A WAY FORWARD FOR FIRE-CAUSED TREE MORTALITY PREDICTION: MODELING A PHYSIOLOGICAL CONSEQUENCE OF FIRE

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ABSTRACT

Current operational methods for predicting tree mortality from fire injury are regression-based models that only indirectly consider underlying causes and, thus, have limited generality. A better understanding of the physiological consequences of tree heating and injury are needed to develop biophysical process models that can make predictions under changing or novel conditions. As an illustration of the benefits that may arise from including physiological processes in models of fire-caused tree mortality, we develop a testable, biophysical hypothesis for explaining pervasive patterns in conifer injury and functional impairment in response to fires. We use a plume model to estimate vapor pressure deficits (D) in tree canopies during surface fires and show that D are sufficiently high to cause embolism in canopy branches. The potential implications of plume conditions and tree response are discussed.

Keywords: cavitation, crown scorch, fire plume, tree mortality, vapor pressure deficit

INTRODUCTION

Latent tree mortality from wildfire and prescribed fire can be difficult to predict. Initial mortality due to crown combustion and stem girdling is obvious, but an incomplete understanding of the causes of latent mortality has hampered our ability to predict the amount of long-term mortality under a wide variety of conditions following fires. Independent assessment of current tree mortality models points out their strengths such as ease of application and moderate accuracy within their realm of applicability (±20%) in addition to their weaknesses (e.g., Hood *et al* 2007, Breece *et al*. 2008). Models using a mechanistic understanding of underlying biophysical processes may improve predictions of latent mortality by accounting for mitigating effects associated with tree size, fire severity, and climatic conditions. Many unique, regression-based models exist that predict tree mortality as a function of such variables as crown scorch, bole scorch, diameter at breast height (as an indicator of

bark thickness), and species (e.g., Ryan *et al.* 1988, Ryan and Reinhardt 1988, Reggelbrugge and Conard 1993, Fowler and Sieg 2004; see review in Michaletz and Johnson [2006*a*]). These observable model parameters are surrogates of the physiological processes that may cause mortality but are not direct measures of the actual mortality agents or their physiological impacts. In addition, it is difficult to decide which biophysical impacts to measure and model if there are lingering questions about the actual causes of latent mortality and how they are inter-related. Fire related mortality due to the combined effects of heat-caused vascular cambium necrosis around the circumference of the stem and complete mortality of canopy buds has been predicted using a process model with promising results (Michaletz and Johnson 2006*b*). However, as the authors point out, the lack of process-based approaches is limiting our ability to both predict tree functional impairment and mortality where injury from fire alone is sub-lethal, and to define and validate potential mechanisms of post-fire tree mortality.

For example, there are several potential causes of latent tree mortality associated with duff consumption at the base of a tree during prescribed and wildfires. It has been hypothesized that cambial injury leads to a lack of carbohydrate transport from the needles to the roots, and thus to root starvation (Ryan and Fransden 1991). A second potential cause is heat-related disruption of sapwood by a wounding response that, for instance, may lead to resinosis (Shigo and Marx 1977) or direct sapwood consumption in recurrent fires (Rundel 1973), thus interrupting water transport and inducing water stress. Knowing the major causes of mortality is crucial because process-based models of post-fire damage associated with a lack of water transport would be very different from process-based models that predict latent mortality due to a loss of phloem transport and due to direct root mortality.

Experimental studies designed to mimic fire injury give us some clues to potential physiological impacts of fire. Two studies involving heat girdling of the stem indicate that it takes close to 100 % cambial injury to kill a tree (Ryan 2000, Ducrey *et al.* 1996). Sap flux measurements of heat girdled trees indicate that there was an immediate disruption in sapwood water conductance following 100 % heat girdling, but no disruption associated with 37 % to 78 % heat girdling relative to the controls (Ducrey *et al.* 1996). Trees with reduced sap flux and 100 % heat girdling also had lower stomatal conductance and died within five months of treatment, indicating that root death from carbon starvation was not the likely cause. Intermediate girdling caused no change in stomatal conductance relative to controls (Ducrey *et al.* 1996, Ryan 2000), and the subject trees did not die over the life of the experiment (7 months to 2 years). These results indicate that it takes nearly complete cambial girdling to kill a tree and that the main physiological response preceding death is stomatal closure due to disruption of water flow in the sapwood.

In another study that examined the physiology of ponderosa pine (*Pinus ponderosa* C. Lawson) trees following wildfire, it was found that only trees with crown scorch in excess of 50 % showed a positive response in plant hydraulics (e.g., stomatal opening) and photosynthesis rates per unit of leaf area (Wallin *et al.* 2003) relative to trees with less or no defoliation. The lack of response on the foliage remaining on trees with 50 % or less scorch indicates that there may have been internal impairment to the water conducting system on trees exposed to fire. If the water conducting system was fully functioning after a wildfire, higher sapwood to leaf area ratios on the trees with 50 % or less scorched foliage should increase stomatal conductance in foliage on partially defoliated trees relative to non-defoliated trees (Pataki *et al.* 1998).

A Xylem Cavitation Hypothesis

Direct measures of physiological impacts of fire may improve our understanding of the causes of latent mortality and improve our ability to predict it. One physiological process that can be disrupted without outward indications is water transport within a tree. This physiological response may not cause direct mortality, but may have long-term detrimental effects on overall photosynthetic processes and tree productivity. By understanding the causal mechanisms, managers will be better able to model the effects of various fuel treatments and post-fire stressors on tree mortality, identifying the conditions that cause risk. We present a physical model that predicts a potential cause of latent tree mortality associated with a loss of sapwood conductance.

Movement of water from the soil into the roots and throughout a tree is fundamental to its survival. According to the cohesion tension theory, water is pulled to the top of the tree under tension (e.g. Tyree 1997). Liquid water can withstand high tensions because water molecules form hydrogen bonds with each other. However, hydrogen bonds between water molecules, analogous to links on a chain, are under very high tension during periods of drought, when the demand for water exceeds supply, resulting in liquid water that is in a meta-stable state. When the tension becomes too great, air bubbles are sucked into water-conducting conduits through micropores in the cell wall (Cochard *et al*. 1992). The air then nucleates an air embolism when the liquid water is converted to a vapor state.

Xylem cavitation has often been referred to as the unambiguous limit to water transport in trees (Tyree and Sperry 1988). Once a tracheid cavitates, it is no longer able to transport water because of the air embolism that forms (Kavanagh and Zaerr 1997). If a tree cannot transport water to its leaves, it will not survive. Therefore, natural selection has favored trees that minimize cavitation by, for example, cur-

tailing water loss from the leaves during drought (Wang *et al*. 2003, Kavanagh *et al* 2009).

Trees minimize water loss rates, and thus prevent tension on the water column capable of causing cavitation, by closing stomata. Stomata perform a dual function by allowing water to exit and CO_2 to enter the leaf. The stomata close when drought occurs, thereby minimizing water loss but also limiting photosynthesis because CO_2 no longer enters the leaf. In trees, stomata close before the tension in the tracheids reaches a point where excessive cavitation occurs (Tyree and Sperry 1988, Bond and Kavanagh 1999). However, the difference between the tension at which stomata close and the tension at which hydraulic failure occurs is relatively small (Sperry 2004), thus small increases in tension on the water column can initiate cavitation and embolism formation. Although stomatal closure limits photosynthesis, it allows trees to protect their water transport systems so that they can resume transportation of water when the limitations are relieved.

Although trees have adapted to drought conditions by closing stomata, what happens to their water transport systems when atmospheric water demand is rapidly intensified by wildfire? Wildfire increases water demand by causing sudden shifts in atmospheric vapor pressure in the heated plume that rises above the flames. For example, atmospheric temperature and relative humidity have been recorded at $100\,^{\circ}C$ and $0\,\%$ relative humidity, respectively, during a wildfire (Kremens *et al*. 2003), resulting in a vapor pressure deficit (D) of 270 kPa. In addition, it took two hours for atmospheric conditions to return to pre-fire levels. Maximum atmospheric D rarely exceeds 6 kPa in forested environments in the western USA (Kavanagh *et al*. 2007); therefore, the hot plume generated by a wildfire may place a significant strain on a tree's drought stress mechanisms.

The degree of sapwood cavitation and the impact on water conductance associated with

fire-induced atmospheric heating can be predicted given plume D and data relating xylem water potential (Ψ_x) to plume conditions. The relationship between D, soil water potential (Ψ_{soil}) and Ψ_x can be described mathematically as:

$$\Psi_x = \Psi_{soil} - \frac{GsD}{K_L} \qquad (1)$$

where Gs is canopy stomatal conductance (mmol m^{-2} s^{-1}), D is the vapor pressure deficit representing the leaf-to-air vapor pressure gradient (kPa), and K_L is leaf specific conductance (mmol m^{-2} s^{-1} MPa^{-1}) (Jones and Sutherland 1991, Dewar 1995, Whitehead 1998, Bond and Kavanagh 1999). It is evident that if stomata are open or cuticular water loss is significant (e.g., high Gs), high D will increase the tension on the water column in the sapwood (i.e., more negative Ψ_x).

High temperature and low relative humidity (i.e., very high D) associated with fire plumes can cause a rapid loss of water from foliage. For example, lodgepole pine (*Pinus contorta* Dougl.) stems placed in a 250 °C oven had a water loss rate 25 times the rate of normal transpiration (Cohen *et al.* 1990). Water loss rates of this magnitude from living foliage should result in xylem water potentials (Ψ_x) that can cause xylem cavitation. Like clogged arteries in humans, this loss in the water transport system due to cavitation may not be immediately evident but may make the tree more prone to future stresses. For instance, in a crown scorch experiment, it was noted that the buds that survived on the scorched branches produced shortened needles and branches with little internode growth (Ryan 2000). These symptoms are consistent with a loss of branch water conductance due to cavitation (Kavanagh and Zaerr 1997). The irreversible loss in water movement caused by large-scale cavitation will result in reduced productivity as stomatal closure increases (Kavanagh and Zaerr 1997, Bond and Kavanagh 1999), thereby lim-

iting photosynthesis. Excessive heating of the sapwood could also induce cavitation near a tree's base where heating from flames is most intense and, thus, potentially explain the rapid drop in sapwood conductance associated with heat girdling (Ducrey *et al* 1996).

It should be noted, however, that if soil moisture is not limiting, a tree may not experience high rates of cavitation during a wildfire because water supply may balance high rates of moisture loss from the leaves. This may be one reason why fire is less likely to cause mortality on sites with high soil moisture (Cohen and Omi 1991). In addition, riparian trees on sites with relatively high soil moisture may limit cavitation by replacing water that is rapidly lost from foliage. In short, pre-existing conditions may influence the level of cavitation in an individual tree and, therefore, its subsequent mortality.

METHODS

To examine the potential for xylem cavitation in trees exposed to forest fire, we used a fire plume model to estimate atmospheric vapor pressure, and a hydraulic conductance model to predict the corresponding xylem water potential. These xylem water potentials were then compared to cavitation vulnerability curves to determine the potential loss of hydraulic conductance within the tree canopy.

Plume Model

An integral plume model (Mercer and Weber 1994) was used to generate average D through the canopy for typical surface-fire conditions (Table 1). The model simulates a plume arising from a line source of heat of specified intensity (kW m^{-1}) on flat terrain and involves solution of six coupled ordinary differential equations based on the conservation of mass, momentum, and energy. Cross-winds result in down-wind displacement of the plume (e.g., Mercer and Weber 1994) and, conse-

Table 1. Characteristics of fires and resulting plume-model boundary conditions used to predict xylem cavitation. Fuel consumption was held constant at 0.75 kg m^{-2} while wind speed (W) and flame rate of spread (R) varied, creating a range of fireline intensites (I). Flame height (h_f) is determined by wind speed and fireline intensity while initial plume velocity (w_i) is dependent on fireline intensity and initial plume half width (b_i) is dependent on flame width.

W m s^{-1}	R m min^{-1}	I kW m^{-1}	h_f m	w_i m s^{-1}	b_i m
0	1	200	0.9	2.2	0.2
0	2	400	1.2	2.8	0.3
0	4	800	1.7	3.5	0.6
0	8	1600	2.3	4.4	1.2
3	1	200	0.5	2.2	0.2
3	2	400	0.8	2.8	0.3
3	4	800	1.2	3.5	0.6
3	8	1600	1.8	4.4	1.2

quently, no-wind conditions will result in the highest D at a given height within the canopy. We compared wind (3 m s^{-1}) and no-wind plume simulations. When wind was applied, its velocity was constant with height. The coupled equations were solved with the Bulstoer function in MathCad (PTC, Needham, Massachusetts, USA).

To generate water vapor and heat, the model was run over a range of fireline intensities (kW m^{-1}) prescribed by increasing rate of spread at a fixed fuel consumption of 0.75 kg m^{-2} (Table 2). There was no feedback between wind and fire rate of spread. Heat of combustion for convective heat release was constant at 16 000 kJ kg^{-1} (Nelson 2002). Boundary conditions for the plume model (Table 2) include flame velocity (w_i), plume half-width (b_i), flame-tip temperature (Tp_0), and flame density (ρ_i). Plume half-width is one-half of flame depth. Flame tip temperature (K) was estimated as $T_i = 860 + T_a$, where ambient (T_a) was set to 298 K (DePuy *et al* 2003). Average flame temperature (K) for biomass burning through the continuous and intermittent zones was set to $T_f = 1000 + T_a$ (DePuy *et al*. 2003). Flame density was proportional to average flame temperature from the ideal gas law. For this calculation, ambient air pressure at an elevation of 500 m above sea level was used (Campbell and Norman 1998) and, given average flame temperature, flame density was 0.31 kg m^{-3}. Variation in ambient air pressure has minimal effects on the results and so was left constant. Flame velocity was calculated from Nelson (2002) and plume half-width was one-half of flame depth. Flame depth (D_p, m) was calculated from:

Table 2. Parameters used to predict stem water potential and degree of cavitation in Douglas-fir (DF), western larch (WL) and lodgepole pine (LPP). Biophysical parameters include soil water potential (Ψ_{soil}) set at a typical late summer value, canopy conductance to water vapor (G_s) set at approximately 30 % of maximum for the species of interest to reflect mid-day stomatal closure, leaf specific conductance (K_L) determined from values for mature trees in North Idaho, and the water potential where a 50 % loss in hydraulic conductance can be expected ($\Psi_{50\%}$).

Species	Ψ_{soil} (MPa)	G_S (mmol m^{-2} s^{-1})	K_L (mmol m^{-2} s^{-1} MPa^{-1})	$\Psi_{50\%}$ (MPa)
Douglas-fir	-1.0[a]	15[b]	0.93[a]	-5.2[c]
Western larch	-1.0[a]	26[b]	1.34[a]	-4.3[c]
Lodgepole pine	-1.0[d]	30[e]	2.2[b]	-3.0[c]

[a] Kavanagh *et al.* 2007.
[b] Unpublished data Kavanagh
[c] Pinol and Sala 2000
[d] Pataki *et al.* 2000
[e] Reid *et al.* 2006

$$D_f = \frac{RW}{c} \qquad (2)$$

where R is rate of spread (m s^{-1}), W is fuel consumption (kg m^{-2}), and c is combustion rate (kg m^{-2} s^{-1}).

Water vapor was assumed to mix immediately into a flame zone control volume defined in two dimensions by flame depth and length. Flame length (equivalent to height with no wind) was estimated from fireline intensity using Byram (1959). The two-dimensional flux of water vapor (kg m^{-1} s^{-1}) was determined from:

$$\dot{m}_w = \frac{W_{2D} R Y_w}{D_f} \qquad (3)$$

where W_{2D} is two-dimensional loading (kg m^{-1}) and Y_w is yield of water vapor (kg kg^{-1}). Water vapor yield was set to 0.609 kg kg^{-1} based on typical combustion stoichiometry and a fuel moisture content of 5 % of dry weight (Byram 1959).

Water vapor concentration in the flame control volume was calculated as follows:

$$Cf_w = \frac{n_w}{n_{CV}} \qquad (4)$$

where Cf_w is the concentration of water vapor, n_w is the number of moles of water, and n_{CV} is the number of moles of all gases in the flame control volume. The number of moles of water vapor in the two-dimensional control volume was calculated as:

$$n_w = \frac{\dot{m}_w (h_f D_f) \frac{1}{2}}{M_w w_i} \qquad (5)$$

where h_f is flame height (m) and M_w is the molecular weight of water (18 g mol^{-1}). The number of moles of all gases in the two-dimensional control volume is determined from the ideal gas law and flame temperature:

$$n_{CV} = \frac{p_a (h_f D_f) \frac{1}{2}}{R_{2D} T_f} \qquad (6)$$

where p_a is ambient air pressure, R_{2D} is the gas constant for the two-dimensional control volume (8.314 m^2 Pa K^{-1} mol^{-1}), and T_f is defined above. Ambient vapor concentration was added to vapor concentration arising from combustion and fuel moisture.

Because mixing is turbulent, we assume that mass and heat transfer rates between the plume and ambient air are similar. Thus, water vapor concentrations decline toward ambient with height above the flame in proportion to declines in plume temperature:

$$C_{wh} = Cf_w \left(1 - \frac{Tp_0 - Tp_h}{Tp_0 - T_a} \right) \qquad (7)$$

where C_{wh} is concentration of water vapor at height h above the flame and Tp_h is flame temperature at height h above the flame. Flame height for fires in wind (Table 2) was determined from flame length and Nelson's (1986) relation for flame tilt angle. Vapor pressure at height within the plume is the product of ambient pressure and vapor concentration. Vapor pressure deficit is the difference between plume vapor pressure and saturation vapor pressure (Campbell and Norman 1998).

Plume model output is a centerline value that can be considered an average across the width of the plume perpendicular to the centerline axis (a top-hat profile). A Gaussian profile is fit to the top-hat results (Figure 1; Mercer and Weber 1994) and the average gas concentrations and temperatures over the residence time of the plume as it travels at the fire's rate of spread are calculated horizontal to the ground across the plume at 1 m increments in height above the flame tip (Figure 1). The plume in no-wind conditions moves across the frame of reference with no horizontal distortion in contrast to the plume in a cross-wind
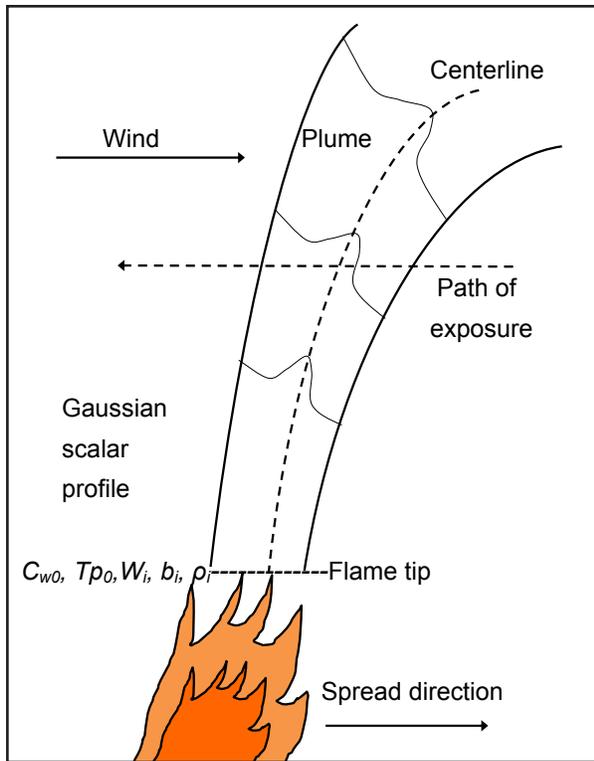
Figure 1. Structure of a modeled plume in a cross wind. The wind blows from left to right causing plume deflection to the right. Flame conditions determine initial flame-tip temperature (T_{p0}), flame density (ρ_i). vertical velocities (w_i), and plume half width (b_i) (Table 1). Fuel moisture, fuel consumption, and ambient vapor pressure determine plume water vapor content (C_{wo}). A Gaussian profile is fit to the top-hat (averaged) output of the plume model and used to calculate average plume vapor pressure deficits at a given height above ground.

represented in Figure 1. The residence times and average vapor pressure deficits mimic what a fixed object, for instance, a branch tip with foliage, would be exposed to as a fire spreads underneath.

Hydraulic Conductance Model

The canopy D profiles generated by the plume model were used in a hydraulic conductance model as described in Equation 1 (Bond and Kavanagh, 1999) to determine Ψ_s. Three species were chosen for the initial model parameterization: Douglas-fir (*Pseudotsuga men-*

ziesii [Mirb.] Franco), western larch (*Larix occidentalis* Nutt.) and lodgepole pine. An integral plume model (Mercer and Weber 1994) was used to generate average D through the canopy for typical surface-fire conditions (Table 1). We chose typical late summer ecophysiological parameters for Ψ_{soil}, G_s, and K_L, as presented in Table 2.

Finally, the Ψ_s value needs to be related to the degree of xylem cavitation. This can be done using a vulnerability curve expressing the degree of loss in water conductance as a function of Ψ_s. Vulnerability curves are available for several tree species including Douglas-fir (Sperry and Ikeda 1997), western larch, and lodgepole pine (Pinol and Sala 2000). The stem water potentials where xylem cavitation causes a 50 % loss in hydraulic conductance for these three species are presented in Table 2.

Of interest were plume exposures above the height at which foliage necrosis would be caused by the direct effects of foliage heating. Van Wagner (1973) determined that foliage necrosis from heat would occur at the height at which 60 °C was reached in a plume above a surface fire, the 60 °C threshold being the temperature at which tissue necrosis would occur nearly instantaneously. Because foliage temperature tracks plume temperatures closely, necrosis (scorch) heights predicted from the 60 °C plume temperature compare favorably with scorch height predictions generated from a series of linked models including plume model predictions of gas temperature and velocity, needle heating from a lumped capacitance heat-transfer model, and tissue necrosis from a thermal tolerance model (Butler and Dickinson 2010).

RESULTS AND DISCUSSION

The effects of the plume are substantially ameliorated by wind because the flow of the plume is inclined and dilution is enhanced (Figure 1). The plume model assumes a con-

stant heat release from a line-source flaming front. Clearly, this is an idealization with fire rate of spread and intensity, and canopy exposures, varying across a burning landscape as fuels, winds, and topography change. We use the plume model only to illustrate that substantial xylem cavitation is possible within a range of surface fire intensities typical of management fires (Johnson 1992).

The models predict Ψ_x capable of causing xylem cavitation under several fire scenarios (Figure 2). The degree of predicted injury due to xylem cavitation is related to plume temperature rise that, in turn, is related to the wind speed and fireline intensity (Figure 2). Stem water potential does not exceed the point of 50 % xylem cavitation very frequently when wind speeds are 3 m s^{-1} and the fire intensity is relatively low. The only impairment expected would be in foliage very close to the ground. As fire intensity increases, Ψ_s declines to a point where cavitation occurs in the canopy up to 10 m above the ground in lodgepole pine and western larch. Finally, at the highest fire intensities, the model predicts foliar necrosis from heat alone up to 30 m when wind is absent. However, when fire intensity is high and wind speeds reach 3 m s^{-1}, foliage necrosis is limited to lower heights but significant amounts of cavitation can be expected in the surviving lodgepole pine and western larch crowns.

Vulnerability to cavitation varies widely between species (Table 2). Of the three species examined, Douglas-fir is least likely to reach values of Ψ_s corresponding to cavitation (Pinol and Sala 2000), even during high intensity fires. Direct mortality of foliage due to heating, rather than xylem cavitation, is more likely to occur in Douglas-fir canopies. Lodgepole pine is the most vulnerable to cavitation and therefore more likely to incur cavitation damage when exposed to a hot plume. When fire intensity is moderate and there is no wind, the models predict that lodgepole pine will suffer 50 % or greater loss of stem hydraulic con-

ductance in the tree canopy below 25 m above ground.

There are several mechanisms that may limit xylem cavitation in trees exposed to excessive D during a fire. Xylem walls in the leaves of the trees may collapse, preventing the propagation of the negative water potential beyond the leaf. Cochard *et al*. (2004) found that, as xylem pressure decreased past a certain pressure threshold ($P_{collapse}$), xylem walls in pine foliage collapsed and so avoided or delayed the risk of cavitation within the tree. Wall collapse dramatically reduced xylem conductance temporarily, and was rapidly reversible upon rehydration. Water storage in the bole and branches is an adaptation that helps trees to overcome hydraulic stress (Holbrook 1995). Phillips *et al*. (2003) found that water stored in the xylem accounted for as much as 25 % of the total daily water use in large Douglas-fir trees. Water stored in elastic tissues in close proximity to leaves may be utilized during periods of high atmospheric D and thus limit the amount of cavitation. This mechanism may work synergistically with xylem collapse to prevent fire-injured trees from reaching Ψ_x where cavitation occurs. Finally, segmentation of xylem-damaged tissue may protect the main bole from irreversible loss. Plants preferentially cavitate xylem in more expendable branches, thus improving the likelihood of maintaining functioning xylem in the main bole (Zimmermann 1983 and Tyree and Sperry 1988). The post-fire mortality of foliage (crown scorch) and lower branches, where tissue heating does not cause necrosis, may reflect all of these processes.

Stomatal aperture at the time when the plume reaches the canopy will have an impact on the degree of damage. In this modeling exercise, we chose an aperture that reflects stomatal conductance at 30 % of maximum. This level of stomatal closure reflects the canopy conductance rate that can be expected once D reaches approximately 3.5 MPa in several western conifers (Pangle 2008). This D may
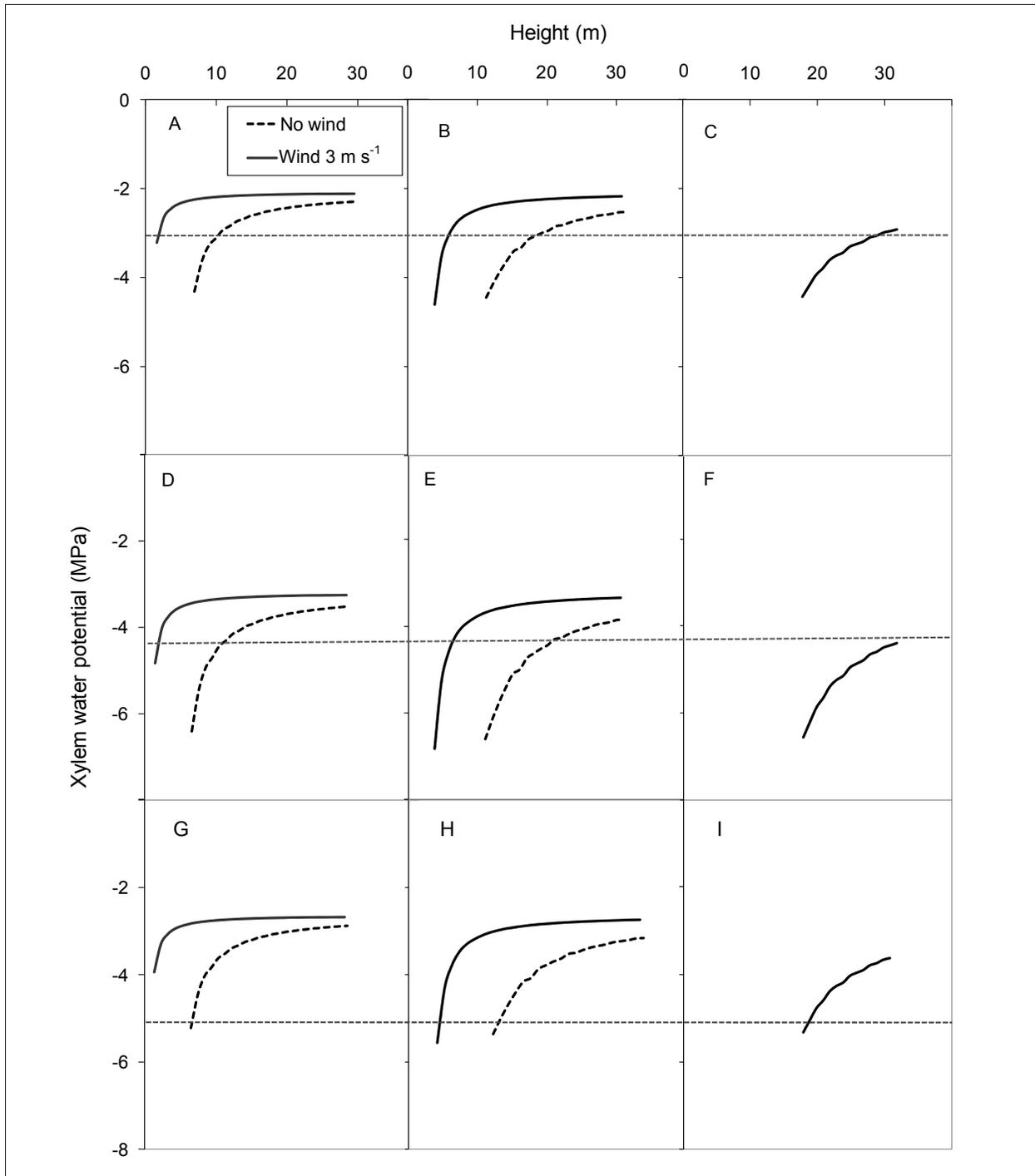
Figure 2. Modeled xylem water potential (MPa) in lodgepole pine (A-C), western larch (D-F) and Douglas-fir (G-I) canopies exposed to plumes arising from firelines with various rates of spread (R, m min^{-1}) and intensities (I, kW m^{-1}). $R = 1$ and $I = 200$ (A, D, G); $R = 2$ and $I = 400$ (B, E, H) and $R = 8$ and $I = 1600$ (C, F, H). Only the foliage elevated enough to have survived heating in the plume is included in this figure. Two wind conditions were simulated: no wind (dashed line) and 3 m s^{-1} (solid line). A plume model was used to estimate atmospheric vapor pressure deficit as an input to a stem hydrologic model to predict stem water potential. The dashed line represents the water potential where a 50 % loss in hydraulic conductivity is expected (Pinol and Sala 2000). Fire and physiological parameters used in the models are in Tables 1 and 2, respectively.

not reflect the daily maximum, which can reach 6 MPa, but the maximum only occurs for a brief period during the day. Atmospheric water deficits in excess of 3.5 MPa will result in higher levels of stomatal closure and therefore lower rates of cavitation.

The response of stomata to a heated plume may also ameliorate its impacts. If stomata close rapidly and cuticular water loss is not too great, the rate of water loss would be severely curtailed, thus Ψ_x could be maintained above a cavitation threshold. Stomatal closure is triggered by water loss rates (Mott and Parkhurst 1991) and high CO_2 concentrations (Morrison 1998). The correlations between rates of stomatal closure and very high rates of leaf water loss generated by high D have not been studied thoroughly. However, there are some studies that indicate that stomatal closure may not be rapid enough to prevent sudden water loss and stem cavitation during fires. Stomata on excised ponderosa pine branches took approximately one hour to close to a point where transpiration rates approached zero (Lopushinsky 1969). When lodgepole branches were exposed to air heated to 225 °C to simulate fire, there was a rapid increase in water transport from the non-heated portions of the tree to the heated portions (Cohen *et al*. 1990). This could not have occurred if water was not also being lost from the foliage. This may indicate a lack of rapid stomatal closure, or deformation of leaf cuticle waxes or stomata due to excessive heat. It is also plausible that stomata may remain open to cool the leaf during sudden periods of high temperature exposure.

There is a lack of literature on the effects of non-lethal high temperatures on stomatal closure rates and cuticle wax integrity in conifers. If excessive heat deforms its cuticle or stomatal waxes, a tree's ability to conserve water may be impaired for a longer time. Our models, under the assumption that cuticles maintain their integrity, suggest that cuticular water loss was not sufficient to cause significant cavitation (results not shown). However, longer-term expo-

sures to high D where exposures are affected by combustion over large areas and long range transfer of high plume temperatures upslope (not modeled plumes arising from line sources of heat) should be investigated.

Differences in stomatal control among species and higher taxa may also be important for determining the effects of fire plumes. Sperry (2004) suggests that angiosperms rely on tighter stomatal control than gymnosperms; that is, the difference in water potential at which stomatal control begins and hydraulic failure occurs is small in angiosperms relative to conifers. Where this generalization holds, and if rates of stomatal control are similar, angiosperms would be more vulnerable to the effects of plumes than gymnosperms.

Although these models predict that xylem cavitation will occur under some conditions, it is not evident where the cavitation will occur within the xylem. It has been demonstrated that branch junctions and leaf connections are points of high resistance to water flow within the stem (Zimmermann 1983, Tyree and Sperry 1988) and thus would be the most likely location for xylem cavitation. The older branches in the lower canopy are also found to have more resistance to water flow relative to the upper canopy (Zimmermann 1983). Therefore, the hydraulic architecture of the tree suggests that cavitation would occur at branch and leaf junctions especially in older branches and perhaps older needles. The loss of older branches and foliage would not be as detrimental compared to loss of newer foliage and branches that are typically located in full sun.

The loss of foliage from a tree with an undamaged water conducting system can actually improve water relations on the remaining foliage. Up to 40 % of the live crown can be removed in conifers without reducing diameter growth (Heidmann 1963, Pearson *et al*. 1972, Wyant *et al*. 1986). This occurs because stomatal conductance on the remaining foliage increases relative to pre-defoliated conditions (Pataki *et al*. 1998, Hubbard *et al*. 1999).

Higher stomatal conductance can result in an increase in photosynthesis per unit foliage, especially during periods of water stress. This increase in foliar productivity mitigates the effects of foliage loss. However, in the case where the stem hydraulic conductance is reduced through cavitation, stomatal conductance may not improve on the remaining foliage, thereby limiting the ability of the remaining foliage to maintain tree productivity (Thompson 2007). Further research on the physiological responses of trees exposed to fire will address the potential of this mechanism to offset the impacts of fire damage.

Refilling of cavitated xylem elements may prevent long-term damage to the water conducting system following a fire. Winter freeze-thaw cycles commonly cause annual xylem cavitation in some conifers, however the cavitated tracheids refill by spring (Sparks and Black 2000, Sperry *et al*. 1994). Refilling has been demonstrated in detached segments in several conifer species (Edwards *et al*. 1994, Zwieniecki and Holbrook 1998); however, the mechanism has not been fully described (Holbrook and Zwieniecki 1999), and no comprehensive studies have been done on intact segments (see summary in Clearwater and Goldstein [2005]). The mechanisms currently hypothesized involve close proximity to either water-filled tracheids to supply water to the cavitated tracheid or close proximity to living parenchyma cells that can provide the energy to drive the refilling process (Holbrook and Zwieniecki 1999). The conditions required by the above mechanisms may not be present if widespread cavitation occurs during exposure to a heat plume. Further research is needed to determine the degree of refilling that can occur *in vivo* following either high levels of cavitation or combinations of different kinds of fire-caused injury.

CONCLUSION

Xylem cavitation is an invisible and potentially underappreciated agent in delayed fire-caused mortality and, along with other injuries, may lead to long term decline in tree vigor. Future efforts needed to validate the cavitation model include measuring cavitation rates in trees subjected to heated plumes, determining the locations within a tree that are most susceptible to injury, determining whether refilling of cavitated xylem elements is occurring, gaining a better understanding of how fast stomata close once exposed to a heat plume, and determining whether variation in pre-fire stomatal conductance reduces injury. Research should also be conducted to determine if cavitation occurs in roots exposed to smoldering fires in the duff and basal stems and if improved water relations follow partial defoliation. Better understanding of cavitation and other biophysical processes associated with changes in tree function and mortality rates after fire is needed. With this understanding, we can better model changes in post-fire carbon dynamics, and managers will have a tool to help them determine which trees may be available for salvage.

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