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Understanding how fire behavior characteristics shape tree population dynamics, diversity and forest patterns

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E.A. Johnson, D.F. Greene and K. Miyanishi

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Sustainable Forest Management Network
G208 Biological Sciences Building
University of Alberta
Edmonton, Alberta, T6G 2E9
Ph: (780) 492 6659
Fax: (780) 492 8160
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Understanding how fire behavior characteristics shape tree population dynamics, diversity and forest patterns

by

E. A. Johnson[1], D. F. Greene[2] and K. Miyanishi[3]

[1]Dept. Biological Sciences, University of Calgary, Calgary, Alberta
[2]Dept. Geography & Biology, Concordia University, Montreal, Quebec
[3]Dept. Geography, University of Guelph, Guelph, Ontario

August 2000

INTRODUCTION

This final report reviews one year of research carried out by three principal investigators and their graduate students, each located at different universities.

Our study area encompasses the Weyerhaeuser FMLA and Prince Albert National Park, an area of about 3.7 million ha.

The projects reported here continue the research program reported last year (May 1999) under the same name.

Five projects are reported here:

- The relative importance of terrain and forest fire on plant biodiversity. The project also discusses the implications for forest management of plant biodiversity.

- The effects of weather, hillslope position, stand density on the amount of duff removed by smouldering combustion. The importance of this in patterns of tree regeneration is considered.

- Methods of determining dispersal and tree recruitment into burns is given so foresters can determine regeneration immediately after a fire or cut.

- The population dynamics project compares different methods of studying forest succession and shows misunderstandings that can result. Important for understanding the basis of succession.

- A model of forest fragmentation predicts the decision rules used by settlers. The wetness values show that fragmentation by settlement is determined by the needs of mechanized agriculture not the moisture-nutrient regime. Nesting in the landscape will probably follow a similar pattern.

Each project can be read separately and has its own executive summary.

These projects have been helped by logistic and information by Saskatoon Timberlands (Weyerhaeuser Canada) and Prince Albert National Park.

A Spatially Realistic Distributed Model of Fragmentation Resulting from Human Disturbance in the Mixedwood Boreal Forest of Saskatchewan

SFM Network Project:

Understanding how fire behavior characteristics shape tree population dynamics, diversity and forest patterns

by

T.L. Tchir and E.A. Johnson

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

August 2000

EXECUTIVE SUMMARY

A decision-based model of the fragmentation process using empirical land-use maps from 1900-1963 was developed to determine which parts of the landscape were more likely to experience human disturbance and which were more likely to be left as forested remnants. Although socioeconomic and biophysical attributes (i.e. nearness to neighbours, transportation networks, moisture and nutrient gradients) strongly influence the quality of land, reliable measures of these attributes were not all available to settlers. Instead, settlers relied on surrogate measures of moisture and nutrient status, such as vegetation, soil texture and stoniness. Using these surrogate measures as decision rules, the model determined that soil texture, soil formation and the amount of stoniness govern the fragmentation process with 71%-94% accuracy.

To predict the distribution of moisture and nutrient gradients that underlie the settlement process, a spatially realistic slope wetness model (TOPMODEL) was used. Incorporating easily measured physical variables, TOPMODEL captures the variability of soil properties by redistributing the soil water and nutrients according to hillslope position, thereby predicting variations in surface soil water. Tolerance of the crops to the wetness values of these areas meant that the productivity of the landscape did not influence the decision rules of the settlers. Instead, the highly mechanized agriculture practiced meant that the physical characteristics such as stoniness, soil formation and slope were more influential than the productivity of the land in determining the location of settlement.

The wetness index we know predicts the distribution of native vegetation by relating hillslope position and surfical material to moisture-nutrient gradients. Given that settlers select wetness values in proportion to their occurrence on the landscape, native vegetation will be fragmented in proportion to their occurrence on the specific wetness values.

INTRODUCTION

Fragmentation is of interest to ecologists because of its widespread prevalence and influence on ecosystem processes in forested areas. In the past, studies of fragmentation have simply described spatial patterns on specific landscapes (*e.g.* Franklin and Forman 1987, Krummel et al. 1987, Turner and Ruscher 1988).

Recognizing that the large scale clearing of forested land for agricultural settlement is the most prevalent type of human disturbance, fragmentation is defined here as the physical manifestation of the decision-based settlement process.

The specific moisture and nutrient requirements of crops and the highly mechanized form of agriculture used in the study region suggests that the decision rules of the settlement process should reflect: 1) the productivity of the landscape (*i.e.* the distribution of moisture and nutrients), and 2) the ease with which the landscape could be cultivated (*e.g.* variables such as slope and stoniness).

OBJECTIVES

The objectives of the study were two fold: (1) To determine if settlers were basing their decisions on the productivity of the landscape, a topographic index **(WETNESS)** was used to distribute the water and surficial materials that control productivity. By comparing the proportion of wetness values available to the settlers to the proportion of wetness values that are chosen by settlers, we can determine how settlers use the variation in productivity of the landscape. (2) To determine if settlers were basing their decisions on the ease with which the landscape could be settled, a spatially exact transition model of fragmentation **(FRAGMENT)** was used to determine which physical characteristics of the landscape (*i.e.* both socioeconomic and biophysical variables) are important in characterizing areas of settlement and cultivation.

STUDY SITE

The study area consists of five rural municipalities covering 3260 km^2 of land. It is located in the agricultural region on the southern edge of the mixedwood boreal forest, just south of Prince Albert National Park in central Saskatchewan, Canada (Figure 1). The topography ranges in elevation from 510 to 580 m above m.s.l.

Prior to 1890, the study area was covered by continuous mixedwood boreal forest (Weir and Johnson 1998). Between 1890 and 1940, most of the homesteads in this area were claimed for settlement (Vanderhill 1958, Fitzgerald 1965) and cleared for grain (wheat and oats) and livestock operations (Stutt and Van Vliet 1945). Currently, the study area is primarily composed of agricultural land with small isolated fragments of forest.

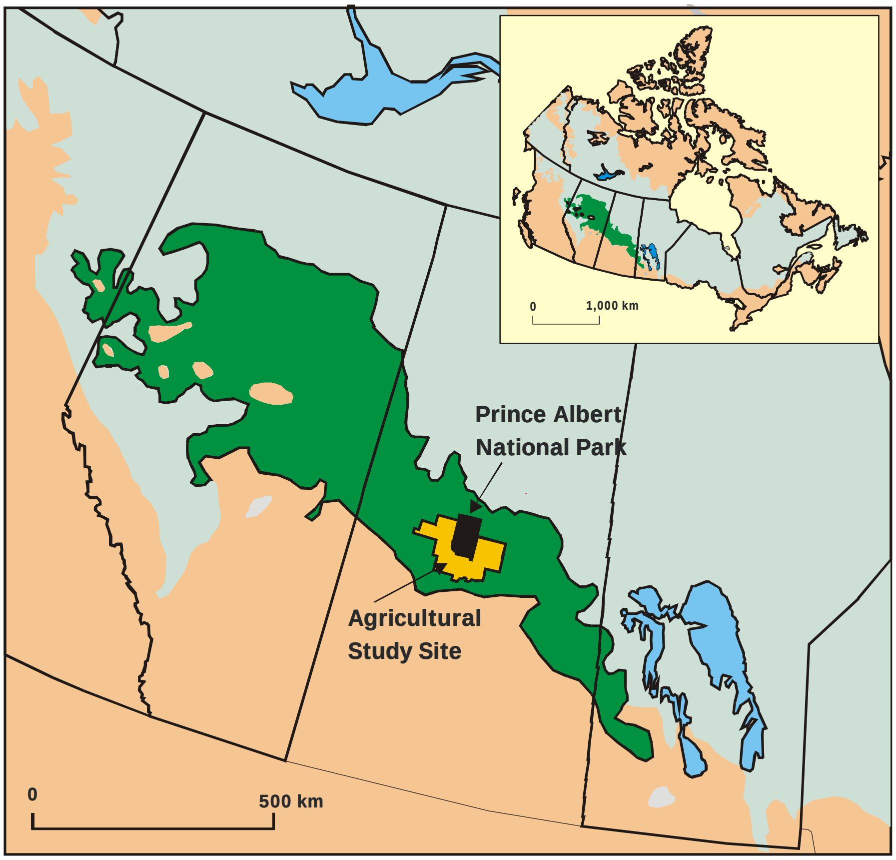


Figure 1. The study area is located in the agricultural region on the southern edge of the mixedwood boreal forest, south of Prince Albert National Park in central Saskatchewan, Canada. The light grey area represents the extent of the boreal forest in Canada and the hatched area is the southern mixedwood boreal forest.

METHODS

The topographic index is a quantitative method of showing hillslope position and accounts for variation in relief and drainage by determining the flow of water, solutes and sediments to a particular point on a hillslope.

The Data Input consists of a Digital Elevation Model (DEM) that represents the spatial distribution of elevations above some arbitrary datum in the landscape. To run the index on the landscape, the drainage network of hillslopes, streams and ridgelines was derived from the DEM in a 2-step process: 1) Pits were removed from the DEM to ensure water flow reached a logical destination using a flow algorithm (either distributed or non-distributed) that produced the most realistic stream network. 2) Flow algorithms were used to define: ridgelines (cells with no contributing cells), stream channels (cells with accumulations above a certain drainage threshold) and hillslopes (the area between the ridge and the stream).

The topographic index predicts the distribution of water, solutes and sediments within a watershed:

$$\mathbf{W}_{i} = \mathit{ln}\ (\mathbf{A}_{s} / \tan\beta) \qquad (1)$$

where:

In is the natural logarithm.

A_s is the specific catchment area per unit contour length (*i.e.* the upslope contributing area per unit width of contour)

tan is the tangent function of the local surface slope angle (^{o}).

The specific catchment area per unit contour length **(A_s)** is used to measure the surface and shallow subsurface runoff at any given point on the landscape:

$$\mathbf{A}_{s} = (\mathbf{A}_{v} * \mathbf{C}_{a}) / \mathbf{C}_{s} \qquad (2)$$

A_v is the accumulation value (*i.e.* the total number of cells that drain through a cell).

C_a is the area of each cell in the raster layer (m^2).

C_s is the linear size of cells in the raster layer (m).

RESULTS

Given that the elevation range of the study area is only 70 m, it is expected that the wetness values would not be as variable as in a region characterized by greater topographic relief. Figure 2 shows that this prediction is correct, the subdued topography of the study area produces a narrow distribution of wetness values.

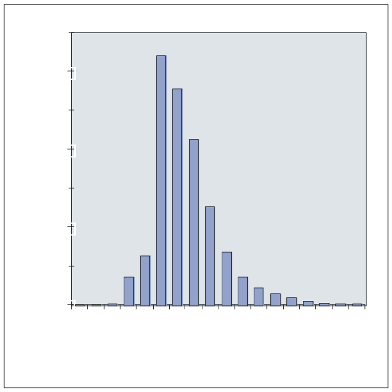


Figure 2. The frequency distribution of wetness cells on the landscape before settlement (pre-1900).

In Figure 3, we see that the proportion of wetness values that are settled reflects the proportion of wetness values remaining available to the settler at the time of settlement.

Therefore, settlers select wetness values in this area in proportion to their occurrence on the landscape.

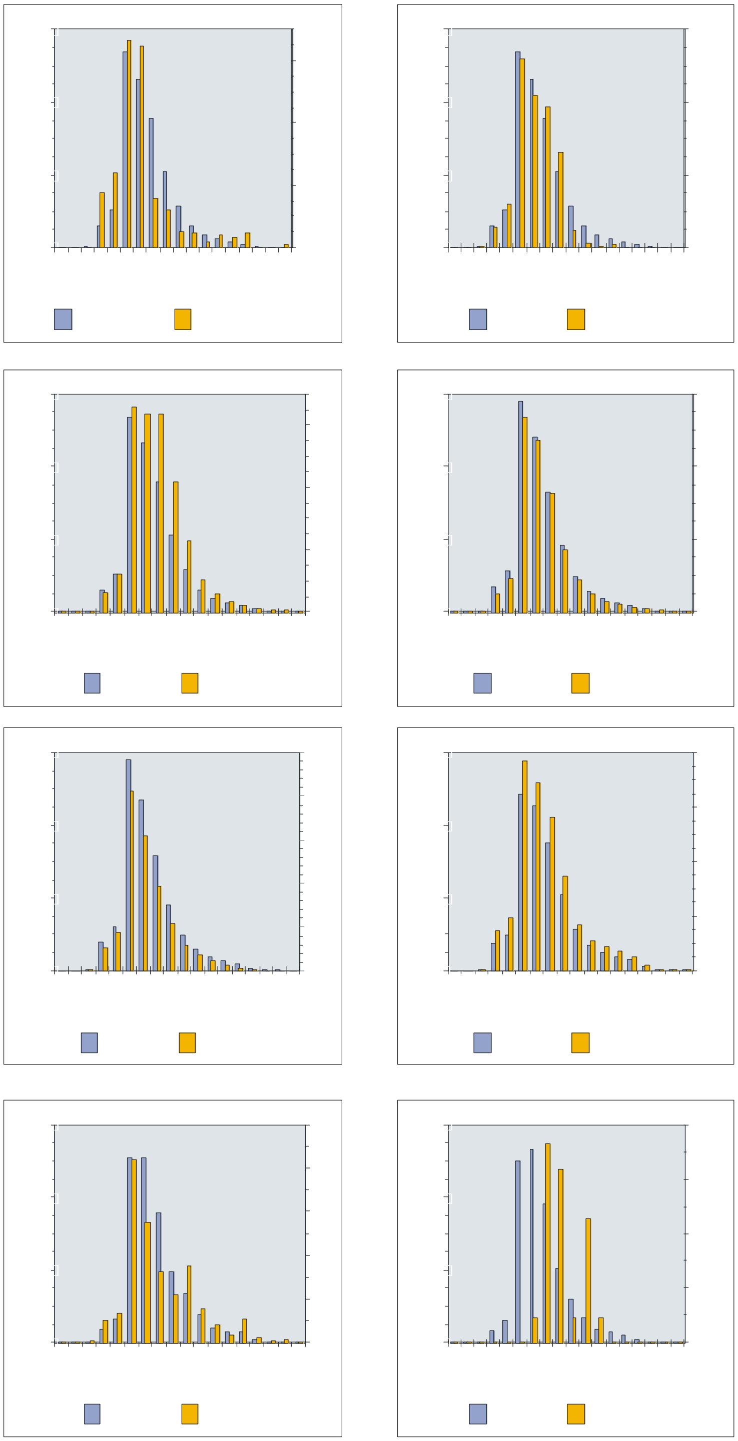


Figure 3.The proportion of wetness values available to the settlers for each decade (*i.e.* wetness values that were not previously settled) and the corresponding proportion of wetness values settled for each decade.

Recognizing that the landscape is characterized by a narrow distribution of wetness values and that the crops used by settlers in this region (*i.e.* wheat, oats and alfalfa) are able to tolerate the range of wetness values found on this landscape (Matz 1969, Percival 1921), all wetness values were considered equally suitable by the settlers. Therefore, all locations were considered equally productive by the settlers in this study area.

The model fragment is spatially realistic in that the socioeconomic and biophysical variables of a specific location are based on actual empirical values for a real landscape. The data input consists of historical settlement maps and socioeconomic and biophysical variables. Homestead records and forest conversion rates from 1900-1960 were used to create the historical settlement maps by decade following the methods of Weir and Johnson (1998) (Figure 4). In this study, homestead is defined as 160 acres (1 acre = 0.405 hectares) and settled means that 30 acres had to be in agriculture for a minimum of 3 years. The empirical settlement maps were integrated into a GIS-based model to determine which decision rules settlers used to choose their homesteads.

To maximize their agricultural return per energy investment, the decisions to settle an area are universal in that they reflect the productivity and the methods used to cultivate the land. Past studies (*e.g.* Ellis and Clayton 1970, Bylund 1960) have shown the following variables to be correlated to settlement: Proximity to transportation (road/railroad), Soil texture and formation, Slope, Stoniness, Adjacency to neighbors. All of these socioeconomic and biophysical variables were available to the settlers at the time of settlement.

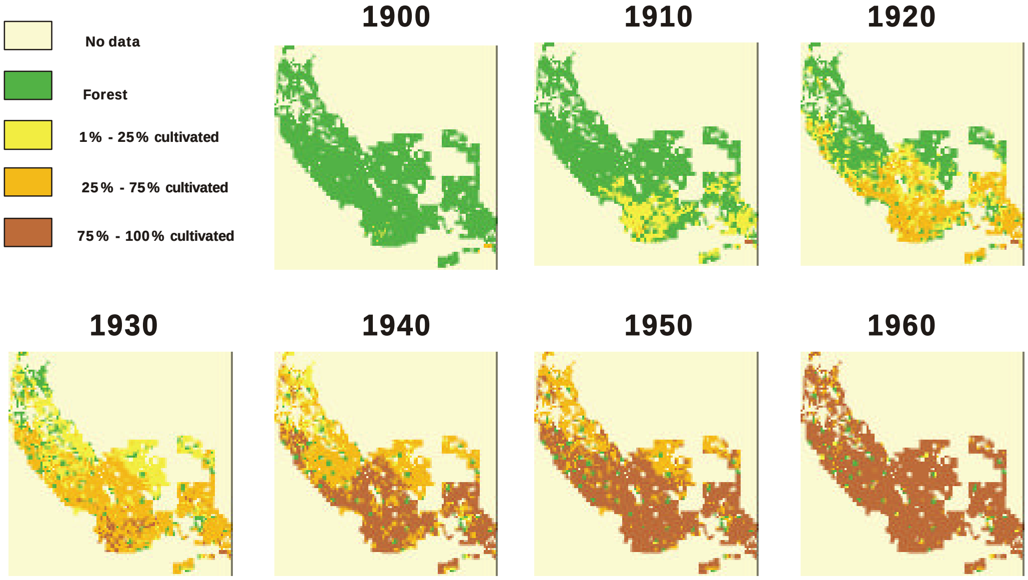


Figure 4. The historical settlement pattern for the 2928 homesteads in the mixedwood boreal forest south of Prince Albert National Park as determined from homestead records and forest conversion rates.

The governing equation of the settlement decision process is a settlement suitability index **(S_i)** that represents the likelihood a particular location **(i)** will be selected for settlement:

$$\mathbf{S_i = \sum^{n}_{j=1}(X_{ij}\, W^*_j)} \qquad \mathbf{(3)}$$

where:

X_{ij} is the socioeconomic and biophysical variables used to determine productivity.

W^*_j is the relative importance (weight) of the socioeconomic and biophysical variables used by the settlers.

The **S_i** values are ranked from largest to smallest on the landscape and those with the largest values are settled. Given that settlement tends to develop near land that is already developed, an adjacency algorithm was incorporated into the model (Figure 5). The number of locations settled in any time period (decade) are given by the actual number of homesteads settled during that time period.

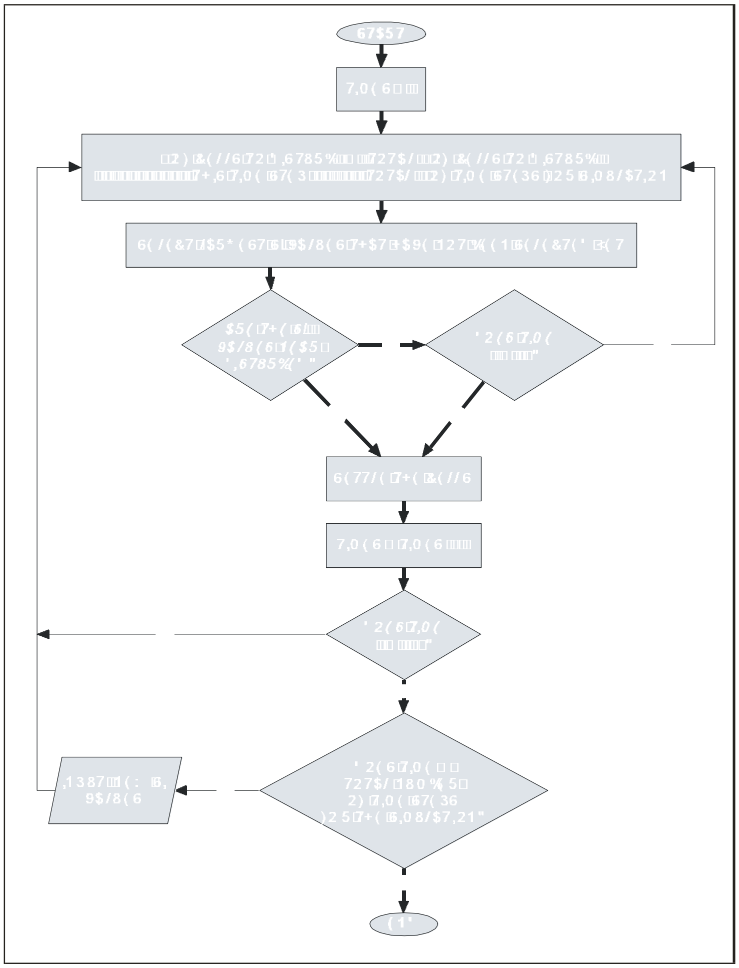


Figure 5. Flow chart of the fragmentation model (FRAGMENT) showing the incorporation of an adjacency algorithm.

Step 1: Determining X_{ij}

Variable categories were compared to empirical records of past settlement and converted to a percent settled variable value by determining the proportion of categories **(k)** within each variable **(j)** that were more likely to be settled:

$$\mathbf{X_{ij} = N^*_{kj} / N_{kj}} \qquad (4)$$

where:

$\mathbf{N^*_{kj}}$ is the number of pixels of a particular category **(k)** that have been settled for each socioeconomic or biophysical variable **(j)**.

$\mathbf{N_{kj}}$ is the total number of pixels of a particular category **(k)** for each socioeconomic or biophysical variable **(j)**.

Step 2: Determining W^*_j

Recognizing that certain socioeconomic or biophysical variables are more important to settlement than others, relative importance of the socioeconomic and biophysical variables **(W^*_j)** was determined by:

$$\mathbf{W^*_j = W_j / \sum^{n}_{j=1} W_j} \qquad (5)$$

where:

$\mathbf{W_j}$ is the importance of **(X_{ij})** on the <u>first</u> principal component which is defined as:

$$\mathbf{W_j = \mu_j(\lambda / S_{jj})^{1/2}} \qquad (6)$$

where:

μ_j is the eigenvector of percent settled variable for the <u>first</u> principal component.

λ is the eigenvalue of the <u>first</u> principal component.

$\mathbf{S_{jj}}$ is the covariance matrix score for the percent settled variable **(X_{ij})**.

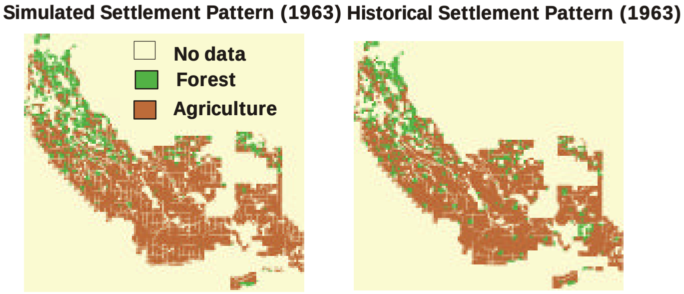
The relative importance of each variable **(W_j)** was determined for each run of the model at decade intervals (Table 1). The first principal component accounted for 46-59% of the variation and the majority of analysis had large positive loadings for stoniness, soil formation, soil texture and slope. Therefore, physical features influence the settlement suitability of a particular location.

Simulations of settlement were carried out for all decades using the settlement suitability index **(S_i)** and the adjacency algorithm. In general, the simulations showed settlement moving from south to north (as a result of the adjacency algorithm) on land with fine-textured soil and few stones.

Simulations were compared to empirical maps of settlement which were not used to calculate the model (*e.g.* Figure 6). The percent of total cells classified correctly for each run of the model at varying time intervals ranged from 44-93%. Therefore, the model performed well in predicting settlement, confirming that the model correctly identified the variables driving the settlement process and that the assumption of adjacency was valid.

Table 1. The proportion of the variation explained by the first principal component and the adjusted loadings of the variables calculated from an initial empirical settlement map of the entire study area (where the definition of settled varies according to what proportion of the cell is deforested). All loadings were adjusted to relative importance values (weights) to reflect the correlation between each variable and the principal component (see equation 6). The largest weights for each simulation are in bold.

Year of settlement map	% deforested defined as settled	(Percent of variance) PC 1	Adjusted loading (weight) of Soil Form (W_j)	Adjusted loading (weight) of Rail (W_j)	Adjusted loading (weight) of Road (W_j)	Adjusted loading (weight) of Slope (W_j)	Adjusted loading (weight) of Stone (W_j)	Adjusted loading (weight) of Texture (W_j)
1910	> 0%	59.3	**87.2**	29.7	12.3	22.0	**93.9**	**68.4**
1920	> 0%	56.1	**89.6**	22.3	13.8	18.7	**93.3**	**65.8**
1920	> 25%	57.7	**89.2**	27.4	13.6	22.5	**93.9**	**66.0**
1930	> 25%	51.1	**88.3**	28.6	14.3	19.6	**93.0**	**64.2**
1940	> 25%	46.2	**71.2**	9.1	16.5	**87.4**	37.2	29.8
1930	> 50%	57.2	**89.4**	24.7	13.8	21.8	**93.8**	**65.4**
1940	> 50%	46.9	**86.8**	29.3	15.4	23.8	**92.6**	**59.4**
1940	> 75%	56.8	**89.4**	22.5	13.9	20.9	**93.7**	**64.5**
1950	> 75%	45.6	**87.9**	24.4	16.2	27.6	**91.6**	**57.1**
1950	100%	55.6	**89.4**	23.4	13.9	20.2	**93.4**	**65.2**
1960	100%	47.1	**88.9**	8.3	18.1	**50.4**	**78.7**	**50.2**



Difference between Historical and Simulated Maps

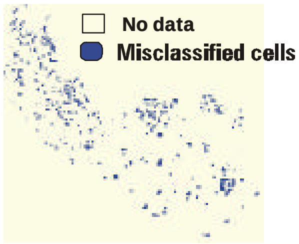


Figure 6. An example of the land use change maps in the mixedwood boreal forest south of Prince Albert National Park, Saskatchewan where1963 map of <u>simulated</u> land use change,1963 map of <u>empirical</u> land use change (not used in the calculation of the model) and locations of the misclassified cells (*i.e.* difference between the simulated and empirical maps from above).

CONCLUSIONS

The tolerance of the crops to the wetness values of this area meant that the productivity of the landscape did not influence the decision rules of the settlers. Instead, the highly mechanized form of agriculture practiced in this region meant that physical characteristics such as stoniness, soil formation and slope were more influential than the productivity of the land in determining the location of settlement.

The topographical index (WETNESS), which incorporates hillslope position, can be used to predict the distribution of vegetation on the landscape since vegetation is related to hillslope position and surficial materials (Figure 7). Given that we know how the settlers are choosing the wetness values, we can predict how the native vegetation will be removed from the landscape. In our study area, therefore, we would expect that the native vegetation was eliminated by the settlement process in proportion to the occurrence of wetness values on the landscape (*i.e.* no specific type of vegetation was selected preferentially over other vegetation types).

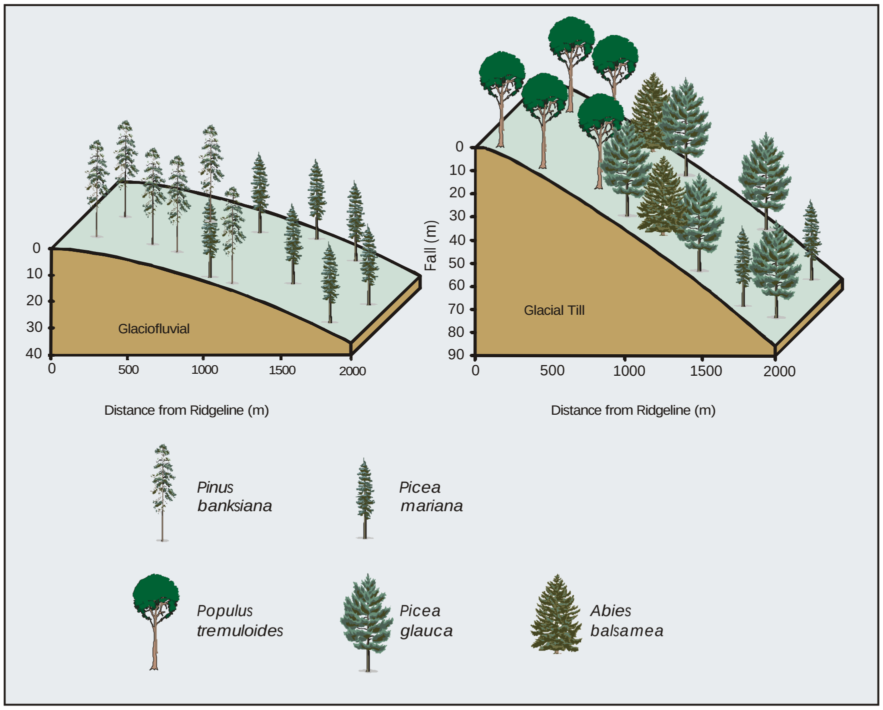


Figure 7. General landscape patterns of vegetation composition where the shapes of the hillslopes depict the actual profile of most hillslopes in the southern mixedwood boreal forest. The tree symbols depict the general change in dominant canopy species down the hillslope, and are based on the relationship between stand positions on the abstract moisture and nutrient gradients and on the distances of the stand from the ridgeline (cf. Bridge and Johnson 2000).

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Duff consumption in *Pinus banksiana* and *Picea mariana* stands in the mixedwood boreal forest

SFM Network Project:

Understanding how fire behavior characteristics shape
tree population dynamics, diversity and forest patterns

by

K. Miyanishi
Department of Geography
University of Guelph
Guelph, Ontario, N1G 2W1

E.A. Johnson
Department of Biological Sciences and Kananaskis Field Stations
University of Calgary
Calgary, Alberta, T2N 1N4

August 2000

EXECUTIVE SUMMARY

Canopy trees in the boreal forest are recruited primarily within the first few years after a crown fire and recruitment is largely restricted to patches from which the organic F and H layers (duff) have been removed by fire. Thus, duff consumption is a key factor in the population dynamics of these species and in post-fire forest regeneration.

Duff consumption is very patchy and the size of the burned patches (and thus the area of seedbed) is determined by factors controlling propagation of smoldering combustion. We used published models of smoldering combustion to identify the variables (bulk density, moisture content and depth) and their interactions which control duff consumption. We predicted a positive relationship between the fuel moisture contents and minimum fuel depths required for sustained smoldering; this relationship was empirically tested and supported by a lab study that used peat as an analog of duff.

We also used data collected from two wildfire burns and comparable unburned areas of mixedwood forest in central Saskatchewan to investigate both patterns of duff consumption and of unburned duff density and depth within stands and between stand types. Top slope stands on glaciofluvial hillslopes are dominated by *Pinus banksiana* and *Picea mariana* while the mid to bottom slopes have almost pure *Picea mariana* stands.

In unburned stands, duff bulk density did not vary significantly along the hillslopes. However, duff depths were significantly greater in the lower slope *Picea* stands than in the upper slope *Pinus-Picea* stands. Duff moisture is also greater in the lower slope *Picea* stands. Since depth and moisture content of duff vary between slope positions, duff consumption should correspondingly vary.

Duff consumption was significantly greater in the *Picea* stands than in the *Pinus-Picea* stands in the burn that occurred during relatively moist duff conditions. However, in the burn that occurred during drier duff conditions, there was no difference in duff consumption between the two stand types. The moisture-depth relationship indicates that, in the moist duff burn, duff depth was a factor limiting smoldering propagation in the thin duff of the *Pinus-Picea* stands. Under the drier duff conditions of the latter burn, depth was not a limiting factor and smoldering was propagated in both stand types.

Patches of duff consumption in all stands in both burns were also found to be spatially correlated to fire-killed trees. Duff moisture levels in unburned stands were significantly lower directly beneath tree crowns than in gaps. A precipitation throughfall study showed that interception by tree crowns resulting in drier duff directly beneath trees could explain this within stand variation in duff consumption.

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INTRODUCTION

North American boreal forest trees recruit primarily in the first six years after wildfires (Black and Bliss 1980; Morneau and Payette 1989; St-Pierre et al. 1991). The initial post-fire cohort forms the canopy of the mature forest and is not subsequently replaced by later establishing trees due to the length of the fire cycle which is generally shorter than the lifespan of the tree species (Johnson 1992). Therefore, recruitment within the first few years after a fire is critical in post-fire forest regeneration. Recruitment of *Pinus banksiana*, *Picea mariana* and *Picea glauca* is inversely related to the amount of duff remaining after the fire (Jameson 1961; Chrosciewicz 1970, 1974, 1976; Zasada et al. 1983; Thomas and Wein 1984; Weber et al. 1987; Charron 1998). Duff is defined as the layer of organic matter on the forest floor between the litter and the mineral soil, consisting of an F-layer of partially decomposed litter that is still distinguishable as to its origins and an H-layer of well decomposed organic matter (Van Wagner 1972; Canada Soil Survey Committee 1978).

Past studies of duff consumption have taken a strictly empirical correlational approach (e.g., Little et al. 1986; Reinhardt et al. 1989; Brown et al. 1991). Such studies lack generalizability as they do not investigate the process by which duff is consumed and thus can only provide site- and situation-specific empirical relationships. Furthermore, they cannot explain the observed patchiness of duff consumption (Fig. 1) nor differences in the spatial patterns of consumption under different conditions. In this study, we used models of smoldering combustion to identify the controlling variables and to explain these patterns of duff consumption, both within stands and across the landscape.

Fig. 1. Post-fire forest floor showing patchiness of duff consumption.

Most duff consumption is due to post-fire smoldering combustion (Dyrness and Norum 1983; Frandsen 1991; Hungerford et al. 1995) and not to flaming combustion during passage of the flaming front. Studies of smoldering combustion (e.g., Moussa et al. 1976; Ohlemiller 1990) have led to the conclusion that the rate-limiting factor for smoldering of *dry* fuels is oxygen availability (i.e., the rate of diffusion of oxygen to the char oxidation zone). However, Peter

(1992) found that, for smoldering in fuel beds with varying moisture contents, fuel moisture, rather than oxygen availability, becomes the limiting factor since latent heat of vaporization constitutes a significant heat sink and thus decreases the heat available for smoldering propagation. Since heat transfer within the fuel bed between the exothermic oxidation zone and the endothermic pyrolysis zone is primarily by conduction (Moussa et al. 1976), thermal diffusivity of the fuel, which is a function of fuel density, plays an important role in propagation of smoldering. Finally, heat losses from the surface of very thin fuel beds can be significant enough to prevent smoldering propagation. Thus, Palmer (1957) and Peter (1992) found critical minimum depths of fuel beds that could propagate smoldering.

These studies of the smoldering combustion process indicate that three controlling variables of smoldering propagation in duff are **moisture content**, **density** and **depth**. Also, from the heat transfer models of smoldering, we hypothesize a positive relationship between fuel moisture content and the minimum depth required for smoldering propagation; i.e., the higher the fuel moisture level, the greater the minimum depth of fuel bed required for propagation of smoldering.

Potentially, all three of these variables (moisture content, density and depth) might be expected to vary due to both hillslope position and canopy coverage. Soil moisture varies along hillslopes (O'Loughlin 1981; Quinn et al. 1992; Bridge and Johnson 2000) and soil and duff moisture have been shown to be connected by capillary movement of water between the duff and mineral soil (Samran et al. 1995). In the mixedwood boreal forest of western Canada, Bridge and Johnson (2000) found a moisture-nutrient gradient on glaciofluvial substrate that ran from drier, less nutrient rich stands at the top slopes dominated by *Pinus banksiana* and *Picea mariana* to the wetter, more nutrient rich, almost pure stands of *Picea mariana* on mid to bottom slopes. Duff moisture would also be expected to exhibit within-stand variability due to interception by tree crowns of precipitation and radiation. Thus, we hypothesize that duff moisture would generally be drier a) in top slope *Pinus-Picea* stands than in mid to bottom slope *Picea* stands, and b) directly beneath tree crowns than between tree crowns.

Bulk density of duff and duff depth may also vary both between and within stands. Both properties are influenced by relative rates of litter input and decomposition which in turn are influenced by litter characteristics and stand density; e.g., duff depths in *Pinus* stands are generally less than that found in *Picea* stands in the eastern Canadian boreal forest (Van Wagner 1972, 1974). Duff depths may also vary within stands since needle litter from the trees would accumulate directly beneath tree crowns and to a lesser extent between tree crowns.

Therefore, if the three controlling variables of duff moisture, bulk density and depth vary both along hillslopes and within stands, we should expect duff consumption to vary also at both scales.

The <u>first objective</u> of this study was to apply what is known about the process of smoldering combustion to predict some general patterns of duff consumption (e.g., the relationship between moisture content and depth). We conducted a laboratory experiment using commercial peat as an analog of duff to test the hypothesis that critical values of moisture content and depth required for smoldering propagation are positively related. Different depth-moisture combinations were tested to determine which combinations supported self-sustained smoldering.

The second objective was to investigate how duff moisture, bulk density and depth vary along hillslopes on well-drained glaciofluvial substrate in the mixedwood boreal forest of western Canada. We collected data from 8 unburned stands dominated by *Pinus banksiana* and *Picea mariana* located on hillslope tops and 8 unburned stands dominated by *Picea mariana* located at mid to bottom slope on glaciofluvial substrate. Within 10 x 10 m plots in each stand, 81 measures of duff depth were recorded at 1 m intervals. Samples of duff were also collected at each of the 81 points, dried and weighed to determine bulk density. We investigated within stand variation in duff moisture within two *Picea* stands using a ThetaProbe inserted into the duff at 0.5 m intervals for a total of 361 readings per stand. The position of each sample point was recorded as either beneath the canopy or in a gap.

The third objective was to apply these results to explain observed patterns of duff consumption in two areas burned by natural wildfires in this region, the first Bittern Creek fire started on June 5, 1996 and the second Waskesiu Lake fire started on July 7, 1998. Both were crown fires in which all trees were killed. Within each burn, 8 *Pinus-Picea* stands and 8 *Picea* stands on glaciofluvial substrate were sampled. All standing fire-killed stems and all burned patches of duff were mapped within a 10 x 10 m plot in each stand. Duff depths were also recorded at 1 m intervals with 81 measures per plot.

SUMMARY OF DATA ANALYSIS

The results of the laboratory experiment supported the hypothesized relationship between the critical values of fuel moisture and depth required for smoldering propagation (Fig. 2). The linear regression was highly significant ($p<0.0001$) with an R^2 of 0.74. The line in Fig.2 indicates the boundary between smoldering propagation and extinction. What this relationship means is that the higher the moisture content of the fuel, the greater the depth of fuel required for smoldering propagation. Thus, for example, at 18% moisture level, the graph indicates that smoldering will only be propagated in this fuel if the fuel depth is greater than 3 cm. Also notice the lower limit of smoldering at 10-12% volumetric moisture content at very thin fuel depths.

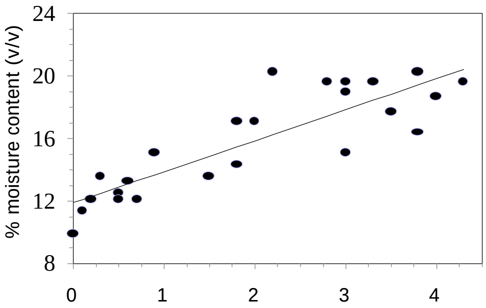

Fig. 2. Relationship between volumetric fuel moisture content and minimum depth of fuel bed required for propagation of smoldering combustion.

For objective 2, we then looked at the distributions of duff bulk density and depth in unburned *Pinus-Picea* and *Picea* stands (i.e. different hillslope positions). As indicated by Fig. 3, the distributions for duff density were similar. Mean density was 0.092 g cm^{-3} for *Pinus-Picea* stands and 0.094 g cm^{-3} for *Picea* stands. These means were not significantly different ($t = 0.66$, $p > 0.05$). Thus, duff density would not appear to be a significant factor in explaining any differences in duff consumption between these stand types.

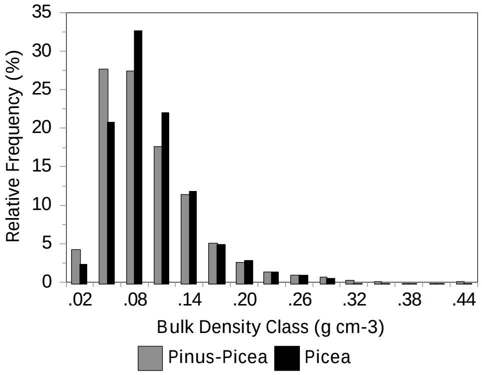

Fig. 3. Distributions of duff bulk density for unburned *Pinus-Picea* and *Pinus* stands.

However, as shown in Fig. 4, the distributions of duff depth were different; mean duff depths (±SE) of 6.9 ± 0.12 cm for *Pinus-Picea* stands and 10.3 ± 0.11 cm for *Picea* stands were significantly different ($t = 20.31$, $p < 0.0001$). Thus duff depth varies along hillslopes with top slope *Pinus-Picea* stands having thinner duff than mid to bottom slope *Picea* stands.

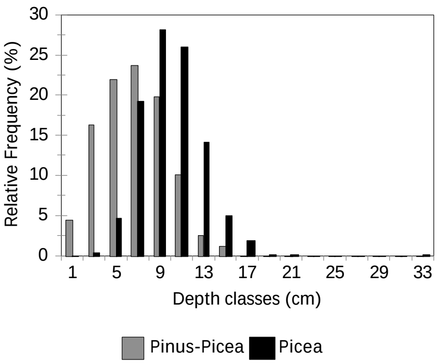

Fig. 4. Distributions of duff depth for unburned *Pinus-Picea* and *Picea* stands.

Although we were not able to determine duff moisture differences along hillslopes, Sang Vo (unpublished study) found in a hillslope water budget study that duff in *Pinus-Picea* stands would be drier than duff in *Picea* stands.

In our study of within stand variation in duff moisture, the two stands were measured on different days; thus, the overall mean volumetric moisture contents for the duff differed significantly between the two stands (12.8% vs 10.8%, $t = 7.54$, $p < 0.001$). Within both stands, mean moisture contents of duff beneath *Picea* tree crowns were significantly lower than in gaps. In one stand, the moisture contents were 12.4% beneath *Picea* and 13.5% in gaps ($t = 2.68$, $p < 0.01$), while in the other stand, the moisture contents were 10.4% beneath *Picea* and 11.2% in gaps ($t = 1.69$, $p < 0.05$).

To explain this within stand variation in duff moisture, we measured precipitation interception by individual *Pinus banksiana* and *Picea mariana*. We collected data for two to five storms per tree with a total of 10 tree-storms per species. Precipitation from each storm, as measured in the gauges in large openings, ranged from 0.8 mm to 24.1 mm. Throughfall, as percentage of precipitation, ranged from 0% to 70 % (mean 23%) beneath *Pinus banksiana* and from 0% to 41% (mean 16%) beneath *Picea mariana*. Thus, both species intercepted approximately 77-84% of the precipitation and there was no significant difference found between the two species in their percentage interception of precipitation ($t = 1.05$, $p > 0.05$). The proportion of precipitation intercepted was negatively correlated with the amount of precipitation ($r = -0.51$, $p < 0.05$). Thus, decreased precipitation throughfall directly beneath tree crowns would explain the observed drier duff beneath trees compared to the duff in gaps.

To indicate the patchiness of duff consumption, we compared the distributions of duff depths in unburned and burned stands. In unburned *Pinus-Picea* stands, the distribution of duff depths (Fig. 4) was normal (symmetric) with a Z_{g1} value of 1.64 ($p > 0.05$). Although the distribution of duff depths in the unburned *Picea* stands was found to be skewed ($Z_{g1} = 9.84$, $p < 0.001$), this skewness was largely a result of a couple of very deep depth measurements (Fig. 4). Removing just the two highest (of 621) depth values changed the Z_{g1} value to 1.17 ($p > 0.05$).

Therefore, both distributions of duff depth in the unburned stands are essentially normally distributed.

In the burned stands at both Bittern and Waskesiu, duff depth distributions were highly positively skewed (Fig. 5). The Z_{g1} values at Bittern were 11.81 ($p < 0.0001$) for *Pinus-Picea* and 14.15 ($p < 0.0001$) for *Picea* stands, while at Waskesiu they were 8.51 ($p < 0.0001$) for *Pinus-Picea* and 7.73 ($p < 0.0001$) for *Picea* stands. From these figures, it is obvious that even removal of the few extreme values would still result in highly skewed distributions. Consequently, assuming that the unburned stands are representative of the burned stands before the fire, duff depths before the fire would have been more or less normally distributed (Fig. 4). After both fires, duff depth was much reduced and skewed towards the lowest depth classes (Fig. 5). The high proportion of zero and near zero duff depths was due to complete, or nearly complete, duff consumption, creating the patches seen in Fig.1.

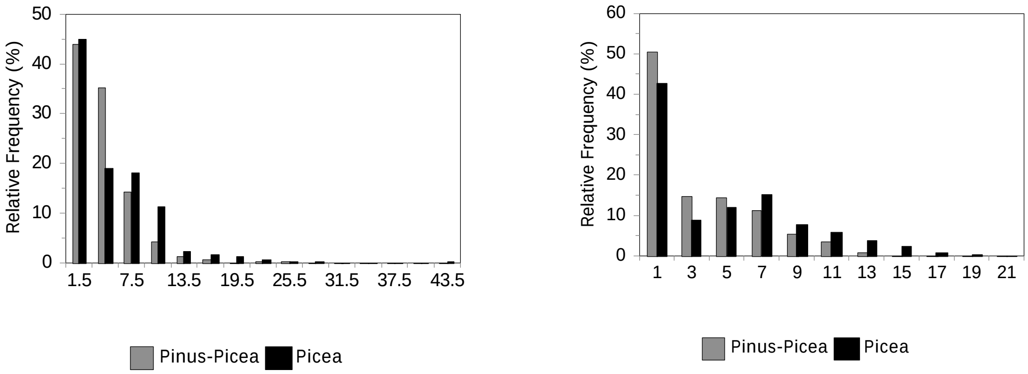

Fig. 5. Distribution of duff depths in *Pinus-Picea* and *Picea* stands in the Bittern Creek burn (left) and the Waskesiu Lake burn (right).

We also compared distributions of the sizes of the burned holes (patches) in the duff (Fig. 6). In the Bittern burn, which occurred during wetter duff conditions, most of the area of duff consumption was attributable to patches in the smallest size classes. The largest patch recorded was 15 m^2 in *Pinus-Picea* stands and 28 m^2 in *Picea* stands.

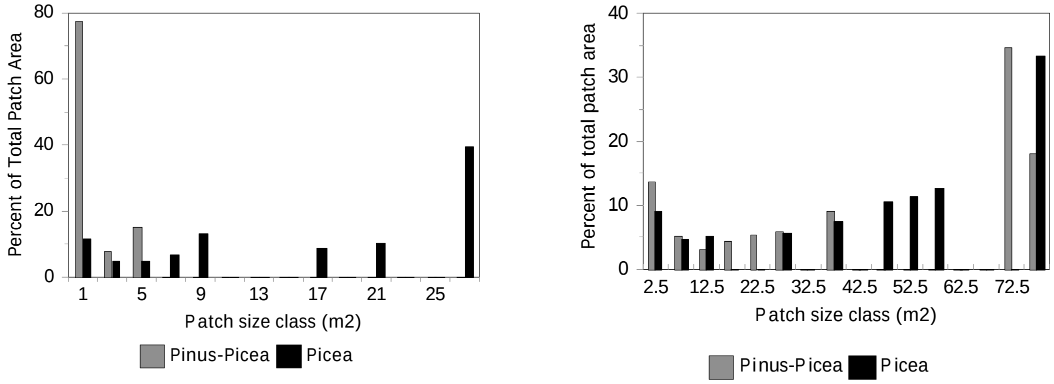

Fig. 6. Distribution of burned duff patches in *Pinus-Picea* and *Picea* stands in the Bittern Creek burn (left) and the Waskesiu Lake burn (right).

The Waskesiu burn, which occurred during drier duff conditions, had a wider range of patch sizes with a maximum of 77 m^2 in *Pinus-Picea* stands and 81 m^2 in *Picea* stands. Furthermore, 78% (*Pinus-Picea*) and 75% (*Picea*) of the total area of duff consumption in the Waskesiu burn were in patches greater in size than the largest patches in the Bittern burn (i.e., drier duff conditions result in larger burned patches). The patch size distributions differed more between stand types in the wetter duff burn (Bittern); all of the burned duff area in top slope *Pinus banksiana* stands were in patches smaller than 6 m^2 while the mid to bottom slope *Picea mariana* stands had only 22% of the total area of duff consumption in patches smaller than 6 m^2. On the other hand, in the drier duff burn (Waskesiu), the patch size distributions were more evenly distributed, irrespective of species and slope position.

The total area in burned patches in the duff was significantly greater in the Waskesiu burn than in the Bittern burn, regardless of stand type (Fig. 7). Furthermore, the area of burned duff differed significantly between *Pinus-Picea* and *Picea* stands in the Bittern burn but did not differ in the Waskesiu burn.

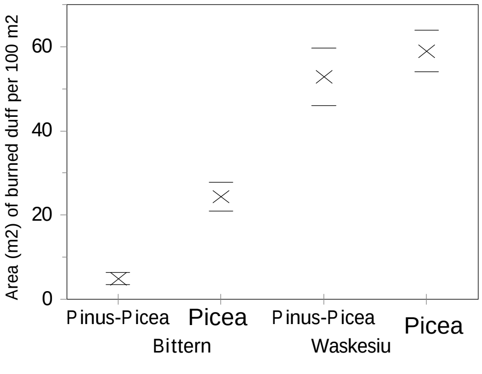

Fig. 7. Mean (± S.E.) area covered by burned patches in the duff within 100 m2 plots (n = 8) by stand type within the two burns at Bittern Creek and Waskesiu Lake.

The explanation for these patterns of duff consumption in the two stand types within the two burns lies in the relationship found between duff moisture and minimum duff depth required for smoldering propagation. As indicated by Fig. 8, the Duff Moisture Code (DMC) was considerably lower in 1996 when the Bittern Creek fire occurred (Julian dates 157-159) than in 1998 when the Waskesiu Lake fire occurred (Julian dates 188-191).

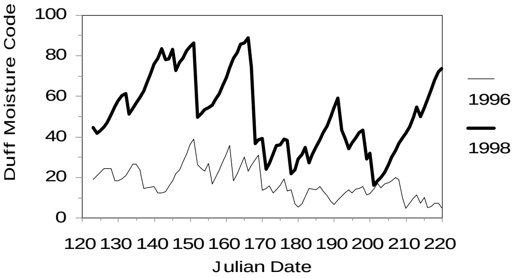

Fig. 8. Daily Duff Moisture Code values during the fire seasons of 1996 and 1998.

Under the low duff moisture conditions (high DMC) of the Waskesiu burn, not only was more duff consumed but also differences in duff depth between the *Pinus-Picea* and *Picea* stands did not play a role. Smoldering was propagated in both stand types. Therefore, there were no differences between stand types in the burned patch sizes (Fig. 6) or in the total area covered by the burned patches (Fig. 7). However, under the higher moisture conditions (low DMC) of the Bittern burn, duff depth was a factor in limiting smoldering propagation. Thus, the burned patches were smaller in the thinner duff of *Pinus-Picea* stands than the thicker duff of *Picea* stands (Fig. 6) and the total area of duff consumption was significantly less (Fig. 7).

Finally, we looked at the spatial distribution of burned patches within stands by looking for spatial relationships between the locations of the burned patches and the locations of standing stems of fire-killed trees. We obtained χ^2 values in the Bittern burn ranging from 50.12 to 381.27 in *Pinus-Picea* plots and from 0.40 to 52.94 in *Picea* plots. All were significant at the 0.01 level except two *Picea* plots. In the Waskesiu burn, the χ^2 values ranged from 5.70 to 37.78 in *Pinus-Picea* plots and from 7.10 to 75.54 in *Picea* plots. All were significant at the $p < 0.01$ level except for two of the *Pinus-Picea* plots which were significant at the $p < 0.05$ level. Thus, 30 of the 32 plots showed a significant spatial relationship between the burned patches and fire-killed trees. In other words, more tree stems were either within patches or touching patches than would be expected if the stems and patches were independently distributed. Thus, as had been anecdotally reported in past studies, the duff burns out preferentially around the bases of trees. This is not surprising since we showed earlier that duff directly beneath tree crowns is drier due to the interception of precipitation by the canopy.

MANAGEMENT APPLICATIONS

As discussed in the Introduction, removal of duff from the forest floor is critical for establishment of most boreal forest tree species. Thus, an understanding of the process of smoldering combustion can lead to an ability to predict duff consumption in wildfires and the resulting availability of seedbed for post-fire regeneration. In turn, this can provide guidelines for when site preparation would be required to increase seedling recruitment if little duff consumption is expected to occur (e.g. as happened in the *Pinus-Picea* stands in the Bittern burn where relatively little area of seedbed was exposed).

CONCLUSIONS

This study showed that spatial patterns of duff consumption both within stands and between stands along hillslopes could be explained by variation in duff depth and moisture. Although this study did not find significant differences in duff bulk density along glaciofluvial hillslopes, density is a controlling factor in smoldering propagation as indicated by heat transfer models of smoldering combustion and therefore would have to be considered in a more general model of duff consumption. The relationship between duff depth and moisture we found was for a constant fuel density. We would expect a family of such curves for varying fuel densities.

This study also provided an explanation for the unexpected results of significantly less duff consumption in the stands dominated by *Pinus banksiana* and *Picea mariana* at the tops of glaciofluvial hillslopes despite the significantly shallower duff compared with the mid to bottom-slope stands dominated by *Picea mariana*. Without an understanding of the factors controlling propagation of smoldering combustion and of the relationship between fuel moisture and depth, these results would have been inexplicable.

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The Local Population Dynamics of Trees in the Mixedwood Boreal Forest

SFM Network Project:
Understanding how fire behaviour characteristics shape
tree population dynamics, diversity and forest patterns

by

S.L. Gutsell and E.A. Johnson

Dept. Biological Sciences and Kananaskis Field Stations,
University of Calgary, Calgary, Alberta

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EXECUTIVE SUMMARY

The proposal that forest management practices should simulate disturbance and ecological processes requires that we first understand how the disturbance and ecological processes create the forest ecosystem patterns. With a clear understanding of the processes underlying the time-since-fire mosaic and the distribution of tree species, in this study we have gained an understanding of how the local scale population dynamics, i.e. the recruitment and mortality of individuals, between fires, affects the abundance of individuals through time.

Evidence from 42 stand reconstructions challenge our beliefs regarding patterns of species replacement through time, i.e. forest succession. We show that the invalid assumptions underlying methods used to study patterns of forest succession, namely a spatial array of stands, size class ordinations, static diameter distributions and static age distributions, have led to questionable conclusions. Since the conclusions reached by these studies have guided forest management practices, our results have important implications for forest management.

Much of forest management is based on when individuals recruit into a population and on the future vegetation composition expected on a particular site. Our results have shown that successful recruitment of all canopy trees occurs within the first few years after wildfire. Consequently, the future composition of the forest is determined within the first few years after stand initiation, whether by wildfire or logging practises. In mixed stands there may be a conspicuous change in canopy composition, but this is simply a result of differences in height growth rates between species. Our results also show that gap phase replacement does not play an important role in the boreal forest, particularly because of the slow growth rates of understorey trees, their high mortality rates, and the relatively short fire cycle.

INTRODUCTION

It has been proposed that sustainable forest management practices should simulate disturbance and ecological processes in order to maintain forest ecosystem structure, function and biodiversity. To achieve this goal we must first understand how the disturbance and ecological processes generate the forest ecosystem patterns. Our other studies have shown how forest fires produce the mosaic pattern of time-since-fire on the landscape (see Weir et al. 2000), and how surficial geology and geomorphic processes create the moisture and nutrient gradients which control the distribution of plant species on the landscape (see Bridge and Johnson 2000). With a clear understanding of the processes underlying the time-since-fire mosaic and the distribution of tree species, in this study we have sought to understand how the local scale population dynamics, i.e. the recruitment and mortality of individuals, and their growth rates affect the abundance of individuals through time.

Clearly the best way to study the changing abundance patterns of individuals is to follow a population from the time of stand initiation (i.e., after a disturbance) until the next stand replacing wildfire. In long-lived plants such as trees, however, the tracking of individuals requires a much longer time period than is practical. To get around this difficulty ecologists have developed a variety of methods to infer patterns of succession. Although most studies acknowledge that the assumptions of these methods limit their ability to make inferences about succession (i.e., the patterns of recruitment and mortality of individuals), they often then proceed to make such inferences.

One of the oldest methods uses a series of spatially separate sites that have been initiated at different times in the past (e.g., Huff 1995; Frenot et al. 1998). It is assumed that the changes in species composition observed over sites of increasing age are the same changes one would see at each site if it was followed through it's lifetime. For this to be true, all sites must follow the same history in terms of the recruitment and mortality of individuals. This means that all individuals within each site have recruited and grown up under the same environmental conditions, regardless of their time of recruitment. Changes in species abundance patterns are usually estimated using one or more measures of abundance, i.e., basal area, stem density.

Another method has been to record individuals by their size. By measuring the diameter at breast height or at the base of each live individual within a stand, and then dividing individuals into size classes, patterns of succession are inferred based on the individuals which dominate each size class. Diameter data are commonly presented in one of two ways: as a static diameter distribution (e.g., Stewart 1986; Platt et al. 1988; Kuuluvainen et al. 1998), or as a size class ordination (e.g., McCune and Allen 1985, Bergeron and Dubuc 1989). A static diameter distribution is simply a frequency histogram of live individuals in diameter classes representing a single stand at one point in time. A size class ordination uses a series of stands, each of which is divided into size-classes based on diameter. All stands in the series are ordinated according to the relative abundances of species within each diameter class. On the ordination diagram, points representing diameter classes from the same stand are linked with vectors, from the largest diameter class to the smallest diameter class. In both static diameter distributions and size-class ordinations, the assumption within a stand is the same: there is a positive correlation between diameter and age, with larger diameters representing older ages. Larger individuals represent the early stages of succession and the smaller individuals represent a future successional stage.

Another method has been to record individuals by their age. By coring all live individuals within a stand (at breast height or at the base), and then dividing individuals into age classes, patterns of succession are inferred based on the individuals which dominate each age class. Such age data are most commonly presented as a static age distribution (e.g. Whipple and Dix 1979; Veblen 1986; Engelmark et al. 1998), which is simply a frequency histogram of live individuals in age classes from a single stand at one point in time. It is assumed that age, determined by coring an individual at the base (typically 30 cm above ground level), accurately represents an individual's time of recruitment. And, it is assumed that within a stand the older individuals represent the early stages of succession, while the younger individuals represent a future successional stage.

A fourth method, called stand reconstruction, tracks changes in species abundance patterns in each of series of stands by reconstructing the age distribution back in time (Johnson and Fryer 1989; Johnson et al. 1994). It requires the ability to detect and date trees that have died in the past. Patterns of recruitment and mortality are determined by aging at the root collar all live and dead individuals (standing, fallen and buried), and using dendrochronology to determine the date of recruitment and mortality of the dead individuals.

The **purpose** of this study was to test the assumptions of each of the different methods used to study forest succession: a spatial array of stands, static diameter distributions, size class ordinations, static age distributions and stand reconstructions. With the same set of data we tested the validity of the assumptions within each method and examined the implications for interpretations of succession. Using old growth stands we also examined whether gap dynamics plays an important role in the changes in species abundance over time.

SUMMARY OF DATA ANALYSIS

Using the stand reconstruction method (Johnson and Fryer 1989) we have reconstructed the recruitment and mortality of individuals within 42 upland stands in the southern mixedwood boreal forest of Saskatchewan. The stands selected for study were chosen based on the distributions of the five dominant upland tree species along the moisture and nutrient gradients (see Bridge and Johnson 2000), and the time-since-fire map by Weir et al. (2000). Twenty-five stands were sampled on glaciofluvial hillslopes, and seventeen stands on glacial till hillslopes. For each hillslope position (top, mid, and bottom), stands were chosen to represent a range in time-since-fire of 1 to 160 years.

Within each stand all live and dead (standing and downed) trees, saplings and seedlings were mapped and their height and diameter at base determined. Disks were taken at 1-metre intervals from the base to the top of each tree for stem analysis. All sapling and tree stumps were excavated to locate the root collar and determine the date of recruitment. Finally, the forest floor was excavated to locate and sample all dead buried boles. In total, the field sampling took 4 field workers twelve months. There were between 60 and 1050 individuals sampled within each stand, including the stem disks and stumps for every individual.

In the laboratory all stem discs were sanded and rings counted (up to 450 grain). All stumps were cross-sectioned and each cross section was sanded (up to 600 grain). A skeleton plot was constructed for each stump cross section. A master skeleton plot was constructed for each species in each stand to determine the date of recruitment and death of each dead tree and to locate any locally missing rings on both live and dead trees. In total, the laboratory analysis took two technicians 4 years.

Stands were chosen to construct a spatial array of stands based on time since fire (2-154 years), geomorphic substrate (glacial till and glaciofluvial), and hillslope position (top, mid, and bottom). Stands were divided by geomorphic substrate and hillslope position based on the results of the gradient analysis study (see Bridge and Johnson 2000 for details). On glacial till hillslopes, top-slope stands made up one spatial array, and mid-slope stands made up a second spatial array. On glaciofluvial hillslopes, mid-slope stands made up a third spatial array, and bottom-slope stands made up a fourth spatial array. For each geomorphic substrate and hillslope position basal area and density was calculated for species in each stand. A regression line was drawn for each species across all stands and patterns of succession were based on the species changes in dominance across increasing stand age. The younger stands in each spatial array were assumed to represent early stages of succession, while older stands were assumed to represent later stages of succession.

For brevity we will only show the spatial array for stands on mid-slope positions. From the spatial arrays of stands the patterns of succession can be interpreted as follows. On glaciofluvial mid-slopes jack pine dominates early in succession, it co-dominates with black spruce in mid-succession, and in late succession jack pine, black spruce and white spruce co-dominate (Figure 1a). On glacial till mid-slopes, white spruce and trembling aspen dominate from early to mid succession, while white spruce and balsam fir dominate in late succession (Figure 1b). We will examine the assumption of spatial arrays in the section on static age distributions.

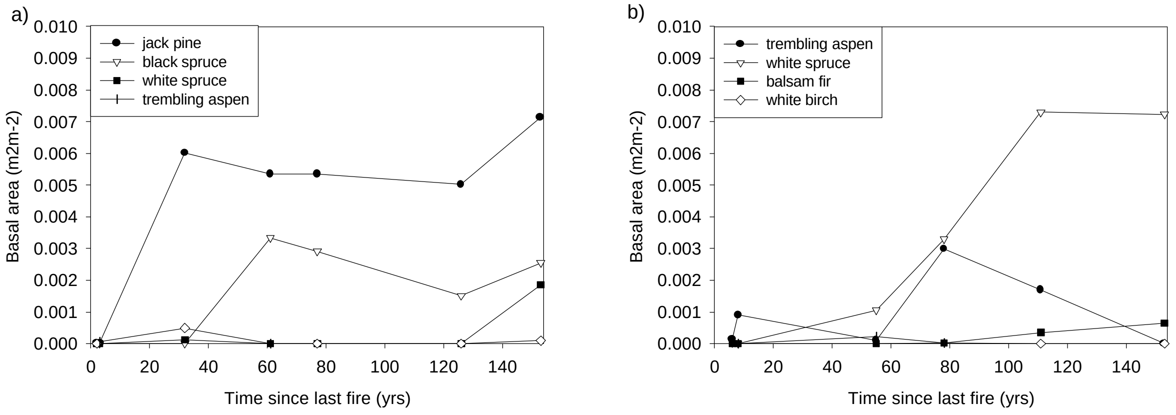

Figure 1: Basal area by species for two spatial arrays midslope on: a) glaciofluvial and b) glacial till.

A static diameter distribution was constructed within each of our stands by dividing all live individuals into 5 cm diameter classes, using diameter at one metre. Patterns of succession were interpreted based on the individuals which dominate each size class, with large and small diameter classes representing the past and future successional stages, respectively. Next, a size association analysis was performed on all stands. Variation in tree species composition was analysed using ordination and classification techniques. Untransformed frequency values (number of occurrences within each stand) were ordinated. Species that occurred in fewer than 10% of stands were excluded. Sites belonging to the abiotic subset (glacial till and glaciofluvial substrates) were re-ordinated using size-class ordination. Within each stand individuals were divided into 5 cm diameter classes. Species frequencies were then considered for each of these size classes, increasing the number of stands five-fold. On the ordination diagram, points representing diameter classes of the same stand were linked in decreasing order of diameter classes. Patterns of succession were interpreted based on the individuals which dominate each size class, with large and small diameter classes representing the past and future successional stages, respectively. The static diameter distributions and size class ordinations make at least one key assumption: there is a good correlation between diameter and age, i.e. larger diameter individuals are older than smaller diameter individuals.

For brevity, we will show the static diameter distribution for only two of our oldest mixed-species stands, one dominated by jack pine and black spruce, and the other dominated by white spruce and balsam fir. Patterns seen in both stands are the same as the patterns seen in our other stands that are similar in species composition. Also, we will not show the size class ordination since the assumptions and interpretations of succession are the same as in the diameter distribution. From the diameter distributions and size class ordinations the patterns of succession can be interpreted as follows. In jack pine-black spruce mixed stands, jack pine dominates early in succession, followed by black spruce, which dominates from mid to late succession (Figure 2a). In white spruce-balsam fir dominated stands, white spruce dominates early in succession followed by balsam fir, which dominates in late succession (Figure 2b).

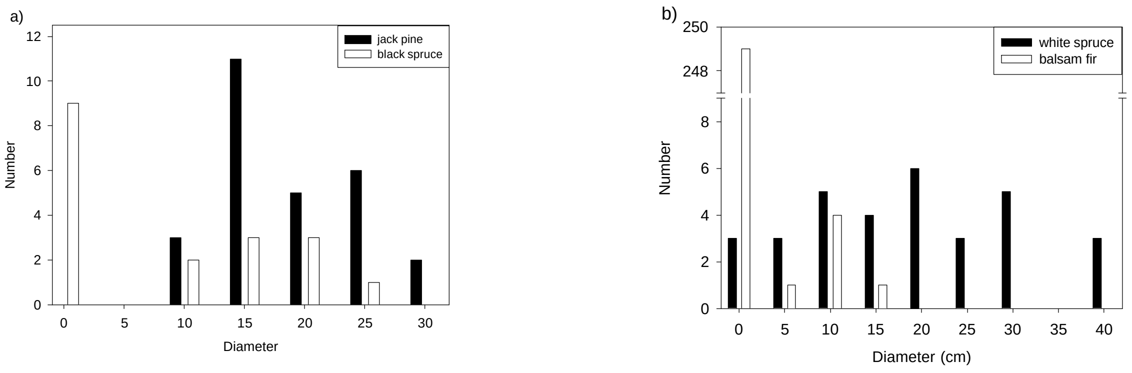

Figure 2: Static diameter distributions for a 126 year old jack pine-black spruce stand and a 154 year old white spruce-balsam fir stand.

We tested the assumption of the static diameter distribution and size class ordinations by examining the relationship between diameter and age for each species in each stand. The diameter-age relationship of individuals in the 126 year old jack pine-black spruce stand shows that the diameter of jack pine individuals ranges from 14-34 cm, however, all are very close in age, 121-125 years (Figure 3a). Similarly, the diameter of the oldest group of black spruce individuals ranges from 12-26 cm, however, they are also very close in age, 122-125 years. In addition, notice that the diameter of the youngest group of black spruce individuals are all less than 1 cm, however, they range in age from 4-30 years. Figure 3b shows that the diameter-age relationship of individuals in the 154 year old white spruce-balsam fir stand. The diameter of the larger white spruce individuals ranges from 8-43 cm, however all are close in age, 140-154 years. Also, notice that the diameters of the smallest group of white spruce individuals are all less than 0.5 cm, and they range in age from 2-22 years. The diameter of the larger balsam fir ranges from 10-17 cm, however they are close in age, 135-153 years, while the smaller balsam fir ranges from 0.1-5 cm and range in age from 1-88 years. Our results show that for all species diameter and age are very poorly correlated. In all mixed-species stands there appears to be one group of individuals (of both species) with a wide range of diameter who are older and all roughly the same age, and a second group with a narrower range of diameter who are much younger. We will address the question of whether the first group of individuals replaces the second group in the next section.

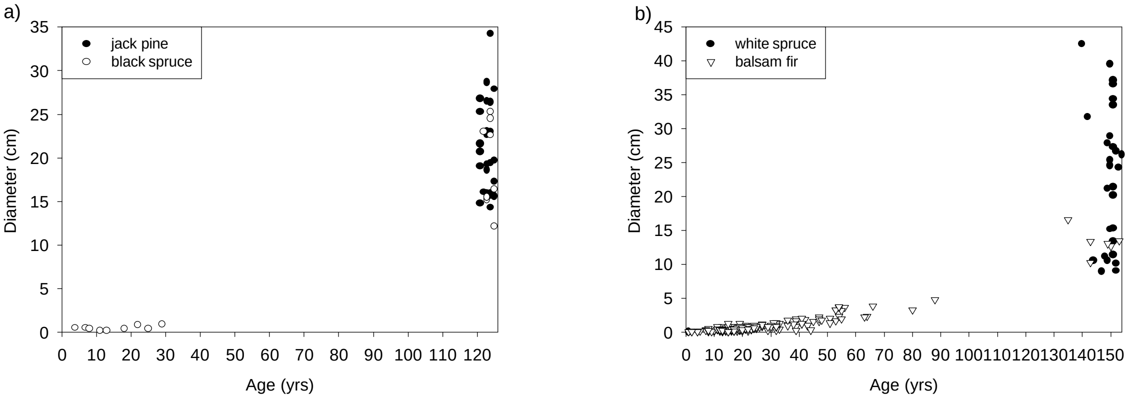

Figure 3: Diameter-age relationship for individuals within: a) 126 year old jack pine-black spruce stand, and b) 154 year old white spruce-balsam fir stand.

Within each of our stands we constructed a static age distribution using the age of all live individuals, where age was determined by counting rings at 30 cm above the root collar, the height at which trees are typically cored. Patterns of succession are based on the individuals that dominate each age class. The static age distribution method makes at least two assumptions: 1) the number of annual growth rings counted on each tree core or disk is an accurate estimate of tree age; and 2) within a stand the older individuals represent the early stages of succession, whereas the younger individuals represent a future successional stage.

For brevity, we will show the static age distribution for the same two stands shown above. Patterns seen in both stands are the same as the patterns seen in our other stands that are similar in species composition. The patterns of succession can be inferred from the static age distributions as follows. In jack pine-black spruce mixed stands jack pine recruits first after fire

(Figure 4a). After some time lag black spruce recruits and co-dominates with jack pine by mid-succession. In late succession a second group of black spruce individuals recruit and the stand becomes dominated by black spruce. In white spruce-balsam fir mixed stands white spruce recruits first after fire (Figure 4b). By mid-succession there is low and sporadic recruitment of balsam fir, and by late succession a second group of balsam fir individuals recruit and the stand becomes dominated by balsam fir.

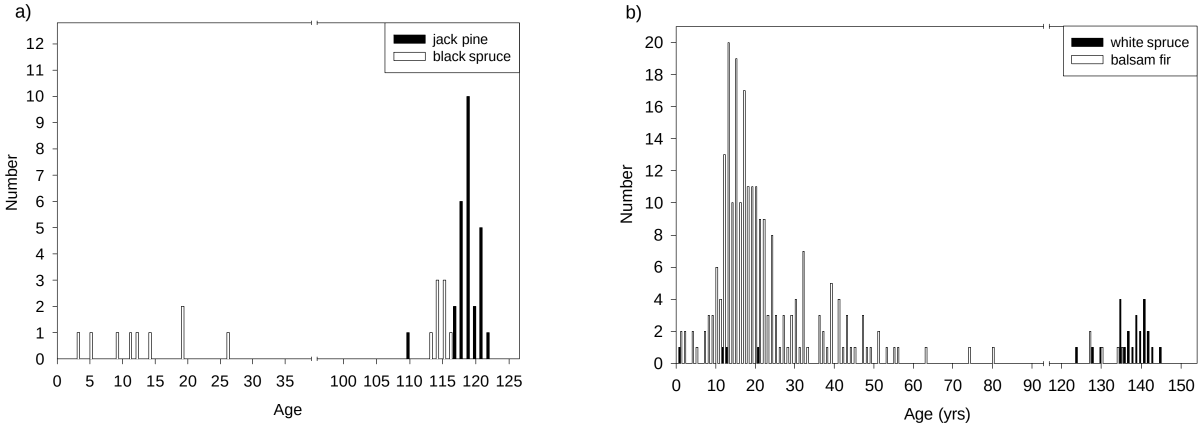

Figure 4: Static age distributions, where individuals are aged at 30 cm above the root collar: a) 126 yr old jack pine-black spruce stand, b) 154 yr old white spruce-balsam fir stand.

We tested the first assumption of the static age distribution by examining whether the number of annual growth rings counted 30 cm above the root collar matches the number of rings counted at the root collar. In all of our stands, we found that aging a tree by simply counting rings at 30 cm will almost always underestimate the true age of a tree for two reasons: 1) rings laid down below 30 cm are missed when counting at 30 cm; and 2) some trees have locally missing rings. Figure 5a compares, for our 126 year old jack pine-black spruce stand, the static age distribution of individuals aged at 30 cm and at the root collar. Notice that the pattern of recruitment in the individuals aged at 30 cm shows that there is a lag in recruitment of five years for jack pine and ten years for black spruce. However, the patterns of recruitment for the same individuals aged at the root collar shows that most individuals of both species recruit within the first 5 years after fire. This pattern of recruitment is consistent among all of our stands dominated by jack pine and black spruce. In our stands dominated by white spruce and balsam fir, most canopy individuals recruit within the first 10 years after fire (Figure 5b). With the exception of balsam fir, very little successful recruitment occurs after this period. Balsam fir appears to be the only species capable of a significant amount of recruitment after the first few years. These patterns are also consistent with studies of recruitment done in other areas of the boreal forest (e.g. Gagnon and Morin 1990; St-Pierre et al. 1992; DesRochers and Gagnon 1996).

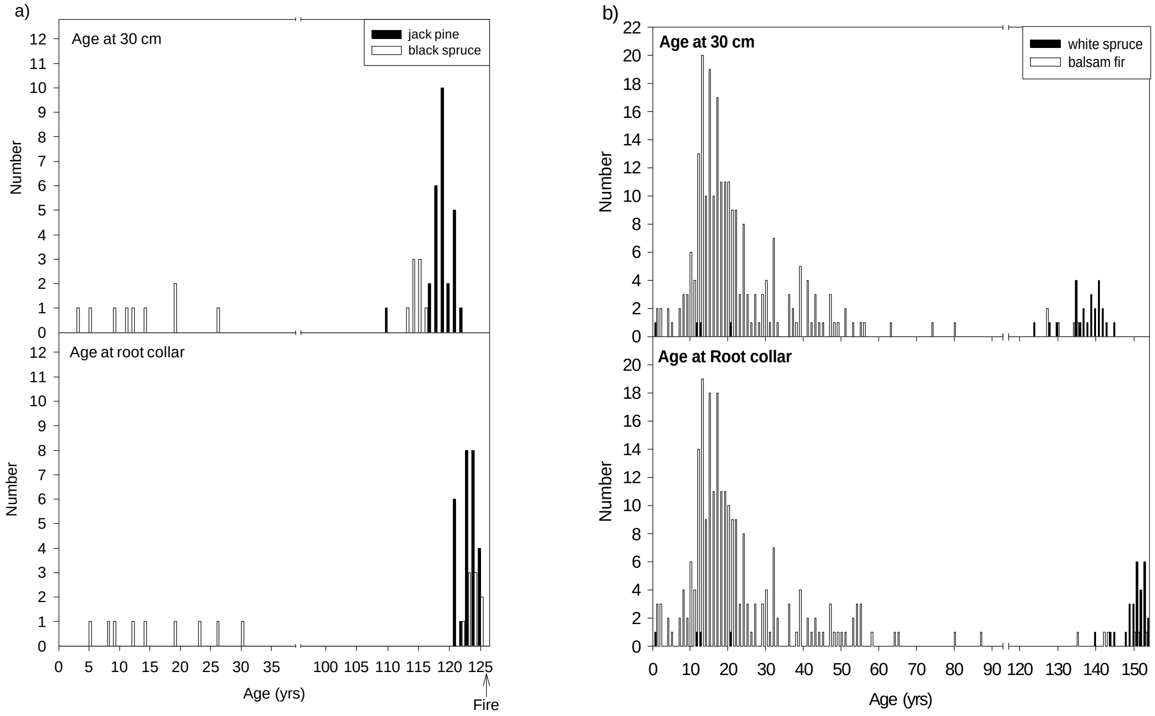

Figure 5: Static age distributions comparing individuals aged at 30cm (top) and at the root collar: a) 126 yr old jack pine-black spruce stand, and b) 154 yr old white spruce-balsam fir stand.

The inaccuracy of aging individuals at coring level has important implications when one is interpreting patterns of succession. Slow growing tree species will always appear to recruit much later after fire compared to fast growing species. In mixed species stands there is often a conspicuous change in canopy composition (for example, from a canopy dominated by jack pine to one with both jack pine and black spruce), however, these changes are simply due to differences in the height growth rates between species. Stem analysis data from our 126 year old jack pine-black spruce stand for example (Figure 6a), shows that while both species recruit within the first 5 years after fire, jack pine grows much faster in the first several years. Similarly, data from our 154 year old white spruce-balsam fir stand shows that while both species recruit within the first 10 years after fire, white spruce grows faster in the first several years (Figure 6b). Consequently, unless trees are aged at the root collar, and dendrochronology is used to account for locally missing rings, we must question the accuracy of the data and the conclusions of studies that are based on trees aged above the root collar.

We tested the second assumption of the static age distribution, that older individuals represent early stages of succession and younger individuals represent later stages of succession by examining the possibility that understorey individuals will eventually make it into the canopy. Note that this is the same as the assumption of the spatial array of stands, and the second assumption of diameter distributions and size class ordinations. To establish whether the understorey individuals might replace the canopy individuals, we looked at the height growth of individuals within each stand using our stem analysis data. In all stands it appears that the likelihood of understorey individuals making it into the canopy is very low for at least two reasons: because of the slow growth rates of understorey trees, and the relatively short fire cycle in our study area (see Weir et al. 2000). For example, data from our 126 year old jack pine-black spruce stand shows that the initial cohort of black spruce took about 80 years to enter the canopy of jack pine (Figure 6a). If we assume that the understorey individuals will grow at the same rate as the canopy individuals, then we estimate that the understorey will also take 80 years to enter the canopy. Given that the understorey individuals began to establish about 15 years ago, the chance of the stand surviving another 65 years, to 191 years, is about 1% (i.e., 1% of the study area is older than 191 years, see Weir et al. 2000). Similarly, data from our 154 year old white spruce-balsam fir stand shows that the few individuals from the initial cohort of balsam fir that made it into the canopy took about 120 years to enter the canopy of white spruce (Figure 6b). Given that the 2nd cohort of balsam fir began to establish about 50 years ago, the chance of the stand surviving another 70 years, to 225 years, is about 0.25% (i.e., 0.25% of the study area is older than 230 years, see Weir et al. 2000). Our results show that in both jack pine-black spruce stands and white spruce-balsam fir stands it appears very unlikely that the understorey individuals will ever replace the canopy cohort. In light of our results, we conclude that the conclusions of studies that use a static age distribution must be re-examined.

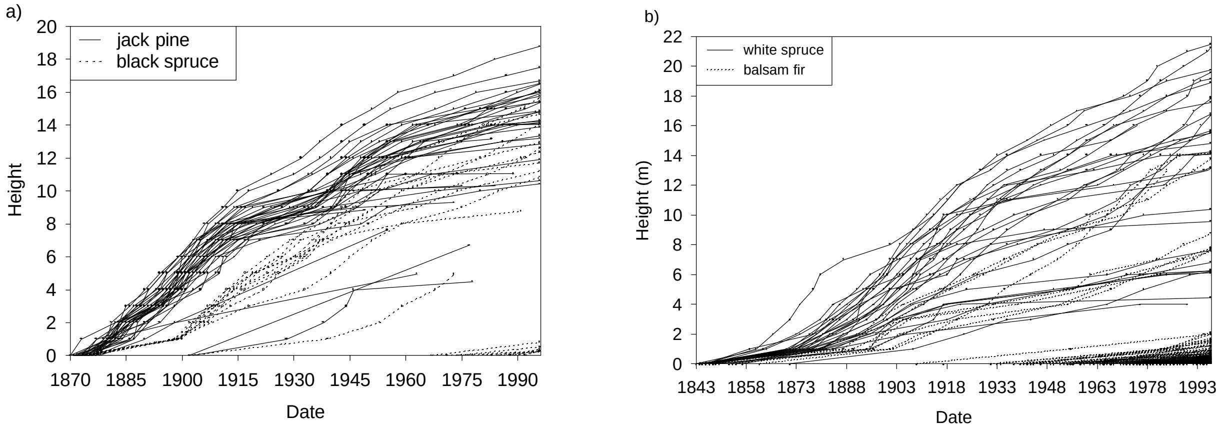

Figure 6: Height-growth curves for individuals in: a) 126 yr old jack pine-black spruce stand, and b) 154 yr old white spruce-balsam fir stand.

Recent studies have also indicated that gap-phase replacement, that is, the replacement of canopy individuals who die and leave a canopy gap, with advance regeneration or later recruiting individuals, may play an important role in the dynamics of these forests. The relatively short fire cycle within our study area however, indicates that given the relatively slow growth rates of understorey individuals, there is little chance that they will make it into the canopy to fill in the gap. If however, individuals within the understorey are capable of releasing, that is, increasing their growth rates once a gap forms, then gap replacement may be possible. We examined this possibility by determining whether the mortality of canopy individuals within old stands is followed by an increase in the height growth rate of understory individuals, thereby filling the gap. In all of our old stands we saw no evidence to suggest that the mortality of canopy individuals leads to understory individuals releasing such that they fill in the gap (e.g., Figure 6a & 6b). Consequently, it does not appear that gap phase replacement plays an important role in the forest dynamics within our study area.

We reconstructed the age distribution back in time of all stands greater than 30 years of age. Using dendrochronology we determined the dates of recruitment and death of each of the dead individuals (standing, downed and buried). The stand reconstruction method makes no assumptions regarding the replacement sequence of tree species. Instead it allows us to look back in time to see when individuals recruited and died. Stand reconstructions are limited in how far back in time individuals can be tracked, since individuals that die and decompose cannot be sampled. This reconstruction limit is roughly half the age of the stand (Johnson and Greene 1989). For brevity we will again only show data for two of our older stands. Figure 7a gives the reconstruction of the age distribution for our 126 year old jack pine-black spruce stand. Notice that the species composition of the stand does not change as we move back in time. Both jack pine and black spruce establish within the first few years after fire and there is little recruitment after this time. From this stand and other stands, both younger and older, it appears that the few understorey black spruce individuals have recruited relatively recently and survived up to the time we sampled the stand. These individuals appear able to survive at most 30 years. Thus it appears that individuals may be recruiting continuously, however they suffer very high rates of mortality. The same pattern exists in stands dominated by white spruce and balsam fir (Figure 7b). White spruce recruits within the first few years after fire and there is little successful recruitment after this period. Balsam fir also recruits within the first few years after fire, but thereafter it appears able to recruit in much higher numbers and/or it suffers relatively lower mortality compared to white spruce. The stand reconstructions show that individuals of all species appear to recruit within the first few years after fire and it is these individuals that form the canopy. Any individuals who recruit in the understorey appear to suffer very high rates of mortality, and never make it into the canopy.

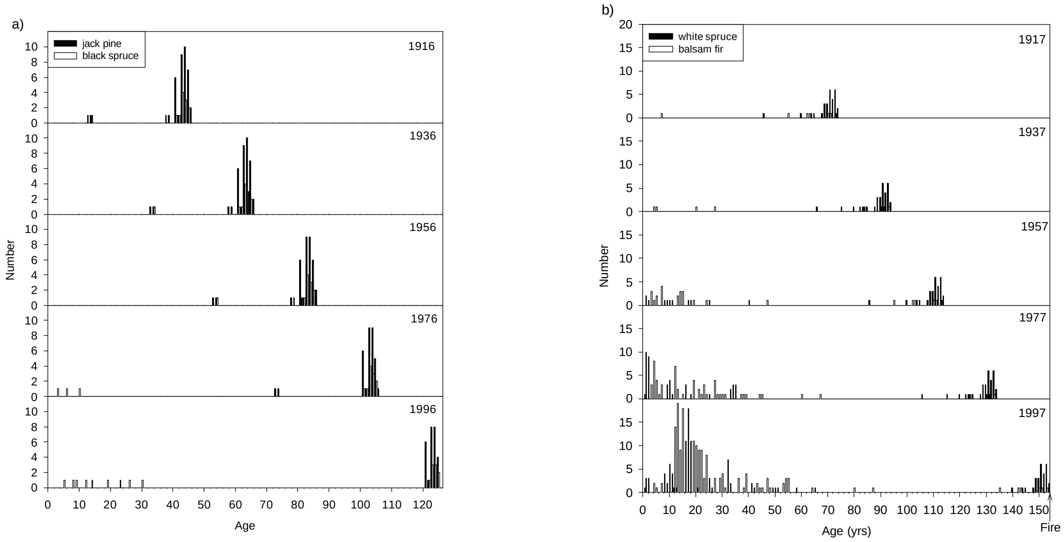

Figure 7: Stands reconstructions for: a) 126 yr old jack pine-black spruce stand, and b) 154 yr old white spruce-balsam fir stand.

MANAGEMENT APPLICATIONS

A clear understanding of the population dynamic processes of recruitment and mortality of individuals is critical to adopting appropriate forest management practises. Up to now, studies of forest dynamics have used a spatial array of stands, size class ordination, static diameter distribution or static age distribution, all of which are based on a number of untested assumptions. Whenever the assumptions of these methods have been rigorously tested they have been shown to be invalid (e.g., Fastie 1995, Jackson et al. 1985, Pickett 1989). Foresters seem to be unaware of these results. Our data also showed no evidence to support the assumptions of these methods, bringing into question conclusions reached by studies using any of the above methods.

Much of forest management is based on when individuals recruit into a population and on the future vegetation composition expected on a particular site. As our results have shown, the recruitment of individuals that successfully make it into the canopy occurs within the first few years after wildfire. Consequently, the future vegetation composition of the forest is determined within the first few years after disturbance. In mixed stands there may be a conspicuous change in canopy composition, but this is simply a result of differences in height growth rates between species. As we have shown in our other studies (Greene and Charron 1999), early recruitment is dependent on the availability of appropriate seedbeds (exposed mineral soil and thin humus) and seed sources (unburned residuals stands and burn edges) (Greene and Johnson 1994). With an understanding of how fire creates patterns of appropriate seedbeds (Miyanishi and Johnson in this report) and unburned residual stands (i.e. seed sources), we can now recommend the kind of site preparation required to mimic regeneration processes in forest management.

Forest management proposals considering a two pass harvesting system must demonstrate that individuals left behind in the first pass are young and vigorous enough such that they will release, i.e. increase their growth rates, after the first pass and form the next canopy. If, as our results show, individuals within a stand are the same age, despite a wide range in their diameters, it is likely that these smaller individuals (that are as old as the larger individuals) left behind in the first pass will not release, but will simply continue to grow slowly or die. If on the other hand individuals are young enough to release, what is the likelihood of those individuals making it into the canopy, given their growth rates and the fire cycle of the area? Our results show that slow growth rates and a relatively short fire cycle make this possibility unlikely, even with a management strategy that includes fire suppression.

CONCLUSIONS

The proposal that forest management practises should simulate disturbance and ecological processes requires that we have a clear understanding of how the disturbance and ecological processes create the forest ecosystem patterns. With a clear understanding of the processes underlying the time-since-fire mosaic and the distribution of tree species, in this study we have gained an understanding of how the local scale population dynamics, i.e. the recruitment and mortality of individuals, between fires, affects the abundance of individuals through time.

Data from 42 stand reconstructions have allowed us to critically examine the assumptions of the most common methods used to study forest succession. Our study demonstrates that the assumptions made using these methods are questionable and can lead to inaccurate conclusions regarding patterns of forest succession and gap dynamics. As we show, many of the strongly held beliefs about forest succession and gap dynamics are misconceptions stemming from studies that have made, but not validated, critical assumptions. Since the conclusions reached by such studies have been used, at least in part, as a basis for forest management practises, our results have important implications for forest management.

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Recruitment Curves of Trees into Burns

SFM Network Project:

Understanding how fire behavior characteristics shape tree population dynamics, diversity and forest patterns

by

D.F. Greene

Departments of Geography and Biology
Concordia University
Montreal, Quebec
Canada H3G 4M8

E.A. Johnson

Department of Biological Sciences, and
Kananaskis Field Stations
The University of Calgary
Calgary, Alberta
Canada T2N 0J2

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EXECUTIVE SUMMARY

We developed and tested a wind dispersal model of tree recruitment into burns from living sources at the fire edge or from unburned residual stands. The model was also tested on recruitment of serotinous *Pinus banksiana* within a burn. The model assumes that source strength is proportional to basal area density and that an individual (point source) recruitment curve can be expressed as a log-normal distribution. The model makes good predictions of the recruitment curves of *Picea engelmannii*, *Picea glauca* and *Abies balsamea* to distances as great as 2.0 km although it tended to underpredict *Abies* and overpredict *Picea*. At shorter distances, the model gave significant prediction of recruitment for *Pinus banksiana* within burns (seeds derived from aerial seed banks), and of *P. glauca* and *Larix laricina* up to 100 m from residual stands. By forestry standards, burns are poorly stocked by those species which must obligately recruit from edges. Nonetheless, the far tail of the recruitment curve insures no net loss in abundance in large burns at the landscape scale if (and only if) these obligate species do not experience serious thinning mortality during the first 70 years.

Keywords: fire, regeneration, seed dispersal, germination, seed production.

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INTRODUCTION

Wildfires are the leading cause of catastrophic canopy mortality in the mixedwood boreal forest of western Canada. Fires exceeding 5,000 ha, while few in number, account for the great majority of the area burned in the last 30 years (Johnson et al. 1998). This means that burns cover large areas in which few seed trees have survived. Consequently, species such as black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*) which have serotinous cones, or trembling aspen (*Populus tremuloides*) which sprouts from underground roots, can easily colonize large burns as long as they were present in the stand before the fire. Greene and Johnson (in press) have found that pre-burn basal area density (basal area per area) of these tree species is a good predictor of the number recruiting and surviving in the first years after the fire. This suggests that trees with serotinous cones and vegetative sprouts have an important advantage in colonizing large burns.

White spruce (*Picea glauca*), balsam fir (*Abies balsamea*) and larch (*Larix laricina*) have neither serotinous cones nor effective means of vegetative reproduction. Instead, their seeds must disperse into a burn from surviving trees. Consequently, their regeneration in large burns will be limited by the seed dispersal distances from the burn edge or unburned remnants in the burn. Thus, it is not clear how these three species persist through repeated fires. Any explanation for their persistence requires an understanding of: (1) the means of dispersal, source strength and density of the initially recruited cohorts immediately after the fire, (2) the rate of decrease in initial density due to mortality as the cohort ages, and (3) differences in the characteristic oldest age. In this paper, we will only model the dispersal, source strength and densities of individuals in the initially recruited cohorts.

We have two objectives in this paper. The first is to develop a micrometeorological seed dispersal model from burn edges and unburned remnants to determine the recruitment curve (stem density versus distance from source). The second step is to test the model against empirical recruitment curves using our own data as well as some previously published curves that extend for more than a kilometer from any source. In addition, we will test the model for jack pine recruitment from burnt trees within a fire. We have already validated the seed dispersal model (see Greene and Johnson 1989, 1994, 1995, 1996) and found it performed well at distances less than about 500 m. At larger distances, the model tended to underpredict seed density as the observed dispersal curve flattened more strongly than predicted.

Models

The point source (single tree) model will give recruitment (stems per m^2 per distance from tree) using two terms: source strength (the product of seed number and survivorship) and dispersal distance. The area source model will consist of the summation of the point source recruitment curves with the forest edge treated as the start of the dispersal distance (x=0).

Greene and Johnson (1996) modeled the dispersal of seeds from a forest into a clearing, taking into account the acceleration of the wind at the leeward edge of the forest. In the case of burnt forests with standing dead tree boles, there is no empirical studies upon which we can model the wind acceleration. Instead, we will follow Greene and Johnson (1995) and assume that for distances greater than about 100 m, the seeds involved will be the fraction of the crop which was moving primarily within or above the canopy (before it entered the burnt forest) and, consequently, there is no abrupt change in wind speed near the forest border. Further, we can greatly simplify the modelling effort by assuming the source forest has the same drag coefficient as the burnt forest. This assumption of a homogenous wind regime means that we will tend to overpredict seed deposition within approximately the first 20 m into the burn.

A further assumption of our model will be that the survivorship of seeds and post-germinant stems will be independent of distance into the burn. That is, the slope of the *dispersal* and *recruitment* curves will be identical.

The point source model

Following Greene and Johnson (1989), we assume a log-normal distribution of recruit density (F_{Dx}) as a function of distance (x) from an individual tree,

$$F_{Dx} = (F / (2\pi)^{1.5} \sigma_x x^2) \exp \left[(-0.5 / \sigma_x{}^2) (\ln (x / x_{0.5}))^2 \right] \qquad [1]$$

where F is the product of terms for seed production by a single tree and seed and seedling survivorship (see below), σ_x is the standard deviation of the logarithms of the distances traveled by seeds, x is distance from the point source, and $x_{0.5}$ is the median distance traveled by the seed crop.

As in Greene and Johnson (1996), we assume that at a meteorological reporting station at 10 m height there is a median and mean horizontal wind speed of 4.3 and 5.0 m/sec, respectively, with a standard deviation of the logarithms of the speeds of 0.55. The mean and median speed are multiplied by 1.83 to account for the dependence of seed abscission on wind speed. This distribution of horizontal wind speeds is made a function of vertical position in the forest using the protocol of Greene and Johnson (1996), assuming a drag coefficient of $\alpha=2$. This coefficient is typical of leafless forests and thus we are explicitly treating both the intact and burnt forests as leafless stands.

Averaging the median horizontal wind speed ($\bar{u}_{0.5}$) from the assumed abscission height ($z_a = 0.75\ z_h$ where z_h is forest height) to the ground, we obtain for a 30 m tall forest, $\bar{u}_{0.5} = 2.51$ m/sec. We define the median distance traveled ($x_{0.5}$) as

$$x_{0.5} = z_a\, \bar{u}_{0.5} / f \qquad [2]$$

where $\bar{f}$ is mean terminal velocity (m/sec). The terminal velocity is 0.66 (m/sec) for white spruce and 0.83 (m/sec) for balsam fir (both are study area estimates). The median distance traveled for white spruce is thus $x_{0.5} = 86$ m and for balsam fir is $x_{0.5} = 68$ m.

The standard deviation of the logarithms of the horizontal distances traveled (σ_x) is given as

$$\sigma_x = ((\sigma_w^2 / f^2) + \sigma_u^2)^{0.5} \qquad [3]$$

where σ_w is the standard deviation of the vertical wind speeds and σ_u is the standard deviation of the logarithms of the horizontal wind speeds (assumed to be 0.55). Following Greene and Johnson (1996), σ_w is a function of the mean horizontal wind speed at a particular height in the forest. If we account for the abscission effect, and estimate σ_w at the assumed mean abscission height (0.75 z_h), then $\sigma_w = 0.78$ for a 30 m tall forest and thus white spruce has $\sigma_x = 1.30$ and balsam fir, $\sigma_x = 1.09$.

The source strength of a single tree, F, in equation [1] is given by

$$F = QS_jT \qquad [4]$$

where Q is mean annual filled seed production, S_j is the juvenile survivorship of a regeneration cohort in a recent burn, and T is the number of regeneration cohorts (years) available for colonization before the seedbeds become so poor that colonization effectively ceases.

Greene and Johnson (1994) defined Q as a function of seed mass (m) and tree size (basal area):

$$Q = 3067\ m^{-0.58}\ B^{0.92} \qquad [5]$$

with seed mass in grams and basal area in meters squared.

Greene and Johnson's (1998) model for juvenile survivorship (S_j) assumes that mortality is dependent on seed size (proportionate to germinant size) and seedbed type, with mineral soil, humus, well-decomposed logs, and certain mosses (e.g. Sphagnum) resulting in much higher survivorship than high-porosity seedbeds such as litter, feather mosses, or charred duff. For recent site-prepared clearcuts, they obtained

$$S_j = 0.28\ m^{0.52} \qquad [6]$$

and, as we have no evidence that the proportional representation of the optimal seedbeds in clearcuts (≈17%) is greatly different from burns (Charron, 1998; K. Miyanishi, unpublished data for Saskatchewan fires; D. Greene and Y. Bergeron, unpublished data for Quebec fires), we will apply equation [6] to recent burns.

We idealize the recruitment process as a set of T consecutive (yearly) cohorts. The number of cohorts T depends on how rapidly the developing litter and feathermoss layers reduce the juvenile survivorship to, effectively, zero. An ongoing (unpublished) study by S. Gutsell

(University of Calgary) using stand reconstructions in central Saskatchewan indicates that the great majority of canopy trees of pine, spruce and fir recruit within the first four years. Tentatively, then, we set T=4.

Explicitly, we will assume that the subsequent thinning mortality for spruce and fir can be ignored because these are very young stands (except for the Galipeau et al. (1997) burn that was 68 years old), and because the densities are so low that they are unlikely to strongly self-thin. We assume that the shade of over-topping *Populus*, *Betula* or pine may reduce growth but not greatly affect mortality.

Thus, we re-write the point source strength (F) in equation [4] using equation [5], [6] and T=4,

$$F = 3312\ m^{-0.06}\ B^{0.92}. \qquad [7]$$

Note that the seed mass terms in seed production and juvenile survivorship have essentially cancelled each other out. In what follows, we will ignore the inconsequential term $m^{-0.06}$.

The area source model

The area source recruitment curve is the summation of the individual recruitment curves using equation [1] for a uniformly distributed array of point sources adjacent to a burn. The intact forest edge is x=0. The density of recruits (F_{Dx}) as a function of distance can be reasonably expressed by the function

$$F_{Dx} \approx (F_D / 2) \exp(-a (x\bar{f})^{b}) \qquad [8]$$

(Greene and Johnson, 1996) where F_D is the potential source strength (on a density basis) within the unburnt forest, and a and b are empirical coefficients from a regression of $x\bar{f}$ on F_{Dx}. At the burn edge (x=0), we expect the seedling density to be half of what it would be deep inside the area source. In fact, of course, F_D in the forest ought to be, because of the intact litter layers, a good deal less than at small distances into the burn. It should be understood that F_D is the product of seed density and cumulative survivorship. Thus, well inside the forest, the *seed* density is double that of the edge.

From equation [5] remember that the exponent B (individual basal area) is so close to 1.0 that we can, with much less than two-fold inaccuracy, write

$$B_D^{0.92} \cong (\Sigma B^{0.92}) /A$$

where A is the area examined and B_D is the dimensionless basal area per area. Therefore, F_D in equation [8] becomes

$$F_D = 3312\ B_D^{0.9} \qquad [9]$$

Two other factors must be accounted for in equation [8]. The first involves the proportion of the landscape that is forested. Estimates of B_D are, of course, made only in stands and we cannot extrapolate to a source area (the scale of a few kilometers) without an overestimate of B_D because of roads, lakes, meadows, young (not reproductively mature) stands, etc. For two burns in central Saskatchewan, Johnson and Greene (unpublished data) used forest inventory maps, and calculated that only about 60% of the area had been seed sources prior to the burn for tree species. Thus, the expected source strength for each species must be multiplied by the proportion of the landscape that is seed producing forest, g = 0.6.

The final consideration involves residual (unburnt) stands within the nominal burn perimeter. Eberhart and Woodard (1987) reported that such stands are quite common in boreal fires. Johnson and Greene (unpublished data) found that residual stands constituted about 5% of the burn area for Saskatchewan fires exceeding 8,000 ha. (This result is similar to that of Eberhart and Woodward (1987) for Alberta fires.) As we will see, these stands should provide a large fraction of the expected recruitment at distances far from the nominal burn edge. However, for the data sets we will use in our test of the recruitment model, the authors ignored the very small residual stands. MacArthur (1964) reported which sampling plots were near *large* residual stands, and we have removed those plots from the analysis. Galipeau et al. (1997) re-evaluated the distance (x) in relation to any large source (including very large residual stands). Therefore, for both these studies, we need to account for the contribution of only the smaller residual stands. Johnson and Greene (unpublished data) found that residual stand sizes have a logarithmic distribution and that residual areas less than 0.5 ha comprise only 0.003 of the total burn area (6% of the total residual area).

Thus, our area source equation [8] for recruitment within a burn as a function of distance becomes

$$F_{DX} = (F_D\, g/2) \exp \left[(-a\,(xf)^b) + R\right] \qquad [10]$$

where R is the proportion of the area in small residual stands, and is assumed to be, in this exercise, R = 0.003.

Examples of the expected area source recruitment curves from equation [10] are given in Figure 1 for spruce and fir with R = 0.003 or R=0, and $F_D g = 1.0$. The regression results for the two coefficients in equation [10] yield for white spruce a = 0.42, b = 0.37 and for balsam fir a = 0.59, b = 0.33.

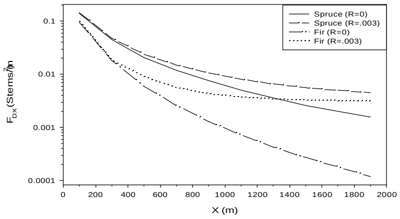

Figure 1

Figure 1. Area source recruitment curves (F_{Dx}) from the model assuming that the source strength ($F_D g$) is 1/m^2. The terminal velocities ($\bar{f}$) were 0.66 (spruce) and 0.85 (fir) m/sec. Each pair of curves is for R=0 or R=0.003, where R is the proportion of the burn comprised of small residual stands.

We should mention that a major source of error in the model validation concerns empirical measures of B_D (basal area/area) for the species of interest. The data sets we use (including our own) rely on sampling the forest edge near the origin of a transect into the burn. This is acceptable for prediction of recruitment within a few hundred m, but at distances exceeding say, 500 m the source area in question is greatly magnified. Field sampling of B_D across such a large area is prohibitive and one ought to rely instead on forestry inventories (although these also are problematic). In short, in this exercise we do not know if the sampled B_D is representative of a much larger area, and we cannot even estimate adequately the potential error.

METHODS

We used an unpublished data set of the present authors (collected in 1985) on recruitment of Engelmann spruce (*Picea engelmannii*) in the 1968 Vermilion Pass burn in the southern Canadian Rockies near Banff, Alberta. A description of the study site can be found in Greene and Johnson (1996). As Engelmann spruce has a terminal velocity and a seed mass similar to white spruce, we have lumped the results with studies of white spruce recruitment into burns from Galipeau et al. (1997) and MacArthur (1964). Galipeau et al. (1997) examined a Quebec fire that was 68 years old and we only use the portion of their data set that represented the initial post-fire recruitment event. MacArthur's (1964) burn in eastern Quebec was 16 years old at the time of his recruitment survey. Both MacArthur (1964) and Galipeau et al. (1997) also obtained data on balsam fir recruitment.

We studied germinant recruitment of jack pine in 1997 following the June rainy season in a 1996 fire (Bittern Creek) 30 km east of Prince Albert National Park in the southern boreal forest in central Saskatchewan. We used a 50 m long transect in a primarily black spruce burned forest. The transect was deliberately chosen so it would pass through a stand of jack pine (about 50% of the total tree basal area in the center of the transect). Jack pine trees within 50 m to either side of the transect were assigned Cartesian coordinates, and their basal areas were measured. Additionally, potential pine source trees at distances greater than 50 m beyond either end of the transect were identified. Germinants were tallied 1.0 m to either side of the 50 m transect. We sampled the germinants in 5 m long transect segments in order to diminish the effect of seedbed conditions (mineral soil and humus are much better seedbeds than thick burnt fibric organic layers) which vary at the scale of inter-bole distances, 1-3 m (Charron, 1998).

Recruitment of white spruce and larch was studied in 1995 at the 1989 Muskeg Fire 40 km east of the northeast corner of Prince Albert National Park. We used three residual stands for spruce and two for larch. Stands were chosen so that they were at least 200 m from a nominal burn edge or another residual stand containing either species. At each stand, four 100 m long transects radiated out along cardinal azimuths. Along each transect, recruitment density was sampled in 3 m radius circular plots at 10, 20, 30, and 40 m, and then at 60, 80, and 100 m. Within the residual stands, the number of source trees and their basal area were measured. All residual stands were about 0.1 ha in size (the modal size for residual stands in Saskatchewan fires, Johnson and Greene unpublished data).

RESULTS

Dispersion of jack pine recruits in a recent fire

The measured terminal velocity of the jack pine seeds was 0.73 m/sec. The mean height of the canopy trees was 14 m, and thus from equations [2] and [3], the median distance traveled ($x_{0.5}$) and standard deviation of log distances (σ_x) were, respectively, 35 m and 1.12.

As the trees are serotinous, we could not use equation [5]. The source strength term for the aerial seed bank of this species has been estimated by Greene and Johnson (in press) as

$$Q = 35{,}100\ B^{0.86} \qquad [12]$$

where Q is the stored seed production and B is the maternal parent's basal area (m^2). In an ongoing regeneration study at this fire, Charron (1998) estimated that 76% of the total aerial seed bank (Q) was available for germination in the early summer of 1997. Further, sowing experiments (200 m from the present study site) indicated that the initial survival rate (S_o) of the seeds from late spring to the end of the June rainy season (i.e. during the transition from abscised seed to censused germinant) was 0.33 (a weighted average across seedbed types). Note that equation [6] for juvenile survivorship will underestimate because it applies to the first three summers for a cohort (Greene and Johnson, in press).

Thus, the fecundity (F = germinants per tree) in equation [1] for the 1997 cohort can be estimated as

$$F = 0.76\ QS_o = 8803\ B^{0.86} \qquad [13]$$

and we sum the contribution of each pine tree to the transect given their Cartesian coordinates and basal area.

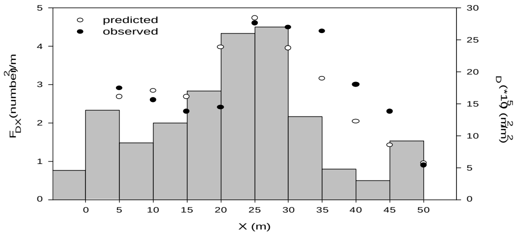

Figure 2. Jack pine recruitment (F_{Dx}) of germinants along the 50 m transect in a one-year-old burn in Saskatchewan. Also shown is the model prediction for F_{DX}, as well as the histogram of dimensionless basal area density, B_D (m^2/m^2).

The results of the transect through the pine stand are shown in Figure 2. As mentioned earlier, the transect was placed so as to bisect a stand of higher pine density (roughly equal to the black spruce density in the distance interval $20 < x < 30$) with no pine sources at $x>50$ m. A regression of predicted recruit density (F_{Dp}) from equation [13] on observed fecundity (F_{DO}) yielded a significant result

$$F_{DO} = 0.58 + 0.86\, F_{Dp} \qquad [14]$$

($r^2 = 0.64$; $p<0.05$; N=10) where neither the intercept nor slope are significantly different from 0 and 1.0, respectively. In Figure 2 there is a rough congruence of B_D (basal area density) and observed recruitment density, but the 9-fold range in B_D is reduced to a 5-fold range in F_{DO} because of dispersal (i.e. the dense pine source in the center of the transect is a net exporter of seeds).

There is clearly some directionality in the recruitment as we tend to overpredict the first 25 m of the transect and underpredict in the subsequent 25 m. The prevailing westerly winds are from the direction of low x to high x. We can remove this azimuthal bias (due, undoubtedly, to abscission events) by taking an average (for both observed and predicted) at x=25, 30; x=20, 35; etc., and then, again, regress observed on predicted. We now obtain

$$F_{DO} = 0.17 + 1.0\, F_{Dp}$$

($r^2 = 0.992$; $p<0.05$; N=5).

Spruce and fir recruitment from burn edges

Empirical results for white spruce and balsam fir are shown in Figures 3 and 4, and expressed using equation [8]:

$$\text{(spruce)} \quad F_{Dx} = (gF_D / 2) \exp(-0.5\,(x\bar{f})^{0.36}) \qquad [15]$$

$$\text{(fir)} \quad F_{Dx} = (gF_D / 2) \exp(-0.26\,(x\bar{f})^{0.41})$$

with $r^2 = 0.52$ (N=27; $p<0.05$) for spruce and $r^2 = 0.72$ (N=27; $p<0.05$) for fir. The 95% confidence intervals on the coefficient a (0.23 – 1.1 for spruce; 0.1 – 0.65 for fir) include the model prediction (equation [10]). Likewise, the confidence intervals for b (0.22 to 0.50 for spruce; 0.26 to 0.57 for fir) span the model estimates. Nonetheless, as can be seen in Figures 3 and 4, there is a tendency to overpredict spruce and underpredict fir (especially with the oldest fire (Galipeau et al. 1997)).

We assume that the shape of the empirical curve (the magnitude of a and b) is determined by dispersal rather than distance-dependent or density-dependent mortality. Using the seed dispersal data of Greene and Johnson (1996) at the Vermilion Pass burn for Engelmann spruce, we obtain a=0.27 and b=0.47. Neither value is significantly different from the regression results (Figure 3) or the model (equation [10]).

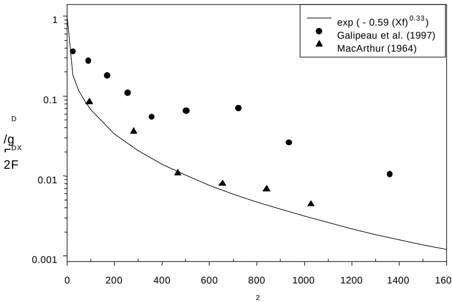

figure 4

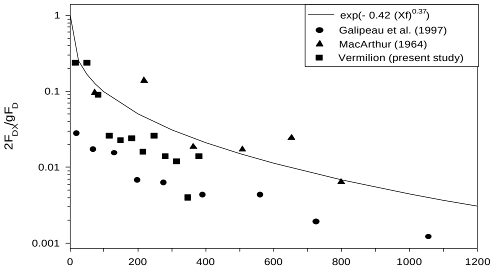

Figure 3

Figure 3. Observed and predicted recruitment curves of spruce (F_{Dx}) at three fires.

Figure 4. Observed and predicted recruitment curves of fir (F_{Dx}) at two fires.

It is of interest to compare these results with a recruitment curve for spruce in a clear-cut. In this case, we set R=0 (no residual stands) and the model coefficients then become a=0.15 and b=0.52. A regression using the results of Timoney and Peterson (1996) for clearcuts in Wood Buffalo National Park yielded a=0.152 and b=0.59 (r^2=0.65; N=8; p<0.05). The data set of Timoney and Peterson extends to 400 m from any source tree. These coefficients are not significantly different from those of our model. Likewise, a study of seed dispersal of Engelmann spruce into a clear-cut (Squillace, 1954) yielded for x >100 m, a=0.13 and b=0.60 (r^2=0.683; N=5), values which are almost exactly the same as those for Timoney and Peterson (1996).

Spruce and larch recruitment from small residual stands

Finally, we turn to the recruitment of white spruce and larch, from residual stands at the 1989 Muskeg Fire in Saskatchewan. In this modelling exercise, we assume g=1.0. Our sampling plots (3 m diameter) were clearly too small for white spruce as we observed no recruitment in about 40% of the sampling plots. Given that the residual stands were about the same size (0.095 to 0.146 ha) and that total number of white spruce canopy trees (about 30) was roughly the same, we have averaged the results for all three stands (Figure 5). Equation [1] was used to model the recruitment at any distance as the sum of the individual point source contributions in a square residual stand of 0.1 ha with 30 source trees of 15 m height and mean basal area of 0.015 m^2 distributed in a uniform manner. The fecundity (F) in equation [1] is 70 recruits/tree. The logarithmic regression of predicted on observed (Figure 5) recruitment density was significant (r^2 = 0.92; N=5; p <0.05) with neither the slope nor intercept significantly different from 1.0. However, as in Figure 3, there is a tendency to overpredict spruce recruitment.

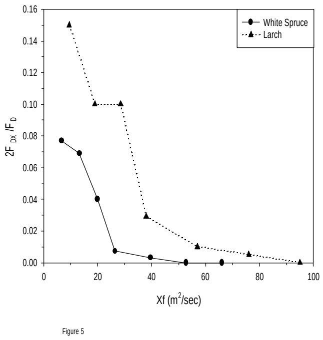

Figure 5. Observed recruitment density near residual stands at a 5-year-old fire in Saskatchewan for larch and white spruce. Given the sampling intensity, the minimum density of stems we can observe is 0.0044/m^2 for larch, and 0.003/m^2 for spruce.

Turning now to the two larch stands, we will again average the results for the regeneration density (as with white spruce, there were too many zero values). Average values for the two larch residual stands were 27 trees per 0.095 ha stand with a height and basal area of 13 m and 0.011 m^2, respectively. Thus, we expect an average of 52 recruits/tree. A logarithmic regression of predicted F_{Dx} on observed F_{Dx} provided a significant result (r^2=0.94; $p<0.05$; N=5) where neither the intercept nor slope are significantly different from 1.0.

DISCUSSION

Three main conclusions can be drawn from this study. The first conclusion is that recruitment curves broadly mimic dispersal curves at large spatial scales. Density-dependent mortality (e.g. granivores or the initial local thinning mortality) and distance-dependent mortality (seeds germinating on sites which are, on average, poorer than that of their maternal parents) may well be occurring, but it is less important (at this scale) than the greater decline in seed deposition with distance.

The second conclusion is that the model predictions were not significantly different from the observed recruitment from burn edges (nominal edges or residual edges) for spruce, fir, and larch, and also predicted well the recruitment from serotinous jack pine trees within a burn. Nonetheless, there was in Figures 3 and 4 a marked tendency to underpredict fir and overpredict spruce. The worse examples involve the Galipeau et al. (1997) observations on fir and spruce. We point out that their estimates of B_D (basal area/area) of the sources were made 68 years after the fire with a devastating spruce budworm outbreak intervening in a period centered on 1980. Thus, our strong underprediction of their fir recruitment could well be due to recent budworm losses. As for white spruce, if it significantly increased its B_D during the last 68 years, this would explain our overprediction of recruitment density.

The third conclusion is that for spruce, both seed dispersal and recruitment have more gentle slopes in burns than in clearcuts. This is initially surprising because we expect horizontal wind speeds in clear-cuts to be substantially greater than in burns because of the absence of drag-producing boles and branches. We think the reason for the observed difference is the presence of the small residual stands. The model predicts that at a distance of 1 km the residual stands sponsor about half of the recruits.

Stocking of white spruce

Foresters have had great difficulty obtaining acceptable stocking levels in cuts with natural regeneration, and they may take some comfort from knowing that burns are similarly poorly stocked by this species.

Let us take a typical stocking criterion of one seedling per 4 m^2 plot in at least 40% of the random plots. For an infinitely wide burn, where white spruce sources had $B_D=0.0005$ (20% of a forest with 25 m^2 of basal area per ha), then $gF_D/2$ in equation [15] becomes 0.89. There will be a 40% chance for a stocked plot at $x=62$ m with a simple Poisson argument:

$$\text{prob (stocked)} = 1 - \exp(-4F_{Dx})$$

Roughly, then, across the distance interval $0<x<124$ m the stocking criteria would be satisfied. (Note that a numerical solution across the burn will not change this approximate distance.) Extrapolating from fire to clearcut, a square clearcut intended to be naturally regenerated could not be larger than about 6 ha (248 m on a side).

It is of some interest that Johnson and Greene (unpublished data) found that the average distance between edges (nominal or residual) and random points within large burns (5,000 to 13,000 ha.) in Saskatchewan was about 150 m. The distance is so short because small residual stands are very common and because the nominal burn perimeter is markedly invaginated. An outstanding problem in boreal ecology has been the explanation of the persistence of the three species (white spruce, balsam fir, and larch) that possess neither aerial seedbanks nor a reliable method of asexual regeneration. Appeals to classical succession are misplaced in landscapes such as the western boreal forest where fire return time is typically less than 100 years (Johnson, 1996) and thus only a small fraction of the landscape becomes old forest. We argue here that a species such as white spruce may well comprise only a small minority of the total regeneration density (typically, $F_D>3$ for aspen, jack pine, and black spruce in areas where their pre-burn B_D was large) across the fire, but if its thinning mortality is small relative to the species with higher abundance, then it can persist at a temporal scale demarked in units of fire cycles.

Imagine that at 69 years old, half a landscape burns (a negative exponential time-since-fire distribution with a 100-year return time). At this age, assume 0.1 canopy trees per m^2 (all species, of which white spruce has $0.02/m^2$ (20%)). We require that this species achieves an average recruitment density of 0.01 (there is another area source on the other side of the burn), and we assume thinning losses from years 5 to 69 are small enough to be ignored. Using equation [15] to solve for the distance at which F_D=0.01, we have x=637 and thus the mean fire diameter could be 1.3 km. Large burns commonly have residual stands sufficiently large that equation [12] would apply, and burns >7,000 ha have only a small proportion of their areas with distances to a large source (nominal or large residual edge) greater than 637 m (Johnson and Greene, unpublished data; Eberhart and Woodard, 1987). We note that this argument is independent of the initial white spruce forest proportion because a doubling of source strength would merely require a doubling of the recruitment density required for self-replacement.

We make one last point regarding the persistence of white spruce and fir. As they have no mechanism for persisting *in situ* through a fire, white spruce will be found at different densities in different locations from one fire cycle to the next. By contrast, species such as jack pine, black spruce and aspen tend to replace themselves *in situ* through a fire (Greene and Johnson, in press). We must remember that each of these five species have different tolerance curves and grow best on different substrates (mainly glaciofluvial and glacial till in the mixedwood forest) and different hillslope positions (moisture and nutrient regimes) (Bridge and Johnson, in press).

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