

Simulating the effects of future fire regimes on western Canadian boreal forests

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Abstract. Effects of future fire regimes on boreal tree species and plant functional types were studied in W Canada using a simulation approach. Present (1975-1990) and future (2080-2100) fire regimes were simulated using data from the Canadian Global Coupled Model (CGCM1). The long-term effects of these fire regimes were simulated using a stand level, boreal fire effects model (BORFIRE) developed for this study. Changes in forest composition and biomass storage due to future altered fire regimes were determined by comparing the effects of present and future fire regimes on forest stands over a 400-yr period. Differences in the two scenarios after 400 yr indicate shifting trends in forest composition and biomass that can be expected as a result of future changes in the fire regime. The ecological impacts of altered fire regimes are discussed in terms of general plant functional types. The Canadian Global Coupled Model showed more severe burning conditions under future fire regimes including fires with greater intensity, greater depth of burn and greater total fuel consumption. Shorter fire cycles estimated for the future generally favoured species which resprout (fire endurers) or store seed (fire evaders). Species with no direct fire survival traits (fire avoiders) declined under shorter fire cycles. The moderately thick barked trait of fire resisters provided little additional advantage in crown fire dominated boreal forests. Many species represent PFTs with multiple fire survival traits. The fire evader and avoider PFT was adaptable to the widest range of fire cycles. There was a general increase in biomass storage under the simulated future fire regimes caused by a shift in species composition towards fast-growing re-sprouting species. Long-term biomass storage was lower in fire exclusion simulations because some stands were unable to reproduce in the absence of fire.

Keywords: Biomass; Climate change; Fire effects; Forest composition; Plant functional type.

Introduction

As a result of climate change in the Canadian boreal forest region, a general increase in fire intensity, fire severity (depth of burn) and fire season length (Flannigan & Van Wagner 1991; Wotton & Flannigan 1993; Stocks et al. 1998; Flannigan et al. 2001) is expected. Change in the fire regime is also expected to have an effect on the

forest disturbance rate, or annual area burned. In Canada, stand replacing crown fires burn ca. 2M ha (0.5% of total forest area) each year (Stocks 1991; Amiro et al. 2001) with typical fire cycles of 75-150 yr depending on the local fire regime. Over millennia, tree species have adapted to this fire environment in different ways and can be classified into plant functional types (PFTs) by their fire survival and post-fire regeneration strategy. In N American boreal forests, tree species exist in an environment of recurrent fire by storing seed in the canopy, resprouting, producing large quantities of long distance wind dispersed seed to invade newly disturbed sites (i.e. shade-intolerant pioneers) or by constant regular seed release to establish seedlings in the understorey of post-fire stands (i.e. shade tolerant, late successional species). Protection of parent seed trees by thick, fire resistant bark is a rare survival strategy.

Because of differences in fire survival and post-fire regeneration strategy, a change in the future fire regime will favour some PFTs and may cause a shift in forest composition (Weber & Flannigan 1997). This can affect carbon sequestration rates due to different growth rates in tree species. A change in biomass (or fuel) dynamics will also have a feedback effect on fire regime through flammability and fuel load which affect fire occurrence and fire intensity. Current research on fire and climate change has focused on the physical aspects of altered fire regimes rather than on the ecological impacts. The purpose of this study was to examine the physical and ecological effects of future altered fire regimes on boreal tree communities and biomass dynamics. Fire effects on tree species representing different PFTs were studied using a simulation approach in four National Parks in the western boreal region of Canada.

Study area and Methods

The four study areas were located across a wide geographical range in W Canada (Fig. 1). The mean July temperature (mid fire season) ranges from 14.0 °C in Wood Buffalo National Park to 16.5 °C in Riding Moun-

Table 1. Summary of forest stand types in the four study areas. All values are given in ha.

Stand type	Wood Buffalo National Park	Elk Island National Park	Prince Albert Mountain National Park	Riding National Park
<i>Pinus banksiana</i>	694 293		24 201	
<i>Populus tremuloides</i>	807 830	11 230	93 967	91 947
<i>Picea mariana</i>	1 187 333	320	32 213	
<i>Picea glauca</i>	201 570		5378	38 710
<i>Betula papyrifera</i>		241		
<i>Pinus banksiana</i> / <i>Populus tremuloides</i>			17 675	
<i>Pinus banksiana</i> / <i>Picea mariana</i>			36 946	
<i>Pinus banksiana</i> / <i>Picea glauca</i>			3531	
<i>Picea glauca</i> / <i>Populus tremuloides</i>	546 436	186	59 134	73 296
<i>Populus tremuloides</i> / <i>Betula papyrifera</i>		207		
Other Forest	499 187	71	37 477	71 815
Non Forest	1 019 850	6569	84 913	32 955
Unclassified	99 334			
Total	5 055 833	18 824	395 435	308 723

tain National Park (Anon. 1993). Mean annual precipitation ranges from 353 mm in Wood Buffalo National Park to 508 mm in Riding Mountain National Park, most of which occurs in summer. The majority of the forest in all study areas is comprised of *Picea mariana*, *Pinus banksiana*, *Populus tremuloides* and *Picea glauca* in mixed or pure stands (Table 1). *Betula papyrifera*, *Larix laricina* and *Abies balsamea* are common associates, but only in smaller numbers. Topography in all four study areas is flat to gently rolling with many small waterbodies scattered across the landscape. The fire season ranges from April to September in southern areas and May to August in the north but burning conditions commonly reach very high levels in all study areas (Simard 1973; Harrington et al. 1983; McAlpine 1991). The Wood Buffalo and Prince Albert National Park fire regimes are dominated by natural fire, although Prince Albert National Park is increasing the use of prescribed fire to manage ecosystems. The Elk Island National

Park fire regime is dominated by prescribed burns which are mainly conducted in the spring, although some burns occur in autumn. Riding Mountain National Park has relatively few natural wildfires and prescribed burns are conducted infrequently.

Fire regimes and Plant Functional Types

Fire regime has been defined using characteristics of frequency, intensity, severity, season of burn, fire type and fire size (Malanson 1987; Whelan 1995; Weber & Flannigan 1997). Fire regime has usually been described in relative terms using general classes such as low, moderate or high fire intensity and short, medium or long fire frequency (e.g. Heinselman 1981). In this study, we quantify fire regime by summarizing head fire intensity, time since last fire (fire cycle), fire severity and Julian burn date (season of burn) for all fires occurring in a simulation period. Fire regime effects on PFTs were simulated in a boreal fire effects model through the cumulative impacts of individual fires on boreal tree species over a long period of time (400 yr). Different fire regimes were simulated using current and future climate scenarios, and PFTs were represented by different boreal tree species.

The effects of fire on plant species is largely based on the interaction of physical fire parameters, plant vital attributes important to survival or regeneration, and physiological plant condition at the time of burning (Noble & Slatyer 1980; Trabaud 1987; Johnson 1992; Weber & Flannigan 1997). Many plants adapted to living in an environment of recurrent fire share common traits, and they can be collectively grouped into a small number of different PFTs in relation to fire. Rowe (1983) suggested a classification of species groups by relative fire cycle length using examples of north American boreal plants. In brief, each group had unique functional adaptations to fire. *P. tremuloides* and *B. papyrifera*

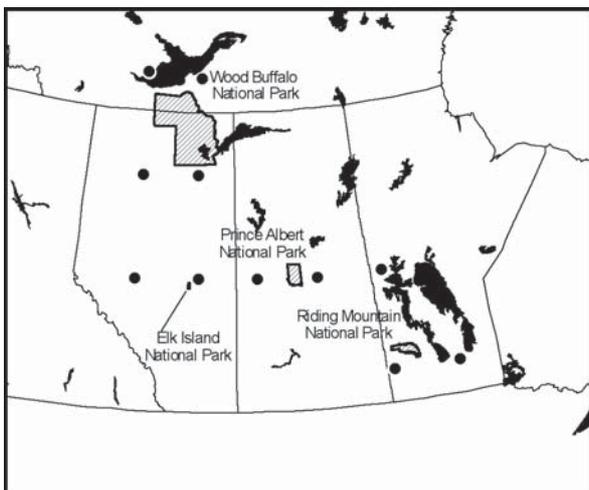


Fig. 1. Location of study areas and gridpoint locations (●) for the Canadian Global Coupled Model estimates used.

were classed as invaders because of their short-lived, wind-disseminated propagules and shade intolerance. These pioneer species can survive a wide range of fire cycle lengths and fire intensities. Both species also resprout after fire (fire endurers), a trait which is favoured by short fire cycles. Fire evaders such as *P. banksiana* and *P. mariana* store seed in the canopy. These species require 20-25 yr to produce a reliable seed crop, so they are most successful in intermediate fire cycles. *P. banksiana* was also classified as a fire resister species because its relatively thick bark protects it from low intensity ground fires. *A. balsamea* and *P. glauca* are late-successional, disseminule based species with no direct adaptation to fire. These were classed as fire avoiders and are favoured by long fire cycles. Their shade tolerance allows them to establish in the understorey of established deciduous stands or *P. banksiana* stands which have a sufficient amount of available light. *P. mariana* also acts as a fire avoider because it releases seed after storing it for some years, so it regularly disseminates seed during its life span which allows it to regenerate in the absence of fire. Because many species possess multiple functional adaptations to fire (or traits), PFT descriptions used for these species represent their multiple fire strategies (e.g. *P. tremuloides* is a fire invader and endurer PFT; Table 2).

If future fire regimes are characterized by shorter fire cycles and higher fire intensities (Flannigan & Van Wagner 1991; Weber & Flannigan 1997; Stocks et al. 1998), then there should be a decrease in fire avoider PFTs and an increase in PFTs with strategies directly related to fire survival and post-fire regeneration. The impact of putative future altered fire regime on boreal PFTs is assessed by comparing long-term (400 yr) differences in species composition and stand condition under 1975-1990 and 2080-2100 fire regime scenarios.

BORFIRE Model Inputs and Datasets

Forest stand dynamics were simulated using BORFIRE, a boreal fire effects model. The model requires a number of datasets to parameterize processes and several inputs to establish the initial simulation conditions. This includes data on vegetation, climate, fire weather, fire behaviour and fire cycles.

Vegetation

Forest inventories of the four National Park study areas (Table 1) were used to determine the major stand types in each National Park. A total of 21 pure and mixed stand types (three to eight in each Park) were identified and simulated in the study.

Climate, fire weather and fire behaviour

Data output from the Canadian Global Coupled Model (CGCM1) (Flato et al. 2000) was used to represent present (1975-1990) and future (2080-2100) climate conditions in the study areas. These two time periods have been used to approximate 1× and 3× CO₂ scenarios in previous climate change studies (Flannigan et al. 1998). CGCM1 data included daily temperature, precipitation, relative humidity, wind speed and growing degree days (mean of maximum and minimum temperatures above 5°C) for gridpoint locations around the study areas (Fig. 1). The data covered April 1 - Sept 30 for every year during both time periods. Growing degree days data was used in BORFIRE to estimate dates for leaf flush and leaf fall of *P. tremuloides* and *B. papyrifera*, seed ripening of *P. glauca*, and spring green-up and autumn curing of herbaceous understorey plants. Daily temperature, precipitation, relative humidity and wind speed were applied to the Canadian Forest Fire Weather

Table 2. Summary of important life history and plant functional traits in relation to fire for tree species simulated in BORFIRE¹. Plant functional types are the composite of important functional traits, as described by their fire strategy. Most species are plant functional types which have multiple fire survival or regeneration strategies (e.g. *Picea mariana* is a fire evader and avoider plant functional type).

	<i>Pinus banksiana</i>	<i>Picea mariana</i>	<i>Picea glauca</i>	<i>Populus tremuloides</i>	<i>Betula papyrifera</i>	<i>Abies balsamea</i>
Fire strategy ²	Fire evader, fire resister	Fire evader, fire avoider	Fire avoider	Fire endurer, fire invader	Fire endurer, fire invader	Fire avoider
Regeneration method	Canopy-stored seed	Canopy-stored seed; periodic seeding	periodic seeding	Re-sprouting from roots; wind-disseminated seed	Re-sprouting from root collar; wind-disseminated seed	Periodic seeding
Bark protection from fire	Moderate	Low	Low	Very low	Very low	Very low
Seasonal fire effect	None	None	Self-seeds only after autumn fire	Does not resprout if burned prior to leaf flush ³	Does not resprout if burned prior to leaf flush	None
Age to reproduction (yr)	20	25	25	5	5	25
Maximum life span (yr)	150	250	350	150	150	200
Shade tolerance	Intolerant	Moderately tolerant	Tolerant	Intolerant	Intolerant	Tolerant
FBP system fuel type	Jack pine	Boreal spruce	Boreal spruce	Deciduous	Deciduous	Boreal spruce

¹ Data sources explained in the text; ² 'Fire resister' strategy due to bark protection from fire; other fire strategies relate to regeneration method; ³Weber (1990).

Index System (Van Wagner 1987) to calculate daily fire danger parameters, or burning conditions. This included the Duff Moisture Code which represents the moisture content of loosely compacted forest floor organic matter; the Buildup Index which indicates the total amount of fuel available for combustion and the Initial Spread Index which indicates rate of fire spread. The daily Duff Moisture Code and Buildup Index were summarized to provide a mean monthly distribution by study area and time period. The Initial Spread Index data was similarly summarized using monthly high values. When a fire event occurred in BORFIRE simulations, this Fire Weather Index System dataset was used to calculate physical fire characteristics.

Fire behaviour, or the physical characteristics of individual fires, was calculated in BORFIRE by applying the Fire Weather Index System parameters to fuel types of the Canadian Forest Fire Behaviour Prediction System (Anon. 1992) and fire behaviour models. This resulted in depth of burn, fuel consumption and rate of spread values for each fire. Head fire intensity was calculated using heat of combustion, fuel consumption and rate of fire spread (Byram 1959).

Fire cycles

The actual 1975-1990 area burned in each National Park was used as the annual burn rate in the 1975-1990 simulations (Table 3). BORFIRE used the annual rate of area burned as the probability rate that a simulated stand would burn in any given year. If a fire event occurred in a simulation year, the month of fire occurrence was similarly determined using the monthly distribution of area burned. Julian fire date was then randomly determined within that month.

Harrington et al. (1983) studied the correlation of monthly area burned to monthly Fire Weather Index System parameters during 1953-1980. Mean monthly Duff Moisture Code values had the strongest relationship to monthly area burned in west-central Canada with correlations of 0.29-0.65. Therefore, mean monthly Duff Moisture Code values for 2080-2100 were used to estimate future monthly area burned in this study. To do this, the difference in mean monthly Duff Moisture

Code values between 1975-1990 and 2080-2100 was proportionately reflected in the mean monthly area burned between those two time periods. Annual area burned and fire cycles are summarized in Table 3. The fire cycles in Prince Albert National Park were extremely long because the annual area burned during 1975-1990 was very low, and the 2080-2100 fire cycle used the 1975-1990 fire cycle as an estimate basis.

BORFIRE Model

BORFIRE quantitatively simulates tree community dynamics (species composition and stand density, mean tree height and diameter) and biomass (above and below-ground, live and dead organic material) (de Groot et al. 2002). Changes in these two state variables were based on processes of tree mortality, tree recruitment, tree growth, biomass decomposition and biomass consumption by fire (Fig. 2). Fire, climate and competition were the variables driving model processes. Tree community dynamics were driven by fire disturbance events which affected recruitment and mortality, and natural thinning due to competition. Biomass increased with tree growth and decreased with decomposition of dead organic material and fuel consumption during fire. The model is process driven using an annual time step and simulates conditions of a 1-ha forest stand.

Tree community dynamics

The model simulates the community dynamics of six major boreal tree species: *P. mariana*, *P. banksiana*, *P. tremuloides*, *P. glauca*, *B. papyrifera* and *A. balsamea*. Each simulated stand may include any number of species. Stand density at the end of each annual time step was a result of recruitment and mortality to the initial condition. Recruitment occurred after a fire event as new *P. banksiana* and *P. mariana* seedlings and new *P. tremuloides* and *B. papyrifera* sprouts. *P. glauca*, *P. mariana* and *A. balsamea* recruitment was possible at each time step in the understorey of deciduous trees (*P. tremuloides* and *B. papyrifera*) or *P. banksiana* if a seed source was available, but recruitment could not occur under other coniferous trees due to limited light. All

Table 3. Summary of annual area burned¹ and fire cycles used in the study. The 1975-1990 data are actual values for each National Park, and the 2080-2100 values were determined from future estimated Duff Moisture Code values (see text).

Study site	1975-1990		2080-2100	
	Actual annual area burned (%)	Actual fire cycle (yr)	Estimated annual area burned (%)	Estimated fire cycle (yr)
Wood Buffalo National Park	1.282	78	1.786	56
Elk Island National Park	0.741	135	1.754	57
Prince Albert National Park	0.007	14 286	0.008	12 987
Riding Mountain National Park	0.461	217	0.730	137

¹ Data provided by each National Park (unpubl. records).

other tree species are shade intolerant and could not regenerate under any tree canopy. Mortality was separated into fire and natural thinning. The latter followed the fully stocked stand density algorithms of the Alberta Phase III Inventory (Anon. 1985) for *P. tremuloides*, *P. glauca*, *P. mariana*, *P. banksiana* and mixed wood stands (any conifer/deciduous mix). *A. balsamea* and *B. papyrifera* used Ontario algorithms by Plonski (1974), MacDonald (1991) and Payandeh (1991). In the case of non pure stands, thinning occurred proportionately to stand density by species.

Biomass dynamics

Biomass was separated into live and dead, and above and below-ground components. Live above-ground tree growth rates followed the Alberta Phase III Inventory and Ontario algorithms. Live below-ground (root) biomass was a proportion of above-ground biomass (Kurz et al. 1996). Thinned trees were transferred to the appropriate above-ground and below-ground dead biomass pools. Standing dead stems fell at a rate of 10% annually and were transferred to surface slash pools of branchwood (10%) and coarse woody debris (90%). Respiration of slash branchwood used the maximum decay rate of the fast soil carbon pool (half life of 3-20 yr) in the boreal west region of the Carbon Budget Model of the Canadian Forest Service (Kurz et al. 1992; Kurz & Apps 1999). The coarse woody debris respired at the maximum decay rate of the medium soil carbon pool (half life of 20-100 yr) and standing dead stems respired at the medium soil carbon pool minimum decay rate.

Dead below-ground biomass was separated into three pools: a surface litter layer of dead foliage and fine (< 1 cm) woody material, a duff layer of loosely compacted surface organic matter and dead roots. Leaf and needle detritus was an annual input to the litter layer, and litter was transferred to duff using the rates of Keane et al. (1989). Through decomposition, branchwood and coarse woody debris was transferred from above-ground slash to the duff pool at a rate of 10% and 5% per year, respectively. In each time step, 10% of dead root biomass and 73.5% of live fine roots (Kurz et al. 1996) were input to the duff layer. Respiration of litter and duff used the rates of fine and medium soil carbon pools for the west boreal region (Kurz et al. 1992) with the maximum rate occurring in the first year after fire and declining to the minimum rate by year 100. Dead root respiration similarly used the medium soil carbon pool rate.

Fire ecology and effects

Fire ecology traits for each species (Table 2) were quantified in the model as it affected tree mortality and recruitment under different fire conditions. Recruitment of *P. tremuloides*, *P. banksiana* and *P. mariana* followed

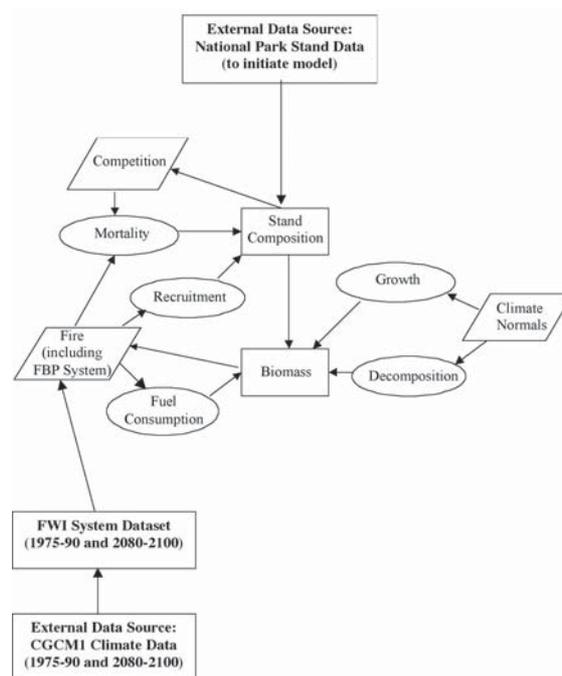


Fig. 2. Simplified structure of the BORFIRE model (inside large box) showing state variables (squares), processes (ellipses), driving variables (parallelogram) and external data inputs.

the algorithms of Greene & Johnson (1999). To simulate post-fire resprouting from the root collar in *B. papyrifera*, recruitment was incorporated as a replacement of surviving individual trees. There are no good recruitment models for *A. balsamea* or *P. glauca*, so a basal area approach was used in a similar fashion to Greene & Johnson (1999). *A. balsamea* used the same algorithm as *P. mariana*, and *P. glauca* used a ratio factor of surviving tree basal area to basal area of a fully stocked pure stand. Long distance seeding of *P. tremuloides* and *B. papyrifera* was considered of minimal importance (Greene & Johnson 1997; Greene et al. 1999) and was not included in these model simulations. In order for regeneration to occur, a propagule bank (*P. tremuloides*, *P. banksiana*, *P. mariana*, *B. papyrifera*) or a surviving individual (*P. glauca*, *A. balsamea*) was required. Reproductive age and maximum life span were used to define the reproductive period for each species. Tree mortality was based on the amount of crown scorch and cambium death during fire (Ryan & Reinhardt 1988). Crown scorch height was calculated using Van Wagner's (1973) equation and fire intensity. Crown scorch was estimated from crown scorch height (Peterson 1985). Cambium mortality was based on bark thickness (Kozak & Yang 1981) and fire intensity. For resprouting species (*P. tremuloides* and *B. papyrifera*), season of burn was important to tree mortality and resprouting ability as low intensity fires prior to leaf flush have been shown to girdle

P. tremuloides stems and prevent suckering (Weber 1990). Pure deciduous stands did not burn after spring understorey green-up but they could burn after autumn leaf fall when herbaceous plants dry quickly with increased solar radiation reaching the forest floor.

Biomass impacts

Fuel (or biomass) consumption during a fire was estimated using fuel load and burning condition parameters. Slash consumption as correlated to Buildup Index (McRae 1980) was used to calculate biomass losses in branchwood and coarse woody debris pools. Depth of burn was calculated using forest floor depth and duff moisture content (estimated by Duff Moisture Code) using FIRESUM (Keane et al. 1989) procedures. All biomass in the litter layer was lost during combustion. The amount of duff biomass lost was determined using duff fuel load, duff bulk density (97 kg.m^{-3}), litter depth (based on 36 kg.m^{-3}) and depth of burn.

Fine aerial fuels were also lost during fire. In the case of a crown fire, this amount was estimated as the foliage and stem bark components (Ter-Mikaelian & Korzukhin 1997) for conifers and *B. papyrifera*, and only the foliage for *Populus tremuloides* (which does not have flammable bark). In non crowning fires, the model estimates no live biomass loss in *P. tremuloides* and a 2% loss representing bark in all other tree species. Live trees killed by fire were transferred to the dead standing biomass pool and dead standing trees were transferred to branchwood and coarse woody debris pools during a fire.

Physical fire parameters

Fire occurrence was simulated using the procedures described in the Fire Cycles section. Julian fire date was used to determine the state of hardwood flushing, understorey condition and the burning conditions as measured by the Fire Weather Index System. The model then selected the Buildup Index, Initial Spread Index and Duff Moisture Code values for the fire event from the Fire Weather Index System dataset using a probability weighted by the distribution of those values for the month of fire occurrence.

The Duff Moisture Code was used to calculate forest floor consumption, and Buildup Index was used to calculate above-ground dead biomass consumption. The mean fire rate of spread (weighted by species) was calculated with the Initial Spread Index and tree species data using procedures of the Canadian Forest Fire Behaviour Prediction System (Anon. 1992). Fire intensity was calculated using fire rate of spread and fuel consumption during the fire. Fuel consumption was calculated in several steps following Canadian Forest Fire Behaviour Prediction System procedures (Anon.

1992). Critical surface fire intensity was determined using foliar moisture content and live crown base height. Actual surface fire intensity was determined from rate of fire spread (using stand composition, age and season of burn) and surface fuel consumption (litter, duff, dead and downed branchwood and coarse woody debris). If surface fire intensity was greater than the critical surface fire intensity, then a crown fire occurred and total fire intensity was calculated using rate of fire spread and total fuel consumption (surface fuels plus bark and foliage fuels).

Model simulations

Each simulation was started with initial conditions of 1000 seedling.ha⁻¹ for each species and a standard duff biomass of 80 t.ha⁻¹. This was to simulate the first year of a stand regenerating after fire. Separate simulation scenarios were run for each stand type in each National Park and for both simulation periods, resulting in a total of 42 simulation scenarios. For each simulation scenario, a total of 25 separate simulations were run using the same model initializing criteria (i.e. replicates) and mean values were calculated from their resulting output. Each of the 25 simulations was run for 400 yr to allow the stand dynamics to reach equilibrium under the driving variables. Mean tree densities by species and stand biomass during the final 100 yr of the simulation period were summarized to compare the different simulation scenarios.

Results

There was a slight decrease in the highest monthly Initial Spread Index values in Elk Island National Park and Prince Albert National Park, but this had minimal impact on fire behaviour. There was a slight decrease in mean monthly Duff Moisture Code and Buildup Index values in Elk Island National Park in the autumn but this had minimal impact since almost all fires occurred in the spring as prescribed burns. All other Fire Weather Index System parameters increased under future fire regimes in all Parks. Higher Duff Moisture Code, Buildup Index and Initial Spread Index values resulted in greater depths of burn, fuel consumption and fire intensities (Table 4). The latter were also highly variable, indicating fire regimes were a mix of low intensity surface fires and high intensity crown fires.

Overall, *P. tremuloides* stem densities (Table 4) increased in Wood Buffalo National Park and Riding Mountain National Park under future fire regimes, but *P. tremuloides* biomass (Table 5) increased greatly in Riding Mountain National Park and only slightly in

Table 4. Summary of mean (S.D.) physical fire characteristics in the model simulations and mean tree density in forest stands during the final 100 yr of the 400 yr simulations. Species unable to survive under the simulated fire regime for 400 yr show stand density = 0.

Study site	Stand type	Fire regime	Depth of burn (cm)	Fuel consumption (kg.m ⁻²)	Head fire intensity (kW.m ⁻¹)	Mean stand density(stems.ha ⁻¹)
Wood Buffalo National Park	<i>Populus tremuloides</i>	1975-1990	3.7 (3.1)	4.3 (3.9)	1198 (2444)	230
		2080-2100	4.5 (3.6)	5.5 (4.6)	1351 (2301)	454
	<i>Pinus banksiana</i>	1975-1990	2.5 (2.3)	3.3 (3.2)	15 076 (15 980)	310
		2080-2100	5.0 (4.1)	6.6 (5.7)	26 214 (24 330)	714
	<i>Picea mariana</i>	1975-1990	2.7 (2.7)	4.2 (4.0)	22 229 (22 863)	2665
		2080-2100	2.5 (2.3)	3.8 (3.5)	21 533 (20 188)	1842
	<i>Picea glauca</i>	1975-1990	2.4 (2.2)	3.7 (3.4)	22 652 (27 542)	6
		2080-2100	2.6 (2.2)	3.8 (3.3)	20 638 (20 307)	25
	<i>Populus tremuloides/ Picea glauca</i>	1975-1990	4.3 (2.8)	5.4 (3.8)	9296 (15 773)	0/112 ¹
		2080-2100	5.3 (3.7)	6.7 (4.8)	9353 (22 517)	17/694
Elk Island National Park	<i>Populus tremuloides</i>	1975-1990	1.6 (0.7)	1.2 (0.8)	303 (242)	0
		2080-2100	1.4 (1.0)	1.2 (1.2)	430 (362)	5
	<i>Picea mariana</i>	1975-1990	1.1 (1.6)	1.7 (2.6)	6127 (9784)	0
		2080-2100	0.7 (0.6)	1.3 (1.3)	4679 (6097)	33
	<i>Betula papyrifera</i>	1975-1990	1.8 (4.7)	2.5 (6.2)	768 (1168)	4873
		2080-2100	2.0 (2.6)	2.8 (3.4)	888 (1016)	4277
	<i>Betula papyrifera/ Populus tremuloides</i>	1975-1990	1.6 (1.1)	1.6 (1.5)	380 (276)	130/38
	<i>Populus tremuloides</i>	2080-2100	1.7 (1.9)	1.7 (2.4)	515 (489)	0/0
	<i>Populus tremuloides/ Picea glauca</i>	1975-1990	1.7 (2.0)	1.7 (2.7)	4287 (8271)	0/0
	2080-2100	1.3 (1.0)	1.3 (1.4)	2518 (4636)	35/0	
Prince Albert National Park	<i>Populus tremuloides</i>	1975-1990	- ²	-	-	0
		2080-2100	-	-	-	0
	<i>Pinus banksiana</i>	1975-1990	-	-	-	0
		2080-2100	-	-	-	0
	<i>Picea glauca</i>	1975-1990	-	-	-	4455
		2080-2100	-	-	-	4632
	<i>Picea mariana</i>	1975-1990	-	-	-	683
		2080-2100	1.5 (- ³)	2.1 (-)	28 987 (-)	683
	<i>Pinus banksiana/ Picea mariana</i>	1975-1990	0.4 (0.1)	0.2 (0.1)	110 (49)	0/4588
	<i>Picea mariana</i>	2080-2100	5.4 (-)	7.3 (-)	46 752 (-)	0/4479
	<i>Pinus banksiana/ Picea glauca</i>	1975-1990	-	-	-	0/683
	<i>Picea glauca</i>	2080-2100	3.0 (-)	5.2 (-)	4675 (-)	0/655
	<i>Pinus banksiana/ Populus tremuloides</i>	1975-1990	-	-	-	0/0
	<i>Populus tremuloides</i>	2080-2100	-	-	-	0/0
<i>Picea glauca/ Populus tremuloides</i>	1975-1990	1.4 (-)	0.9 (-)	681 (-)	653/0	
2080-2100	-	-	-	-	680/0	
Riding Mountain National Park	<i>Populus tremuloides</i>	1975-1990	1.9 (1.2)	1.9 (1.5)	3269 (3170)	0
		2080-2100	4.6 (3.9)	5.2 (5.0)	5423 (8167)	520
	<i>Picea glauca</i>	1975-1990	1.4 (1.7)	2.8 (2.9)	26240 (27 606)	129
		2080-2100	2.4 (1.9)	4.2 (3.2)	38 563 (31 649)	34
	<i>Picea glauca/ Populus tremuloides</i>	1975-1990	2.2 (2.9)	3.1 (3.9)	26 317 (27 314)	73/0
	2080-2100	4.4 (2.8)	5.8 (3.7)	22 550 (23 778)	35/293	

¹ Numbers represent first species/second species in mixed stands;² No fires during the simulation period;³ Only one fire during the simulation period; no S.D.

Wood Buffalo National Park. In contrast, *P. tremuloides* density was very low in Prince Albert National Park and Elk Island National Park under future fire regimes, resulting in very little tree biomass. *P. banksiana* density increased in Wood Buffalo National Park but it did not survive the long simulated fire cycles of Prince Albert National Park. *P. mariana* stem density decreased substantially under future fire regimes in Wood Buffalo National Park but remained very similar in Elk Island National Park and Prince Albert National Park. *P. glauca* stem densities and stand biomass were high in Prince Albert National Park. *P. glauca* stem density was very low in all other study areas. In mixed stands of *P. tremuloides* and *P. glauca*, shorter fire cycles in the future increased *P. tremuloides* stem density and decreased *P. glauca*, but total biomass increased. Some stands increased in total biomass and others decreased under shorter fire cycles, but the overall effect was an increase in total biomass storage in all Parks.

Discussion

The Fire Weather Index System values for the current (1975-1990) simulation scenarios were within the normal range of historical conditions (Harrington et al. 1983). The increasing fire danger trend of future fire regimes found in this study is in agreement with the predictions of other published literature (Clark 1988; Flannigan & Van Wagner 1991; Price & Rind 1994; Weber & Flannigan 1997; Stocks et al. 1998). Future fire regimes resulted in fires with greater depths of burn, greater fuel consumption and higher fire intensities. Elk Island National Park was an exception to some of the results because the simulated fire regimes were based on the early spring prescribed burn program being implemented there. The Duff Moisture Code and Buildup Index values at that time of year were generally very low, so future depth of burn and fuel consumption showed little change from current values.

Table 5. Mean forest stand biomass (t.ha⁻¹) values during the final 100 yr of the 400 yr simulation under current (1975-1990) and future (2080-2100) fire regimes. Biomass values indicate different levels that would be achieved over a 400 yr period due to differences in fire regime. Species unable to survive under the simulated fire regime for 400 yr have zero biomass.

Study area	Species	Fire regime	Dead wood	Forest floor	Pt	Pb	Tree species ¹			Total
							Pm	Pg	Bp	
Wood Buffalo National Park	<i>Populus tremuloides</i>	1975-1990	4.14	42.37	40.60					87.10
		2080-2100	6.44	48.93	41.17					96.55
Elk Island National Park	<i>Pinus banksiana</i>	1975-1990	9.14	51.80		10.87				71.82
		2080-2100	12.87	49.99		15.91				78.78
	<i>Picea mariana</i>	1975-1990	13.42	58.80			19.36			91.58
		2080-2100	11.20	48.64			17.19			77.03
	<i>Picea glauca</i>	1975-1990	1.99	8.66				2.79		13.43
		2080-2100	1.31	5.97				1.89		1.22
	<i>Picea glauca</i>	1975-1990	4.72	43.05	42.78			0.00		90.54
	<i>Populus tremuloides</i>	2080-2100	8.62	56.52	51.15			1.71		117.99
	<i>Populus tremuloides</i>	1975-1990	0.40	4.73	2.24					7.37
		2080-2100	0.93	9.05	9.38					19.35
Prince Albert National Park	<i>Betula papyrifera</i>	1975-1990	0.01	11.01					0.42	11.43
		2080-2100	1.21	38.12					23.9	63.26
	<i>Picea mariana</i>	1975-1990	31.18	180.08			75.12			286.38
		2080-2100	20.65	98.32			34.14			153.10
	<i>Picea glauca</i>	1975-1990	3.83	43.38	16.42			25.87		89.50
	<i>Populus tremuloides</i>	2080-2100	0.05	2.84	0.12			0.11		3.12
	<i>Betula papyrifera</i> / <i>Populus tremuloides</i>	1975-1990	0.09	2.70	1.40				0.45	4.64
	<i>Populus tremuloides</i>	2080-2100	1.08	9.97	11.08				0.35	22.48
	<i>Populus tremuloides</i>	1975-1990	0	0.37	0					0.37
		2080-2100	0	0.37	0					0.37
Riding Mountain National Park	<i>Pinus banksiana</i>	1975-1990	0	12.28		0				12.28
		2080-2100	0	12.28		0				12.28
	<i>Picea mariana</i>	1975-1990	26.80	214.21			143.35			384.36
		2080-2100	27.06	215.58			141.26			383.91
	<i>Picea glauca</i>	1975-1990	49.55	203.21				80.87		333.62
		2080-2100	49.55	203.21				80.87		333.62
	<i>Pinus banksiana</i> / <i>Populus tremuloides</i>	1975-1990	0	0.98	0	0				0.98
	<i>Populus tremuloides</i>	2080-2100	0	0.98	0	0				0.98
	<i>Pinus banksiana</i> / <i>Picea mariana</i>	1975-1990	22.46	198.89		0	142.51			363.86
	<i>Picea mariana</i>	2080-2100	21.88	195.78		0	141.52			359.17
	<i>Pinus banksiana</i> / <i>Picea glauca</i>	1975-1990	49.39	201.48		0		80.87		331.73
	<i>Picea glauca</i>	2080-2100	47.41	193.89		0		77.63		318.93
	<i>Picea glauca</i> / <i>Populus tremuloides</i>	1975-1990	45.00	177.76	0			76.72		299.49
	<i>Populus tremuloides</i>	2080-2100	46.42	181.33	0			79.83		307.59
Riding Mountain National Park	<i>Populus tremuloides</i>	1975-1990	0.22	5.20	4.76					10.18
		2080-2100	7.01	67.21	104.5					178.77
	<i>Picea glauca</i>	1975-1990	11.02	52.12				15.89		79.03
		2080-2100	4.80	24.84				6.02		35.65
	<i>Picea glauca</i> / <i>Populus tremuloides</i>	1975-1990	9.03	38.12	0.00			13.52		60.67
	<i>Populus tremuloides</i>	2080-2100	10.99	69.82	45.80			6.65		133.26

¹ Pt = *Populus tremuloides*, Pb=*Pinus banksiana*, Pm = *Picea mariana*, Pg = *Picea glauca*, Bp = *Betula papyrifera*.

The stand density, biomass and species composition results show stand conditions after 400 yr under each simulated fire regime scenario. Species which could not survive under the simulated fire regime for 400 yr had stem densities and biomass of zero. For stands that were self-sustaining after 400 yr under the 1975-1990 fire regimes, live tree biomass ranged from 11 t.ha⁻¹ in *P. banksiana* stands of Wood Buffalo National Park (mean age 39 yr) to 143 t.ha⁻¹ in *P. mariana* stands in Prince Albert National Park (mean age 125 yr). These values are consistent with other current, mean boreal estimates of 65 t.ha⁻¹ (Kurz & Apps 1999), 56-108 t.ha⁻¹ (Bonnor 1985) and 30-170 t.ha⁻¹ (others cited in Bonan 1990).

The Prince Albert National Park simulations were different because of extremely long simulated fire cycles. This was an artifact of the fire cycle sample period (1975-1990) when very few fires occurred in the Park. Although the simulated fire cycles are unrealistic over longer time scales, the simulations provide insight into the effects of fire exclusion. Under such a regime, the fire

evader *P. banksiana* (Rowe 1983) quickly became locally extinct because there was no fire to open cones and release canopy stored seed. The resprouting fire endurers *P. tremuloides* and *B. papyrifera* eventually became locally extinct as well because fire did not provide the stimulus to resprout and old stands declined in their resprouting ability. These two species are also classed as fire invaders because of their prolific annual seed production. However, they were unable to reproduce by seed under extremely long fire cycles because there was little fire disturbance to remove competition and allow these shade-intolerant species to become established. *P. glauca*, a fire avoider, reproduced well in the absence of fire because regular seed dispersal allowed seedlings to take advantage of newly available growing space from other declining PFTs. *P. mariana*, which is normally referred to as a fire evader due to its semi-serotinous cones, performed as a fire avoider under extremely long fire cycles because of annual seed release and shade tolerant seedlings. In terms of biomass, the results

indicate that fire exclusion would cause an overall decrease in biomass storage from current levels over a 400-yr period because many stands would not be able to reproduce in the absence of fire.

The resprouting fire endurers were most advantaged over other PFTs by shorter fire cycles of future fire regimes. They survive by quickly sprouting after fire to dominate recently disturbed sites. This PFT reproduced under the shortest fire cycles and will benefit the most from any decrease in fire cycle length. The seed storing fire evaders were also promoted by shorter fire cycles. However, these species are restricted to fire cycles that are longer than the earliest age of seed production. Fire invaders should also be promoted by shorter fire cycles due to the greater opportunity for seedling establishment, but the success of long distance seed dispersal at a spatial landscape scale was not tested in this stand level simulation model. Higher fire intensities of future fire regimes provided a small advantage to the one relatively thicker barked fire resister species in this study (*P. banksiana*), but the majority of boreal fires are very high intensity so this advantage had minimal impact.

P. mariana represented the fire evader and avoider PFT. This combination of fire strategies made it adaptable to the widest range of fire cycles, from 25 yr (age of seed production) to fire exclusion. Fire avoiders declined quickly under shorter future fire cycles. The only way this PFT can survive in a fire prone environment is through individual survival of low intensity fires or off site seeding. The latter is of minimal consequence beyond 100-200 m from the fire boundary (Greene & Johnson 1997). However, the chance for individual tree survival during fire is greatly increased if it grows in a deciduous dominated stand where fire intensities are generally very low. Additionally, the fire season of deciduous stands is almost exclusively spring and autumn because of understorey green-up during the summer, and this also is an advantage to *P. glauca* because trees can reproduce after autumn fire with seed ripened at the end of summer. This may be a reason why *P. glauca* is often found in association with *P. tremuloides* in W Canada.

Increased depth of burn under future fire regimes will result in greater mortality rates in all PFTs through cambium death at the root collar or around roots by smouldering fires. This may provide an advantage for resprouting, fire endurer PFTs that produce new shoots from deeper buried roots (*P. tremuloides*) but not for root collar resprouters (*B. papyrifera*). Increased fuel consumption in the future will result in higher fire intensities and greater mortality of all species. Most area burned in N American boreal forests is by high intensity crown fires, and this is likely to continue in the future.

The resprouting, fire endurer PFT was most advantaged by future fire regimes, and this produced two

secondary effects. The first was a change in forest composition which resulted in a fuel type feedback to fire regime. A shift towards resprouters increased the deciduous component of the forest and this tended to promote more spring and autumn fires, and fires of lower intensity. However, the latter effect was small in comparison to the general increase in fire intensity caused by an increase in burning conditions.

The other secondary effect of a shift towards resprouters was a general increase in biomass storage. This PFT was characterized by fast growing intolerant species so an increase in the forest composition of those species increased the overall forest biomass accumulation rate. Greater live tree biomass resulted in greater detrital input to the forest floor, and this also increased dead biomass storage.

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