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LETTER

Xylem heating increases vulnerability to cavitation in longleaf pine

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Alexandra G Lodge^{1,3} , Matthew B Dickinson² and Kathleen L Kavanagh¹¹ Ecosystem Science and Management Department, Texas A&M University, College Station, TX 77843, United States of America² US Forest Service, Northern Research Station, Delaware, OH 43015, United States of America³ Author to whom any correspondence should be addressed.E-mail: lodge@tamu.eduKeywords: *Pinus palustris*, fire, vulnerability curve, cavitation, surface tension, roots

Abstract

Improved understanding of the physiological mechanisms of tree mortality following fires is important with the predicted increase in wildfires under climate change, as well as continued use of prescribed fire for forest management. Disruption of water transport in the xylem from exposure to the heat plume of a fire has been hypothesized as a mechanism of delayed tree mortality. This heat plume rapidly increases vapor pressure deficit in the canopy, increasing transpiration and tension on the xylem causing cavitation, thus reducing water transport and leading to eventual tree death. We aimed to increase understanding of the mechanisms behind such unintended mortality by determining whether branches and roots of longleaf pine are more vulnerable to cavitation when exposed to temperatures expected to occur during prescribed or wild fires. Additionally, we modeled expected branch cavitation under fire conditions based on measured cavitation vulnerability. We heated branch and root segments in a water bath to 41 °C and 54 °C and simulated the negative xylem water potentials experienced during exposure to a heat plume using a double-ended pressure chamber. When branches and roots were pressurized under elevated temperatures, xylem in both organs was more vulnerable to cavitation. In branches, as temperature was increased from 23 °C–54 °C, the pressure at which 50% conductivity was lost (P_{50}) increased from −3.55 MPa to −2.79 MPa, while in roots, P_{50} increased from −2.08 MPa to −1.36 MPa. When the P_{50} values measured under elevated temperatures were included in plume and hydraulic models, branches were predicted to experience conditions leading to 50% loss of conductivity up to two meters higher into the canopy than under ambient temperatures. Overall, these results suggest that heating of branches and roots during fires can increase vulnerability to xylem cavitation, potentially leading to hydraulic disruption and delayed tree mortality.

Introduction

Tree mortality following wild and prescribed fires is likely due to impacts of heat on roots, branches, stems, and foliage, but the mechanisms of mortality that are not associated with direct heating of plant parts are poorly understood (Michaletz and Johnson 2007, Butler and Dickinson 2010, Kavanagh *et al* 2010). A major mechanism for tree mortality is cambial necrosis due to direct exposure to high temperatures (Dickinson and Johnson 2004). However, recent research has suggested that disruption in water transport due to xylem cavitation may be an additional

mechanism (Kavanagh *et al* 2010, Michaletz *et al* 2012, West *et al* 2016). A tree canopy in the heat plume of a fire can experience very rapid changes in atmospheric vapor pressure deficits (VPD) up to approximately 14 kPa without experiencing temperatures high enough for cambial necrosis (Kavanagh *et al* 2010). This puts high tension on the water held in the xylem, which can lead to cavitation via air seeding (Sperry and Tyree 1988, Zimmermann 1983). Additionally, heating of water in xylem in branches or roots exposed to heat at temperatures below those which cause cambial necrosis could further increase vulnerability to cavitation by reducing surface

tension of the water (Vargaftik *et al* 1983, Michaletz *et al* 2012).

Previous work has examined xylem vulnerability to cavitation in branches exposed to temperatures $>60^{\circ}\text{C}$ which are high enough to cause conduit wall deformation (Michaletz *et al* 2012, West *et al* 2016, Bär *et al* 2017) and immediate tissue necrosis. Vulnerability has not been investigated for the lower branch temperatures that are reached above the height at which foliage reaches 60°C (scorch height; Van Wagner 1973) and that may lead to increased vulnerability to cavitation in transpiring branches. Michaletz *et al* (2012) heated *Populus balsamifera* branches in 65°C and 95°C water baths while under pressure (simulating xylem tension) and observed a significant reduction in conductivity accompanied by conduit wall deformation at both treatment temperatures. West *et al* (2016) observed 40%–80% reductions in conductance when *Eucalyptus cladocalyx* and *Kiggelaria africana* were exposed to 70°C and 100°C heat plumes. When they exposed the branches to water baths heated to the same temperature, they observed conduit deformation in one species at 100°C exposure. While these studies suggest increased vulnerability to cavitation at high temperatures, branch temperatures $>60^{\circ}\text{C}$ are expected to cause immediate necrosis of physiologically active plant tissues (Caldwell 1993, Dickinson and Johnson 2004). As such, it is not clear how relevant conduit wall deformation is to the process of tree injury and mortality in fires.

Less research has been done on the impacts of heat on root vulnerability to cavitation. Soil is generally thought to insulate roots from the heat from fires (Stephan *et al* 2010), but smoldering duff can lead to long fire residence times and heat transfer into the soil (Michaletz and Johnson 2007, Varner *et al* 2009). Due to differences in physiology—namely larger diameter conduits—roots are typically more vulnerable to cavitation than branches (Zimmermann 1983, Kavanagh *et al* 1999). In this manuscript, we investigate the impacts of temperatures from ambient to less than 60°C on xylem cavitation vulnerability in shoots and roots of a fire dependent tree species.

Longleaf pine (*Pinus palustris*) forests were once found across 90 million acres of the southeastern United States (USDA and NRCS 2011), but they now occupy less than 5% of their historic range (Klepzig *et al* 2014). Longleaf pine is a fire-dependent species—during its unique grass stage, a seedling looks like a clump of grass with long, densely packed needles that protect its bud from historically frequent low-intensity surface fires. However, longleaf pines are subject to being outcompeted by oaks and other hardwoods that overtop the small longleaf pine if fires are excluded (Chapman 1932). Therefore, prescribed fire is a common management tool in restoration of this important ecosystem (Klepzig *et al* 2014, Kirkman *et al* 2004, Dell *et al* 2017). However, managers sometimes observe unintended mortality of mature pines

in the months or years following a prescribed burn (Hood 2010). Our study aimed to increase understanding of the mechanisms behind such unintended mortality by determining whether branches and roots of longleaf pine are more vulnerable to cavitation when heated to temperatures that they could reasonably be expected to be exposed to in the canopy during low to moderate intensity surface fires or in the soil below smoldering duff, respectively, either in wild or prescribed fires. Based on laboratory measurements, we modeled expected branch cavitation under prescribed fire conditions based on measured cavitation vulnerability.

Methods

Branches were collected over multiple days between May 2016 and March 2017 from a natural forest in the Roy E Larsen Sandyland Sanctuary in Silsbee, Texas. They were collected early in the morning during or after recent rainfall to minimize likelihood of embolism related to diurnal or episodic water stress. Branches at least 1 m in length were cut using an extension pole pruner from longleaf pine trees over 25 cm in diameter at breast height. One branch was collected from forty trees. Five bolting ('rocket stage') longleaf pine saplings were excavated by hand on February 10 and March 13, 2017. Multiple root segments were excised from each sapling. Roots were collected from saplings instead of mature trees due to logistical limitations of excavation, necessity of ensuring sampled roots were from the target species, and limitations on root size to fit into the cavitation chamber. All samples were transported on ice, surrounded by wet paper towels, and stored at 4°C for up to ten days until processing.

All needles were removed from branches and one segment ~ 20 cm long and <14 mm in diameter was excised under water from each branch. Bark was removed from the ends of each segment and the segment was inserted into a double-ended pressure chamber (Cavitation Chamber; PMS Instrument Company, Albany, Oregon). A type K thermocouple was inserted inside the chamber, secured to the sample under the bark using parafilm, and attached to a handheld digital thermometer during treatments (HH200A, Omega, Norwalk, Connecticut). Lateral longleaf pine roots were processed similarly, with the adjustment that multiple samples were cut from each individual sapling. A one to two centimeter segment of each sample was excised under water and attached to Tygon tubing attached to a reservoir of 0.05% Safranin-O stain 1 m above the lab bench. Stained samples were visually inspected to ensure no pre-treatment embolisms were present.

Each sample (enclosed in the double-ended pressure chamber) was immersed in a water bath at one of three temperatures: ambient (23°C , $N=16$ branches and 12 roots), moderate (41°C , $N=11$ branches,

8 roots), and high (54 °C, $N=19$ branches and 18 roots). Unequal sample sizes were due to expansion of the experiment from only ambient and high temperature treatments to include an intermediate temperature treatment, and a limited number of samples. Four branch samples were discarded due to procedural failures (e.g. insufficient seal in the cavitation chamber). We recognize that the hot water bath treatment is not equivalent to the hot and dry conditions found in a fire plume, however we were interested in isolating the potential effects of heat alone on vulnerability to cavitation. Once the thermometer indicated that the sample had reached the target temperature, it was removed from the water bath and attached to a modified Sperry apparatus to measure the hydraulic conductance through the sample (Sperry *et al* 1988). Filtered (0.20 μm), degassed (MiniModule, Liqui-Cel, Charlotte, North Carolina), deionized water was contained in an IV bag 1 m above the lab bench. Water flowed from the IV bag, through the sample, and into a graduated cylinder on an analytic balance. Flow was recorded automatically by the balance at ten-second intervals and averaged across six consecutive readings. When this value stabilized, the initial flow rate (K_{max}) was recorded. The sample was then returned to the water bath, allowed to reach the prescribed temperature, and then pressurized using industrial nitrogen to either 0.5 or 1 MPa and held at that pressure for 5 min. The pressure was released and the sample was allowed to relax for at least 3 min, until outgassing ceased. The sample was then hooked back up to the Sperry apparatus and flow was measured. This process was repeated, with pressures increasing at 1 MPa intervals, until no flow was recorded. The pressure chamber utilizes the air injection method to induce cavitation by using positive pressure to simulate negative pressures experienced by xylem under tension (Sperry and Tyree 1988).

Percent loss of conductivity (PLC) was calculated based on,

$$\text{PLC} = (K_{\text{max}} - K)/K_{\text{max}} * 100. \quad (1)$$

Vulnerability curves were constructed using the *fit-plc* package in R (Duursma 2017, R Core Team 2016) separately for branches and roots at each of the three treatment temperatures using the Weibull function. P_{50} , or the pressure at which 50 percent of conductivity is lost was calculated using the *coef()* function. We used regression to examine the relationship between temperature and P_{50} for branches and roots. The expected changes in P_{50} based only on reductions in surface tension with increases in temperature were calculated based on the surface tension of water equation presented in Vargaftik *et al* (1983).

We applied parameters from the vulnerability curves to a plume model (Mercer and Weber 1994) and a hydraulic model (Bond and Kavanagh 1999) to assess if branches are likely to experience VPD sufficient

for xylem cavitation (Kavanagh *et al* 2010). Briefly, we determined the xylem water potential (Ψ_x) as,

$$\Psi_x = \Psi_{\text{soil}} - G_s D / K_L. \quad (2)$$

Where Ψ_{soil} is soil water potential (MPa), G_s is canopy stomatal conductance ($\text{mmol m}^{-2} \text{s}^{-1}$), D is the vapor pressure deficit between the leaf and the air (kPa) and K_L is leaf specific conductance ($\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$) (Kavanagh *et al* 2010). Soil water potential was set at -1.0 MPa to simulate drought conditions. Stomatal conductance was set at $24 \text{ mmol m}^{-2} \text{s}^{-1}$, approximately 30% of maximum for longleaf pine to reflect mid-day stomatal closure (Addington *et al* 2004). Leaf specific conductance was set at $1.2 \text{ mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$ (Addington *et al* 2004).

We examined the effect of branch heating on vulnerability to cavitation in the plume above a fire using a two-dimensional plume model (Mercer and Weber 1994) over a range of fireline intensities and ambient wind speeds as described in Kavanagh *et al* (2010). Gaussian time-series fit to plume centerline VPD, velocity, and temperature were used to determine branch exposures (see figure 1 in Kavanagh *et al* 2010). Branch heating was simulated with a numerical conduction model in cylindrical coordinates. Branch thermal properties (heat capacity, thermal conductivity, density) were taken to be similar to bark thermal properties and quantified using equations from Martin (1963). The boundary condition was either forced (during plume residence) or natural convection (after plume departure). Engineering correlations are from Incropera and DeWitt (2002) where natural convection is that for a long, horizontal cylinder (p 516) and forced convection is for a long cylinder generally (p 384). Forced convection was a function of plume velocity and temperature and needle or branch diameter at the height of interest. Natural convection was a function of needle or branch temperature and diameter. Maximum needle necrosis height was estimated using a lumped-capacitance conduction heat-transfer model, also with natural and forced convection as boundary conditions. Necrosis was predicted when modeled needle temperatures reached 60 °C. The dependence of P_{50} on branch temperature was assessed using the results of laboratory experiments reported below. The average sapwood temperature at the time of peak VPD and minimum xylem tension were used to assess vulnerability. Average sapwood temperature (from cambium to pith) was used to assess vulnerability for the thinnest and thickest longleaf pine branch in the sample. These two branch diameter classes provided a range of branch thicknesses for which to exercise the model.

Results

Under all three temperature conditions, longleaf pine roots were 50%–60% more vulnerable to cavitation

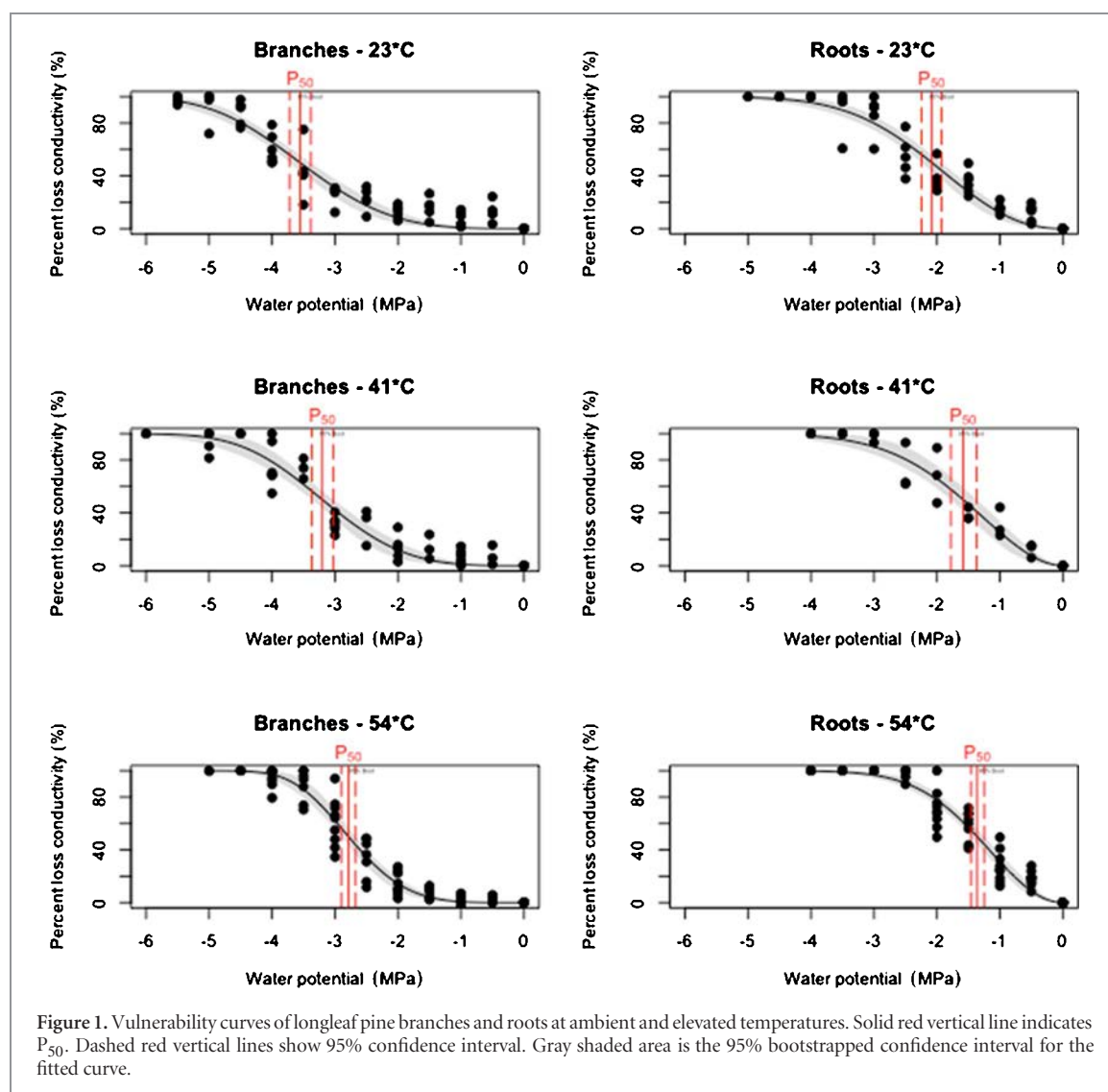


Table 1. P_{12} , P_{50} , P_{88} values for longleaf pine branches and roots at ambient and elevated temperatures. (MPa, mean $\pm$ standard error).

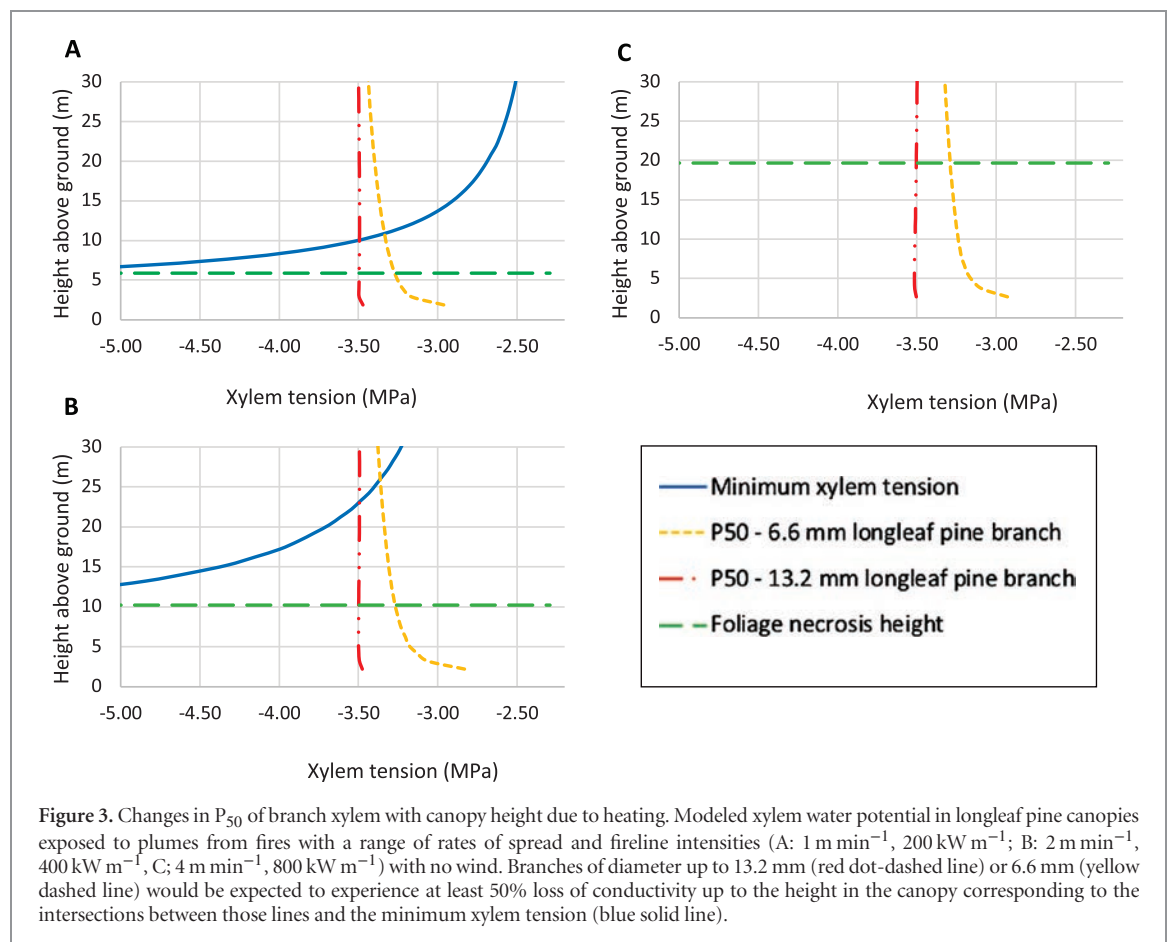
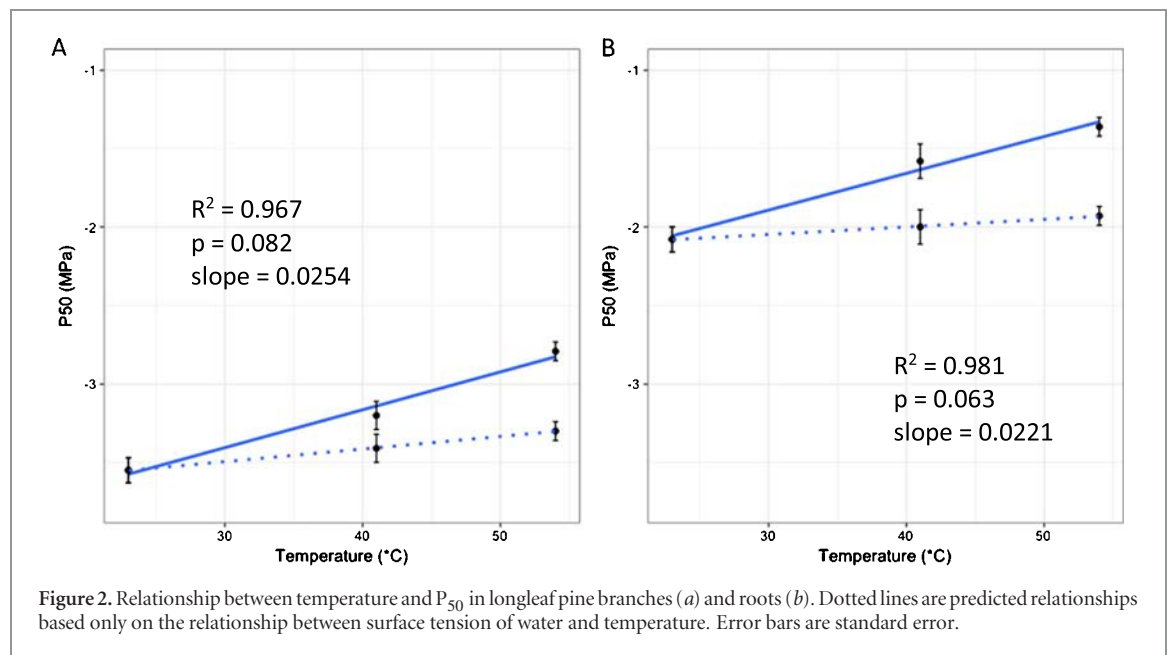
Branches				
Temperature:	23 °C	41 °C	54 °C	
P_{12}	$-2.23 (\pm 0.14)$	$-2.00 (\pm 0.15)$	$-1.92 (\pm 0.07)$	
P_{50}	$-3.55 (\pm 0.08)$	$-3.20 (\pm 0.09)$	$-2.79 (\pm 0.06)$	
P_{88}	$-4.83 (\pm 0.12)$	$-4.37 (\pm 0.19)$	$-3.57 (\pm 0.12)$	
Roots				
Temperature:	23 °C	42 °C	54 °C	
P_{12}	$-1.00 (\pm 0.08)$	$-0.65 (\pm 0.09)$	$-0.59 (\pm 0.06)$	
P_{50}	$-2.08 (\pm 0.08)$	$-1.58 (\pm 0.11)$	$-1.36 (\pm 0.06)$	
P_{88}	$-3.39 (\pm 0.14)$	$-2.87 (\pm 0.22)$	$-2.37 (\pm 0.09)$	

than branches. P_{50} of branches under ambient temperature was -3.55 MPa, while roots experienced 50% cavitation at -2.08 MPa (table 1).

When branches and roots were pressurized under elevated temperatures, xylem in both organs was more vulnerable to cavitation (figure 1). Temperature and P_{50} of branches and roots were positively correlated. In branches, as temperature was increased from 23°C – 54°C , the pressure at which 50% conductivity was lost increased from -3.55 MPa to -2.79 MPa

(figure 2(a); $p=0.082$, $R^2=0.967$). Across the same temperature range, root P_{50} increased from -2.08 MPa to -1.36 MPa (figure 2(b); $p=0.063$, $R^2=0.981$). The slope of the regression line for branches was significantly greater than the slope for roots ($F_{(2,4)}=317$, $p<0.05$). Branches were 22% more vulnerable to cavitation at 54°C than at 23°C , while roots were 34% more vulnerable at 54°C than at 23°C . However, the absolute change in P_{50} was similar for both organs— 0.77 MPa for branches and 0.72 MPa for roots. Based on a decrease in surface tension of water at elevated temperatures, we calculated a 4% and 7% increase in vulnerability to cavitation at 41°C and 54°C , respectively (dotted line, figure 2).

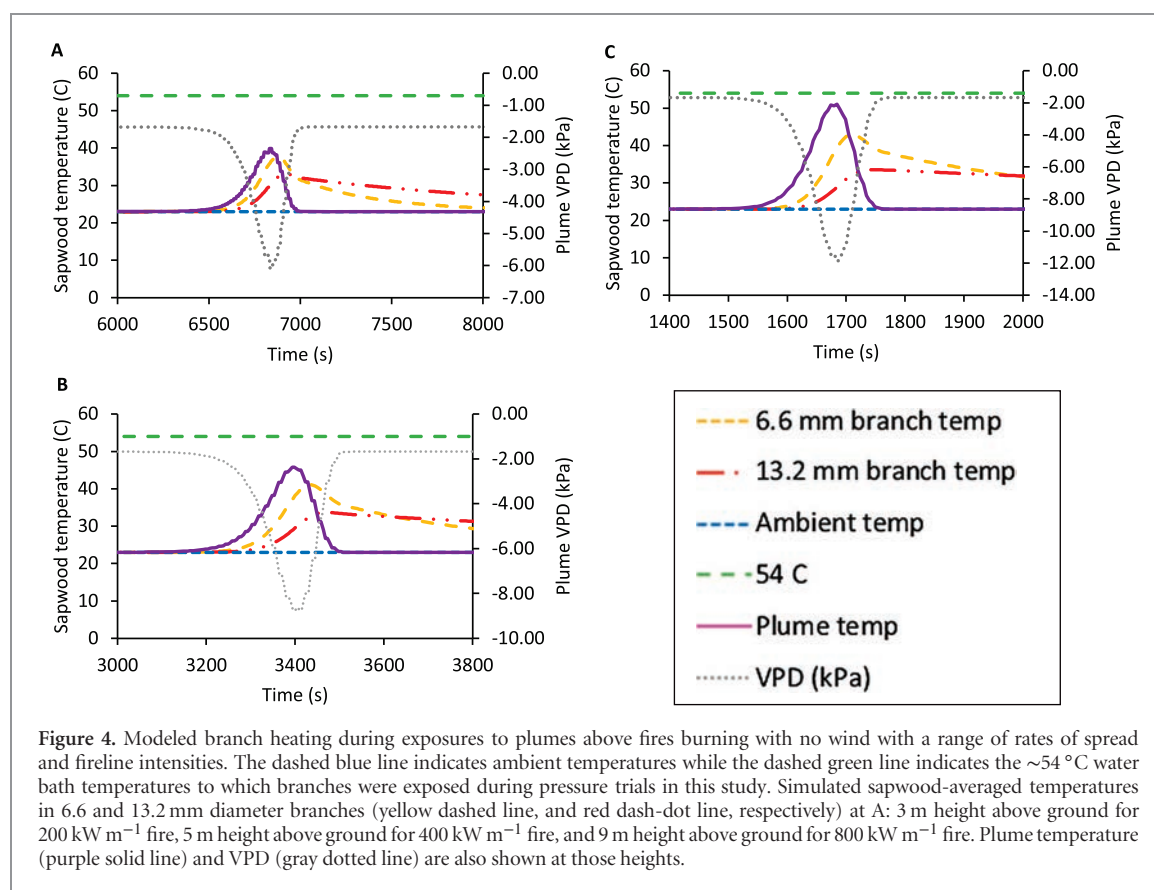
Sapwood vulnerability to cavitation in branches heated by plumes above surface fires was found to increase with fire intensity and as branch thickness decreased (figure 3). Plumes flow faster and plume gas temperatures are higher at a given height above more intense fires resulting in greater convective heat transfer into needles and branches. Based on average sapwood temperatures, the thinnest branches were most vulnerable to cavitation as seen from the



increasing height of the intersection of the curve describing xylem water tension and those of P_{50} for different branch diameters. Peak sapwood temperatures occurred after peak VPD (and corresponding minimum xylem tension), particularly for thick branches, which heat less quickly than thin branches (figure 4).

Discussion

A linear increase in vulnerability to cavitation with heating is consistent with hydraulic disruption being a causal agent of tree mortality following exposure to temperatures that are 6°C – 19°C below 60°C , where immediate cambial necrosis is expected to occur.



Given that the surface tension of water decreases with increasing temperature (Vargaftik *et al* 1983) and that surface tension contributes to xylem cavitation resistance, it was expected that vulnerability to cavitation in longleaf pine xylem would increase approximately 4%–7% under heated conditions. However, we observed a larger increase in cavitation vulnerability; up to 22% and 34% in heated stem and root xylem, respectively.

Based on our laboratory results and a plume and branch heating model, we expect that vulnerability to cavitation is increased by heating above surface fires, particularly for thinner branches whose sapwood heats most quickly. Vulnerability was assessed for sapwood-averaged temperatures, a conservative standard because the outermost sapwood heats more quickly than the inner sapwood as conduction proceeds during plume exposure. The lag in branch heating reduces vulnerability because, based on our Gaussian exposures, peak VPD and minimum xylem tension occur before peak sapwood temperatures are reached during plume exposure. All branches are at the ambient temperature before plume arrival and even the thickest branches show increased vulnerability to cavitation. Branch cavitation is expected up to 9 m above the height at which foliage necrosis would occur from heat alone, opening the possibility that branch cavitation will increase the fraction of tree canopies experiencing injury during surface fires above that indicated by ‘scorch’ heights alone. Scorch height is a commonly used indicator of the probability of tree mortality (Woolley *et al* 2012,

Hood *et al* 2007, Knapp *et al* 2013) and, while useful, may be a misleading indicator of tree vulnerability if it does not reflect the underlying mechanisms.

This study suggests that longleaf pine roots exposed to heat from a fire for a sufficient time to reach 54°C will experience 50% loss in hydraulic conductivity at water potentials as high as -1.36 MPa . We do not know of any studies where root temperatures have been monitored during a fire; however, the long-duration heating of mineral soil under smoldering duff can lead to substantial heating, reaching over 60°C for up to two minutes 20 cm deep in the mineral soil, and for almost an hour 5 cm deep in mineral soil (Hartford and Frandsen 1992, Varner *et al* 2009). In addition, roots do not have insulating bark that is as thick as that of stems (following Trockenbrodt 1995). As such, roots in close proximity to smoldering duff near the soil surface have the potential to reach temperatures sufficient to reduce the safety margin for cavitation. Although bark thickness at the stem base of large, old individuals of certain species is exceedingly thick and resistant to tissue injury from elevated temperatures during smoldering (Ryan and Frandsen 1991, Varner *et al* 2009), sub-lethal heating may increase vulnerability to cavitation even for these individuals. A localized reduction in hydraulic conductance at the root collar can lead to a reduction in function of all the roots distal to the embolism.

There is evidence that root xylem water potentials could approach or exceed -1.36 MPa during a fire. Predawn leaf water potentials (Ψ_{PD}) are a good

estimator of daily maximum root water potential since roots and soils are at equilibrium. Measurements of longleaf pine indicate the Ψ_{PD} typically hover around -0.5 MPa throughout the year (Addington *et al* 2004) and they can get as low as -0.9 MPa in dry conditions (Gonzalez-Benecke *et al* 2011). Midday stem water potentials (Ψ_{MD}) commonly reach -1.8 MPa as VPD increases during the daylight hours (Addington *et al* 2004). Even though roots have higher water potentials relative to stems, it would not take much of a water potential gradient to go from a predawn value of -0.9 MPa to -1.36 MPa at the onset of transpiration, especially during the drier summer months when fire is most likely to occur. One can imagine a scenario where a low-intensity surface fire causes minimal effects in the canopy but ignites duff accumulated after long fire-free periods and the trees continue to transpire as root systems are heated over hours as smoldering progresses (Ryan and Frandsen 1991, Varner *et al* 2009). Heating and cavitation of roots in this scenario could combine with reductions in fine root biomass and attendant stress where fine roots are concentrated in consumed duff (O'Brien *et al* 2010).

The combined plume and hydraulic conductance models demonstrated that VPD in fire plumes under operational prescribed fires could lead to cavitation in longleaf pine branches, even without xylem heating. However, the portion of the canopy that is at risk to damage increases as branches heat, extending an addition 2 m above the ground, based on our wide range of modeled plume exposures and branch heating. The exposure of stems with relatively thin bark could preferentially cause cavitation to be localized in distal branches during a fire, thus protecting the main bole. Researchers should also examine the possibility that massive cavitation in foliage prevents exposures of branches to high tensions during fires (Kavanagh *et al* 2010). Such an effect would provide a mechanistic explanation for 'crown scorch', a ubiquitous fire effect typically ascribed to elevated foliage temperatures during fires and resulting tissue necrosis (Van Wagner 1973, Dickinson and Johnson 2001).

As longleaf pines reach the overstory they typically shed their lower branches. He *et al* (2012) suggest that this trait evolved to create a gap in fuels to limit spread of surface fires into the crown; we hypothesize that this strategy of self-pruning could be an evolutionary strategy to limit the impacts of lower-branch cavitation or be caused by repeated fires and cavitation in lower branches limiting the ability of their buds to resprout. Our study demonstrates that loss of hydraulic conductance can occur in branches even at temperatures below that which would cause rapid necrosis of the cambium. We acknowledge that our 54°C laboratory exposures would likely have resulted in cambium necrosis given the length of time required for branches to reach water bath temperatures.

We observed an increase in xylem vulnerability to cavitation greater than would have been expected

based on temperature-dependent decreases in surface tension alone. In similar experiments, other researchers cite deformation of xylem conduits as a mechanism for loss of conductivity due to thermal softening of lignin and hemicellulose in xylem cell walls (Michaletz *et al* 2012, West *et al* 2016, Bär *et al* 2017), however these studies were all conducted at temperatures higher than 70°C . The 'glass transition' of lignin shifting from a solid to a liquid occurs typically around 90°C – 100°C , with hemicellulose softening at lower temperatures due to its chemical structure (Hillis and Rozsa 1985). Due to differences in chemical composition of the cell wall matrix, hardwoods soften at lower temperatures than softwoods (65°C – 77°C , 79°C – 83°C , respectively; Hillis and Rozsa 1985, Olsson and Salmen 1997). In the current study, water bath temperatures never exceeded 60°C , therefore softening and accompanying deformation of lignin and hemicellulose would not be expected to occur. Deformation of the torus or changes in pit margo membrane structure have also been hypothesized in other studies (Bär *et al* 2017), but these organs are made of cell wall material such as lignin and cellulose and therefore would also not be expected to soften or deform at such low temperatures.

Recent research has emerged on the role that phospholipids in xylem sap may play in reducing expansion of nanobubbles within xylem under tension, inhibiting or delaying cavitation (Schenk *et al* 2017, 2015). Amphiphilic proteins, glycoproteins, and phospholipids have been observed on xylem conduit walls and concentrated on inter-conduit pit membranes (Schenk *et al* 2017). Aggregates of these molecules surround nanobubbles, stabilizing the nanobubbles and preventing them from expanding and causing xylem cavitation (Schenk *et al* 2017). We hypothesize that heating may degrade some of these surfactants or disrupt their function (e.g. Rosenberg *et al* 1971), allowing for increased nanobubble expansion and therefore increased vulnerability to cavitation at less negative pressures.

Given the expected increase in droughts and fires in this region, as well as globally, an improved understanding of the physiological mechanisms leading to post-fire tree mortality is necessary for understanding ecosystem resilience (Mitchell *et al* 2014, Burkett *et al* 2014). Such expanded understanding of the mechanisms of mortality can be incorporated into improved biophysical process models predicting post-fire tree mortality (Michaletz and Johnson 2007, Butler and Dickinson 2010).

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ORCID iDs

Alexandra G Lodge  <https://orcid.org/0000-0002-0769-4821>

References

- Addington R N, Mitchell R J, Oren R and Donovan L A 2004 Stomatal sensitivity to vapor pressure deficit and its relationship to hydraulic conductance in *Pinus palustris* *Tree Physiol.* **24** 561–9
- Bär A, Nardini A and Mayr S 2017 Post-fire effects in xylem hydraulics of *Picea abies*, *Pinus sylvestris* and *Fagus sylvatica* *New Phytol.* **217** 1484–93
- Bond B J and Kavanagh K L 1999 Stomatal behavior of four woody species in relation to leaf-specific hydraulic conductance and threshold water potential *Tree Physiol.* **19** 503–10
- Burkett V R *et al* 2014 Point of departure *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* ed C B Field *et al* (Cambridge: Cambridge University Press) pp 169–94
- Butler B W and Dickinson M B 2010 Tree injury and mortality in fires: developing process-based models *Fire Ecol.* **6** 55–79
- Caldwell C R 1993 Estimation and analysis of cucumber (*Cucumis sativus* L.) leaf cellular heat sensitivity *Plant Physiol.* **101** 939–45
- Chapman H H 1932 Is the longleaf type a climax? *Ecology* **13** 328–34
- Dell J E, Richards L A, O'Brien J J, Loudermilk E L, Hudak A T, Pokswinski S M, Bright B C, Hiers J K, Williams B W and Dyer L A 2017 Overstory-derived surface fuels mediate plant species diversity in frequently burned longleaf pine forests *Ecosphere* **8** e01964
- Dickinson M B and Johnson E 2001 Fire effects on trees *Forest Fires: Behavior and Ecological Effects* ed E A Johnson and K Miyanishi (New York: Academic) pp 477–525
- Dickinson M B and Johnson E A 2004 Temperature-dependent rate models of vascular cambium cell mortality *Can. J. Forest Res.* **34** 546–59
- Duursma R 2017 fitplc: Fit Hydraulic Vulnerability Curves. R package version 1.1–3 (<https://CRAN.R-project.org/package=fitplc>)
- Gonzalez-Benecke C A, Martin T A and Cropper W P 2011 Whole-tree water relations of co-occurring mature *Pinus palustris* and *Pinus elliotii* var. *elliottii* *Can. J. Forest Res.* **41** 509–23
- Hartford R A and Frandsen W H 1992 When it's hot, it's hot... or maybe it's not! (Surface flaming may not portend extensive soil heating) *Int. J. Wildl. Fire* **2** 139–44
- He T, Pausas J G, Belcher C M, Schwilk D W and Lamont B B 2012 Fire-adapted traits of *Pinus* arose in the fiery cretaceous *New Phytol.* **194** 751–9
- Hillis W E and Rozsa A N 1985 High temperature and chemical effects on wood stability *Wood Sci. Technol.* **19** 57–66
- Hood S M 2010 Mitigating old tree mortality in long-unburned, fire-dependent forests: a synthesis *Gen. Tech. Rep. RMRS-GTR-238* (Fort Collins, CO: US Department of Agriculture, Forest Service, Rocky Mountain Research Station) p 71
- Hood S M, McHugh C W, Ryan K C, Reinhardt E and Smith S L 2007 Evaluation of a post-fire tree mortality model for western US conifers *Int. J. Wildl. Fire* **16** 679–89
- Incropera F and DeWitt D 2002 *Introduction to Heat Transfer* (New York: Wiley)
- Kavanagh K L, Bond B J, Aitken S N, Gartner B L and Knowe S 1999 Shoot and root vulnerability to xylem cavitation in four populations of Douglas-fir seedlings *Tree Physiol.* **19** 31–7
- Kavanagh K L, Dickinson M B and Bova A 2010 A way forward for fire-caused tree mortality prediction: modeling a physiological consequence of fire *Fire Ecol.* **6** 80–94
- Kirkman L K, Goebel P C, Palik B J and West L T 2004 Predicting plant species diversity in a longleaf pine landscape *Écoscience* **11** 80–93
- Klepzig K, Shelfer R and Choice Z 2014 Outlook for coastal plain forests: a subregional report from the southern forest futures project *Gen. Tech. Rep. SRS-GTR-196* (Asheville, NC: USDA-Forest Service, Southern Research Station) p 68
- Knapp E E, Skinner C N, North M P and Estes B L 2013 Long-term overstory and understory change following logging and fire exclusion in a Sierra Nevada mixed-conifer forest *Forest Ecol. Manage.* **310** 903–14
- Martin R 1963 Thermal properties of bark *Forest Prod. J.* **13** 419–26
- Mercer G and Weber R 1994 Plumes above line fires in a cross-wind *Int. J. Wildl. Fire* **4** 201
- Michaletz S T and Johnson E A 2007 How forest fires kill trees: a review of the fundamental biophysical processes *Scand. J. Forest Res.* **22** 500–15
- Michaletz S T, Johnson E A and Tyree M T 2012 Moving beyond the cambium necrosis hypothesis of post-fire tree mortality: cavitation and deformation of xylem in forest fires *New Phytol.* **194** 254–63
- Mitchell R J, Liu Y, O'Brien J J, Elliott K J, Starr G, Miniati C F and Hiers J K 2014 Future climate and fire interactions in the southeastern region of the United States *Forest Ecol. Manage.* **327** 316–26
- O'Brien J J, Hiers J K, Mitchell R J, Varner I I J M and Mordecai K 2010 Acute physiological stress and mortality following fire in a long-unburned longleaf pine ecosystem *Fire Ecol.* **6** 1–12
- Olsson A-M and Salmen L 1997 The effect of lignin composition on the viscoelastic properties of wood *Nord. Pulp Pap. Res. J.* **12** 140–4
- R Development Core Team 2016 *R: A Language and Environment for Statistical Computing* (Vienna: The R Foundation for Statistical Computing) (www.R-project.org)
- Rosenberg B, Kemeny G, Switzer R C and Hamilton T C 1971 Quantitative evidence for protein denaturation as the cause of thermal death *Nature* **232** 471–3
- Ryan K and Frandsen W 1991 Basal injury from smoldering fires in mature *Pinus ponderosa* Laws *Int. J. Wildl. Fire* **1** 107
- Schenk H J *et al* 2017 Xylem surfactants introduce a new element to the cohesion-tension theory *Plant Physiol.* **173** 1177–96
- Schenk H J, Steppe K and Jansen S 2015 Nanobubbles: a new paradigm for air-seeding in xylem *Trends Plant Sci.* **20** 199–205
- Sperry J S, Donnelly J R and Tyree M T 1988 A method for measuring hydraulic conductivity and embolism in xylem *Plant Cell Environ.* **11** 35–40
- Sperry J S and Tyree M T 1988 Mechanism of water stress-induced xylem embolism *Plant Physiol.* **88** 581–7
- Stephan K, Miller M and Dickinson M B 2010 First-order fire effects on herbs and shrubs: present knowledge and process modeling needs *Fire Ecol.* **6** 95–114
- Trockenbrodt M 1995 Structure and identification of root bark of *Quercus robur* L *Trees* **9** 341–7
- USDA and NRCS 2011 Longleaf Pine Initiative (www.nrcs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb1045845.pdf)
- Vargaftik N B, Volkov B N and Voljak L D 1983 International tables of the surface tension of water *J. Phys. Chem. Ref. Data* **12** 817–20
- Varner J M, Putz F E, O'Brien J J, Kevin Hiers J, Mitchell R J and Gordon D R 2009 Post-fire tree stress and growth following smoldering duff fires *Forest Ecol. Manage.* **258** 2467–74
- Van Wagner C E 1973 Height of crown scorch in forest fires *Can. J. Forest Res.* **3** 373–8
- West A G, Nel J A, Bond W J and Midgley J J 2016 Experimental evidence for heat plume-induced cavitation and xylem deformation as a mechanism of rapid post-fire tree mortality *New Phytol.* **211** 828–38
- Woolley T, Shaw D C, Ganio L M and Fitzgerald S 2012 A review of logistic regression models used to predict post-fire tree mortality of western North American conifers *Int. J. Wildl. Fire* **21** 1
- Zimmermann M H 1983 *Xylem Structure and the Ascent of Sap* (Berlin: Springer)