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Bark heat resistance of small trees in Californian mixed conifer forests: testing some model assumptions

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Abstract

An essential component to models of fire-caused tree mortality is an assessment of cambial damage. Cambial heat resistance has been traditionally measured in large overstory trees with thick bark, although small trees have thinner bark and thus are more sensitive to fire. We undertook this study to determine if current models of bark heat transfer are applicable to small trees (<20 cm diameter at breast height (dbh)). We performed this work in situ on four common species in the mixed conifer forests of the Sierra Nevada, California.

The allometric relationship between bole diameter and bark thickness for each species was linear, even for very small trees (5 cm dbh). Heating experiments demonstrated that bark thickness was the primary determinant of cambial heat resistance. We found only slight, but statistically significant, among species differences in bark thermal properties. Our most significant finding was that small trees were more resistant to heating than expected from commonly used models of bark heat transfer. Our results may differ from those of existing models because we found smaller trees to have a greater proportion of inner bark, which appears to have superior insulating properties compared to outer bark. From a management perspective, growth projections suggest that a 50-year fire-free interval may allow some fire intolerant species to achieve at least some degree of cambial heat resistance in the Sierra Nevada.

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Keywords: Cambial damage; Fire effects; Mortality models; Prescribed fire

1. Introduction

Fire is a long-standing feature of many forest types, and is thought to play an important role in determining the structure and successional pathways of forests (Agee, 1993). One of the most obvious effects of burning is an increase in post-fire tree mortality. Trees

subjected to burning may be directly or indirectly killed from the effects of multiple fire-caused injuries. Fire may simultaneously result in damage to crowns, cambial tissue in the stem, and roots. There is a clear relationship between the severity of these injuries and probabilities of post-fire tree mortality (e.g., Peterson and Ryan, 1986; Ryan and Reinhardt, 1988; Ryan et al., 1988; Swezy and Agee, 1991; Regelbrugge and Conard, 1993, and many others).

Developing an accurate understanding of fire-caused tree mortality depends largely on knowing

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exactly how fire causes damage to plant tissues (Dickinson and Johnson, 2001). The process of cambial damage may be especially important in the context of prescription fire, where relatively low fire intensities generally do not result in large amounts of crown damage. Of particular interest is how the process of cambial damage occurs in small trees, because reducing densities of small trees is often a target of management actions. Little work, however, has been done on the cambial heat resistance of small trees (<20 cm diameter at breast height (dbh)) in any community.

Fires typically damage cambial tissues in tree stems by conductive heat transfer (Dickinson and Johnson, 2001). Heat stress to cambial tissues causes cell necrosis, with extensive damage resulting in stem girdling and tree death. The main source of cambial protection from fire is the insulating layer of bark. Thermal diffusivity of bark, the ease in which a temperature pulse moves through a given thickness of bark, decreases with increasing bark density and increasing moisture content (Reifsnyder et al., 1967). Hare (1965) found significant among species differences in bark insulating ability independent of thickness due to varying bark physical properties. The importance of these differences, however, is unclear due to relatively large interspecific differences in bark thickness. Most researchers assume that species differences in bark thermal properties are negligible, so that the de facto determinant of cambial heat protection is bark thickness alone (Vines, 1968; Uhl and Kaufmann, 1990; Hengst and Dawson, 1994).

Researchers modeling heat transfer in the bole have often relied on one-dimensional heat transfer equations (Dickinson and Johnson, 2001). This is an analytically simple approach that describes conductive heat flow in one direction. These models often simplified to ignore thermal contact resistance (i.e., resistance to heat transfer at the bark surface due to the presence of air pockets along the interface), and can be written as

$$\frac{\theta}{\theta_0} = \operatorname{erf}\left(\frac{x}{2\sqrt{\alpha\tau}}\right) \quad (1)$$

where x is the bark thickness, α the bark thermal diffusivity, τ the duration of heating, and erf the Gaussian error function found in texts of mathematical tables (Abramowitz and Stegun, 1964). The value of

the Gaussian error function depends on the excess temperature ratio, θ/θ_0 , which is defined as

$$\frac{\theta}{\theta_0} = \frac{T - T_f}{T_0 - T_f} \quad (2)$$

where T is the temperature of the cambium at bark depth x , T_0 the ambient temperature, and T_f the flame temperature. If we assume that cambial cell death occurs at a certain temperature threshold, rearrangement of Eq. (1) allows us to derive the relationship between bark thickness and the amount of time needed to kill the cambium given a fire with a constant temperature. For example, Peterson and Ryan (1986) found this relationship to be

$$\tau_c = 2.9x^2 \quad (3)$$

where τ_c is the time (in min) required to kill the cambium, and x the bark thickness in cm, given $\alpha = 0.06 \text{ cm}^2 \text{ min}^{-1}$ (from Martin, 1963), $T = 60 \text{ }^\circ\text{C}$, $T_0 = 20 \text{ }^\circ\text{C}$, and $T_f = 500 \text{ }^\circ\text{C}$. This result has a good deal of empirical support, with many researchers finding the amount of insulation afforded by bark to be roughly proportional to the square of bark thickness (Hare, 1965; Vines, 1968; Uhl and Kaufmann, 1990; Hengst and Dawson, 1994). Thus, heat resistance of the bole is achieved by having thick bark, and interspecific differences are mainly attributed to the fact that some species produce thicker bark than others at similar bole diameters.

The analytically simple one-dimensional heat transfer equations rest on a number of simplifying assumptions. The most important assumptions involve the use of a simplified geometry, known as a semi-infinite solid. A semi-infinite solid is an idealized shape that has uniform thermal properties and extends to infinity in all but one direction, and is thus characterized by one identifiable surface. One-dimensional models therefore assume: (1) heat transfer occurs only at right angles to the bark surface; (2) thermal properties are uniform within bark tissues; and (3) there is no contact resistance between the flames and the bark surface, so that the bark surfaces instantaneously reach flame temperatures when exposed to fire. Open flames have high convective heat transfer rates, so this final assumption is probably not unreasonable in many circumstances (Dickinson and Johnson, 2001). We know each of these assumptions misstates the actual mechanisms of bark heat transfer. In spite of these

limitations, this approach adequately approximates conductive heat transfer in many situations (Incropera and DeWitt, 1996).

There is reason to believe, however, that these assumptions may not be suitable when describing bark heat transfer in small trees. Small stem diameters may require us to consider conductive heat flow from other directions in addition to right angles from the bark surface, forcing us to adopt two-dimensional models (e.g., Costa et al., 1991). Further, bark development is a complex process (Esau, 1965), perhaps leading to differences in bark physical characteristics that may affect thermal properties as growth progresses. Particularly important may be the relative thickness of inner bark compared to the thickness of the outer bark layer. Inner bark is known to be much more dense and have a higher moisture content compared to the corky outer bark (Reifsnyder et al., 1967), which would logically lead to differences in thermal properties. Finally, the effects of contact resistance, which may be safely ignored for large trees, may be important for small trees. Small trees with thin bark imply short heating durations needed to damage cambial tissues, so the lag time before bark surface temperatures reach flame temperatures may become significant relative to overall heating times.

We sought to address two basic questions concerning bark heat resistance in small trees. First, are there detectable interspecific differences in bark heat resistance in small trees, and what bark properties might account for these differences? Second, how well do one-dimensional models of bark heat transfer apply to small trees? We attempted to answer these questions by field and laboratory measurements of bark physical properties. We also subjected trees in situ to experimental heating trials using a method that attempts to mimic as closely as possible the conditions assumed by one-dimensional heat flow models.

2. Methods

2.1. Study sites

We conducted measurements in the white fir mixed conifer forests of the central Sierra Nevada, California. We chose these forests as our study system because fires are common in this forest type and there

exists a combination of naturally co-occurring species that vary in bark thickness and expected fire resistance. The climate of this area is Mediterranean, with long, dry summers and wet, snowy winters. A large proportion of the precipitation in these forests arrives in the form of snow (Major, 1977). The average January and July air temperatures for this region are 2 and 22 °C, respectively. The soils of this region are primarily derived from granite. White fir mixed conifer forests are found at elevations between 1250 and 2200 m along the western slope of the Sierra Nevada (Rundel et al., 1977). The forests are dominated by *Abies concolor* (Gord. and Glend.) Lindley (white fir), with most areas showing an inverse J-shaped stem size distribution for this species. *Calocedrus decurrens* (Torrey) Florin (incense cedar), *Pinus ponderosa* Laws. (ponderosa pine), and *Pinus lambertiana* Douglas (sugar pine) are also typically found in significant numbers. *Quercus kelloggii* Newb. (black oak), and *Pseudotsuga menziesii* [Mirbel] Franco var. *menziesii* (Douglas fir) are common in lower elevation stands of this forest type. Shrub and herbaceous cover are generally low in these forests, with litter and duff compromising the majority of the ground cover.

We took measurements of incense cedar, ponderosa pine and white fir at Calaveras Big Trees State Park, California. Douglas fir is not found at this site, though in other respects the stands are representative of white fir mixed conifer forest across the western slope of the Sierra Nevada. We sampled Douglas fir at Jenkenson Lake in the El Dorado National Forest, California, approximately 50 km north of Calaveras Big Trees State Park.

We performed the sampling primarily during the spring (April through June), with some additional measurements taken in the fall (September and October). Tree stem diameter was measured basally (10 cm above the ground) and at breast height. We measured basal and breast height bark thickness to the nearest 1 mm on at least 45 individual trees of sizes <50 cm dbh using a standard bark gauge. Roughly 20 trees of each species were haphazardly selected to test bark physical properties and cambial heat resistance.

We expected white fir to be the least fire-tolerant tree species, followed by incense cedar, ponderosa pine and Douglas fir. These fire tolerance ratings arise from our own experience in the field and from published accounts of fire tolerances (Peterson and Ryan,

1986; Thomas and Agee, 1986; Ryan and Reinhardt, 1988).

2.2. Measurement of bark physical properties

At each selected tree a 2 cm × 2 cm bark sample was taken. We measured bark thickness to the nearest 0.01 cm using calipers. Fresh bark weight was determined immediately in the field. Samples were stored in airtight plastic bags and stored frozen until laboratory analysis. Samples were placed in a drying oven for 48 h at 60 °C to insure a uniform drying. Comparisons of fresh and oven dry weights were then used to calculate moisture content on a dry mass basis [percentage of moisture = ((fresh mass – dry mass)/dry mass) × 100]. Dry bark volume was measured by the mass displacement of water method and used to calculate bark density (g cm⁻³) (Hengst and Dawson, 1994). Although immersion times were short, the bark samples may have absorbed water during these measurements, so the exact values of the density measurements should be viewed with some caution.

2.3. Experimental heat applications

We measured in situ responses to bark surface heating using a 7 cm × 10 cm electrical copper heating pad powered by a portable generator. Initial trials using the wick method (e.g., Uhl and Kaufmann, 1990; Hengst and Dawson, 1994) produced heat outputs with unacceptably high levels of variation for our needs. To measure cambial temperatures during the heating trials a sheathed type J thermocouple (Inconel Corporation) was inserted between the bark and the wood 5–10 cm upward under the bark in the gap left from the bark sample. To measure outside bark temperatures a second thermocouple was placed on the outside of the bark at an area visually estimated to be directly opposite the inner bark thermocouple. Immediately before each measurement ambient air and cambial temperatures were recorded. The flexible copper heating pad was pre-heated to 400 °C and was then tightly placed over the thermocouples. A constant 400 °C was applied to the outer bark by means of a digital switch that regulated the power supply to the heating pad. This design allowed for a precise control over the outer bark temperatures. Inner and outer bark temperatures were recorded every 5 s, using a Campbell 21X data

logger. Heating stopped when cambial temperatures exceed 60 °C, a temperature assumed to be lethal (Wright and Bailey, 1982). The actual measurement used for analysis, τ_{60} , was the time required to raise the cambial temperature from 18 °C (the highest pretreatment ambient cambial temperature observed) to 60 °C.

An assumption of one-dimensional models of bark heat transfer is that bark thermal properties are constant within all bark tissues. To verify this assumption we placed several thermocouples at different depths within a single bark sample in ponderosa pine, a species with thick, corky bark. As described above, one thermocouple was placed at the bark surface, and a second thermocouple was placed at the cambial layer. Two additional thermocouples were inserted in the bark sample, one directly in the corky outer bark, the second at the interface between the inner and outer bark. The inner and outer bark layers are distinctive in this species, so the interface between these layers was found visually. A space was created in the bark for the insertion of the additional thermocouples by driving a small diameter nail into the bark sample. The nail was of a slightly smaller diameter than the thermocouples, so it was possible to insert the thermocouples snugly in the proper locations within these solid bark layers. If bark heat resistance were constant within a bark sample, we would expect uniform heating rates within both the inner and outer bark layers.

3. Results

Regression analysis showed a strong positive, linear relationship between basal tree diameter and basal bark thickness for Douglas fir ($r^2 = 0.59$, $P < 0.001$, $n = 48$), incense cedar ($r^2 = 0.72$, $P < 0.001$, $n = 45$), ponderosa pine ($r^2 = 0.71$, $P < 0.001$, $n = 45$), and white fir ($r^2 = 0.64$, $P < 0.001$, $n = 45$) (Fig. 1). These relationships held equally as well with measurements taken at breast height. Analysis of the homogeneity of regression slopes showed large differences among species (F -ratio = 31.2, d.f. = 3, $P < 0.01$, $n = 180$), with the model slope for white fir being much shallower than that of the other species. Because these data did not meet the assumption of parallelism, we did not attempt further analysis with ANCOVA.

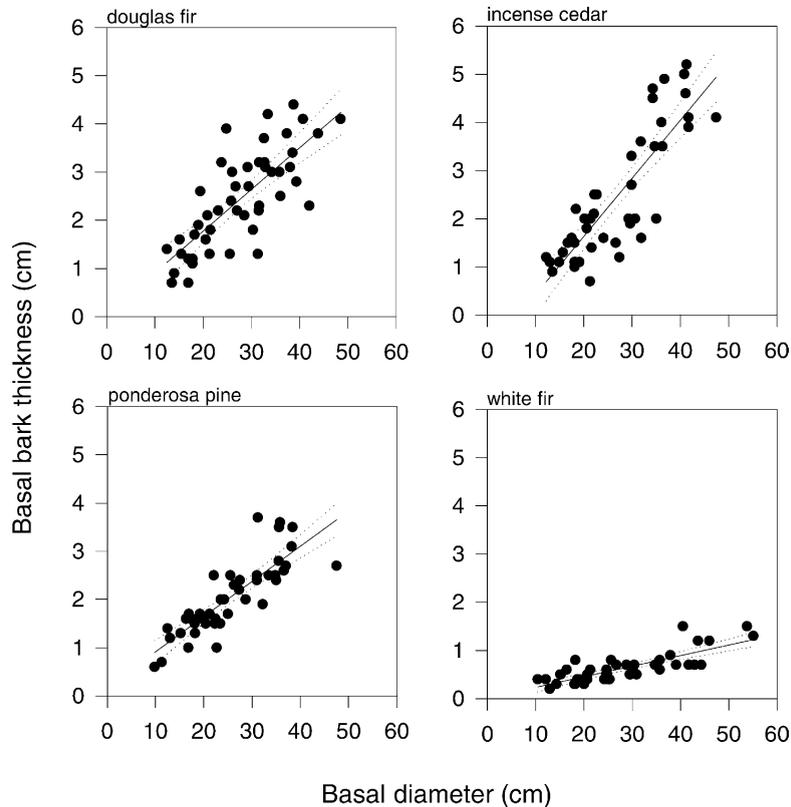


Fig. 1. The relationship between basal diameter and bark thickness for four tree species common to mixed conifer forests of the Sierra Nevada, California. The solid line represents the regression model, while the dotted lines are 95% confidence intervals.

3.1. Fire resistance trials

Fig. 2 displays a representative time/temperature profile used to measure τ_{60} , the amount of time needed to raise cambial temperatures to 60 °C. For all observations there was a fairly consistent amount of time required for the bark surface temperatures to reach 400 °C (mean (\pm S.D.) = 179 (\pm 70) s). This time lag represents initial contact resistance between the heating element and the bark surface. Once a 400 °C bark surface temperature was attained, the bark surface temperatures were uniform during the heating trials (mean (\pm S.D.) = 404.5 (\pm 5.6) °C). The low variability in this measure demonstrates the appropriateness of this method for comparative studies. Bark physical properties varied among the species used for our heating trials. Analysis of variance demonstrated incense cedar had the highest moisture content, while Douglas fir and white

fir possessed significantly greater bark density (Table 1).

We used linear regression with bark thickness as an independent variable to predict τ_{60} , the time to lethal cambial temperatures. Graphical inspection of the data showed an exponential relationship between bark thickness and τ_{60} for all species, so the values for τ_{60} were log-transformed for further analysis (Fig. 3). Bark thickness explained large amounts of variation in τ_{60} for each species (Douglas fir, $r^2 = 0.87$, $P < 0.001$, $n = 17$; incense cedar, $r^2 = 0.76$, $P < 0.001$, $n = 19$; ponderosa pine, $r^2 = 0.67$, $P < 0.001$, $n = 21$; white fir, $r^2 = 0.96$, $P < 0.001$, $n = 20$). Including additional terms for bark moisture content or bark density did not significantly improve the fit of the regression models. Analysis of the homogeneity of the regression slopes and elevations showed significant differences among species, with Douglas fir and white fir having a steeper slopes than

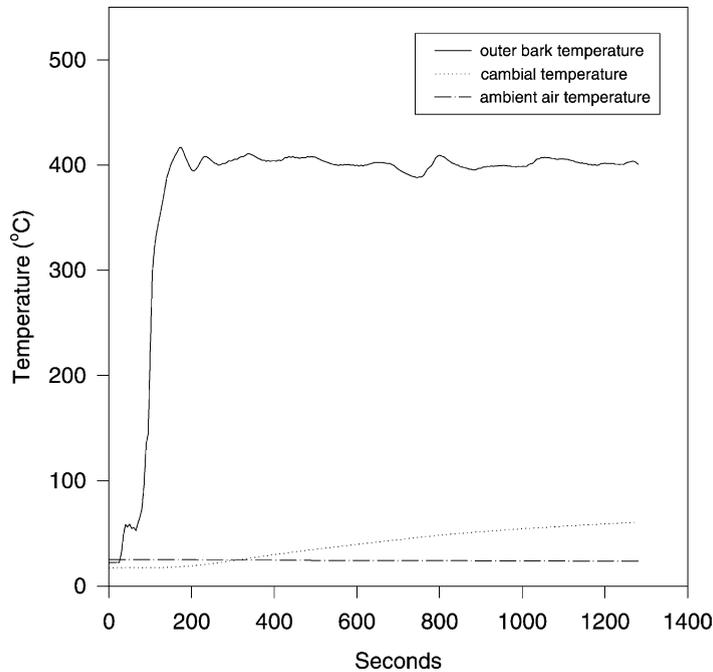


Fig. 2. A typical time–temperature profile used to generate values for seconds to lethal cambial temperatures of 60 °C (τ_{60}).

incense cedar and ponderosa pine. Douglas fir and white fir were therefore more resistant to heat than the other species per unit thickness of bark, although the magnitude of this difference was not large. Among species differences appears to be consistent with observed patterns in bark density (Table 1).

The strong relationship between stem diameter and bark thickness allows us to use basal stem diameter as a predictor of the time needed to reach lethal cambial temperatures. Regression analysis showed a strong positive, linear relationship between basal tree diameter and log-transformed values of τ_{60} for Douglas fir ($r^2 = 0.73$, $P < 0.001$, $n = 17$), incense cedar ($r^2 = 0.76$, $P < 0.001$, $n = 19$), ponderosa

pine ($r^2 = 0.49$, $P < 0.001$, $n = 21$) and white fir ($r^2 = 0.82$, $P < 0.001$, $n = 20$). Regression slopes did not differ significantly among the models. We tested among species differences using analysis of covariance, which adjusted for sample differences in basal diameter. The test indicated a significant difference in heat resistance among species (Table 2). Bonferroni adjusted pair-wise comparisons between species showed that Douglas fir was significantly more heat resistant compared to the other species (all pair-wise comparisons with Douglas fir, F -ratio ≥ 19.7 , d.f. = 1, $P \leq 0.0001$, $n \geq 36$). All other pair-wise comparisons were not significant. Thus, in spite of its thin bark, when accounting for differences in stem size

Table 1

Mean (\pm S.D.) of stem size and bark physical characteristics for four species used to test bark insulating abilities during fire simulations^a

Species	<i>n</i>	Basal diameter (cm)	Bark moisture (%)	Bark density (g cm ⁻³)
Douglas fir	17	15.7 (5.4) a	42 (14) bc	0.37 (0.05) a
Incense cedar	19	19.6 (6.9) a	116 (27) a	0.17 (0.04) c
Ponderosa pine	21	19.5 (6.0) a	28 (6) c	0.25 (0.07) b
White fir	20	17.3 (7.0) a	61 (45) b	0.37 (0.11) a

^a Different letters denote significant differences ($P < 0.05$) among species.

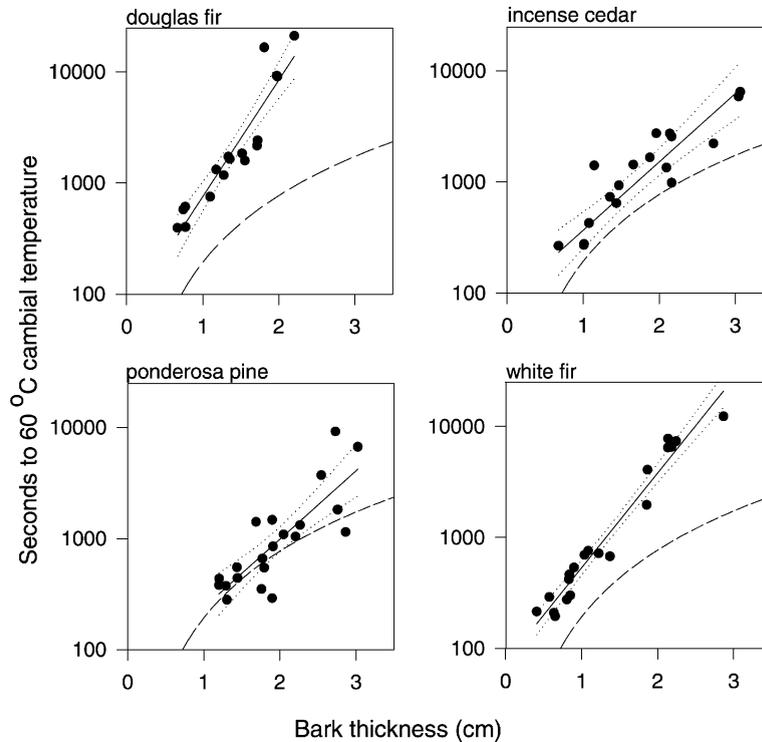


Fig. 3. The relationship between bark thickness and time required to reach the presumed lethal cambial temperatures of 60 °C given a constant 400 °C outer bark temperature. The solid line represents the regression model, while the dotted lines are 95% confidence intervals. The dashed line represents expected values of τ_{60} generated from a one-dimensional model (Eq. (3), $\alpha = 0.06 \text{ cm}^2 \text{ min}^{-1}$ (from Martin, 1963), $T = 60 \text{ }^\circ\text{C}$, $T_0 = 18 \text{ }^\circ\text{C}$, and $T_f = 400 \text{ }^\circ\text{C}$).

white fir was not less heat resistant than incense cedar or ponderosa pine (incense cedar vs. white fir, F -ratio = 2.9, d.f. = 1, $P = 0.10$, $n = 39$; ponderosa pine vs. white fir, F -ratio = 3.0, d.f. = 1, $P = 0.09$, $n = 41$).

We performed additional heating trials in October 1999 to assess possible differences between spring

and fall cambial heat resistance. We examined eight individual trees per species for incense cedar, ponderosa pine, and white fir. We could not detect any differences between observed fall values for τ_{60} vs. expected values given by the spring regression models (incense cedar, $t = 0.930$, $n = 8$, $P = 0.37$; ponderosa pine, $t = 1.102$, $n = 8$, $P = 0.29$; white fir, $t = 0.196$, $n = 8$, $P = 0.85$).

To test if the preceding results were dependent on the size of the heating pad used in the experimental heating trials, we repeated the trials increasing the area of the heating pad from 7 cm × 10 cm to 15 cm². The smaller heating pad appeared to have larger values for τ_{60} compared to the larger pad for trials with very thick bark (>2.5 cm), but there was no detectable overall difference for the range of bark thickness used in this study. Results using five ponderosa pines, five white fir and six incense cedars showed no significant difference between τ_{60} for the larger heating element and the

Table 2
Analysis of covariance for among species differences in the relationship between basal diameter and seconds to cambial temperatures of 60 °C (τ_{60}) given a constant 400 °C outer temperature. The interaction term was not significant

	Sum of squares	d.f.	Mean square	F-ratio	P
Species	19.04	3	6.34	14.36	<0.001
Basal diameter	74.29	1	74.29	168.09	<0.001
Error	31.82	72	0.442		

expected time given by the smaller heating pad ($t = 0.740$, d.f. = 31, $P = 0.465$). Additionally, there were no significant differences in τ_{60} for any of the individual species (incense cedar, $t = 0.216$, d.f. = 11, $P = 0.835$; ponderosa pine, $t = 0.393$, d.f. = 9, $P = 0.709$; white fir, $t = 0.616$, d.f. = 9, $P = 0.556$).

We compared our results against estimates given by one-dimensional models of bark heat transfer (e.g., Peterson and Ryan, 1986). We calculated model equations to allow for a constant 400 °C fire and a starting temperature of 18 °C. We used a constant for bark thermal diffusivity of 0.06 cm² min⁻¹ (Martin, 1963). Sample bark thickness was used to generate predicted time to a cambium temperature of 60 °C (τ_{60}). These estimated figures were compared against the empirical data from the experimental heating trials. While the analytical model provided the correct general shape of the response, the model results were much lower than our measured values for τ_{60} (Fig. 3). For each species the analytical model underestimated τ_{60} (Douglas fir, $t = 11.17$, $P < 0.001$, d.f. = 16; incense cedar, $t = 6.43$, $P < 0.001$, d.f. = 18; ponderosa pine, $t = 2.26$,

$P < 0.001$, d.f. = 20; white fir, $t = 6.94$, $P < 0.001$, d.f. = 18).

Bark morphologies may change with increasing stem diameters, which may in turn affect bark thermal properties. One readily observable feature of bark structure that changed with stem size was the relative proportion of inner bark thickness to total bark thickness. The proportion of inner bark tended to decrease with increasing stem size (all species combined, $r^2 = 0.11$, $P < 0.05$, $n = 40$). A single data point for Douglas fir was identified as an outlier, if this observation was removed the relationship became stronger (all species combined, $r^2 = 0.30$, $P < 0.001$, $n = 39$) (Fig. 4). We subsequently compared inner and outer bark characteristics that may influence thermal properties. Compared to the outer bark, inner bark was significantly denser (all species combined, paired t -statistic = 7.9, $P < 0.0001$, $n = 40$), and had a higher moisture content (all species combined, paired t -statistic = 13.6, $P < 0.0001$, $n = 40$).

We tested thermal differences between the bark layers by placing multiple thermocouples in situ

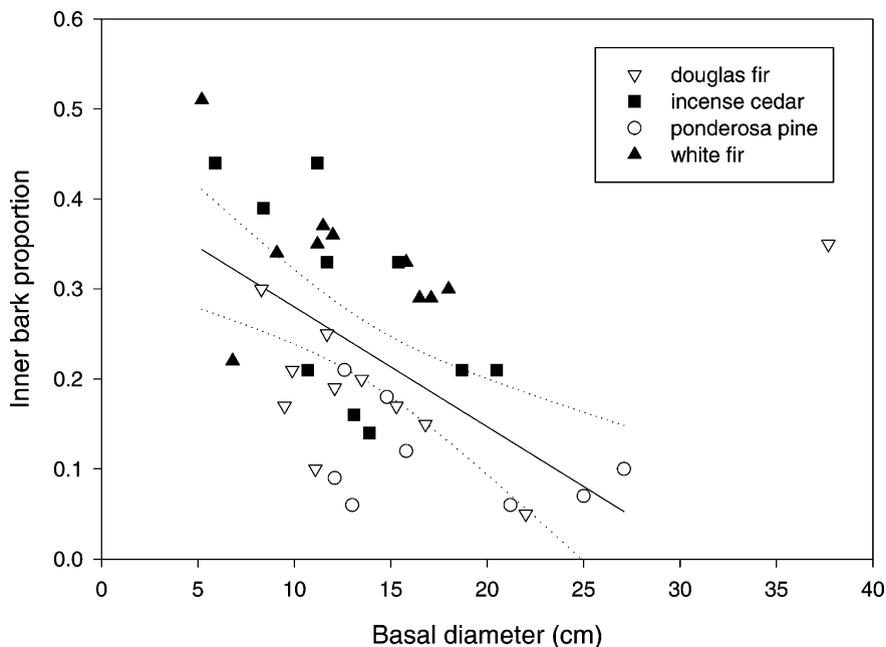


Fig. 4. Proportion of inner bark thickness (cm) to total bark thickness (cm) over a range of stem sizes for Douglas fir, incense cedar, ponderosa pine, and white fir. The solid line represents a regression model, with the dotted lines representing 95% confidence intervals. A single data point for Douglas fir, identified as an outlier, is not included in the model, although a statistically significant regression model can be constructed if this data point is included (see text).

Table 3

Two sample *t*-tests for observed vs. expected values for seconds to required to reach the cambial temperatures of 60 °C (τ_{60}) for thermocouples placed at various depths within the bark of ponderosa pine^a

Thermocouple placement	Observed average, τ_{60} (s)	Expected average, τ_{60} (s)	<i>t</i> ^b	<i>P</i> ^c
Corky outer bark	135	600	9.50	<0.001
Inner/outer bark interface	354	806	5.03	<0.001

^a Thermocouple placement refers to the bark tissue layer where the temperature probes were inserted. Observed values were generated empirically, while expected values were derived from a regression model of whole bark heating.

^b Tests used separate variance *t*, and values for τ_{60} were log-transformed to normalize the data. For each comparison, *n* = 11.

^c Bonferroni adjusted probabilities were used to determine *P*-values.

within individual ponderosa pine bark slabs. It was extremely difficult to accurately measure the precise pre-burn thermocouple depth within the bark samples. Therefore, we removed and measured the exact depth of the thermocouples after heating. Because there was a loss of bark due to smoldering, expected values for the time to lethal cambial temperatures were not generated using the relationships for ponderosa pine described earlier. Instead, expected values were determined directly from the scorched samples. The relationship between scorched bark thickness and τ_{60} was determined by linear regression ($r^2 = 0.53$, $P < 0.001$, $n = 11$). This relationship was then used to calculate expected times for each of the other bark depths to reach 60 °C (Table 3). The expected values were significant overestimates, with the data indicating that the outer layers of the bark transferred heat more quickly than the inner bark. From these data it is apparent that heat transfer rates are not uniform between the inner and outer bark layers in ponderosa pine.

4. Discussion

4.1. Comparisons with large tree studies

In broad terms our findings agree with previous studies of bark heat transfer in large trees. For each species there was a strong, positive linear trend between stem diameter and bark thickness. Further, bark thickness alone could be used as the determinant of heat transfer rates within a species. Douglas fir and white fir had slightly higher than expected heat tolerance. The high thermal resistance found in Douglas fir and white fir may be in part related to the high bark densities in these two species. It is also likely that thick

cork layers had not sufficiently developed in the small diameter “fire-tolerant” species used in this study. In sum, the expected interspecific differences in small tree heat tolerances failed to emerge (i.e., Douglas fir > ponderosa pine > incense cedar > white fir). Instead we found, with the exception of Douglas fir, that at small stem diameters the species were roughly equivalent with respect to heat resistance (i.e., Douglas fir > ponderosa pine = incense cedar = white fir). At this size the magnitude of the difference between Douglas fir and the other species was small, and may not be biologically significant.

While the overall species differences were slight, it is important to note that even these small trees possessed a surprising amount of bark thermal resistance. While the heat output of an actual fire will be much greater than trees encountered in our experimental heating trials, the relatively large values for τ_{60} for all species indicate a higher than expected level of cambial heat tolerance. Our heating experiments showed that trees with a bark thickness of only 1 cm could withstand temperatures of 400 °C for approximately 10 min, a time–temperature profile that could be achieved during smoldering combustion. Actual post-fire mortality rates will, of course, also be governed by the severity of crown and root damage.

We found that one-dimensional analytical models of bark heat transfer provide the correct general shape of the relationship between bark thickness and τ_{60} for small trees. If we had found that one-dimensional models consistently overestimated values for τ_{60} , it could have been interpreted as evidence showing that a two-dimensional modeling approach is needed for small trees. Since this was not the case, it appears that one-dimensional solutions are adequate. A separate concern was that heating times would be of such short

duration for small trees that it would be necessary to account for the initial effects of contact resistance in our models. However, on average it took only 179 s (approximately 3 min) for the bark surface to reach 400 °C, showing that this effect would only be important for trees with extremely thin bark. It might be reasonable to expect that the effects of contact resistance would be less during an actual fire, where the flame vertical velocity and associated turbulence leads to high rates of convective heat transfer (Dickinson and Johnson, 2001).

In spite of these findings, we were not able to fully support a one-dimensional modeling approach for small trees. The expected times generated by one-dimensional models consistently underestimated the times for τ_{60} for small trees in our study. At least four possible explanations could account for this discrepancy: (1) There was a large amount of thermal translocation slowing the rate of heat transfer to the cambium. This phenomenon was first described by Vines (1968), who noticed that when a heat source was applied to a relatively small area on a stem surface, the movement vascular fluids could transfer the heat vertically away from the heat source. However, we could not find support for this idea in our data, because significant differences in τ_{60} were not observed when using a larger heating pad. Additional trials with an even larger heating element, or a different heating method (see Greene and Shilling, 1987) would provide stronger evidence for or against this proposition. (2) Analytic models assume perfect contact between bark and the heat source, in spite of the fact that contact resistance was readily observable during our heating trials. However, the duration of initial contact resistance at the bark surface (i.e., the amount of time needed for the bark surface to reach 400 °C) was of such short duration relative to overall heating times that it is unlikely that it had a significant influence on our results. (3) The semi-infinite solid assumption is questionable because of the variable thermal properties within the bark. Analytical models of bark heat transfer assume that heating rates are uniform within a given bark sample. This is a necessary condition when using simplified geometries (i.e., semi-infinite solids) in order to obtain analytical solutions to heat transfer problems. Initial modeling of our data show that finite-difference models (Cengel, 1998) that do not use the semi-infinite solid assumption provide improved fits to

the data. (4) The greater relative amount of inner bark found in small trees may have lead to greater than expected overall heat resistance. In agreement with Reifsnyder et al. (1967), we found inner bark to be more dense and moist compared to outer bark. Our results showed that at least in ponderosa pine the physical differences between the bark layers translated into different rates of heat movement. The proportion of the total bark thickness composed of inner bark appeared to increase with smaller stem diameters, perhaps effectively lowering the thermal diffusivity of the total bark sample.

4.2. Implications for forest management

Fire exclusion in the Sierra Nevada of California is generally believed to have resulted in an overabundance of small white fir and incense cedar (Barbour, 1988). The explanation for this shift centers on the observations that white fir and incense cedar are extremely shade tolerant but fire intolerant, characteristics that allow them to flourish in a fire-free environment. This has led to the purposeful reintroduction of fire into these forests, in order to reduce wildfire risks and restore these forests to pre-European settlement conditions.

Measurements taken from long-term monitoring plots in crowded low-elevation mixed conifer forests at Sequoia National Park, California, demonstrate the understory growth patterns (Nathan L. Stephenson, unpublished data). Observations of small trees (≤ 5 cm dbh) over a 5-year period showed large differences in interspecific average annual diameter growth rates (incense cedar = 0.7 mm, S.E.: ± 0.09 , $n = 118$; ponderosa pine = 0.3 mm, S.E.: ± 0.03 , $n = 47$; white fir = 1.4 mm, S.E.: ± 0.06 , $n = 641$; no data were available for Douglas fir). Bark thickness is strongly related to stem diameter, so divergent growth rates will lead to bark thickness being added at different rates. Using the relationships between stem diameter and bark thickness it is possible to roughly project how quickly understory trees may achieve cambial resistance to low-intensity fires at this site (Fig. 5). If a 1 cm layer of bark confers at least some degree of fire resistance, it would take a 5 cm dbh incense cedar approximately 25 years to reach this stage. Ponderosa pine grows slowly in understory conditions, and while this species has relatively thick bark, a 5 cm dbh tree

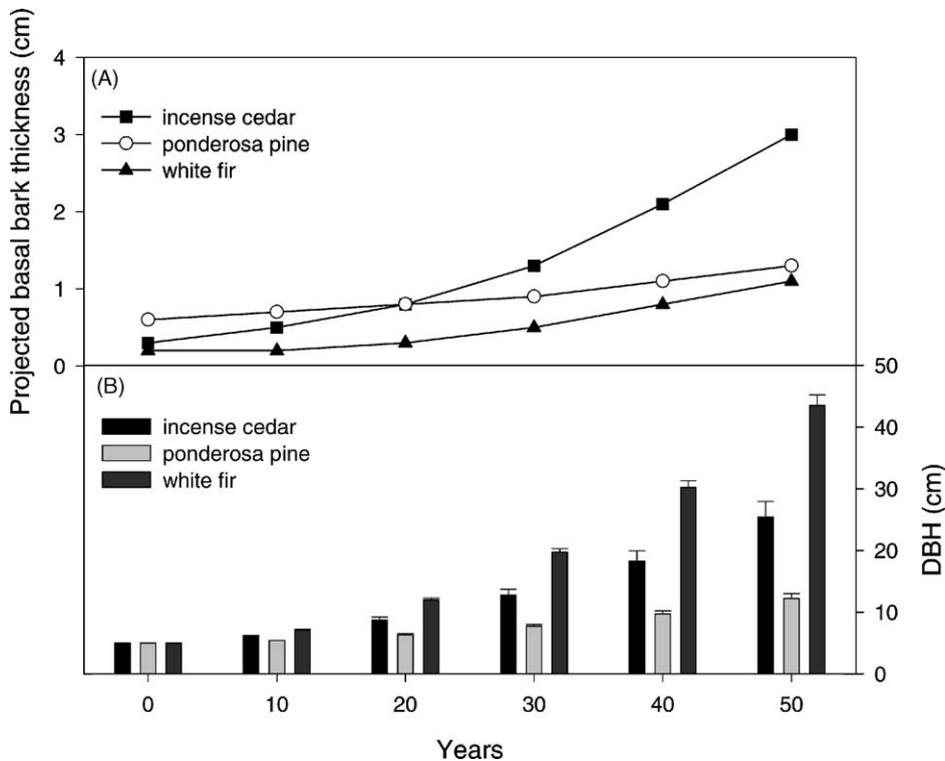


Fig. 5. (A) Projected bark thickness development and (B) radial diameter growth (dbh cm \pm S.E.) for small (≤ 5 cm dbh) incense cedar, ponderosa pine and white fir. Growth data are taken from mixed conifer forests in Sequoia National Park, California (Stephenson, unpublished data). Basal bark thickness was calculated using the relationships presented in Fig. 1. Basal diameter, used to calculate basal bark thickness, was estimated using the relationship between dbh and basal diameter (for each species $r^2 \geq 0.95$, $P < 0.001$, $n = 45$).

would take about 35 years to grow 1 cm thick bark layer. White fir grows quickly but has relatively thin bark, so this species would require about 50 years to develop 1 cm bark thickness. Although growth rates will vary across sites and with stand development, this demonstration shows that where understory conditions favor the growth of shade tolerant species, such as incense cedar and white fir, these species may become resistant to cambial damage relatively quickly.

While there is a clear need to restore these forests, there is an on-going debate involving the choice of restoration tools (i.e., fire alone, silvicultural thinning, or both) (Stephenson, 1999). Proponents for mechanical thinning as a precursor to the reintroduction of fire have noted that it may be difficult for fire alone to reduce the abnormally dense cohort of firs that have grown since fire exclusion has occurred (Bonnicksen and Stone, 1978, 1982). However, several other

authors have reported successes reducing trees in this cohort using fire as their only management tool (Kilgore, 1973; van Wagtenonk, 1983; Keifer, 1998). Our results suggest that it will become increasingly difficult to remove these trees using fire alone, although presently there has probably been insufficient time for firs to become resistant to cambial damage from most prescribed fires.

It is possible to modify the application of prescribed fire to vary the amount of tree mortality. Our results, however, indicate that adjusting the season of burn will probably not have a great affect on the severity of cambial damage in these forests. We were also unable to detect large among species differences in cambial fire tolerance for small trees. This finding suggests that it may prove difficult to favor understory trees of shade intolerant species over shade tolerant species by modifying prescribed fire intensity.

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