y que nuestros resultados deben ser ubicados en el contexto de grandes esfuerzos para restaurar grandes áreas de bosques proclives al fuego.

Background

Drought and wildfire are two of the most significant disturbances affecting forests globally (Allen et al. 2015; Jones et al. 2022). As global climate change alters the dynamics of these disturbances, leading to more frequent droughts and greater wildfire area burned (Chiang et al. 2021; Pausas and Keeley 2021), forest management is increasingly recognized for its potential to increase resilience and buffer disturbances' undesirable impacts (Davis et al. 2022; Millar et al. 2007; Seidl et al. 2016). Specifically, management actions that reduce forest density, change species composition, or manipulate fuels can mitigate adverse effects, such as high levels of tree mortality, from wildfire (Prichard et al. 2010), and actions that decrease forest density may additionally lessen drought vulnerability by reducing competition for water (Bradford et al. 2022). These types of management actions are of particular importance in seasonally dry conifer forests of western North America that historically burned frequently at low severity. These forests have become increasingly dense, in part due to fire suppression, leading to higher severity wildfire, suppressed tree growth, increased competition for water and nutrients, and exacerbated drought-related mortality (Bradford et al. 2022; Young et al. 2017; Hagmann et al. 2021). In these systems, prescribed fire and silvicultural techniques such as thinning are the two primary modes of forest management used to address these challenges. In addition, it is increasingly recognized that low to moderate severity wildfire may achieve similar goals (North et al. 2021). Importantly, mechanical thinning does not reduce surface fuels and is not as effective as prescribed fire in reducing future fire severity (Davis et al. 2024). Thus, addressing these forest management challenges requires a suite of approaches, many of which include the use of fire (North et al. 2021; Bernal et al. 2025). Yet, our knowledge of how fire and its impacts on tree function affect post-fire growth and vulnerability to drought remains incomplete.

While both thinning and prescribed fire typically decrease future wildfire severity (Prichard et al. 2020; Brodie et al. 2024), they may also simultaneously enhance growth and lessen forest vulnerability to drought due to fire-induced decreases in forest density which reduce competition for water and nutrients (Sohn et al. 2016; van Mantgem et al. 2021; Camarero et al. 2023). Growth typically decreases under drought, but reducing forest density may dampen this effect (Tepley et al. 2020). Minimizing growth declines is particularly important, as slower growth often increases the likelihood of drought- (Cailleret et al. 2017) and fire-related mortality (van Mantgem et al. 2018). Mechanical thinning can increase water availability and growth of remaining trees, thus mitigating negative impacts of drought (Chase et al. 2016; Sohn et al. 2016; Cabon et al. 2018; Sankey and Tatum 2022). However, the potential for fire (either prescribed or low to moderate severity wildfire), without prior thinning, to have these same benefits is not as clear (Zald et al. 2022; Knapp et al. 2021; Valor et al. 2018). As prescribed fire use and area burned by wildfires increase, it is important to understand whether and when fire-caused reductions in forest density can be expected to reduce drought vulnerability and enhance growth.

Two primary factors separate mechanical forest density reductions from fire: trees that survive fire typically incur some level of fire-caused injury during burning, and fire-caused density reductions unfold over multiple years, as many trees that initially survive fire die in later years (Hood et al. 2018). Additionally, many prescribed fires do not substantially reduce forest density, as they are often implemented under conditions that lower fire intensity (Knapp et al. 2009; Grupenhoff et al. 2025). The potential for prescribed fire or low-to-moderate-severity wildfire to decrease drought vulnerability and increase growth is thus likely dependent on the magnitude of density reductions, the severity of fire injuries, the degree to which physiological impacts from fire injuries affect growth and drought vulnerability (Bär et al. 2019), and the timeframe over which the costs and benefits of burning are examined (Fig. 1). Importantly, we know very little regarding the physiological effects of fire injuries on post-fire growth and drought vulnerability, nor the length of time required for recovery from these injuries, which will likely influence the timeframe over which potential benefits are realized. This limits the ability to accurately model, estimate, and forecast forest vulnerability to climate-related stressors during the recovery period, as well as essential forest ecosystem and economic services, such

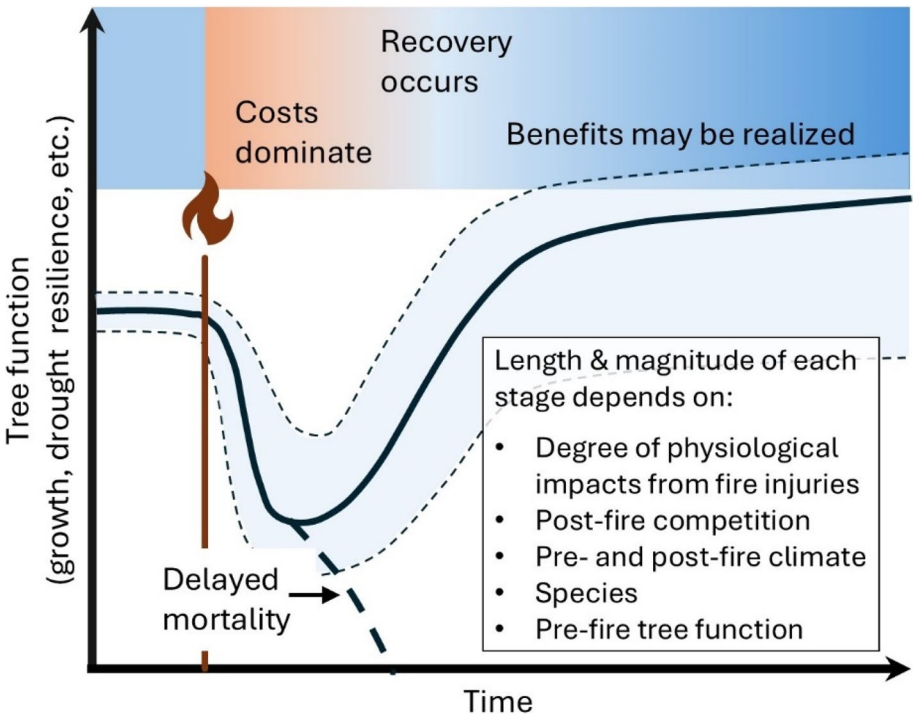

Fig. 1 Conceptualization of tree function (e.g., growth, drought resilience) versus time before and after fire. Shading around the curve represents variability in the magnitude of tree response at each stage. During the first stage after fire, costs due to fire-related injuries may dominate, but after recovery occurs benefits can be realized. The length and magnitude of each stage is dependent on numerous factors. The bold dashed line indicates a scenario in which delayed mortality occurs. The vertical red line denotes the time of fire

as carbon pools, forest growth and yield, and wildlife habitat.

Non-lethal fire-caused injuries can impact tree physiological function in ways that could affect both post-fire growth and drought vulnerability. Fire injuries are a product of fire intensity, exposure to heat plumes, and subsequent heat transfer to tree tissues that can result in leaf, bud, and phloem and cambium necrosis (Smith et al. 2017; Michaletz and Johnson 2007). These injuries have the potential to impact tree carbon balance and hydraulic function, and thus impact both growth and tree water relations (Bär et al. 2019; Reed et al. 2025). Fire-caused leaf necrosis (i.e., crown scorch) temporarily reduces carbon uptake (Reed and Hood 2024), while bud necrosis may slow the recovery time to grow new tissues. Phloem death can also affect carbon balance by obstructing transport of non-structural carbohydrates (soluble sugars, starch; NSC) to locations where NSC are needed for tissue maintenance and repair (Partelli-Feltrin et al. 2023). Thus, fire-caused injuries can affect both production and translocation of NSC necessary for maintaining tree metabolism and growth (Sala et al. 2012; Hartmann and Trumbore 2016; Galiano et al. 2011). In addition, because NSC have been implicated in the maintenance of fine roots for water uptake and in turgor maintenance and osmoregulation (Sword and Haywood 1995; Sapes et al. 2021), changes in NSC could affect tree hydraulic function and responses to drought. For example, the magnitude of NSC drawdowns after fire relates to the level of fire injury a tree sustains, and these reductions may lead to indirect effects on hydraulic function and possibly delayed mortality (Reed and Hood 2024; Reed et al. 2025). These and other fire-induced negative effects on tree physiology could deteriorate hydraulic function and responses to future drought (Partelli-Feltrin et al. 2021). In contrast to these negative effects, tree water status could be temporarily improved if leaf area, but not root area, is sufficiently reduced during fire (Bryant et al. 2022; Wallin et al. 2003), although the length of time this benefit may persist has not been explored. Importantly, the magnitude of fire-caused injuries and their physiological impacts likely affect the recovery time needed before fire-related thinning benefits can be realized (Fig. 1).

There has been much recent interest in examining drought vulnerability and growth after fire (wildland and prescribed), yet most studies that do so are retrospective and quantify either differences in drought-related mortality after fire (van Mantgem et al. 2021; Steel et al. 2021) or differences in radial growth between burned and unburned trees (Becker and Lutz 2023; Camarero et al. 2023; Valor et al. 2020). This work shows that fire-caused forest density reductions can improve drought resistance and growth. However, increased drought-related mortality for some tree species after fire can also occur (Steel et al. 2021), suggesting that the propensity for increased growth post-fire may be related to differences in site productivity and climate or the level of fire-caused injuries a tree sustains (Valor et al. 2018; Alfaro-Sánchez et al. 2015). Additionally, the benefit of burning might not be realized immediately post-fire, and the timeframe over which this benefit is realized may depend on the time needed for recovery from fire-caused injuries (Furniss et al. 2022; Wenderott et al. 2022) (Fig. 1). While retrospective studies are important, they do not directly address the relationship between post-fire recovery and the magnitude of fire-caused injuries (but see Valor et al. 2018). These uncertainties further highlight the need for a more experimental approach to gain a better mechanistic understanding of fire-caused physiological impacts, how site and species differences affect outcomes, and the variables that influence recovery time.

We explored these questions by following two widespread western North American conifer species before and after two prescribed burns in western Montana, USA. We examined how fire-caused injuries and their physiological impacts interact with fire-caused changes in competition to affect tree water relations and growth over the first two growing seasons post-fire. Additionally, we implemented a rainfall exclusion treatment to explicitly examine whether fire-caused injuries exacerbate post-fire drought effects. We followed Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) pre-fire and at multiple timesteps up to 22 months post-fire to assess short-term changes in water status and growth as a function of changes in tree carbon balance (i.e., NSC), fire injuries (i.e., crown scorch, bud kill, cambium kill), and changes in competition. The two prescribed burns differed in timing, with one occurring in the spring and one in the fall, allowing us to capture the range of prescribed fire seasonality typical in our study area. The fall burn occurred under conditions more similar to those experienced during late summer wildfires, and the spring burn occurred at the end of the dormant season. Each burn site was paired with a nearby unburned "control" site. We hypothesized that the beneficial effects of density reductions on tree water status will not be realized in the short-term post-fire due to the physiological impacts of fire-caused injuries. We thus predicted that: (i) fire-caused reductions in tree density will lead to improved tree water status only when fire injuries are minimal, (ii) burned trees are more negatively affected by drought due to the physiological impacts of fire on tree water relations, and (iii) given the importance of stored carbohydrate reserves for tree growth and overall function, initial fire-caused growth declines and subsequent recovery are

related to fire injuries and associated changes in tree carbon balance. Our work highlights the potential for short-term impacts to drought vulnerability and growth in the years following fire and suggests areas that require further study to develop a more comprehensive understanding of when and how management activities can best increase forest resilience to drought.

Methods

Site description and study species

We selected two sites dominated by ponderosa pine and Douglas-fir in western Montana, USA that were scheduled to be prescribed burned the following fall or spring. Sites had no recent fire or other forest management activity. One site was burned in mid-October 2022 and the other in early May 2023. Both sites are characterized by relatively open ponderosa pine and Douglas-fir in the overstory, with dense clusters of regenerating trees of both species interspersed throughout the understory. Each burned site was paired with a nearby site of similar forest structure, species composition, and aspect that remained unburned (henceforth, controls). Paired burned and control sites were no more than 800 m apart and at similar elevations. The spring and fall burn sites were approximately 8.5 km apart, at similar elevations (~1300 m), and with similar climatic conditions. Most rainfall in this area occurs in May and June, and snowfall typically occurs from December to March. The average total precipitation over the water year (October through September) averaged 225 mm from 2017 to 2022 (Agrimet; https://mesonet.climate.umt.edu/dash/lubrecht/). Total precipitation over the 2022–2023 water year was 120% of average (27.2 cm), whereas total precipitation over the 2023–2024 water year was 55% of average (12.4 cm). See Reed et al. (2025) for additional site details.

Tree characteristics and neighborhood competition

At each of the four sites (fall-burn, fall-control, spring-burn, spring-control), we tagged 20 ponderosa pine and 20 Douglas-fir approximately 1 month prior to burning, for a total of 40 trees per site. We selected trees 7–16 cm diameter at breast height (1.37 m, DBH). We chose smaller trees to increase the likelihood of crown scorch, and to capture a range of levels of competition around each focal tree, as these trees were more likely to be growing in relatively dense clusters. Prior to the prescribed fires, we measured tree size (DBH, height), bark thickness, and compacted crown ratio. Approximately 3 weeks, post-fire we measured crown volume scorched and the percent of buds killed. We only assessed bud kill on ponderosa pine, as we assumed that scorched Douglas-fir branches had no bud survival due to their small bud size; this was confirmed by observations post-fire. We retrospectively estimated cambium kill rating (CKR) in 2024 on live trees. We additionally cut sections from the base of dead trees and carefully examined evidence of post-fire radial growth and obvious cambium death (e.g., from bark consumption) in order to retrospectively assess CKR on these trees. Cambium kill rating is a measure of the number of quadrants around the base of the main stem with fire-killed cambium (Hood et al. 2010). We grouped CKR into two categories for analyses: low (0–1 quadrant killed) and high (2–4 quadrants killed), as only a few trees had CKR ratings of 3 or 4. We assessed tree status (live, dead) 3 weeks post-fire, the first spring post-fire (May 2023), at the end of the first growing season (September 2023), and following the second growing season post-fire (September 2024).

As a result of higher-than-expected fire intensity at the fall-burn site, 22 of the 40 originally tagged trees died in the fire (100% crown consumption or 100% bud kill). We replaced these trees with similarly sized live trees (i.e., some green foliage) of the same species haphazardly selected immediately post-fire. The patchy nature of the spring burn resulted in six trees not experiencing fire (i.e., no needle scorch or bark char). We similarly replaced these trees immediately post-fire with live trees that had some crown scorch. Original and replacement trees did not vary in tree characteristics (Reed et al. 2025), but pre-fire physiological measurements were taken from original trees only, while post-fire physiological measurements included a mixture of original and replacement trees.

We selected trees with a range of levels of neighborhood competition, with some occurring in relatively open conditions, while others occurred in patches of dense regenerating trees. We quantified neighborhood competition within 5 m of each focal tree using the Hegyi index (Hegyi 1974). We chose this competition index as is has been shown to relate well to growth of ponderosa pine and Douglas-fir (Contreras et al. 2011), and because it considers both neighbor tree size and distance to the focal tree. We additionally calculated stand density index (SDI; Reineke 1933) within the same radius around each focal tree. We assessed competition pre-fire (including a retrospective assessment of pre-fire competition for replacement trees), and at the end of both the first and second growing seasons post-fire. A full sampling timeline is included in the Supporting Information (Table S1).

Fire intensity and fuel moisture information

Detailed information on burn day weather, fire intensity, and fuel moisture is included in Reed et al. (2025). Briefly, burn units were broadcast burned by either hand ignitions (fall burn) or aerial ignitions (spring burn), and sampling sites occurred in a relatively small area (0.05 km^2) within the larger burn units. Both litter and live fuel

moisture values were higher during the fall burn compared to the spring burn (25% vs. 8% and 133% vs. 99%, respectively), but duff moisture was higher at the time of the spring burn (51% vs. 36%). Although fuel moisture was generally higher at the time of the fall burn, the spring burn was considerably patchier. Both burns were primarily surface fires with some individual and group tree torching (i.e., crown consumption via flaming). In addition to direct observations of fire intensity during the burn and post-burn observations of fire severity, we also sampled litter and duff at dripline (outer edge of tree crown width) on the north side of each focal tree before and immediately after fire, and differences in crown scorch height on overstory trees post-fire within our study sites. These data show that the fall burn was more intense, with crown scorch heights up to 24 m compared to 10 m at the spring-burned site, and higher litter consumption (48% decrease) compared to a 19% decrease at the spring-burned site.

Drought experiment

We selected half of the 40 focal trees at each of the four sites for a rainfall exclusion treatment after the prescribed burns. Trees were selected such that drought-exposed and ambient trees had similar mean size and similar mean crown scorch for burned trees. We constructed rainfall exclusion shelters around the base of each focal tree (Fig. S1). Shelter sizes were determined based on an estimate of tree crown widths (Hann 1999). We multiplied estimated crown width by 1.2 to calculate the length of one side of the square shelter (i.e., 120% of crown width) to ensure that shelters extended beyond dripline, where most roots are assumed to occur (Smith 1964). Shelters were constructed using 6 mil (0.15 mm) clear greenhouse plastic (Green-Tek, Clinton, WI, USA). Shelters were attached to the stem of the focal tree and corners and edges staked so that some air flow could still occur under the shelters (Fig. S1). Shelters were installed in late May of 2023. We flattened shelters to the ground prior to snowfall in October 2023 to prevent infiltration of snowmelt within the shelter footprint, and we reconstructed shelters in April 2024. Shelters were removed in September 2024 once all measurements were completed. We repaired shelters every 2–4 weeks during the snow-free period as needed. Wind and animal damage did occasionally occur, so rainfall exclusion cannot be assumed to be 100%. We assessed shelter effectiveness by measuring soil volumetric water content at 12 cm depth using a HydroSense II soil moisture sensor (Campbell Scientific, Logan, UT, USA) in July 2023 and June 2024 approximately 1 m from the stem of the tree at two points on opposite sides of the tree. We measured soil moisture for both droughted and ambient trees.

Drought stress and water availability

Changes in water availability and water stress were assessed via needle pre-dawn water potential (Ψ_{pd}) and mid-day (12:00–14:00) water potential (Ψ_{md}), respectively. We measured Ψ_{md} pre-burn, the first spring post-burn (May 2023), at the end of the first summer (September 2023), and during the second summer post-burn (July 2024). Pre-dawn measurements were taken at the same timesteps within a week of Ψ_{md} measurements at each site. However, we did not assess Ψ_{pd} pre-burn at the spring-burn and spring-control sites as the sites were challenging to access due to snow. Samples were clipped from the upper half of the tree crown on all focal trees and stored in humidified bags until measurement approximately 30 min later with a Scholander pressure chamber (PMS Instruments, Albany, OR, USA). We used 1-year old needles (single fascicle for ponderosa pine, small branch end for Douglas-fir) for all measurements.

Radial growth

In fall 2024, we took two, 4.5 mm-diameter increment cores from the base of live trees (or where there was live phloem) on the cross-slope and cut sections from the base of dead trees for analyses of radial growth and to estimate tree age. Cores were mounted and both sections and cores were sanded with progressively finer grits until cell structure was visible through a binocular microscope. Sections and cores were then scanned at 1200 DPI using an Epson platform scanner. Ring widths were measured using CooRecorder v9.8, and series were crossdated using CDendro (Cybis Elektronik & Data AB, Saltsjöbaden, Sweden). We checked crossdating with COFECHA (Holmes 1983). We converted annual raw ring widths to basal area increment (BAI) to account for decreasing ring widths with increasing tree size (Biondi and Qeadan 2008). We calculated BAI using the "dplR" package in R (Bunn 2008), and averaged BAI for two radii (sections) or two cores per tree. For analyses, we calculated mean pre-fire growth (mean BAI over 5 years pre-fire), as well as growth resistance (BAI of first year post-fire/BAI of 1 year pre-fire), growth recovery (BAI of second year post-fire/BAI of first year post-fire), and resilience (BAI of second year post-fire/BAI of 1 year pre-fire) via Lloret et al. (2011). We divided these values at the burn site by means of unburned trees at the paired control site to account for year-to-year climatic variability.

Non-structural carbohydrates

To assess how fire-caused changes in carbon stores related to post-fire growth, we sampled tissue from both the phloem and xylem of the main stem for non-structural carbohydrate (NSC; soluble sugars, starch) analysis. We did not sample needles since prior analyses

had shown minimal effects of fire on needle NSC (Reed and Hood 2024). We took samples from all focal trees approximately 1–2 weeks pre-burn, 3 weeks post-burn, the first spring post-fire (May 2023), and at the end of the first (September 2023) and second (August 2024) growing seasons post-fire. All samples had visually live phloem. Samples were transported to the lab on ice, where they were then microwaved for three 30-s intervals to stop respiration and hydrolysis and denature enzymes (Landhäusser et al. 2018; Piper and Reyes 2020), before being frozen until further processing. Samples were dried at 60 °C for 48–72 h, and then coarsely ground with a Wiley mill (Thomas Scientific, Swedesboro, NJ, USA). We then ground samples to a fine powder using a mixer mill (Retsch, Hann, Germany) and dried again overnight prior to weighing for NSC quantification. We followed the Landhäusser et al. (2018) protocol as described in Reed and Hood (2024), following the enzyme method for quantifying soluble sugars. Tissue concentrations are expressed on a dry matter basis.

Fine-scale growth and water deficit (dendrometers)

In late May 2023, we installed point dendrometers (TOMST, Prague, Czech Republic) at approximately 1 m height on five droughted and five ambient ponderosa pine at all four sites, for a total of 40 trees. We chose ponderosa pine as it is a species that managers often aim to promote with prescribed fire in the study region. We removed outer bark prior to installation and ensured placement in areas with live phloem. Dendrometers were loaded as suggested by the manufacturer (200–1000 µm) and recorded measurements every 15 min. Many burned tree stems contracted by an unexpectedly large degree over the first summer post-fire, and thus dendrometers fell off some trees. Although we re-installed dendrometers to higher levels of loading after this issue arose, this resulted in small sample sizes in the data and thus larger error during the first summer post-fire, particularly for the spring-burned site. To process the data, we adjusted all dendrometer series to start at 0 µm 1 week after installation to allow for initial settling of the dendrometer. When dendrometers fell off, we removed the associated zero-values from the data. After reinstallation, we adjusted values to start at the most recent value prior to falling off. If the dendrometer fell off for more than 2 weeks prior to re-installing or large changes in growth occurred during this time period for other trees, we calculated the average percent change in growth over the time period from the other trees at that site and adjusted the last measured value by the same amount to get the new starting value. After these adjustments had been made, we further flagged any radial diameter changes larger than 30 µm from one timestep to the next and investigated each, adjusting as necessary. We chose 30 µm based on observations from functioning dendrometers rarely having jumps of this magnitude or greater. We then separated the irreversible growth signal (GRO) from the diurnal shrinking and swelling of the stem caused by changes in tree water deficit (total water deficit, TWD) in the timeseries (Zweifel 2016; Ziegler et al. 2024). Calculation of TWD follows the zero-growth concept and assumes that no growth occurs when a stem contracts (Zweifel et al. 2016). TWD has been found to correlate well with water potential to provide a fine-scale measurement of water stress (Ziegler et al. 2024). Dendrometers were not removed until the end of August 2025, with the aim of capturing a longer recovery timeframe post-fire.

Data analyses

Pre-burn differences in tree attributes (DBH, height, crown ratio, neighborhood competition, tree age estimate) were assessed via two-way ANOVAs with site (fall-burn, fall-control, spring-burn, spring-control), tree treatment (ambient, drought), and their interaction as predictor variables. A Tukey HSD test was used for multiple pairwise-comparisons. All analyses were conducted in R v.4.4.1 (R Core Team 2024). We took a similar approach to assess post-burning differences in crown ratio at the burned sites. We assessed changes in neighborhood competition around focal trees from pre-burn to the end of the study via paired *t*-tests for each of the four sites. Differences in soil moisture near the base of drought and ambient trees were assessed for each site and both measurement years (2023, 2024) using Wilcox rank-sum tests. We quantified differences in water potential between burned and control sites over time using linear mixed-effects models and a difference-in-differences approach (Butsic et al. 2017; Donald and Lang 2007), which accounts for pre-burn water potential differences between trees at burn and control sites. This approach calculates the treatment effect as the difference between the differences of observations at burned and control sites before and at each timestep after the burns. We modeled water potential (Ψ_{md}, Ψ_{pd}) as a function of site treatment (burned, control), timestep, and their interaction, building separate models for each species and site combination so as to separate out fire effects specific to each species and site. We included a dispersion formula to account for differences in variances for site treatments. Standard errors of the parameters were adjusted to account for temporal correlation due to remeasures of the same trees at each of the post-burn timesteps by incorporating a heterogenous compound symmetry covariance structure. We compared differences between the burned and control trees from pre-burn to each timestep post-burn

via the difference-in-differences approach by building custom contrasts using the "emmeans" package (Lenth 2022). Because we did not have pre-burn measurements for Ψ_{pd} from the spring sites, we did not use the difference-in-differences approach for these analyses. We tested for overdispersion using simulation-based tests from the "DHARMa" package (Hartig 2022) and examined model residuals via quantile-quantile plots. We used the "glmmTMB" package for building models (Brooks et al. 2017).

We observed greater water potential (Ψ_{md}, Ψ_{pd}) variability at the burned sites relative to the controls. We quantified this variability using linear mixed-effects models to determine whether it was due primarily to differences in fire injury or changes in competition; thus, these models were not meant to be predictive. We modeled each timestep (pre-burn, May 2023, September 2023, July 2024) separately to determine whether specific factors influencing water potentials changed over time, using a Bonferroni correction for *p* values. We modeled pre-burn Ψ_{md} separately for spring and fall sites due to the different times of year in which they were measured. We modeled water potential as a function of species, tree treatment (drought, ambient), tree height, crown ratio (pre-burn only), crown scorch (post-burn only), CKR (post-burn only), and changes in competition. We selected the best-fit model by AIC. If multiple models had similarly low AIC, we selected the one with the fewest parameters. We examined model residuals via quantile-quantile plots. Values were scaled and centered prior to inclusion in models to allow for comparisons of effect size.

We took a similar approach to model both pre-fire growth (mean BAI for 5 years pre-burning) and growth resistance, recovery, and resilience. We modeled each growth variable individually, as a function of species, tree treatment, DBH, crown ratio (pre-burn), crown scorch (post-burn), CKR (post-burn), changes in competition, and changes in total NSC of the phloem and xylem. Phloem NSC was consistently a better predictor than xylem NSC; therefore, we show only these results, as both NSC variables are highly colinear. The pre-burn model included measured values for NSC and competition, while the post-burn models included the percent change of these variables from pre-burn to the end of the first summer post-burn (BAI resistance) or to the end of the second summer post-burn (BAI recovery, resilience). For the trees for which we did not have pre-burn data (e.g., those that replaced trees that died during the burn), we calculated within-species means from the pre-burn timestep and used those values as the pre-burn values with which to calculate percent change. We included NSC in these models, but not the water potential models, as we expected growth to be more strongly related to tree carbon balance, which was confirmed as pre-burn growth was positively related to pre-burn NSC.

Results

Tree attributes, delayed mortality, and soil moisture

Almost twice as many trees died after the spring burn than the fall, despite tree characteristics being similar between the two sites. Prior to burning, basic tree characteristics (DBH, height, bark thickness, crown ratio) were similar across sites (spring, fall), site treatments (burn, control), and species, although ponderosa pine tended to have thicker bark and lower crown ratio than Douglas-fir (Reed et al. 2025). Ambient and droughted trees did not differ in any tree characteristics, but trees were on average older at the spring sites (burned and control) than the fall (Table S2), suggesting that the fall sites may have higher productivity due to their larger size relative to their age. At the end of the first summer post-fire, 5 of 40 trees had died at the fall-burned site and 6 of 40 at the spring-burned site. By the end of the second summer post-fire, 10 of the 40 trees (15% ponderosa pine; 35% Douglas-fir) had died at the fall-burned site (4 ambient, 6 droughted), whereas 17 of 40 (50% ponderosa pine, 35% Douglas-fir) had died at the spring-burned site (8 ambient, 9 droughted). Lastly, soil volumetric water content was lower under rainfall exclusion shelters at the fall-burned site in 2023 (6.0% ± 0.6 vs. 9.8% ± 0.8) and at both sites in 2024 (fall: 2.0% ± 0.3 vs. 6.9% ± 0.7, spring: 1.0% ± 0.4 vs. 4.2% ± 0.6) (Fig. S2).

Prescribed burning caused small but significant declines in neighborhood competition

Neighborhood competition around focal trees decreased by an average of 31% (± standard error of 0.46) at the fall-burn site and 28% (±0.65) at the spring-burn site by the end of the second summer post-fire (Fig. 2). Stand density index (SDI) similarly decreased from a mean of 163 (±18) to 129 (±15) at the fall-burn site and from 192 (±18) to 152 (±15) at the spring-burn site by the end of the second growing season post-fire. Competition did not change at the unburned control sites over this time period. Although competition declines were similar in magnitude at both sites when assessed after two seasons post-fire, declines were initially (after one season) greater at the fall-burn site (24% vs. 8%), whereas mortality was more delayed at the spring-burn site.

Burning negatively affects water status, but the magnitude of the effect is small

Burning led to more negative Ψ_{md} (higher water stress) relative to unburned control sites, particularly for spring-burned ponderosa pine, after accounting for pre-burn differences in mid-day water potential between burn and

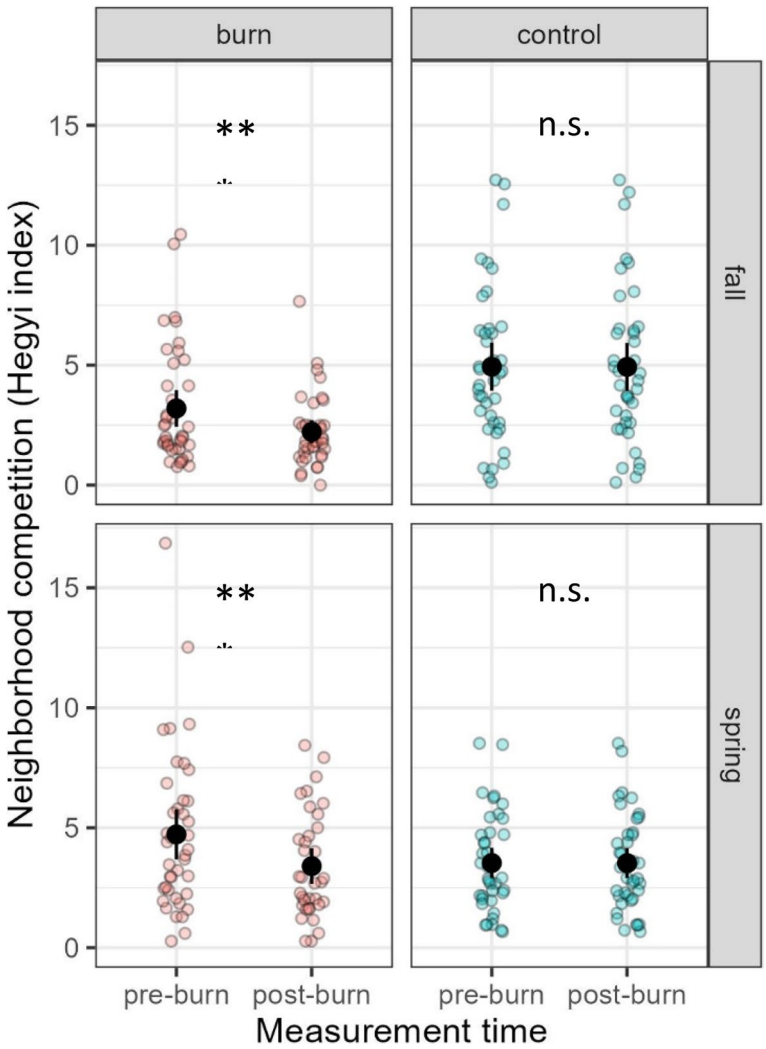

Fig. 2 Hegyi competition index around focal trees pre- and two seasons post-burn for burn (left) and control (right) sites and for both fall (top) and spring (bottom) sites. Black points are means with 95% confidence interval error bars. Asterisks denote significant change from pre-burn to post-burn ($p < 0.001$; *t*-tests); n.s. = not significant

control sites (Fig. 3). By the second summer post-fire, burned trees had consistently more negative Ψ_{md}, with the exception of fall-burned ponderosa pine, which did not differ from unburned controls. We saw similar patterns when we assessed changes in Ψ_{pd} over time, with burned trees generally having more negative values. However, the magnitude of these effects appeared to lessen over time (Fig. 4). Importantly, the magnitude of the differences between burned and control trees was generally small (0.02–0.55 MPa of difference), but the level of variability in water potentials of burned trees was consistently greater than unburned controls. We explored differences in water potentials between drought-treated and ambient trees as well, but differences between tree treatments were not significant (data not shown).

Variability in water stress related to crown scorch but only for the first summer post-burn

Pre-burn Ψ_{md} was best explained by species, and to a lesser degree, by crown ratio and tree height (Table 1). Pre-burn Ψ_{pd} was not well explained by any of the measured variables. Species was included in best-fit Ψ_{md} models from each timestep, although the direction of the relationship with Ψ_{md} changed over time. By the first spring post-burn, crown scorch emerged as a significant predictor in the Ψ_{md} best-fit model, with trees with higher crown scorch having less negative Ψ_{md} (Table 1 and Fig. 5). This pattern held for the end of the first summer post-burn, but the relationship between Ψ_{md} and crown scorch had become neutral by the second summer post-fire (Table 1 and Fig. 5). Few predictors explained post-fire Ψ_{pd}, with only high CKR relating

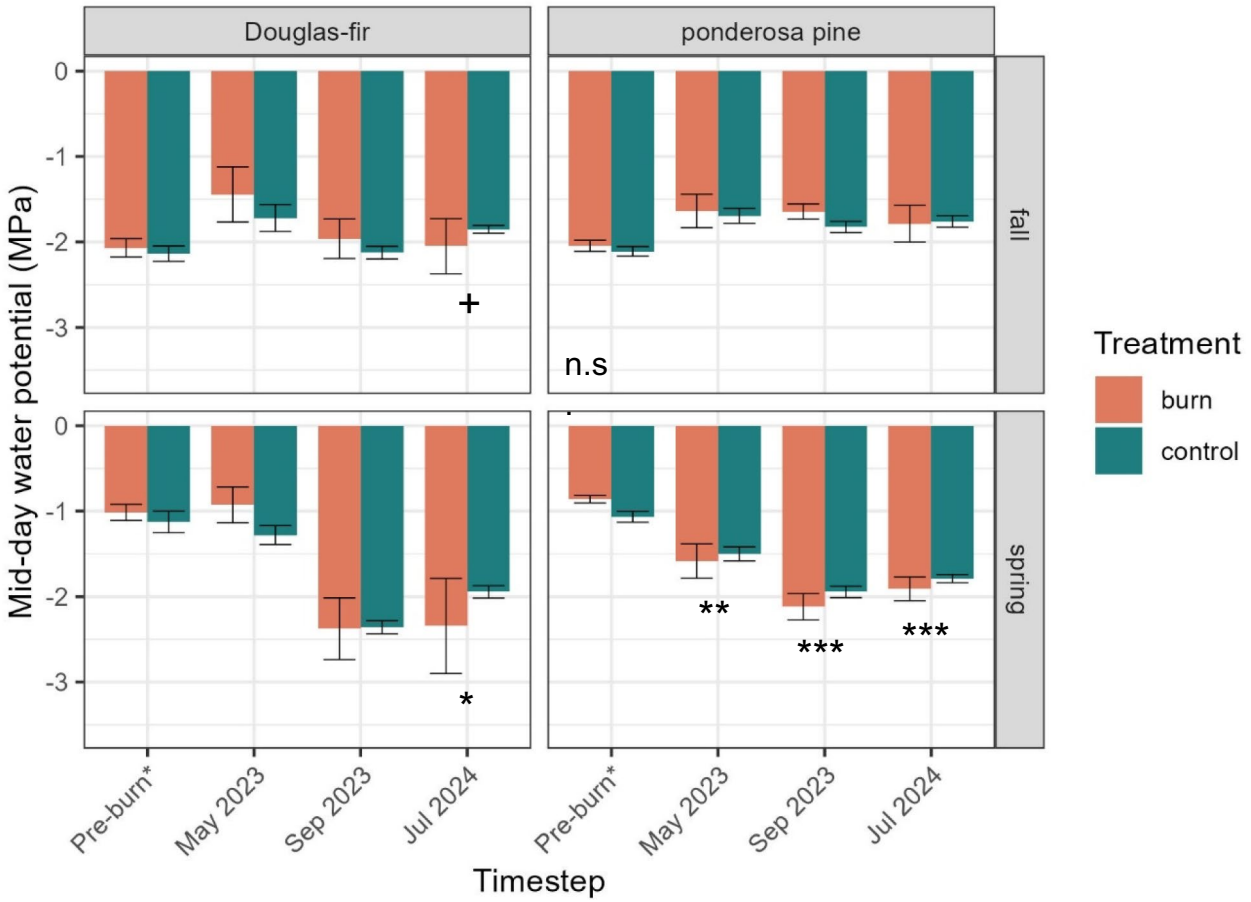

Fig. 3 Mid-day water potential over time at burned and unburned control sites. Pre-burn measurement times vary between fall and spring sites: fall = October 2022, spring = April 2023. Values are means and error bars are 95% confidence intervals. Analyses used a difference-in-differences approach to account for pre-burn differences between burn and control sites. Significance levels: + = $p < 0.1$, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, n.s. = not significant

to more negative Ψ_{pd} values, though not significantly (Table 1). Interestingly, tree treatment (drought, ambient) was not included in any of the models, suggesting that the rainfall exclusion treatment, despite lowering soil moisture at 12 cm, did not affect water potential, at least at the timesteps measured. Similarly, competition was not included in any of the best-fit water potential models.

Burned trees exhibit higher total water deficit

Consistent with pre-dawn water potential observations for ponderosa pine, fine-scale measurements of total water deficit (TWD) measured from point dendrometers on surviving ponderosa pine also showed higher water deficit for burned trees relative to unburned controls, although surviving spring-burned trees appear to have recovered by the second growing season post-fire (Fig. 6A). Interestingly, droughted trees at the fall-burned site had higher TWD relative to ambient-burned trees and all unburned controls, and these trees appeared to be driving the generally higher TWD of fall-burned trees (Fig. 6B). This pattern did not hold true for spring-burned trees, although when trees that eventually died were included, droughted-burned trees tended to have the highest TWD the second growing season post-fire (Fig. S3).

Fire-caused growth declines relate to levels of fire injury

Fire caused clear declines in radial growth at both fall- and spring-burned sites relative to unburned controls, with steeper declines at the fall-burned site (Fig. 7). This decline was temporary, as radial growth recovered to similar levels as control trees by the second growing season post-burn at the spring-burned site, and recovery was also occurring at the fall-burned site (Fig. 7). We observed generally similar patterns for fine-scale growth measured via dendrometers on ponderosa pine, which consistently showed lower growth for burned trees over the first two seasons post-fire, with recovery beginning

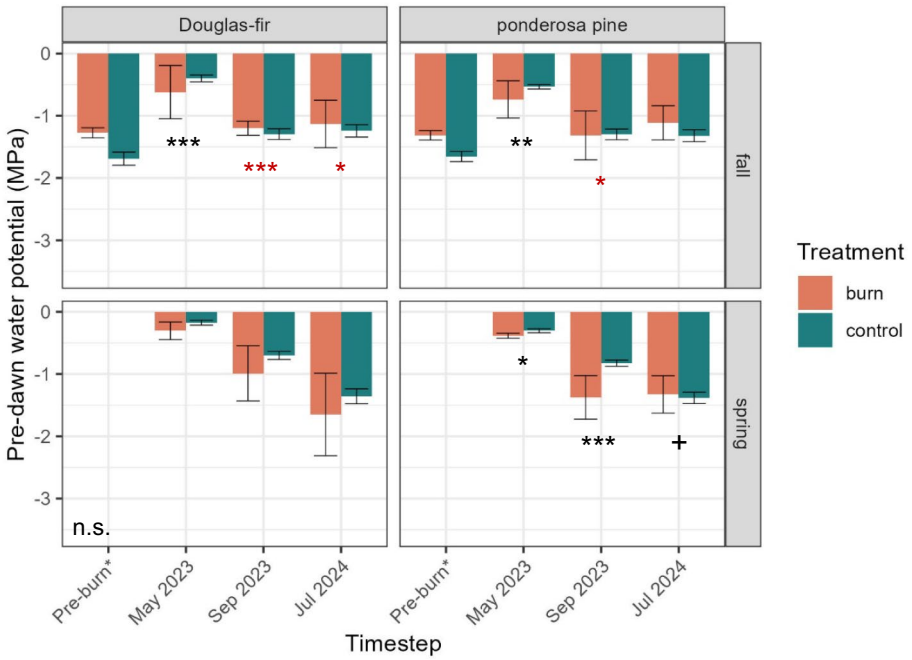

Fig. 4 Pre-dawn water potential over time at burned and unburned control sites. Pre-burn measurements occurred in October 2022; no pre-burn measurements were made at the spring sites. Values are means and error bars are 95% confidence intervals. Analyses used a difference-in-differences approach to account for pre-burn differences between burn and control sites (fall only). Red asterisks indicate that burned trees have more negative water potential than controls after accounting for pre-burn differences between the burn and control sites. Significance levels: + = $p < 0.1$, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$

Table 1 Coefficients for best-fit pre-dawn (PD) and mid-day (MD) water potential models

Ψ	Time	Species	Height	Crown ratio (%)	Crown scorch (%)	CKR
MD: fall	Pre-burn	−0.480		−0.335	–	–
MD: spr	Pre-burn	**−0.276**	−0.130		–	–
PD: fall	Pre-burn		0.060		–	–
MD	May '23	**0.996**		–	**0.556**	
PD	May '23					−0.509
MD	Sep '23	**−0.562**		–	**0.326**	
PD	Sep '23					
MD	Jul '24	−0.540		–		
PD	Jul '24					

Bold indicates statistical significance. All continuous variables scaled and centered prior to inclusion in models. Species is equal to 1 if Douglas-fir and 0 if ponderosa pine; CKR (cambium kill rating) is equal to 1 if high and 0 if low. Dashes indicates variable not included in model; blank indicates included in full model but not best-fit model. Competition index not included in any best-fit model. Bonferroni correction of p values. $p < 0.0125$

to occur by the third growing season post-fire for spring-burned trees (Fig. S4). We saw no differences in radial growth between droughted and ambient trees (data not shown).

Prior to burning, radial growth (BAI) was greater for trees with larger DBH, higher crown ratio, and higher phloem NSC (Table 2). As expected, growth resistance was negatively related to crown scorch, with trees with higher resistance (i.e., less of a growth decrease after fire) having lower levels of crown scorch (Table 2 and Fig. 8A). Resistance was also explained by species, with Douglas-fir having generally higher resistance than ponderosa pine, as well as DBH, with larger trees having higher resistance. Growth recovery was weakly negatively related to both competition and DBH but unrelated to crown scorch and NSC (Table 2 and Fig. 8B). Similar to resistance, growth resilience was also negatively related to crown scorch (Table 2 and Fig. 8C).

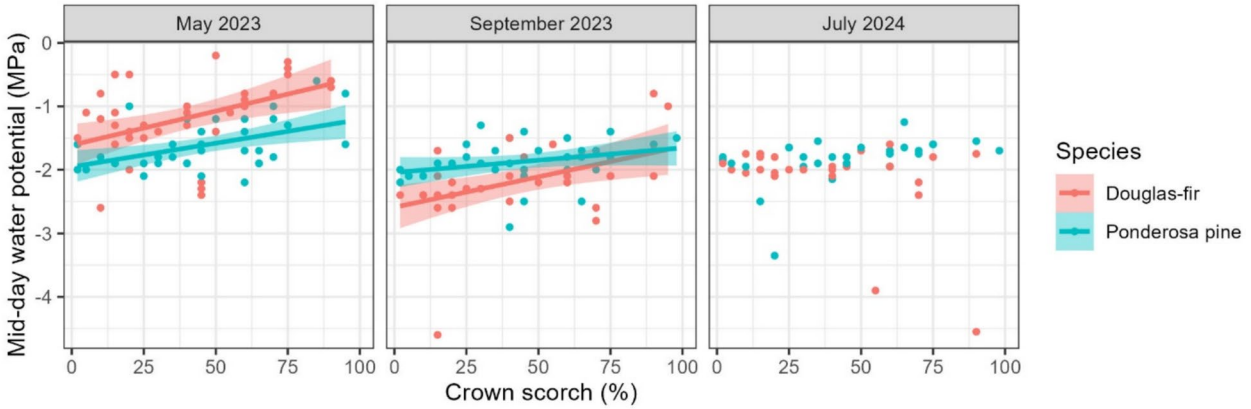

Fig. 5 Relationships between mid-day water potential and crown scorch at the three post-burn timesteps separated by species. Burns occurred in mid-October 2022 and early May 2023. Trends are linear models with shaded 95% confidence intervals. Only trends that were significant in the best-fit models are shown

Discussion

We show that burning can at least temporarily have some negative effects on tree water status and growth, and that benefits of fire-induced density reductions may not be fully realized until surviving trees recover from fire-caused injuries. While there are clear demonstrated benefits of prescribed fire for forest health and reduction in future fire hazard (North et al. 2021; Prichard et al. 2010; Hood et al. 2016), our results highlight that the balance of costs and benefits from fire, which is highly context-dependent (Fig. 1), may open a temporary window of increased post-fire vulnerability to drought and reduced growth. We found that burned trees in general exhibited higher water stress and greater total water deficit relative to unburned controls over the first 1–2 years post-fire, and that post-fire drought may exacerbate these differences in some cases (Figs. 3, 4 and 6), regardless of changes in competition. Consistent with other post-fire dendrochronological studies (Willson et al. 2024), burning also caused a transient reduction in radial growth, which was strongly related to the level of crown scorch that a tree sustained (Figs. 7 and 8), and weakly with NSC. Interestingly, while growth recovery in the second year after fire was not related to fire injuries, it was weakly related to changes in competition (Table 2). This suggests that the benefits of decreased competition may be more fully realized once recovery from fire-caused injuries takes place or if competition is more strongly reduced (Fig. 1). Given projected increases in drought, our work highlights the critical need for more research on how specific management approaches may minimize these risks while optimizing longer-term outcomes.

Both isolated measurements of water potential and continuous measurements of total water deficit (TWD) indicate that burned trees experience greater water stress relative to unburned controls (Figs. 3, 4 and 6A). This could be explained by reduced access to soil water if fine root dieback occurs as a result of impaired NSC supply or translocation (Reed et al. 2025) or soil heating (Swezy and Agee 1991). Increased carbon demand to compensate for post-fire NSC declines could also enhance carbon assimilation at the expense of increased water loss (transpiration rate). Indeed, Niccoli et al. (2023) observed higher sap flow after fire in another conifer with high levels of fire-caused defoliation, suggesting increased transpiration post-fire. We also observed that pre-dawn water potentials were consistently more negative in burned trees relative to controls, particularly at the fall-burned site, after accounting for pre-burn differences between sites, although these differences were small (Fig. 4). This, along with prior work showing that trees that died at these sites often had lower pre-dawn water potentials and NSC prior to death, suggests that greater post-fire water stress may more likely be an indirect effect of NSC depletion on maintenance of fine roots post-fire (Reed et al. 2025). More work is needed to further explore the magnitude and duration of time over which any impacts from fire-caused injuries negatively affect tree water status, and the mechanisms of these effects.

In partial contradiction of our first prediction and despite generally higher water stress in burned trees, we found that trees with higher levels of crown scorch initially had lower levels of water stress (Table 1 and Fig. 5). This suggests that fire-caused decreases in live leaf area can at least initially improve tree water status, potentially overriding any negative impacts of burning on hydraulic function. This is consistent with other studies that have quantified post-fire water status in ponderosa pine in relationship to crown injuries (Wallin et al. 2003; Bryant et al. 2022). However, our work suggests that this benefit

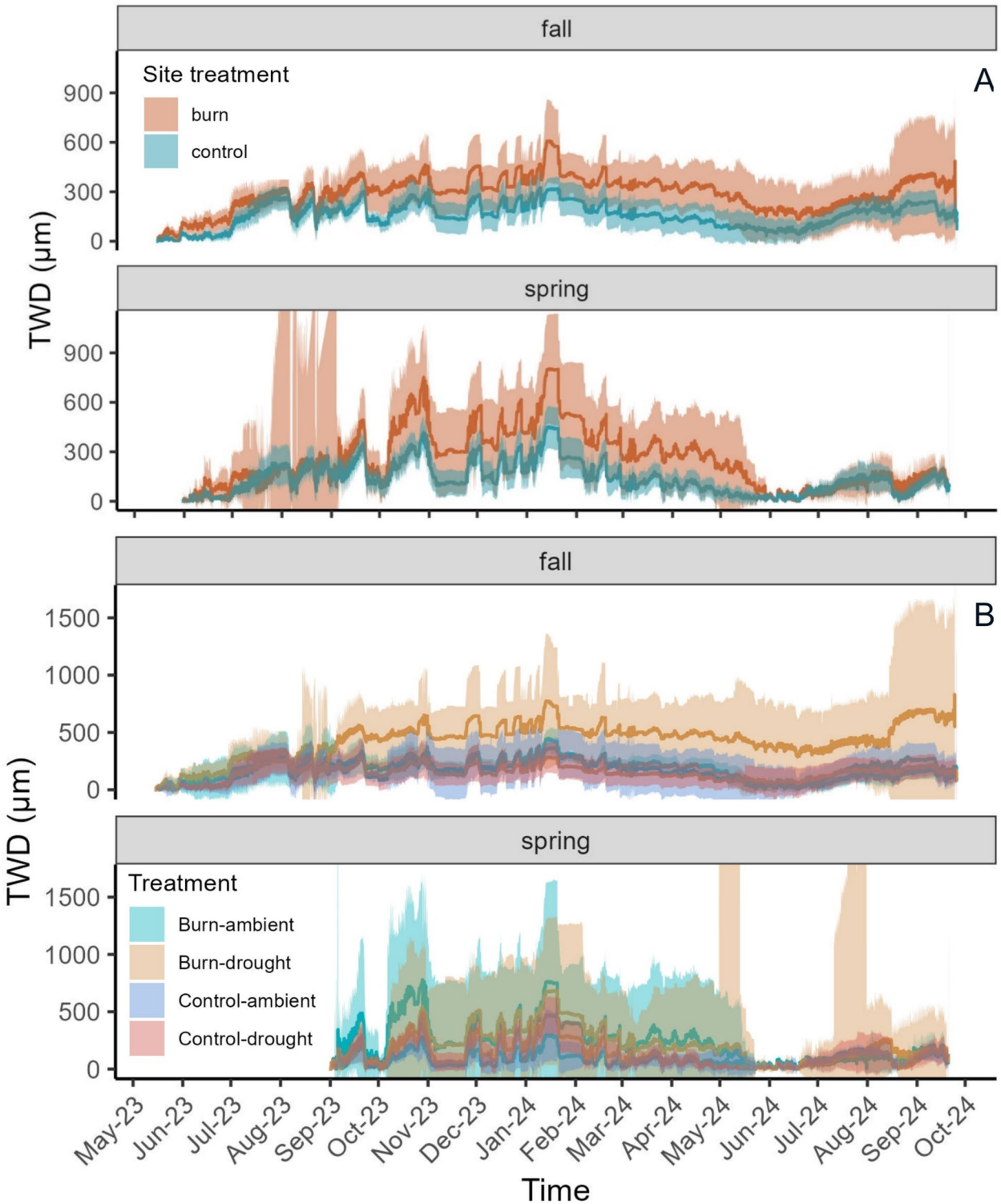

Fig. 6 Total water deficit (TWD) over time separated by site treatment (**A**) and tree treatment (**B**). Only trees still alive at the end of the study period are shown. Lines are means with shaded 95% confidence intervals. Considerable error due to burned tree shrinkage during the first growing season at the spring-burned site occurred and thus prevented further separating spring-burned trees into drought and ambient categories prior to September 2023. Y-axes for spring-burned trees truncated to match fall-burn and to more clearly show treatment differences

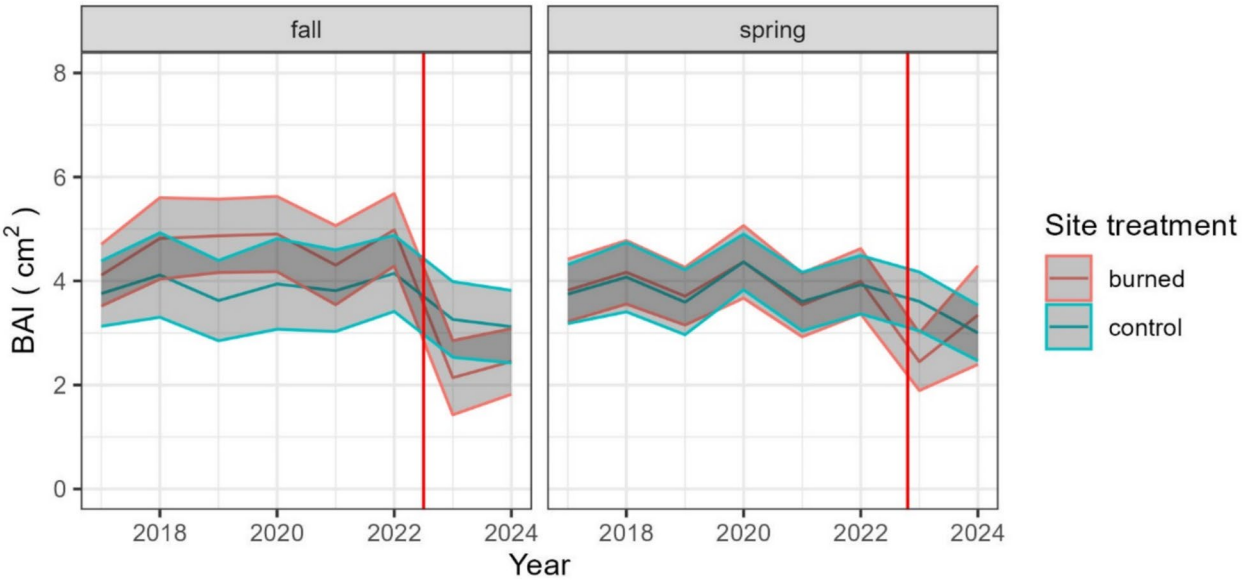

Fig. 7 Basal area increment (BAI) of trees at fall and spring-burned sites and paired control sites. Lines are means with shaded 95% confidence intervals. Red line denotes approximate time of fire relative to growth year

Table 2 Basal area increment (BAI) model coefficients

Time	Species	DBH	Age	Crown ratio (%)	Crown scorch (%)	Competition	Phloem NSC
Pre-burn BAI		**0.496**	−0.112	**0.285**	–		**1.133**
BAI resistance	**0.477**	**0.276**		–	**−0.684**		0.146
BAI recovery		**−0.195**		–		**−0.174**	
BAI resilience				–	**−0.614**		0.210

Bold indicates significance ($p < 0.05$). All post-burn BAI variables are relativized by means at control sites to account for climatic variation from year to year. All continuous variables scaled and centered prior to inclusion in models. Species is equal to 1 if Douglas-fir and 0 if ponderosa pine. Dashes indicates variable not included in model; blank indicates included in full model but not best-fit model

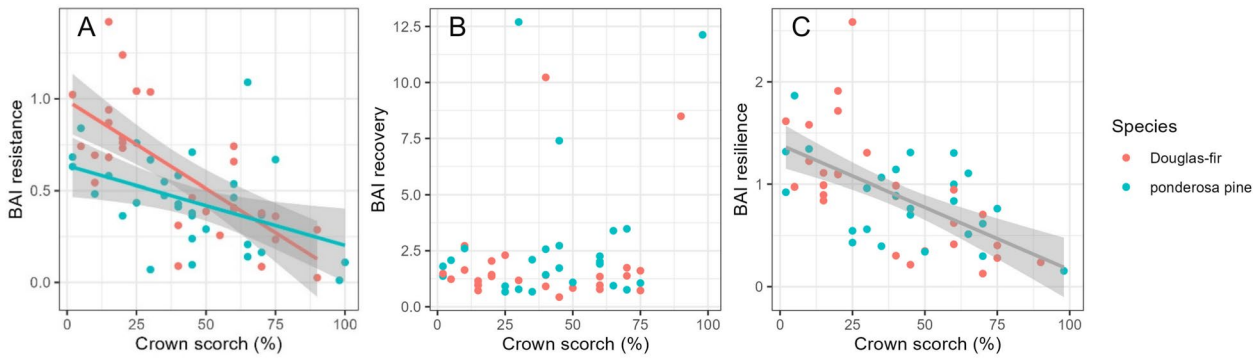

Fig. 8 Relationships between crown scorch and radial growth (BAI) resistance (**A**), recovery (**B**), and resilience (**C**). Values were divided by site-specific means of unburned controls to account for year-to-year climatic variability. Points colored by species. Trends are linear models with shaded 95% confidence intervals. **C** includes a single trend line as species was not a predictor in the best-fit model. Only trends that were identified as significant in the best-fit models are shown

may not persist beyond the first growing season post-fire, possibly due to adjustments in root-to-shoot ratios as foliage re-grows, or if tree-level carbon imbalance causes death of fine roots (Reed et al. 2025).

The generally negative impact of burning on tree water status suggests that trees may experience a period of heightened drought vulnerability immediately post-fire. This is consistent with work showing higher levels of drought-related mortality in the first few years post-fire (Furniss et al. 2022; Knapp et al. 2021). While our drought treatment did not have a detectable effect on water potential during the time periods it was measured, our continuous measurements of TWD suggest that water deficit may be exacerbated in burned trees that experience post-fire drought, at least at the fall-burned site (Fig. 6B). This result provides tentative support for our second prediction that post-fire drought impacts would be more negative in burned trees. The fact that we did not detect a clear drought impact on spring-burned trees could be a result of differences in site characteristics, or some physiological impact from burning that was more pronounced at the fall-burned site. This is supported by greater differences in pre-dawn water potential (Fig. 4) and stronger growth declines associated with burning at the fall-burned site (Fig. 7). The spring-burned site is on average steeper than the fall-burned site, potentially making the rain exclusion shelters less effective if significant upslope rainfall infiltration occurred. At the same time, differences in soil composition where deep roots occur could have affected the time needed for deep soils to dry out. While we did not detect significant differences between ambient and drought tree soil moisture during the first growing season post-burn at the spring-burn site, we did by the second growing season (Fig. S2). Thus, it is also possible that the drought treatment was only effective the second growing season at this site, and this shorter duration resulted in less pronounced effects. Interestingly, when we include trees that eventually died at the spring-burn site, the drought effects appear more pronounced during the second season post-fire (Fig. S3). Alternatively, higher fire intensity at the fall-burned site may have resulted in greater damage to fine roots, although duff consumption was similar to the spring-burned site (Fig. S5) indicating that soil heating was similar. Still, the clear impact of the post-fire drought at the fall-burn site combined with the generally negative effect of burning on water status across both sites supports the idea that trees may experience a period of heightened drought vulnerability at least in the first few years post-fire.

Burning had a negative impact on growth during the first year post-fire (Fig. 7, Fig. S4), consistent with our expectations and with other studies that have observed radial growth declines in the first year or two post-fire, followed by a period of recovery (Willson et al. 2024; Wenderott et al. 2022; Seifert et al. 2017). We find partial support for our third prediction in that the initial post-fire growth decline (resistance) and the degree to which growth recovers to pre-fire levels (resilience) are strongly related to the level of crown scorch that a tree sustains and weakly related to NSC (Fig. 8 and Table 2). However, the degree of growth recovery during the second year post-fire was more strongly related to changes in competition than NSC or fire injuries. These results are generally consistent with a study that followed *Pinus halepensis* Mill. post-fire and found that trees that sustained crown scorch showed a marked decrease in post-fire growth, but that, after this initial decline, burned trees that experienced a relevant decrease in competition and lower crown scorch grew faster (Valor et al. 2018). Importantly, past work has found a strong relationship between the level of crown scorch a tree sustains and NSC levels post-fire (Reed et al. 2025; Reed and Hood 2024). It seems likely then that the fire-induced radial growth decrease is a product of the effects of fire injuries on tree-level carbon balance, particularly as trees require stored NSC to regrow leaves and repair tissues post-fire (Sala et al. 2012; Ruehr et al. 2019; Galiano et al. 2011). It is interesting then that the magnitude of recovery in the second year post-fire is not related to degree of crown scorch nor NSC depletion. This may be due to the short timeframe over which we assessed recovery or a product of the preferential investment of NSC in the regrowth of new tissues (e.g., leaves), leaving radial growth uncoupled from NSC dynamics (Wiley et al. 2013). Further, the inclusion of changes in competition in the growth recovery model suggests that post-fire radial growth may also be responding to changing water or nutrient availability. This dynamic between post-fire recovery and fire-induced NSC depletions requires further study, and our results highlight the importance of better understanding the physiological effects of fire over a longer post-fire recovery period.

Most work examining fire effects on tree physiology have focused on impacts to tree function that can lead to post-fire mortality (Nolan et al. 2024). However, our work highlights the importance of understanding non-lethal impacts to physiological function that influence the post-fire recovery period (Hood 2021). Prior studies highlight clear differences in post-fire growth dynamics across sites and species (Valor et al. 2020; Willson et al. 2024; Alfaro-Sánchez et al. 2015; Camarero et al. 2024), suggesting that there is much we do not understand about what drives these patterns. Some work has suggested that site climate may be important in the recovery period and in determining whether reduced forest

density can increase tree growth (Alfaro-Sánchez et al. 2015), while other work suggests that the time needed for post-fire growth recovery may vary by species (Willson et al. 2024) (Fig. 1). Therefore, a better understanding of how site and species differences combine with altered forest density and lasting physiological impacts on tree function is needed. As many studies that examine tree recovery and drought vulnerability post-fire take a retrospective approach using dendrochronological techniques, it will be particularly important to better understand whether recovery of radial growth is in fact a good indicator of recovery of physiological function, and particularly tree carbon balance, post-fire.

Our results highlight the potentially negative impact of fire injuries on both post-fire water status and tree growth, even if these effects are temporary. However, forest management actions that minimize fire-caused injuries may ameliorate some of these effects, and the benefits of prescribed burning in fire-dependent forests are supported by a broad body of evidence (Hood et al. 2016; Tepley et al. 2020; Hagmann et al. 2021). While our results show a fire-induced window of susceptibility to drought, we caution that our results should be placed in the context of larger efforts to restore vast areas of fire-prone forests. While studies that have examined tree growth and drought vulnerability after fire alone have found mixed results (van Mantgem et al. 2021; Zald et al. 2022; Alfaro-Sánchez et al. 2015), those that include prescribed fire after mechanical thinning have shown clearer improvements to both growth and tree water status (Rodman et al. 2025, Vilà-Vilardell et al. 2024, Wallin et al. 2003, Zausen et al. 2005), or at a minimum, less negative impacts than burning alone (Steel et al. 2021). This is likely due to the tendency of pre-fire thinning to moderate prescribed fire behavior and thus the magnitude of fire injuries, although it may also be due to more consistent decreases in stand density when thinning precedes fire, as prescribed burns can be highly variable in their effectiveness at reducing stand density (Vaillant et al. 2009). Indeed, recent work has found that trees growing in denser neighborhoods are particularly susceptible to drought-related mortality (Furniss et al. 2022; Knapp et al. 2021). While fire that is intense enough to cause substantial mortality can lead to great reductions in stand density, this type of fire often results in high levels of injury. Therefore, where feasible, prior silvicultural treatments to reduce stand density or repeated prescribed burning (Greenler et al. 2023; Chamberlain et al. 2024) is likely needed to achieve a balance between reduced levels of fire injury and sufficient levels of stand density reduction to achieve a benefit during drought. Future research should directly compare approaches (thin and burn, burn only, repeated burning) to assess which best improves physiological function under post-fire drought.

Conclusions

Prescribed fire is an important tool to reduce fuel loads and fire hazard, and low to moderate severity wildfire can have similar effects (Ryan et al. 2013; North et al. 2021). Low severity fire may also have other benefits like stimulating tree defenses against bark beetles (Hood et al. 2016, 2015) and increased nutrient cycling (Deluca and Sala 2006). However, whether and when fire-caused reductions in forest density can affect post-fire drought vulnerability and tree growth is less certain. Our research advances understanding of how fire-caused injuries and changes in competition affect post-fire recovery and susceptibility to drought. Such knowledge is needed to refine burn prescriptions towards meeting management objectives and improving predictions of how fire and drought affect tree physiology. We show that trees likely experience a period of both low growth and heightened drought vulnerability in the first few years post-fire, and that the magnitude of this impact is likely related to the level of fire injury a tree sustains, and possibly the effects of fire-caused changes in tree-level carbon balance. Importantly, the decreases in competition we observed did not result in less water stress or increased growth for burned trees relative to unburned controls in the two growing seasons post-fire. This may be due to the relatively small magnitude of stand density decreases, or the impacts of fire injuries overriding this effect. Thus, it is still possible that this benefit might materialize over longer timescales as trees recover from fire-caused injuries. Our work highlights the need to better understand the physiological impacts of fire on post-fire recovery of tree function and the length of time needed for recovery to occur. Management decisions that affect either the level of stand density reduction (e.g., pre-fire thinning or repeated prescribed burning), or the level of fire injuries trees sustain (e.g., ignition patterns or conditions under which burning occurs) should therefore be considered when managing for greater forest resilience to future drought.

Abbreviations

AIC	Akaike information criterion
BAI	Basal area increment
CKR	Cambium kill rating
DBH	Diameter at breast height
GRO	Irreversible growth signal
NSC	Non-structural carbohydrates
SDI	Stand density index
TWD	Total water deficit
Ψ_{md}	Mid-day water potential
Ψ_{pd}	Pre-dawn water potential

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-026-00487-3.

Supplementary Material 1.

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Authors' 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: https://doi.org/10.5061/dryad.qv9s4mws1.

Declarations

Competing interests
The authors declare no competing interests.

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