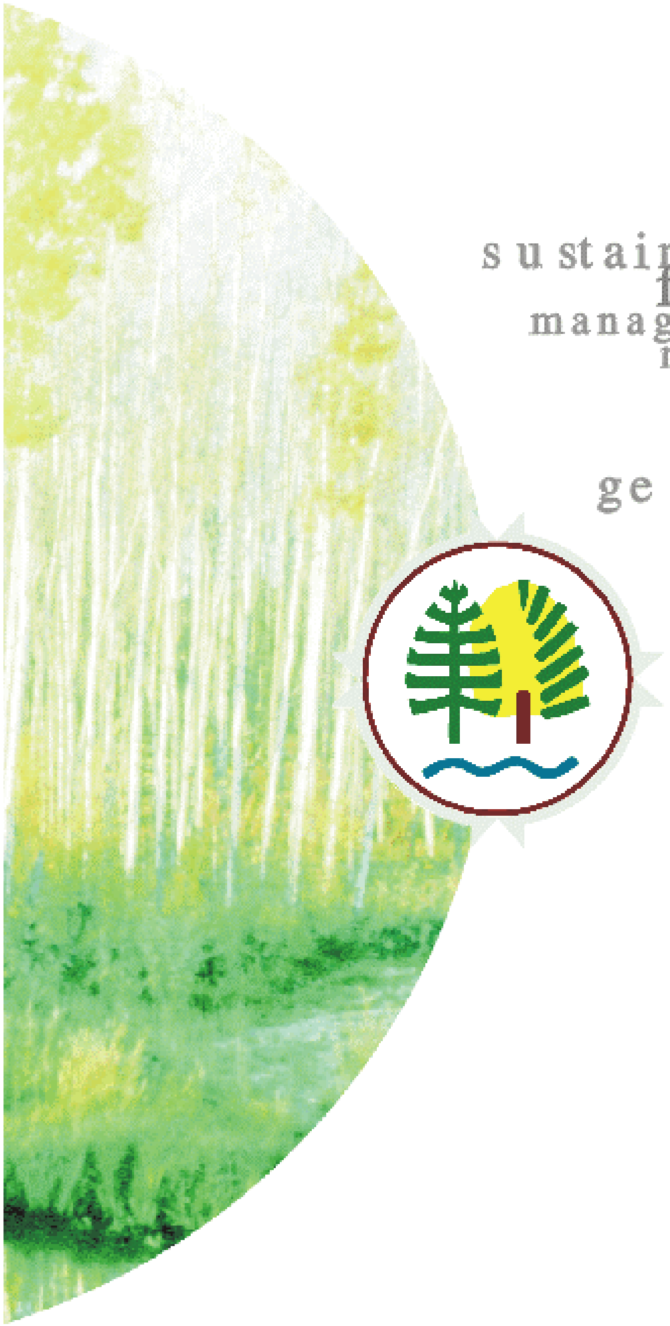
PROJECT REPORT
2000-43
FINAL PROJECT REPORT



sustainable
forest
management
network

réseau
sur la
gestion durable
des forêts

Fire caused mortality in boreal trees

M.B. Dickinson and E.A. Johnson

For copies of this or other SFM publications contact:

Sustainable Forest Management Network
G208 Biological Sciences Building
University of Alberta
Edmonton, Alberta, T6G 2E9
Ph: (780) 492 6659
Fax: (780) 492 8160
http://www.ualberta.ca/sfm

ISBN 1-55261-105-1

Fire-Caused Mortality in Boreal Trees

by

M. B. Dickinson and E. A. Johnson

Department of Biological Sciences and Kananaskis Field Stations
University of Calgary, Calgary, Alberta, T2N 1N4, Canada

December 2000

EXECUTIVE SUMMARY

We use a **surface-fire extinction model** to ask whether differences among surface fuels in aspen and conifer stands in the Saskatchewan mixedwood boreal forest are sufficiently large to affect patterns of burning across the landscape (i.e., where fires spread and where they go extinct). The key variables in the extinction model are fuel-bed surface area (a measure of the loading of fine fuels) and fuel moisture (determiined by weather and live-to-dead fuel ratios). A larger fuel-bed surface area means that fires should propagate at higher fuel moisture levels. Surface fuels were sampled in 56 stands spanning the range in upland fuel variability. Dead-fuel moisture was estimated from weather data and fuel-drying models for periods during large-area-burned years when large fires made runs. We assume that it is during these periods when the vast majority of forest area burns that fuel differences have the potential to cause large effects on landscape-level patterns of burning. All stands ≥30 years-since-last fire were predicted to carry a surface fire during large-area burned years when actual fires made runs. Aspen stands had lower fuel-bed surface areas than conifer stands but fuel moisture levels were low enough that the differences did not matter. In contrast, fires were not predicted to spread in many recently burned stands under any weather conditions. Our results imply that increasing aspen dominance on the mixedwood boreal landscape may not be effective as a strategy to encourage fire extinction and, thereby, reduce area burned and tree mortality in fires (Fechner and Barrows 1976, DeByle et al 1987).

When surface fires spread past trees, tree components (i.e., roots, boles, and crowns) are heated, causing cell mortality, tissue necrosis, and tree death. We used a **heat-transfer model** and a **biophysical cell-survivorship model** to derive quantitative predictions of cell survivorship in the boles of trees in fires of a range of residence times and for trees with a range of bark thicknesses. The cell-survivorship model was parameterized with live-bark cell survivorship data from aspen and spruce. We assume that survivorship of live bark cells closely approximates survivorship of adjacent vascular cambium cells. We found that live-bark cell survivorship in surface fires can be described by a relatively simple relationship between bark thickness and fire residence time. We expect two thresholds relative to bark thickness: complete vascular-cambium cell mortality would be expected in all fires for trees with bark thickness <6 mm while trees with bark thickness >20 mm are expected to be immune to vascular-cambium necrosis during surface fires. Our mechanistic approach could provide managers with a tool for predicting vascular-cambium necrosis and tree death from bark thickness and fire residence time, variables that are readily estimated in the field or from models.

ACKNOWLEDGEMENT

Financial and logistical support for this project was provided by Weyerhaeuser Canada, Prince Albert National Park, the Natural Science and Engineering Research Council of Canada (through the Sustainable Forest Management Network), and the Kananaskis Field Stations and Department of Biological Sciences of the University of Calgary.

INTRODUCTION

A key goal of the Sustainable Forest Management Network is to develop a better understanding of how to mimic natural disturbances (e.g., fire) in forest management practices. We currently know a lot about the spatial mosaic of stand ages (e.g., Bergeron 1991, Larsen 1997, Weir et al. 2000) and the temporal patterns in fire frequency and area burned (e.g., Stocks and Street 1983, Flannigan and Wotton 1991, Stocks 1991, Bergeron and Archambault 1993, Nash and Johnson 1996, Reed et al. 1998) in Canadian boreal forests. However, little is known about surface-fire extinction and tree mortality in fires despite their importance in determining the landscape mosaic of stand ages. We use mechanistic models to guide our study of surface-fire extinction and tree mortality.

Forest managers need to know how fuel differences among stands affects extinction of surface fires. Aspen fuels are widely thought to cause surface-fire extinction more readily than conifer fuels (e.g., Fechner and Barrows 1976, DeByle et al. 1987). We use a physically-based **surface-fire extinction model** (Wilson 1985) to address two questions. First, do aspen stands have surface-fuel characteristics that would cause surface-fire extinction at lower moisture levels than in conifer stands? Second, do these surface-fuel differences matter when considered in the context of weather during periods in which the vast majority of area burned in the past?

An adequate tree death model is needed to understand the effects of natural and prescribed fires (Dickinson and Johnson 2001). Incomplete tree mortality that results from surface fires of low to moderate intensity is of primary interest in our study while complete mortality is typical in high-intensity fires. Death of a tree in a surface fire depends on heat transfer into the bole from the flames and vascular-cambium response to elevated temperatures. We use a **heat-transfer model** to simulate temperature regimes at the vascular cambium and a **biophysical cell-survivorship model** to predict cell survivorship. The cell-survivorship model is tested with data from aspen and spruce. Our results point the way towards a mechanistic model of vascular-cambium necrosis and tree death during surface fires.

MODELS AND METHODS

Surface-Fire Extinction

The surface-fire extinction model is based on a heat budget defined by the ratio of a heat source and a heat sink (Wilson 1985):

$$n_x = \frac{heat\ source}{heat\ sink} \qquad \textbf{(1)}$$

where n_x is an extinction index (dimensionless), the heat source (kJ kg^{-1}) indicates both the amount of heat available to heat the unburned fuel and how quickly the fuel bed can be heated to ignition, and the heat sink (kJ kg^{-1}) is the energy required to dry a unit mass of fuel and carry the fuel through the pyrolysis process. Different ranges of the extinction index correspond approximately to three states of fire spread by flaming combustion: steady-state spread, in which the rate of spread does not vary appreciably through time ($n_x \geq 8$); marginal spread, in which the fire front breaks up and combustion becomes erratic ($6 \leq n_x < 8$); and extinction, in which fires do not spread ($n_x < 6$).

The variables determining the heat source are as follows:

$$heat\ source \propto h_v S \qquad \textbf{(2)}$$

where h_v is the heat of combustion of the volatiles during flaming combustion (kJ kg^{-1}) and S is the fuel-bed surface area (dimensionless). The heat of combustion (h_v ~ 12700 kJ kg^{-1}) is held constant because it has been found to vary minimally among natural cellulosic fuels. The fuel-bed surface area S quantifies the total amount of surface area in the fuel bed:

$$S = \frac{ó w}{ñ_p} \qquad \textbf{(3)}$$

where $ó$ is the average fuel particle surface-area-to-volume ratio (m^{-1}), w is the fuel loading (kg m^{-2}), and $ñ_p$ is the fuel particle mass density (kg m^{-3}). Mass density of the fuel particles is held constant at 400 kg m^{-3} because we assume that it, like the heat of combustion, varies minimally among natural cellulosic fuels. Fuel-bed surface area is a key variable in our study of surface-fire extinction because we hold the other variables in the heat source constant. The rationale for the fuel-bed surface area is that heat-transfer rates from the flames to the fuel are highest when the fuel bed is composed of high loadings of fine fuels. For instance, radiation heat-transfer from the flames to the fuel is highest in fuel beds with high optical densities (i.e., where most radiation is absorbed near the surface of the fuel bed).

The heat sink is determined by the following variables:

$$heat\ sink \propto Q_p + Q_w M \tag{4}$$

where Q_p is the total heat required to completely pyrolyze the fuel (kJ kg^{-1}), Q_w is the heat required to vaporize the water in the fuel (kJ kg^{-1}), and M is the proportional moisture content of the fuel (dimensionless). Fuel moisture is determined by both live and dead fuel. The heat of pyrolysis ($Q_p \sim 640$ kJ kg^{-1}) is held constant because it has been found to vary minimally among natural cellulosic fuels.

Fuel-bed surface area of the herb and litter layers was estimated using methods in Brown et al. (1982) in 56 upland stands in Prince Albert National Park, Saskatchewan, and the surrounding Weyerhaeuser Forest Management Area. We sampled across the entire upland moisture and nutrient gradient to ensure that the stands spanned the range of variability in tree-species composition (see Bridge and Johnson 2000). We also sampled across the time-since-fire gradient, from 2 to 226 years (Weir et al. 2000). Stands were divided into those $\leq$12 years since-last-fire and those $\geq$30 years-since-last fire. No stands were available between 12 and 30 years since-last-fire. The older stands were classified by the relative importance of tree species that formed their canopies.

We sampled fuels during May and June because this is the historical fire season in the mixedwood boreal forest (Johnson et al. 1999). No significant changes in live-to-dead fuel ratios were detected during the May to June sample period. Live-fuel moisture was set to values appropriate for conifer, herbaceous, and deciduous foliage and wood (e.g., Bradshaw et al. 1983).

The moisture of fine, dead fuels varies over short time scales (e.g., hours and days) while fuel characteristics such as chemical properties, fuel loading, and average fuel particle surface-area-to-volume ratios vary over longer time scales (e.g., years to decades). Clearly, not all of the substantial variation in fuel moisture is relevant to understanding the effects of fuel variability on surface-fire extinction because, at minimum, fires have to be burning somewhere on the landscape

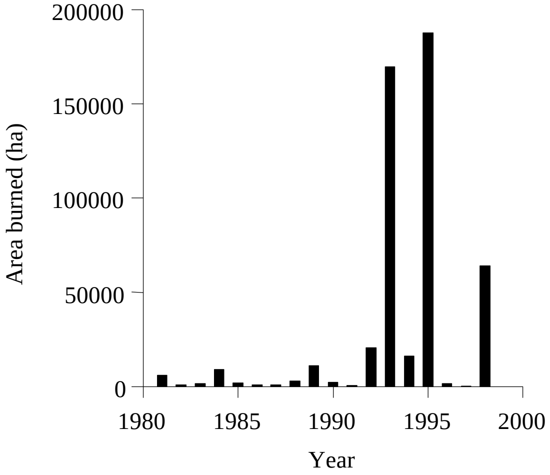


Figure 1. Area burned during the spring fire season in the mixedwood boreal region of Saskatchewan from 1981 to 1998 (data from Saskatchewan Environmental Resource Management).

for fuel variability to have any effects. Further, we assume that, if aspen stands have surface-fuel characteristics that increase the likelihood of surface-fire extinction relative to conifer stands, those differences will have the greatest potential for affecting where fires spread and where they go extinct during periods when the majority of forest area burns. In contrast, there would appear to be little scope for large effects on patterns of burning during periods when area burned is small. A handful of large fires that occur during occasional years (large-area-burned years, Figure 1) account for the vast majority of area burned (Strauss et al. 1989, Johnson et al. 1998). We use only weather during these periods in our analyses of the effects of fuel differences on surface-fire extinction. Dead-fuel moisture was estimated from fuel-drying models following methods of Bradshaw et al. (1983) and Van Wagner (1987). In the fuel-drying models, we used standard observations from the Environment Canada or Saskatchewan Environment and Resource Management (SERM) weather station nearest each of a sample of large fires (N = 18). Each fire burned between 25,000 and 301,000 ha south of latitude 57 in Saskatchewan during large-area-burned years (1981, 1993, 1995, and 1998). Weather from the one to two periods during which these fires made runs were used in the models. Fire behavior information was from SERM records.

Tree Death

Vascular-cambium necrosis occurs when the bark surface is bathed in flame during a surface fire and heat transfer into the bole causes a rise in vascular cambium temperatures. After the flames have passed the tree, vascular cambium temperatures fall gradually as the bole cools (e.g., Fahnestock and Hare 1964, Gill and Ashton 1968, Vines 1968). The bole heating process is unsteady, that is, temperature gradients through the bole are not constant through time. The simplest model of the unsteady-state heating of tree boles is (e.g., Holman 1986):

$$\frac{\partial T}{\partial t} = á \; \frac{\partial^2 T}{\partial x^2} \qquad \textbf{(5)}$$

where T is temperature (°C) at a given depth x (m) within the bark, t is time (s), and *á* is thermal diffusivity ($m^2\ s^{-1}$). The model shows that the change in temperature through time within the bark $\partial T/\partial t$ is proportional to the gradient in temperature through the bark $\partial^2 T/\partial x^2$. Thermal diffusivity quantifies the ease with which a given temperature gradient produces a rise in temperature within the bark and is determined by the following variables:

$$á = \frac{k}{ñc} \qquad \textbf{(6)}$$

where k is thermal conductivity ($W\ m^{-1}\ °C^{-1}$), *ñ* is mass density ($kg\ m^{-3}$), and c is heat capacity ($J\ kg^{-1}\ °C^{-1}$). Heating in Equation 5 is one-dimensional in the sense that heat is transferred perpendicularly to the bark surface. As such, heat-transfer through the center of the bole and the effects of bole curvature are assumed to be minimal. One can see that, according to the relatively simple heat-transfer model (Equation 5), temperatures within the bole are determined by the bark surface temperature regime, thermal diffusivity, and bark thickness. It is known from a variety of studies that temperature regimes below the bark are primarily determined by variation in fire residence time and bark thickness while variation among trees in thermal diffusivity is of limited importance because it varies minimally among trees (e.g., Martin 1963, Reifsnyder et al. 1967).

Heat transfer into the bole has been linked with tree death by assuming that vascular-cambium necrosis occurs around the bole if a threshold temperature (~60 °C) is reached at the vascular cambium (e.g., Peterson and Ryan 1986, Brown and DeByle 1987). A relatively simple solution to Equation 5 can be used to predict whether the threshold temperature is reached during the residence time of the flames. Equation 5 can be solved by the Laplace transform technique given several boundary conditions, an important one being that the bark surface temperature rises rapidly to its maximum and remains there (e.g., Holman, 1986):

$$\frac{è}{è_0} = erf\ \left(\frac{x}{2\ \sqrt{á\ t}}\right) \qquad \textbf{(7)}$$

where $è/è_0$ is the excess temperature ratio (dimensionless), *erf* is the Gauss error function whose argument can be found in mathematical tables for a given value of the excess temperature ratio (e.g., Abramowitz and Stegun, 1964), and the other variables are defined above. The excess temperature ratio is defined as:

$$\frac{\text{è}}{\text{è}_0} = \frac{T - T_f}{T_0 - T_f} \tag{8}$$

where T is the temperature (°C) at the depth x of the vascular cambium, T_f is the average flame temperature, and T_0 is the initial temperature of the tree bole. The flame temperature T_f is usually set to around 500 °C (e.g., Peterson and Ryan 1986, Brown and DeByle 1987). The vascular cambium temperature T is set to the threshold for vascular-cambium necrosis and Equation 7 is solved for the fire residence time t required to reach that temperature.

Use of Equation 7 and 8 as a tissue necrosis model is problematic for several reasons. First, the model only predicts peak vascular cambium temperatures during the residence time of the flame and does not include the heat-transfer process after the flames have passed and the bark begins to cool. Thus, peak temperatures predicted from the model are often lower than actual peak temperatures, particularly in trees with thick bark (unpubl. data). Second, we expect that using a threshold temperature to predict tissue necrosis is too simplistic given that cell mortality occurs continuously and at increasingly high rates as temperatures rise above the level at which cell mortality rates are appreciable (~40 °C, e.g., Lorenz 1939, Levitt 1980, Martin et al. 1969). Only if vascular cambium temperature regimes were the same among trees in fires could a single threshold temperature be strictly valid as an index of tissue necrosis.

We propose an alternative tree-death model that is consistent with what we know about fire behavior, heat transfer, and cell mortality at elevated temperatures. The model involves using (1) a heat-transfer model to predict the rise and fall of temperatures at the vascular cambium in response to bark surface heating by the flames and (2) a cell-survivorship model to predict cell mortality resulting from the elevated temperatures. We use a numerical approach for predicting vascular cambium temperatures that involves a forward-difference solution to Equation 5 (Hanks and Ashcroft 1980, Holman 1986, Rego and Rigolot 1990):

$$T_i^{j+1} = T_i^j + \frac{1}{\text{á}} \frac{\text{Ä}t}{\text{Ä}x^2} \left(T_{i-1}^j - 2T_i^j + T_{i+1}^j\right) \tag{9}$$

where T is temperature (°C), i subscripts refer to depth increments of Äx millimeters, and j superscripts refer to time increments of Ät seconds. Bark surface temperatures were constrained below 100 °C for the duration of heating under the assumption that the temperatures of materials do not rise above the boiling point while liquid water is present (e.g., Albini and Reinhardt 1995).

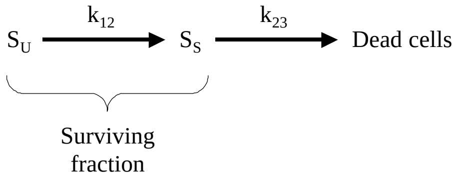


Figure 2. Three-population cell-survivorship model (e.g., Gutfreund 1995). Cells unaffected by heat S_U (population 1) are converted to cells susceptible to death S_S (population 2) at a given rate k_{12}. Susceptible cells, in turn, are killed at a rate k_{23}. The surviving fraction of cells at any given time S(t) is the sum of the fractions of cells in the unaffected and susceptible populations.

This simplification has been found to give good results, indicating that the bulk of tree bark is not desiccated during fires (unpubl. data, Rego and Rigolot 1990). We treated cooling of the bark surface after passage of the flames as a Newtonian cooling process using parameters appropriate for surface fires in a cooling equation (see Weber et al 1995). We used Equation 9 to simulate the rise and fall of vascular cambium temperatures for fires of a range of fire residence times and trees of a range of bark thicknesses.

It is hypothesized that cell mortality at elevated temperatures occurs primarily because of the accumulation of "lesions", particularly protein denaturations (e.g., Rosenberg et al. 1971). As lesions accumulate, the probability of cell mortality increases (e.g., Jung 1986). We approximate this process with a three population cell-survivorship model adapted from the protein denaturation literature (see Figure 2). Unaffected cells become susceptible to being killed (i.e., they have accumulated enough lesions) at a temperature-dependent rate:

$$\frac{dS_U}{dt} = -k_{12}S_U(t) \tag{10}$$

where S_U is the fraction of live cells that are unaffected by heating and k_{12} is the temperature-dependent transition rate between the unaffected (first) and susceptible (second) populations. The fraction of unaffected cells is 1 at the initiation of heating while the fraction of susceptible cells is initially 0. The change in the fraction of susceptible cells is dependent on both the rate at which they are produced from unaffected cells and also by the rate at which they are killed:

$$\frac{dS_S}{dt} = k_{12}S_U(t) - k_{23}S_S(t) \tag{11}$$

where S_S is the fraction of cells that are susceptible to being killed and k_{23} is the temperature-dependent transition rate between the susceptible cells (second population) and dead cells (third population). Equations 10 and 11 are integrated and the surviving fraction at a given time $S(t)$ is the sum of the unaffected and susceptible fractions at that time:

$$S(t) = \frac{k_{23}\exp(-k_{12}t) - k_{12}\exp(-k_{23}t)}{k_{23} - k_{12}} \tag{12}$$

We used Equation 12 and a nonlinear least-squares routine to estimate the rate parameters k_{12} and k_{23} from data on cell survivorship in thin cross-sections of live aspen and spruce bark heated in a water bath at a series of constant temperatures between 40 to 71 °C. We estimated the fraction of surviving cells S_t at a series of exposure times by staining tissues with a vital stain and counting live cells under a microscope. Cell counts in unheated controls served as the basis for estimating surviving fractions. Surviving fractions were estimated in live bark tissue adjacent to the vascular cambium because it was not possible to count the small vascular cambium cells themselves. We assume that the rate parameters k_{12} and k_{23} we estimated from live bark cells closely approximate those of vascular cambium.

The temperature dependence of the rate constants can be expressed in terms of a standard biophysical rate-theory equation (e.g., Johnson et al. 1974):

$$k_{12}\ or\ k_{23} = \frac{k_B T}{h}\exp(\frac{\text{Ä}S}{R})\exp(\frac{-\text{Ä}H}{RT}) \tag{13}$$

where k_B is the Boltzman constant (erg °K^{-1}), T is temperature (°K), h is Planck's constant (erg sec), *ÄS* is the activation entropy (J mol^{-1}), R is the universal gas constant (J mol^{-1} °K^{-1}), and *ÄH* is the activation enthalpy (J mol^{-1}). Values of *ÄS* and *ÄH* in Equation 13 were estimated from data by a nonlinear least-squares routine.

We describe live bark cell survivorship in terms of flame residence time and bark thickness by linking a heat-transfer model and a biophysical cell-survivorship model. We used Equations 10 and 11 in a numerical routine to predict the reduction in cell survivorship for a range of simulated vascular cambium temperature regimes. The rate parameters k_{12} and k_{23} and their temperature dependence (Equation 13) were estimated as described above. We tested the modeling approach against data on cell survivorship in thin sections of live aspen and spruce bark heated over temperature regimes characteristic of those experienced by the vascular cambium during fires.

SUMMARY OF DATA ANALYSIS
AND MANAGEMENT APPLICATIONS

Surface Fire Extinction

Surface fires were predicted to spread across all upland mixedwood boreal forest stands $\geq$30 years-since-last fire during periods when the majority of area burned in the past (Figure 3). Spread was predicted to occur in all stands because values of the extinction index were above those found to allow steady-state spread (Wilson 1985). The extinction index is a heat budget described by the ratio of a heat source and a heat sink term (Equation 1). Fire spread was predicted for all stands despite the fact that aspen stands had lower values of the heat-source term than conifer stands. The differences between aspen and conifer stands were not large enough to cause differences in whether fires spread or went extinct because fuel moisture levels and, consequently, the heat sink term were low.

Our results imply that increasing aspen dominance on the mixedwood boreal forest landscape may not be effective as a strategy to encourage fire extinction and, thereby, reduce area burned and tree mortality in fires (Fechner and Barrows 1976, DeByle et al 1987). We base this conclusion on the assumption that aspen stands would only have the potential to cause large effects on area burned if those effects operated during periods when the vast majority of forest area burned (i.e., during large-area-burned years when surface-fuel moisture levels are low and large fires make runs). It is conceivable that, when fuel-moisture levels are moderate, aspen stands could cause surface-fire extinction at the same time that fires would spread through conifer stands. One

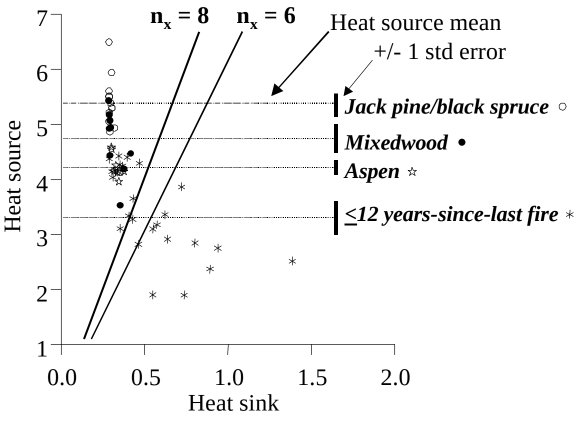


Figure 3. We here present the extinction index n_x as the ratio of the heat source and the heat sink (Equation 1). Steady-state spread is predicted for n_x values $\geq$8 and extinction is predicted for values < 6 while marginal spread is predicted for intermediate values (Wilson 1985). Shown are heat source and sink values for surface fuels in upland stands in the Saskatchewan mixedwood boreal forest during large-area-burned years when fires $\geq$25000 ha made runs.

can see this from Figure 3 where smaller increases in surface-fuel moisture (i.e., the heat sink) are required to move aspen stands into the marginal spread region than would be necessary for many conifer stands. However, differences among aspen and conifer stands in ability to carry a fire would only occur during periods when rates of spread and intensities were unlikely to be extreme because of relatively moist fuels. Consequently, it is unlikely that area burned would be large during these periods even if conifer fuels were the only fuels on the landscape.

Many recently-burned stands were not predicted to carry a surface fire because the extinction index was below the threshold for surface-fire spread (Figure 3). Surface fuels in recently-burned stands had relatively low values of the heat-source term and high values of the heat-sink term during large-area-burned years when large fires made runs. Low values of the heat-source term resulted primarily from low fuel loadings. High values of the heat-sink term resulted from high live-to-dead fuel ratios during the spring fire season and, thus, high fuel-moisture levels even while dead fuels were relatively dry. Recently-burned stands that were not predicted to carry a fire during periods when the majority of forest area burned would not be predicted to carry a fire during any weather conditions because dead-fuel moisture levels would not often be lower than they are during large-area-burned years when large fires made runs. We caution that the recently-burned stands in our sample had not experienced a short fire cycle as would be the case under frequent prescribed burning. Frequent prescribed burning would be expected to have large effects on the herb layer (e.g., increases in grass and herb biomass) that would render invalid any extrapolation of our results.

Tree Death

Survivorship of live bark cells can be predicted for a range of bark thicknesses and for fires of a range of residence times by linking the heat-transfer and biophysical cell-survivorship models (Figure 4). We assume that live-bark cell survivorship closely approximates the survivorship of the adjacent vascular cambium cells (see above). We expect that vascular-cambium cell mortality would be complete in trees with bark <6 mm thick over a range of fire residence times. In contrast, minimal vascular-cambium cell mortality would be expected in trees with bark >20 mm thick during surface fires and crown scorch must then become the primary cause of their death (see Van Wagner 1973). Our mechanistic approach could provide managers with a tool for predicting vascular-cambium necrosis and tree death during surface fires from bark thickness and fire residence time, variables that are readily estimated in the field or from models.

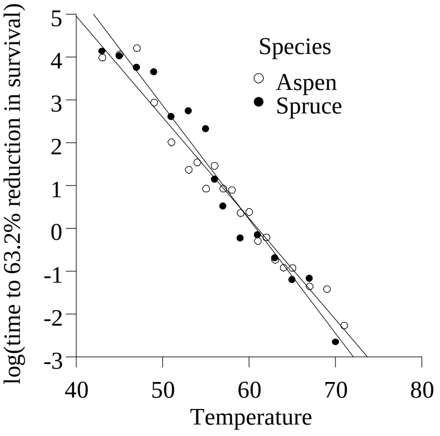


Figure 6. Relationship between temperature and the time required to reduce live-bark cell survivorship by 63.2%.

We expect that cell-survivorship predictions derived from the biophysical cell-survivorship model are reasonable because our live-bark cell survivorship data are consistent with the model in three key respects. First, the data show an initial period of reduced cell mortality rates exhibited by an obvious shoulder in many of the lines (Figure 5). The lag in the onset of high cell-mortality rates is consistent with our understanding of the cell-mortality process in which cells must accumulate protein denaturations (or some other type of lesion) before mortality rates become appreciable (e.g., Jung 1986). In the literature, a lag in cell mortality rates is generally observed but is typically ignored so that a simple, though unrealistic, negative exponential model can be used (e.g., Dewey et al. 1977).

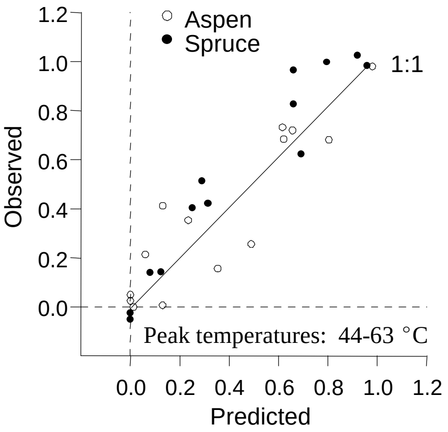


Figure 7. Fit between observed survivorship of live-bark cells and survivorship predicted from the biophysical cell-survivorship model after exposure to time-varying temperature traces typical of those experienced by the vascular cambium in fires. Replicates for which observed and predicted survivorship were near zero are offset for clarity.

Second, the biophysical cell-survivorship model captures the expected temperature-dependence of live-bark cell survivorship (Figure 6, see Equation 13). The time required to cause a given reduction in cell survivorship decreases continuously with temperature in both aspen and spruce bark. It is doubtful that a threshold temperature for vascular-cambium necrosis has general utility because cell mortality occurs continuously at elevated temperatures. As is apparent in Figure 4, any number of vascular-cambium temperature regimes with different peak temperatures can result in the same reduction in cell survivorship. Only if vascular cambium temperature regimes were consistent among trees in fires would a single threshold temperature for vascular-cambium necrosis be valid.

Finally, the cell-survivorship model can be used to predict aspen and spruce live-bark cell survivorship after exposure to temperature regimes approximating those at the vascular cambium during fires (Figure 7). This new result is important because it opens the door to linking heat-transfer models with cell-survivorship models as we have done in Figure 4.

CONCLUSIONS

Surface Fire Extinction

All stands $\geq$30 years-since-last fire were predicted to carry a surface fire during periods when the majority of forest area burned in the past. The vast majority of area burned occurs during large-area-burned years when large fires make runs. We assume that it is during these periods that fuel differences would have the greatest potential to affect landscape-level patterns of burning. Aspen stands had lower values of the heat-source term in the surface-fire extinction model than conifer stands but the differences were not large enough to matter because fuel moisture levels were low during periods when area burned was large. In contrast, many recently-burned stands would not be expected to carry a surface fire during any weather because of low fuel loadings and high live-to-dead fuel ratios.

Tree death

Survivorship of live bark cells can be predicted from fire residence time and bark thickness by linking a heat-transfer model with a biophysical cell-survivorship model. We assume that live bark cell survivorship closely approximates survivorship of the adjacent vascular cambium cells. The biophysical cell-survivorship model is consistent with key aspects of our data on aspen and spruce live-bark cell survivorship at elevated temperatures. First, there is a lag in the onset of high cell mortality rates at constant temperatures from about 43 to 70 °C. Second, cell mortality rates are a continuous function of temperature. Finally, the model predicts aspen and spruce cell survivorship after exposure to temperature regimes such as those experienced at the vascular cambium during fires. Our mechanistic approach could provide managers with a tool to predict vascular-cambium necrosis and tree death in surface fires.

REFERENCES

Abramowitz, M., and Stegun, I. A. 1964. Handbook of mathematical functions. Applied Mathematics Series No. 55. US Department of Commerce, National Bureau of Standards, Washington, D.C.

Albini, F. A., and Reinhardt, E. D. 1995. Modeling ignition and burning rate of large woody natural fuels. Int. J. Wildland Fire 5:81-91.

Bergeron, Y. 1991. The influence of island and mainland lakeshore landscapes on boreal forest fire regimes. Ecology 72:1980-1992.

Bergeron, Y., and Archambault, S. 1993. Decreasing frequency of forest fires in the southern boreal zone of Quebec and its relation to global warming since the end of the 'Little Ice Age'. Holocene 3:255-259.

Bridge, S. R. J., and Johnson, E. A. 2000. Geomorphic principles of terrain organization and vegetation dynamics. J. Vege. Sci. 11:57-70.

Bradshaw, L. S., Deeming, J. E., Burgan, R. E., and Cohen, J. D. 1983. The 1978 National Fire-Danger Rating System: technical documentation. USDA For. Serv. Gen. Tech. Rep. INT-169.

Brown, J. K., Oberheu, R. D., Johnston, C. M. 1982. Handbook for inventorying surface fuels and biomass in the Interior West. USDA For. Serv. Gen. Tech. Rep. INT-129.

Brown, J. K., DeByle, N. V. 1987. Fire damage, mortality, and suckering in aspen. Can. J. For. Res. 17:1100-1109.

DeByle, N. V., Bevins, C. D., Fischer, W. C. 1987. Wildfire occurrence in aspen in the interior Western United States. West. J. Appl. For. 2:73-76.

Dewey, W. C., Hopwood, L. E., Sapareto, S. A., and Gerweck, L. E. 1977. Cellular responses to combinations of hyperthermia and radiation. Radiology 123:463-474.

Dickinson, M. B., and Johnson, E. A. 2001. Fire effects on trees. In E. A. Johnson, and K. Miyanishi (eds) Forest fires: behavior and ecological effects. Academic Press, in press.

Fahnestock, G. R., and Hare, R. C. 1964. Heating of tree trunks in surface fires. J. For. 62:799-805.

Fechner, G. H., and Barrows, J. S. 1976. Aspen stands as wildfire fuel breaks. Eisenhower Consortium Bulletin 4, USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

Flannigan, M. D., and Wotton, B. M. 1991. Lightning ignited fires in nortwest Ontario. Can. J. For. Res. 21:277-287.

Gill, A. M., and Ashton, D. H. 1968. The role of bark type in relative tolerance to fire of three central Victoria eucalypts. Aust. J. Bot. 16:491-498.

Gutfreund, H. 1995. Kinetics for the life sciences: receptors, transmitters and catalysts. Cambridge University Press.

Hanks, R. J., Ashcroft, G. L. 1980. Applied soil physics. Springer-Verlag, Berlin.

Holman, J. P. 1986. Heat transfer. McGraw-Hill Book Company, New York.

Johnson, E. A., Miyanishi, K., and O'Brien, N. 1999. Long-term reconstruction of the fire season in the mixedwood boreal forest of Western Canada. Can. J. Bot. 77:1185-1188.

Johnson, E. A., Miyanishi, K., and Weir, J. M. H. 1998. Wildfires in the western Canadian boreal forest: landscape patterns and ecosystem management. J. Vege. Sci. 9:603-610.

Johnson, F. H., Eyring, H., and Stover, B. J. 1974. The theory of rate processes in biology and medicine. Wiley, New York.

Jung, H. 1986. A generalized concept for cell killing by heat. Rad. Res. 106:56-72.

Larsen, C. P. S. 1997. Spatial and temporal variations in boreal forest fire frequency in northern Alberta. J. Biogeog. 24:663-673.

Levitt, J. 1980. Responses of plants to environmental stresses, Volume 1, chilling freezing, and high temperature stresses. Academic Press, New York.

Lorenz, R. W.   1939. High temperature tolerance of forest trees. Technical Bulletin 141, Minnesota Agricultural Experiment Station.

Martin, R. E. (1963). Thermal properties of bark. For. Prod. J. 13:419-426.

Martin, R. E., Cushwa, C. T., and Miller, R. L. 1969. Fire as a physical factor in wildland management. In Proceedings of the Ninth Annual Tall Timbers Fires Ecology ConferenceTall Timbers Research Station, Tallahassee, Florida, pp. 271-288.

Nash, C. H., and Johnson, E. A. 1996. Synoptic climatology of lightning-caused forest fires in subalpine and boreal forests. Can. J. For. Res. 26:1859-1874.

Peterson, D. L., and Ryan, K. C. 1986. Modeling postfire conifer mortality for long-range planning. Env. Manage. 10:797-808.

Reed, W. J., Larsen, C. P. S., Johnson, E. A., and MacDonald, G. M. 1998. Estimation of temporal variations in historical fire frequency from time-since-fire map data. For. Sci. 44:465-475.

Rego, F., Rigolot, E. 1990. Heat transfer through bark - a simple predictive model. In J. G. Goldammer and M. J. Perkins (eds) Fire in ecosystem dynamics. SPB Academic Publishing, The Hague, pp. 157-161.

Reifsnyder, W. E., Herrington, L. P., and Spalt, K. W. (1967). Thermophysical properties of bark of shortleaf, longleaf, and red pine. Yale University School of Forestry, Bull. No. 70.

Rosenberg, B., Kemeny, G., Switzer, R. C., and Hamilton, T. C. 1971. Quantitative evidence for protein denaturation as the cause of thermal death. Nature 232:471-473.

Stocks, B. J. 1991. The extent and impact of forest fires in northern circumpolar countries. In J. S. Levine (ed.) Global biomass burning: atmospheric, climatic, and biospheric implications. MIT Press, Cambridge, MA, pp. 197-202.

Stocks, B. J., and Street, R. B. 1983. Forest fire weather and wildfire occurrence in the boreal forest of northwestern Ontario. In R. W. Wein, R. R. Riewe, and I. R. Methven (eds) Resources and dynamics of the boreal zone. Association of Canadian Universities Northern Studies, Ottawa, Ontario, pp. 249-265.

Strauss, R. A., Bednar, L., and Mees, R. 1989. Do one percent of forest fires cause ninety-nine percent of the damage? Forest Science 35:319-328.

Van Wagner, C. E. 1973. Height of crown scorch in forest fires. Can. J. For. Res. 3:373-378.

Van Wagner, C. E. 1987. Development and structure of the Canadian Forest Fire Weather Index System. Can. For. Serv. For. Tech. Rep. 35, Ottawa.

Vines, R. G. 1968. Heat transfer through bark, and the resistance of trees to fires. Australian Journal of Botany 16:499-514.

Weber, R. O., Gill, A. M., Lyons, P. R. A., and Mercer, G. N. 1995. Time dependence of temperature above wildland fires. CALMScience Supplement 4:17-22.

Weir, J. M. H., Johnson, E. A., and Miyanishi, K. 2000. Fire frequency and the spatial age mosaic of the mixed-wood boreal forest in western Canada. Ecol. Appl. 10:1162-1177.

Wilson, R. A., Jr. 1985. Observations of extinction and marginal burning states in free burning porous fuel beds. Comb. Sci. Tech. 44:179-193.