

Moving beyond the cambium necrosis hypothesis of post-fire tree mortality: cavitation and deformation of xylem in forest fires

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Summary

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- It is widely assumed that post-fire tree mortality results from necrosis of phloem and vascular cambium in stems, despite strong evidence that reduced xylem conductivity also plays an important role.
- In this study, experiments with *Populus balsamifera* were used to demonstrate two mechanisms by which heat reduces the hydraulic conductivity of xylem: air seed cavitation and conduit wall deformation. Heat effects on air seed cavitation were quantified using air injection experiments that isolate potential temperature-dependent changes in sap surface tension and pit membrane pore diameters. Heat effects on conduit wall structure were demonstrated using air conductivity measurements and light microscopy.
- Heating increased vulnerability to cavitation because sap surface tension varies inversely with temperature. Heating did not affect cavitation via changes in pit membrane pore diameters, but did cause significant reductions in xylem air conductivity that were associated with deformation of conduit walls (probably resulting from thermal softening of viscoelastic cell wall polymers).
- Additional work is required to understand the relative roles of cavitation and deformation in the reduction of xylem conductivity, and how reduced xylem conductivity in roots, stems, and branches correlates and interacts with foliage and root necroses to cause tree mortality. Future research should also examine how heat necrosis of ray parenchyma cells affects refilling of embolisms that occur during and after the fire event.

Introduction

Tree mortality in forest fires results from an interaction of heat injuries to the roots, stem, and crown, but the processes by which these injuries occur and interact are poorly understood (Dickinson & Johnson, 2001; Michaletz & Johnson, 2007, 2008; Butler & Dickinson, 2010; Kavanagh *et al.*, 2010; Midgley *et al.*, 2010). Most research has focused on stem injury, and it has been well established that heat conduction through bark can cause necrosis of phloem and vascular cambium tissues at a temperature of *c.* 60°C (Dickinson & Johnson, 2004; Dickinson *et al.*, 2004; Bova & Dickinson, 2005; Jones *et al.*, 2006). Necrosis around the entire stem circumference prevents downward translocation of photosynthates, which eventually causes stem mortality via root starvation and desiccation (Kramer & Kozlowski, 1960; Nobel, 2005). For this reason, tree mortality is generally assumed to result from cambium necrosis, and this has become the standard mortality mechanism considered by models of post-fire tree mortality (Spalt & Reifsnyder, 1962; Reifsnyder *et al.*, 1967; Vines, 1968; Peterson & Ryan, 1986; Rego & Rigolot, 1990; Costa *et al.*, 1991; Ryan & Frandsen, 1991; van Mantgem & Schwartz, 2003; Dickinson & Johnson, 2004; Dickinson *et al.*,

2004; Jones *et al.*, 2004, 2006; Bova & Dickinson, 2005; Michaletz & Johnson, 2007, 2008).

However, evidence suggests that reduced xylem conductivity is another important mechanism of post-fire tree mortality. For example, stem heating has been shown to reduce sap flux density (Ducrey *et al.*, 1996) and functional xylem (sapwood) area (Smith & Sutherland, 1999, 2001; Ryan, 2000; Schoonenberg *et al.*, 2003; Balfour & Midgley, 2006), both of which imply a concomitant reduction in xylem conductivity. Crown mortality has also been strongly correlated with fire scar size (Rundel, 1973), which is consistent with crown dieback resulting from sapwood area reduction (Tyree *et al.*, 1994; Rood *et al.*, 2000; Sperry *et al.*, 2002). And finally, stem heating has caused mortality within weeks (Ducrey *et al.*, 1996), but trees with phloem and cambium necrosis around their entire circumference should survive for a longer period until stored carbon reserves are depleted and fine-root production ceases (in some cases trees have survived for decades; Kramer & Kozlowski, 1960; Noel, 1970; Tyree & Zimmermann, 2002; Nobel, 2005). Although it is clear that fires can cause mortality by reducing xylem conductivity (even in the absence of crown injury), the mechanisms by which this occurs have not yet been

demonstrated (Ducrey *et al.*, 1996; Balfour & Midgley, 2006; Midgley *et al.*, 2010).

Cavitation is one mechanism by which heat can reduce xylem conductivity. According to the cohesion–tension theory (Dixon & Joly, 1894), transpiration induces surface tension forces at the evaporative surfaces in the leaf (parastomata and mesophyll surfaces) that are transmitted via cohesion and tension forces (hydrogen bonding) through a continuous water column, so that water is effectively pulled up from the soil, into the roots, and through the xylem (Tyree & Zimmermann, 2002; Nobel, 2005). This requires tensile sap water, which is metastable and subject to cavitation (Oertli, 1971; Pickard, 1981). When cavitation occurs, air comes out of solution to fill the cavity and embolize the xylem conduit (Tyree & Zimmermann, 2002). Because embolized conduits cannot conduct water, embolism reduces the cross-sectional area and (by definition) hydraulic conductivity of the sapwood.

Xylem cavitation generally occurs by air seeding, which is the aspiration of air into a water-filled conduit (Cochard *et al.*, 1992; Sperry & Saliendra, 1994; Tyree & Zimmermann, 2002). The cavitation pressure P_{cav} is the pressure difference required to displace an air–water meniscus from a pit membrane pore, which is determined by the capillary force of the meniscus according to (Oertli, 1971; Pickard, 1981; Tyree & Zimmermann, 2002):

$$P_{\text{cav}} = \frac{4\sigma \cos(\theta)}{D_{\text{pore}}} \quad \text{Eqn 1}$$

σ , the air–water surface tension; θ , the contact angle between the meniscus and wall; D_{pore} , the pit membrane pore diameter. Cavitation occurs when the pressure difference across the air–water interface ($P_{\text{air}} - P_{\text{sap}}$) exceeds the cavitation pressure

$$P_{\text{air}} - P_{\text{sap}} > P_{\text{cav}} \quad \text{Eqn 2}$$

P_{air} , the air pressure; P_{sap} , the sap water pressure. There is some evidence that cavitation occurs by this same air seed mechanism for both angiosperms and gymnosperms, despite their major differences in pit membrane structure (effective pore size in gymnosperms appears to be determined by sealing of the torus and pit wall aperture; Tyree & Zimmermann, 2002; Cochard *et al.*, 2009; Delzon *et al.*, 2010). Eqn 2 suggests that heating by fire could enhance cavitation by increasing the air pressure P_{air} or decreasing the cavitation pressure P_{cav} (Eqn 2). Heat effects on air pressure are not considered here because preliminary calculations using the ideal gas law suggested these would have relatively minor effects on cavitation. Heat effects on cavitation pressure are considered via changes in both the air–water surface tension σ and the pit membrane pore diameter D_{pore} (Eqn 1). The air–water surface tension is inversely proportional to temperature and decreases *c.* 22% between 0 and 100°C (Vargaftik *et al.*, 1983), so heating by fire should cause a corresponding reduction in cavitation pressure and make the xylem more vulnerable to cavitation. Pit membrane pore diameters might also be affected by heat as a result of thermal softening of lignin, hemicellulose, and cellulose polymers in conduit walls (Hillis & Rozsa, 1985; Lewin & Goldstein, 1991). These polymers are viscoelastic and

exhibit properties of both elastic solids and viscous fluids (Wolcott *et al.*, 1990; Riande *et al.*, 2000); at low temperatures they are hard and glassy, and at high temperatures they are soft and gel-like. The transition between these states is a temperature-dependent kinetic process characterized by the glass transition temperature. Thermal softening of lignin is probably the most relevant for trees in forest fires, as the glass transition of *in situ* lignin occurs between 60 and 90°C (variation reflects glass transition kinetics as well as differences in measurement technique; Irvine, 1984; Salmén, 1984; Kelley *et al.*, 1987). Softening of lignin permits movement of cellulose microfibrils in the conduit walls (Hillis & Rozsa, 1985), so forces acting on pit membranes may affect pore diameters by displacing and/or rupturing the pit membrane (including the torus–margo membrane in gymnosperms); another possibility is that softened lignin might flow from the cell walls into the pit membrane, reducing pore diameters. It should be noted that pit membranes themselves do not contain lignin as they derive from the primary cell wall (Sperry & Tyree, 1988; Tyree & Zimmermann, 2002; Sperry & Hacke, 2004).

Conduit deformation is another mechanism by which heat can reduce xylem conductivity. In transpiring trees, sap tension causes corresponding stresses in xylem conduit walls (Innes, 1995; Hunter, 2001; Alméras & Gril, 2007) that could cause wall deformation upon thermal softening of viscoelastic cell wall constituents (Wolcott *et al.*, 1990). Deformation could reduce conduit diameters or cause conduit rupture or collapse (Hacke *et al.*, 2001; Cochard *et al.*, 2004; Sperry & Hacke, 2004; Brodribb & Holbrook, 2005). Any of these possibilities would reduce the hydraulic conductivity of the xylem, and the changes would become permanent once the xylem cools and the viscoelastic polymers return to a glassy state.

In this study, we demonstrated heat effects on air seed cavitation and conduit wall deformation using experiments with *Populus balsamifera*. *Populus balsamifera* is an appropriate model species because it has relatively low cavitation pressures (Tyree *et al.*, 1994) and is not subject to complications associated with torus–margo aspiration and resinosis (Sperry & Tyree, 1990; Mayr *et al.*, 2007). Heat effects on air seed cavitation were shown using the single-ended air injection method, which causes cavitation by increasing air pressure relative to sap pressure (Eqn 2). As correlated changes in surface tension and pit membrane pore diameters would confound results, experiments were designed to test each of these in isolation. To test for surface tension effects, branch segments were perfused with an ethanol–water mixture having a surface tension equal to that of water at 95°C; this temperature is a suitable upper bound for these experiments because surface tension varies continuously with temperature, and water vaporization prevents stem temperatures from rising above the saturation temperature (100°C at sea level) until the water is evaporated. To test for pore diameter effects (via thermal softening of lignin), pressurized branch segments were exposed to 65 or 95°C heat treatments, cooled, and perfused with water to rewet pit membranes and refill pit pores; these temperatures were chosen to span the range within which the glass transition of *in situ* lignin is thought to occur (Irvine, 1984; Salmén, 1984; Kelley *et al.*, 1987). Heat effects on conduit wall deformation were shown

using air conductivity measurements and light microscopy to compare unheated controls with branches subjected to 65 or 95°C heat treatments.

Materials and Methods

Plant material

Experiments were conducted using *Populus balsamifera* L. branches collected in the Bow River valley in Calgary, Alberta, Canada (51°03'41"N 114°09'23"W). Branches were trimmed to 60 cm, defoliated, and transported in plastic bags to the laboratory where they were submerged in deionized water and stored at 3–5°C until experimentation (within 5 d). Maximum vessel length was measured using low-pressure air perfusion (Zimmermann & Jeje, 1981). Before measurement, branches were flushed with pressurized (0.14 MPa) water filtered to 0.2 µm (PN 12112; Pall Corporation, Port Washington, New York, USA) to rewet all pit membranes and refill pit pores. Branches were flushed with approximately four times their volume of water. The proximal end of each branch was then shaved with a fresh razor blade, fitted to Tygon tubing (Saint-Gobain Performance Plastics, Paris, France), and 0.14 MPa of air pressure was applied. The distal end of each branch was submerged in water and slowly trimmed in 1-cm increments until air bubbles could first be seen to emerge. The maximum vessel length measured was 37 cm ($N = 20$), which is consistent with previously reported values for *P. balsamifera* (33–36 cm; Hacke & Sauter, 1995). Branch segments 40 cm long (longer than the longest vessel) were used for all experiments.

Heat effects on air seed cavitation

Cavitation pressure was measured using the well-established single-ended air injection method (Crombie *et al.*, 1985; Sperry & Tyree, 1988, 1990; Sperry *et al.*, 1988, 1991, 1996; Cochard *et al.*, 1992; Jarbeau *et al.*, 1995). This method causes cavitation via the air seed mechanism described in Eqns 1 and 2. It should be noted that the air seed mechanism works in the same way here as it does for water-stressed trees in the field, except that here cavitation pressure P_{cav} is achieved by increasing air pressure (P_{air}) instead of sap tension ($-P_{\text{sap}}$; Eqn 2). Results are plotted as air permeability curves (Sperry & Tyree, 1988; Sperry *et al.*, 1988), which show the cumulative proportion of conduits having a particular cavitation pressure (defined by the largest pore) as relative air conductivity $L_a/L_{a,\text{max}}$.

Air conductivity L_a ($\text{m}^4 \text{s}^{-1} \text{MPa}^{-1}$) is calculated according to (Siau, 1984):

$$L_a = Q_a \left(\frac{Pl}{\Delta P \bar{P}} \right)^n \quad \text{Eqn 3}$$

Q_a , the mass flow rate of water (kg s^{-1}); l , the branch length (m); P , the pressure at which Q_a was measured (MPa); ΔP , the pressure difference (applied air pressure; MPa); $\bar{P}$, the stem mid-point pressure ($\bar{P} = (P + \Delta P)/2$; MPa). Note that Eqn 3 is an empirical scaling relationship and is not dimensionally

homogeneous. The scaling exponent n is obtained empirically and characterizes the flow regime as laminar when $n = 1$, turbulent when $n = 0.57$, or nonlinear when $n = 0.5$. Scaling exponents n were estimated for $N = 7$ branches. Branches were first air-dried at 45°C to a constant mass so that all conduits could conduct air regardless of the pressure difference (i.e. flow not restricted by air–water interfaces; Sperry & Tyree, 1988). Air flow through the pith was diverted by a radial drill hole into the pith; a second hole distal to the first was filled with epoxy to prevent pith flow out of the distal end of the branch. To estimate scaling exponents n , Eqn 3 was rearranged to give

$$Q_a = L_a \left(\frac{\Delta P \bar{P}}{Pl} \right)^n \quad \text{Eqn 4}$$

Eqn 4 was $\log_{10}$ -transformed and rearranged to give the linear form

$$\log(Q_a) = \log(L_a) + n \log \left(\frac{\Delta P \bar{P}}{Pl} \right) \quad \text{Eqn 5}$$

where the slope n and y -intercept $\log(L_a)$ were obtained by ordinary least squares (OLS) linear regression. Linear regression is more appropriate than reduced/standardized major axis estimation in situations where fitted parameters are to be used in a predictive manner (Warton *et al.*, 2006). To test for a common slope among branches, an F -statistic compared sums of squares when a common slope was fitted with sums of squares when each branch was fitted with a unique slope (Sokal & Rohlf, 1995). Regression analyses were performed using SMATR (Falster *et al.*, 2006; Warton *et al.*, 2006). Supporting Information Fig. S1 shows the relationship between the mass flow rate of water displaced by air and the applied air pressure gradient for $N = 7$ branches (OLS linear regression; for each branch $r^2 \geq 0.996$). Differences in elevation (y -intercepts) reflect differences in the cross-sectional area (i.e. air conductivity) of sapwood. Slopes n of individual branches are significantly heterogeneous ($F_{(6,77)} = 47.110$, $P = 0.001$), so a mean ($\pm$ SEM) scaling exponent of $\bar{n} = 0.706 \pm 0.016$ was used to characterize flow in air conductivity calculations (Eqn 3).

To measure air conductivity using the single-ended air injection method, branch segments were trimmed at both ends with a fresh razor blade and the proximal ends inserted *c.* 3 cm into a pressure chamber. Distal ends were connected via Tygon tubing to a 5000-ml Erlenmeyer flask filled with water. The flask contained a bottom hose outlet that was connected via water-filled tubing to a Sartorius CP2202S digital balance (Sartorius AG, Goettingen, Germany). In this way, the mass flow rate of water displaced by air could be logged using a desktop PC. Air conductivity L_a was measured according to Eqn 3 for ΔP in 0.35-MPa increments between 0 and 4.48 MPa. During these experiments, air was not observed passing through the pith or bark.

To isolate surface tension and pore diameter effects on air seed cavitation (Eqn 1), four treatments were compared.

Control ($N = 5$) Cavitation pressures measured for this 'initial' treatment provide the baseline air permeability curve to which all

other treatments are compared. Branches were flushed with water as already described to rewet pit membranes and refill pit pores. Air injection experiments were conducted at 20°C. Water surface tension ($72.55 \pm 0.007 \text{ mN m}^{-1}$; mean $\pm$ SEM) was measured at 20°C using a Krüss K12 tensiometer (A. Krüss Optronic GmbH, Hamburg, Germany) using the Wilhelmy plate method. After measurement, these same branches were reflushed with water (branches now called 'reflushed') and the air injection experiments repeated ($N = 5$). Comparison of permeability curves for 'initial' and 'reflushed' branches demonstrated whether the air injection method altered pit membrane pore diameters, and whether flushing treatments were sufficient to rewet pit membranes (note that the presence of some air/water mix in conduits would not in theory alter the air pressure needed to displace pit pore water, assuming that the pit membranes are undamaged).

3.75% (w/w) ethanol perfusion ($N = 8$) This treatment demonstrates the temperature dependence of water surface tension in the absence of potential heat effects on pit membrane pore diameters. Branches were perfused with pressurized (0.14 MPa) 3.75% (w/w) ethanol (mixture based on Vázquez *et al.*, 1995), which has approximately the same surface tension as water at 95°C (59.87 mN m^{-1} ; Vargaftik *et al.*, 1983); branches were perfused with approximately four times their volume of the mixture. Surface tensions of prepared mixtures ($59.84 \pm 0.002 \text{ mN m}^{-1}$ (mean $\pm$ SEM)) were measured as described above for control branches. Air injection experiments were conducted at 20°C. At 20°C, 3.75% (w/w) ethanol has a 0.75% lower density and 0.05% higher viscosity than pure water (based on the simple rule of mixtures; Speight, 2005; Lide, 2006); such minor differences are not expected to affect n . To confirm that observed effects were a result of surface tension alone and not ethanol-induced changes to pit membrane pore diameters, branches were reflushed with water (branches now called 'reflushed') and air injection experiments repeated ($N = 5$).

65°C heat treatment ($N = 6$) This treatment tests for heat effects on pit membrane pore diameters in the absence of temperature-dependent changes in water surface tension. A temperature of 65°C was used for these experiments because it bounds the lower end of the range in which the glass transition of *in situ* lignin is thought to occur (Irvine, 1984; Salmén, 1984; Kelley *et al.*, 1987); in addition, sapwood heating simulations forced by cambium temperature data from experimental fires suggest that sapwood can attain this temperature (Fig. S3). Branch segments of *c.* 55 cm in length were trimmed and shaved as described in the 'Plant material' section. The proximal end of each branch was inserted *c.* 3 cm into a pressure chamber and 1.72 MPa of pressurized air was applied; thus, the force induced by the air pressure on the pit membranes was similar in magnitude but opposite in direction to the force exerted by the sap in *Populus* on a typical summer afternoon (Tyree *et al.*, 1994). The distal 40 cm of the branch was then submerged into a 65°C water bath for 5 min followed by an ice water bath for 5 min; during this time, the branch was continuously pressurized so that forces acting to deform conduit walls persisted through the cooling phase just as

they are expected to do following a forest fire. Note that here we are interested in simply reducing sapwood temperatures below the glass transition temperature of lignin (between 60 and 90°C; Irvine, 1984; Salmén, 1984; Kelley *et al.*, 1987), and cooling by ice water or ambient air will produce the same results provided the branch is pressurized throughout the cooling phase. The distal 40 cm of the branch was then removed and both ends trimmed with a fresh razor blade. Branches were flushed as described in the 'Plant material' section and air injection experiments were conducted at 20°C.

95°C heat treatment ($N = 12$) Similar to the 65°C treatment above, this treatment tests for heat effects on pit membrane pore diameters in the absence of temperature-dependent changes in water surface tension. A temperature of 95°C is a suitable upper bound for these experiments as water vaporization prevents stem temperatures from rising above the saturation temperature (100°C at sea level) until all water is evaporated. Aside from the temperature difference of the heat treatment, branch sample preparation and measurement were conducted as described above for the 65°C heat treatment.

Heat effects on conduit wall structure

To quantify heat treatment effects on branch conductivity, air conductivity curves were plotted using the same data from control and 95°C heat treatments. These curves are not intended to show changes in cavitation pressure among treatments, but instead heat treatment effects on air conductivity. Air conductivity is a proxy for hydraulic conductivity because the same geometric factors govern the flow of air and water through xylem (Siau, 1984; Tyree & Zimmermann, 2002).

To visualize heat treatment effects on xylem conduit structure, control and heat treatment branches used in air conductivity experiments were hand-sectioned and stained with toluidine blue O (Yeung, 1998). Sections were examined using a Leitz Aristoplan photomicroscope (Ernst Leitz Wetzlar GmbH, Wetzlar, West Germany). Images were captured using a Leica DFC490 digital camera (Leica Microsystems GmbH, Wetzlar, Germany) and processed using Adobe Photoshop CS5. Captured images were not randomly chosen from the entire section but were instead chosen to demonstrate the maximum degree of observed deformation.

Results

Air permeability curves for initial and reflushed control branches are shown in Fig. 1(a). The initial control curve shows that, for water at 20°C, relative air conductivity increases approximately linearly with applied air pressures $> 1.38 \text{ MPa}$. When these control branches were reflushed to rewet pit membranes and refill pit pores, the curve was not different from the initial curve (i.e. the 95% confidence intervals overlap), showing that the air injection method did not alter pit membrane pore diameters, and that the 0.14-MPa water flushing technique was sufficient to rewet pit membranes. Note that, for the air injection method used in this

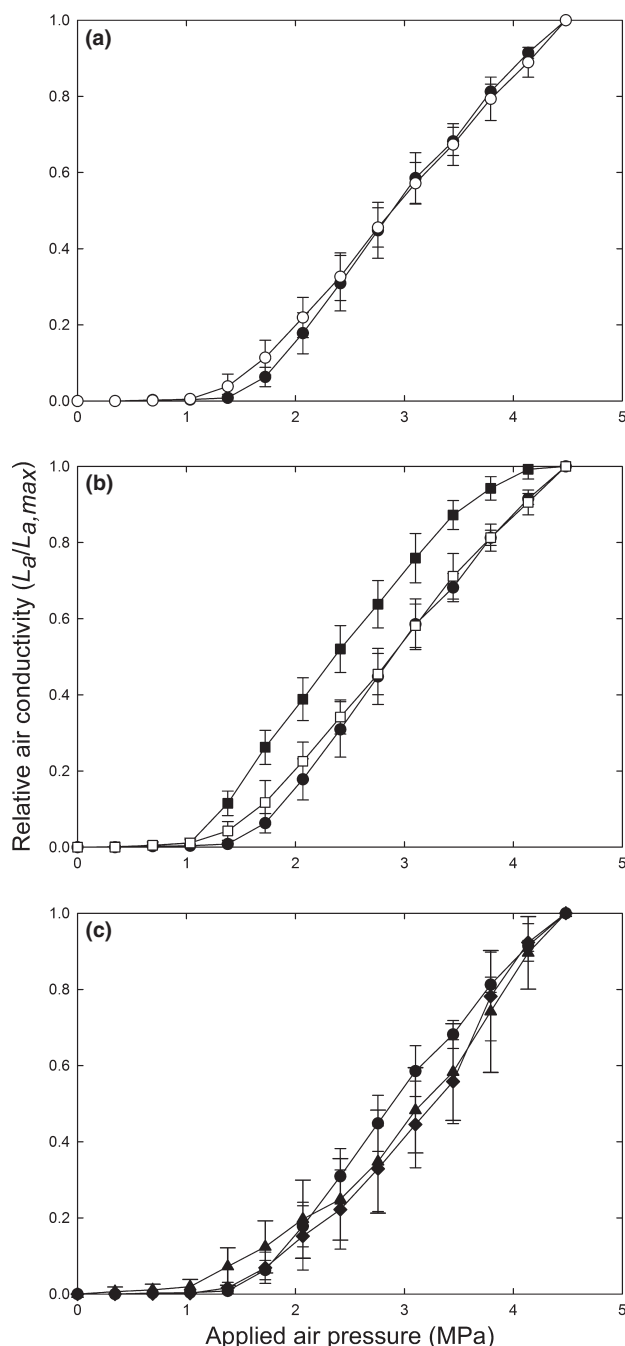


Fig. 1 Air permeability curves for *Populus balsamifera* showing the cumulative distribution of conduits having a given cavitation pressure (P_{cav} , where applied air pressure $\Delta P = P_{cav}$). Curves are means ($N \geq 5$) and error bars are 95% confidence limits. (a) Initial (closed circles) and reflushed (open circles) control branches; (b) initial control branches (closed circles), and initial (closed squares) and reflushed (open squares) 3.75% (w/w) ethanol branches; (c) initial control branches (circles), 65°C heat treatment branches (diamonds), and 95°C heat treatment branches (triangles). All air permeability curves were measured at 20°C.

study, it is not necessary to remove all air bubbles from conduit lumina because air seed cavitation is controlled by capillary forces and pressure differences across pore menisci (Eqns 1, 2).

Reducing the air–water surface tension via perfusion with 3.75% (w/w) ethanol significantly increased relative air

conductivity as compared with controls (Fig. 1b); for each applied pressure between 1 and 4.48 MPa, 11–21% more conduits were cavitated in ethanol-perfused branches than in controls. When these branches were rinsed and refushed with water, the curve was not different from the control curve, showing that differences between the 3.75% ethanol and control curves were attributable to surface tension effects alone, and not alteration of pit membrane pore diameters by the ethanol.

The 65 and 95°C heat treatments did not significantly change relative air conductivity as compared with controls (Fig. 1c), although the 95°C treatment exhibited a marginal increase in the proportion of conduits with a cavitation pressure < 2.07 MPa, and both heat treatments exhibited a marginal decrease in the proportion of conduits with a cavitation pressure > 2.07 MPa. Heated branches exhibited more residual variation in relative air conductivity (Fig. 1c) and significantly lower air conductivity than controls (Fig. 2). Note that the reduced air conductivity in Fig. 2 would also be accompanied by reductions in hydraulic conductivity, because the flows of air and water through xylem are governed by the same geometric factors (Siau, 1984; Tyree & Zimmermann, 2002). These results suggest that thermal softening of *in situ* lignin probably occurred at or below 65°C, allowing for deformation of conduit walls and a concomitant reduction in xylem conductivity.

Conduit wall deformation was observed qualitatively in branches from both the 65 and 95°C heat treatments (Fig. 3). In control branches, conduit walls were relatively straight and well defined, but in branches from both heat treatments, conduit walls were deformed and degraded. Deformation was especially apparent in the internal walls of grouped conduits, which have lower thickness-to-span ratios and are more rupture-prone than solitary conduits (Hacke *et al.*, 2001). Deformation was more apparent in the 95°C heat treatment than in the 65°C heat treatment (Fig. 3), although both heat treatments had an equal reduction in air conductivity (Fig. 2). The degree of deformation was not constant within the sapwood of individual branches and appeared to

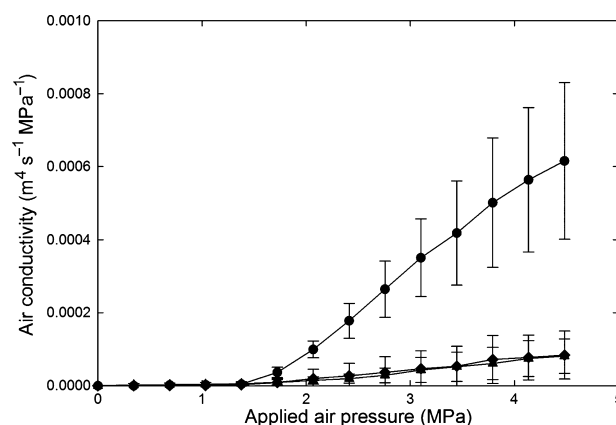


Fig. 2 Air conductivity (L_a) plotted against applied air pressure (ΔP) for control (circles, $N = 5$), 65°C (diamonds, $N = 6$) and 95°C (triangles, $N = 12$) heat treatment branches of *Populus balsamifera*. Curves are means and error bars are 95% confidence limits. The 65 and 95°C heat treatments significantly reduced air conductivity as compared with controls. Air conductivity was measured at 20°C.

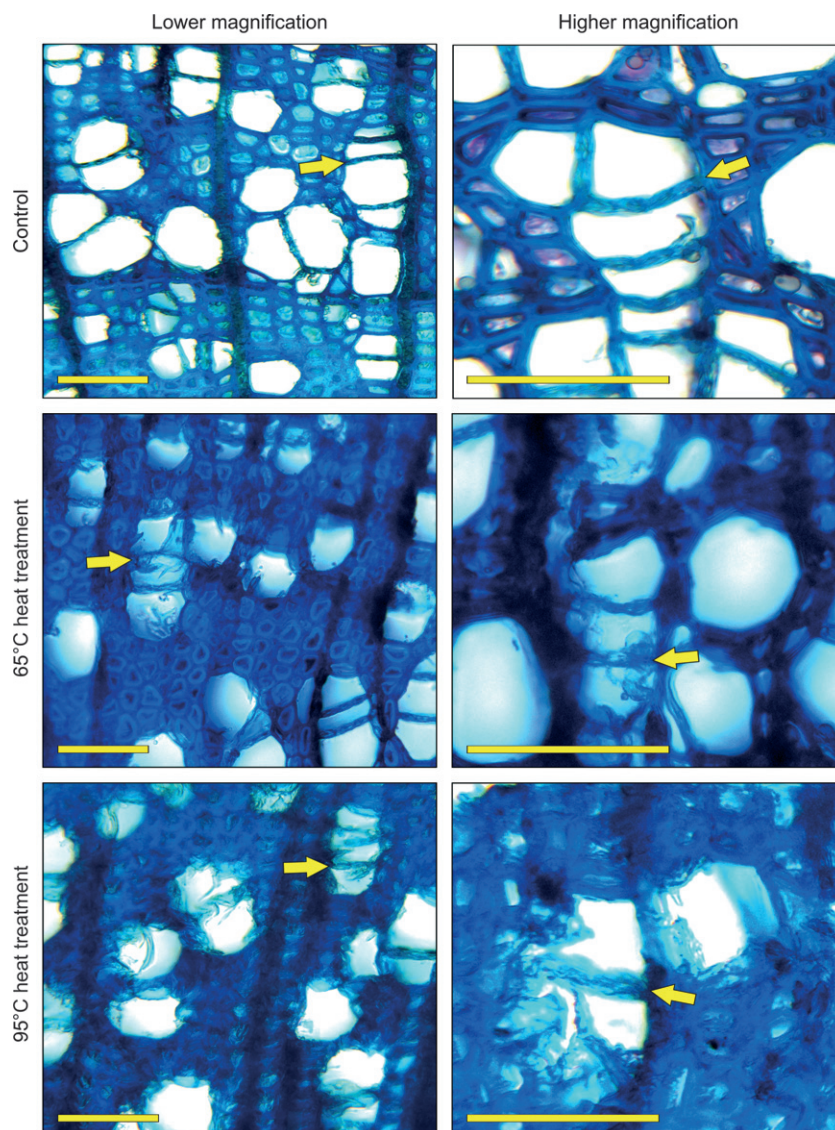


Fig. 3 Xylem conduit structure in control, 65°C heat treatment, and 95°C heat treatment branches of *Populus balsamifera*. Cross-sections were stained with toluidine blue O and are oriented with the cambium to the top and the mature xylem to the bottom. The left column is a lower magnification view showing the spatial extent of conduit wall deformation; the right column is a higher magnification view showing details of conduit wall deformation. Photographs in the same column (i.e. control, 65°C heat treatment, and 95°C heat treatment) are not before-and-after photographs of the same branch, but are instead comparisons between similar geometries from different branches. Arrows indicate conduit wall structures typically observed in each treatment. Bars, 50 μ m.

increase with radial distance from the branch center. It is unclear whether the residual variation in Fig. 1(c) results from changes to pit membrane pore diameters, or other effects of thermal softening such as slippage and/or compression of the branch in the pressure chamber. It is clear, however, that heating caused significant reductions in xylem conductivity (Fig. 2), and that this was associated with visible deformation of conduit walls (Fig. 3), probably a result of thermal softening of lignin.

Discussion

The experiments reported here show that heating reduces xylem conductivity via at least two mechanisms: cavitation resulting from temperature-dependent changes in sap surface tension (Fig. 1b), and conduit wall deformation resulting from thermal softening of viscoelastic cell wall polymers (Figs 2, 3).

Reducing sap surface tension to that of water at 95°C (i.e. the 3.75% ethanol perfusion) caused a $14.97 \pm 2.14\%$ (mean $\pm$ SEM) increase in the number of embolized conduits (relative air

conductivity) for applied pressures above 1.03 MPa (Fig. 1b). These results were expected from Eqn 1 and the inverse relationship between temperature and air–water surface tension, which decreases *c.* 18% between 20 and 95°C (Vargaftik *et al.*, 1983). Assuming changes in surface tension correspond to an equal per cent increase in the number of embolized conduits, calculations suggest that more modest temperature increases of 60 and 70°C would cause 8.9 and 11.4% increases in embolized conduits, respectively. Cavitation caused by temperatures above 60°C would be particularly harmful, because these temperatures would cause necrosis of living ray parenchyma cells thought to assist in conduit refilling (Dickinson & Johnson, 2004; Clearwater & Goldstein, 2005). In such cases, heat-induced cavitation would probably result in permanent disruption of xylem flow.

Similar increases in cavitation have been observed in other studies where surface tension was manipulated by heating between 1 and 50°C (Cochard *et al.*, 2007) or by perfusion with surfactants having surface tensions much lower than that of water

at 95°C (Crombie *et al.*, 1985; Sperry & Tyree, 1988; Sperry *et al.*, 1988; Cochard *et al.*, 2009). However, the surface tension ranges considered by these studies are either much smaller or much larger than would be expected for trees heated by fire, because water vaporization limits stem temperatures to the saturation temperature (100°C at sea level) until the water is evaporated; consequently, results of these studies do not clearly quantify how heating by fire is expected to alter vulnerability to cavitation. The surface tensions used in our experiments were chosen to bound the range possible for xylem sap in a fire, and these results demonstrate that forest fires can significantly increase vulnerability to cavitation.

Heating caused thermal softening of viscoelastic polymers in the conduit walls, which deformed in response to stresses induced by air injection (Fig. 3). Although this increased the residual variation around permeability curve means, it did not change pit membrane pore diameters enough to significantly alter vulnerability to cavitation (Fig. 1c). This is not surprising given that pit membranes are nonlignified (Sperry & Tyree, 1988; Tyree & Zimmermann, 2002; Sperry & Hacke, 2004). Heating did, however, significantly reduce air conductivity (Fig. 2), and during the experiments we also observed radial air flow from the xylem out through the bark. Thus, it appears that thermal softening of stressed conduit wall polymers causes a catastrophic breakdown of conduit structure. In our experiments, xylem lumens were pressurized so that forces acting on conduit walls were opposite in direction but equal in magnitude to those induced by the transpirational tension of sap. For transpiring trees, thermal softening could allow conduit walls to deform in response to sap tension, reducing conduit diameter or allowing conduit rupture or collapse (Hacke *et al.*, 2001; Cochard *et al.*, 2004; Sperry & Hacke, 2004; Brodribb & Holbrook, 2005); these changes would become permanent once the xylem cools and the viscoelastic polymers become glassy. Further work is required to understand the glass transition kinetics of *in situ* lignin, hemicelluloses, and cellulose, and how these control conduit wall geometry in response to mechanical stresses induced by the sap tension of transpiring trees (e.g. Innes, 1995; Hunter, 2001; Alméras & Gril, 2007).

The temperature dependence of air seed cavitation and conduit wall deformation highlights the need to better understand how different fire behavior characteristics control radial temperature gradients in sapwood. We are not aware of any published data documenting sapwood temperatures in forest fires. However, cambium temperatures have been observed to approach and even exceed 100°C in surface fires (Fahnestock & Hare, 1964; Vines, 1968; Rego & Rigolot, 1990; Costa *et al.*, 1991) and in kerosene wick fires (Hare, 1965; Uhl & Kauffman, 1990; Hengst & Dawson, 1994; Pinard & Huffman, 1997); measurements of maximum cambium temperatures from 45 stem heating experiments are summarized in Table S1. In Notes S1, cambium temperature data measured in three forest fires (Fig. S2) are used to force simulations of sapwood heating. These simulations suggest that sapwood can attain temperatures capable of enhancing air seed cavitation and permitting conduit wall deformation (Figs 1–3, S3). Furthermore, as a consequence of the scaling of

area with thickness for an annulus (Notes S2, Figs S4, S5, Eqn S13), even seemingly small depths of cavitation or deformation can result in considerable reductions in cross-sectional sapwood area, particularly for small-diameter stems and branches (Notes S3, Fig. S6). It is important to note that the heat transport model used in Notes S1 is a simplification of the processes that occur when a real tree stem is heated in a forest fire. Importantly, the model does not consider the possibility of convection and/or advection in the xylem sap water. It is not known how these processes affect sapwood temperatures in forest fires, but it is possible that heated water could be replaced with unheated water so that sapwood temperatures would be lower than our simulations suggest. Thus, the simulation results in Notes S1 should not be interpreted as absolute proof that sapwood attains such temperatures in forest fires; instead, they should be interpreted as evidence that such temperatures are a possibility. It is hoped that the results encourage measurement of sapwood temperatures in forest fires as well as development of three-dimensional coupled heat transport and hydrodynamics models capable of characterizing the pertinent processes.

The possibility that heating by fire might somehow restrict xylem water transport has long been recognized (Rundel, 1973; Ducrey *et al.*, 1996; Ryan, 2000; Balfour & Midgley, 2006), but only now have two of the causal mechanisms been demonstrated. Reduced xylem conductivity creates a hydraulic bottleneck that can cause desiccation and death of distal parts of the tree (Tyree *et al.*, 1994; Rood *et al.*, 2000; Sperry *et al.*, 2002); consequently, heat effects on xylem conductivity should be considered in models of post-fire tree mortality (Spalt & Reifsnyder, 1962; Reifsnyder *et al.*, 1967; Vines, 1968; Peterson & Ryan, 1986; Rego & Rigolot, 1990; Costa *et al.*, 1991; Ryan & Frandsen, 1991; van Mantgem & Schwartz, 2003; Dickinson & Johnson, 2004; Dickinson *et al.*, 2004; Jones *et al.*, 2004, 2006; Bova & Dickinson, 2005; Michaletz & Johnson, 2007, 2008). This will necessitate an understanding of fire effects on hydraulics of roots, stems, and crowns, and how injuries in all of these areas interact within whole-tree water budgets. Our understanding of fire effects on roots is limited (Michaletz & Johnson, 2007), which may be acceptable as a first approximation because root heating is generally limited to cases where smoldering combustion of duff causes soil heating for extended periods of time (Hartford & Frandsen, 1992; Miyaniishi, 2001; Choczynska & Johnson, 2009). Our understanding of fire effects on tree crowns is growing (Van Wagner, 1973; Michaletz & Johnson, 2006a,b), but our understanding of the hydraulic implications of these is limited. Recently, however, Kavanagh *et al.* (2010) suggested that vapor pressure deficits (i.e. water potential gradient; analogous to $P_{\text{air}} - P_{\text{sap}}$ in our Eqn 2) in fire plumes may be sufficient to cause cavitation in tree crown foliage. Understanding how forest fire effects on roots, stems, and crowns correlate and interact within the whole-tree water budget remains an outstanding question that should motivate the next generation of process-based models of tree mortality in forest fires. This is particularly important because of the increasing need in forest management to understand how fire behavior can be controlled to produce desired effects.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Mass flow rate of water displaced by air (Q_a) plotted against air pressure gradient ($\Delta P \bar{P} / Pl$).

Fig. S2 Time series of cambium temperatures measured in three experimental forest fires.

Fig. S3 Maximum simulated sapwood temperatures in three surface fires.

Fig. S4 Sapwood thickness plotted against outside diameter for stems and branches of *Populus tremuloides* Michx.

Fig. S5 Sapwood area plotted against outside diameter for stems and branches of *Populus tremuloides* Michx.

Fig. S6 Simulated sapwood area reduction in three experimental forest fires.

Table S1 Maximum cambium temperatures measured in surface fires and kerosene wick fires

Notes S1 Simulated sapwood heating in three experimental forest fires.

Notes S2 Sapwood allometry.

Notes S3 Simulated sapwood area reduction in three experimental forest fires.

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