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Timing of fire relative to seed development controls availability of non-serotinous aerial seed banks

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Abstract

The existence of non-serotinous, non-sprouting species in fire regimes where serotiny confers an adaptive advantage is puzzling, particularly when these species recruit poorly from soil seed banks or from burn edges. In this paper, white spruce (*Picea glauca* (Moench) Voss) was used to show that the timing of fire relative to seed development can control aerial seed bank availability for non-serotinous species. To estimate seed survival in closed cones during crown fires, cone heating was simulated using a one-dimensional conduction model implemented in a computational fluid dynamics (Navier–Stokes) fire spread model. To quantify the area burned when germinable seed would be contained in closed cones, empirical fire occurrence and seed development (germinability and cone opening) data were compared for multiple locations across the white spruce range. Approximately 12 % of cones contained viable seed following crown fire simulations (0.072 $\mathrm{m\,s^{-1}}$ mean spread rate; 9147 $\mathrm{kW\,m^{-1}}$ mean intensity), and roughly half of the historical area burned resulted from fires that occurred when closed cones would contain germinable seed. Post-fire recruitment from in situ aerial seed banks can occur for non-serotinous species, and may be an important cause of their existence in fire regimes to which they otherwise seem poorly suited.

1 Introduction

Serotiny is the retention of germinable seed within the cones or fruits of a plant crown for a period longer than the interval between successive seed cohorts (Le Maitre, 1985; Lamont et al., 1991). Serotiny is a fire-adaptive trait for non-sprouting (obligate seeding) species in some fire regimes (Enright et al., 1998; Gill, 1981; Lamont and Enright, 2000; Keeley et al., 2011; Schwilk and Ackerly, 2001), as it not only provides a persistent aerial seed bank for post-fire recruitment, but can also insulate seeds against heat necrosis (e.g. with thickened cone scales or fruit walls; Mercer et al., 1994; Beaufait, 1960; Judd, 1993; Bradstock et al., 1994; Despain et al., 1996; Fraver, 1992).

Theory suggests that serotiny is favored when mean fire return intervals are longer than a species' time to reproductive maturity but shorter than its lifespan, and inter-fire recruitment is rare and/or unsuccessful at producing reproductively mature individuals (Enright et al., 1998; Lamont and Enright, 2000); in contrast, non-serotiny should be favored when mean fire return intervals are longer than a species' lifespan and inter-fire recruits can survive to reproductive maturity.

However, this theory does not explain the existence of some non-serotinous species like white spruce (*Picea glauca* (Moench) Voss), which co-exists with the serotinous trees jack pine (*Pinus banskiana* (Lamb.)), lodgepole pine (*Pinus contorta* Dougl. ex. Loud.), and black spruce (*Picea mariana* (Mill) B.S.P.), and is common throughout the North American boreal forest where mean fire return intervals (< 150 yr; Payette, 1992; Gauthier et al., 1996) are shorter than the lifespans of constituent tree species (Johnson, 1992). Inter-fire recruitment does occur for white spruce, but has little adaptive value as these seedlings have a low probability of reaching reproductive maturity before the next fire event (Johnson et al., 1994, 2003; Youngblood, 1995; Gutsell and Johnson, 2002). Thus, the ubiquity of white spruce is paradoxical as the species should either exhibit serotiny, or be rare and relegated to small, unburned patches of old forest where inter-fire recruits might survive to reproductive maturity (Enright et al., 1998; Lamont and Enright, 2000).

The prevalence of white spruce must be accounted for by additional seed sources for post-fire recruitment. However, soil seed banks are not available, as they are limited by seed predation and loss of viability (Johnson and Fryer, 1996; Nienstadt and Zasada, 1990), or are consumed by smoldering combustion of the upper organic soil horizons (Miyanishi, 2001). Therefore, it is widely assumed that recruitment occurs via wind dispersal of seed from live sources on burn edges (including residual unburned areas within the fire; Galipeau et al., 1997; Wirth et al., 2008). However, it is unlikely that dispersal alone is responsible for the widespread existence of white spruce; recruitment in high densities requires a fire during a mast year (Peters et al., 2005), and the large size of fires responsible for most of the area burned in the boreal forest (Johnson, 1992) imposes a dispersal constraint that would limit high densities of recruitment to areas near burn edges (Greene and Johnson, 2000).

We suggest another possibility: germinable seed contained within closed cones can survive fire to provide transient aerial seed banks (Thompson and Grime, 1979) for post-fire recruitment. A number of studies have shown that the onset of seed germinability begins before the onset of cone opening in white spruce, so that germinable seed is contained within closed cones for part of each growing season (Zasada, 1973, 1978; Winston and Haddon, 1981; Cram and Worden, 1957; Crossley, 1953). Such seeds may be insulated against heat necrosis in fires, since white spruce cone diameter (and presumably radial heat transfer characteristics; Incropera et al., 2006) is nearly identical to that of black spruce cones (Parker and McLachlan, 1978), which often contain high proportions of viable seed after crown fire (Lutz, 1956; Greene and Johnson, 1999). This suggests that the timing of fire relative to seed development (germinability and cone opening) governs post-fire aerial seed bank availability. We hypothesize that white spruce colonizes burns in situ if a fire occurs when seeds can germinate but are still contained in closed cones; i.e. under such circumstances, it behaves as a serotinous species.

Thus, our objectives are to: (1) use a physical process simulation approach to demonstrate theoretically that seeds in closed cones can survive heating by crown fire, and (2) demonstrate empirically that forest fires occur when germinable white spruce seed would be contained within immature, closed cones. Cone heating in crown fires was simulated using a one-dimensional conduction model implemented in a computational fluid dynamics (CFD) model of forest fire spread. These simulations simply provide theoretical evidence that seeds in cones can survive heating by fire; effects of variation in cone properties and fire behavior characteristics on seed survival were beyond the scope of the paper. Timing of fire and seed development was compared using historical fire occurrence and area burned data with seed germination studies at several locations across the range of white spruce. This is one of the first attempts to couple a relatively complete understanding of physical fire processes with vegetation heat transfer processes to characterize the ecological effects of fire. Although the current analysis is limited to white spruce, these processes are general to cones and fruits of other species and the same arguments should inform understanding of the community dynamics of other types of fire-prone vegetation.

2 A one-dimensional model of cone heating in forest fires

White spruce seeds are located around the longitudinal cone axis, with seed embryos located immediately adjacent to the axis (Fig. 1). In a forest fire, heat received at the cone surface via radiation and convection is conducted inward towards the longitudinal axis in response to radial temperature gradients. Endothermic thermal degradation reactions (evaporation and pyrolysis) act to limit the rate of temperature increase. However, seed necrosis can occur if embryos are heated to sufficiently high temperatures for sufficiently long periods.

White spruce cones have low Reynolds numbers *Re* (ratio of inertia to viscous forces in the boundary layer) and large length-to-radius ratios, so it can be assumed that heat fluxes are uniform around the circumference of the cone and that conduction occurs in the radial direction only. Cone heating can thus be characterized as one-dimensional conduction in cylindrical coordinates (Incropera et al., 2006; McGrattan et al., 2010a):

$$\rho_c c_c \frac{\partial T_c}{\partial t} = \frac{1}{r}\frac{\partial}{\partial r}\left(r k_c \frac{\partial T_c}{\partial r}\right) + \dot{q}''' \tag{1}$$

where ρ_c is cone density (kg m^{-3}), c_c is cone specific heat capacity (J kg^{-1} K^{-1}), k_c is cone thermal conductivity (W m^{-1} K^{-1}), T_c is cone temperature (°C), t is time (s), and r is radial position (m). A similar approach was used by Mercer et al. (1994) to study seed survival in woody fruits during fires. The energy source term $\dot{q}'''$ accounts for heat loss or gain per unit volume (W m^{-3}) via evaporation, pyrolysis, or combustion.

The boundary condition along the longitudinal axis is

$$k_\mathrm{c}\frac{\partial T_\mathrm{c}}{\partial r} = 0 \tag{2}$$

and the boundary condition at the surface is

$$-k_\mathrm{c}\frac{\partial T_\mathrm{c}}{\partial r}(0,t) = \dot{q}''_\mathrm{conv} + \dot{q}''_\mathrm{rad} \tag{3}$$

The convective flux $\dot{q}''_\mathrm{conv}(\mathrm{W\,m^{-2}})$ is given by

$$\dot{q}''_\mathrm{conv} = h(T_\mathrm{a} - T_\mathrm{surf}) \tag{4}$$

where T_a (°C) is the temperature of air adjacent to the cone surface and T_surf (°C) is the cone surface temperature. The convective heat transfer coefficient h ($\mathrm{W\,m^{-2}\,K^{-1}}$) is taken as the greater of free and forced components (Holman, 1997; Incropera et al., 2006)

$$h = \max\left[C(\Delta T)^{1/3}, \left(\frac{k_\mathrm{a}}{D}\right)\left(0.664 Re^{1/2}\mathrm{Pr}^{1/3}\right)\right] \tag{5}$$

where C is a free convection coefficient (1.52 or 1.31 for horizontal or vertical surfaces, respectively), D (m) is cone diameter, $k_\mathrm{a}(\mathrm{W\,m^{-1}\,K^{-1}})$ is the thermal conductivity of air, and the Prandtl number Pr (dimensionless) is the ratio of momentum and thermal diffusivities. The radiative flux $\dot{q}''_\mathrm{rad}$ ($\mathrm{W\,m^{-2}}$) is given by

$$\dot{q}''_\mathrm{rad} = \varepsilon_\mathrm{c}\dot{q}''_\mathrm{i} - \varepsilon_\mathrm{c}\sigma T^4_\mathrm{surf} \tag{6}$$

where ε_c is the cone emissivity (dimensionless), $\dot{q}''_\mathrm{i}(\mathrm{W\,m^2})$ is the radiative heat flux incident from the fire and plume to the cone surface, and σ is the Stefan–Boltzmann constant ($5.67 \times 10^{-8}\,\mathrm{W\,m^{-2}\,K^{-4}}$).

3 Materials and methods

3.1 Cone collection

Cones used for model parameterization (Eqs. 1–6) and germination studies (see below) were collected during the summers of 2006 and 2010. During 2006, cones for germination studies were collected between 23 July and 1 September (757.35 to 1121.19 accumulated degree days) from a mature white spruce stand in Kananaskis Country, Alberta, Canada (51° 01′ 32″ N 114° 52′ 22″ W; Fig. 2). Accumulated degree days (beginning ordinal day 1) were calculated using the double-sine method with a lower threshold of 5 °C (Allen, 1976; Zasada, 1973) and maximum and minimum daily temperature data obtained from the Barrier Lake Station of the Biogeoscience Institute of the University of Calgary (11.33 km away from the collection site). Each week, five randomly-chosen trees were felled and approximately 100 cones were collected from each. Cones were placed in paper bags and transported to the laboratory, where they were stored at approximately 22 °C until the date of natural cone opening (Zasada, 1973, 1978); cone drying thus occurred in a manner similar to the drying of cones on a dead tree following a forest fire. Seed extraction and germination studies began once the scales reflexed on cones from the last sampling date (see below). During 2010, cones for model parameterization and germination studies were collected between 14 June and 9 September (345.32 to 1221.27 accumulated degree days) from open-grown trees at the University of Calgary campus in Calgary, Alberta, Canada (51° 04′ 49″ N 114° 07′ 27″ W; Fig. 2). Accumulated degree days were calculated as above using temperature data from the Calgary International Airport (8.16 km from the collection site; http://climate.weatheroffice.gc.ca). Each week, five cones were sampled from each of five trees that had been selected on the first sampling date. Cones were transported to the laboratory, where four cones from each tree were stored and processed as described for the 2006 cones, and one cone from each tree was enclosed in a plastic zipper bag and frozen at −22.4 °C for measurement of parameters for the cone heat transfer model (see below).

3.2 Simulation of cone heating by crown fire

Cone heating and crown fire spread were simulated using the Wildland-Urban-Interface Fire Dynamics Simulator (WFDS), which is a joint product of the US Forest Service and the National Institute of Standards and Technology (NIST). The WFDS is a CFD model of fire spread through thermally-thin vegetative fuels, which provide momentum drag and heat and mass fluxes to the fluid (Mell et al., 2007, 2009). The model is an extension of the NIST Fire Dynamics Simulator 6 (FDS), which numerically solves Navier–Stokes approximations that are appropriate for the low-velocity, thermally-driven flows characteristic of fires (McGrattan et al., 2010b; Rehm and Baum, 1978). An explicit predictor-corrector scheme (second-order accurate in space and time) is used to march the solution forward in time through a three-dimensional rectilinear grid. Turbulence is modeled by large eddy simulation (LES), which resolves flow at scales larger than the grid cell size and parameterizes flow at subgrid scales (direct numerical simulation may also be used with grid cells of sufficiently fine resolution). Fluid flow solutions are coupled with solid-phase evaporation and pyrolysis models, a gas-phase mixture fraction combustion model, and a radiation transport equation solver. Detailed descriptions of the WFDS and the FDS are given in Mell et al. (2007, 2009) and McGrattan et al. (2010a).

The one-dimensional conduction model used to characterize cone heating (Eqs. 1–6) was implemented within WFDS. For every WFDS timestep, cone temperatures were updated using the implicit Crank–Nicolson method (cf. Chapra and Canale, 2009), which is second-order accurate in space and time. Cell sizes were uniform and chosen to satisfy

$$\delta r < \sqrt{\frac{k_\mathrm{c}}{\rho_\mathrm{c} c_\mathrm{c}}} \tag{7}$$

The conduction model is coupled to WFDS via the boundary condition described in Eq. (3); convective flux $\dot{q}''_\mathrm{conv}$ (Eq. 4) is calculated from properties of the cone surface

(T_{surf}) and the gas adjacent to the cone surface (T_{a}, Re, and Pr), whereas radiative flux $\dot{q}''_{\mathrm{rad}}$ (Eq. 6) is based on solution of the radiation transport equation. Additional details on the conduction model, numerical scheme, and coupling to WFDS can be found in McGrattan et al. (2010a).

The FDS has undergone extensive validation (McGrattan et al., 2010b; McDermott et al., 2010), and the WFDS extension has been validated for fire spread through grasslands (Mell et al., 2007) as well as the burning of individual tree crowns (Mell et al., 2009). The one-dimensional conduction model and Crank–Nicolson scheme have been validated using analytical solutions of the conduction equation (McDermott et al., 2010) and heating experiments with cylindrical geometries (electrical cables; McGrattan, 2008). The WFDS is increasingly being used as a physics-based "laboratory" for conducting experiments on fire spread through vegetation (Mell et al., 2007, 2009; Parsons et al., 2011; Hoffmann et al., 2012).

Parameter values used for the cone heating model are shown in Table 1. Physical properties were measured using the cones collected during 2010. In preliminary cone heating simulations, maximum seed temperatures varied less than 10 % between the first and last sampling dates (345.32 and 1221.27 degree days, respectively; Fig. A1), so means calculated during the entire 2010 sampling period (Table 1) were used for subsequent simulations. To measure physical properties, cones were removed from −22.4 °C storage and allowed to warm to approximately 22 °C. Fresh mass, length, diameter, and volume (via mass displacement of water) were measured for each cone. Longitudinal sections (Fig. 1) were used to measure seed depth (defined as embryo depth). Dry mass was measured after oven-drying at 95 °C to a constant mass. Bulk density was calculated from dry mass and fresh volume, and the mass fractions of water and dry cone were calculated from fresh and dry masses. Variation in physical properties throughout the sampling period was consistent with that reported for white spruce cones from Chalk River, Ontario (Winston and Haddon, 1981; Fig. B1). Thermal properties (Table 1) were obtained from the literature. Specific heat capacities c and thermal conductivities k of cone constituents (i.e. char, dry cone, and water) varied with temperature (Table 1), and the density ρ_c, specific heat capacity c_c, and thermal conductivity k_c (Eq. 1) of the composite cone varied with simulated time in accordance with varying temperature and mass fractions of char, dry cone, and water (simple rule of mixtures). The heat of combustion (kJ kg^{-1} of *gaseous* fuel; Mell et al., 2009) was taken as the mean of values reported for conifer foliage, wood, and bark (Susott, 1982a).

Cone heating in crown fires was simulated in five 102 × 50 × 40 m computational domains at a resolution of 0.5 × 0.5 × 0.5 m (Fig. 3). Each simulation comprised 1.632 million grid cells, and 2000 s of simulated time required between 58 and 69 h on 48 3.0 GHz Intel® Xeon® X5450 processors. A mature, closed canopy white spruce forest was generated within each domain (Fig. 3) using forest inventory data, allometry models, and thermophysical properties from the literature (see below). For each simulation, 6259 independent random points (trees) were uniformly distributed across the 102 × 50 m area using the runifpoint function from the package spatstat (Rolf and Adrian, 2005) in the statistical software R (R Development Core Team 2011); thus, the five simulations shared a common size-frequency distribution, but each had a unique spatial arrangement of trees. A homogeneous surface fuelbed (see below) was positioned on the $z = 0$ plane between $x = 5$ to 100 m and $y = -25$ to 25 m, and an ignition source (500 kW m^{-2} for 70 s) was positioned on $z = 0$ between $x = 4$ to 5 m and $y = -25$ to 25 m (Fig. D1). White spruce cones were positioned in vertical arrays located at $x = 25.5$, 42.5 m, 59.5 m, and 76.5 m along $y = -12.5$ and 12.5 m planes (Figs. 3 and D1); cones were positioned at heights $z = 8.7$ and 17.7 m, which roughly bounds the range within which most cones would be present in this canopy (Boggs et al., 2008; Greene et al., 2002). Open boundaries were located on the $x = 102$ and $z = 40$ m planes, an inflow boundary was located on the $x = 0$ m plane, and mirror boundaries were located on the $y = -25$ and 25 m planes. A time-averaged wind profile (Albini and Baughman, 1979; Fig. C1) was prescribed at the inflow boundary $x = 0$

according to

$$\bar{U}(z) = \max\left[\left(\frac{U_*}{K}\right)\ln\left(\frac{z-0.64H}{0.13H}\right), \frac{0.306U_{\mathrm{ref}}}{\sqrt{fH}\ln\left(\frac{10+0.36H}{0.13H}\right)}\right] \tag{8}$$

where K is the von Kármán constant (0.41; dimensionless), z is height (m), and H is the maximum canopy height (17.7 m). U_{ref} is the wind velocity at the reference height z_{ref} = 27.7 m (10 m above canopy height; Lawson and Armitage, 2008); U_{ref} was taken as 10 m s^{-1}, which is a typical value during actively crowning wildfires (Cruz and Alexander, 2010). The volume filling fraction f (dimensionless) was taken as 0.12, which gives the same ratio of canopy velocity to reference velocity U_c/U_{ref} (Albini and Baughman, 1979) that was observed in a *Picea* stand (Norum, 1983) having the same percent crown closure (80 %) as the forest inventory data used to generate the forest canopy structure (see below). The friction velocity U_* is given by (Monteith and Unsworth, 2008)

$$U_* = \frac{U_{\mathrm{ref}}K}{\ln\left(\frac{z_{\mathrm{ref}}-0.64H}{0.13H}\right)} \tag{9}$$

In all simulations, ignition occurred at 100 s to allow this inflow wind profile to establish steady state air flow within the domain (Fig. E1).

The mirror conditions prevent flow across y = −25 and 25 m boundaries, which restricts flow in the y-direction. This can lead to higher u-velocities, rates of spread, and fire intensities as compared to cases with open boundaries. To quantify these effects, rate of spread and mean fire intensity for a 102×50×40 m domain with mirror boundaries at y = −25 and 25 m were compared to those for a 153×75×60 m domain with open boundaries at y = −25 and 25 m. Rates of spread and intensities were compared for x = 5 to 50 m, because the fire stopped crowning at approximately x = 50 m for the case with open boundaries. Rate of spread R (m s^{-1}) was estimated as

$$R = \frac{x_2 - x_1}{t_2 - t_1} \tag{10}$$

Mean global fire intensity $\bar{I}$ (kW m^{-1}) was calculated as

$$\bar{I} = \frac{\sum_{i=1}^{n} \left(\frac{\dot{Q}_i}{L} \right)}{n} \tag{11}$$

where $\dot{Q}_i$ is the total heat release rate (kW) at timestep i, L is the fireline length in the y-direction (50 m), and n is the number of timesteps. Here, $i = 1$ corresponds to the timestep when the surface fire front reached $x = 5$ m and n corresponds to the timestep when the surface fire front reached $x = 50$ m. Rate of spread and fire intensity were 1.71 and 2.52 times greater, respectively, for the case with mirror boundaries.

Canopy structure was generated from forest inventory data and allometric fuel biomass models. Forest inventory data for a mature white spruce stand with 80 % crown closure were obtained from site WS 04 of Ottmar and Vihnanek (1998; Table 2). Data did not include crown base height CBH of dead trees, so this was estimated as

$$\mathrm{CBH}_{\mathrm{dead}} = Z - \mathrm{CR}(Z) \tag{12}$$

where Z is total tree height and CR is the crown ratio of live trees in the same DBH size class

$$\mathrm{CR} = \frac{Z - \mathrm{CBH}_{\mathrm{live}}}{Z} \tag{13}$$

Forest canopies comprised four DBH size classes, each having a constant DBH, height, and crown base height defined as size class means from Table 2. Individual tree crowns were modeled as cones (Mell et al., 2009) using height and crown base height data from Table 2 with crown width w (m) estimates from an ordinary least squares regression of log-transformed data for *P. englemannii* ($R^2 = 0.888$; Brown, 1978)

$$w = 0.797\mathrm{DBH}^{0.444} \tag{14}$$

The physical properties of crown fuels are given in Tables 3 and 4. For each DBH size class, crown fuel masses were estimated from allometric equations for suppressed trees (DBH ≤ 5.1 cm; Woodard and Delisle, 1987) and codominant/dominant trees (DBH > 5.1 cm; Johnson et al., 1990). Four crown fuel size classes were considered: foliage, 0–0.5 cm roundwood, 0.5–1.0 cm roundwood, and 1.0–3.0 cm roundwood. All crown fuels ≤ 1.0 cm diameter were considered available for combustion, since these diameters were completely consumed in tree burning experiments and mass loss rates were best predicted by WFDS with inclusion of these diameters (Mell et al., 2009). The 1.0–3.0 cm roundwood class was not available for combustion, but was included as a source of radiation absorption and momentum drag. The bulk density of each size class (Table 3) was calculated as the quotient of fuel mass and crown volume (calculated for conical geometries, as above). Bulk densities varied with DBH (Table 3) due to DBH-dependent variation in fuel masses (Johnson et al., 1990; Woodard and Delisle, 1987) and crown volumes (Eq. 14); all other physical properties of crown fuels (Table 4) were constant with DBH. The surface-area-to-volume ratio of white spruce foliage was calculated from data of Michaletz and Johnson (2006). Surface-area-to-volume ratios of the roundwood size classes were estimated using white spruce branches growing in a closed canopy forest at the University of Calgary Biogeoscience Institute Barrier Lake Field Station in the Southern Canadian Rocky Mountains of Alberta, Canada; values were calculated from length and diameter measurements of 20 branches per size class that were randomly chosen from the crowns of 20 individual trees. Water content of foliage was taken as the minimum value observed for white spruce after 600 accumulated degree days (Chrosciewicz, 1986); degree days were calculated as above using daily temperature data from 1974 at Slave Lake, Alberta (http://climate.weatheroffice.gc.ca). Water contents for live roundwood were obtained from Titus et al. (1992), and water contents for dead roundwood were taken as those typical of 1- (0–0.5 cm roundwood) and 10-h (0.5–1 and 1.0–3.0 cm roundwood) fuels during actively crowning wildfires (Cruz and Alexander, 2010). Char fraction of foliage was taken as the mean of conifer foliage values reported by Susott (1982a), and char fraction of roundwood was taken as the value for *P. abies* wood reported by Grønli et al. (2002). Particle density of foliage was obtained from Michaletz and Johnson (2006), and particle density of wood was calculated using relationships from Simpson and TenWolde (assuming 0 % water content; 1999). For all crown fuels, emissivity was taken as 0.9 (Mell et al., 2009), heat of combustion was calculated as above (Table 1), maximum dehydration and burning rates were taken as 0.4 $\mathrm{kg\,s^{-1}\,m^{-3}}$ (Mell et al., 2009), and the drag force factor was taken as 3/8 (Mell et al., 2007, 2009; Morvan and Dupuy, 2001, 2004; Linn et al., 2002).

Surface fuels were modeled using the vegetation boundary fuel method in WFDS. Fuel data typical of 100- to 200-yr-old closed white spruce stands with feathermoss understories (Viereck et al., 1992) were obtained from fuelbed 101 of the Fuel Characteristic Classification System 2.1 (FCCS 2.1; Ottmar et al., 2007). Fuels comprised 1-h woody fuels, 10-h woody fuels, feathermosses, ladder fuels, lichen, litter, white spruce saplings (height ≤ 1.4 m), dead primary shrubs (*Alnus viridis* ssp. *crispa*, *Betula nana*, and *Salix* spp.; height ≤ 4.6 m), and dead secondary shrubs (*Empetrum nigrum*, *Ledum groenlandicum*, *Linnaea borealis*, *Vaccinium ulginosum*, and *Vaccinium vitis-idaea*; height ≤ 0.6 m). Surface fuels are listed in Table 5 along with their physical properties required for parameterization of the WFDS vegetation boundary fuel model. These physical properties were combined into a single homogeneous fuelbed following Rothermel's (1972) surface-area-weighting approach, modified to include Albini's (1976) revisions and Wilson's (1980) SI unit conversions; characteristic values for the homogeneous fuelbed are given in Table 5. It was assumed that all fuels ≤ 1.0 cm diameter were available for combustion (see above; Mell et al., 2009); consequently, loadings of feathermosses, lichen, litter, white spruce saplings, primary shrubs and secondary shrubs were obtained directly from FCCS data, whereas loadings for 10-h and ladder fuels ≤ 1.0 cm diameter were estimated from FCCS data assuming a uniform distribution of fuel mass among diameters (20 and 39 % of total loadings of 10-h and ladder fuels, respectively). Fuel depths for feathermosses, lichen, and litter were taken from FCCS data, and depths for white spruce saplings and woody fuels were assumed to be equal to the largest diameter of the fuel category (i.e. 1 cm; Keane and Dickinson, 2007). Char fractions were obtained from Susott (1982a); values for moss and lichen were taken as that of feathermosses, values for woody fuels were taken as the mean of conifer wood and bark, and the value for litter was taken as the mean of all conifer foliage. Particle densities of 1-h, 10-h, and ladder fuels were calculated as above (Simpson and TenWolde, 1999), particle density of litter was obtained from Michaletz and Johnson (2006), and the mean of these values was used for white spruce saplings. Particle densities of moss and lichen were calculated as the quotient of feathermoss bulk density and packing ratio (O'Donnell et al., 2009), and particle densities of primary and secondary shrubs were calculated as the mean of *Salix* spp. wood (Singh, 1987) and foliage (quotient of leaf specific mass and leaf thickness; Koike, 1988). Surface-area-to-volume ratios for 1- and 10-h fuels were taken as those measured for crown fuels (described above), for moss and lichen as the value measured for feathermosses by Sylvester and Wein (1981), for ladder fuels as the mean of 1- and 10-h fuels (see above), for white spruce saplings as the mean of measured 1- and 10-h fuels and foliage (Michaletz and Johnson, 2006), and for litter as the value for white spruce foliage (Michaletz and Johnson, 2006). Water content of white spruce saplings was taken as the mean of live foliage and branches (see above) and water contents of all other fuels were taken as those typical of 1- and 10-h fuels during crown fires (as above; Cruz and Alexander, 2010). Heat of combustion, specific heat, and emissivity were taken as above for crown fuels. Maximum mass loss rate data were not available for the fuelbed type used here; therefore, this parameter was adjusted to $0.42\,\mathrm{kg\,s^{-1}\,m^{-3}}$ so that simulated rates of spread agreed with observations from *Picea* stands with feathermoss surface fuels (Norum, 1982; Kiil, 1975; Alexander et al., 1991). The drag force factor was taken as 0.1(3/8), which accounts for the approximate 1 : 10 ratio of fuelbed height to grid cell height (Mell et al., 2007, 2009; Morvan and Dupuy, 2001, 2004; Linn et al., 2002).

Five simulations were conducted, each containing 16 cones. Each simulation had a unique spatial arrangement of trees, but all simulations shared a common size-frequency distribution (see above). For each simulation, rate of spread (Eq. 10) and mean fire intensity (Eq. 11) were calculated for $5 \leq x \leq 95$ m; note that for each simulation, fire spread was not steady state and both rate of spread and intensity varied through time and space. For each cone, surface temperature, seed temperature, total convective heat flux, and total radiative heat flux were recorded every 1 s. Time-integrated total heat fluxes were calculated for each cone by summing (since $\Delta t = 1$ s) total convective and radiative heat fluxes. The necrosis kinetics of white spruce seeds have not been established, so cones from all simulations were combined and the cumulative proportion of cones containing viable seed $\hat{F}_N(T_\mathrm{n})$ was plotted as a function of threshold necrosis temperature T_n:

$$\hat{F}_N(T_\mathrm{n}) = \frac{\text{number of cones with } T_\mathrm{max} \leq T_\mathrm{n}}{\text{total number of cones}} = \frac{1}{N}\sum_{i=1}^{N} 1\left\{T_{\mathrm{max},i} \leq T_\mathrm{n}\right\} \tag{15}$$

where T_max is the maximum seed temperature of each cone i, N is the total number of cones ($N = 80$), and $1\left\{T_{\mathrm{max},i} \leq T_\mathrm{n}\right\}$ is the indicator of $T_\mathrm{max} \leq T_\mathrm{n}$. This approach is useful given the lack of necrosis kinetics data, as it permitted estimation of the proportion of cones containing viable seeds $\hat{F}_N(T_\mathrm{n})$ for any seed necrosis temperature. Here we assume a threshold necrosis temperature of 70 °C, which was observed for non-stratified *Picea abies* (Norway spruce) seeds subjected to a 10 min exposure (Granström and Schimmel, 1993). In reality, the threshold necrosis temperature is probably higher, because exposure times are lower for seeds in cones heated by forest fires (maximum of approximately 3 min; see discussion).

3.3 Timing of fire occurrence and seed development

The timing of fire occurrence and seed development (germinability and cone opening) were examined for multiple locations across the range of white spruce (Fig. 2). Timing of fire occurrence was estimated using climate and fire data for Canada and Alaska from 1959 to 2009. Climate (daily temperature) data were obtained from

Environment Canada (http://climate.weatheroffice.gc.ca) and the National Ocean and Atmospheric Administration National Climatic Data Center (http://www.ncdc.noaa.gov). Data for each year were available for Jasper and Yellowknife, but at other locations data were missing for one to four years (Bagotville, Fairbanks, Fort Smith, and Sioux Lookout), eight years (Schefferville), and eleven years (La Ronge). For each annual record, accumulated degree days were calculated as above; these data were then used to calculate the mean accumulated degree days for each ordinal day at each site. Fire data from Canada and Alaska were obtained from the Canadian National Fire Database (formerly the Canadian Large Fire Database, Stocks et al., 2002; http://cwfis.cfs.nrcan.gc.ca/nfdb) and the Bureau of Land Management Alaska Fire Service (http://fire.ak.blm.gov/predsvcs/maps.php). Data were truncated to include only lightning fires ≥ 200 ha that originated within 2° latitude × 2° longitude "fire observation areas" centered around weather stations used for degree day calculations (except for Yellowknife, where the area was centered 1° north of the station to avoid Great Slave Lake). For each fire observation area, the area burned per ordinal day was estimated by assuming a steady state rate of spread between fire start and end dates; although this is an unrealistic assumption, it provides a better estimate of area burned per day than do fire start or end dates alone (which would necessarily assume that all area burned occurs on day of ignition or extinction). Start dates were available for all fires in all fire observation areas. End dates were available for some fires at Fairbanks, Fort Smith, La Ronge, and Sioux Lookout; for these areas, fires without end dates were excluded from the analysis. End dates were not available for fires at Bagotville, Jasper, Schefferville, and Yellowknife, so they were estimated using a backwards stepwise multiple regression equation ($F_{13,2558} = 49.53$, $P < 2.2\times10^{-16}$, $R^2 = 0.2011$) based on data from all fires in Canada for which start and end dates were available ($N = 2572$); area burned, latitude, longitude, start date, and year were used as explanatory variables because they characterize the processes controlling fuel drying, ignition, rate of spread, and extinction (Macias Fauria et al., 2011; Macias Fauria and Johnson, 2006; Johnson, 1992). Timing of fire occurrence was expressed as the cumulative distribution

$$\hat{S}(t) = \frac{\text{area not yet burned}}{\text{total area burned}} = \frac{1}{A_{\text{total}}} \sum_{i=1}^{n} A_i 1\{t_i > t\} \tag{16}$$

where t is ordinal day (in accumulated degree days), A_{total} is the total area burned, n is the total number of ordinal days, A_i is the area burned on ordinal day i, and $1\{t_i > t\}$ is the indicator of $t_i > t$.

Timing of seed development was estimated using germination studies of seeds from cones collected at Kananaskis Country during 2006 and Calgary during 2010 (see above; Fig. 2). Seed extraction occurred after the last sampling date (i.e. date of cone opening), by which time previously-collected cones had dried and cone scales had reflexed open. Mechanical shaking was used to extract seeds from most of the cones, but manual extraction was required for immature cones with non-reflexed scales. Wings were removed by rubbing seeds in a cotton bag and blowing away debris with a fan; seeds were then individually inspected with a hand lens to remove those with signs of physical damage or seed predation. Germination studies commenced immediately following seed extraction and were conducted according to International Seed Testing Association (ISTA) standards for *P. glauca* (ISTA, 2003). Seeds from each tree were randomly divided into either 4 replicates of 100 seeds (2006) or 8 replicates of at least 10 seeds (2010; the low seed numbers during 2010 resulted from infestation by the spruce seed moth *Cydia strobilella*). Seeds of each replicate were placed on two layers of filter paper (Fisher 09-795A; Fisher Scientific International, Inc., Hampton, New Hampshire) in a covered 60 × 15 mm petri dish (Fisher 0875713A; Fisher Scientific International, Inc., Hampton, New Hampshire), and filter papers were saturated with deionized water. To prevent water loss, petri dishes were sealed in 5 3/4″ × 3″ plastic zipper bags. During 2006, seeds were stratified prior to commencement of germination studies, whereas during 2010 seeds were subjected to "double tests" (ISTA, 2003) in which four of the replicates from each tree were stratified and four were not. Stratification consisted of 21 days storage in a 3–5 °C Conviron E7/2 plant growth chamber (Conviron, Winnipeg, Manitoba) with an 8 h photoperiod at 200 lux (measured using LI-COR LI-185B with quantum sensor LI-190SB; LI-COR Biosciences, Lincoln, Nebraska). Germination studies were conducted during 21 days in the same growth chambers at 25 °C with a 16 h photoperiod at 750 lux. Germination was assessed daily between days 7 and 21. Seeds were considered to have germinated when the radicle was four times longer than the seed (Zasada, 1973; Winston and Haddon, 1981), and germinated seeds were removed daily from each petri dish. Germination rate was plotted as a cumulative function of accumulated degree days, calculated as above using daily temperature data from 2006 (University of Calgary Biogeoscience Institute, Barrier Lake Station) and 2010 (Calgary International Airport; http://climate.weatheroffice.gc.ca). As we were interested in the timing of seed development (and not for example in differences between treatments, replicates, trees, or dates), germination rates were calculated by pooling seeds collected on each sampling date.

Germination data were also obtained from the literature for several additional locations (Fig. 2), including Chalk River, Ontario (45° 59′ 00″ N 77° 26′ 00″ W), Fairbanks, Alaska (64° 48′ 54″ N 147° 51′ 23″ W), Indian Head, Saskatchewan (50° 33′ 00″ N 103° 39′ 00″ W), and Kananaskis Country, Alberta (51° 01′ 39″ N 115° 02′ 05″ W). These data include the real germination results of Crossley (1953) and means (±SEM) calculated from trees W-1 and W-2 of Cram and Worden (1957), trees 1–3 from treatment 4 of Zasada (1973), trees 2 and 4–6 from the T-field site of Zasada (1978), and weeks 4, 8, and 12 of the “shack-air” treatment of Winston and Haddon (1981). In these studies, cone sampling began at various times during the spring or summer, but consistently ended upon observation of cone opening. To compare data among locations, sampling dates were expressed in accumulated degree days (as above) using daily temperature data obtained for the appropriate year from weather stations located within 8 km of each sampling site http://climate.weatheroffice.gc.ca, http://www.ncdc.noaa.gov).

4 Results

4.1 Simulation of cone heating by crown fire

Simulated fires spread as passive crown fires (Van Wagner, 1977). Crown fuel combustion was dependent on the spreading surface fire, since the product of spread rate and effective bulk density was much less than empirical estimates of the fuel mass flow rate required for crown fire spread (Van Wagner, 1977; Thomas, 1967). For the five simulations, rate of spread was 0.072 ± 0.004 (mean ± SEM) $\mathrm{m\,s^{-1}}$ and fire intensity was 9146.81 ± 1165.00 (mean ± SEM) $\mathrm{kW\,m^{-1}}$; these values agree with empirical data from *Picea* stands with feathermoss surface fuels (Norum, 1982; Kiil, 1975; Alexander et al., 1991). Note that in each simulation, fire spread was not steady state and that both rate of spread and intensity varied in time and space. Typical time series of cone surface and seed temperatures are shown in Fig. 4. Temperature-time histories at cone surfaces varied widely, but relatively little variation was observed in maximum seed temperatures, which ranged from 46.00 to 95.65 °C (Fig. F1). Variation in maximum seed temperatures varied with time-integrated total heat flux on cone surfaces (Fig. G1). In general, maximum seed temperatures were greater for cones at 8.7 m than for cones at 17.7 m (Figs. F1 and G1), which was expected given the greater bulk density (per canopy volume) of crown fuels at 8.7 m and the inverse relation between temperature and height as characterized by classical plume theory (cf. Mercer and Weber, 2001).

Simulation results suggest that white spruce seed contained in closed cones can survive heating by crown fire (Fig. 5). Seed survival is expected for any necrosis temperature greater than 46 °C (a value of 60 °C is generally assumed in fire effects research; Dickinson and Johnson, 2004). For a given seed necrosis temperature, viable seed would be contained in a larger proportion of cones at a height of z = 17.7 m than a height of z = 8.7 m. Assuming a threshold necrosis temperature of 70 °C for *Picea* seeds (Granström and Schimmel, 1993), viable seed would be contained in approximately 7.5 % of cones at 8.7 m, 19 % of cones at 17.7 m, and 12 % of cones for both heights combined. This should be considered as a conservative estimate given our use of 70 °C for the threshold necrosis temperature (see discussion). The proportion of cones containing viable seed increased with assumed seed necrosis temperature so that all cones at height $z = 17.7$ m would contain viable seed for a necrosis temperature of 81.25 °C, and all cones at height $z = 8.7$ m would contain viable seed for a necrosis temperature of 95.65 °C.

4.2 Timing of fire occurrence and seed development

The timing of fire occurrence (assuming steady state rate of spread) and seed development at eight locations across the range of white spruce are shown in Fig. 6 (the timing of fire occurrence estimated using other assumptions is shown in Fig. H1). Temporal patterns of seed development (in accumulated degree days) were highly consistent among locations. The onset of germinability in Calgary occurred at 633.12 degree days for non-stratified seeds and at 705.65 degree days for stratified seeds. Although cone collections at other locations began too late in the year to determine the onset of germinability, extrapolation of results suggests that roughly 600 degree days are required for seed germinability. In general, germination rates increased sigmoidally and saturated prior to cone opening (Fig. 6). Accumulated degree days required for cone opening varied among locations, with a mean of 1177.29 (±71.38 SEM) degree days. Differences in date of cone opening may result from local differences in growing season length (i.e. total accumulated degree days per year) or differences in how investigators perceived cone opening.

The proportion of total area burned resulting from fires that occur when seeds are germinable but still contained within closed cones can be estimated for each area as the difference between area burned after 600 degree days (onset of cone opening) and area burned after 1177 degree days (cone opening; Fig. 6). This proportion varies from 0.14 at Schefferville to 0.90 at Jasper, with a mean of 0.52 (±0.091 SEM). Thus, across the range of white spruce, approximately half of the total area burned resulted from fires that occurred when seeds would be sufficiently developed to germinate but still insulated within closed cones.

5 Discussion

In this paper, white spruce was used to demonstrate how the availability of non-serotinous aerial seed banks after fire is governed by the insulating ability of cones and fruits and the relative timing of fire and seed development. Numerical simulations of cone heating in crown fires showed that approximately 12 % of cones would have contained viable seed, assuming a threshold necrosis temperature of 70 °C (Fig. 5). Fire occurrence and seed germination data suggest that a substantial proportion of the area burned within eight fire observation areas (Fig. 2) resulted from fires that occurred when germinable seed would be contained within closed cones (Fig. 6). Thus, white spruce can colonize burned areas from in situ aerial seed banks, provided the fire occurs when germinable seed is contained within closed cones. This is probably rare, however, as it depends on the joint probability (perhaps 0.05) of a mid- to late-season fire (i.e. a fire when germinable seed is still contained in closed cones; mean probability of 0.52) coinciding with a mass seeding event (probability of 0.1, depending on how masting is defined; Greene and Johnson, 2004). This explains why white spruce is typically present in low densities across the landscape as would be expected if they relied on long distance dispersal to colonize large burn areas from the edge (Galipeau et al., 1997; Greene and Johnson, 2000; Peters et al., 2005), and yet rarely can be found in quite dense stands that approach a monoculture.

Two assumptions in our reasoning need to be justified. First, we assume that the period when seeds can survive fires ends with the onset of ovulate scale opening. Seed abscission in this species is a slow process, with the 50th percentile of abscission occurring at least a month after the onset of cone opening (Greene et al., 1999). However, this is probably unimportant since relatively small proportions of the total area burned result from fires occurring after cone opening (Fig. 6). Furthermore, once the scales begin to reflex open (a result of differential hygroscopic expansion of sclerid and fibre cells; Dawson et al., 1997), cones will combust as fine fuels (Almeida et al., 2011; Fonda and Varner, 2004) and any seeds they contain will be killed.

Second, our simulations considered the heating of isolated cones, but the vast majority of white spruce cones develop during mass seeding events (Greene and Johnson, 2004) and are thus not isolated, but instead located within dense clusters that contain up to several hundred cones. Such clustering is expected to provide even greater more insulation than our results suggest, particularly for cones not located on the periphery of the cluster (Judd and Ashton, 1991). A case in point is black spruce, a serotinous species for which cones characteristically accumulate in a large cluster at the top of the crown. Approximately 50 % of black spruce seeds survive stand-replacing crown fires (Greene and Johnson, 1999; D. F. Greene, unpublished data), a much higher survival rate than our simulations suggest for isolated cones. Given the similarity of scale thickness and cone diameter for white and black spruce (Parker and McLachlan, 1978), this difference probably reflects the insulating properties of the cluster and not just of the individual cones. This does not, however, change the conclusion that the joint probability of mid- to late-season fires and mass seeding events makes in situ white spruce recruitment rare; it merely means that the density of regeneration during these rare events would be higher than our simulation results suggest.

Maximum seed temperatures varied with time-integrated total heat flux on cone surfaces (Fig. G1). Because integrated heat fluxes result from convective and radiative heat transfer from the flame and plume to cone surfaces, it is desirable to relate integrated flux to some measure of heat output from the fire. The most widely used measure is fire intensity (Byram, 1959), which was initially developed as a time- and space-averaged approximation of heat output for management and suppression purposes (Van Wagner, 1965). However, intensity can vary extensively within fires due to changes in wind velocity and fuel bulk density (Fig. 3; Byram, 1959; Van Wagner, 1965), and the relation between intensity and cone heat flux also varies in accordance with flame geometry, cone location, and patterns of air and plume flow. This makes it difficult to identify relevant fire intensities and their contributions to cone surface heat fluxes. Although it is possible to obtain reasonable relations between time-integrated heat flux and cone heating time, height, and fire intensity (Appendix I), it is still not clear exactly how or why they contribute to cone surface flux. A better approach might be to identify the areas of the forest from which the cone surface fluxes could have originated. Methods similar to those used for flux footprint modeling (Schmid, 2002; Vesala et al., 2008) are particularly appropriate for use with the CFD approach, as CFD models already compute the paths of convective and radiative heat transfer from the fire to the cone surfaces.

The proportion of cones containing viable seed following crown fire was estimated by comparing variation in maximum seed temperatures (Fig. G1) to an assumed threshold necrosis temperature (Fig. 5). This approach was used in lieu of a more appropriate rate-process approach (Dickinson and Johnson, 2004; Dickinson et al., 2004), because cellular necrosis kinetics have not been established for white spruce seeds. A threshold necrosis temperature of 70 °C (Granström and Schimmel, 1993) was assumed in this study, but this should be considered a conservative estimate as it was measured using a heat exposure time of 10 min, which is much longer than the simulated exposure time of seeds in cones (maximum of approximately 3 min; Fig. 4). Given this relatively short exposure time, and the exponential increase of cell necrosis rates with temperature (Dickinson and Johnson, 2004; Johnson et al., 1974), a necrosis temperature greater than 70 °C is expected for seeds in cones. This means that the proportion of cones with viable seed (12 %; Fig. 5) is also expected to be greater. Nevertheless, during a mass seeding event, even this small proportion of cones could contribute an enormous number of seeds for post-fire recruitment. For example, if each tree in the 13.5 and 25.1 cm DBH size classes ($n = 2116$; Table 2) produces 10 000 cones, and each cone contains 20 viable seeds (Nienstadt and Zasada, 1990), the 12 % survival rate would equate to roughly 50.8 million seeds ha^{-1} in a monoculture of mature white spruce.

The onset of germinability is apparently highly consistent across the range of white spruce (Fig. 6). Better agreement might be obtained if calculations began on pollination dates (Zasada, 1973; Edwards, 1980) as opposed to ordinal day 1, but unfortunately these data were not available. Nevertheless, if these patterns hold across the range of white spruce, onset of germinability at Schefferville (approximately 240 km south of the arctic tree line; Vowinckel et al., 1975) would not occur until early September, because degree days accumulate much slower at higher latitudes. This would support previous results (Black and Bliss, 1980) that suggest that tree line represents the climatic regime where degree day accumulation over the growing season is insufficient for seed maturation to be completed. Thus, tree line may be maintained or expanded during rare, very warm summers (so that 600 degree days is reached unusually early) that coincide with a mast year.

Despite consistency in the onset of germinability, the timing of cone opening appeared to vary throughout the range of white spruce (Fig. 6). It is unclear whether these differences result from differences in how investigators perceived cone opening, or whether phenological differences actually do exist. Because the retention of germinable seed in closed, insulative cones is adaptive in boreal fire regimes, one might expect seed release to be timed with the end of the fire season. For example, earlier dates of seed release may be expected at Bagotville and Yellowknife, whereas later release dates may be expected at La Ronge and Sioux Lookout. Additional work is required to understand the degree to which variation in regional fire seasons might control variation in regional seed release dates.

Much of the variation in germination rates among locations (Fig. 6) was probably due to differences in calculation method used in different studies. For example, the highest reported rates (Zasada, 1973, 1978) were real germination rates for which unfilled seeds were excluded from calculations, whereas the lowest reported rates (Crossley, 1953; 2010 samples) were apparent germination rates for which unfilled seeds were included. Additionally, the relatively low germination rates observed in our 2010 samples reflect an outbreak of the spruce seed moth (*C. strobilella*) and their preferential selection of filled seeds (Tripp and Hedlin, 1956).

In this study, the WFDS CFD modeling software was used as a physics-based "laboratory" for conducting virtual experiments on forest fire spread, cone heating, and seed necrosis. This approach has several advantages that make it a valuable complement to traditional field experiments. For example, simulated fire experiments are safe, relatively fast (particularly when tens or hundreds of different fire experiments are desired), not limited to the fire season, and easily re-run if changes are desired (to parameter values, boundary conditions, experimental design, etc.). It is also possible to address questions that would be difficult or impossible to address in the field (as in this study, for example). The approach also considers the causal mechanisms linking combustion, fluid dynamics, and heat transfer to the physiological effects in organisms and the consequent effects at higher levels of organization such as forest stands. The relevant variables and their functional relationships are clearly defined, and sensitivity analyses can be used to identify the most important variables in a particular scenario. The use of CFD modeling has been growing in the fire behavior literature (e.g. Mell et al., 2007, 2009; Dupuy et al., 2011; Linn et al., 2010; Morvan et al., 2011; Hoffmann et al., 2012), but we are aware of only one paper that has applied the approach to questions of fire ecology (Bova et al., 2011). It is hoped that the use of this approach will continue to grow and help foster a more mechanistic and predictive fire ecology.

We have proposed that the retention of germinable seed in closed, insulative cones is a fire-adaptive trait (Keeley et al., 2011) that may enable non-serotinous species to exist in fire regimes for which serotiny is currently thought to be favored. This contrasts with the commonly held belief that non-serotinous cones have little to no fire-adaptive value (Fonda and Varner, 2004). However, the success of this colonization strategy relies on the coincidence of a mast year and a fire that occurs when germinable seed is contained in closed cones; consequently, serotiny provides a greater advantage as it helps ensure that seeds will consistently be available for colonization of burned areas regardless of the timing of either fire or seed development.

Supplementary material related to this article is available online at: http://www.biogeosciences-discuss.net/9/16705/2012/ bgd-9-16705-2012-supplement.pdf.

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Table 1. Parameter values used for the cone heating model (Eqs. 1–6)[a].

Definition	Symbol	Value (units)	Source
Char fraction	χ_{char}	0.234 (dimensionless)	(Grønli et al., 2002)
Density, char	ρ_{char}	$46.31\,\mathrm{kg\,m^{-3}}$	(Ragland et al., 1991)
Density, dry cone	ρ_{dc}	$308.712\,\mathrm{kg\,m^{-3}}$	Measured
Density, water	ρ_{w}	$997\,\mathrm{kg\,m^{-3}}$	(Incropera et al., 2006)
Depth, seed	r_{s}	0.005 m	Measured
Diameter, cone	D	0.013 m	Measured
Emissivity, char	$\varepsilon_{\mathrm{char}}$	0.95 (dimensionless)	(Gupta et al., 2003)
Emissivity, cone	ε_{c}	0.94 (dimensionless)	Measured
Heat of combustion	Δh_{c}	$17936\,\mathrm{kJ\,kg^{-1}}$	(Mell et al., 2009; Susott, 1982a)
Heat of pyrolysis	Δh_{pyr}	$418\,\mathrm{kJ\,kg^{-1}}$	(Morvan and Dupuy, 2004)
Heat of vaporization	Δh_{vap}	$2257\,\mathrm{kJ\,kg^{-1}}$	(Incropera et al., 2006)
Length, cone	l	0.044 m	Measured
Mass fraction, dry cone	χ_{dc}	0.31	Measured
Mass fraction, water	χ_{w}	0.69	Measured
Specific heat, char	c_{char}	$c_{\mathrm{char}} = 3.8\times10^{-6}T^2 + 0.004T + 0.555\,\mathrm{kJ\,kg^{-1}\,^{\circ}C^{-1}}$	(Gupta et al., 2003)
Specific heat, dry cone	c_{dc}	$c_{\mathrm{dc}} = 1.16 + 3.867\times10^{-3}T\,\mathrm{kJ\,kg^{-1}\,^{\circ}C^{-1}}$	(Simpson and TenWolde, 1999)
Specific heat, water	c_{w}	$c_{\mathrm{w}} = -5\times10^{-11}T^5 + 2\times10^{-8}T^4 - 2\times10^{-6}T^3 + 1\times10^{-4}T^2 - 3.5\times10^{-3}T + 4.217\,\mathrm{kJ\,kg^{-1}\,^{\circ}C^{-1}}$	(Incropera et al., 2006)
Temperature, boiling		100 °C	(Incropera et al., 2006)
Temperature, pyrolysis		200 °C	(Susott, 1982b)
Thermal conductivity, char	k_{char}	$0.095\,\mathrm{W\,m^{-1}\,^{\circ}C^{-1}}$	(Gupta et al., 2003)
Thermal conductivity, dry cone	k_{dc}	$k_{\mathrm{dc}} = 0.085 + 2.25\times10^{-4}T\,\mathrm{W\,m^{-1}\,^{\circ}C^{-1}}$	(Incropera et al., 2006)
Thermal conductivity, water	k_{w}	$k_{\mathrm{w}} = -7\times10^{-6}T^2 + 0.002T + 0.570\,\mathrm{W\,m^{-1}\,^{\circ}C^{-1}}$	(Incropera et al., 2006)

[a] Measured properties are means calculated over 757.35 to 1121.19 accumulated degree days.

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Table 2. Forest inventory data used to generate the white spruce canopy in model simulations.

DBH size class (cm)	Status	DBH (cm)	Density (ha^{-1})	Crown base height (m)	Crown width (m)	Height (m)
≤ 5.1	live	3.3	1327	3.30	1.35	5.3
	dead	2.5	3316	2.43	1.20	3.9
5.1–10.2	live	7.6	2777	5.20	1.96	8.7
	dead	6.4	250	4.02	1.82	6.8
10.2–22.9	live	13.5	1908	6.60	2.53	12.6
	dead	10.9	42	5.29	2.30	10.1
> 22.9	live	25.1	208	6.90	3.34	17.7

Table 3. Crown fuel bulk densities (kg m^{-3}) used in model simulations[a].

Crown fuel size class DBH size class (cm)	Status	Foliage	0–0.5 cm roundwood	0.5–1.0 cm roundwood	1.0–3.0 cm roundwood
≤ 5.1	live	0.332	0.141	0.038	0.154
	dead	n.a.	0.131	0.040	0.125
5.1–10.2	live	1.850	1.150	0.299	0.363
	dead	n.a.	1.236	0.330	0.372
10.2–22.9	live	1.249	1.193	0.286	0.449
	dead	n.a.	1.200	0.297	0.423
> 22.9	live	0.814	1.236	0.270	0.560

[a] n.a. = not applicable.

Table 4. Physical properties of the four crown fuel size classes used in model simulations[a].

Crown fuel size class	Status	Char fraction (dimensionless)	Particle density ($kg\,m^{-3}$)	Surface-area-to-volume ratio (m^{-1})	Water content (dimensionless)
Foliage	live	0.260	628	4239.29	1.220
0–0.5 cm roundwood	live	0.234	410	1434.66	0.781
	dead	0.234	410	1434.66	0.050
0.5–1.0 cm roundwood	live	0.234	410	529.65	0.781
	dead	0.234	410	529.65	0.06
1.0–3.0 cm roundwood	live	n.a.	410	188.79	n.a.
	dead	n.a.	410	188.79	n.a.

[a] The 1.0–3.0 cm size class was included as a source of radiation absorption and momentum drag only (combustion was not considered). Water content and char fraction are not listed for 1.0–3.0 cm fuels as these could not combust in model simulations.
n.a. = not applicable.

Table 5. Fuel types, categories, and physical properties used to generate the homogeneous surface fuelbed[a].

Type	Category	Bed depth (m)	Char fraction (dimensionless)	Loading ($kg\,m^{-2}$)	Particle density ($kg\,m^{-3}$)	Surface-area-to-volume ratio (m^{-1})	Water content (dimensionless)
1-h woody	Woody	0.01	0.266	0.07	410	1434.66	0.06
10-h woody[1]	Woody	0.01	0.266	0.02	410	529.65	0.07
Feathermosses	Moss	0.064	0.355	0.59	1818.18	25 000	0.06
Ladder fuels[1]	Woody	0.01	0.266	0.04	410	982.15	0.07
Lichen	Lichen	0.051	0.355	0.01	1818.18	25 000	0.06
Litter	Litter	0.025	0.286	0.67	628.11	4239.29	0.06
White spruce saplings	Live	0.01	0.274	0.01	519.06	2478.34	0.87
Primary shrubs	Woody	0.01	0.266	0.40	622.77	746.85	0.06
Secondary shrubs	Woody	0.01	0.266	1.20	622.77	746.85	0.06
Homogeneous fuelbed	n.a.	0.045	0.323	3.01	1296.44	15048	0.06

[a] Properties pertain to $D \leq 1$ cm. n.a. = not applicable

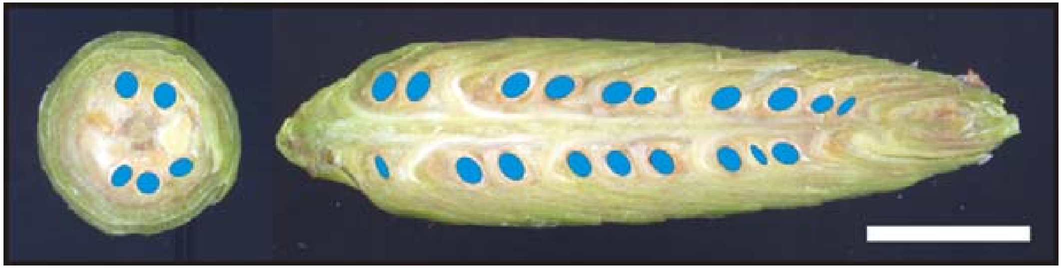

Fig. 1. White spruce cone anatomy in cross (left) and longitudinal (right) sections. Blue areas approximate the intersections of seeds and sections. For cones heated in a fire, radial conduction occurs from the cone surface towards the longitudinal cone axis. Scale bar represents 1 cm.

Fig. 2. Map showing the range of white spruce (Little, 1971) with cone collection locations, weather station locations, germination study locations, and forest fire observation areas.

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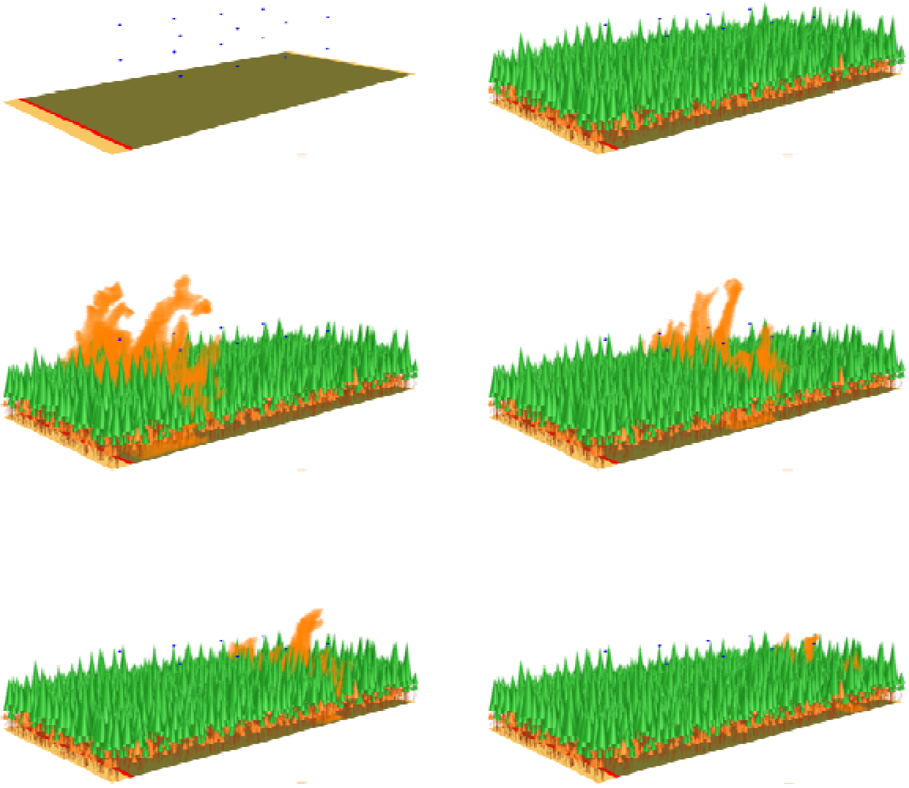

Fig. 3. Example of computational domains, cone locations **(a)**, forest canopy structure **(b)–(f)**, and visualization of WFDS output at $t = 0\,\mathrm{s}$ **(b)**, $t = 250\,\mathrm{s}$ **(c)**, $t = 500\,\mathrm{s}$ **(d)**, $t = 750\,\mathrm{s}$ **(e)**, and $t = 1000\,\mathrm{s}$ **(f)**. Blue ellipsoids (not to scale) represent cone locations, green crowns represent live trees, and orange crowns represent dead trees. Smoke plume is not shown.

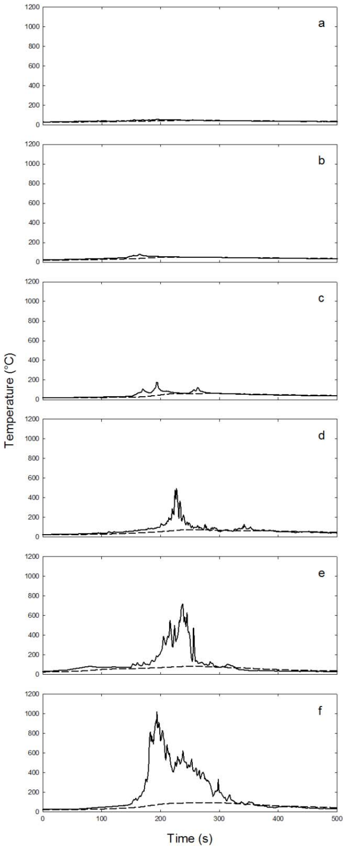

Fig. 4. Typical time series of temperatures for cone surfaces (T_{surf}; solid lines) and seeds (T_{seed}; dashed lines). Time series are shown for cones having maximum seed temperatures that span the range of observed values: 46.00 °C **(a)**, 51.17 °C **(b)**, 64.09 °C **(c)**, 75.85 °C **(d)**, 84.62 °C **(e)**, and 93.90 °C **(f)**.

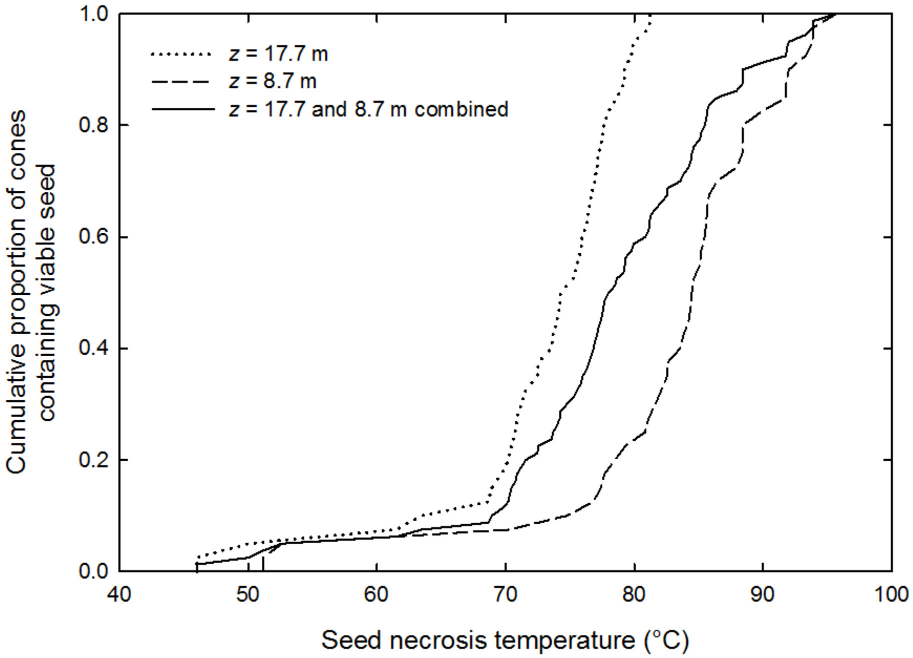

Fig. 5. Cumulative proportion of cones containing viable seeds as a function of seed necrosis temperature, for cones in five simulated forest fires at heights of $z = 8.7$ m ($N = 40$), $z = 17.7$ m ($N = 40$), and $z = 8.7$ and 17.7 m combined ($N = 80$).

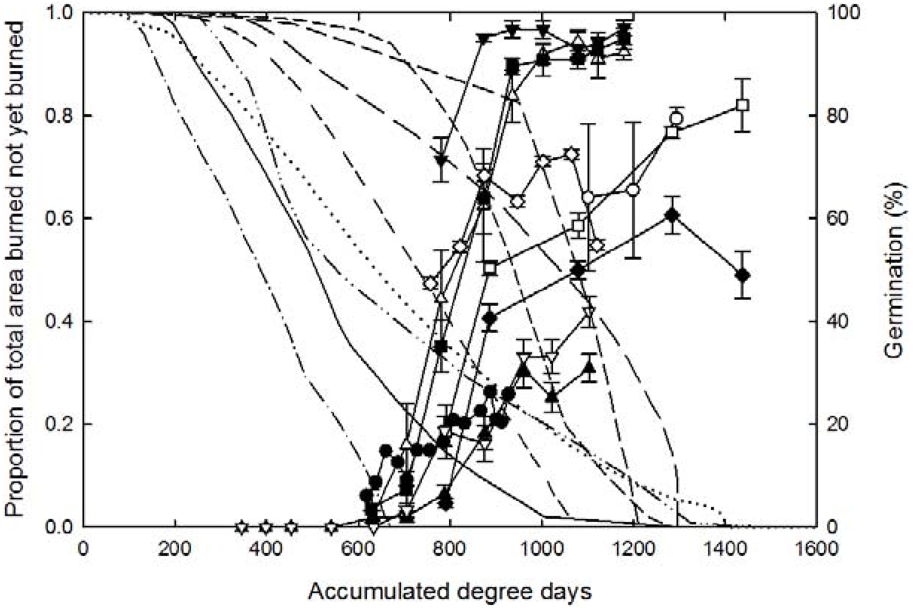

Fig. 6. Timing of fire occurrence (descending lines) and white spruce seed development (mean and SEM). Fire occurrence data were estimated assuming steady state rate of spread between fire start and end dates. Error bars are standard error. ▲ Calgary, non-stratified (2010 data); ▿ Calgary, stratified (2010 data); ♦ Chalk River, non-stratified (Winston and Haddon, 1981); ☐ Chalk River, stratified (Winston and Haddon, 1981); ■ Fairbanks, non-stratified (Zasada, 1978); ▼ Fairbanks, stratified (Zasada, 1973); △ Fairbanks, stratified (Zasada, 1973); ∘ Indian Head, stratified (Cram and Worden, 1957); • Kananaskis Country (Crossley, 1953); ◊ Kananaskis Country, stratified (2006 data); ——— Bagotville; — — — Fairbanks; – – – – Fort Smith; - - - - - - - Jasper; ········· La Ronge; –·–·–·–·– Schefferville; –··–··–··– Sioux Lookout; -- -- -- Yellowknife.