

Prediction and measurement of thermally induced cambial tissue necrosis in tree stems

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Abstract. A model for fire-induced heating in tree stems is linked to a recently reported model for tissue necrosis. The combined model produces cambial tissue necrosis predictions in a tree stem as a function of heating rate, heating time, tree species, and stem diameter. Model accuracy is evaluated by comparison with experimental measurements in two hardwood and two softwood species: red maple (*Acer rubrum*), chestnut oak (*Quercus prinus*), ponderosa pine (*Pinus ponderosa*), and Douglas-fir (*Pseudotsuga menziesii*). Results are promising, and indicate that the model predicts stem mortality/survival correctly in ~75–80% of the test cases. A limited sensitivity analysis of model kill depth predictions suggests that the model is more sensitive to required input data for some species than for others, and that the certainty in predicting vascular cambium necrosis decreases as stem diameter decreases.

Introduction

Methods for predicting tree or shrub mortality caused by thermal injury from fire can be useful for understanding and predicting post-fire forest composition and to guide land managers' decisions (Martin 1963; Peterson and Ryan 1986; Hengst and Dawson 1994; Durcey *et al.* 1996). A tree may be killed by the effects of heating on the roots and crown individually or by the combined effects of root, stem, and crown heating (Dickinson and Johnson 2001). In the present study, we focus on stem vascular cambium necrosis as one cause of tree death in fires. What is needed for predicting vascular cambium necrosis from flames is a heat transfer prediction linked with some method for predicting cambial tissue necrosis (Martin 1963). The linking of thermal transport models and tissue necrosis models was proposed by Martin (1963) for stems and further developed by Mercer *et al.* (1994) and Dickinson and Johnson (2004). However, such a linked deterministic model has not yet been presented and validated. This paper describes a research model consisting of a thermal simulator that includes a more complete accounting of energy sink terms than previously published models (Jones *et al.* 2004), and a cellular necrosis model that accounts for the rate dependence of tissue necrosis during heating (Dickinson and Johnson 2004; Dickinson *et al.* 2004). The development, validation, and sensitivity analysis of such a linked model has

not been reported previously nor is the model in its present form formulated to be used operationally by land managers.

Models for predicting fire-induced tree mortality may be loosely classified into two general categories: empirical and theoretical. For the purposes of this study, empirical models are defined as those based primarily on statistical correlations of experimentally measured fire behavior and tree mortality. It is presumed in their development that the biological and physical processes governing the heating and subsequent plant injury are implicitly included in the correlations. Empirical models and methods presented to date have attempted to utilize visual indicators of fire intensity such as surface fuel consumption, stem height scorch or degree of canopy scorch to predict tree mortality. Theoretical models, on the other hand, are based primarily on a mathematical treatment of the physical processes that govern the energy transfer through the stem, yielding a prediction of the local temperature history within the stem and the resulting local tissue response. Some empiricism is always present in the submodels comprising the theoretical model (e.g. correlations for thermal conductivity).

Empirical methods

Early efforts to predict fire effects on trees focused on developing rules for predicting tree mortality based on observed fire indicators (Flint 1925; Starker 1934; McCarthy and Sims

1935), and quantifying the thermal environment characteristic of fires and the response of plant stems to fire-induced heating (Shirley 1936; Martin and Davis 1961; Kayll 1963; Martin 1963; Fahnestock and Hare 1964; Hare 1965a, 1965b; Gill and Ashton 1968; Ryan and Frandsen 1991). Others sought to measure the thermal and physical characteristics of wood and bark required by theoretical models (Spalt and Reifsnnyder 1962; Kayll 1963; McArthur 1967; Lamb and Marden 1968; Martin and Crist 1968; Vines 1968). Still others explored the interaction between low intensity fires and scarring of tree stems (Nelson 1952; Gill 1974; Tunstall *et al.* 1976; Peterson and Arbaugh 1986, 1989; Wyant *et al.* 1986; Harrington 1987, 1993; Saveland *et al.* 1990; Hengst and Dawson 1994; Russell and Dawson 1994; Gutsell and Johnson 1996; Ryan 1998). Peterson and Ryan (1986) combined the work of these earlier studies with additional experimental observations to develop empirical correlations for predicting the probability of plant mortality due to heating. The correlations developed by Peterson and Ryan (1986), Ryan and Reinhardt (1988), and Greene and Schilling (1987) form the primary basis for the tree mortality prediction systems currently used by forest managers in North America. Very recent work by Bova and Dickinson (2005) follows a correlative approach to linking fire behavior and subsequent tissue necrosis.

Theoretical methods

Theoretical models for predicting fire-induced tissue heating have included both analytical and numerical modeling efforts. Mercer *et al.* (1994) and Mercer and Weber (2001) solved the one-dimensional differential heat conduction equation analytically, and estimated mortality of fruit from definitions of time-to-necrosis at a range of fixed temperatures. Dickinson and Johnson (2001, 2004) coupled an analytical solution for the unsteady temperature distribution in an infinite-slab approximation of the stem with a rigorous, thermally induced tissue necrosis model. Rego and Rigolot (1990) used Taylor-series finite differencing to solve numerically the heat conduction equation to predict thermal response to heating, but no prediction of mortality was made. Costa *et al.* (1990) employed a two-dimensional numerical control-volume approach with temperature-dependent thermal properties, but did not account for spatial variations in moisture and its effect on energy transfer. Keane (1991) included a spatially varying treatment of moisture and its non-linear temperature dependence, but this numerical model was not compared against experimental data. Steward *et al.* (1990) examined root heating, developing a numerical model to predict the temperature-time behavior as a function of root depth for mineral soil exposed to a fire. Potter and Andresen (2002) followed a two-dimensional approach to numerically simulate the temperature variation in a tree stem due to diurnal variations in solar heating.

Their model was not intended to predict temperature variations due to heating by fire and, therefore, included no prediction of thermal damage. Jones *et al.* (2004) presented a one-dimensional heat conduction model that included temperature- and moisture-dependent thermophysical properties, incorporating submodels for desiccation, charring, pyrolysis, and spatially varying moisture distribution. Three of the theoretical models described previously use a known surface temperature boundary condition (Costa *et al.* 1990; Rego and Rigolot 1990; Keane 1991). By contrast, Steward *et al.* (1990), Potter and Andresen (2002) and Jones *et al.* (2004) specified an energy flux boundary condition rather than temperature. This is significant from a thermal modeling standpoint as incident energy flux is more readily obtained from fire behavior descriptors than stem surface temperatures, and further, prediction of the local temperature history in a stem subject to an imposed surface heat input requires a more rigorous accounting of energy than is the case for an imposed surface temperature.

Tissue necrosis

The traditional methodology for defining mortality due to fire-induced heating of tree stems has been to define a temperature typically between 55°C and 60°C as the lethal temperature limit at which tissue necrosis occurs instantaneously (Brown and DeByle 1987; Gutsell and Johnson 1996). While the lethal temperature concept may give a useful estimate for predicting tree mortality, Shirley (1936), Lorenz (1939), and later Martin (1963) recognized the shortcomings of such an approach. Dickinson and Johnson (2001) showed that this approach is not intuitively sound from a biological perspective. The process of thermally induced cell and tissue impairment in plants is rate-dependent, governed both by the heating rate (and thus, temperature magnitude) and duration of exposure (Lorenz 1939; Hare 1961; Kayll 1963; Martin 1963; Levitt 1980; Caldwell 1993; Dickinson and Johnson 2004; Dickinson *et al.* 2004).

Recognizing the shortcomings of a simple lethal temperature threshold approach, Martin (1963) built on earlier work by Silen (1960), proposing a method for predicting tissue necrosis that simulates the cumulative thermal injury to the cambium. The advantage of this method is that it accounts for the effect of both long-term, low-temperature heating and/or short-term, high-temperature heating on plant tissue mortality. However, Silen's model included data only from Douglas-fir (*Pseudotsuga menziesii*). While the coupling of thermal transport models and cell necrosis models was proposed by Martin (1963), such a coupled model was not developed.

Using the large body of theory and data on thermal tolerance of both plant and animal tissues (e.g. Johnson *et al.* 1974; Levitt 1980), Dickinson (2002), Dickinson and Johnson (2004) and Dickinson *et al.* (2004) proposed a rate-process model to describe the impairment of tissues exposed to

time-varying, elevated temperatures. In that methodology cambial tissue impairment is based on species-specific, temperature-dependent rate parameters. This is the model utilized in the present study.

Because no models linking thermal transport with tissue necrosis have been presented, techniques for quantifying the accuracy of the model have not been established. In the past, thermal model performance was evaluated by comparing measured and predicted cambial temperature histories (Costa *et al.* 1990; Rego and Rigolot 1990; Jones *et al.* 2004). However, such an approach does not evaluate the linking between thermal and tissue necrosis simulators.

For this study two indicators of model accuracy were explored by comparing measured and predicted (i) depth-of-kill, and (ii) local cambial tissue viability. Comparisons are made for red maple (*Acer rubrum*) and chestnut oak (*Quercus prinus*) with depth-of-kill measurements determined post-mortem using a chemical stain technique (Kayll 1963). This technique was determined to be unreliable for ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) and, therefore, a modified approach was developed to assess the accuracy of the linked model predictions for these species. For these softwood species, the model's capability to accurately predict whether or not the cambial tissue is killed subject to predicted and measured cambial temperature histories was compared. The results of the model evaluations are presented and their implications are discussed.

Stem heating model

The numerical heat transfer model used in this research is described and validated in detail elsewhere (Jones *et al.* 2004), and is only summarized here. The model is a one-dimensional heat conduction prediction in a cylindrical coordinate system where temperature is a function only of radial position in the cylindrical approximation of the stem, $T = T(r)$. The simulation includes various temperature-dependent phenomena such as desiccation, devolatilization, charring, and bark swelling (where appropriate), all of which represent energy absorption mechanisms. Jones (2003) showed that asymmetric heating around the stem can be simulated with one-dimensional heat transfer provided that the stem diameter is greater than ~ 4 cm. Thus, non-uniform, two-dimensional heating can be simulated by applying the one-dimensional model at discrete circumferential locations around the stem. This is the protocol that would be followed for operational use of this model. Required inputs to the model include geometric information (stem diameter, inner and outer bark thickness), thermophysical properties (thermal conductivity, density, and specific heat) and their moisture and temperature dependence for the various layers, and radial variation of moisture content in the stem. While the model is capable of simulating the stem response to an imposed stem surface temperature history or an imposed

time-dependent heat flux boundary condition at the stem surface, the heat flux boundary condition is employed here.

The stem heating model is capable of predicting temperatures as a function of time for discrete numerical grid points deployed radially within the tree stem. The appropriate differential equation governing the conservation of energy through the stem is 'discretized' or formulated to simulate the continuous temporal response through discrete but small computational steps in both space and time, resulting in an energy balance on each cell. After a thorough study, 600 spatial cells were used with a time step of 1/16 s (Jones *et al.* 2004). The resulting nominally linear algebraic equations are then solved for local temperatures within the small spatial cells at discrete time steps during the heating process, thereby providing a prediction of the temperature profile within the stem at each time step. Kayll (1963) described the exterior surface of many trees as consisting of a 'plate-fissure' structure where 'plate' refers to the outermost region of maximum bark thickness and 'fissure' to the crevasses between the plates. Kayll concluded that energy transfer through the plates rather than the bark fissures is the limiting factor. The model described herein adheres to Kayll's assumption.

Tissue necrosis model

The thermally caused impairment of tissues or mortality in populations of cells may be described by a rate equation that models the rate of decline in tissue viability (i.e. tissue impairment) as being proportional to current viability (Dickinson and Johnson 2001, 2004; Dickinson *et al.* 2004)

$$\frac{dV}{dt} = -\kappa V(t), \quad (1)$$

where V is viability ($-$), t is time (s), and κ is a species-specific, temperature-dependent rate parameter (s^{-1}). Since tissue temperature varies with time as trees are heated in fires, the rate parameter is thus time-dependent. The temperature-dependence of the rate parameter has been described using an Arrhenius relation (Dickinson *et al.* 2004):

$$\kappa(t) = A \exp \left[-\frac{E}{RT(t)} \right], \quad (2)$$

where A is the pre-exponential factor (s^{-1}), E is the activation energy ($J \text{ mol}^{-1}$), R is the universal gas constant ($8.31 J \text{ mol}^{-1} K^{-1}$), and $T(t)$ (K) is the temperature at time t . The rate parameters (A and E) in Eqn (2) are species specific, and must be determined in laboratory experiments. These parameters have been measured experimentally for the four species for which the combined model has been evaluated here (Dickinson *et al.* 2004) and are summarized in Table 1.

Linked model

The stem heating model predicts the temperature-time history at discrete radial locations through the tree stem. Given

Table 1. Arrhenius parameters in Eqn (2) for the species considered here
From Dickinson *et al.* (2004)

Species	A (s^{-1})	E ($J\ mol^{-1}$)
Red maple (<i>Acer rubrum</i>)	1.0903×10^{24}	166 729
Chestnut oak (<i>Quercus prinus</i>)	7.1466×10^{34}	235 446
Ponderosa pine (<i>Pinus ponderosa</i>)	2.1970×10^4	46 402
Douglas-fir (<i>Pseudotsuga menziesii</i>)	1.4413×10^{12}	95 217

a predicted temperature as a function of time at any location in the stem, a prediction of relative tissue impairment or cell mortality can be made by integrating Eqn (1) with respect to time. The tissue necrosis model was therefore discretized in time in order to couple it to the stem heating model previously developed (Jones *et al.* 2004). The discrete analog of Eqn (1) is

$$V_t = V_{t-\Delta t} - \kappa(t)V_{t-\Delta t}\Delta t, \quad (3)$$

where V_t is the local tissue viability at the current time step, $V_{t-\Delta t}$ is the viability at the previous time step, Δt is the discrete time step size, and $\kappa(t)$ is calculated using Eqn (2) based on the local temperature at the current time step $T(t)$ for a given species. As tissue is heated, it loses viability over time. Initially, the (living) tissue's viability is assigned a value $V = 1$. Viability drops as thermal damage accumulates, approaching $V = 0$ as heating progresses. It is assumed arbitrarily in this study that tissue necrosis will occur when viability drops below $V = 0.5$. Model predictions (Jones 2003) and prior experimental data (Dickinson and Johnson 2004) reveal that, under heating conditions typical of wildland fires, the decrease in tissue viability is rather rapid, such that the decrease in local viability V from 1 to 0 is quite sudden. Thus, the prediction of necrosis is not terribly sensitive to this arbitrary criterion defining necrosis at $V = 0.5$ for high incident heat fluxes. However, it will be shown that the viability limit defining mortality for lower-intensity, sustained heating scenarios is less clear.

At each time step in the stem heating model, the viability at each of the numerical grid points is recalculated according to Eqn (3). As the stem is heated, tissue necrosis is predicted first near the stem surface. With further heating, tissue damage proceeds inward through the bark and, if the heating is of sufficient magnitude and duration, reaches the cambium. Thus, the result of the combined stem heating and tissue necrosis models is a prediction of tissue mortality as a function of time and depth into the stem. The distance from the bark surface inward to the deepest radial location with viability less than $V = 0.5$ is thus defined as the kill depth. Of course, a kill depth that penetrates beyond the vascular cambium and into the sapwood is of little significance, since this scenario yields overall stem mortality. Therefore, accurate modeling of cambial tissue mortality is of principal importance from the standpoint of predicting fire-induced tree mortality. To

extrapolate the local cambial tissue necrosis prediction to a whole-stem survival/mortality prediction, it is necessary to either apply the model at many circumferential locations around the stem or to assume that all other locations around the stem suffer equal or greater necrosis. For the purposes of this study, the second option has been followed. It is thus assumed that the calculation is made for the location with the lowest level of heating, suggesting that if cambial necrosis occurs at this location, all other locations around the stem will also be killed, girdling the tree.

Experimental methods

The combined stem heating and tissue necrosis model was evaluated by comparison with experimental data. The experiments included (i) characterization of the thermal response to external heating by experimentally recording the temperature–time history at the cambium for various heating magnitudes and durations, and (ii) characterization of tissue necrosis in the stems through the use of chemical stains that identify respiring tissue. The following paragraphs summarize the experimental approach.

Stem heating procedure

Thermal response of tree stems subjected to heating was characterized by measuring the timewise variation of both the incident heat flux at the exterior surface and the temperature at the cambium. Generally speaking, ponderosa pine and Douglas-fir heating experiments were conducted in the laboratory on freshly cut tree sections (Jones *et al.* 2004), whereas the red maple and chestnut oak data were collected in controlled burns conducted in field experiments (Bova and Dickinson 2005). Samples were collected randomly from populations of trees in relatively small geographical areas, and from necessarily finite areas on the stem. In both cases the heating source was fire, usually produced by the presence of combustible fuels manually placed around the stem. In these experiments, either sections of freshly cut stems or live-standing trees were instrumented with heat flux sensors at the stem surface and thermocouples under the bark. Instrumentation for both the laboratory tests, and the field tests was similar. The experiments are described for both in paragraphs to follow.

The ponderosa pine measurements were conducted at the USDA Forest Service Research Laboratory in Missoula, MT, and have been summarized previously in a work seeking to validate the thermal transport model alone (Jones *et al.* 2004). The heat source for these experiments was generated by soaking cotton rope in kerosene until saturation, affixing the rope to the base of the stem, and igniting the kerosene-soaked rope. After ignition, the rope burned for 10–12 min, with peak heat fluxes typically of magnitude 40–45 $kW\ m^{-2}$. Timewise variations in both heat flux and cambial temperature were measured at 1-s intervals.

The chestnut oak and red maple experiments were conducted in the Vinton Furnace Experimental Forest in southern Ohio through a series of plot and rope burns, with instrumentation similar to the ponderosa pine experiments. Rectangular plots ranged from 3×7 m to 4×8 m. The fire was generated with a fuel bed consisting of leaves, straw, poplar excelsior, corn stalks, and wooden cribbing or a combination of these (Bova and Dickinson 2005). Fires were started by drip torch at one end of the plot and allowed to burn well past the target tree. The plots were constructed such that the approaching fire typically had ample time to reach a relatively uniform rate of spread. Experimental conditions were deliberately varied in the plot burns to produce a range of heating regimes, and the resulting peak total (convective plus radiative) heat fluxes were between 19 and 93 kW m^{-2} . In general, peak fluxes for packed leaf fuel beds were in the range $19\text{--}30 \text{ kW m}^{-2}$, while burns involving straw, wood, and/or excelsior fuel beds produced peak total fluxes in the $35\text{--}90 \text{ kW m}^{-2}$ range. The chestnut oak and red maple rope burns consisted of a single or double circumference length of fuel-oil soaked cotton rope coiled around the instrumented tree 8 cm below the heat flux sensor. The rope was attached using nails and the tree was instrumented identically to those studied in the plot burns, although the thermocouple probes were inserted ~ 5 cm to the side of the heat flux sensor so that the tips were positioned along the sensor's horizontal centerline. After ignition, the rope typically burned several minutes, in contrast to the relatively short flame residence times (10–20 s) in the plot burns. Additional details of the plot and rope burn experiments on chestnut oak and red maple may be found elsewhere (Bova and Dickinson 2005).

Stem diameter and bark thickness were carefully measured for all experiments, as were inner and outer bark moisture levels. The sample sizes for each species was necessarily finite, and reflected a random sample of trees in the stands investigated. The mean stem diameters for the red maple, chestnut oak, ponderosa pine and Douglas-fir samples were 10.4 cm, 7.9 cm, 15.2 cm, and 30.1 cm, and the average ratio of bark thickness-to-stem diameter for the samples was, respectively, 0.039, 0.079, 0.068, and 0.049. It is acknowledged that low-intensity, long-duration heating occurs when the duff layer around tree stems burns by smoldering combustion, rather than flaming combustion around the exposed portion of the tree stem. In fact, this may be as important to tree mortality prediction as flame-induced stem heating; however, in its current formulation, this model only simulates heating of the stem and subsequent cambial tissue mortality caused by flaming combustion around the exposed portion of the tree stem.

Characterization of stem survival and mortality

Following the controlled burns on chestnut oak and red maple, a tetrazolium trichloride (TTC) staining procedure

was employed to determine the radial penetration of thermally induced tissue necrosis, hereafter termed depth-of-kill (or kill depth). Live (respiring) plant tissues incubated in a TTC solution for ~ 18 h turn a deep pink color as the TTC is chemically reduced to formazan (Kayll 1963). Tissues that are not respiring remain unstained. Kill depths beyond the cambial tissue thus result in overall stem mortality. Depth-of-kill within the fire-exposed stem is indicated by the interface between pink and unstained tissue (Bova and Dickinson 2005). For the validation of the model, the depth-of-kill was measured from the surface of the stem (bark surface) to the transition between stained and unstained tissue in thin (~ 4 mm thick) cross-sections of heated tree stems. Measurements of depth-of-kill were made at heights of 10 cm and 20 cm above the soil surface (5 cm above and below the heat flux sensor) following the chestnut oak and red maple plot burn experiments. Three samples were collected in most instances; however, for some experiments, only two complete samples were available. The depth-of-kill measurements from each height were then averaged. Depth-of-kill measurements were made at locations that reflect a compromise between proximity to the heat flux measurements and sufficient distance from the heat flux sensors that their presence would not appreciably influence the thermal transport in the stem. Bark thickness measurements were made at the same locations as the depth-of-kill TTC stain measurements. Pre-burn bark thickness is the value required by the model; consequently, all bark thickness measurements were made prior to heating. This method represents a direct approach to measuring tissue necrosis. Depth-of-kill thus determined was used to evaluate the model accuracy for red maple and chestnut oak.

The TTC stain technique is not applicable to ponderosa pine or Douglas-fir because the staining is obscured by discoloration caused by a tissue wounding response. Rather, an alternative approach was employed to evaluate the model. The predicted and experimentally measured cambial temperature histories can be compared to assess the accuracy of the energy transport model, as has been done previously (Jones *et al.* 2004). However, survival/mortality was determined for both experiment and linked model prediction by numerically integrating Eqn (1), once subject to the experimentally measured cambial temperature history, and a second time subject to the predicted cambial temperature history. The result is two independent determinations of the cambial viability history, one based on measured temperature history and one based on the predicted cambial temperature history produced by the thermal model of Jones *et al.* (2004). The rate parameters for the respective species in Table 1 were used in the integration of Eqn (2). Although this is a less direct approach to determining fire-induced tissue necrosis than the staining technique, it nevertheless provides a test of the accuracy of the linked model for predicting stem survival or mortality in softwood species.

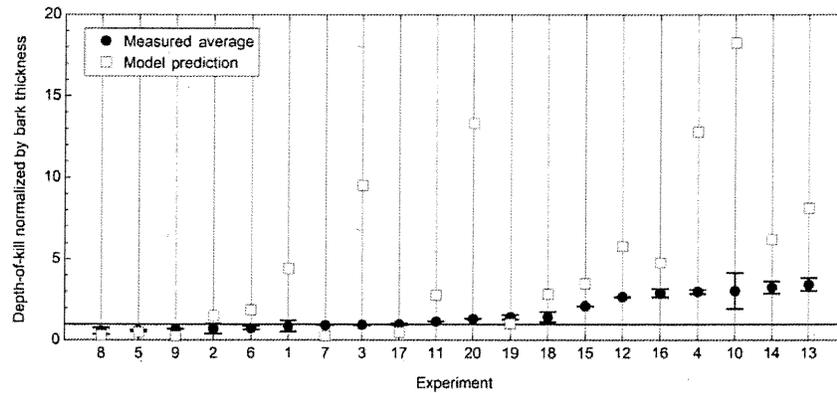


Fig. 1. Normalized depth-of-kill for red maple (*Acer rubrum*). Error bars indicate the minimum and maximum of the depth-of-kill measurements.

Results and discussion

Red maple

Red maple tissues stain readily in TTC, revealing the radial extent of thermal damage. As stated previously, stem survival/mortality is a binary phenomenon as absolute depth-of-kill becomes irrelevant for scenarios where thermal damage penetrates deeper than the vascular cambium. Therefore, it is instructive to examine the model's ability to predict survival/mortality. Figure 1 shows the predicted and measured depth-of-kill for the 20 red maple experiments, plotted in order of ascending measured depth-of-kill. The depth-of-kill shown represents the average of the two TTC stain measurements, and the error bars indicate the minimum and maximum of the two measurements. To facilitate comparison among the various tests for red maple trees of diameter and bark thickness ranging, respectively, from 4.1 to 15.0 cm and from 0.16 to 0.70 cm, the depth-of-kill for each experiment has been normalized by the average bark thickness measured for that experiment. Thus, a normalized depth-of-kill value of unity indicates that thermally induced tissue necrosis has penetrated to the cambium. Normalized depth-of-kill less than unity indicates that tissue death did not reach the cambium, while values greater than unity indicate that the tissues on the radial interior of the cambium (i.e. sapwood) have suffered necrosis. If, in Fig. 1, both the measured and predicted values of normalized depth-of-kill are on the same side of unity, the model correctly predicts stem survival/mortality. The figure shows that stem survival or mortality (model prediction and experimental data on the same side of the unity normalized depth-of-kill line in Fig. 1) is correctly predicted in 15 of the 20 tests. If the variation in depth-of-kill experimental measurements is accounted for (i.e. measured depth-of-kill measurements that straddle the cambial radial location), there are perhaps 18 of 20 correct predictions of survival or mortality for the red maple. The data of Fig. 1 indicate that, for this species and heating scenario, the linked stem heating

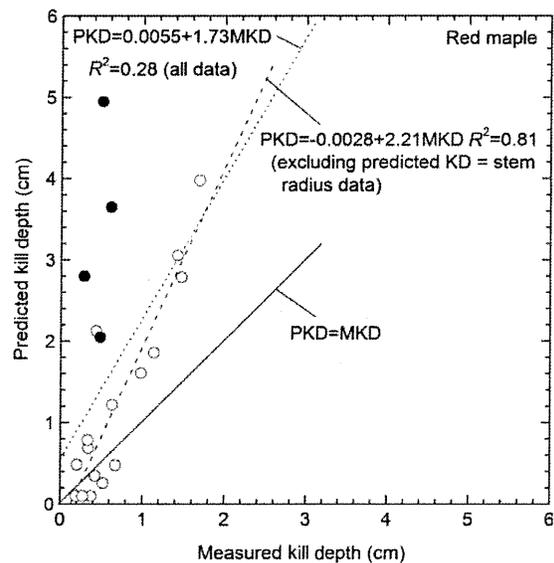


Fig. 2. Comparison between predicted and measured depth-of-kill for red maple (*Acer rubrum*). MKD, measured kill depth; PKD, predicted kill depth. The filled symbols are those for which the PKD reached the stem centerline.

and tissue necrosis model predicts stem mortality accurately in more than 75% of the cases.

The most rigorous test of the linked stem heating/tissue necrosis model accuracy is the comparison between predicted and experimentally measured kill depth (defined here as the radial location corresponding to $V = 0.5$). Figure 2 shows the predicted (absolute) kill depth for red maple *v.* measured kill depth. Perfect accuracy in model predictions would be reflected by the predicted kill depth (PKD) matching the measured kill depth (MKD), i.e. all data lying on the PKD = MKD line. Included in the figure are two linear regressions. The

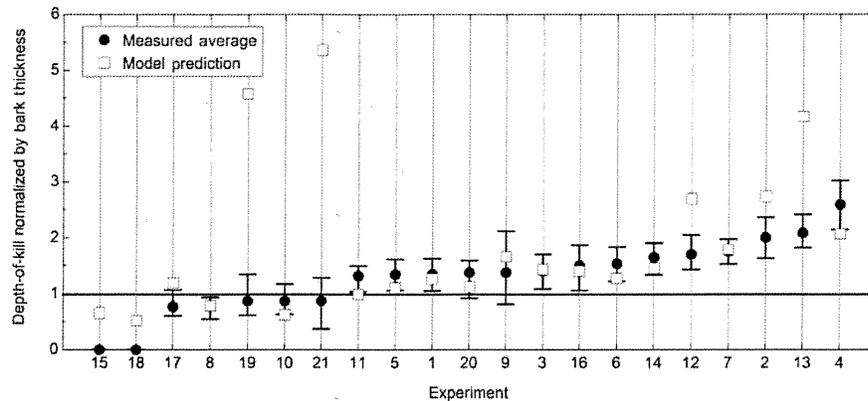


Fig. 3. Normalized depth-of-kill for chestnut oak (*Quercus prinus*). Error bars indicate the minimum and maximum of the depth-of-kill measurements.

first regression includes all predicted/measured kill depth data. The second regression excludes data for which predicted kill depth reached the stem centerline, which are shown as filled symbols. Agreement between model prediction and these experimental data may be compromised by one or more of the following:

Initial temperatures measured by a single thermocouple near the stem surface for two of these cases were abnormally high ($\geq 30^{\circ}\text{C}$), probably due to stem exposure to solar irradiation prior to the test burns. The temperatures throughout each stem were initialized with this single measured temperature, which was probably not representative of initial temperatures on the stem interior.

Two of the outlier data were for small (juvenile) stems, with bark thicknesses of 2 mm or less. As reported by Jones *et al.* (2004), juvenile stems exhibit different moisture profiles than mature stems, and this is more difficult to generalize. Further, the bark for such juvenile stems is much thinner than for more mature stems (< 2 mm). Thus, errors made in characterizing the bark thickness and its moisture content (which represents the primary resistance to penetration of energy to the cambium) in thin-bark stems may result in large errors in predicted depth-of-kill. The sensitivity of the predictive model to bark thickness, moisture content, and other model inputs will be explored in detail in a section to follow.

As will also be demonstrated shortly, the $V = 0.5$ criterion defining depth-of-kill may or may not be appropriate particularly for smaller stems where the temperature rises more uniformly under heating conditions. The sensitivity of this arbitrarily selected kill depth criterion was assessed by varying the $V = 0.5$ tissue necrosis threshold by 50%, which resulted in quite different predictions for kill depth particularly for small stems.

Both linear regressions shown in Fig. 2 exhibit zero intercept with reasonable accuracy. However, the slope for the

regression should be unity. The data and linear regressions reveal that, in general, the model over-predicts depth-of-kill (as seen by slope greater than unity) for the red maple, particularly at higher measured kill depths. As was reported previously, the stem heat transfer model is quite sensitive to a number of model inputs, with bark thermal conductivity and moisture content exercising a particularly strong influence on the predicted thermal transport (Jones *et al.* 2004). The error in predicted absolute depth-of-kill may be the result of inappropriate modeling of bark structure, uncertainty in thermophysical properties, inaccurate assumptions of initial temperature profiles, and/or assumed moisture distribution in the stem. As presented previously, red maple exhibits thinner bark than any of the other species studied in the investigation, suggesting that accuracy of model inputs is more critical for thin-bark species. Further, tissue necrosis model rate parameter κ for red maple is substantially higher than for the other three species in the temperature range of significant thermal damage, $45\text{--}60^{\circ}\text{C}$. Again, the sensitivity of predicted kill depth to model inputs will be fully characterized subsequently.

Chestnut oak

As indicated in the description of experimental procedure, the chestnut oak experimental results were obtained in a similar manner to those of red maple (Bova and Dickinson 2005). Figure 3 illustrates the normalized depth-of-kill predictions of chestnut oak survival/mortality, again in order of ascending measured depth-of-kill. As before, the error bars indicate the measured range of two or three depth-of-kill measurements. From a stem survival/mortality perspective, the results for chestnut oak yield 17 of 21 correct predictions of cambial death based on the average normalized measured depth-of-kill (measured and predicted kill depth on the same side of unity normalized depth-of-kill). The two cases for which measured depth-of-kill is zero (Experiments 15 and 18) reflect the fact that the TTC stain reveals nothing if the depth-of-kill does not reach the living inner bark layer.

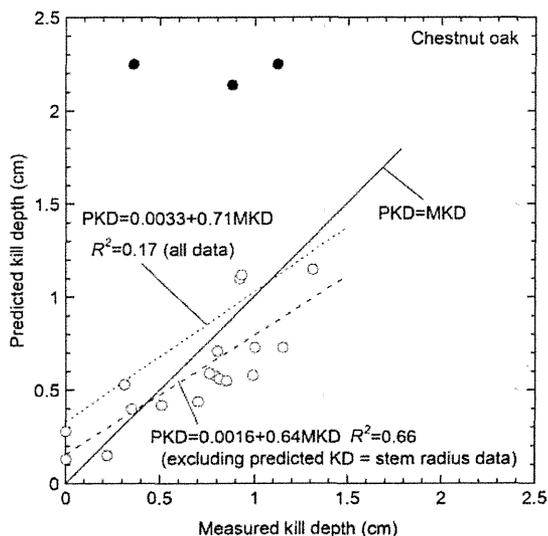


Fig. 4. Comparison between predicted and measured depth-of-kill for chestnut oak (*Quercus prinus*). MKD, measured kill depth; PKD, predicted kill depth. The filled symbols are those for which the PKD reached the stem centerline.

A comparison between predicted and measured absolute depth-of-kill is shown in Fig. 4. Again, perfect accuracy between model prediction and measured data would be indicated by experimental data lying on the $PKD = MKD$ line. Linear regressions of the data are also included in the figure. As was done for the red maple, the two regressions are (i) for all prediction data, and (ii) for data excluding the cases where predictions reached the stem centerline (again shown as filled symbols). These three outliers are juvenile stems, for which predictions may be compromised for the reasons explained previously. The calculated slope in both linear regressions is not radically different from unity. Figure 4 reveals that the linked thermal transport/tissue necrosis model predicts absolute depth-of-kill with better accuracy for chestnut oak than was observed in the red maple data. Absolute depth-of-kill is predicted to within the TTC stain test reproducibility in 11 of 21 cases for the chestnut oak.

Ponderosa pine

As stated previously, evaluation of the linked model predictions for ponderosa pine was not possible with the TTC stain technique. Figure 5 shows the predicted and measured cambial temperature histories for four of the 11 ponderosa pine experiments. Although not all of the 11 cases are included in Fig. 5, the cases shown are typical of the data. Experiments 4 and 6 (Fig. 5*a,b* respectively) are typical of the best agreement between measured and predicted cambial temperatures (Experiments 2, 3, 4, and 6 all exhibited good agreement). Experiments 7 and 8 (Fig. 5*c,d*) are representative of the worst agreement (Experiments 5, 7, 8, and 11 exhibited poor

agreement). Agreement in Experiments 1, 9, and 10 was marginal. In light of the mixed agreement in predicted temperatures, it is instructive to consider the results in terms of final cambial mortality. Although the TTC stain cannot readily reveal depth-of-kill for ponderosa pine, it is possible to draw some conclusions about the model's ability to correctly predict mortality based on simulation of the cambial viability history. Figure 6 illustrates a comparison between final (post-burn) cambial viability calculated according to Eqn (3) from predicated temperature histories (PCV) and that calculated from measured cambial temperature histories (MCV). Perfect accuracy in model predictions would be reflected by the cambial viability from predicted temperatures (PCV) matching the cambial viability determined from measured temperatures (MCV) (e.g. $PCV = MCV$ line). The final cambial viability is slightly over-predicted. The consistent under-prediction of cambial temperatures (Fig. 5) suggests that the discrepancy between predicted and measured cambial viability may be due to the thermal transport model, and that the tissue necrosis model will yield correct simulations of tissue impairment if the temperature history is correctly predicted. The prediction of stem survival/mortality for the 11 ponderosa pine experiments is shown in Fig. 7, where again the final cambial viability is calculated by the integration of the tissue impairment model, Eqn (1), subject to (i) the experimentally measured cambial temperature histories, and (ii) cambial temperature histories predicted by the stem heating model. The figure reveals that, for eight of the 11 ponderosa pine cases, the model's predictions of tree survival/mortality match those based on measured cambial temperature histories, as indicated by predicted and measured viability on the same side of the $V = 0.5$ line. It should be underlined that the viabilities shown on this plot do not indicate experimentally determined values but, rather, cambial viabilities calculated using the tissue impairment model based on measured cambial temperature histories.

Douglas-fir

Following the same linked model evaluation approach as that applied to ponderosa pine in the foregoing section, the Douglas-fir data reported by Jones *et al.* (2004) were used to explore the model's predictive accuracy for this species. Figure 8 shows the variation of average measured cambial temperatures with time (solid symbols) and predicted cambial temperatures as reported by Jones *et al.* (2004) for four different heating cases. The figure also illustrates corresponding cambial viability histories as predicted from (i) experimentally measured cambial temperatures (open symbols), and (ii) predicted cambial temperatures (lines). The solid and dashed lines (for both viability and temperature) are predictions based on the two different heat flux histories measured at the stem exterior surface during the experiments. As expected, cambial viability drops due to

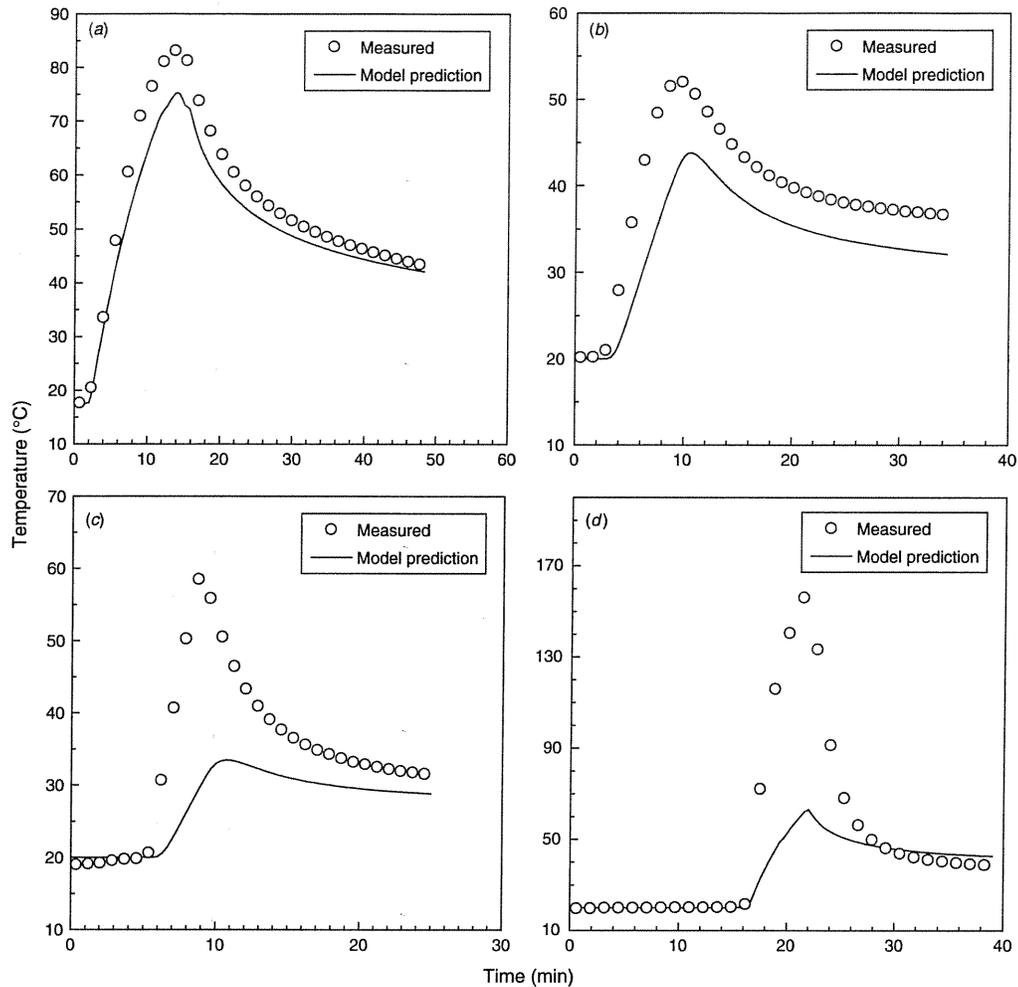


Fig. 5. Predicted and measured cambial temperatures for ponderosa pine (*Pinus ponderosa*). (a) Experiment 4; (b) Experiment 6; (c) Experiment 7; and (d) Experiment 8.

thermal damage as the temperature rises. Predictions of cambial viability based on predicted cambial temperatures (using the two different incident flux series as input) agree closely with predictions of viability determined from measured cambial temperatures in Cases (a) and (c). As expected from the temperature dependence of the tissue necrosis model, under-predictions in cambial temperature by the stem heating model in Cases (b) and (d) result in over-predictions of cambial viability. For the heating intensity and durations of these tests, cambial viability never reaches $V = 0.5$, defined arbitrarily here as the threshold for cambium necrosis. It is interesting to note that, even for these heating scenarios which resulted in relatively low temperatures (peak cambial temperature in the four cases is $\sim 45^\circ\text{C}$ – well below the 60°C threshold traditionally accepted for thermal tissue damage),

the rate-dependent tissue necrosis model predicts thermal damage, indicated by a loss in tissue viability ($V < 1$). For these low-intensity, longer duration heating scenarios, however, it is apparent that the choice of particular threshold viability for tissue necrosis may have a large effect on necrosis predictions. Further work is needed to characterize how tissues respond to long-term, low-temperature heating.

Sensitivity of predictions to model inputs

A model sensitivity study was undertaken to characterize the effect of potential errors in experimentally measured model inputs on kill depth predictions. Measurements of the stem bark thickness, inner bark moisture level, stem radius, initial stem temperature, and heat flux input history are required for linked model simulation. The heat flux input may in the

future be supplied by a fire behavior model. It should be mentioned that these inputs are in addition to the species-dependent rate parameters required for the tissue necrosis model. The sensitivity study undertaken here examined a number of experiments for the four species investigated, increasing and decreasing each required model input by an amount representative of a realistic error in the measurement.

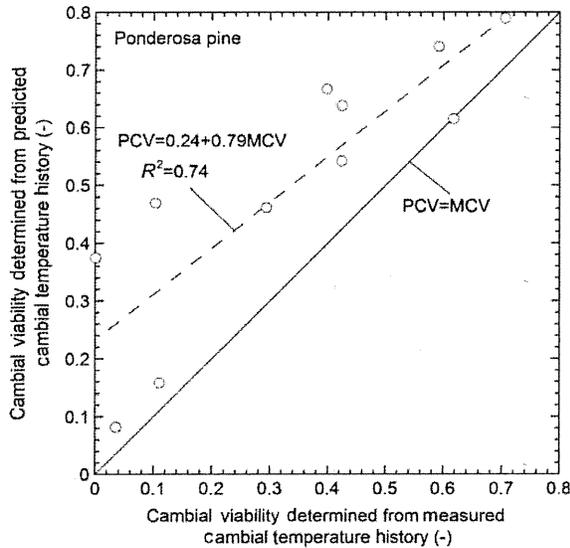


Fig. 6. Comparison between cambial viability determined from the predicted and measured cambial temperature history for ponderosa pine (*Pinus ponderosa*). MCV, cambial vitality based on measured cambial temperature history; PCV, cambial mortality based on predicted cambial temperature history.

Thus, predictions were conducted for a given experimental condition with the model input for bark thickness first increased by 1 mm, then decreased by 1 mm, to determine the effect of such a positive or negative change in bark thickness relative to the base case. Likewise, the inner bark moisture was increased/decreased by 25% (absolute), the stem radius by 5 mm, the initial stem temperature by 5°C, and the heat flux input to the stem by 10%. Results are shown in Fig. 9 for experiments with stems of a size near the mean of all experiments for each species (red maple, Experiment 18, 9.0 cm diameter; chestnut oak, Experiment 2, 9.5 cm diameter; ponderosa pine, Experiment 5, 20.8 cm diameter; and Douglas-fir, Experiment 1, 29.2 cm diameter). Results are presented in the left panel of Fig. 9 as the dependence of predicted kill depth on perturbed model input, $(KD - KD_{base\ case})$ in mm, where KD is the predicted kill depth for the perturbed model input, and $KD_{base\ case}$ is that for base case conditions (measured bark thickness, stem radius, inner bark moisture, stem initial temperature, and flux history). This representation explores the sensitivity in predicted absolute kill depth to model input, attempting to assess the impact of uncertainty in model inputs on kill depth predictions independent of variations in bark thickness across species. The right panel in the figure illustrates the sensitivity of prediction in kill depth normalized by bark thickness, $(KD - KD_{base\ case})/Bark\ thickness$. Defined in this fashion, the sensitivity $[(KD - KD_{base\ case})/Bark\ thickness]$ with magnitudes greater than unity indicates that the perturbation in specific model input produces differences in predicted kill depth greater than the bark thickness, and would thus certainly impact the mortality prediction. It should be noted that the sensitivity data in Fig. 9 are for a single experiment in each species class. A more complete sensitivity analysis was

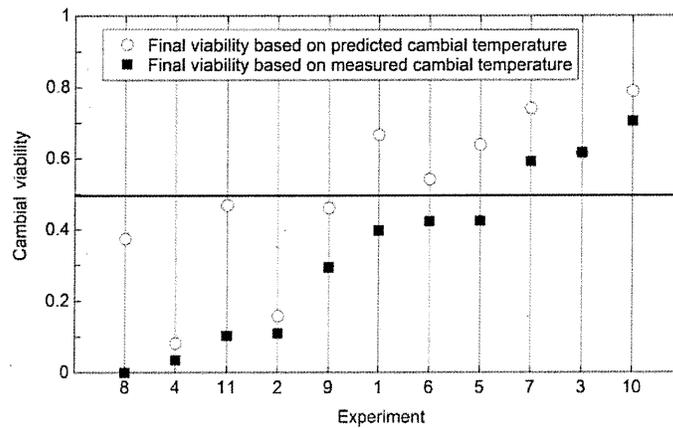


Fig. 7. Final cambial viability generated using both experimentally measured and predicted (stem heating model) cambial temperature histories for ponderosa pine (*Pinus ponderosa*).

not warranted, since (i) the sample size for each species was necessarily finite and rather small, and (ii) the species and heating regime are confounded in the data. Thus, species comparisons of sensitivity for different model inputs should be seen as suggestive rather than conclusive. However, the trends shown are based on data from stems that were representative of each species sample.

For the variations in model input perturbations chosen, the data of Fig. 9 suggest that kill depth predictions are quite sensitive to bark thickness, inner bark moisture, and initial stem temperature. Perhaps of greater interest is the relative magnitude of the kill depth prediction sensitivity among the different species, a result that justifies further study. The predictions for the representative softwood species stems (ponderosa pine and Douglas-fir) appear to be rather insensitive to model inputs, with $KD - KD_{base\ case}$ generally less than 1 mm, and $(KD - KD_{base\ case})/Bark\ thickness$ less than 10%. Predictions for the representative chestnut oak stem are somewhat more sensitive to model inputs than the softwoods, although the normalized sensitivity $(KD - KD_{base\ case})/Bark\ thickness$ is still generally less than 50%. Kill depth predictions for representative red maple stems exhibit the highest sensitivity, with absolute sensitivities, $KD - KD_{base\ case}$, as high as 10 mm, and normalized sensitivities, $(KD - KD_{base\ case})/Bark\ thickness$, in the range 100% to over 300% for all model inputs shown. In general, red maple stems exhibited rather thin bark and relative low moisture. Further, as stated previously, the rate constant κ for red maple is highest of all four species in the temperature range of significant thermal damage, 45–60°C.

Combined, these characteristics may render red maple particularly susceptible to significant variations in predicted kill depth for rather small perturbations in prescribed model input (for the range of stem sizes studied here). These data suggest that, for the general size ranges explored, model inputs for red maple must be known with much higher accuracy than for the other three species studied. It may thus be concluded that the discrepancy observed between model prediction and experimental measurement presented in Figs 1 and 2 for red maple is the result of uncertainty in model inputs. Further, if the results of Fig. 9 are representative of the species in general, red maple is more susceptible to thermally induced stem mortality than the other species in the size ranges for each investigated, since small tree-to-tree variations in bark thickness, bark moisture, stem diameter, initial stem temperature and heating level yield large variations in predicted penetration of thermally induced tissue necrosis.

The dependence of the kill depth prediction sensitivity to stem size is also of interest, and normalized data $(KD - KD_{base\ case})/Bark\ thickness$ are illustrated in Fig. 10 for red maple of stem diameters 4.1 cm, 9.0 cm, and 15.0 cm. The red maple data presented in the figure are generally representative of the trend observed in model sensitivity with stem diameter observed in the limited sample populations for the other three species. For the smallest-diameter red maple stem (4.1 cm), the predicted penetration of tissue necrosis for the base case reached the stem center ($KD = \text{stem radius}$, r_o), so changes in model input that would result in greater kill depth are indicated in the figure as ' $KD = r_o$ '. The data

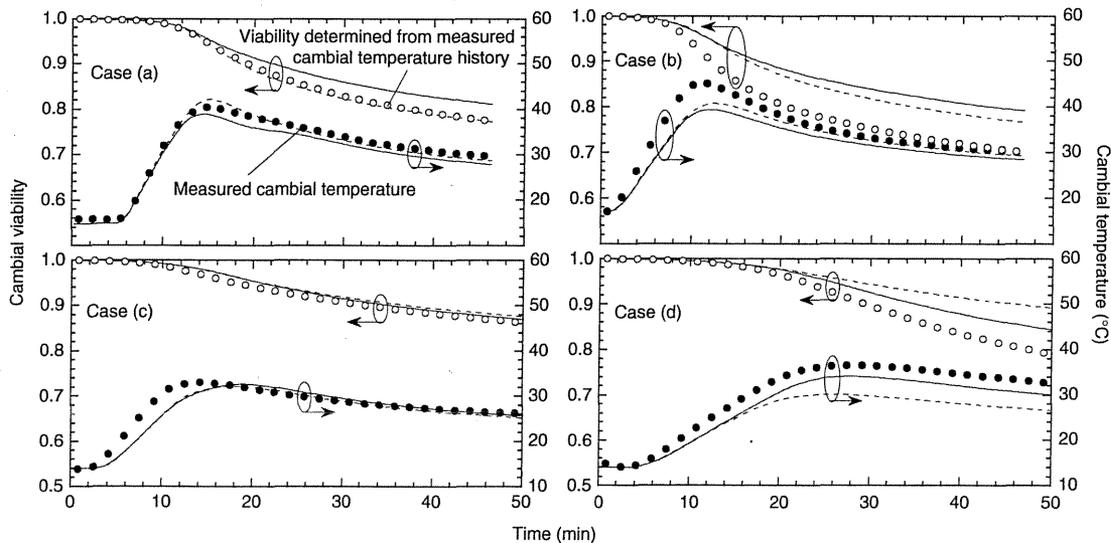


Fig. 8. Measured cambial temperatures (\bullet) and predicted cambial temperatures for Douglas-fir (*Pseudotsuga menziesii*) from Jones *et al.* (2004), and cambial viability histories as predicted from measured cambial temperature (\circ) and predicted cambial temperatures. The solid and dashed lines (for both viability and temperature) are predictions based on two different incident flux series measured during the experiments. The ovals and attached arrows indicate which axis applies to which data.

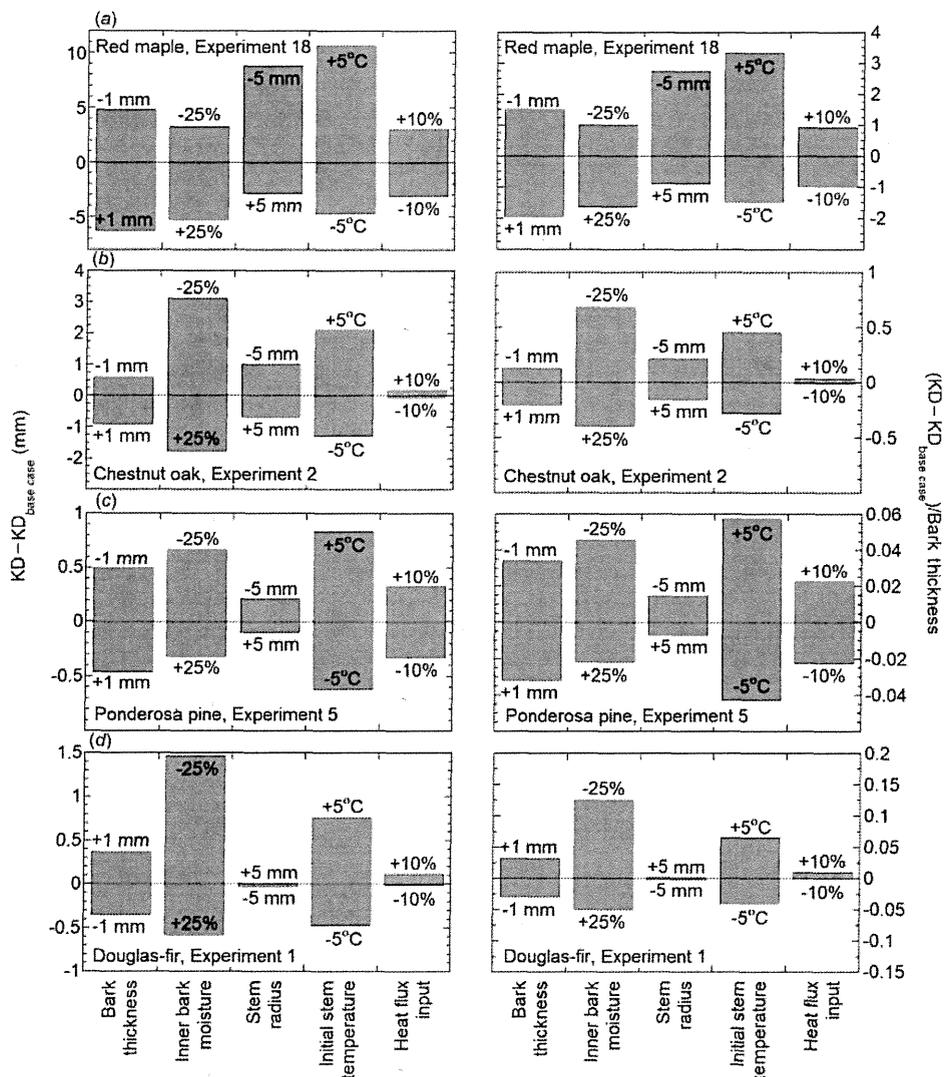


Fig. 9. Sensitivity of linked model prediction of kill depth for (a) red maple (*Acer rubrum*, Experiment 18), (b) chestnut oak (*Quercus prinus*, Experiment 2), (c) ponderosa pine (*Pinus ponderosa*, Experiment 5), and (d) Douglas-fir (*Pseudotsuga menziesii*, Experiment 1). KD is the predicted kill depth for the perturbed model input, while $KD_{base\ case}$ is that for base case conditions (measured bark thickness, stem radius, inner bark moisture, stem initial temperature, and flux history).

of Fig. 10 reveal that the sensitivity of predicted kill depth to model inputs increases rather significantly as the stem diameter decreases. Whereas for the 15.0 cm diameter red maple sample the maximum deviation from base case kill depth prediction never exceeded one bark thickness (for the model input perturbations studied), the corresponding normalized kill depth sensitivity for the 4.1 cm diameter was often between 300 and 800% of the base case. This confirms that juvenile stems are significantly more vulnerable to fire-induced mortality and, further, reveals the difficulty in making stem mortality predictions for juvenile stems.

Inaccuracy in the combined models comes from uncertainty in the experimental measurement of model input data, approximation in the stem heating model, and approximation in the tissue necrosis model and error in the associated parameter measurements. Trees are composed of anisotropic, non-homogeneous materials for which physical properties are poorly understood. Even the geometry of the tree stem poses difficulty for measurements; the insulating bark layer can have large variations in thickness. The fire that is heating the stem is almost always highly turbulent and variable in intensity. Error and approximation in the stem heating model

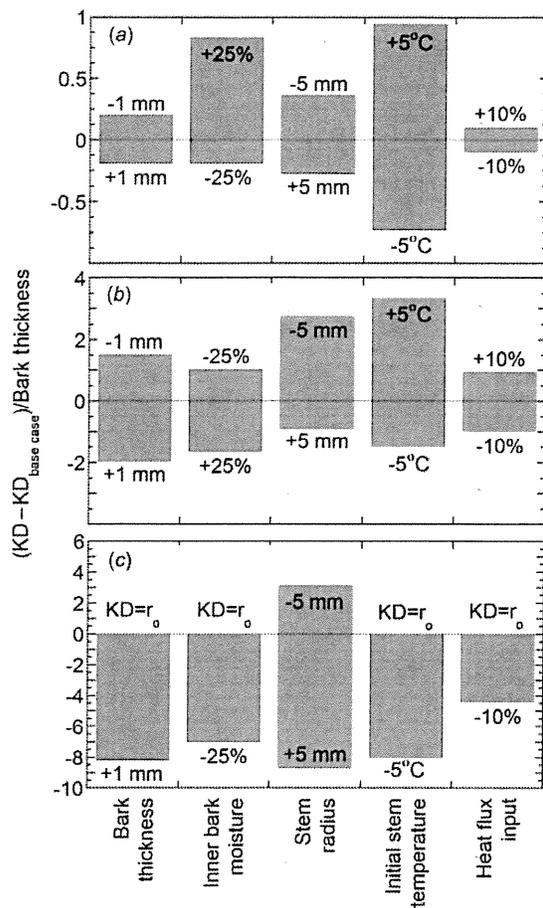


Fig. 10. Sensitivity of linked model prediction of kill depth for red maple (*Acer rubrum*) of three different diameters: (a) 15.0 cm, (b) 9.0 cm, and (c) 4.1 cm. KD is the predicted kill depth for the perturbed model input, while $KD_{base\ case}$ is that for base case conditions (measured bark thickness, stem radius, inner bark moisture, stem initial temperature, and flux history).

have been discussed in detail by Jones *et al.* (2004), and limited parametric studies as part of this work have revealed sensitivity of kill depth predictions to thermal transport model inputs. Error and approximation associated with the tissue necrosis model comes from tree-to-tree variation in tolerance to elevated temperatures and the approximate correspondence between the tissue necrosis model and the actual necrosis process. The errors associated with the stem heating model, tissue necrosis model, and experimental measurement can be cumulative or multiplicative. However, the data suggest that, even with the uncertainty inherent in the process, the linked models have the ability to correctly predict cambial tissue necrosis most of the time.

Conclusions

The stem heating model previously outlined by Jones *et al.* (2004) has been linked to the tissue necrosis model of Dickinson and Johnson (2004). The resulting model makes it possible to predict the decline in cambial tissue viability at any location in the stem based on an imposed time-varying heat flux at the exterior surface of the stem. This model is unique relative to currently used tree mortality prediction tools in that it has been developed primarily from a physics (deterministic) basis rather than an empirical basis. One of the limitations of such a model is that it requires physical parameters for the species of interest (i.e. thermal conductivity, moisture distribution, density, mortality rate parameters). There is a paucity of such data. Experimental data from red maple, chestnut oak, Douglas-fir, and ponderosa pine were used to evaluate model performance. In its current form the model is one-dimensional and therefore provides a local estimate of tissue survival/mortality around a stem. The model does not provide estimates of the extent of cambial tissue mortality, which is needed to estimate tree survival/mortality. If the model is to be used to estimate whole tree survival or mortality it must either be applied at many discrete locations around the stem or simulate the location with the lowest heat flux and subsequent injury, implying that all other peripheral locations will sustain damage. The results of the linked model presented herein indicate a better than 75% success rate in predicting local cambial mortality, on par with previously published empirical models. A limited sensitivity analysis based on representative stems suggests that predicted kill depth exhibits greater sensitivity to model input parameters for red maple than for the other three species explored, as well as for stems of decreasing diameter. The results of this work suggest that, with more accurate input data for the thermal transport model, the linked model predictions may be further improved. If indeed a deterministic model like that presented here can provide tree mortality estimates with accuracy comparable to empirically based approaches, it opens the door to the possibility of developing a comprehensive tree and stand fire-induced mortality prediction system that can be applied across a wide variety of species.

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References

- Bova AS, Dickinson MB (2005) Linking surface fire behavior, stem heating, and tissue necrosis. *Canadian Journal of Forest Research* 35, 814–822.

- Brown JK, DeByle NV (1987) Fire damage, mortality, and suckering in aspen. *Canadian Journal of Forest Research* **17**, 1100–1109.
- Caldwell CR (1993) Estimation and analysis of cucumber (*Cucumis sativus* L.) leaf cellular heat sensitivity. *Plant Physiology* **101**, 939–945.
- Costa JJ, Oliveira LA, Viegas DX, Neta LP (1990) On the temperature distribution inside a tree under fire conditions. In 'Proceedings of the international conference on forest fire research, 19–22 November 1990, Coimbra, Portugal'. pp. c14.1–c14.16.
- Dickinson MB (2002) Heat transfer and vascular cambium necrosis in the boles of trees during surface fires. In 'Forest fire research and wildland fire safety'. (Ed. X Viegas) pp. 1–10. (Millpress: Rotterdam) [CD-ROM]
- Dickinson MB, Johnson EA (2001) Fire effects on trees. In 'Forest fires: behavior and ecological effects'. (Eds EA Johnson, K Miyanishi) pp. 477–525. (Academic Press: New York)
- Dickinson MB, Johnson EA (2004) Temperature-dependent rate models of vascular cambium cell mortality. *Canadian Journal of Forest Research* **34**, 546–559. doi:10.1139/X03-223
- Dickinson MB, Jolliff J, Bova AS (2004) Vascular cambium necrosis in forest fires: using hyperbolic temperature regimes to estimate parameters of a tissue-response model. *Australian Journal of Botany* **52**, 757–763. doi:10.1071/BT03111
- Durcey M, Duhoux F, Huc R, Rigolot E (1996) The ecophysiological and growth responses of Aleppo pine (*Pinus halepensis*) to controlled heating applied to the base of the trunk. *Canadian Journal of Forest Research* **26**, 1366–1374.
- Fahnestock GR, Hare RC (1964) Heating of tree trunks in surface fires. *Journal of Forestry* **62**, 799–805.
- Flint HR (1925) 'Fire resistance of northern Rocky Mountain conifers.' USDA Forest Service, Northern Rocky Mountain Forest Experiment Station Applied Forestry Note 61. Missoula, MT.
- Gill AM (1974) Toward an understanding of fire-scar formation: field observation and laboratory simulation. *Forest Science* **20**, 198–205.
- Gill M, Ashton DH (1968) The role of bark type in relative tolerance to fire of three Central Victorian eucalypts. *Australian Journal of Botany* **16**, 491–498.
- Greene TA, Schilling CL (1987) Predicting girdling probability for pine and hardwood saplings in low-intensity backfires. *Forest Science* **33**, 1010–1021.
- Gutsell SL, Johnson EA (1996) How fire scars are formed: coupling a disturbance process to its ecological effect. *Canadian Journal of Forest Research* **26**, 166–174.
- Hare RC (1961) 'Heat effects on living plants.' USDA Forest Service, Southern Forest Experimental Station Occasional Paper 183. New Orleans, LA.
- Hare RC (1965a) Contribution of bark to fire resistance of southern trees. *Journal of Forestry* **63**, 248–251.
- Hare RC (1965b) Bark surface and cambial temperatures in simulated forest fires. *Journal of Forestry* **63**, 437–440.
- Harrington MG (1987) Ponderosa pine mortality from spring, summer, and fall crown scorching. *Western Journal of Applied Forestry* **2**, 14–16.
- Harrington MG (1993) Predicting *Pinus ponderosa* mortality from dormant season and growing season fire injury. *International Journal of Wildland Fire* **3**, 65–72.
- Hengst GE, Dawson JO (1994) Bark properties and fire resistance of selected tree species from the central hardwood region of North America. *Canadian Journal of Forest Research* **24**, 688–696.
- Johnson FH, Eyring H, Stover BJ (1974) 'The theory of rate processes in biology and medicine.' (John Wiley and Sons: New York)
- Jones JL (2003) Development of a model for prediction of stem mortality under fire conditions. MS Thesis, Brigham Young University, Provo, UT.
- Jones JL, Webb BW, Jimenez D, Reardon J, Butler B (2004) Development of an advanced one-dimensional stem heating model for application in surface fires. *Canadian Journal of Forest Research* **34**, 20–30. doi:10.1139/X03-187
- Kayll AJ (1963) 'Heat tolerance of Scots pine seedling cambium using tetrazolium chloride to test viability.' Department of Forestry Publication No. 1006. (Canada Department of Forestry, Forest Research Branch: Ottawa, ON)
- Keane RE (1991) 'Plant adaptation engineering—are trees optimally protected from girdling by fire?' An Environmental Biophysics Project. March. USDA Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, Missoula, MT.
- Lamb FM, Marden RM (1968) Bark specific gravities of selected Minnesota tree species. *Forest Products Journal* **18**, 77–82.
- Levitt J (1980) 'Responses of plants to environmental stresses. Volume 1: Chilling, freezing, and high temperature stresses.' 2nd edn. (Academic Press: New York)
- Lorenz R (1939) 'High temperature tolerance of forest trees.' Technical Bulletin 141. (University of Minnesota Agricultural Experiment Station: St Paul)
- Martin RE (1963) A basic approach to fire injury of tree stems. In 'Proceedings of the 2nd annual tall timbers ecology Conference 14–15 March 1963, Tallahassee, FL. Volume 2, pp. 151–162. (Tall Timbers Research Station: Tallahassee, FL)
- Martin RE, Crist JB (1968) Selected physical-mechanical properties of eastern tree barks. *Forest Products Journal* **18**, 54–60.
- Martin RE, Davis LS (1961) 'Temperature near the ground during prescribed burning.' Papers of the Michigan Academy of Science, Arts and Letters. Vol. XLVI.
- McArthur AG (1967) 'Fire behaviour in eucalypt forests.' Leaflet No 107. (Forest Research Institute, Forestry and Timber Bureau: Canberra, Australia)
- McCarthy EF, Sims IH (1935) The relation between tree size and mortality caused by fire in southern Appalachian hardwoods. *Journal of Forestry* **33**, 155–157.
- Mercer GN, Weber RO (2001) Fire plumes. In 'Forest fires: behavior and ecological effects'. (Eds EA Johnson, K Miyanishi) pp. 225–255. (Academic Press: New York)
- Mercer GN, Gill AM, Weber RO (1994) A time-dependent model of fire impact on seed survival in woody fruits. *Australian Journal of Botany* **42**, 71–81.
- Nelson RM (1952) 'Observations of heat tolerance of southern pine needles.' USDA Forest Service, Southeastern Forest Experiment Station Paper 14. Asheville, NC.
- Peterson DL, Arbaugh MJ (1986) Postfire survival of Douglas-fir and lodgepole pine: Comparing the effects of crown and bole damage. *Canadian Journal of Forest Research* **15**, 596–598.
- Peterson DL, Arbaugh MJ (1989) Estimating postfire survival of Douglas-fir in the Cascade Range. *Canadian Journal of Forest Research* **19**, 530–533.
- Peterson DL, Ryan KC (1986) Modeling postfire mortality for long-range planning. *Environmental Management* **10**, 797–808. doi:10.1007/BF01867732
- Potter BE, Andresen JA (2002) A finite-difference model of temperatures and heat flow within a tree stem. *Canadian Journal of Forest Research* **32**, 548–555. doi:10.1139/X01-226
- Rego F, Rigolot E (1990) Heat transfer through bark—a simple predictive model. In 'Fire in ecosystem dynamics'. (Eds JG Goldammer, MJ Perkins) pp. 157–161. (SPB Academic Publishing: The Hague)
- Russell MS, Dawson JO (1994) The effects of artificial burning on cambial tissue of selected tree species of the central hardwood region of North America. In '1994 Proceedings

- of the North American Conference on Savannas and Barrens'. (US Environmental Protection Agency: Chicago, IL) Available at <http://www.epa.gov/glnpo/ecopage/upland/oak/oak94/Proceedings/> [Verified 20 June 2002]
- Ryan KC (1998) Analysis of the relative value of morphological variables in predicting fire-caused tree mortality. In 'Proceedings of the III international conference on forest fire research and 14th conference on fire and forest meteorology, Luso-Coimbra, Portugal'. (Ed. DX Viegas) pp. 1511–1526. (ADAI-Associação para o Desenvolvimento da Aerodinâmica Industrial: Coimbra)
- Ryan KC, Frandsen WH (1991) Basal injury from smoldering fires in mature *Pinus ponderosa* Laws. *International Journal of Wildland Fire* 1, 107–118.
- Ryan KC, Reinhardt ED (1988) Predicting postfire mortality of seven western conifers. *Canadian Journal of Forest Research* 18, 1291–1297.
- Saveland JM, Bakken SR, Neuenschwander LF (1990) 'Predicting mortality from scorch height from prescribed burning for ponderosa pine in Northern Idaho.' University of Idaho College of Forestry, Wildlife and Range Sciences Bulletin Number 53. Moscow, Idaho. pp. 9–18.
- Shirley HL (1936) Lethal high temperatures for conifers, and the cooling effect of transpiration. *Journal of Agricultural Research* 53, 239–258.
- Silen R (1960) Lethal surface temperatures and their interpretation for Douglas-fir. Doctoral Dissertation, Oregon State University, Corvallis, OR.
- Spalt KW, Reifsnnyder WE (1962) 'Bark characteristics and fire resistance: a literature survey.' Southern Forest Experiment Station. (US Department of Agriculture in cooperation with the School of Forestry, Yale University)
- Starker TJ (1934) Fire resistance in the forest. *Journal of Forestry* 32, 462–467.
- Steward FR, Peter S, Richon JB (1990) A method for predicting the depth of lethal heat penetration into mineral soils exposed to fires of various intensities. *Canadian Journal of Forest Research* 20, 919–926.
- Tunstall BR, Walker J, Gill AM (1976) Temperature distribution around synthetic trees during grass fires. *Forest Science* 22, 269–276.
- Vines RG (1968) Heat transfer through bark, and the resistance of trees to fire. *Australian Journal of Botany* 16, 499–514.
- Wyant JG, Omi PN, Laven RD (1986) Fire induced tree mortality in a Colorado ponderosa pine/Douglas-fir stand. *Forest Science* 32, 49–59.