

RESEARCH ARTICLE

Divergent shifts in hydraulic versus carbon acquisition functional traits after wildfire in four Rocky Mountain tree species

Annapurna C. Post-Leon¹  | William R. L. Anderegg^{1,2} 

¹School of Biological Sciences, University of Utah, Salt Lake City, Utah, USA

²Wilkes Center for Climate Science and Policy, University of Utah, Salt Lake City, Utah, USA

Correspondence

Annapurna C. Post-Leon

Email: annapurna.post-leon@utah.edu

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Abstract

1. Climate change has increased the frequency and severity of drought and large wildfire events across western North America. Despite the increasing concurrence of drought and wildfire events and the importance of forests as a global carbon sink, the impacts of fire on tree drought and carbon acquisition traits are not well understood, particularly on multi-year time-scales.
2. In 2022–2024, we leveraged a natural experiment at a large 2018 wildfire in southwestern Colorado, comparing leaf and xylem functional traits related to drought resistance and carbon acquisition in burned and unburned ponderosa pine, quaking aspen, subalpine fir, and Engelmann spruce trees.
3. Relative to unburned trees of the same species, we found reduced xylem vulnerability to embolism (P_{50}) in burned ponderosa pine and subalpine fir; decreased leaf heat tolerance (T_{50}) in burned quaking aspen and ponderosa pine; and increased investment in leaf structural over photosynthetic components (leaf C:N isotopic ratio) in burned quaking aspen, subalpine fir, and Engelmann spruce.
4. In contrast to previous studies, our results suggest that wildfire positively impacts functional traits related to drought resistance and water movement in surviving burned trees. However, generally negative impacts of wildfire were found with respect to leaf physiological and photosynthetic traits, suggesting divergent water and carbon responses to fire.

KEYWORDS

carbon assimilation, drought, ecophysiology, fire ecology, functional traits, pyroecophysiology, wildfire, xylem hydraulics

1 | INTRODUCTION

Warming temperatures due to anthropogenic climate change have already caused increased drought and large wildfire activity across the forests of the American West, leading to substantial and widespread

tree mortality events across many western North American forests (Abatzoglou & Williams, 2016; Goulden & Bales, 2019; Williams et al., 2015). While substantial prior and ongoing research has elucidated many of the key physiological mechanisms by which trees respond to drought (Groover et al., 2025), the impacts of wildfire

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on tree functional traits remain poorly understood (Bär et al., 2019; Smith et al., 2025).

Functional traits are measurable characteristics of plants that indirectly impact the plant's reproductive or growth success (Violle et al., 2007) and include physiological traits that pertain to hydraulic transport and carbon assimilation capacity, as well as a wide variety of other aspects of plant growth and reproduction. For the purposes of this work, we focus on a suite of hydraulic and carbon functional traits that allow us to gain insight into how fire may impact tree water transport and xylem drought resistance, as well as carbon assimilation and growth.

Given future predictions for increasingly large and severe wildfire and drought events worldwide under climate change (Pörtner et al., 2022; Wu et al., 2021) and therefore the potential for greater co-occurrence of wildfire before, after, and alongside drought events, understanding how fire impacts tree hydraulic functional traits and thus forest drought resilience is crucial to understanding disturbance interactions and the long-term future dynamics of forests under climate change. While some past studies (e.g., Bär et al., 2018; Michaletz et al., 2012; Partelli-Feltrin et al., 2021; Reed et al., 2025; Salladay & Pittermann, 2023) have attempted to elucidate the hydraulic responses of various tree species to wildfire, simulated fire or prescribed fire, these studies have reached varying conclusions, suggesting fire only weakly impacts hydraulic traits. While Bär et al. (2018) found that wildfire-scorched branches, compared with unscorched branches from the same mature tree, had reduced resistance to embolism 1 year after fire in two out of three European forest species studied (Bär et al., 2018), Reed et al. (2025) found no impact of prescribed fire on mature ponderosa pine resistance to embolism or hydraulic conductivity immediately or up to 15-month postfire, and a significant increase in resistance to embolism in Douglas-fir immediately postfire, although this shift was not maintained in later timepoints (Reed et al., 2025). Partelli-Feltrin et al., working with ponderosa pine saplings exposed to a laboratory fire treatment, saw no impacts at all of fire on xylem hydraulic traits, regardless of whether the measurements were conducted 1 day or 22 months after fire (Partelli-Feltrin et al., 2021, 2022). However, differences in tree age, type of fire exposure and time since fire can and likely do influence diverging findings across studies.

Globally, forests represent the largest terrestrial carbon sink; however, this role is being increasingly threatened by the impacts of climate change (Pan et al., 2024). Carbon emitted directly from wildfires is known to be responsible for a substantial portion of global emissions (Byrne et al., 2024), but the longer-term impacts of wildfire on the global carbon budget through delayed postfire tree mortality and fire-induced impacts on carbon assimilation in surviving burned trees is far more difficult to quantify. Recent studies have found more consistently negative impacts of fire on carbon-related traits, primarily with respect to concentrations of non-structural carbohydrates (NSCs) in plant tissues, which several studies have observed to decrease after fire, potentially in response to phloem transport disruption (Partelli-Feltrin et al., 2022; Reed et al., 2025). NSC levels can be difficult to directly link to stress (Hartmann & Trumbore, 2016), however, so it can be useful to evaluate other carbon acquisition-related traits to more accurately assess the impact of fire or other stressors on tree

and ecosystem carbon balance. For example, leaf stable isotope concentrations of carbon and nitrogen can provide important insights into how trees prioritize relative investment into tissue structural components (higher carbon to nitrogen ratio) versus photosynthetic proteins (lower carbon to nitrogen ratio) (Evans, 1989); as well as stomatal closure due to hydraulic disruption from fire or drought, which is indicated by higher $\delta^{13}\text{C}$ (greater intrinsic water use efficiency) (Anderegg et al., 2014; Evans, 1989; Kannenberg et al., 2021; Pu & Lyu, 2023).

In this study, we aimed to quantify the multi-year impacts of a wildfire on tree hydraulic and leaf physiological traits in mature, established trees in a natural forest environment and to explore potential species differences in fire response by harmonizing methods across the species in our study. We focused on four widespread tree species native to the western United States that span a gradient of climatological and fire ecological niches: ponderosa pine ('PIPO'; *Pinus ponderosa* P. & C. Lawson), quaking aspen ('POTR'; *Populus tremuloides* Michx.), subalpine fir ('ABLA'; *Abies lasiocarpa* (Hook.) Nutt.) and Engelmann spruce ('PIEN'; *Picea engelmannii* Parry ex Engelmann). Ponderosa pine is generally considered highly adapted to withstand frequent, low-severity fire, and is broadly distributed at low-mid elevations across western North America (Keeley, 2012; McKinney, 2019). Quaking aspen is the most widely distributed tree species in North America and has experienced recent widespread mortality events linked to drought (Anderegg et al., 2013). Aspen is an early seral species that relies on infrequent, high-severity fires to clear out encroaching conifers to resprout from its underground root system but is not generally considered well adapted to survive fire as an individual stem (Shinneman et al., 2013). The fire adaptations of subalpine fir and Engelmann spruce fall somewhere in between ponderosa pine and quaking aspen, with both species possessing moderately thick bark but are often found in dense forests that rarely experience high-severity fires and when they do, reseed from surviving 'seed bank' trees instead of regrowing or withstanding fire (Pelz, 2016).

The different fire adaptations of these four tree species create an ideal study system to answer our primary research questions: (1) Do trees that survive fire events experience shifts in functional traits on multi-year time-scales, and if so, what are potential underlying mechanisms for these shifts? (2) Are shifts in functional traits consistent across species, and if not, do differential levels of adaptation to fire explain observed species differences? (3) Are hydraulic and carbon acquisition traits similarly or differentially impacted by wildfire?

2 | MATERIALS AND METHODS

2.1 | Study design, location and establishment of forest monitoring and data collection plots

We measured a range of functional traits at a pair of burned and unburned transects. Each transect, respectively, spanned three forest types and four tree species in the Rocky Mountains of the San Juan National Forest (SJNF) in southwestern Colorado (Figure S1). These steep mountains possess a substantial temperature and precipitation gradient that creates a high diversity of different forest

types in a relatively small spatial region, including open ponderosa pine-dominated woodlands at low elevations, dense quaking aspen stands at mid elevations and subalpine mixed Engelmann spruce-subalpine fir forests at high elevations.

In 2018, 4 years prior to the beginning of our study, the 416 and Burro wildfires burned nearly 60,000 acres across all three of these dominant forest types in this region, creating an ideal study system for understanding wildfire-driven shifts in physiological and hydraulic traits in species with varying adaptations to fire but that are found in close spatial proximity.

The unburned transect (henceforth referred to as 'unburned sites') consisted of a subset of existing long-term forest monitoring plots on the west slope of the San Juan Mountains in southwestern Colorado, USA (Huang & Anderegg, 2012; Anderegg et al., 2013; Kerr et al., 2022). These plots were established between 2014 and 2022 along an elevation gradient of three forest types (ponderosa pine, quaking aspen, subalpine fir-Engelmann spruce). No permits or licenses were needed for this work, all of which was conducted in the San Juan National Forest. [Correction added on 27 February 2026, after first on-line publication: Three citations (Huang & Anderegg, 2012; Anderegg et al., 2013 and Kerr et al., 2022) have been added, and Huang, C.-Y. and Anderegg, W.R.L. (2012) has been included in the References.]

We established a corresponding burned transect ('burned sites') on the east side of San Juan Mountains within burn perimeters (416 and Burro fires, burned in summer 2018) in summer 2022 (Engelmann spruce-subalpine fir) and 2023 (ponderosa pine and quaking aspen). Burned Engelmann spruce-subalpine fir plots were relatively close (7.2 km) to unburned plots of the same forest type, while quaking aspen and ponderosa pine plots were further away (37–42 km) to ensure that elevation, aspect and climate conditions were similar between burned and unburned sites for each forest type (Table S1). Burned plots were selected to contain as many living trees with visible bole char as possible (for conifers), or, for aspen, to contain living trees where the fire apparently occurred, based on visible ground fuel charring (direct fire damage on aspen is difficult to quantify due to non-char bark blackening on aspen). We chose to measure mortality and functional traits 4–6 years after fire due to the absence of substantial prior studies that have explored physiological impacts more than 2 years after wildfire.

Three to six plots total were used or established in each forest type ($N=5$ for burned Engelmann spruce-subalpine fir; $N=3$ for unburned Engelmann spruce-subalpine fir; $N=3$ for burned quaking aspen; $N=6$ for unburned aspen; $N=5$ for burned ponderosa pine; $N=5$ for unburned ponderosa pine). While some metrics are reported at the plot level (e.g. mortality, basal area, both of which are standardized for plot area), all ecophysiological measurements are reported at the individual tree scale. A map of all plots (Figure S1) and a table of plot characteristics measured (Table S1) can both be found in the supplemental information.

2.2 | Collection of tree-level demographic data

We used ground-based surveys adapted from Forest Inventory and Analysis (FIA) protocols (Forest Inventory and Analysis, 2024) to

collect tree-level demographic data that, while not the primary focus of this study, allow us to better contextualize the ecophysiological data. Surveys estimated recent canopy dieback, living vs. dead status of each tree, diameter at breast height (dbh), bole char percent and direction, and estimations of scorch height at all (burned and unburned) Engelmann spruce-subalpine fir plots in summer 2022, and all quaking aspen and ponderosa pine plots in summer 2023. Only trees over 2 inches dbh were used for demographic data, including mortality and plot basal area. Mortality and canopy dieback causes were not always easy to establish and thus were not analysed. All ecophysiological measurements were collected on burned and unburned trees of the same species within 2–4 weeks of each other to reduce potential seasonal impacts on physiology.

2.3 | Extraction of publicly available plot data

Plot elevation, aspect, climate and fire severity data can allow us to better contextualize the results of a natural experiment study such as this one. We extracted elevation and aspect for all plots from USGS 1/3 arcsecond 3D digital elevation maps (U.S. Geological Survey, 2022) using the programme QGIS (QGIS version 3.34.13-Prizren). We also extracted satellite-based 2018 fire severity at burned plots from Monitoring Trends in Burn Severity (MTBS) (Eidenshink et al., 2007) 30 m rasters using QGIS. MTBS data are categorical, with higher values (scale of 1–5) representing higher burn severity; we averaged these values across plots for each forest type. One plot (burned POTR) was mapped as outside the MTBS burn perimeter despite trees in the plot showing visible fire damage; for averaging purposes, this plot was assigned a MTBS value of 1, which corresponds to a to unburned-low-severity burn classification. Because sites were selected on the edges of the burn for accessibility and for living tree presence, MTBS classified burn severities as relatively low (1–2, corresponding to unburned-low-severity fire) for all plots, despite plots containing fire-charred and fire-killed trees. We also extracted precipitation and minimum and maximum temperature data for all plots from 2000 to 2024 from TerraClimate (Abatzoglou et al., 2018) at 4 km resolution using the Google Earth Engine API and the geemap module (Wu, 2020) in Python. The code used to extract TerraClimate data was edited by a publicly available generative AI (ChatGPT) (OpenAI, 2025). We estimated mean monthly temperature by averaging monthly minimum and maximum temperatures and subsequently calculated mean annual temperature by averaging mean monthly temperatures for the period of record of the dataset. All plot data can be found in Table S1.

2.4 | Vulnerability curve and xylem hydraulic conductivity measurement

We constructed xylem vulnerability curves and measured native and maximum xylem hydraulic conductivity to understand how

burned and unburned trees differed in drought resistance, maximum water transport capacity and reduction in water transport capacity under field conditions due to embolism. Hydraulic measurements were conducted only on branches collected from trees with visible bole char for conifers. Medium-sized branches (~0.5 m length) were sampled using pole pruners from canopy branches (~5–8 m above-ground) at plots in summer 2022 (Engelmann spruce and subalpine fir) and 2023 (ponderosa pine and quaking aspen). Canopy branches, which were selected to be light-exposed when possible, were used due to their greater importance in hydraulic and carbon assimilation function than below-canopy branches (Lichtenthaler et al., 1981). Branches were not visibly scorched, but most likely would have experienced significant heating during the fire (Banerjee et al., 2020). Nine branches were collected from each site (burned and unburned) and species for Engelmann spruce, subalpine fir and quaking aspen, and 12 branches were collected from each site for ponderosa pine. Each branch was collected from a different tree. The cut ends of sampled branches were wrapped in wet paper towels, and the branches were sealed into plastic bags and placed into coolers with ice. After transporting samples back to the laboratory, bagged samples were placed in a refrigerator (approximately –0.7–5.1°C) and processed within 7 days of collection.

Branch segments (0.5–1.5 cm diameter, ~15 cm length) were cut underwater from branch samples using razor blades. The age of these segments was not measured, but similar segments collected at the same time were all old enough to have directly experienced the 2018 wildfire (Table S2). Hydraulic conductivity (K_h) was directly measured on each branch segment using a Sperry apparatus and degassed 10 mmol KCl perfusion solution (Sperry et al., 1988). Native measurements of hydraulic conductivity ($K_{h, \text{native}}$) were taken first, then stem segments were vacuum infiltrated in 10 mmol KCl overnight (8–16 h) and maximum hydraulic conductivity ($K_{h, \text{max}}$) was measured. Wood and pith diameter were measured on each segment, and the xylem area was calculated for each end of the branch and averaged to standardize hydraulic conductivity by xylem area (i.e. stem-specific hydraulic conductivity, K_s). Native percent loss in conductivity (PLC_{native}) was calculated using Equation (1) for calculating PLC of points on vulnerability curves. To ensure only biologically relevant values were reported, PLC data were filtered: $-10 < \text{PLC} < 110$. Only filtered PLC data were statistically analysed and reported in results.

Following overnight vacuum infiltration, vulnerability curves were constructed by repeatedly spinning the same stem samples used for PLC_{native} and $K_{s, \text{max}}$ measurements in a centrifuge (Sorvall RC-5C Plus Superspeed Centrifuge, Kendro Laboratory Products, Newtown, CT, USA) with the ends kept moist by wet sponges (Alder et al., 1997) to induce embolism formation. Samples were spun to –0.5, –1.0, –2.0, –3.0, –5.0, –7.0 and –9.0 MPa and the hydraulic conductivity measured after each spin. Samples were either spun until breakage, >95% of maximum hydraulic conductivity was lost, or –9.0 MPa was reached. PLC was calculated at each spin as follows:

$$\text{PLC} = 100 * \frac{1 - K_h}{K_{h, \text{max}}} \quad (1)$$

Weibull curves were fit individually to the vulnerability curve (PLC vs. spin) of each stem using the *fitplc* package in the program R (Duursma & Choat, 2017).

2.5 | Leaf area: Sapwood area and leaf mass per area measurement

Leaf area: sapwood area ratio (inverse Huber value) was measured in order to provide a better understanding of water use and competition for water resources and balance of investment in leaf versus xylem tissues between burned and unburned trees (Mencuccini et al., 2019; Tyree & Zimmermann, 2002). Leaf mass per leaf area (also known as specific leaf area) was also measured in a subset of these same leaves for each sample; higher leaf mass per area often corresponds to increased drought, heat and cold tolerance alongside a reduction in leaf nitrogen content and photosynthetic capacity (Sastry et al., 2018; Wright et al., 2004). Branches used for hydraulic sampling, as well as additional branches, were used for leaf area sampling. The measured xylem area (sapwood area) from the hydraulic samples was used for leaf area: sapwood area calculations. One-sided conifer leaf areas were calculated by scanning a subset of needles for each sample (Epson Perfection V39 Scanner, Epson America Inc., Los Alamitos, CA, USA), calculating the scanned leaf area using ImageJ or ImageJ Fiji (Schindelin et al., 2012; Schneider et al., 2012), drying these needles and weighing the dry mass of the subset using a semi-micro balance (NewClassic MS, Mettler-Toledo LLC., Columbus, OH, USA; CPA225D and Basic, Sartorius AG, Göttingen, Niedersachsen, Germany). The leaf mass per area obtained from these subsets was used to extrapolate total sample leaf area based on total sample dry mass. Aspen leaf areas were measured directly on all leaves using a leaf area scanner (LI-3100C Portable Leaf Area Meter, LI-COR Environmental Inc., Lincoln, NE, USA). Total sample dry masses were obtained from scanned leaves and leaf mass per area calculated from total sample area and total sample dry mass.

2.6 | Thermotolerance and chlorophyll fluorescence methods

Leaf thermotolerance, a relatively plastic trait that varies based on plant temperature status immediately prior to sampling, drought status of the plant and other environmental factors including leaf mass per area, was measured via construction of chlorophyll fluorescence thermotolerance curves (Marias et al., 2017; Sastry et al., 2018). Small branch samples were collected predawn in summer 2023 for all sites ($N = 6/\text{species/site}$). Immediately after sampling, branch ends were wrapped in moist paper towels to limit water loss, sealed into bags and placed in a cooler with ice until measurement. Minimal light was permitted to reach the leaves after collection; all experimental protocols were followed in a dark room using a headlamp light only. Individual needles (Engelmann spruce, subalpine fir), cut needle

sections (ponderosa pine) or hole-punched leaf rounds (quaking aspen) were sealed into small plastic bags (3 needles/bag). One bag per sample was placed in a water bath for 15 min at each of the following temperatures: 25, 29, 33, 37, 41, 45, 49, 53, 57 and 61°C. The temperature of water baths was maintained using sous vide cookers. After exposure to the water bath treatment, samples were removed from bags and placed on moist filter paper in a covered petri dish in the dark for 18–36 h. Additional control samples (not exposed to water bath treatments) were also placed on filter paper for the same length of time. Dark-adapted chlorophyll fluorescence (F_v/F_m) was measured on each sample after the rest period. Control F_v/F_m measurements were used as predawn fluorescence measurements, which represent the maximum efficiency of photosystem II and a proxy for photosynthetic health of the leaf, with higher values indicating healthier or more photosynthetically capable leaves (Murchie & Lawson, 2013). The remaining F_v/F_m measurements were used to construct thermotolerance curves (plots of F_v/F_m vs. temperature). Weibull curves were fit to each curve using the function in the R programming language, and values of T_{crit} (the temperature at F_v/F_m begins to decline) and T_{50} (the temperature at which 50% of initial fluorescence is lost) were calculated from each fit curve (Vargas-Gutierrez, 2022).

2.7 | Leaf stable isotope methods

We removed leaf samples (6 samples/tree/site) for stable isotope analysis from all branches that we collected for thermotolerance in summer 2023. To avoid nitrogen contamination from human hands, we handled the entire branches with gloves until stable isotope samples were removed (also with gloves). Isotope samples were stored in small plastic bags in a refrigerator (approximately −0.7–5.1°C) for 2–4 weeks (no evidence of decay), then removed and placed into paper envelopes and dried at 60°C for at least 72 h. Needle ages were standardized as much as possible within conifer species, though needle dating was sometimes difficult due to branch morphology. Second-year needles were used for all subalpine fir samples, first-year needles were used for all Engelmann spruce samples, and the youngest mature needles were used for ponderosa pine samples. Fully expanded leaves were used for aspen samples.

For each sample, we froze dried leaves with liquid nitrogen and ground the frozen leaves as finely as possible in a mortar and pestle, then transferred the ground material into individual plastic micro-fuge tubes that were stored sealed at room temperature until analysis. Small amounts of the samples were massed and placed in tin capsules for isotopic analysis using isotopic ratio mass spectrometry at the Stable Isotope Ratio Facility for Environmental Research at the University of Utah. Nitrogen values are reported on the AIR scale where USGS40 = −4.5 per mil and USGS41 = +47.6 per mil. Carbon values are reported on the VPDB scale where USGS40 = −26.24 per mil and USGS41 = +37.76 per mil.

Intrinsic water use efficiency, the ratio between photosynthesis and stomatal conductance and a proxy for stomatal closure, was

calculated according to Equation (2) (Ehleringer & Cerling, 1995; Farquhar et al., 1982; Saurer et al., 2014):

$$iWue = C_a * \frac{b - \frac{\delta^{13}C_{atm} - \delta^{13}C_{leaf}}{1 + \frac{\delta^{13}C_{leaf}}{1000}}}{1.6(b - a)} \quad (2)$$

where a is the isotopic fractionation of CO_2 associated with diffusion through the stomata ($a=4.4\%$), b is the isotopic fractionation of CO_2 from enzymatic carbon fixation in C3 plants ($b=27\%$), C_a is the concentration of CO_2 in the atmosphere ($C_a=421.08$ ppb in 2023; Lan, 2025), and $\delta^{13}C_{atm}$ is the relative amount of the ^{13}C isotope present in the atmosphere (calculated as $^{13}C=-8.36\%$ for 2023, the year all leaves were sampled for isotopes).

2.8 | Replication statement

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Site (species × burn status)	Plot	3–5 plots per site (8 total sites, with 1 site per species per burn status) (for mortality, basal area, site characteristic data)
Site (species × burn status)	Site	6–12 individuals per site (multiple plots within each site pooled) (for physiological measurements)

2.9 | Data analysis

We conducted all data analyses in the programming language R (version 4.5.2) (R Core Team, 2024). Weibull curves were fit for vulnerability curves and thermotolerance curves as described in the individual sections above. Statistical comparisons were conducted between burned and unburned sample groups for each species and variable of interest; statistical comparisons were not conducted between species. QQ plots were constructed for each sample group using the *car* package in R (Fox et al., 2024) and used to assess normality for each group. When groups were normal, statistical comparisons were conducted using two-sample *t*-tests; when groups did not conform to normality, standard transformations were applied to achieve normality and two-sample *t*-tests were then conducted on the transformed data. When normality could not be achieved with standard transformations, non-parametric Wilcoxon signed-rank tests were used to statistically compare between groups. We considered statistical significance to be reached at a confidence level of 95% ($p < 0.05$). Statistical significance level is denoted on all graphs using asterisks, with *, ** and *** representing $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively.

Corrected standardized mean differences (Hedge's g) were also calculated between burned and unburned means for each species

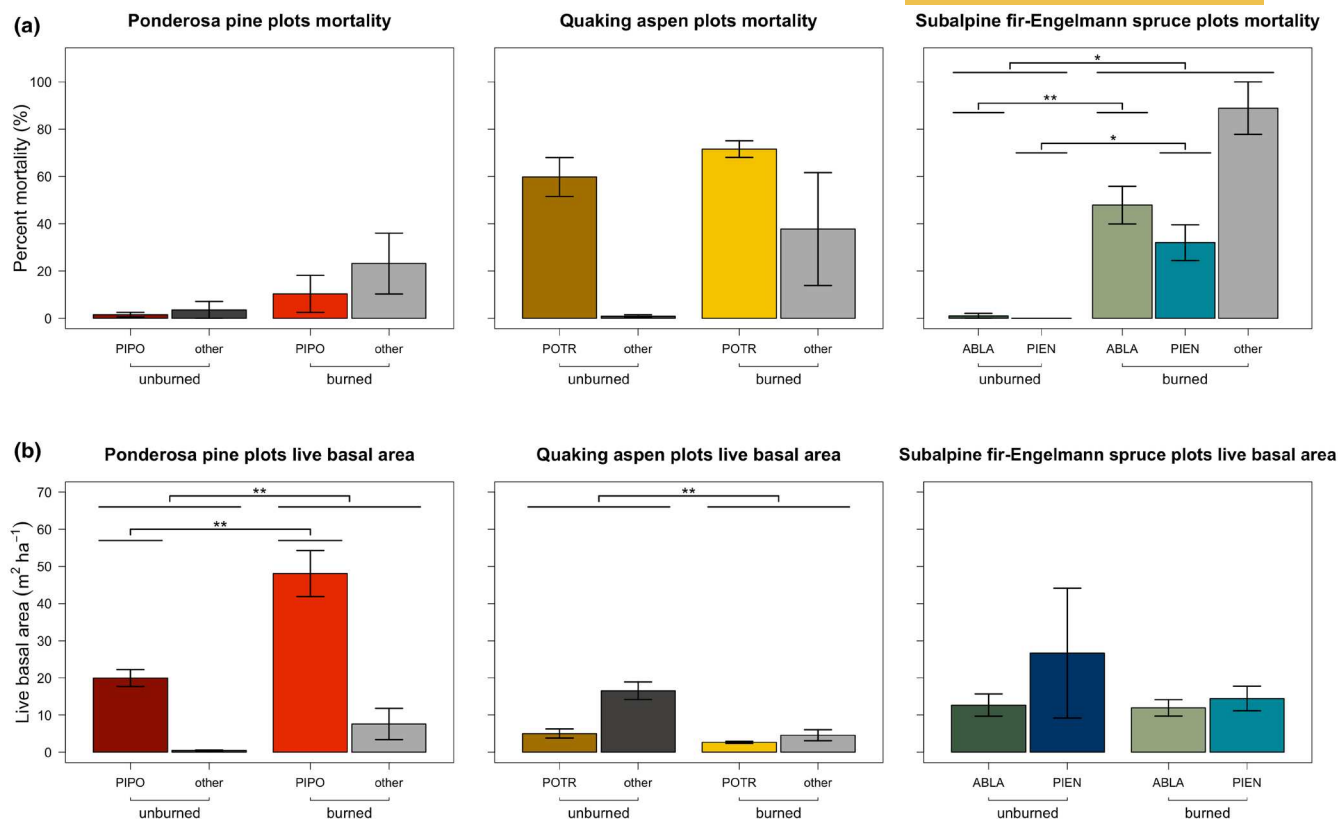


FIGURE 1 (a) Percent of trees dead (100% canopy mortality) out of the total number of trees per plot. Results grouped by species and site. (b) Mean per plot live-tree basal area, grouped by species and site. Significance level of comparisons (*t*-tests) between values denoted above graph (*, **, or *** for $p < 0.05$, $p < 0.01$, or $p < 0.001$, respectively). PIPO = *Pinus ponderosa*; POTR = *Populus tremuloides*; ABLA = *Abies lasiocarpa*; PIEN = *Picea engelmannii*. For more detailed plot-level mortality and plot characteristic data, see Table S1.

for a subset of traits (Borenstein, 2009). *p*-values, sample sizes, data transformations and types of statistical tests used for each comparison can be found in Supporting Information (Tables S4–S7).

3 | RESULTS

3.1 | Plot-level mortality

The percent of dead trees per plot (dead trees were defined as trees with current or previous 100 percent canopy mortality) during the survey year (2022 for subalpine fir-Engelmann spruce plots, 2023 for quaking aspen and ponderosa pine plots) was not significantly different between burned and unburned plots for ponderosa pine or for quaking aspen plots. For subalpine fir-Engelmann spruce plots, plot-level tree mortality was significantly higher at burned plots than unburned plots, both when all species were combined ($p < 0.05$; combined percent mortality across all tree species present at the plot) and at the individual tree species level (percent mortality separated for each of the focal tree species; $p < 0.05$ for Engelmann spruce mortality and $p < 0.01$ for subalpine fir mortality) (Figure 1a).

Live basal area per plot varied between burned and unburned plots for ponderosa pine both when the basal area was combined

across all tree species present at the plot ($p < 0.01$) as well as for basal area of ponderosa pine alone ($p < 0.01$), with greater basal area at the burned than at the unburned plots. For quaking aspen, the live basal area was significantly different between burned and unburned plots only when basal area was combined across all tree species present at the plot ($p < 0.01$). Neither combined nor species-specific live basal areas were significantly different between burned and unburned plots for Engelmann spruce-subalpine fir plots (Figure 1b).

3.2 | Hydraulic traits

Vulnerability curves show a strong decrease in P_{50} , corresponding to an increase in xylem resistance to embolism, in burned ponderosa pine (-3.94 ± 0.09 MPa) relative to unburned (-3.42 ± 0.15 MPa) ponderosa pine ($p < 0.01$) and in burned subalpine fir (-2.9 ± 0.4 MPa) relative to unburned (-1.7 ± 0.1 MPa) subalpine fir ($p < 0.05$; Figure 2), but did not significantly differ ($p > 0.05$) between burned and unburned trees for either quaking aspen or Engelmann spruce.

Maximum xylem area-corrected hydraulic conductivity after removal of emboli via vacuum infiltration ($K_{s,max}$) was significantly

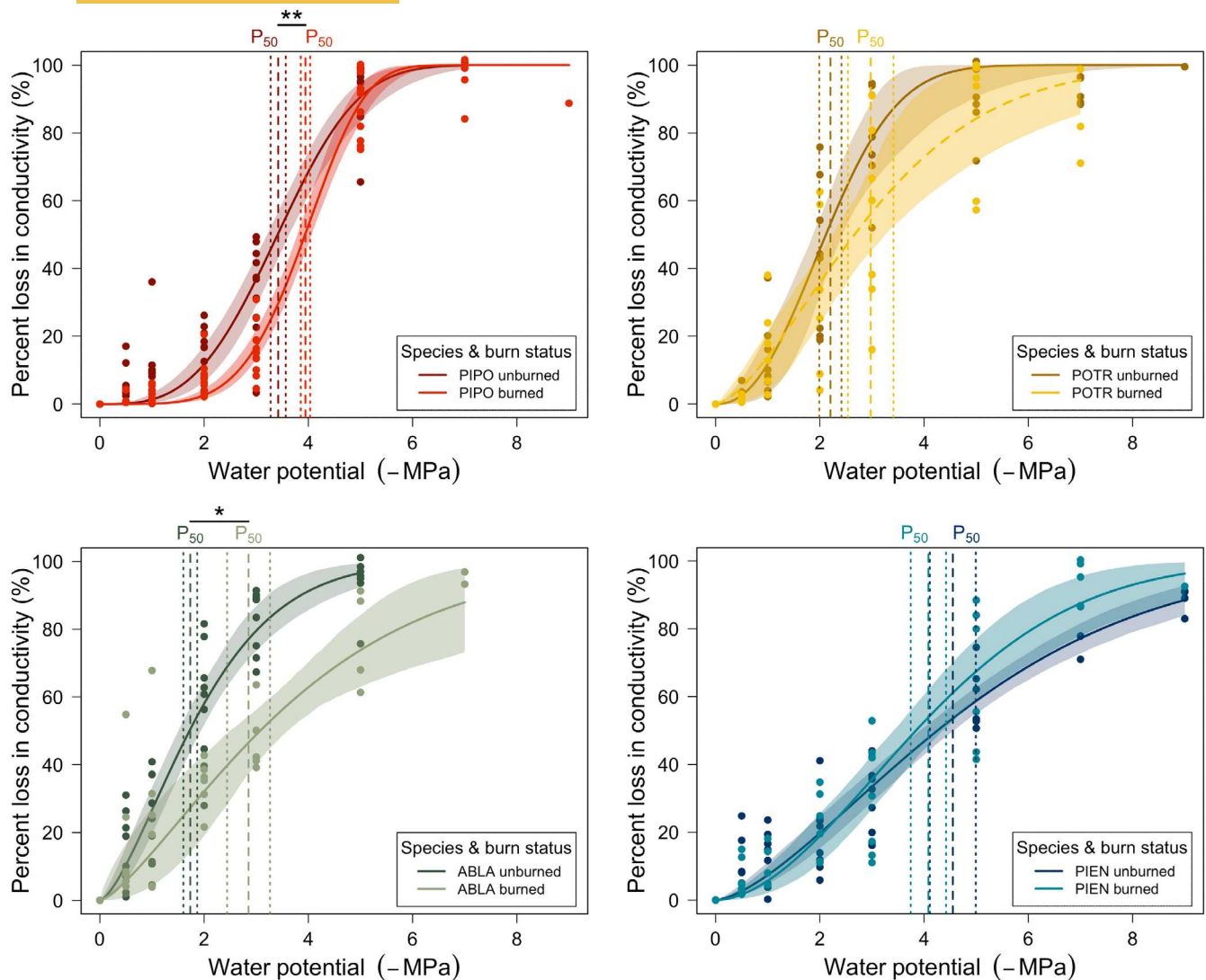


FIGURE 2 Vulnerability curves for each species and burn status. Displayed curves show overall fit for each group. Shaded regions indicate 95% confidence intervals of the overall fitted curve. Vertical dashed lines correspond to mean P_{50} values when curves fit individually for each stem within group; vertical dotted lines correspond to standard error of P_{50} values within group. Significance level of comparisons (t -tests) between P_{50} values denoted above graph (*, **, or *** for $p < 0.05$, $p < 0.01$, or $p < 0.001$, respectively). PIPO = *Pinus ponderosa*; POTR = *Populus tremuloides*; ABLA = *Abies lasiocarpa*; PIEN = *Picea engelmannii*.

($p < 0.01$) higher in burned ($0.43 \pm 0.03 \text{ mg kPa}^{-1} \text{ mm}^{-1} \text{ s}^{-1}$) than in unburned ($0.30 \pm 0.04 \text{ mg kPa}^{-1} \text{ mm}^{-1} \text{ s}^{-1}$) ponderosa pine, but significantly ($p < 0.05$) lower in burned ($0.22 \pm 0.05 \text{ mg kPa}^{-1} \text{ mm}^{-1} \text{ s}^{-1}$) than in unburned ($0.36 \pm 0.03 \text{ mg kPa}^{-1} \text{ mm}^{-1} \text{ s}^{-1}$) subalpine fir (Figure 3a). No significant differences ($p > 0.05$) between burned or unburned trees were observed in quaking aspen or Engelmann spruce.

Native per cent loss in conductivity ($\text{PLC}_{\text{native}}$) was significantly ($p < 0.05$) lower in burned ($10 \pm 4\%$) relative to unburned ($24 \pm 5\%$) Engelmann spruce (Figure 3b). The difference between burned and unburned $\text{PLC}_{\text{native}}$ was marginally statistically significant ($p = 0.053$) in quaking aspen, with values higher in burned trees ($58 \pm 9\%$) than in unburned ($35 \pm 6\%$) (Figure 3b). No significant differences ($p > 0.05$) were observed in either ponderosa pine or subalpine fir.

Leaf area: sapwood area ratio is a proxy for the balance between hydraulic supply and demand, with higher values generally indicating greater water availability and movement (Mencuccini et al., 2019; Tyree & Zimmermann, 2002). The leaf area: sapwood area ratio was significantly ($p < 0.05$) higher in burned ($3000 \pm 500 \text{ cm}^2/\text{cm}^2$) than in unburned ($1700 \pm 200 \text{ cm}^2/\text{cm}^2$) ponderosa pine, as well as significantly ($p < 0.001$) higher in burned ($6500 \pm 700 \text{ cm}^2/\text{cm}^2$) than in unburned ($3300 \pm 400 \text{ cm}^2/\text{cm}^2$) quaking aspen and in burned ($7300 \pm 1000 \text{ cm}^2/\text{cm}^2$) compared to unburned ($4100 \pm 400 \text{ cm}^2/\text{cm}^2$) Engelmann spruce ($p < 0.05$). No significant differences ($p > 0.05$) in leaf area: sapwood area between burned and unburned trees were observed in subalpine fir (Figure 3c).

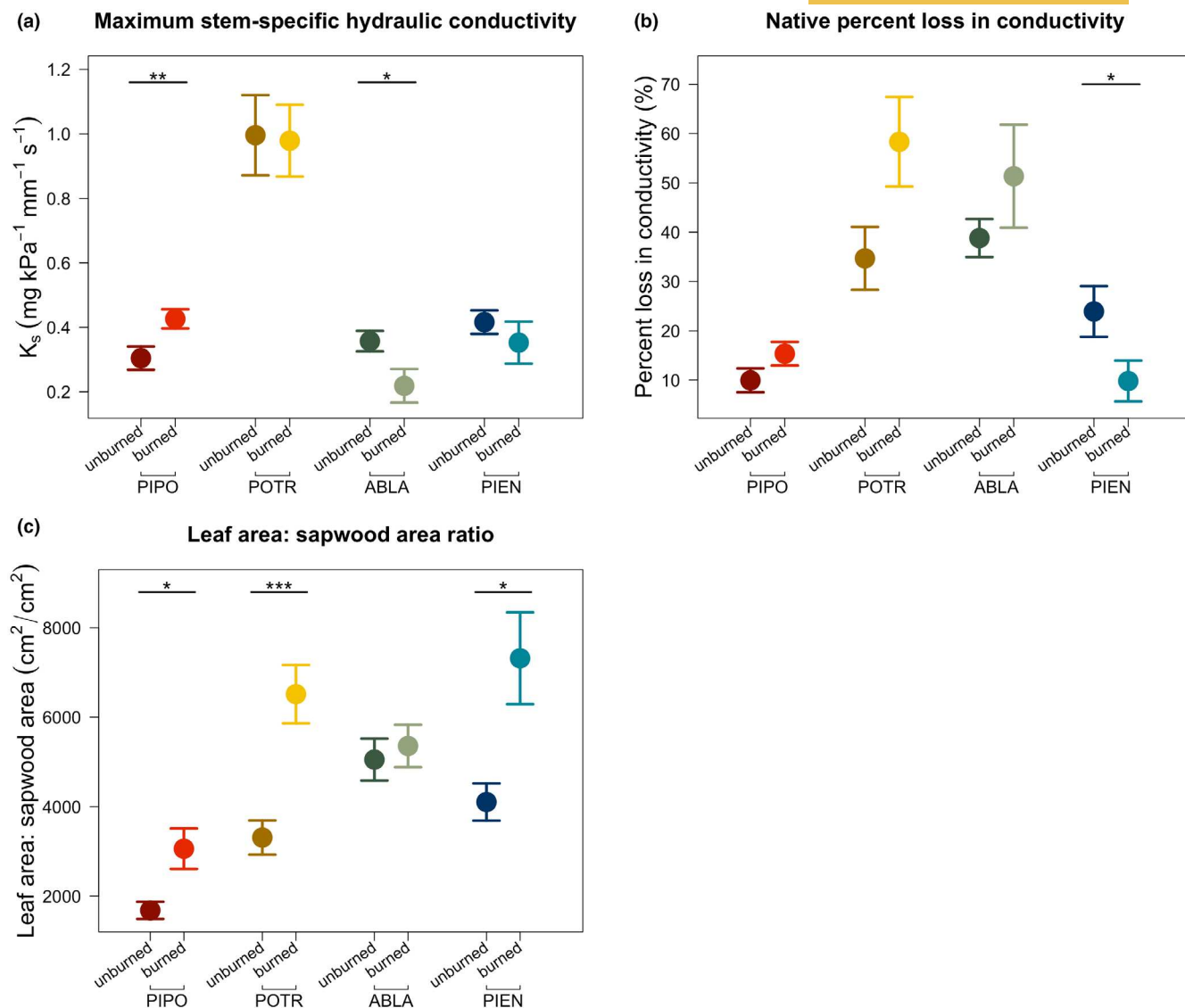


FIGURE 3 (a) Stem-specific conductivity (corrected to mean xylem area, as measured on each end of branch) for each species and site. (b) Native per cent loss in conductivity by species and site. (c) Leaf area: sapwood area ratios for each species and site. The significance level of comparisons (t-tests on raw or transformed data for datasets where raw or transformed data were normally distributed; Wilcoxon tests for non-normally distributed data) between burned and unburned groups for each species are denoted by asterisks (*, **, or *** denote $p < 0.05$, $p < 0.01$, or $p < 0.001$, respectively). PIPO = *Pinus ponderosa*; POTR = *Populus tremuloides*; ABLA = *Abies lasiocarpa*; PIEN = *Picea engelmannii*.

Leaf mass per area, higher values of which often correspond to drought or cold-tolerant traits (Mencuccini et al., 2019), was not significantly different ($p > 0.05$) between burned and unburned trees for any species (Figure S2).

3.3 | Leaf photosynthetic and carbon assimilation traits

Leaf intrinsic water use efficiency (iWUE), which is calculated from leaf $\delta^{13}\text{C}$ as shown in Equation (2), was significantly ($p < 0.05$) higher in burned ($111 \pm 5 \mu\text{mol mol}^{-1}$; than in unburned iWUE: $89 \pm 6 \mu\text{mol mol}^{-1}$) Engelmann spruce, but did not differ significantly in any of the other species (Figure 4a).

Leaf carbon to nitrogen ratio was significantly ($p < 0.05$) higher in burned than in unburned trees for quaking aspen (27.0 ± 0.8 versus 24.1 ± 0.5 , respectively); subalpine fir (66 ± 3 vs. 54 ± 3 , respectively); and Engelmann spruce (56 ± 3 vs. 48 ± 2 , respectively). No significant differences were observed in ponderosa pine, however (Figure 4b).

Bulk leaf carbon concentration was significantly ($p < 0.01$) lower in burned than in unburned trees for subalpine fir ($59.7 \pm 0.3\%$ vs. $61.7 \pm 0.5\%$, respectively) and Engelmann spruce ($52.5 \pm 0.63\%$ vs. $56.2 \pm 0.7\%$, respectively). No significant differences between burned and unburned trees were observed in either ponderosa pine or quaking aspen (Figure 4c).

Bulk leaf nitrogen concentration was significantly ($p < 0.01$) lower in burned than unburned trees for quaking aspen ($1.92 \pm 0.06\%$

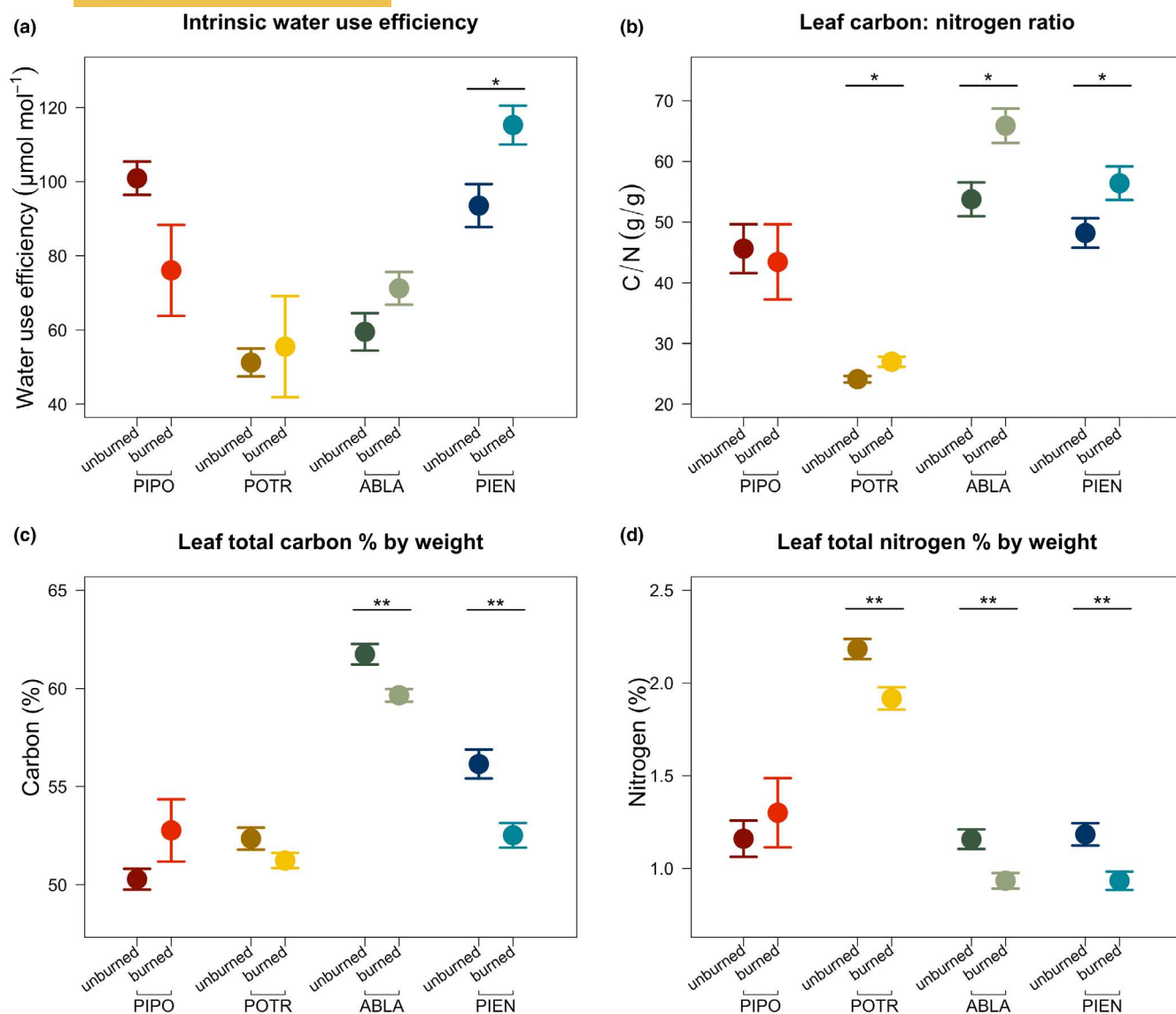


FIGURE 4 (a) Leaf intrinsic water use efficiency, calculated using $\delta^{13}\text{C}$ in Equation (2). (b) Leaf total carbon: nitrogen ratio by mass. (c) Leaf total percent carbon by mass. (d) Leaf total percent nitrogen by mass. For all plots, points denote sample means and error bars are one standard error above and below means. The significance level of comparisons between burned and unburned groups for each species are denoted by asterisks (*, **, or *** denote $p < 0.05$, $p < 0.01$, or $p < 0.001$, respectively). PIPO = *Pinus ponderosa*; POTR = *Populus tremuloides*; ABLA = *Abies lasiocarpa*; PIEN = *Picea engelmannii*.

vs. $2.18 \pm 0.05\%$, respectively); subalpine fir ($0.93 \pm 0.04\%$ vs. $1.16 \pm 0.05\%$, respectively); and Engelmann spruce ($0.93 \pm 0.05\%$ vs. $1.18 \pm 0.06\%$, respectively). No significant differences were observed in ponderosa pine (Figure 3d).

Dark-adapted chlorophyll fluorescence F_v/F_m was significantly ($p < 0.001$) lower in burned quaking aspen (0.731 ± 0.008) than in unburned quaking aspen (0.787 ± 0.004); however, F_v/F_m was significantly ($p < 0.001$) higher in burned (0.754 ± 0.006) Engelmann spruce than in unburned (0.648 ± 0.017) Engelmann spruce, suggesting differences in leaf photosystem response to fire between species. No significant differences between burned and unburned trees were observed in either ponderosa pine or subalpine fir (Figure 5a).

The temperature at which chlorophyll fluorescence begins to decline (T_{crit}) derived from chlorophyll fluorescence thermotolerance curves was significantly ($p < 0.01$) lower in burned ($37 \pm 1^\circ\text{C}$) than in unburned ($44 \pm 2^\circ\text{C}$) ponderosa pine, indicating decreased heat tolerance in burned ponderosa pine. No significant differences were observed in the other tree species (Figure 5b).

The temperature at which 50 percent of maximum chlorophyll fluorescence is lost (T_{50}) derived from chlorophyll fluorescence thermotolerance curves was significantly ($p < 0.05$) lower in burned than unburned trees for both ponderosa pine ($49.4 \pm 0.3^\circ\text{C}$ versus $51.5 \pm 0.5^\circ\text{C}$, respectively) and quaking aspen ($46.4 \pm 0.6^\circ\text{C}$ versus $48.7 \pm 0.3^\circ\text{C}$, respectively), indicating decreased heat tolerance in both burned ponderosa pine and burned quaking aspen. No

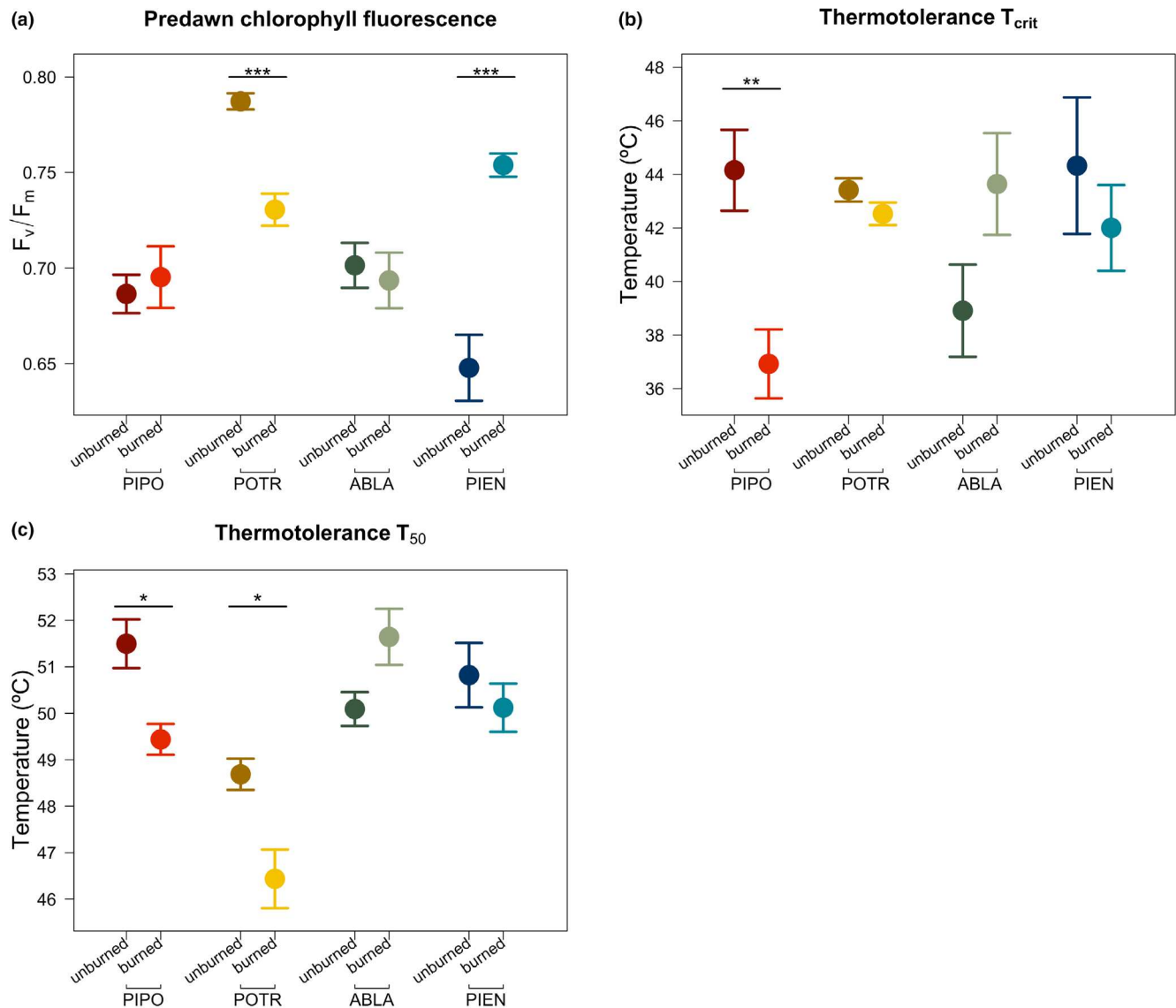


FIGURE 5 (a) Dark-adapted chlorophyll fluorescence (F_v/F_m) measured on unheated (control) sampled leaves. (b) T_{crit} extracted from chlorophyll fluorescence thermotolerance curve. (c) T_{50} extracted from chlorophyll fluorescence thermotolerance curve. For all plots, points denote sample means, and error bars are one standard error above and below means. The significance level of comparisons (t-tests on raw or transformed data for datasets where raw or transformed data were normally distributed; Wilcoxon tests for non-normally distributed data) between burned and unburned groups for each species are denoted by asterisks (*, ** or *** denote $p < 0.05$, $p < 0.01$ or $p < 0.001$, respectively). PIPO = *Pinus ponderosa*; POTR = *Populus tremuloides*; ABLA = *Abies lasiocarpa*; PIEN = *Picea engelmannii*.

significant differences were observed in subalpine fir or Engelmann spruce (Figure 5c).

4 | DISCUSSION

4.1 | Overall trends and potential mechanisms underlying hydraulic trait response to wildfire

Overall, we found that surviving burned trees exhibited more drought-tolerant hydraulic traits than unburned trees (Figures 2 and 6). Burned ponderosa pine and subalpine fir trees were both significantly more resistant to embolism (more negative P_{50}) than

unburned trees of the same species, and burned quaking aspen was non-significantly more resistant to embolism as well. While burned ponderosa pine had a significantly greater hydraulic transport capacity ($K_{s,max}$) than unburned ponderosa pine (Figure 3), we suspect this apparent difference was due to significant differences in hydraulic sample branch size between burned and unburned trees (Table S2), as $K_{s,max}$ is known to increase with increasing branch diameter, while P_{50} does not (Meinzer et al., 2010).

These results are in contrast to the majority of prior studies that have found either no impact of fire on xylem vulnerability to embolism (Bär et al., 2018; Partelli-Feltrin et al., 2021, 2022) or increased vulnerability to embolism in burned trees (Bär et al., 2018; Partelli-Feltrin et al., 2021), with differences depending on species and time

since fire. However, our results align with Reed et al., 2025, who observed a decrease in xylem vulnerability to embolism immediately after fire in Douglas-fir (Reed et al., 2025). Xylem resistance to embolism is considered to be a moderately plastic trait in many species (de la Mata et al., 2022; Kerr et al., 2022; McCullough et al., 2017; Wortemann et al., 2011). We believe the shifts in xylem resistance to embolism we observed several years postfire may arise from one of two potential mechanisms: (1) increased short-term drought stress after fire from heat-plume embolism, leading to adaptive changes in the xylem to increase drought resistance (e.g. smaller vessels or tracheids, smaller and fewer pits) in the postfire xylem of burned trees (Maherali et al., 2002; Wheeler et al., 2005); or (2) survivorship bias, where less embolism-resistant trees are more likely to be killed by heat-plume embolism, leaving only the more resistant trees alive.

We believe that adaptive changes to xylem (mechanism 1) are the major driver for the observed shifts toward increased resistance to embolism in ponderosa pine, subalpine fir, and quaking aspen. Trees that experience a brief but intense embolism event often adapt by building more embolism-resistant xylem (Kerr et al., 2022; Maherali et al., 2002) with smaller vessels or tracheids (Guérin et al., 2020) and/or smaller pit apertures (Roskilly et al., 2019), leading to more negative P_{50} . However, we cannot ignore the possibility that survivorship bias (mechanism 2) may skew postfire sampling in subalpine fir and quaking aspen, given the high rates of postfire mortality observed in the burned subalpine fir-Engelmann spruce and quaking plots. It is possible that the surviving subalpine fir and quaking aspen trees we sampled may have survived the fire in part because they already possessed greater resistance to heat-plume embolism. Both mechanisms are also consistent with the results by Reed et al. (2025), who found decreased xylem vulnerability to embolism in burned Douglas-fir when the prescribed fire treatment was severe enough to kill 14/20 of their originally sampled trees, potentially introducing survivorship bias into their postfire hydraulic sampling. However, we believe mechanism 1 alone is responsible for the increased resistance to embolism (more negative P_{50}) observed in burned ponderosa pine, as mortality in burned ponderosa pine plots was very low (Figure 1). While hydraulic conductivity ($K_{s,max}$) shifts in ponderosa pine appear to not follow the expected hydraulic safety-efficiency trade-off (more negative P_{50} alongside high $K_{s,max}$) (Wheeler et al., 2005), this trade-off is often found to be rather weak at a tissue level within species (Pritzkow et al., 2020), and $K_{s,max}$ can be significantly impacted by branch diameter (Meinzer et al., 2010), which was significantly larger in burned than in unburned hydraulic conductivity samples for ponderosa pine only (Table S2). We therefore suspect that these trends in $K_{s,max}$ for ponderosa are most likely due to sample diameters and should not be considered conclusive of a larger pattern of fire impacts on hydraulic conductivity.

While we cannot exclude the possibility that pre-fire microclimatic, basal area, soil structure, or topographical differences between the burned and unburned transects (Table S1) could be responsible for some of the observed differences between traits at the burned and unburned sites, we carefully chose sites to mirror topographic and climatic conditions between the burned and unburned

transects so this is unlikely to be the main driver of our site-level differences. Future work focusing on the wood anatomical traits of ponderosa pine and subalpine fir before and after fire could help elucidate the mechanisms of this shift and disentangle any pre-fire site differences in growth from tree responses to fire.

Burned Engelmann spruce also exhibited a lower native percent loss in conductivity than unburned Engelmann spruce, indicative of reduced drought stress, although burned quaking aspen, ponderosa pine and subalpine fir non-significantly showed the opposite trend, suggesting species-specific differences in hydraulic supply or water accessibility. These results are not fully consistent with two past studies that found no change in PLC_{native} immediately after fire; however, this could be due to the longer time since fire of our study allowing for postfire reductions in stand basal area and thus hydraulic demand to occur prior to sampling (Partelli-Feltrin et al., 2021, 2022).

Burned ponderosa pine, quaking aspen and Engelmann spruce all showed much higher leaf area: sapwood area ratios than their unburned counterparts, suggesting that reduced competition for water resources allowed for greater hydraulic supply to the leaves (Mencuccini et al., 2019; Tyree & Zimmermann, 2002). However, it should be noted that these branch-level measurements do not account for the total loss of canopy leaf area due to fire, as only healthy undamaged branches were sampled for leaf area: sapwood area and hydraulic measurements. In addition, we did not measure tree-ring sizes in these branches for this study, so it is possible the differences in these ratios could be due to reduced growth in xylem tissues after fire. Future work investigating radial growth in these trees could help elucidate if changes in leaf or xylem area are the main drivers of these differences.

4.2 | Overall trends and potential mechanisms underlying carbon acquisition trait response to wildfire

In contrast to our hydraulic functional trait data suggesting positive impacts of wildfire on most surviving trees, the leaf photosynthetic and carbon acquisition-related traits we measured exhibited overall negative responses to wildfire, with a few exceptions discussed below (Figures 4–6).

Leaf predawn chlorophyll fluorescence responses to fire varied by species, with increased F_v/F_m in burned Engelmann spruce but decreased F_v/F_m in burned quaking aspen, relative to unburned trees, suggesting that burned Engelmann spruce had a greater capacity for photosynthesis, while burned quaking aspen had a lower capacity for photosynthesis, relative to unburned trees of each species, respectively (Murchie & Lawson, 2013).

We found decreased leaf thermotolerance (T_{50}) in burned trees compared to unburned in both ponderosa pine and quaking aspen. Thermotolerance is generally higher in leaves with higher leaf mass per area (which we did not find to be significant in our results) and thus lower nitrogen content—the opposite of the patterns we have seen in this study (Sastri & Barua, 2017). Few prior studies have

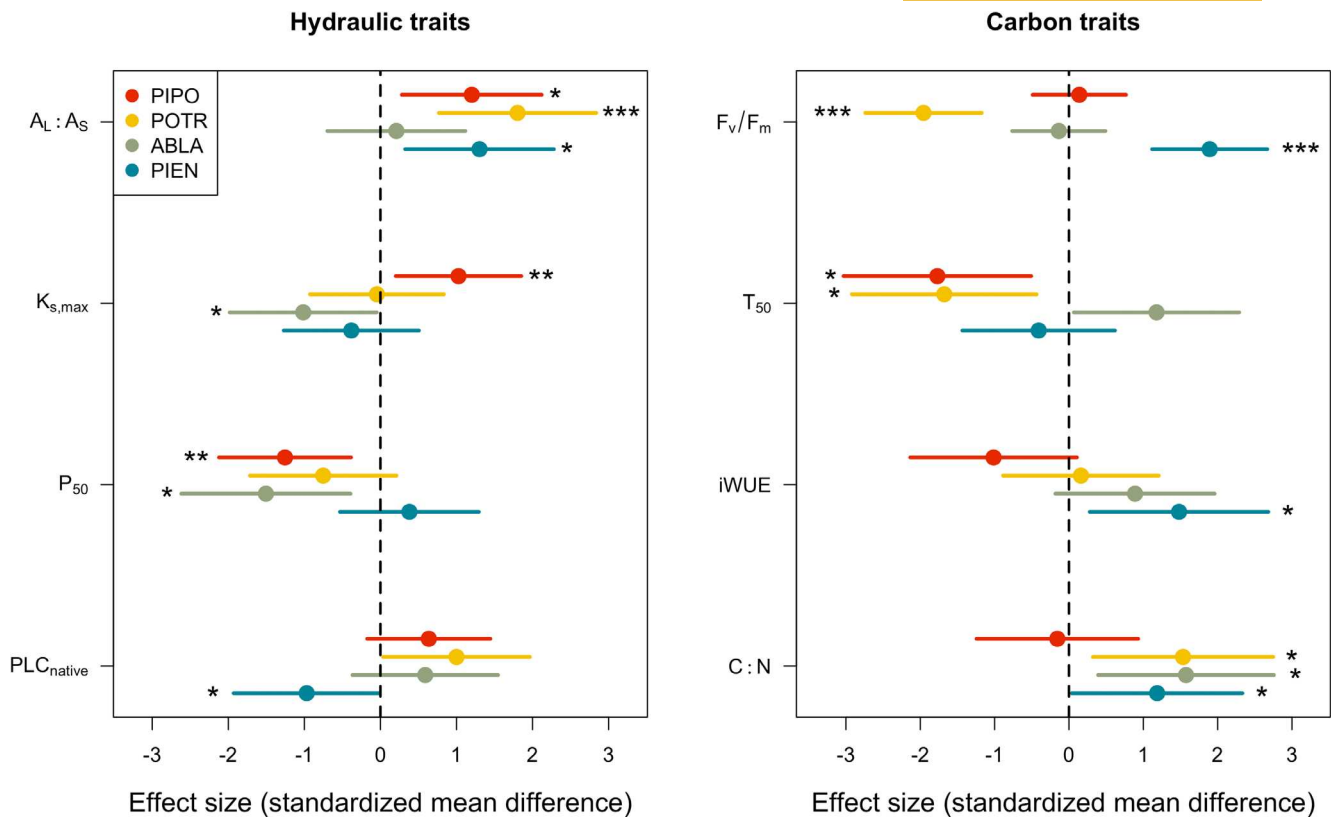


FIGURE 6 Comparisons between burned and unburned means for select hydraulic and carbon acquisition traits for each species. Values are corrected standardized mean differences (Hedge's g) (Borenstein, 2009) between burned and unburned means for each trait and species, with values less than zero representing where burned values are lower than unburned values, and values greater than zero representing where burned values are higher than unburned values. Error bars represent approximate 5% and 95% confidence intervals (calculated as $1.96 \times$ corrected standard error), respectively. Where error bars do not overlap zero (dashed vertical line), traits are most likely statistically significantly different between burned and unburned trees; asterisks indicate the significance level of statistical tests (*, **, or *** for $p < 0.05$, $p < 0.01$, or $p < 0.001$, respectively) between burned and unburned groups. PIPO = *Pinus ponderosa*; POTR = *Populus tremuloides*; ABLA = *Abies lasiocarpa*; PIEN = *Picea engelmannii*.

directly compared leaf C:N ratio or leaf nitrogen content with thermotolerance; however, so it is therefore unclear whether these elemental ratios are a significant driver in leaf thermotolerance. Decreased heat tolerance in burned trees could allow increased heat damage to photosynthetic proteins if heatwaves—especially coupled with drought events that increase stomatal closure and thus reduce leaf evaporative cooling capacity—occur in burned forests, which diverged from our expectation that we would see increased heat resistance after a fire event. The underlying mechanism for this shift is unclear, since it did not trend with nitrogen content or leaf mass per area as expected, but could be due to decreased drought stress causing decreased leaf osmolarity in the burned trees. This would be somewhat consistent with our hydraulic results that found increased leaf area: sapwood area, a proxy for water availability, in both of these species (Sastry et al., 2018; Tarvainen et al., 2022).

Intrinsic water use efficiency was higher in burned than in unburned Engelmann spruce. $iWUE$ is higher when plants are operating with closed stomata in drought conditions (Anderegg et al., 2014; Kannenberg et al., 2021), but increased $iWUE$ can also be due to

increased carbon assimilation and growth, particularly in high-elevation forests where water is less limiting (Pu & Lyu, 2023). Given that burned Engelmann spruce, relative to unburned, exhibited lower PLC_{native} , suggesting decreased water stress; greater leaf area: sapwood area, indicating greater water availability; and higher F_v/F_m , indicating greater photosynthetic capacity, it seems most likely that the increased $iWUE$ in burned Engelmann spruce trees is due to increased carbon assimilation, not decreased water availability. This result is therefore potentially in contrast to our other results as well as other studies that found lower NSC concentrations and reduced photosynthesis after fire (Partelli-Feltrin et al., 2022; Reed et al., 2025).

Leaf carbon to nitrogen ratio—driven by decreased nitrogen in burned trees relative to unburned—was higher in burned trees in all species except ponderosa pine. Site differences in soil nitrogen content or tree nitrogen uptake, due to either pre-fire soil nitrogen content or increased bioavailability after fire, were not measured directly in this study and could theoretically lead to the observed differences in leaf carbon to nitrogen ratios (Cai et al., 2024), although relationships between leaf and soil carbon to nitrogen

ratios are often weak (Ferlian et al., 2017; Gong et al., 2020). However, we found no differences in foliar $\delta^{15}\text{N}$ between burned and unburned trees for any species except Engelmann spruce (Figure S3b). Foliar $\delta^{15}\text{N}$ is known to be correlated with soil nitrogen content on regional scales, and the absence of a clear trend between foliar $\delta^{15}\text{N}$ and carbon to nitrogen ratio suggests that soil N content is likely not the major driver of this pattern (Craine et al., 2009). Additionally, increased nitrogen bioavailability from fire generally only occurs in high-severity fires, which were not experienced at our study sites (Table S1; Cai et al., 2024). We believe a physiological driver of the observed patterns of leaf carbon to nitrogen ratios is most likely. Leaf nitrogen content is known to strongly correlate with RuBisCO activity, so these results strongly suggest decreased photosynthesis in burned trees relative to unburned (Evans, 1989). Leaf carbon content was also significantly lower in burned trees in Engelmann spruce and subalpine fir. Prior work has found that leaf carbon content decreases with increasing cold or aridity, but considered alongside the hydraulic data suggesting decreased $\text{PLC}_{\text{native}}$ in burned Engelmann spruce and the climatological data showing similar site climate at burned and unburned Engelmann spruce-subalpine fir sites (Table S1), it seems unlikely that there is lower water availability in these sites; therefore, the exact mechanism for these patterns remains unclear (Zhao et al., 2018).

Overall, our carbon acquisition and photosynthetic functional traits are relatively consistent with prior studies that have found negative impacts of simulated or actual fire on cambium tissues and non-structural carbohydrate concentrations (Partelli-Feltrin et al., 2022; Reed et al., 2025; Salladay & Pittermann, 2023), with the notable exception of greater iWUE potentially indicating increased photosynthesis in burned Engelmann spruce.

4.3 | Species' fire adaptations may impact physiological responses to wildfire

Past fire physiology studies have found variable tree physiological responses to wildfire, potentially due to a combination of different techniques for fire exposure, species fire adaptations and tree age, which are difficult to disentangle when comparing across studies. As species differ in their relative adaptations to wildfire (e.g. varying bark thicknesses), and given that fire regimes of forests vary widely by ecosystem type and climate, it is unsurprising that studies focused on different species from disparate fire regimes and climate have reached variable conclusions that do not generally align with our results (Bär et al., 2018, 2019; Battipaglia et al., 2016; Michaletz et al., 2012; Niccoli et al., 2023; Partelli-Feltrin et al., 2021, 2022; Salladay & Pittermann, 2023; West et al., 2023). Even within our study, one of the goals of which was to harmonize methodology to compare fire response between our study species, we found variable physiological responses to wildfire that seem to correspond to different species-specific fire adaptations.

Evolutionarily adapted to frequent, low-severity wildfires (Keeley, 2012), ponderosa pine had the most positive response to fire with respect to hydraulic traits, becoming more drought resistant (more negative P_{50}) while also increasing leaf area: sapwood area. However, leaf photosynthetic traits in ponderosa pine were neutral to negative, with a lower T_{50} and T_{crit} in burned trees and no change in isotopic traits.

Quaking aspen, our least fire-resistant species with respect to individual stems (Shinneman et al., 2013), experienced no significant shifts in hydraulic traits except for a strong increase in leaf area: sapwood area ratio in burned trees, suggesting greater water resource availability in these forests after fire, although a non-significant decrease in P_{50} was observed (Figure 2). Quaking aspen also showed decreases in leaf T_{50} , corresponding to a decrease in leaf heat tolerance, in burned trees. Burned quaking aspen had lower leaf F_v/F_m , lower leaf nitrogen content, and lower leaf C:N ratios than unburned trees, corresponding to decreases in leaf photosynthetic health in burned quaking aspen that survive fires. As aspen are highly adapted to postfire resprouting but not fire survival, it is unsurprisingly that stems that did survive fire showed such declines in physiological health with no evidence of acclimation.

Intermediate in terms of fire adaptation, high-elevation mixed spruce-fir forests showed differential species responses to wildfire. Engelmann spruce appears to generally benefit more from fire than subalpine fir, with burned Engelmann spruce having higher leaf area to sapwood area ratio, lower percent loss in conductivity and higher F_v/F_m values than unburned; subalpine fir does appear to increase drought resistance after fire, but trades this for significantly reduced hydraulic conductivity. Subalpine fir was also the only species that did not increase leaf area to sapwood area ratio postfire, suggesting that competitive release of water and/or light resources after fire did not benefit subalpine fir, potentially due to its close coexistence with Engelmann spruce. It is possible that these divergent species responses to fire within a forest ecosystem could have profound impacts on the future species composition dynamics of these forests. For example, Engelmann spruce could potentially outcompete subalpine fir in areas that begin to experience more frequent wildfire events, which is predicted for many of these forests in the future (Perret et al., 2025).

Time since fire exposure may have a particularly notable impact on the conclusions past fire physiology studies have drawn. One of the few studies that compared short and longer-term impacts of fire on the same trees found that structural damage to the xylem cells was only present in growth occurring postfire (Partelli-Feltrin et al., 2021), suggesting that studies only focused on immediate changes after wildfire may be underestimating long-term impacts of fire on xylem structure and function. In four studies where measurements were conducted longer after fire exposure, two found increased xylem vulnerability to embolism in some species (*Pinus ponderosa* saplings, *Pinus sylvestris* mature trees) 1–2 years postfire (Bär et al., 2018; Partelli-Feltrin et al., 2021), while another found no changes in xylem vulnerability to embolism 3 years postfire in *Pinus pinaster*, but some

decreases in tracheid wall thickness and radial growth after fire (Niccoli et al., 2023). The last study, which compared hydraulic conductivity and xylem vulnerability to embolism before, immediately after, and 15–22 months after prescribed fire, found some changes in xylem vulnerability to embolism immediately postfire in *Pseudotsuga menziesii* but no longer-term impacts or impacts in *Pinus ponderosa* (Reed et al., 2025). Our study aimed to understand longer-term (4–6 year postfire) impacts of fire, and our findings suggest that, generalized across our study species on these multi-year time-scales, fire has an overall positive impact on hydraulic traits (e.g. reduced competition and increased drought resistance) but an overall negative impact on carbon acquisition traits (e.g. reduced leaf nitrogen content and reduced heat tolerance) (Figure 6). Our findings suggest that many forests may be more resistant to drought several years after wildfire, but potentially uptake less carbon. These results could provide essential information for ecological models, land managers and others hoping to understand long-term trajectories of forests after fire events and highlight the importance of understanding physiological impacts of disturbances such as wildfire on longer time horizons than are generally studied.

4.4 | Impacts of wildfire on drought physiology provide hope in a changing climate

While prior work on fire impacts on P_{50} and other hydraulic traits has generally found neutral to negative impacts (Bär et al., 2018, 2019; Battipaglia et al., 2016; Michaletz et al., 2012; Niccoli et al., 2023; Partelli-Feltrin et al., 2021; Partelli-Feltrin et al., 2022; Salladay & Pittermann, 2023; West et al., 2023), our work finds generally positive impacts of wildfire on hydraulic traits, most significantly in fire-adapted ponderosa pine, providing some promise for increased forest resilience to wildfire and drought in a changing climate. However, carbon acquisition traits generally had more negative responses to fire, suggesting a potential trade-off between drought resistance and carbon acquisition after wildfire events.

Previous published research on the impacts of wildfire on forest carbon stocks generally takes into account metrics such as mortality, reduction in live basal area, or direct emission from fuels combustion, but rarely considers the long-term impacts on surviving trees (e.g. Davis et al., 2024; Hurteau et al., 2011; North & Hurteau, 2011). Our research finds that while surviving trees may be more resilient to drought stress, the forests may also suffer reduced photosynthetic capacity—and thus reduced carbon uptake—after wildfire events. As large wildfires continue to increase in frequency and severity in the western United States over the twenty-first century, understanding this potential trade-off between carbon uptake and hydraulic safety through ecophysiology will bring greater clarity to our understanding of the forest balance between carbon storage and stability in western US forests (Hurteau et al., 2011) and provide a stronger mechanistic understanding of the impacts of wildfire on forest carbon stocks.

AUTHOR CONTRIBUTIONS

Annapurna C. Post-Leon and William R.L. Anderegg planned and designed the research. Annapurna C. Post-Leon performed experiments and conducted fieldwork. Annapurna C. Post-Leon primarily analysed data, with assistance and troubleshooting by William R.L. Anderegg. Annapurna C. Post-Leon and William R.L. Anderegg interpreted the data. Annapurna C. Post-Leon primarily wrote the manuscript. William R.L. Anderegg edited the manuscript. Annapurna C. Post-Leon and William R.L. Anderegg revised the manuscript and responded to reviewers. Both authors approved the final version of the manuscript to be published.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known competing financial interests or personal relationships that could have influenced or appeared to influence the work reported in this paper.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are freely available through a Figshare digital data repository: <https://doi.org/10.6084/m9.figshare.31160710> (Post-Leon & Anderegg, 2026).

STATEMENT ON INCLUSION

Our study is located in a region of personal and professional interest to the principal investigator and final author on the paper. The contributors named in the Acknowledgements are from all places in careers, from early undergraduate researchers to postdoctoral fellows, representing an effort to involve a variety of researchers with different backgrounds in this research project. However, the authors acknowledge that, despite this study taking place on land traditionally belonging to the Diné, Pueblos and Ute indigenous people, the authors did not consult with indigenous leaders or land managers as a part of this study.

ORCID

Annapurna C. Post-Leon  <https://orcid.org/0000-0003-0647-5165>

William R. L. Anderegg  <https://orcid.org/0000-0001-6551-3331>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Plot characteristics of all field plots sampled in this study. Values are means $\pm$ standard error, and are the means of plot-level values unless otherwise noted. An asterisk (*) denotes individual-tree level characteristics that were averaged at the site (e.g. 'burned ponderosa') level instead of the plot level; two asterisks (**) denotes scorch traits only measured on conifers. Mean annual temperature and mean annual precipitation data extracted from TerraClimate at 4km-resolution. Percent of bole charred is quantified as percentage of the circumference of the bole at the most charred point on the trunk. All plots were circular, with unburned quaking aspen and subalpine fir-Engelmann spruce plots established with 18m radii, and unburned ponderosa pine plots established with 25m radii. All burned plots were established with 15m radii. Species abbreviations: PIPO = *Pinus ponderosa*; POTR = *Populus tremuloides*; ABLA = *Abies lasiocarpa*; PIEN = *Picea engelmannii*.

Table S2. Mean, minimum, and maximum age of branch segments collected at the same time and similar in size to branch segments used for hydraulic conductivity and vulnerability curve measurements, and branch segment xylem area (mean is mean of distal and proximal ends, max is maximum of proximal ends, min is minimum of distal ends) for samples used for hydraulic conductivity measurements (age and xylem area measured on separate segments). Branch age determined by imaging sections under a dissecting microscope and counting growth rings visible in images. Xylem diameter measured using callipers, pith diameter also measured and excluded from xylem area. $N=3$ for each species and burn status for branch age; for branch xylem area, $N=9$ samples for POTR, ABLA, and PIEN, $N=12$ samples for PIPO. Statistics (two-sample t-tests) only performed on xylem area measurements due to small sample size for branch age measurements. The significance level of comparisons between burned and unburned groups for each species are denoted by asterisks (*, **, or *** denote $p<0.05$, $p<0.01$, or $p<0.001$, respectively). Species abbreviations:

PIPO=*Pinus ponderosa*; POTR=*Populus tremuloides*; ABLA=*Abies lasiocarpa*; PIEN=*Picea engelmannii*.

Table S3. P_{12} , P_{50} , P_{88} values (mean $\pm$ standard error, units = MPa) for each species and burn status. Asterisks (*, **, ***) after reported values reflect confidence level ($p < 0.05$, $p < 0.01$, $p < 0.001$) when values for burned and unburned groups within species are compared with a t -test; n.s. denotes comparisons where $p > 0.05$. Outliers removed with the interquartile method where datasets were not normally distributed. Species abbreviations: PIPO=*Pinus ponderosa*; POTR=*Populus tremuloides*; ABLA=*Abies lasiocarpa*; PIEN=*Picea engelmannii*.

Table S4. Statistical tests conducted on plot mortality data. All comparisons are between burned and unburned plots of the same species/ forest type. Species abbreviations: PIPO=*Pinus ponderosa*; POTR=*Populus tremuloides*; ABLA=*Abies lasiocarpa*; PIEN=*Picea engelmannii*.

Table S5. Statistical tests conducted on hydraulic traits. All comparisons are between burned and unburned trees for the same species. Species abbreviations: PIPO=*Pinus ponderosa*; POTR=*Populus tremuloides*; ABLA=*Abies lasiocarpa*; PIEN=*Picea engelmannii*.

Table S6. Statistical tests conducted on photosynthetic traits. All comparisons are between burned and unburned trees for the same species. Species abbreviations: PIPO=*Pinus ponderosa*; POTR=*Populus tremuloides*; ABLA=*Abies lasiocarpa*; PIEN=*Picea engelmannii*.

Table S7. Statistical tests conducted on isotopic traits. All comparisons are between burned and unburned trees for the same species. Species abbreviations: PIPO=*Pinus ponderosa*; POTR=*Populus tremuloides*; ABLA=*Abies lasiocarpa*; PIEN=*Picea engelmannii*.

Figure S1. Map of study plot locations in the San Juan national forest. Black outlines denote fire perimeters. Species abbreviations: PIPO=*Pinus ponderosa*; POTR=*Populus tremuloides*; ABLA=*Abies lasiocarpa*; PIEN=*Picea engelmannii*.

Figure S2. Leaf mass per area for all species. Points denote sample means, and error bars are one standard error above and below means. Two-sample t -tests found no significant differences in leaf mass per area between burned and unburned trees for any species; see Table S5 for more detailed information on statistical tests and sample sizes. Species abbreviations: PIPO=*Pinus ponderosa*; POTR=*Populus tremuloides*; ABLA=*Abies lasiocarpa*; PIEN=*Picea engelmannii*.

Figure S3. (a) Leaf $\delta^{13}\text{C}$; (b) Leaf $\delta^{15}\text{N}$. Points denote sample means, and error bars are one standard error above and below means. The significance level of comparisons between burned and unburned groups for each species are denoted by asterisks (*, **, or *** denote $p < 0.05$, $p < 0.01$, or $p < 0.001$, respectively). Species abbreviations: PIPO=*Pinus ponderosa*; POTR=*Populus tremuloides*; ABLA=*Abies lasiocarpa*; PIEN=*Picea engelmannii*.

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