CSIRO PUBLISHING

International Journal of Wildland Fire **2012**, *21*, 709–721
http://dx.doi.org/10.1071/WF11153

Modelling the effects of surface and crown fire behaviour on serotinous cone opening in jack pine and lodgepole pine forests

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Abstract. A methodology has been developed for defining the various threshold conditions required for the opening of serotinous cones and viable seed release in the overstorey canopies in jack pine (*Pinus banksiana*) and lodgepole pine (*Pinus contorta* var. *latifolia*) forests on the basis of fireline intensity and, in turn, rate of fire spread and fuel consumption. The extent of the effects to the overstorey canopy (i.e. crown scorch height and flame defoliation) and the type of fire (i.e. low- to high-intensity surface, intermittent crown and active crown) vary at any given fireline intensity level and are principally a function of foliar moisture content, canopy base height, stand height and canopy bulk density. The viability of the seed stored in serotinous cones of the two pine species begins to decreases once the flame-front residence time at the ground level of an active crown fire exceeds 50 s.

Additional keywords: convection column temperature, crown scorch height, fire ecology, fireline intensity, flame front residence time, fuel consumption, rate of fire spread, tree regeneration.

Received 25 October 2011, accepted 24 January 2012, published online 5 July 2012

Introduction

The connection between fire and serotinous cones of jack pine (*Pinus banksiana*) and lodgepole pine (*Pinus contorta* var. *latifolia*) represents two of the classical fire ecology relationships found in the coniferous forests of western and northern North America (Wright and Heinselman 1973). Conventional wisdom has it that serotinous cones of jack pine and lodgepole pine, sealed shut by a resinous bond at the tips of the cone scales, typically require exposure to high temperatures in order for the seal to be broken (Carey 1993; Anderson 2003). The reflexing of the cone scales and release of seed do not occur immediately following passage of the flame front. However, a 'seed rain' can be expected to begin within 24 h (Eyre and LeBarron 1944; Chrosciewicz 1988). The resin bond on serotinous cones on or near the ground can also be broken or weakened by normal summertime soil-surface temperatures (Eyre and LeBarron 1944; Crossley 1956).

Cameron (1953) determined that the melting point of the scale bonding material was 50°C for jack pine and 45.5°C for lodgepole pine using a petroleum ether extract procedure. Quantification of the heating requirements for opening serotinous cones of jack pine and lodgepole pine has been undertaken by several investigators using both dry (Beaufait 1960*a*; Hellum 1981) and wet treatments (Clements 1910; Smith and McMurray 2002). These efforts have so far been restricted to simplistic tests carried out in laboratory or artificial environments as opposed to real-world-like situations, although Beaufait (1960*b*) did demonstrate that serotinous cones on standing jack pine trees could be opened with a flame thrower after only 4 s of exposure.

Given our knowledge and experience with respect to fire behaviour and fire effects in jack and lodgepole pine forests (Lotan *et al.* 1985; Rouse 1986), there is considerable potential to begin linking the various quantitative models for predicting forest fire behaviour (e.g. Forestry Canada Fire Danger Group 1992; Alexander and Cruz 2011) to fuel characteristics (e.g. Alexander 1979; Lavoie *et al.* 2010), and in turn information on seed quantity (Roe 1963; Lotan and Jensen 1970) and desired seedbed conditions following fire (Muraro 1971; Chrosciewicz 1974). Such developments would be of value, for example, in simulating wildfire effects (de Groot *et al.* 2003) and in developing prescriptions for prescribed burning in natural forest stands (Dubé 1977; Muraro 1978; Zimmerman 1990; Safranyik *et al.* 2001).

This paper outlines development of a simple methodology to determine the conditions associated with the melting of the resinous bonding material found on serotinous cones in the overstorey canopies of jack pine and lodgepole pine and the degree of crown scorch or consumption in relation to quantifiable surface and crown fire behaviour, and fuel and stand characteristics. It also in turn examines the effect of cone ignition or charring on seed viability in relation to crown fire behaviour in these two conifer forest types.

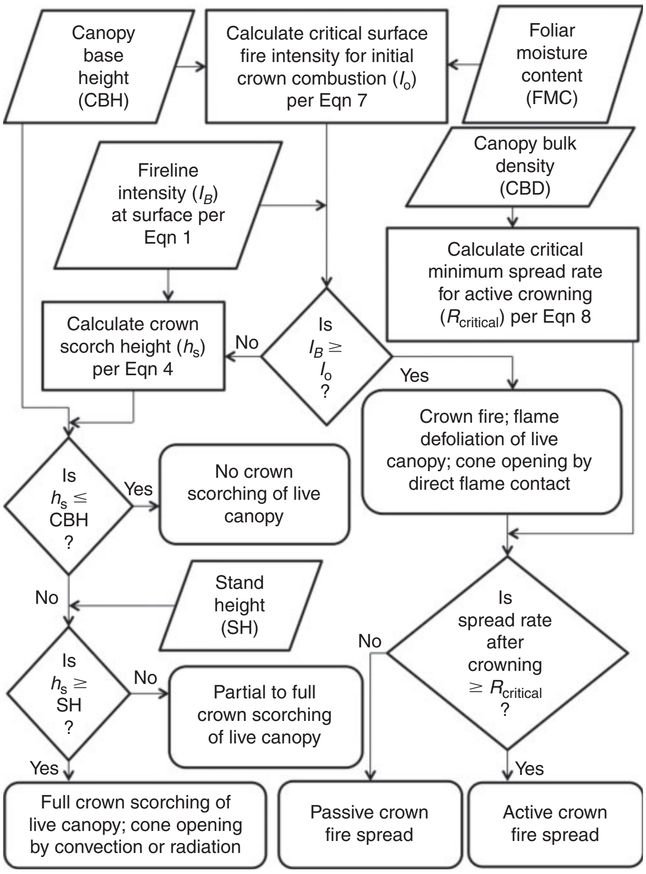

Fig. 1. Flow diagram of the primary processes involved in predicting the effects of surface and crown fire behaviour on the overstorey tree canopy of jack pine and lodgepole pine forests, starting with the calculation of the critical surface fire intensity for initial crown combustion.

Methods

The methodology as developed herein relies on the application of several existing models and fundamental relationships with respect to the following physical fire processes (Fig. 1):

- Surface fire intensity;
- Convective heating as reflected in the height of crown scorch;
- Crown fire initiation and propagation;
- Duration of heating of the live overstorey canopy by convection and by direct flame contact; and
- Time–temperature dependency associated with the melting of the resinous bond that holds the scales of serotinous cones of jack pine and lodgepole pine together.

A description of each of these methodology elements follows. For the convenience of the reader, a summary list of the variables referred to in the equations and text, including their symbols and units, is given at the end of this article.

Basic descriptor of a spreading heat source

One of the most fundamental descriptors of a wildland fire with respect to aboveground fire effects is Byram's (1959) fireline intensity. Effects such as bud and needle tissue mortality result mainly from radiative and convective heat transfer and are thus strongly correlated with fireline intensity (Fig. 2), which dictates the temperature profile above the flame zone as well as the height of crown scorch (Fig. 3*a*) (Van Wagner 1973; Wade 1987; Burrows 1995).

Byram (1959) defined fireline intensity as the rate of heat energy release per unit time per unit length of fire front, regardless of the depth or width of the zone of active flaming combustion (Alexander 1982). Flame length (Fig. 3*a*) is its main visual manifestation (Alexander and Cruz 2012). Fireline intensity cannot be measured directly *per se*, but can be computed by the following formula:

$$I_B = H\,w_a\,r \tag{1}$$

where, in compatible International System (SI) units (Van Wagner 1978), I_B is fireline intensity (kW m^{-1}); H is the

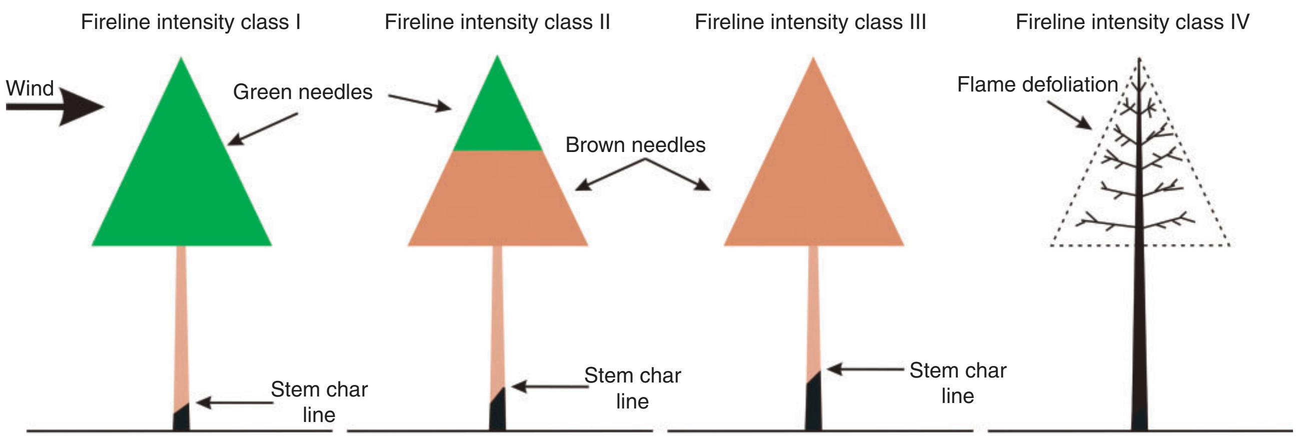

Fig. 2. Schematic diagram of the four fireline intensity classes as recognised in this paper in terms of post-fire effects on the overstorey tree canopy.

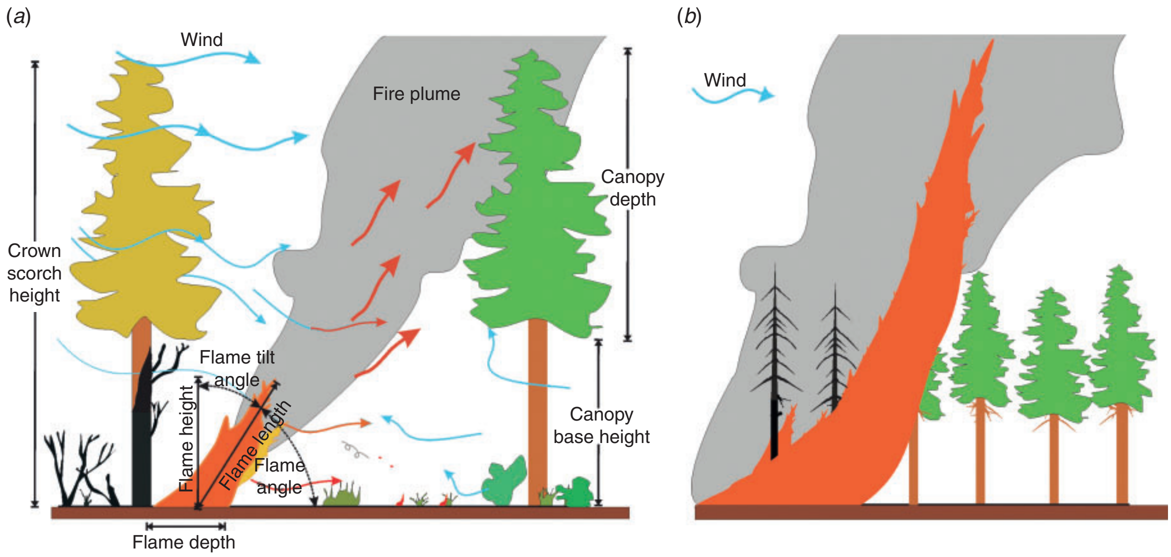

Fig. 3. Cross-sectional views of (*a*) a stylised, wind-driven surface head fire spreading through a conifer forest stand on level terrain and (*b*) a stylised active crown fire on level terrain, illustrating flame-front dimensions in relation to fuel complex structure.

low heat of combustion (kJ kg^{-1}), which when reduced for fuel moisture content becomes the net H; w_a is the 'available fuel' or fuel consumed in the active flame front (kg m^{-2}); and r is the rate of fire spread (m s^{-1}).

Assuming a net $H = 18\,000$ kJ kg^{-1} (Stocks *et al.* 2004) and that the rate of fire spread is in metres per minute (represented by the symbol R), Eqn 1 can be expressed as follows (Forestry Canada Fire Danger Group 1992):

$$I_B = 300\, w_a R \tag{2}$$

The hyperbolic or inverse function represented by Eqn 2 is graphically displayed in Fig. 4 in the form of a fire behaviour characteristics chart (Alexander *et al.* 1991) as patterned after the fire characteristics chart (Andrews *et al.* 2011).

Spread rates slightly in excess of 100 m min^{-1} have been documented in jack pine and lodgepole pine fuel types during wind-driven wildfire runs that have involved extensive crowning activity (Alexander and Cruz 2006). Total ground, surface and canopy fuel consumption values of close to 6.0 kg m^{-2} have been measured on experimental fires (Stocks *et al.* 2004). For photographic examples illustrating a range in I_B and different types of fires (i.e. surface, passive crown and active crown), see Stocks and Hartley (1995).

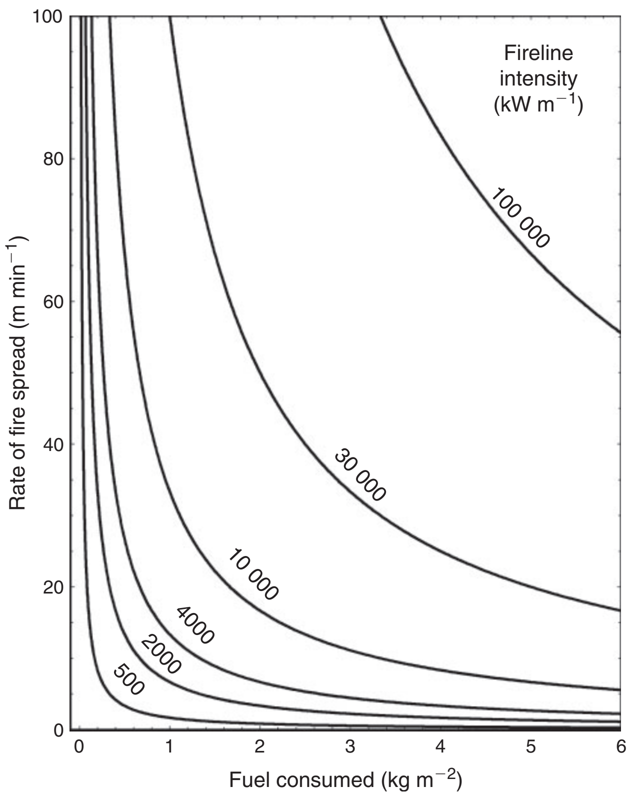

Fig. 4. A fire behaviour characteristic chart illustrating six specified levels of fireline intensity defined as a function of rate of fire spread and fuel consumption, assuming a net low heat of combustion $H = 18\,000$ kJ kg^{-1}, according to Eqn 2. For the sake of operational use in fire and fuel management, it is worth noting that 1.0 kg m^{-2} equals 10 t ha^{-1}.

Convective heating of the overstorey canopy by surface fire

A heat source such as a forest fire produces a plume (Fig. 3*a*) of thermally induced gases, smoke, ash particulates and other debris (Cheney and Sullivan 2008). According to Thomas (1963), the temperature attained at any height in the convection column above a surface fire can be estimated from I_B, in the absence of wind, from the following relation (after Van Wagner 1973, 1975):

$$\Delta T = \frac{b\, I_B^{2/3}}{z} \tag{3}$$

where ΔT is the temperature rise above the ambient air conditions (°C) at height z above the ground (m), and b is an empirical proportionality constant. A value of $b = 3.85$ based on the works of Van Wagner (1973, 1975) is commonly cited (Alexander 1982), although higher values have been reported (Alexander 1998; Michaletz and Johnson 2006). Michaletz and Johnson (2006) attribute this variation to differences in crown components (e.g. needles versus buds), species, season and site. Although these are certainly influential factors, there are several other reasons, of which fuel complex structure is the most important (Alexander and Cruz 2012). The means to account for the effect of wind do exist (Van Wagner 1973; Alexander 1998).

Above any fire, there will be a zone within which the live conifer needle foliage or buds will be killed by hot gases rising upwards from the flames (Van Wagner 1973). This is generally regarded as the height above ground at which a temperature of ~57 to 60°C is maintained for approximately 1 min (Van Wagner 1973; Alexander 1998).

Van Wagner (1973) applied Thomas's (1963) theory of convection column temperature to the prediction of crown scorch height (h_s, m) and presented field evidence that h_s also varies with the 2/3 power of fireline intensity (from Alexander and Cruz 2012):

$$h_s = 0.1483\, I_B^{2/3} \tag{4}$$

Ambient air temperature can have a profound effect on h_s, especially under calm conditions (Byram 1958). The experimental fires used in the development of Eqn 4 were conducted with light to moderate in-stand winds (2.3 to 4.7 km h^{-1}) but moderate to high temperatures of 23.5 to 31°C (Van Wagner 1973).

Given a canopy base height (CBH, m) or stand height (SH, m), the inverse of Eqn 4 can be used to determine the I_B levels for (i) no crown scorch ($h_s <$ CBH); (ii) partial or incomplete crown scorch (CBH $\leq h_s \leq$ SH); and (iii) full or complete crown scorch ($h_s \geq$ SH) (Fig. 2) using the following equation (from Alexander and Cruz 2012):

$$I_B = 17.49\, h_s^{1.5} \tag{5}$$

The assumptions and limitations of this approach are discussed in Alexander and Cruz (2012).

Duration of convective heating by surface fire

Flame-front residence time (t_r, min) is another one of the more important characteristics of the advancing flame front of a wildland fire (Cheney 1981). It represents the length of time it takes for the flame zone to pass a given point (Wade 1987). Some authors have suggested it represents an approximation of the convective heating above a surface fire (Alexander 1998; Michaletz and Johnson 2006). For a fuelbed as opposed to an individual fuel particle, t_r is numerically equal to the horizontal flame depth (D, m) of a spreading fire (Fig. 3*a*) divided by the fire's rate of advance (Fons *et al.* 1963):

$$t_r = \frac{D}{R} \tag{6}$$

Like fireline intensity, t_r is a hyperbolic or inverse function (Fig. 5).

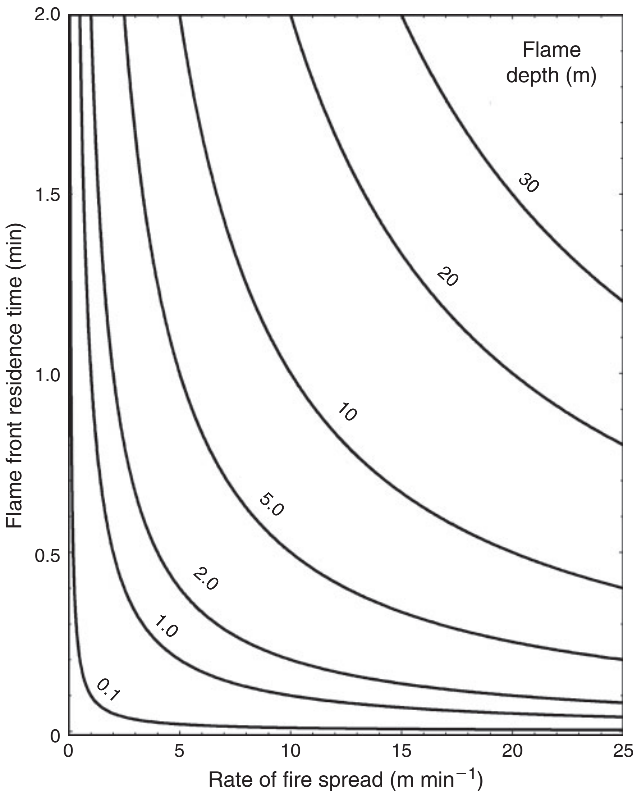

Fig. 5. Flame-front residence time as a function of horizontal flame depth and rate of fire spread according to Eqn 6.

Surface fires in jack pine and lodgepole pine stands typically produce t_r values of 0.5 to 1.0 min (Lawson 1972; Van Wagner 1972; Taylor *et al.* 2004). Head fires in grasslands typically have shorter residence times of 5 to 15 s (Cheney and Sullivan 2008) in contrast to 1 to 2 min in logging slash fuelbeds (Brown 1972). The physical explanation for these differences among broad fuel types lies in available fuel load and fuel particle size-class distribution (Anderson 1969; Burrows 2001; Nelson 2003).

For conifer forest stands with substantial forest floor accumulations, t_r values greater than 1 min are possible (McArthur and Cheney 1966), but this is dependent largely on the amount of ground and surface fuel consumed, which is in turn determined by the gradients in moisture content and bulk density found in the forest floor layer (Cheney 1981; Nelson and Adkins 1988; Nelson 2003). The deepening of the flame front resulting in increasingly residence times is due to the advancing fire edge spreading not only horizontally across the fuelbed, but vertically

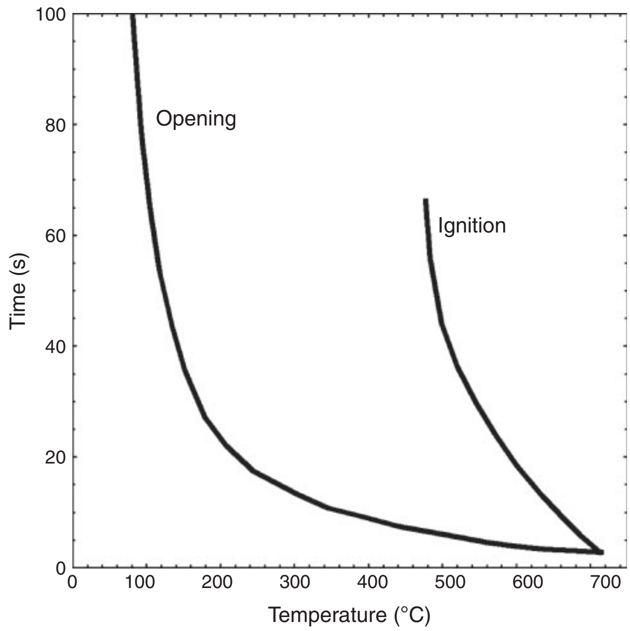

Fig. 6. Cone-opening and ignition curves for jack pine cones at 8.0% moisture content based on heating in an open muffle furnace as derived by Beaufait (1960*a*). The original work was done in Fahrenheit. Ten cones were exposed one at a time to temperatures ranging from 93 to 704°C (200–1300°F) in 68°C (100°F) intervals. After opening, the cones were left in the furnace to furnish data on ignition time. Cones did not ignite at temperatures of 427°C (800°F) or less even after 5 min.

upwards and downwards as well (Van Wagner 1972; Cheney 1990).

Time–temperature dependency relationships

The weakening or breaking of the resin bond that holds the tips of the serotinous cone scales in place is dependent on both the maximum temperature reached as well as the duration of the temperature above the threshold required to initiate the process (Hellum and Pelchat 1979). Perry and Lotan (1977), for example, found that serotinous cones of lodgepole pine open after 2 min in a 60°C water bath. Similarly, LeBarron and Roe (1945) found jack pine cones opened after 10 s of exposure to boiling water (i.e. 100°C). Cone moisture content is also known to influence cone opening (Hellum and Barker 1980). In contrast to these cone-soaking or 'wet' heating treatments, Hellum and Barker (1981) used a wood-drying kiln set at 180°C and found that the average time for resin bonds on lodgepole pine cones to break when exposed to this 'dry' heat was 53 s.

Beaufait (1960*a*) used an open muffle oven or furnace to investigate the opening and ignition of serotinous cones of jack pine and derived an exponential time–temperature relationship in graphical form but offered no corresponding equation (Fig. 6). Assuming for a moment that the temperatures experienced in an open muffle oven were indicative of convection column temperatures experienced above a spreading surface fire, for exposures equivalent to t_r values of 0.5 to 1.0 min (i.e. 30 to 60 s), the corresponding temperatures varied from 112 to 168°C. Johnson and Gutsell (1993) employed the same general methodology as Beaufait (1960*a*) and found a similar curvilinear result, although they made no direct comparison, other than to say that their result 'clearly fits the pattern of cone opening and ignition' given in Beaufait (1960*a*), as they chose to express their results in dimensionless time.

Placing a pine cone inside a muffle oven cannot entirely simulate the thermal environment associated with the convection column or fire plume above the flaming combustion zone of a spreading surface fire as the rising 'wafts' of heated air flow through the overstorey tree canopy (Despain *et al.* 1996). This was, however, exactly the approach taken by Johnson and Gutsell (1993) in linking their cone-heating results with Thomas' (1963) convective heating relationship represented here by Eqn 3. Strictly speaking, the temperature in a muffle oven is not compatible with Eqn 3. This is because heating in the muffle oven is primarily by radiation whereas in a fire plume, it is primarily by convection and it is difficult to ascertain how much of a difference there would in terms of temperature (B. W. Butler, USDA Forest Service, pers. comm., 2011). In this regard, a lumber- or wood-drying kiln (Hellum and Pelchat 1979; Hellum and Barker 1981) may be more suitable. Nevertheless, the lack of an established time–temperature relation for serotinous cone opening is not viewed as a hindrance in the development of the methodology.

Both Beaufait (1960*a*) and Johnson and Gutsell (1993) also utilised a muffle oven to acquire time–temperature data on cone ignition (Fig. 6). However, it's unrealistic to expect to be able to emulate an overstorey tree canopy being engulfed by the advancing flame front of either a passive or active crown fire in such a laboratory setting.

Crown fire considerations

The maximum flame temperatures in the overstorey tree canopy of a crown fire are given to be ~800 to 1000°C (Van Wagner and Methven 1978; Taylor *et al.* 2004). Thus, the resin bond that holds the tips of the scales of a serotinous jack pine or lodgepole pine cone together is far more easily broken from the momentary exposure to direct flame contact (Eyre and LeBarron 1944; Beaufait 1960*b*) than by convective and radiant heating from a surface fire.

The onset of crowning in most jack pine and lodgepole pine stands occurs when fire spread rates exceed ~5 to 10 m min^{-1}, and in turn with fireline intensities greater than ~2500 to 4000 kW m^{-1} (Lawson 1972; Quintilio *et al.* 1977; Stocks 1987, 1989). Continuous active crowning is generally expected in conifer forest fuel types when R reaches 15 to 30 m min^{-1} (Van Wagner 1980), reflecting the fact that R commonly doubles or triples in value following the onset of crowning (Fernandes *et al.* 2004), with fireline intensities exceeding 10 000 kW m^{-1} (Van Wagner 1977; Stocks 1987).

Van Wagner (1977) developed a simple model for determining crown fire initiation on the basis of two crown fuel properties:

$$I_o = (0.010\,\mathrm{CBH}(460 + 25.9\,\mathrm{FMC}))^{1.5} \quad (7)$$

where I_o is the critical surface fire intensity needed for initial crown combustion (kW m^{-1}), CBH is the canopy base height (m) and FMC is the foliar moisture content (% oven-dry weight basis). Thus, the onset of crowning is expected to occur when $I_B \geq I_o$.

Van Wagner (1977) also proposed that a critical minimum spread rate for active or fully developed crowning (R_o, m min^{-1}) could be estimated on the basis of stand canopy bulk density (CBD, kg m^{-3}) using the following simplistic function:

$$R_o = \frac{3.0}{\text{CBD}} \quad (8)$$

CBD represents the available canopy fuel load divided by the canopy depth (Cruz *et al.* 2003). Active crowning occurs when $I_B \geq I_o$ and $R \geq R_o$. Passive crowning, however, represents the spectrum between high-intensity surface fires and fully developed crown fires. This occurs when $I_B \geq I_o$ and $r < R_o$ (Van Wagner 1977; Alexander and Cruz 2011) and can lead to partial fuel consumption in the lower portion of the overstorey canopy depending on the CBD (Alexander 1998). The robustness of the relationship represented by Eqn 8 in differentiating passive from active crown fires has been amply demonstrated (Cruz and Alexander 2010).

One cannot directly infer the duration of direct flame contact at a given point in the overstorey canopy in a crown fire from the t_r value at the ground surface because of the wedge-shaped nature of the flame front in a crown fire (Fig. 3*b*) – i.e. the horizontal flame depth at the ground surface gradually narrows or tapers up to the flame tip some distance above the canopy layer. Anderson (1969) derived the following relationship between flame residence time of an individual fuel particle (t_R, s) and particle thickness (d, cm):

$$t_R = 189\, d \quad (9)$$

For needles of jack pine (Roussopoulos 1978) and lodgepole pine (Brown 1970), $d = 0.051$ and 0.062 cm respectively. Thus, according to Eqn 9, one would expect the flaming residence time in the canopy fuel layer to range from at least 10 to 12 s. This minimum value range matches measurements (Taylor *et al.* 2004) and general observations of experimental crown fires.

Despain *et al.* (1996) analysed segments of video footage taken of the 1988 Yellowstone fires for the duration of flaming in individual tree crowns ($n = 18$) as well as stands of lodgepole pine where all the crowns burned simultaneously as a result of area ignition from spot fires ($n = 84$). He found from a non-random sample that the duration of flaming averaged 24.5 s (s.d. ± 9.6) and ranged from 5 to 48 s with no significant difference between single trees and stands of trees in the time that crowns remained flaming.

An exact physical description of the relationship between t_r at the ground level of a surface fire versus t_r in the overstorey canopy layer associated with an active crown fire does not presently exist. However, based on existing information, one can say with some degree of certainty that the ratio lies between 2 : 1 (Taylor *et al.* 2004) and 3 : 1 (Anderson 1968). In other words, the t_r in the live canopy is approximately equal to the t_r at the ground surface divided by a factor of 2.5 (Fig. 3*b*).

Nominal stand and fuel characteristics

For the purposes of demonstrating the methodology, nominal stand heights of 10 and 20 m were selected for jack pine and lodgepole pine respectively. This represents the mature (C-3) and immature (C-4) jack pine and lodgepole pine fuel types of the Canadian Forest Fire Behaviour Prediction (FBP) System (Forestry Canada Fire Danger Group 1992; Wotton *et al.* 2009) as well as the two western Canadian pine stand types modelled by Johnson and Gutsell (1993). An understorey of spruce (*Picea* spp.) could be present and act as ladder or bridge fuel. CBH values of 8.0 and 4.0 m have been assigned to FBP System fuel types C-3 and C-4 (Forestry Canada Fire Danger Group 1992). In turn, the CBD values for fuel types C-3 and C-4 would be 0.1 and 0.2 kg m^{-3}. Thus, the development of active crown fire spread would be expected to occur at 30 and 15 m min^{-1}.

A FMC of 100% was selected for pine species based on a suggestion of Keyes (2006). This is close to the midpoint of the range in FMC seen, for example, over the course of the fire season in much of the forested region of Canada (Forestry Canada Fire Danger Group 1992). Surface fire t_r was assigned a value of 1.0 min. In the absence of any definitive research on cone distribution within the tree crown, it was assumed (based on general observation) that cones are distributed vertically throughout the live canopy space and that there are no cones below the CBH level. This is in contrast to Johnson and Gutsell's (1993) assumption that most of the cones are borne at the very top of the tree.

Results

The canopy fire effect charts presented in Fig. 7 for the two example stands are patterned after the fire behaviour characteristics chart (Fig. 4) presented earlier. The fireline intensity classes (Fig. 2) identified in Fig. 7 and Table 1 reflect four more or less logical categories of canopy fire effects (Tozzini and Soares 1987) as follows:

- Fireline intensity class I: $h_s \leq$ CBH threshold determined from Eqn 5.
- Fireline intensity class II: CBH $\leq h_s \leq$ SH thresholds determined from Eqn 5.
- Fireline intensity class III: $h_s \geq$ SH threshold determined from Eqn 5 and the $I_B \leq I_o$ threshold determined from Eqn 7.
- Fireline intensity class IV: $I_B \geq I_o$ threshold determined from Eqn 7.

At this stage of their development, the differences between the two canopy fire effect charts are due solely to CBH and SH as opposed to tree species and fuel type characteristics (e.g. forest floor cover, ladder or bridge fuels such as bark features, dead bole branches and the presence of understorey trees).

Discussion

From the perspective of cone opening, fireline intensity classes I and II could be combined into a single category. The description given in Table 1 for fireline intensity class III reflects some of the uncertainty associated with the lack of a precise time–temperature relationship for serotinous jack pine and lodgepole pine cone opening that would be compatible, for example, with Eqn 3. It also reflects the fact the cones are assumed to be distributed throughout the length of the live crown. Convection column temperatures within the crowns of fully scorched trees just before the onset of crowning are estimated to range from ~57 to 60°C at the SH level (Van Wagner 1973; Alexander

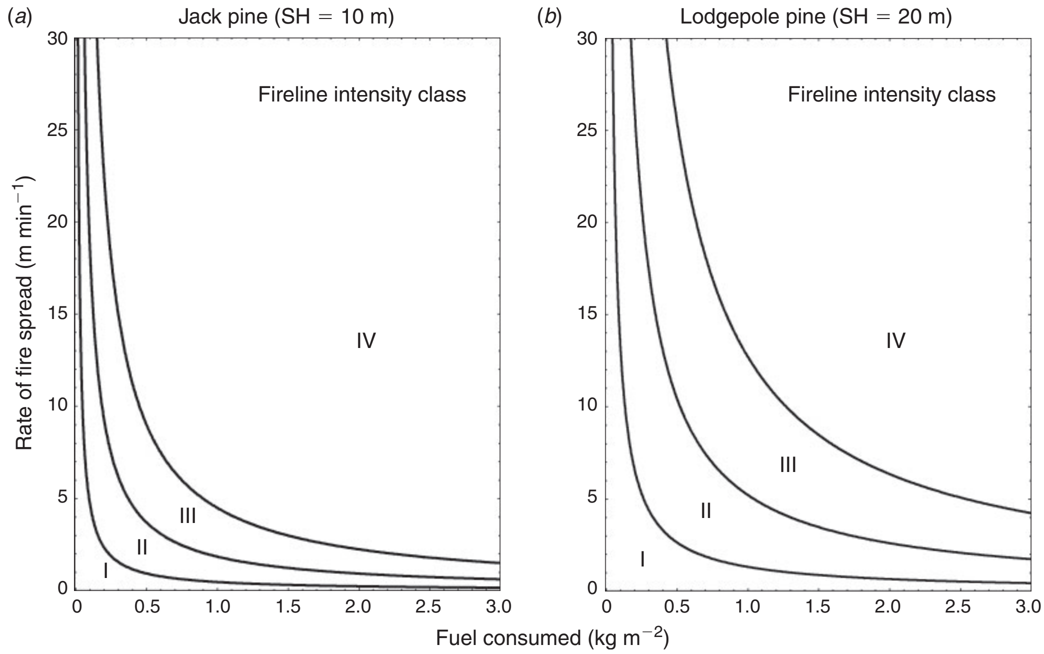

Fig. 7. Canopy fire effect charts for (*a*) 10-m-tall jack pine and (*b*) 20-m-tall lodgepole pine forests based on rate of fire spread and fuel consumption. See Table 1 for a description regarding the type of fire, serotinous cone opening or lack thereof, and degree of crown scorch or flame defoliation associated with each fireline intensity class.

Table 1. Range in fireline intensities linked to canopy fire effects derived for two example pine stand types
SH, stand height; CBH, canopy base height; *R*, rate of fire spread

Fireline intensity class[A]	Type of fire and associated effect on cones and tree crowns	Jack pine stand (SH = 10 m, CBH = 4 m) ($kW\ m^{-1}$)	Lodgepole pine stand (SH = 20 m, CBH = 8 m) ($kW\ m^{-1}$)
I	Low-intensity surface fire; no crown scorch or cone opening	<140	<396
II	Moderate-intensity surface fire; partial to nearly complete crown scorch of the overstorey canopy and no cone opening	140–554	396–1566
III	High-intensity surface fire; full crown scorch of the overstorey canopy and cone opening by convective and radiative heating	554–1348	1566–3811
IV	Crown fire; flame defoliation of the overstorey canopy, full cone opening as a result of direct flame contact and cone charring	≥1348[B]	≥3811[C]

[A]Refer to Fig. 7.
[B]The transition between passive and active crowning occurs when R is $\geq 15\ m\ min^{-1}$.
[C]The transition between passive and active crowning occurs when R is $\geq 30\ m\ min^{-1}$.

1998) to ∼300 to 325°C at the CBH level (Van Wagner 1977; Cruz *et al.* 2006), and thus fall within the range of convective temperatures conducive to melting of the resin bond for exposures of 30 to 60 s. In this regard, it is worth noting that Chrosciewicz (1988) observed some cone opening in jack pine seed trees that had experienced complete crown scorch resulting from the broadcast burning of clear-cut logging slash.

General model validation

Although the results given in Fig. 7 and Table 1 could be viewed as theoretical in nature, they are corroborated by a large body of empirical evidence of fire-induced tree regeneration in relation to quantified fire behaviour. Such an assertion is based on the premise that the resinous bond that holds the tips of the scales of serotinous cones together would have to be broken for viable seed to be released and in turn fall to the ground and germinate for seedlings to become established. Seedling density would first and foremost be a reflection of the total quantity of seed held in the canopy seed bank as dictated by stand characteristics (i.e. age, tree density). The amount of viable seed that actually falls to the ground, germinates to produce the next tree crop, in turn influenced by a host of factors (e.g. seedbed conditions, post-burn climatic conditions) (Carey 1993; Anderson 2003).

Weber *et al.* (1987) for example reported on jack pine regeneration in relation to fire behaviour for six outdoor experimental fires and one wildfire in eastern Ontario where

SH = 19 m. A statistical relationship derived by Weber *et al.* (1987) explained 82% of the variation in post-fire seedling density based on I_B alone. The two most intense fires ($I_B = 17\,000$ kW m^{-1}) exhibited R values of 15 and 24 m min^{-1}, which implies w_a values of 3.78 and 2.36 kg m^{-2} (assuming a net $H = 18\,000$ kJ kg^{-1}). Weber *et al.* (1987) observed ~30 000 to 50 000 regenerated stems ha^{-1} 13 to 16 years after these fires.

Stocks and Alexander (1980) documented fire-induced tree regeneration 5 years following experimental fires in 10- and 20-m-tall jack pine plots located in north-central Ontario. They recorded regeneration densities of up to 4000 and 15 000 seedlings ha^{-1}. On the experimental plots, head-fire rates of spread reached 68 and 15 m min^{-1}, with fireline intensities of ~60 000 and 6000 kW m^{-1} and fuel consumption levels of 3.44 and 2.53 kg m^{-2} (Stocks 1987, 1989; Stocks and Hartley 1995). Similarly, de Groot *et al.* (2004) reported fire-induced regeneration densities of 70 000 to 800 000 jack pine seedlings ha^{-1} 1 year after 10 experimental crown fires in a 12-m-tall jack pine–black spruce (*Picea mariana* (Mill.) BSP) stand in the southern region of the Northwest Territories where spread rates, fireline intensities and fuel consumption levels ranged from ~25 to 70 m min^{-1}, 37 000 to 90 000 kW m^{-1} and 2.8 to 5.5 kg m^{-2} (Stocks *et al.* 2004).

There are also many examples of profuse jack pine (Grafstrom and Hansen 1962; Methven *et al.* 1975; Ohmann and Grigal 1979) and lodgepole pine (Dubé 1976; Lyon 1984; Oswald and Brown 1990) regeneration following high-intensity crowning wildfires. Consider for example the abundance of lodgepole pine regeneration following the 8426-ha Galatea Creek Fire of August 1936 in the Kananaskis Valley of south-western Alberta (Horton 1955). For that fire, Fryer and Johnson (1988) retrospectively estimated that I_B exceeded 7000 kW m^{-1} over 92% of the area burned.

The documentation associated with the cases mentioned above is all in general agreement with the expected outcomes as presented in Fig. 7 and Table 1 with respect to fireline intensity levels III and IV. It is worth noting that on the basis of the fire-induced tree regeneration associated with the low- and moderate-intensity surface fires (70 to 200 kW m^{-1}) in jack pine reported by Weber *et al.* (1987), the possibility exists that serotinous cones were present below the CBH level and releasing some viable seed following their opening as a result of exposure to convective and radiative heating. Another possibility is that the resinous bond on serotinous cones lying on the ground surface are being broken as a result of direct flame contact during the surface fire spread.

Comparison with other similar work

Johnson and Gutsell (1993) set out to analytically define the heating requirements of serotinous cone opening and viable seed release in jack pine and lodgepole pine forests in terms of quantifiable fire behaviour. The authors developed a mechanistic heat budget model for cone opening and ignition by utilising heat-transfer principles and the thermal properties of the cones, coupled with empirical data garnered from heating cones in an open muffle oven as mentioned earlier.

The overriding objective of the Johnson and Gutsell (1993) study was to 'define the types of fires that result in cone opening and viable seed release'. They concluded, on the basis of their modelling, that serotinous cones on jack pine and lodgepole pine trees 10–20 m in height will 'open and release viable seeds in fires with low rates of spread and high fuel consumption but not when the rate of spread is high and fuel consumption low'.

Although the conclusion regarding the 'low spread rate–high fuel consumption' is in general agreement with our modelled results, their conclusion regarding the 'high spread rate–low fuel consumption' type of fire is not, nor does it match the knowledge gained from operational experiences and research studies as described in the previous section on general model validation. To explain, crown fires can occur throughout the year. However, in conifer forest stands in the boreal forest regions of Canada and similar adjacent areas in the Lake States region of the United States, they are a particularly common phenomenon in the spring before green-up when surface fuel consumption is typically low owing to the high moisture content of the duff layer following melting of the winter snowpack (Kiil and Grigel 1969; Simard *et al.* 1983). The propensity for crown fires at this time of year is attributed to several factors (Rowe and Scotter 1973; Fuglem and Murphy 1980), namely longer daylight hours, abundance of cured lesser vegetation, lack of turgid new plant growth, low overstorey foliar moisture contents, and certain synoptic meteorological patterns (e.g. high-pressure systems with little or no rainfall and low relative humidity although not necessarily high ambient air temperatures), which result in conditions that are conducive to relatively rapid drying of fine, dead fuels (Kiil and Grigel 1969; Nimchuk 1983).

Johnson and Gutsell (1993) expressed the final results of their modelling work in graphical form (Fig. 8). They recognised three categories – no cone opening, cone opening and cone ignition – defined by two fire-behaviour variables, namely fireline intensity and rate of fire spread. The modelled outcomes presented in Fig. 8 appear counterintuitive to existing empirical knowledge. The fire spread rates and intensities associated with their 'no cone opening' criteria, for example, are not consistent with the prolific fire-induced regeneration that often follows stand-replacing crown fires in forests of these two tree species (Lotan *et al.* 1985; Rouse 1986). Crown fires typically exhibit a rate of spread greater than 15 m min^{-1} and in turn fireline intensities exceeding 10 000 kW m^{-1} (Van Wagner 1977; Alexander and Cruz 2011). The modelled results obtained by Johnson and Gutsell (1993) predicted 'no cone opening' and in turn no viable seed release and thus, contrary to the actual situation, no fire-induced tree regeneration in any of the cases discussed in the previous section.

The other aspect of Fig. 8 that seems inconsistent with existing empirical knowledge concerns the axis scales of each graph. Regardless of the simple mathematics of Byram's (1959) fireline intensity calculation, certain variable combinations and intensity levels are not possible. For example, assuming $r = 1.0$ m min^{-1} and $I_B = 60\,000$ kW m^{-1}, according to Eqn 2, $w_a = 200$ kg m^{-2}. Fuel consumption levels in natural stands of jack pine and lodgepole pine rarely exceed 6.0 kg m^{-2} (Stocks 1987, 1989; Stocks *et al.* 2004). Even blowdown fuel loads are not likely to exceed 11 kg m^{-2} (Gilmore *et al.* 2003).

The principal reason for the modelled outcomes presented in Fig. 8 is a result of Johnson and Gutsell's (1993) assumption of a constant D value of 2.0 m regardless of the R value. The situation

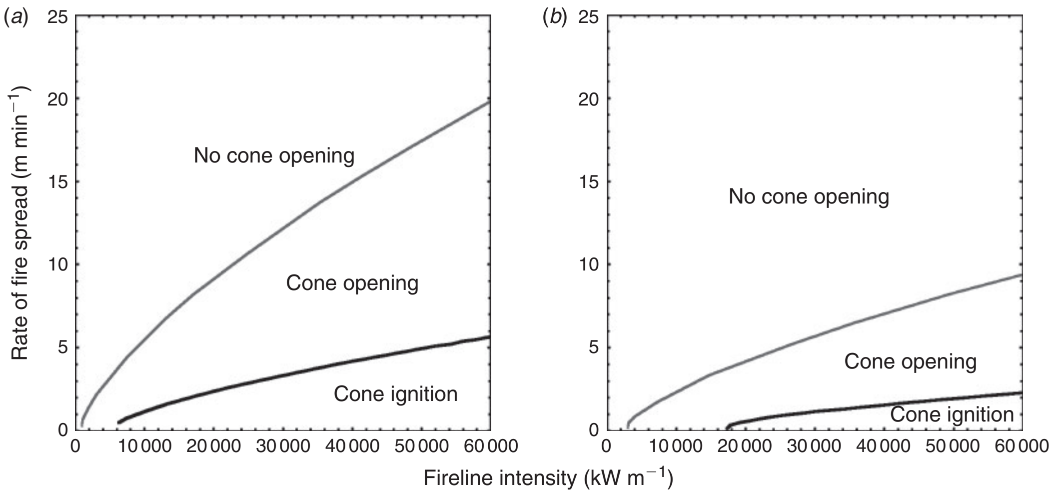

Fig. 8. Johnson and Gutsell's (1993) modelled outcomes relating fireline intensity and rate of fire spread to cone opening or lack thereof and cone ignition in (*a*) 10-m-tall jack pine and (*b*) 20-m-tall lodgepole pine stands.

is exacerbated by an error they made in not correctly converting the equation coefficient derived by Van Wagner (1975) that links ΔT to I_B (kW m^{-1} rather than kcal s^{-1} m^{-1}) represented by Eqn 3, resulting in a 38% underestimate in calculated values.[A]

Johnson and Gutsell (1993) used a rearranged version of Eqn 6 (i.e. $r = D \div t_r$) to relate R directly to t_r and in turn to their empirical data relating time to cone opening to temperature. As mentioned earlier, fires in boreal or subalpine pine stands typically exhibit t_r values of 0.5 to 1.0 min. Thus, Johnson and Gutsell's (1993) assumption that $D = 2.0$ m regardless of the value of R is only valid for spread rates of ~2 to 4 m min^{-1} (Fig. 5), typical of low-intensity heading surface fires (Lawson 1972; Quintilio *et al.* 1977; Stocks 1989). However, for an R of 25 m min^{-1}, according to Johnson and Gutsell's (1993) assumption that $D = 2.0$ m, Eqn 6 implies that $t_r = 0.083$ min or 5 s, a reasonable value for grass fires as mentioned early, but not for natural stands of jack pine and lodgepole pine.

McArthur (1967) has shown experimentally in the field that D and R generally vary in concert with each other for a surface head fire in a given fuel complex. The model of Nelson and Adkins (1988) indicates that both D and R increase with increasing wind speed and w_a. As a result of the Johnson and Gutsell's (1993) modelling assumption, the only way for the criteria for cone opening and cone ignition to be met is to substantially increase w_a, which, in turn, results in extraordinarily high I_B levels as alluded to above.

Rather than setting $D = 2.0$ m, Johnson and Gutsell (1993) might have selected a nominal value or values) (e.g. 0.75 or 0.5 and 1.0 min) for t_r as a means of incorporating the duration of heating into their modelling efforts. In this way, then cone opening and ignition could have been expressed solely a function of I_B rather than in terms of I_B and R or alternatively R and w_a as shown in Figs 4 and 7.

Seed mortality in relation to flame residence times in crown fires

Knapp and Anderson (1980) showed that seed germination was not adversely affected by temperatures required to open the serotinous cones of lodgepole pine. Johnson and Gutsell (1993), however, concluded that once cones ignite, the seeds contained within the cones are killed, although they do not indicate by what mechanisms this occurs or to what degree. Jack pine cones typically have a maximum diameter of ~2.5 cm and the cone shell has a corresponding thickness of ~0.5 cm (Lee and Beaufait 1961). The pyrolysation of woody plant tissue occurs at a rate of ~0.15 cm min^{-1} (Albini 1993). Considering the typical flaming residence times within the canopy fuel layer of crown fires (Despain *et al.* 1996; Taylor *et al.* 2004), it is unlikely that cones contained in the crowns of standing trees would be consumed to any appreciable depth as to physically affect potential seed availability and viability. This is consistent with the prolific post-fire seeding cited previously.

In contrast, cones in cured jack pine and lodgepole pine logging slash treated with prescribed fire typically are partially or wholly consumed (Zimmerman 1982; Chrosciewicz 1988) because of the longer t_r values experienced in these heavier, more compacted fuelbeds (Quintilio 1972; Stocks and Walker 1972). The deliberate or accidental burning of blowdown fuel complexes (Stocks 1975; Gilmore *et al.* 2003) might be expected to produce a more severe result (D'Amato *et al.* 2011) given the heavier, more compacted fuelbeds that produce even longer residence times.

The principal concern regarding a reduction in seed viability with respect to cone ignition or charring by direct flame contact in the crowns of standing trees is the duration of heating at a given temperature. This is also, to some extent, a major concern in commercial seed extraction operations (LeBarron and Roe

[A]The conversion of Van Wagner's (1975) b coefficient of 10 is accomplished as follows, where 4.184 is the factor for converting kilocalories per second per metre to kilowatts per metre (Van Wagner 1978): $10 \div (4.184^{2/3}) = 3.85$. Johnson and Gutsell (1993) inadvertently forgot to take the conversion factor to the 2/3 power (i.e. $10 \div 4.184 = 2.39$). The same type of error was made with respect to Van Wagner's (1973) h_s model represented by Eqn 4.

1945; Hellum 1981; Wang *et al.* 1992). Despain *et al.* (1996) have found that seed viability in serotinous cones of lodgepole pine decreases rapidly once exposure to direct flame contact exceeds 20 s; de Groot *et al.* (2004) obtained a similar result with serotinous cones of jack pine. Viability decreased to between 0.3 and 14%, depending on cone age, after 60-s exposure.

Given a flaming residence time of 20 s in the overstorey canopy of a jack pine or lodgepole pine stand and a ratio of 2.5 : 1, this would in turn equate to a t_r value at the ground surface of ~50 s or 0.83 min. The application of a biophysical fire model such as that of Mercer *et al.* (1994) might produce a more refined result than this first approximation with regard to a threshold condition for the onset of seed mortality resulting from the flame bathing associated with active crowning in jack pine and lodgepole pine forests.

Despain *et al.* (1996) has documented that t_r values in lodgepole pine tree canopies can exceed 20 s. Thus, it is quite possible for temperatures lethal to pine seed to penetrate deep enough within the cone, especially in cases involving large quantities of dead down woody surface fuels and very deep forest floor layers with low moisture contents (Hartford and Rothermel 1991). Although we now see that there are limits to the insulating ability of the cone scales, as Despain *et al.* (1996) point out for lodgepole pine at least, generally enough viable seed remains in the overstorey tree canopy to restock stands even in areas subjected to the most severe crown fire activity. The physical explanation presented here regarding seed mortality in relation to variability in fire behaviour characteristics goes a long way to explaining the relatively higher seedling densities in lodgepole pine following low- to high-intensity surface fires as compared with crown fires reported by Anderson and Romme (1991), for example.

Summary and closing remarks

Wildland fire scientists have long recognised the need to promote a more complete understanding of fire behaviour and ecological effects (McArthur and Cheney 1966; Van Wagner and Methven 1978; Alexander 1982; Wade 1987; Burrows 1995). More recently, it has been suggested that ecologists and foresters themselves have failed to understand the connection between the physical aspects of wildland fires and ecological processes (Miyanishi 2003). However, as Dickinson and Ryan (2010) note, 'This is not to suggest that ecologists need to become combustion engineers or physical scientists to do their work, but it does suggest that it is highly desirable to have a conceptual understanding of how fire effects arise from biophysical processes, and it speaks to the need for interdisciplinary studies that couple fire behaviour with observed effects'.

In this paper, we have described a relatively simple picture of the processes and linkages involved in the opening of serotinous cones of jack pine and lodgepole pine and the release of viable seed in relation to variations in fireline intensity. The mode or mechanisms associated with the breaking of the resinous bond that holds the tips of the cone scales together are dictated by the type of fire. In surface fires, this occurs as a result of convective and radiative heating beginning in the lower portion of the live overstorey canopy once full or complete crown scorch to the SH level has been attained. Cone opening by direct flame contact occurs with the onset of crowning. Seed mortality is expected to occur in active crown fires once flame-front residence times at the ground surface exceed 50 s. As in most wildland fire modelling efforts, the results are an approximation or simplification of the real world as we know it, based on existing knowledge (Wade 2011).

We have described a more structured basis with which to assess and codify how serotinous cone opening and viable seed release in jack pine and lodgepole pine are related to fire behaviour characteristics than previously existed. Such insights have come about as a result of coupling years of field observation with advances in the science of wildland fire behaviour to the fire ecology literature of the two pine species. If this paper inspires others to explore any of the relationships involved in greater depth, we would be most pleased.

List of symbols, quantities and units used in equations and text

b, empirical proportionality constant
CBH, canopy base height (m)
CBD, canopy bulk density (kg m^{-3})
d, fuel particle thickness (cm)
D, horizontal flame depth (m)
FMC, foliar moisture content (% oven-dry weight basis)
h_s, crown scorch height (m)
H, low heat of combustion (kJ kg^{-1})
I_B, fireline intensity (kW m^{-1})
I_o, critical surface fire intensity for initial crown combustion (kW m^{-1})
r, rate of fire spread (m s^{-1})
R, final rate of fire spread, surface or crown (m min^{-1})
R_o, critical minimum spread rate for active crowning (m min^{-1})
SH, stand height (m)
t_r, flame-front residence time (min)
t_R, particle flame residence time (s)
w_a, amount of fuel consumed in the active flaming front (kg m^{-2})
z, height above ground (m)
ΔT, temperature rise above ambient air conditions (°C)

Acknowledgements

This article is a contribution of Joint Fire Science Program Project JFSP 09-S-03-1. A sincere debt of gratitude is owed to C. E. Van Wagner for his pioneering research in forest fire behaviour that is incorporated within the methodology outlined herein. Thanks are extended to R. Arthur, W. Bereska, D. G. Despain, W. N. Droog, P. M. Fernandes, J. S. Gould, C. M. Hoffman, P. J. Murphy, D. L. Peterson, D. Quintilio, K. C. Ryan, N. M. Vaillant, D. D. Wade and R. H. Ziel for reviewing earlier drafts of the paper. Comments on the manuscript by the co-Editor-in-Chief S. G. Conard as well as the associate editor and two anonymous reviewers are gratefully appreciated. Finally, the senior author, M. E. Alexander, gratefully acknowledges his former employer, the Canadian Forest Service, for the opportunities to have gained first-hand experience in observing and documenting experimental fires, prescribed fires and wildfires and their resulting aftermath as a basis for understanding and modelling the impacts and effects of free-burning fires in relation to their behaviour over the course of nearly 35 years (1976–2010).

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