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Methods to assess fire-induced tree mortality: comparing heated water baths to experimental laboratory fires

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ABSTRACT

Background. Recent studies looking to advance knowledge of fire-effects on trees have used both heated water baths and experimental laboratory fires to apply heat to plant tissues. **Aims.** We assessed whether heated water baths and experimental laboratory fires caused xylem cell wall deformation and increased vulnerability to embolism. **Methods.** Using *Pinus ponderosa* and *Pinus monticola* saplings, we measured impacts using both heated water bath treatments and experimental laboratory fires, with parameters elucidated by prior studies that observed effects associated with lethal outcomes. **Key results.** We show that increased vulnerability to embolism only occurred in one of the species tested when using the heated water baths and did not occur in either species when using the laboratory fire treatments. Neither treatment caused xylem cell deformations. **Conclusions.** Heated water baths may generate misleading results in some species and therefore should be used with caution when researching effects due to wildland fires. **Implications.** Future studies should assess the potential of other common fire dynamics proxy methods.

Keywords: artefacts, behavior, cambium, phloem, physiology, severity, water baths, xylem.

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Introduction

The projected increase of wildfire occurrence, and the resultant impacts on woodland and forested ecosystems, have led to many tree physiology studies seeking to further understand the physiological mechanisms driving tree resistance to fire-induced death and/or subsequent post-fire recovery (Smith *et al.* 2016; Hood *et al.* 2018; O'Brien *et al.* 2018). Improved understanding of these mechanisms and how fires and other climate-exacerbated stressors such as heat and drought interact to impact tree physiology (Sparks *et al.* 2018, 2024; Partelli-Feltrin *et al.* 2020; Wilson *et al.* 2022) would greatly improve representation of fire effects within land management, ecosystem and Earth system models (Shuman *et al.* 2022; Dickman *et al.* 2023; Little *et al.* 2025). Land management personnel need improved information on the survival of trees of all ages during wildland fires to assess the costs associated with replanting, the impacts on ingrowth, to model timber growth and yield, among other management needs (Tinkham *et al.* 2018; Steady *et al.* 2019; Gilvarg *et al.* 2025; Sparks *et al.* 2025). Improved information is also needed when assessing species with different morphological and physiological adaptations (Pausas 2018; Smith *et al.* 2018). Notably, Agee (1993) highlighted that if it is possible to group different species by how they respond post-fire, such information would greatly improve the utility of ecosystem and Earth-system models, especially when considering decomposition, biogeochemical and hydrological processes impacted by fire-induced tree mortality (Stenzel *et al.* 2019; Masi *et al.* 2021; Hanan *et al.* 2022; Birch *et al.* 2025).

Multiple syntheses describe the different potential mechanisms of fire-induced tree mortality (Hare 1961; Michaletz and Johnson 2007; Butler and Dickinson 2010; Hood et al. 2018; O'Brien et al. 2018; Bär et al. 2019; Kleynhans et al. 2021; Dickman et al. 2023; Hudiburg et al. 2023; West et al. 2023). In the last decade, it was proposed that fire can increase vulnerability to embolism by increasing air vapor pressure deficit around the tree canopy (Kavanagh et al. 2010), increase in vulnerability to cavitation by heat-induced reductions in sap surface tension, decrease cavitation pressure by heat-induced decrease in water-surface tension and by causing deformation to xylem conduits (Michaletz et al. 2012). To test this hypothesis and particularly deformation of xylem conduits, several studies have made use of heated water baths as a fire dynamics proxy (Michaletz et al. 2012; West et al. 2016; Bär et al. 2018; Lodge et al. 2018). There is a long history of using hot- and cold-water baths to assess tissue injury, with the vast majority using these methods to assess heat and cold impacts on animal tissues (e.g. Silva and Rosenthal 1961; Boykin et al. 1981; Strickler et al. 1990; Burke et al. 2001; Engelland et al. 2020) and to gelatinize plant tissue starches (Pucher and Vickery 1936). As described in Smith et al. (2025), these methods have also been used as proxies of fire dynamics to assess the impacts of fire on plant tissue.

Results from studies that used fires in field or laboratory experiments have often observed conflicting results with those studies that used heated water baths. For instance, studies that have exposed branches and roots of different tree species to heated water baths have shown increased vulnerability to embolism and concluded that this likely occurs during forest fires (Michaletz et al. 2012; West et al. 2016; Bär et al. 2018; Lodge et al. 2018). Later studies using fires in laboratory- and field-based experiments have not observed similar results (Battipaglia et al. 2016; Partelli-Feltrin et al. 2021, 2023; Niccoli et al. 2023; Reed et al. 2025). Specifically, in containerized *Pinus ponderosa* saplings, Partelli-Feltrin et al. (2021, 2023) did not observe induced embolisms, changes to hydraulic efficiency days after the fire, or deformation of xylem conduits. However, saplings exposed to lower intensity fires exhibited a higher vulnerability to embolism after 2 years, likely from fire effects on post-fire xylem growth. In a field experiment, a delayed impact of prescribed fires (i.e. not occurring immediately after fire), was observed on *Pseudotsuga menziesii* and *Pinus ponderosa* hydraulics and was attributed to changes in non-structural carbohydrates rather than direct fire injuries (Reed et al. 2025). Although field and laboratory studies using fire have found changes in hydraulic efficiency (Partelli-Feltrin et al. 2021, 2023; Reed et al. 2025), it was not directly attributed to the heat generated during the fire as proposed and tested in different studies using heated water baths (Michaletz et al. 2012; West et al. 2016; Bär et al. 2018; Lodge et al. 2018). Thus, the conflicting results between prior studies that used heated water baths and studies that used experimental fires have led others to question whether heated water baths can be used to approximate wildland fire dynamics and thus test similar effects on trees (Varner et al. 2021).

Therefore, the objectives of the current study are to:

1. Assess whether heated water baths and experimental laboratory fires cause xylem cell wall deformation and increased vulnerability to embolism in *Pinus ponderosa* and *Pinus monticola*;
2. Discuss potential sources of uncertainty; and
3. Make recommendations for future research.

Materials and methods

Plant material and growth conditions

We used 1.5-year-old *Pinus ponderosa* Douglas ex C. Lawson and *Pinus monticola* Douglas ex D. Don saplings for this experiment. These species were chosen as they represent contrasting levels of fire resistance: *Pinus ponderosa* is broadly considered resistant to fire-induced tree mortality, while *Pinus monticola* is broadly considered susceptible to fire-induced tree mortality (Griffith 1992; Howard 2003; Sparks et al. 2023). To illustrate the differences in fire resistance between these two species, we measured the thermal conductivity of bark in mature *Pinus ponderosa* and *Pinus monticola* trees located on the University of Idaho Arboretum, Moscow, ID, USA, using a KD2-Pro thermal properties analyzer (METER, Pullman, WA, USA). Although we acknowledge the bark thickness of trees generally increases with age, the relative differences in thermal conductivity should be broadly representative across all age groups. *Pinus monticola* had a relatively high thermal conductivity of 0.108 W m^{-1} K (n = 79, at 288 K) as compared to *Pinus ponderosa* of 0.048 W m^{-1} K (n = 29, at 281 K), indicative of the increased ability of heat to penetrate the stem in *Pinus monticola*. Although these two species are different in their resistance to fire, we recognize that at this age (1.5 years old) both are still very vulnerable to fire due to their thin bark. The rationale for using saplings is that they should be more susceptible to fire-induced injuries than mature trees, as they have not yet developed morphological (e.g. thick bark, vertical growth away from flame zone) protections to fire (Pausas 2018; Smith et al. 2018). Hence, if we do not observe any injuries due to fire in saplings, it is highly unlikely that we would observe any injuries from the same fire behavior in mature trees.

We grew 48 saplings in 3.8 L pots in Sun Gro® Professional Growing mix media at the University of Idaho's Center for Forest Nursery and Seedling Research, Moscow, ID. Saplings were cultivated and well-watered for 6 months in an open-sided greenhouse as described in Partelli-Feltrin et al. (2021, 2023). The current study represents new data associated with each species using the heated water baths and new data associated with *Pinus monticola* using fires. The *Pinus ponderosa* data associated with the 1-day post-fire and control data were previously reported in Partelli-Feltrin *et al.* (2021). In fall 2018, six well-watered saplings of each species were randomly selected for each treatment group (unburned, lethal fire, 5-min water bath at 65°C; and 5-min water bath at 95°C). The mean root collar diameter (RCD) of the *Pinus ponderosa* saplings was 1.5 ± 0.04 cm and the height was 0.48 ± 0.01 m. The mean RCD of the *Pinus monticola* saplings were 1.41 ± 0.02 cm and the height was 0.54 ± 0.02 m. Before each fire or heated water bath treatment, predawn leaf water potential (Ψ_p) in saplings was measured using a Model 1505D pressure chamber (PMS Instrument Company, Albany, OR, USA) to ensure that all saplings were not water stressed. Mean Ψ_p for *Pinus ponderosa* ($n = 24$) and *Pinus monticola* ($n = 23$) were −0.47 ± 0.02 MPa and −0.24 ± 0.02 MPa, respectively. A pairwise comparison was conducted among the treatments within each species and no significant difference ($P > 0.05$) in RCD, height and Ψ_p was observed (Supplementary Table S1).

Heated water bath treatment

The night prior to the heated water bath treatment, saplings were taken to a laboratory in the Integrated Research and Innovation Center (IRIC) at the University of Idaho, watered and placed within a black plastic bag. The next morning, Ψ_p was measured (Supplementary Table S1). Main stems were excised at the root collar of each sapling with the bark left intact to limit damage to the phloem and cambium. Under deionized water at ambient temperature (~21.5°C), the stems were defoliated, and the distal ends were cut with a sharp razor blade to remove any potential embolisms associated with the excising the stem, yielding a segment of ~20 cm. Water bath treatments were conducted for 5-min durations at 65 and 95°C using a 10-L digital water bath (Fisher Scientific, Pittsburgh, PA, Fig. 1). Each stem was placed in the water bath individually to avoid pseudoreplication. Studies using different temperatures and longer time exposure, i.e. 6–60 min, found xylem cell deformation in heated water bath experiments (West *et al.* 2016; Bär *et al.* 2018). However, 10–15 min are durations reported in procedures to gelatinize starches in plant samples through immersion in boiling water (Pucher and Vickery 1936; Smith and Zeeman 2006). Therefore, we selected 5-min heat durations at 65 and 95°C as prior studies have reported differences in xylem properties on a range of tree species using these parameters (Michaletz *et al.* 2012; West *et al.* 2016; Lodge *et al.* 2018).

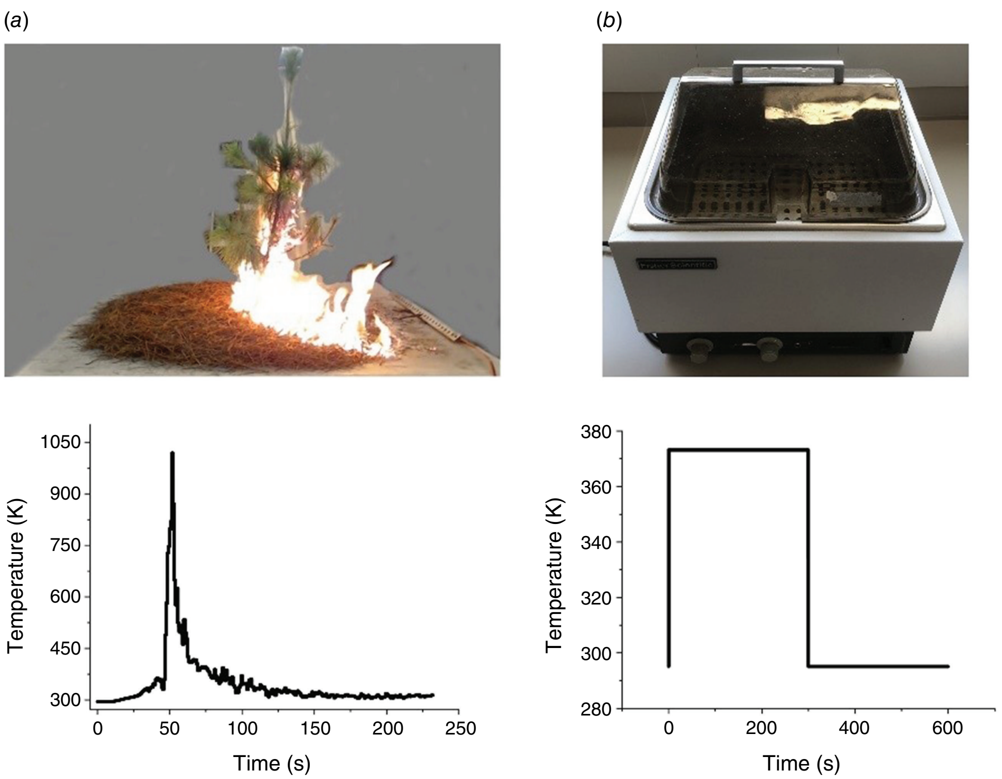

Fig. 1. (*a*) Example of a sapling burning within a laboratory experiment. The bottom graph represents temperatures attained within a sapling under 100% lethal fire conditions. Data obtained from Smith *et al.* (2017) on 2.5-year-old *Pinus contorta* saplings. (*b*) Heated water bath used in this study. The bottom graph represents the idealized temperatures during immersion of a stem in the water bath (assuming the stem is placed in and removed directly and entirely from the hot water).

Although prior heated water bath studies have used cooling durations < 20 min, with ice sometimes added to accelerate cooling (Michaletz *et al.* 2012; Bär *et al.* 2018), we followed the methodology presented by Bär *et al.* (2018) that consecutively cooled down the stems in water at ~20°C for 20 min intervals. As such, stems were placed in an open container with deionized water at room temperature (~21.5°C). After ~20 min the stems were placed in another container containing deionized water at room temperature (~21.5°C) and we repeated this process for at least an hour. No ice was used to avoid shocking the plant components and this extended cooling duration was selected to minimize impacts of elevated temperatures on the dynamic viscosity of water (Balmer 2011).

Fire treatment

In this paper we use the term forest fire dynamics to describe the fire behavior associated with the physical transfer of heat through heat transfer mechanisms. Fire treatments were conducted under controlled conditions at the Idaho Fire Initiative for Research and Education (IFIRE) combustion laboratory and all live plants exposed to the fire followed the same procedure that is described in detail in Partelli-Feltrin *et al.* (2020, 2021, 2023). Specifically, to achieve a known lethal dosage level (i.e. 100% probability of mortality for saplings of these ages) of fire radiative energy (FRE) = 1.4 MJ m^{-2}, 0.304 kg m^{-2} of *Pinus ponderosa* needles were oven dried at 105°C for 48 h and then used as a fuel bed (Matthews 2010; Smith *et al.* 2013). Subsequent studies have demonstrated that lethal FRE dose levels of both these species are attained below 0.8 MJ m^{-2} (Steady *et al.* 2019; Blanco *et al.* 2025). As in Partelli-Feltrin *et al.* (2023), we selected this lethal dosage level to create a baseline of the morphological and physiological effects during real fires. Importantly, not all FRE dosage levels cause fire-induced mortality in saplings, with several species exhibiting zero probability of mortality at FRE levels of ~0.4 MJ m^{-2} (Sparks *et al.* 2023). The needles were evenly distributed across a 1 m^2 circular concrete board surface that had a hole cut within the center to enable seamless fuel continuity over the pot soil surface. Air from below was eliminated through sealing any gaps between the pots and concrete board with a non-combustible material. The fires were ignited with 2 g of ethanol on ~25 cm of the fuel bed perimeter. Each experimental fire lasted approximately 5 min from ignition to extinction. During the experimental fires, the combustion laboratory fan was turned off to limit any forced convection that could impact the fire spread. In addition, as reported in Partelli-Feltrin *et al* (2021), the maximum bark temperature recorded at a height of ~9 cm from the surface of the soil in three different species (*P. monticola*, *Populus tremuloides*, *Quercus macrocarpa*) ranged from 33.2 and 77°C. It is important to note that the bark temperature measurements were taken at least 5-min after the fires to avoid contact with actively burning components and we acknowledge that the bark will have attained higher temperatures.

Hydraulic conductivity

Xylem hydraulic conductivity was measured in all six saplings of each species for each treatment in a climate-controlled wet lab located in the IRIC building at the University of Idaho. The evening prior to xylem hydraulic measurements, control and burned plants were taken to the laboratory, watered and bagged within a black plastic bag. The next morning Ψ_p was measured. Fire treatment caused foliage damage (scorch and combustion) and although we selected the least affected needles, the damage caused could potentially affect the water potential (see Partelli-Feltrin *et al.* 2021). After, the main stem was excised at the root collar, it was placed in the perfusion solution (0.02 M KCl and 0.012 M HCl) at an ambient temperature (~21.5°C) and defoliated. Stems submerged in the perfusion solution had the distal end cut to approximately 14 cm to remove any potential emboli caused during stem collection. Given the height of ~9 cm from the pot soil surface was associated with the maximum temperature measured after the fire, that point was marked, and the distal ends were cut to position that point approximately at the center of the stem segment used for xylem conductivity measurements (see Partelli-Feltrin *et al.* 2021 for more details).

Xylem hydraulic conductivity (k, kg m^{-1} MPa^{-1} s^{-1}) was measured using a Sperry apparatus with a pressure head reservoir of a degassed perfusion solution (0.02 M KCL and 0.012 M HCl). Prior to the measurements, the solution used for hydraulic measurements was connected to a vacuum pump for 48 h for de-gassing. After the stem segments were excised, native conductivity (k_{native}) was measured, then the stems were placed in a vacuum chamber and immersed in perfusing solution overnight to clear any air emboli. The following morning, stems were placed in another container with the solution at ambient temperature. Following Partelli-Feltrin *et al.* (2021), the samples were left in the solution at room temperature (~21.5°C) for 1 h to enable them to thermally equilibrate and then following equilibrium both ends were shaved under water using a fresh razor blade, and maximum hydraulic conductivity (k_{max}) was measured. Following Partelli-Feltrin *et al.* (2021, 2023), all conductivity measurements were corrected for stem length and cross-sectional area and native percentage loss of conductivity (nPLC) calculated using:

$$\text{nPLC} = 100\left[1 - \left(\frac{k_{\text{native}}}{k_{\max}}\right)\right] \tag{1}$$

After k_{max} measurement using the same stems, the vulnerability to embolism curves were generated using the centrifugation technique (Alder *et al.* 1997; Cochard *et al.* 2013). Negative pressure in the stems were induced by spinning the stems at increments of −0.5 and −1 MPa until 4 MPa for *Pinus ponderosa* and −8 MPa for *Pinus monticola*. We calculated xylem pressures needed to cause 12, 50 and 88% loss of xylem hydraulic conductivity to compare the water bath, fire-exposed and unburned control plants.

Xylem anatomy

We investigated whether the lethal intensity fires and heated water bath treatments visibly damaged the xylem conduit structure in *Pinus ponderosa* and *Pinus monticola* using microscopic examination. We imaged the cross-sections of all stem segments used to measure hydraulic conductivity and compared fire-exposed, water bath treatments and unburned control plants. Segments, 5 cm in length, were cut from the stem section that was used to measure xylem hydraulic conductivity and placed in a solution of 1:1:1 of glycerin, ethanol and deionized water for a minimum of 2 weeks. 40 μm thick cross sections were made using a microtome (America Optical Company, Buffalo, NY, USA) and stained with 6% safranin solution. Each stem cross section was examined for tracheid cell wall deformation using an Olympus BX51 (Olympus Cooperation, Tokyo, Japan) confocal microscope equipped with an Olympus DP70 digital camera (Olympus Cooperation, Tokyo, Japan). Images were acquired and the cell structure of unburned control, fire-exposed and heated water bath treated plants were visually compared. Scale bars were added to each image using Olympus MicroSuite Software version 3.1.108 and the Inkscape software version 0.92 (http://www.inkscape.org/).

Statistical analysis

R software version 3.6.0 was used to conduct all statistical analysis. A pairwise comparison using the R package 'emmeans' was used to compare the differences among treatment groups, in terms of mean root collar diameter, height and leaf water potential water conductivity (k) and nPLC (Lenth *et al.* 2020). One point in the treatment water bath 65°C was excluded due to measurement error ($N = 5$) based on Cook's distance test. Vulnerability curves were fitted using R package fitplc (Duursma and Choat 2017). Fitplc package was also used to estimate the stem water potential needed to cause 12, 50 and 88% PLC for each treatment and 95% confidence intervals using the recommended bootstrap resampling approach. Confidence intervals were used to compare the differences in water potential at 12, 50, and 88% PLC among the treatments.

Heat transfer modeling

To better understand the potential heat transfer differences between the heated water bath and fire experiments, we conducted a simple one-dimensional finite difference model (FDM) to illustrate the difference between heat transfer in fires and in water baths. As a first approximation, we modeled heat transfer in MATLAB R2019a (9.6.0.1174912) and created a one-dimensional FDM using a Fourier's heat transfer model in cylindrical (polar) coordinates evaluated along the radial direction to numerically approximate the temporal and spatial temperature profile within a sapling stem under both fire and water bath conditions (see supplemental videos). The general form of the heat transfer equations and the FDM approach to approximate heat conduction in tree stems is well known in the wildland fire science literature (Jones *et al.* 2006; Butler and Dickinson 2010; Chatziefstratiou *et al.* 2013):

$$\frac{\partial T_{(r,t)}}{\partial T} = \frac{\alpha}{r}\frac{\partial}{\partial r}r\frac{\partial T_{(r,t)}}{\partial r} \tag{2}$$

$$T_{(r,0)} = T_{0_{(r)}} \tag{3}$$

$$T_{(R,t)} = T_{BC} \tag{4}$$

$$\frac{\partial T_{(0,t)}}{\partial r} = 0 \tag{5}$$

For an initial condition, it can be assumed that the system is at a fixed initial temperature (which could be a function of (radius increment) r, Eqn 3). The 1st boundary condition (Eqn 4) assumes no external heat transfer resistance such that the outermost bark layer (i.e. $r = R$ (total radiius)) is equal to the fluid temperature (T_{BC}). For the 2nd boundary condition, the derivative of the temperature at the center of the cylinder is zero due to symmetry (Eqn 5).

The FDM model, Eqn 6, is a numerical approximation of Eqn 2 and divides the material of interest into differential spatial (Δr) and temporal (Δt) elements, where $T(r, t)$ is the temperature at the generic point (r) at time (t), where the origin ($r = 0$) is the center of the tree stem (Butler and Dickinson 2010; Chatziefstratiou *et al.* 2013):

$$T_{(r,t)} = T_{(r,t-1)} + \frac{\alpha \times \Delta t}{\Delta r^2}(T_{(r+1,t-1)} - 2 \times T_{(r,t-1)} + T_{(r-1,t-1)}) + \frac{\alpha \times \Delta t}{2 \times r \times \Delta r^2}(T_{(r+1,t-1)} - T_{(r-1,t-1)})$$
$$\text{where, a constraint for stability requires } \frac{\alpha \times \Delta t}{\Delta r^2} < 0.5 \tag{6}$$

FDM parameters were derived from Khattabi and Steinhagen 1993; Quintiere 1997; Kremens *et al.* 2010; Chatziefstratiou *et al.* 2013 and Welty *et al.* 2015. We acknowledge that a one-dimensional FDM is a simplification, but it captures the dominant effects and provides a reasonable proof-of-concept to illustrate the difference between heat transfer in fires and water baths. To calibrate the model, temperature data were collected from 36-gage type K thermocouples (OMEGA Engineering, Norwalk) embedded in the bark of pine saplings of a similar age to the current study in lethal levels of fire intensity (1.2 MJ m^{-2}) during experimental fires (Smith *et al.* 2017). The saplings had an average bark depth of

< 1 mm. The data from Smith *et al.* (2017) represented lethal fires and given we are undertaking a mechanistic approach, this modeling should be transferable to larger trees.

Results

We found no significant difference in nPLC and k_{max} among treatments within each species. As previously reported for *Pinus ponderosa* (Partelli-Feltrin *et al.* 2021) but now extended to a second conifer species, *Pinus monticola*, fire did not increase the vulnerability to embolism of the burned plants (Fig. 2). The shape of the hydraulic vulnerability curves between burned and unburned control saplings were similar for both species (Fig. 2*a*, *b*). Fig. 2*a* also demonstrates that the 65°C heated water bath treatment had no impact on *Pinus ponderosa*, while the 95°C heated water bath treatment appears to show a small difference. As shown in Fig. 2*b*, a clear difference is seen for both the 65 and 95°C heated water bath treatments for *Pinus monticola*. The increase in vulnerability to embolism was only observed for *Pinus monticola* when exposed to the heated water bath at both temperatures. Xylem pressures to cause 50 and 88% were higher (less negative) when compared with control and fire treatments (Table 1, Fig. 2*b*). In our study we did not find significant differences in nPLC among our treatments for both species, but we observed that nPLC for the stems treated in heated water baths had almost 0% loss of conductivity (Fig. 2*c*). We observed no visible damage in the tracheid cell walls of plants exposed to lethal fire intensity or to either heated water bath treatment temperatures (Fig. 3). Likewise, there were no visible differences between unburned control and fire-exposed cell walls (Fig. 3).

The modeling potentially informs why differences are being observed between heated water bath and fire experimental

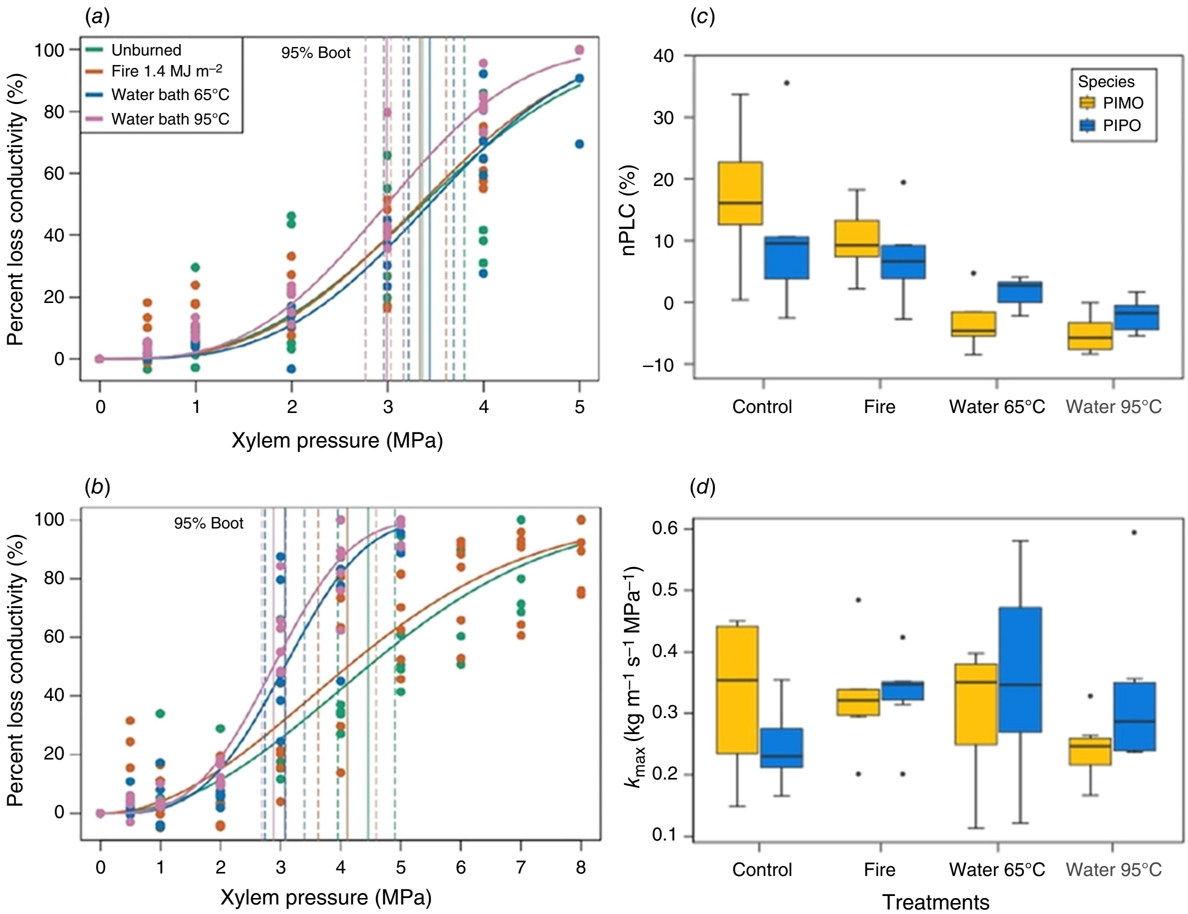

Fig. 2. Plant xylem vulnerability of *Pinus ponderosa* (*a*) and *Pinus monticola* (*b*) displayed by treatment: unburned control (green), lethal fire (orange), the 65°C water bath (blue) and 95°C water bath (magenta). The solid vertical lines represent P50 (the water potential at which the plant reaches 50% loss of hydraulic conductivity). The dotted lines represent the 95% confidence intervals. (*c*) Native percentage loss of xylem hydraulic conductivity (nPLC) and (*d*) maximum conductance (k_{max}) in the unburned (control), lethal fire and the 65°C (65) and 95°C (95) water bath treatments. Note the near-zero nPLC values for the water bath measurements which is likely indicative of a temperature-based artefact. Box plots show the median (horizontal line), first and third quartile (box edges) and 1.5× interquartile (whiskers). One outlier was removed in (*c*) and (*d*) following an extreme studentized deviate test. PIPO = *Pinus ponderosa*, PIMO = *Pinus monticola*.

treatments. Heat incident on live sapling stems during fires is characterized by high temperature pulses over short durations (Figs 1*a*, 4*a*), which broadly describes conditions present in wildland surface fires except when a large quantity of downed wood or belowground fires such as peat is burning (Kreye *et al.* 2014; Sparks *et al.* 2017). As described in Smith *et al.* (2017) the 0.4–1.4 MJ m^{-2} range of fire radiative energy dosage levels broadly captures the range of surface fire conditions across a wide array of fire regimes. Fig. 5*a* shows the radial distribution of cumulative time (or thermal dose) that temperatures in the stem exceeded 65°C. The 65°C is important as its widely assumed in fire ecology studies that heat associated with temperatures exceeding ~60°C for 2 min causes cambium death (Hare 1961). In Fig. 4*b*–*d*, each line represents a different time step. Fig. 4*b*, *c* represents the temperature at the bark surface measured via thermocouples during the 100% survival and 100% mortality fires, respectively. Although the current study focuses on mortality, both scenarios were included to provide context to Fig. 5*b*. Fig. 4*d* shows an FDM simulation of the radial thermal profile for stem heating within a 95°C (368 K) heated water bath based on the temporal conditions shown in Fig. 4*c*. Our modeling results showed that at 90–100% of the radial thermal profile of the stem, where 0% represents the pith and 100% represents the bark surface (Fig. 5*a*), the near-boiling water bath for 5-min produced an increase in exposure time of temperatures exceeding 65°C by ~324 and ~2870% greater than compared to surface fires that caused 100 and 0% mortality, respectively (Fig. 5*b*). Although the data presented in Figs 1 and 5 report immersion in hot water up to 300 s (5 min), Supplementary Video S1 presents the complete finite difference modeling of heat penetrating into a sapling stem within a heated water bath for up to 1 h immersion.

Table 1. Conifer sapling xylem vulnerability.

Treatments	P_x	Species	
		Pinus ponderosa	***Pinus monticola***
Unburned	P_{12}	-1.87 (-1.32, -2.64)	-2.05 (-1.43, -2.64)
	P_{50}	-3.36 (-2.97, 3.82)	-4.45 (-3.93, -4.94)
	P_{88}	-4.96 (-4.37, NA)	-7.44 (-6.63, NA)
Fire	P_{12}	-1.91 (-1.40, -2.36)	-1.77 (-1.18, -2.31)
	P_{50}	-3.34 (-3.05, -3.59)	-4.11 (-3.57, -4.60)
	P_{88}	-4.82 (-4.55, NA)	-7.18 (-6.22, NA)
Water bath 65°C	P_{12}	-2.05 (-1.80, -2.35)	-1.86 (-1.49, 2.32)
	P_{50}	-3.43 (-3.24, -3.73)	-3.07 (-2.75, -3.38)*
	P_{88}	-4.83 (-4.37, NA)	-4.28 (-3.26, -4.76)*
Water bath 95°C	P_{12}	-1.75 (-1.49, -2.05)	-1.72 (-1.48, -1.97)
	P_{50}	-2.99 (-2.75, -3.16)	-2.88 (-2.68, -3.08)*
	P_{88}	-4.27 (-4.02, -4.46)	-4.06 (-3.47, -4.44)*

Xylem pressure (MPa) to cause 12, 50 and 88% loss of xylem hydraulic conductivity in *Pinus ponderosa* and *Pinus monticola* saplings exposed to different heat treatments. Significant differences between unburned treatments and each heat treatment are indicated with asterisks ($P < 0.05$). *Pinus ponderosa* control and fire were reported in Partelli-Feltrin *et al.* (2021).

Discussion

We compared experimental laboratory fires and heated water baths as alternative methods to assess the effect of

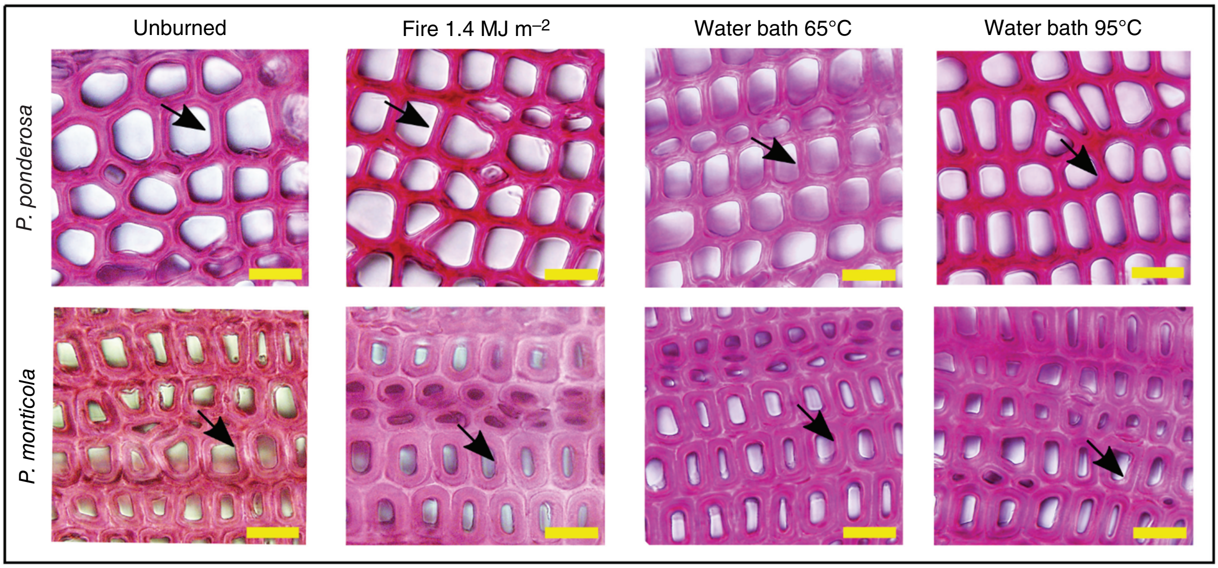

Fig. 3. *Pinus ponderosa* and *Pinus monticola* xylem conduit anatomy of unburned and heat-treated saplings. *Pinus ponderosa* data previously reported in Partelli-Feltrin *et al.* (2021). Arrows indicate the conduits cell walls. Bars are 20 µm. We observed no cell wall damage and no deformation of xylem conduits with exposure to the real fire or hot water bath treatments.

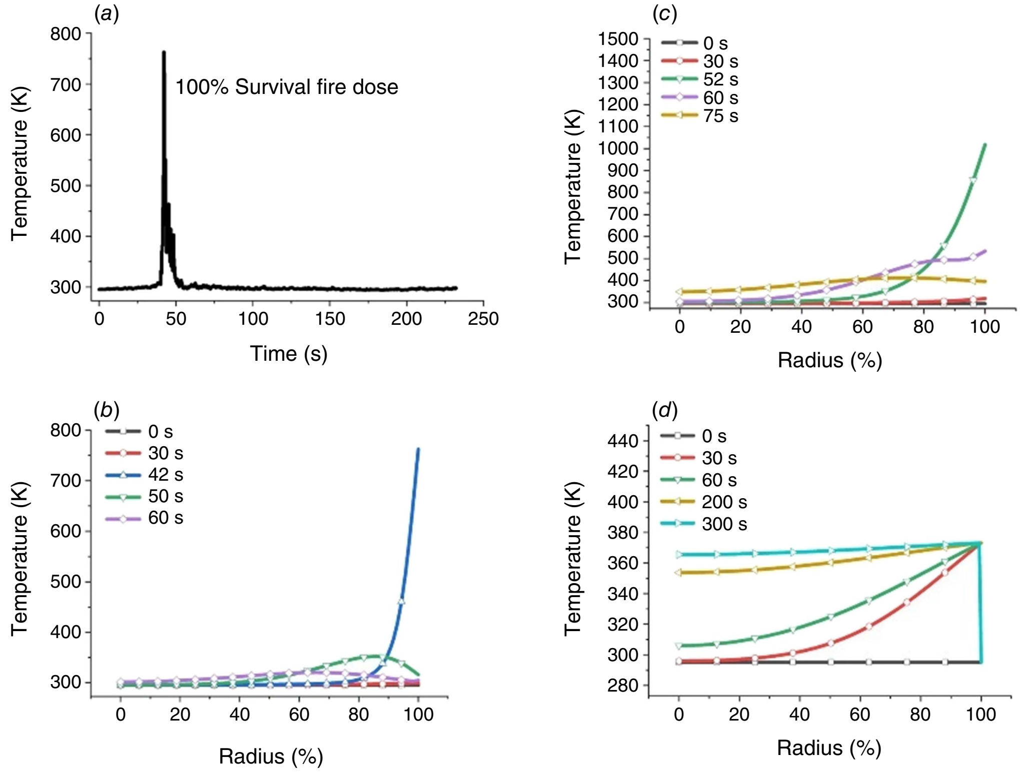

Fig. 4. (*a*) Thermal profiles during a100% survival surface fire obtained from Smith *et al.* (2017) on 2.5-year-old *Pinus contorta* saplings. In (*b*–*d*), each line represents a different temporal condition associated with the FDM simulation of the radial thermal profile for stem heating. (*b*) 100% survival case associated with Fig. 4*a*, (*c*) 100% mortality case associated with Fig. 1*a* and (*d*) 368.15 K (95°C) water bath, where the stem was removed after 300 s.

heat on xylem conduits and vulnerability to embolism. Using tree saplings of two contrasting fire-resistant species, we found no evidence of fire-induced increase in xylem vulnerability to embolism in either species (Partelli-Feltrin *et al.* 2021). The main novel finding in this study is that heated water baths appear to subject stems to considerably higher levels of heat exposure than stems experienced during lethal fire conditions (Fig. 5*b*) and thus likely overestimate the hydraulic impacts of fires on trees. Although we acknowledge that there may be differences when considering fires burning in natural settings, these results agree with past studies that landscape fires do not cause hydraulic failure in trees (Battipaglia *et al.* 2016; Niccoli *et al.* 2023). In our study, heated water bath treatments significantly increased vulnerability to embolism in *Pinus monticola*, whereas *Pinus ponderosa* remained unaffected (Table 1, Fig. 1*a*, *b*).

In terms of explaining the near 0% loss of conductivity in the heated water baths (Fig. 2*c*), although we cooled down the stem for ~1 h prior to the conductivity measurement, it is possible that the inside of the stem did not cool down enough causing a temperature-based water viscosity artefact. For example, the dynamic viscosity of water can vary from 1.0005 mPa s at 20°C to 0.2814 mPa s at 100°C (Balmer 2011) and can cause significant difference in measurements. In our study, we observed that when the stem was placed in the water bath, it initially sank and after 5 min it floated. As previously described in Bär *et al.* (2018), it is possible that the high temperature of the heated water bath caused formation of small bubbles due to decreases in gas solubility with increases in temperature. In addition, xylem cell walls moisture content could potentially increase and cause wood expansion and a decrease in wood density (Yue *et al.* 2024). Thus, it is more likely that in our study, small bubbles and/or wood expansion caused the stems to float and the near-zero nPLC was related to a temperature-based water viscosity artefact. Although further investigation is needed to confirm this hypothesis, this also highlights the importance of properly cooling down the branch/stem samples prior to measurements, regardless of the methodology used. Other explanations could also include heat effects on pit pore structure, dissolution of air embolism or variations introduced by doing conductivity measurements at different temperatures (Bär *et al.* 2019).

Vulnerability to embolism

Bär *et al.* (2018) found that heated water baths increased the vulnerability to embolism in two conifer species. It is

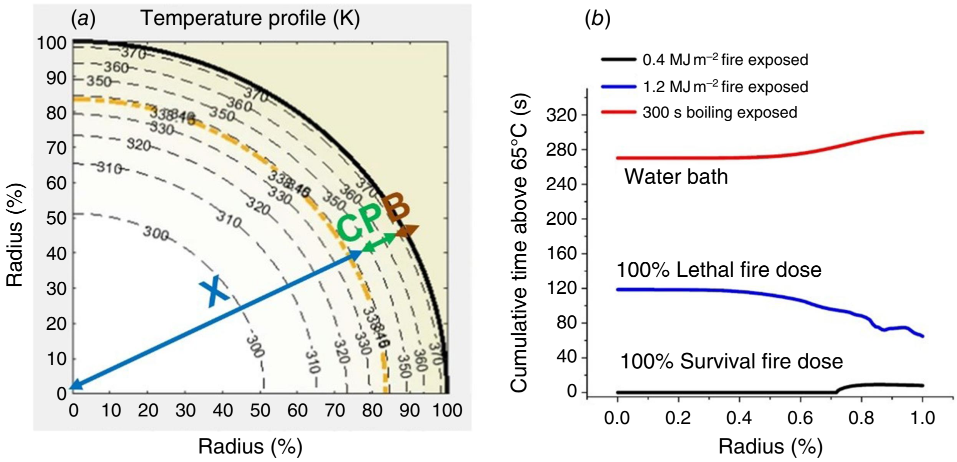

Fig. 5. (*a*) Heat penetration into a stem within a water bath at 232 s, where the yellow dashed line represents temperatures exceeding 338.15 K (65°C). B denotes the bark region, P the phloem, C the cambium and X the xylem. Contour lines denote time in seconds above 65°C. In the saplings in this study, all the xylem was functional. (*b*) Modeled cumulative time that temperatures exceeded 338.15 K (65°C) from 100% survival (fire radiative energy = 0.4 MJ m^{-2}) and 100% mortality (1.2 MJ m^{-2}) surface fires and from exposure to a water bath for 5 min. The water bath temperatures are those shown in Fig. 4d.

important to note that in our study, the heated water bath treatment was 55 min shorter than that in Bär *et al.* (2018). Thus, it is possible that a longer exposure might have affected the vulnerability of *Pinus ponderosa* in our study, especially given that a 95°C water bath slightly increased its vulnerability (Table 2, Fig. 2*a*). However, a 1-h long immersion in a 90°C heated water bath would represent a significant quantity of heat entering the stem that is unrealistically higher than heat transfer associated with a lethal fire behavior condition (Fig. 5*b*, Supplementary Video S1). Moreover, while Bär *et al.* (2018) observed increased vulnerability in two conifer species in heated water baths, only *Pinus sylvestris* reportedly exhibited greater vulnerability when exposed to a forest fire when assessed over a year after the fire. Importantly, Bär *et al.* (2018) only assessed living branches. In contrast, neither species in our study was affected by fire. However, if the saplings survived it is likely that some negative fire effects could be observed, like that observed in other studies that measured vulnerability after at least a year after fire exposure (Bär *et al.* 2018; Partelli-Feltrin *et al.* 2021). The different results in our study combined with the results from previous studies that also used heated water baths and forest fires highlights that heated water bath experiments may overestimate a tree's vulnerability to embolism depending on the species and time of exposure, emphasizing the need for caution when interpreting and applying these results as post-fire responses.

Xylem deformation and structural changes

Xylem deformation observed in heated water bath studies is often used to provide support for the mechanism of xylem hydraulic failure. Our study showed that although a 5-min heated water bath treatment at either 65 and 95°C substantially amplifies the amount of heat transferred through the bark to the xylem as compared to lethal fire conditions (Fig. 5*b*, Supplementary Videos S1 and S2), no noticeable deformation in the xylem cells occurs (Fig. 3). This contrasts with previous heated water bath studies (Michaletz *et al.* 2012; Bär *et al.* 2018). Specifically, Bär *et al.* (2018) reported that heat affected cells surfaces exhibited a 'rough and grainy appearance' and that heat-induced ruptures would be apparent along the inside edges of the cells. However, prior studies using 5-min duration water baths reported no deformation in the fire-adapted *Eucalyptus cladocalyx* F. Muell while deformation was apparent in the non-fire adapted species *Kiggelaria africana* (West *et al.* 2016). The same study found no xylem deformation was observed in *Kiggelaria africana* when exposed to convection oven heating at 70 and 100°C. (West *et al.* 2016). In contrast, 60-min duration water baths resulted in xylem deformation in *Picea abies* (L.) H. Karst, *Fagus sylvatica* L., and *Pinus sylvestris* L. (Bär *et al.* 2018). It was suggested that xylem deformation was the cause of the increase in vulnerability to embolism in these species, but contrary to statements in past commentaries (e.g. O'Brien *et al.* 2018), no evidence of xylem deformation was provided for the branches exposed to forest fires.

Partelli-Feltrin *et al.* (2021) observed nonfunctional xylem in *Pinus ponderosa* saplings after 21-months post-fire and reported an increase in vulnerability to embolism. However, due to lack of evidence of xylem cell wall deformation in *Pinus ponderosa* saplings exposed to fire, a potential mechanism of wound response where resin would clog the tracheids was proposed (Partelli-Feltrin *et al.* 2021). The same wound response was also proposed by a study that used a thin-film resistive heater to apply heat to the stem of *Symplocos tinctoria* saplings (Hoffmann *et al.* 2024), and although they also did not observe any xylem deformation, there was a gradual change in hydraulic conductivity, which was also suggested to be caused by a wound response. These and other studies that used heated water baths and other sources of heat such as convection oven (West *et al.* 2016), illustrate that heated water baths can cause cell wall damage, even when not apparent during forest fire conditions (Bär *et al.* 2018).

It is apparent that the changes in the hydraulic vulnerability curves that were observed in the heated water bath experiments in the current study (Fig. 2*a*, *b*), combined with no changes in xylem deformation, are consistent with results presented by Hoffmann *et al.* (2024). As such, it's possible that the direct and localized heating of these methods are each causing unrealistically high levels of heat to be transferred into the xylem, yielding these potential xylem differences and hydraulic impacts. In a study with a similar result, Zhang *et al.* (2025) sampled five burned trees several months after a wildfire, and while they observed no impacts of xylem deformation, they did observe impacts to the leaf hydraulic conductivity in cut branches, which again may be indicative of a delayed wound response. However, a challenge with interpreting Zhang *et al.* (2025), is that the reported values of (Leaf hydraulic conductance) K_{leaf} and leaf capacitance (which is used in the calculation of K_{leaf} in the method used) are an order of magnitude greater than previously published values from other conifer species, which raises questions about the methods used. Furthermore, the meteorological conditions are not reported, and it's unclear if the selected burned trees were dead or recovering, leading to uncertainty given drought, water stress conditions and delayed wound responses could lead to the same outcomes.

It is important to point out that during fires, trees can lose moisture content unlike samples immersed in a water bath, potentially impacting the glass transition temperature of xylem cell wall polymers (Goring 1965). For instance, the heated water bath could have facilitated the softening of xylem cell walls by preventing the loss of stem moisture content, considering that higher wood moisture content can decrease the glass transition temperature of cell wall components such as lignin, hemicellulose and cellulose (Back and Salmén 1982; Orsa *et al.* 1997); lignin (Börcsök and Pásztory 2021). In addition, some of the prior studies applied pressure during the water bath treatments (Michaletz *et al.* 2012; Lodge *et al.* 2018) which could also increase the chance of cell wall damage. However, it is important to note other studies (West *et al.* 2016; Bär *et al.* 2018) did not describe applying pressure in the stem during the water bath treatment and found evidence of xylem deformation. Thus, it is significant that the heated water bath duration (5 min) in our experiment was insufficient to cause physical damage to the xylem cell walls in *Pinus ponderosa* and *Pinus monticola*. This is especially noteworthy given the higher conductivity associated with the less fire-resistant *Pinus monticola* and that the level of heat exposure was significantly greater than that which would be expected within lethal fire conditions associated with these saplings (Fig. 5*b*). Clearly, any plant material placed under sufficient immersion durations in near-boiling water would likely lead to significant cell wall deformation (e.g. Shomer 1995), where 15 min of immersion in boiling water is sufficient to gelatinize starch in plant tissues (Pucher and Vickery 1936), but this is not reflective of the damage that real wildland fires cause.

Even if heat from actual fires could be shown to deform xylem tissue, such heat would already have had a devastating effect on phloem and cambial tissue (Hoffmann *et al.* 2024). This was experimentally demonstrated by Salladay and Pittermann (2023), who observed that significantly higher heat doses are required to cause xylem dysfunction than is necessary to cause cambium death. Moreover, for fire to induce tree mortality via hydraulic failure, drought studies have demonstrated that >60–80% of xylem hydraulic conductivity must be occluded by embolisms before tree death occurs (Adams *et al.* 2017; Hammond *et al.* 2019). If such extensive embolism were to result solely from heat transferred into the stem, it would likely be accompanied by heat-induced girdling of the tree. Given this, Hoffmann *et al.* (2024) questioned the importance of xylem-based tree mortality mechanisms given tree mortality would already have occurred due to cambium death.

Limitations of water bath experiments

It is possible that multiple aspects of past experimental heated water bath methods may have inadvertently produced experimental artefacts, including immersion in heated water or methods to prepare the samples for dissection and analysis. We are not stating that any of the prior studies caused such artefacts but rather include these explanations as points of discussion on how potential artefacts may arise. We also acknowledge that other factors may also contribute.

Preparing samples for light microscopy may contribute to a xylem deformation artefact in heat treated samples, and differences in the applied sectioning methods may lead to unintended deformation artefacts (e.g. if dull blades are used – see Supplementary Fig. S1). In terms of other sample preparation artefact sources; defoliating, trimming and partial removal of bark at the end of the stems to prevent leaks during conductivity measurement prior to water bath treatments could partially, or even entirely, destroy the phloem and cambium layers in areas where bark is removed, likely allowing direct heat stress on the xylem cells during heated water bath treatments. Even if the bark is only removed from a small part of the stem, there is potential for rapid mass transfer of hot water into the xylem, especially given the diffusion constant of water is dependent on the temperature (Holz *et al.* 2000). This could cause rapid and direct heating of water in the xylem, contributing to embolisms and cell-wall ruptures that are not reflective of real fire conditions.

However, the principal advantage of heated water baths is that specialized equipment is not needed, there is not restrictions due to access or safety and extreme heat transfer conditions can be assessed.

Limitations of laboratory fire experiments

Although fire laboratory experiments use real flames and thus represent the heat transfer modes, temporal dynamics, maximum temperatures and radiative energy associated with surface fires in a wide range of fire regimes (Smith *et al.* 2017, Fig. 1*a*), several limitations exist that are described in detail in Smith *et al.* (2025). Most notably, indoor fire laboratory experiments are limited in inferences associated with meteorological, microclimatic and edaphic conditions. Although not the focus of the current study, many laboratory combustion experiments have, however, assessed combustion of coarse woody debris (e.g. Hyde *et al.* 2012; Brewer *et al.* 2013; Tinkham *et al.* 2016), smoldering and extended exposure to sub-surface soils (e.g. Brady *et al.* 2022). A limitation with laboratory combustion experiments is that they are limited to assessing younger trees (i.e. seedlings and saplings) and assessing plants grown in pots that may not readily transfer to plants grown under natural conditions or in larger trees (Smith *et al.* 2025).

However, the principal advantage of experimental laboratory fires is that they enable an assessment of the physics of heat transfer and the physiological impacts through a series of repeatable and traceable treatments that can be compared to coincident unburned controls (Smith *et al.* 2016). A further advantage is that the 'dose-response' methodology used in these controlled combustion laboratory experiments can provide improved understanding of the mechanisms of fire impacts on tree physiology and the impacts of other stressor interactions (heat, droughts, disease, etc.) with fires, enabling improvement to process models that can, in turn, be used to assess fire impacts on older trees (O'Brien *et al.* 2018).

Heat transfer differences in heated water baths and fire experiments

Heated water baths do not exhibit similar heat transfer dynamics analogous to what is experienced during fires (Drysdale 2011) and several differences exist between these two experimental approaches that make cross-comparisons difficult, and these differences may account for inconsistencies in prior studies. For example, although Bär *et al.* (2018) found that heated water baths increased vulnerability to embolism in *Picea abies*, branches exposed to a forest fire were not affected. Also, although heated water baths were used to assess the effects of heat on cambial cells during fires (Dickinson and Johnson 2004; Dickinson *et al.* 2004; Achchige *et al.* 2021), these cells are not normally directly exposed to fire and therefore it's unlikely such methods would directly translate to plants impacted by fires. When considering examples of heat applied to external plant tissues, a major difference between heated water baths and fire experiments is that in a heated water bath, the heat is applied isotopically to the entire stem segment by convection (conduction within the segment), while during fires heat is transferred to the stem, branches and leaves through convection, radiation and conduction (Smith *et al.* 2025). Also, in wildland fires, the heat flux on living trees is inherently uneven due to the occurrence of air entrainment, occlusion due to branches and other plants, topography, variations in fuel loading, etc.

In terms of heat transfer differences, in heated water baths the heat is transferred through a very high thermal conductivity fluid (water (liquid) at 90°C: 0.673 W m^{-1} K^{-1}), while in wildland fires, the heat is transferred through a comparatively lower thermal conductivity fluid (air at 800°C: 0.051 W m^{-1} K^{-1}). Heat incident on live vegetation during surface fires are characterized by high temperature pulses (~750°C) over short durations (seconds), while heated water baths are characterized by a more uniform heating for set durations (minutes to hours). Also, cut branches and stems immersed in water will retain moisture and given the thermal softening of wood increases with higher moisture content (Chow and Pickles 1971; Back and Salmén 1982), this could result in a greater likelihood of cell wall damage in heated water baths compared to fires.

Living stems versus cut stems and branches

An important difference between experimental laboratory or field fires and heated water bath experiments is that experimental fires expose intact and whole living plants to fire, while only segments of stems are exposed to heat treatments in the water bath. Living plants that experience fire-induced heating may be better equipped to withstand heat than cut samples in heated water. For instance, cut stems and branches cannot transport water that could be used for cooling during fire (e.g. sap flow, transpiration). Different studies have reported that heated branches take up more water than before exposure to heat (Cohen *et al.* 1987, 1990; Hoffmann *et al.* 2024). For instance, studies with detached branches of conifers exposed to 225°C (Cohen *et al.* 1987) and an angiosperm species exposed to fire (Hoffmann *et al.* 2024), found that water uptake was ~50 times and ~22 times higher, respectively, than before the branches were exposed to heat treatments. Another study using a conifer species found that intact branches exposed to 250°C absorbed almost 50% more energy than detached branches, and they concluded that if energy absorbed was proportional to the amount of water vaporized, the intact branches were associated with a greater uptake of water than the detached branches (Cohen *et al.* 1990). In addition, if the air vapor pressure increases during fire, it is expected to have a higher transpiration rate and consequently higher water uptake (Kavanagh *et al.* 2010). Although this may be harmful for plants under drought-stress, for the well-watered plants in our experiment, the increase in transpiration rate could potentially cool down the stems and foliage causing less damage to these tissues. Although the water bath did not cause xylem cell wall damage in our experiment, the increase in water uptake could explain why deformation was observed in some studies using heated water baths, but not when other sources of heat were used, such as convective ovens and resistive heating plates (West *et al.* 2016; Hoffmann *et al.* 2024).

Although studies using heated water baths were not specifically designed to assess post-fire recovery, it is important to emphasize that using intact plants provides a more appropriate approach for evaluating post-fire effects on water transport and the potential for assessing delayed wound responses (Hoffmann *et al.* 2024). For instance, cut branches cannot make use of the hydraulic redundancy within tree hydraulic networks (Tyree and Ewers 1991; McCulloh *et al.* 2011; Johnson *et al.* 2016; Mrad *et al.* 2021). The main trunks and stems in live trees have many alternative flow paths to get around wounds and emboli, while small branches have substantially less and depending on the species, may not have other paths available (Johnson *et al.* 2016, 2022). Furthermore, living trees also have access to post-fire compensatory responses (e.g. root pressure or living tissues providing ions in the transpiration stream) that allow trees to survive at the organismal level (Trifilò *et al.* 2011). A further cause of a difference between the fire acting on live stems and cut branches is that in most wildland fires, the most intense heating of tree boles only occurs on the leeward sides (Michaletz and Johnson 2007), thus limiting the extent of potential xylem injury to a proportion of the tree circumference as compared to the heated water baths that expose the entire circumference of the cut stem or branch to elevated heat.

Implications for future research

The physiological differences between live main stems subjected to turbulent flames versus cut stems and detached branches immersed in heated water baths can potentially be attributed to heat transfer dynamics. The use of heated water baths fundamentally limits the potential mechanisms of fire-induced tree mortality and physiological impacts that can be tested to xylem-based changes due to the rapid destruction of the phloem and cambium preceding immersion. Future research is warranted to conduct a similar comparison between fire experiments and other fire behavior proxies. Notably, the resistive heating plate approach of Hoffmann *et al.* (2024), the use of propane torches and radiative heaters all deserve further investigation. The identification of a valid fire dynamics proxy methodology would greatly assist plant physiologists seeking to further understand fire impacts on a wide array of species.

In terms of the modeling, future research could explore more refined heat transfer models and consider improvements to existing stem heating models. We again acknowledge that the FDM model is a numerical approximation of Eqn 2 but was used as a first approximation to illustrate the differences between real fires and heated water baths. Finite element models (FEM) exist that include water phase change, charring, radiant heat flux exchange, swelling of the bark and desiccation (Chatziefstratiou *et al.* 2013; Butler and Dickinson 2010). As described in detail by Chatziefstratiou *et al.* (2013), FireSTEM2D is an open-source software tool that utilizes an FEM approach to simulate heat transfer within trees during fire conditions. This model allows for estimating the degree of water loss, pyrolysis loss and thermal profiling in multi-dimensional space and includes many published thermal properties for different tree species. Although FireStem2D is widely recognized as a robust stem heating fire-induced tree mortality prediction model (Wei *et al.* 2019), its main limitation is that it does not incorporate vertical fluid transport processes within the tree, producing overestimates in internal stem temperatures (Wei *et al.* 2019). Future research could explore the use of sap flow sensors to increase understanding of how it changes due to fire. Given many sap flow sensors rely on assessing the sap velocity between two heated prongs inserted into the tree, they are generally not used during active fire conditions, which is a challenge that needs to be overcome.

Although the development of the next generation of fire-effects process models like QUIC-FIRE-Effects has the potential to increase understanding of fire-induced tree mortality (Linn *et al.* 2020), the development of new methods to incorporate various cooling mechanisms would improve realism in these models. New methods to assess how internal vertical fluid transport processes within a tree change dynamically alongside methods to assess water content within the bark, degree of air entrainment interacting on the stem, bark air spaces and density, thermal conductivity of sap, and sap heat capacity would enable an improved incorporation of potential cooling mechanisms.

Conclusions

We assessed whether heated water baths and experimental laboratory fires cause xylem cell wall deformation and increased xylem vulnerability to embolism. We observed that the experimental laboratory fires did not increase vulnerability to embolism nor did heat induce damage to xylem cell walls. Although heated water baths at both temperatures did not cause deformation of the xylem cell walls, heated water baths increase the vulnerability in *Pinus monticola* with a noticeable but not significant effect in *Pinus ponderosa*.

The study provided support for concerns over using heated water baths as a fire dynamics proxy to assess xylem dysfunction (e.g. Varner *et al.* 2021; Nolan *et al.* 2024; Smith *et al.* 2025). As a result, more research is warranted to improve our understanding of how, and to what degree, fire causes damage to trees hydraulic systems (Nolan *et al.* 2024). The results of Hoffmann *et al.* (2024) who used a resistive plate fire dynamics proxy approach applied to sapling stems, also raised tangential lines of inquiry regarding the potential role of hydraulics in driving delayed mortality mechanisms following fires, especially in some conifers such as *Pseudotsuga menziesii* that are known to exhibit delayed fire-induced mortality occurring over years (Ember and Varner 2012). As described in Smith *et al.* (2025), several other areas warrant more attention in furthering our understanding of fire-induced mortality mechanisms.

Given the results of this study, we caution the interpretation of results from heated water baths to make conclusions about how plant hydraulics respond to wildland fires. The current study discussed differences associated with four specific cases (i.e. two laboratory fire conditions and two heat water bath conditions). Although the videos in supplemental tables (Supplementary Videos S1 and S2) do illustrate the heat transferred into the stem over a temporal period of seconds to 60 min, we do acknowledge that other factors such as the impacts on different tissues or locations within an actual wildland fire may lead to different results, limiting the ability to generalize these findings. In conclusion, similar cross-comparisons between other fire dynamics proxies (e.g. propane torches) experimental laboratory and wildland fires should also be evaluated

Supplementary material

Supplementary material is available online.

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Data availability. The following additional data are available via supplementary tables and files. Supplementary Table S1: mean RCD, height and predawn leaf water potential. Supplementary Fig. S1: example xylem deformation artefacts that can occur in conifers due to mistakes in sample preparation methods. Supplementary Video S1: finite difference modeling of heat penetrating into a sapling stem within a heated water bath for up to 1 h immersion. Supplementary Video S2: finite difference modeling of heat penetrating into a sapling stem within a lethal fire.

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