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

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

by

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INTRODUCTION

This progress report reviews three years of research carried out by three principal investigators and their graduate students, each located at different universities. The team is interdisciplinary, each principal investigator bringing different backgrounds and disciplines to the projects.

Our study area encompasses the Weyerhaeuser FMLA and Prince Albert National Park, an area of about 3.7 million ha (Figure 1).

The purpose over the last three years has been to understand the **ecological processes** (particularly fire and terrain processes) that produce the **patterns of forest composition and age**. One goal of the SFMN has been to understand ecological processes so that foresters can simulate them in their forest practices and maintain forest ecosystem structure and function within desired bounds. In the past, forest practices have been largely rule (pattern) based. Today an understanding of how ecological processes produce patterns is needed so that managers can reason through what the effects of their actions will be and determine if their goals are likely to be realized. Hence, we are moving from a rule and desired outcome system of management to a conjecture and confirmation management system.

Our projects are not case studies, but attempts at understanding the underlying mechanisms applicable to **forests in general**. The models, however, are explicit and indicate the variables which need to be measured. They are not theoretical simulations. We believe this approach leads to more valid and applicable **tools** for foresters.

There are seven projects reported, divided into three clusters (Figure 2) which ask these general questions:

1) What is and what determines the forest patterns?
    - Biophysical land classification – geomorphic principles of terrain organization and vegetation gradients.
    - Fire frequency and the forest age mosaic pattern.
    - The relative importance of terrain and forest fire in determining plant biodiversity.
    - Forest fragmentation – mechanism and measures.

2) Forest dynamics and fire effects.
    - Patterns of duff consumption and exposed mineral soil after forest fires – the wildfire mechanisms and its implications for regeneration.
    - Recruitment models: seed production, dispersal and juvenile mortality after fire and cutting.
    - Population dynamics of trees in the mixedwood boreal forest.

Figure 1

Study area encompasses the Weyerhaeuser FMLA and Prince Albert National Park. The dark area is the mixedwood boreal forest and lighter area, the boreal forest in total.

Figure 2

Organization of projects into research clusters.

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

The following graduate students, postdoctoral fellows and visiting scientists have taken part:

Postdoctoral Fellows – M. B. Dickinson
Visiting Scientist (Xinjiang University) -- A. Mijit
Graduate Students – M. J. Bajtala, S. R. J. Bridge, I. Charron, S. J. Chipman, S. L. Gutsell, O. Proulx, T. Tchir and A. Warren
Undergraduate Students – N. O'Brien, S. Vo, J. Kresowaty.

Overall, the SFM projects have been enormously helped by the logistic and information help of Saskatchewan Timberlands (Weyerhaeuser Canada) and Prince Albert National Park.

Finally, we extend an invitation to the partners in the NSERC Sustainable Forest Management Network who wish to discuss or consider any of the implications in this report. We can be reached by e-mail at johnsone@ucalgary.ca, phone (403) 220-7635 or at the mail address given at the beginning of the report. As forest ecologists, we need the interaction with operational foresters.

Biophysical land classification – geomorphic principles of terrain organization and vegetation gradients.

SFM Network Project:

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

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May 1999

EXECUTIVE SUMMARY

Moisture and nutrient gradients consistently explain much of the variation in plant species composition and abundance, but these gradients are not spatially explicit and only reveal species' responses to resource levels. This study links these abstract gradients to quantitative, spatial models of hillslope assembly. A gradient analysis in the mixedwood boreal forest demonstrates that patterns of upland vegetation distribution are correlated to soil moisture and nutrient gradients. The physical environmental gradients are related to qualitative positions on the hillslope, i.e. crest, midslope, bottomslope. However, hillslope shape can be quantitatively described and compared by fitting allometric equations to the slope profiles. Using these equations, we show that hillslope profiles on similar surficial materials have similar parameters, despite coming from widely separated locations. We then quantitatively link the moisture and nutrient gradients to the equations. Moisture and nutrients significantly increase as distance downslope from the ridgeline increases. Corresponding vegetation composition changes too. These relationships characterize the general pattern of vegetation change down most hillslopes in the area. Since hillslopes are a universal feature of all landscapes, these principles may characterize landscape scale spatial patterns of vegetation in many environments.

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INTRODUCTION

Landscape ecology is concerned with the spatial arrangement of vegetation on the landscape. One of the issues of forest ecosystem management is also spatial arrangements, particularly between productive (to be harvested) and unproductive (to be left unharvested) forest. This spatial relationship is important for management concerns such as the selection of areas that are most economically feasible for harvesting or the availability of post harvest seed sources for natural regeneration of nonserotinous species.

One of the goals of ecology has been to predict the distribution and composition of species over the landscape. Plant ecologists have been successful at defining the changes in abundance of species along abstract environmental gradients (e.g. Whittaker and Gauch 1973) and in testing ideas about the organizing principles responsible for these gradients (e.g. Tilman 1988). Moisture and nutrients have consistently been the two most important gradients. These gradients are abstract in that stands (specific geographic locations) are arranged along continuously changing values of moisture and nutrients. However, stands next to each other on the gradient need not be next to each other geographically. The difficulty has been to relate the organization of species along these abstract environmental gradients to the organization of the terrain in terms of the physical processes of geomorphology and climate.

Biophysical land classification attempts to produce this linkage of the physical environment (terrain) to the ecology (biology). Unfortunately, biophysicals have been largely unsuccessful because they have taken a classificational rather than a process approach. For example, at the same time that ecology was interested in determining the interactions which organized communities (e.g. McNaughton and Wolf 1970) and in coupling climate and organisms (e.g. Porter and Gates 1969), biophysicals were interested in taxonomy and description of land units which related geographic location to plant communities (Lacate 1969). Biophysicals were not concerned with the geomorphic and hydrologic processes which organize the land. In fact, contemporary geomorphology and hydrology (e.g. Carson and Kirkby 1972; Kirkby 1978; O'Loughlin 1981, 1986; Wood et al. 1988) were largely ignored, probably because these disciplines are mostly process oriented and were not seen as pertinent to land classification.

SUMMARY OF DATA ANALYSIS

The Vegetation Gradients

We sampled canopy and understorey vegetation as well as shrubs and ground cover in 101 stands in and around Prince Albert National Park, Saskatchewan. All stands were > 4 hectares in size and visually homogeneous with respect to age, structure, etc., with no evidence of anthropogenic disturbance in the lifetime of the canopy trees. There was also no evidence of standing water within the top 30 cm of mineral soil. Principal Component Analysis (PCA) was used to derive indirect gradients (ter Braak 1987). These were compared with direct gradients derived using Redundancy Analysis (RDA) (ter Braak 1987, 1988). The soil moisture and nutrient information required for the RDA was derived from soil samples taken from 40 sites chosen to represent a broad range of species compositions. The two techniques produced almost identical ordinations (Spearman rank correlation axis 1: r^2 = 0.98, axis 2 r^2 = 0.95), suggesting that moisture and nutrients explain most of the variation in species abundance and distribution.

The vegetation on the PCA forms two groups based on the geomorphic surface on which it resides (Figure 1). Stands dominated by the canopy species *Populus tremuloides*, *Picea glauca* and *Abies balsamea* reside almost exclusively on unstratified till deposits laid down directly by the glaciers, while stands dominated by *Pinus banksiana* and *Picea mariana* reside almost exclusively on glaciofluvial surfaces produced by flowing glacial meltwater.

Surfaces with different geomorphic histories often support different vegetation (e.g. Whittaker 1960; Marks and Harcombe 1981; Wentworth 1981; McAuliffe 1994). The change in vegetation with geomorphic surface may also explain why texture gradients were so important in other studies in this region (Swan and Dix 1966; La Roi 1991).

Within each surficial type there is also a strong relationship between qualitative measures of topographic position on slope and gradient position (Figure 2). On hillslopes cut into homogeneous surficial material, the primary determinant of soil moisture flux and storage is usually topography (Quinn et al. 1992), while variability in soil hydraulic conductivity and rainfall play only a secondary role (O'Loughlin 1981, 1986; Selby 1982; Wood et al. 1988). The lack of any obvious trend in soil moisture capacities with topographic position or gradient position on each geomorphic surface (Figure 3) indicates that this is true here. This suggests that within each surficial group the first principal component represents a moisture gradient, with dry sites to the left and wet sites to the right. This is consistent with studies in many other forested systems where vegetation composition reflects topographic control over moisture and nutrient gradients (e.g. Day and Monk 1974; Johnson 1981; Marks and Harcombe 1981; Allen and Peet 1990; Busing et al. 1992).

Characterizing Hillslopes With Allometric Equations

In this region, three different geomorphic surfaces have been left on the landscape through the action of glacial ice and glaciofluvial and glaciolacustrine meltwater (Padbury et al. 1978). On each of these different surfaces, the geomorphic processes produce hillslopes which can be described by allometric equations that summarize the relationship between the processes, the surficial material and the climate (Hack and Goodlet 1960; Bull 1975). We estimated the parameters for two allometric equations that describe hillslopes on glacial till and glaciofluvial surfaces (Figure 4). This was accomplished by measuring the log vertical fall and log horizontal distance from the ridgeline down the slope profile (Hack and Goodlet 1960).

Twenty-three hillslopes on glacial till materials and six on glaciofluvial materials were measured in this way from 1:50 000 topographic maps. An analysis of covariance revealed no

Figure 1

The stand scores and species abundance on the first two gradients of the principal components analysis. Each figure shows the abundance of a given species in stands on the ordination. The broken curve running diagonally across the ordination separates stands residing on undifferentiated glacial till deposits from stands residing on highly sorted glaciofluvial deposits.

Figure 2

Centroids for topographic position on slope with the stand loadings on the first two gradients of the principal components analysis. The centroids for topographic position on slope are indicated separately for the two types of surficial deposits.

Figure 3

Soil moisture capacity (% dry weight) at (a) 33 kPa, (b) 1500 kPa and (c) available moisture capacity for stands on the principal components analysis.

Figure 4

Allometric relationships for hillslope profiles on glacial till deposits and glaciofluvial deposits.

significant differences between the slope profiles on a given surficial material, therefore the profiles were pooled to produce the two equations; one for each surficial material. The intercept, or coefficient of steepness (Hack and Goodlet 1960), was significantly higher for hillslopes on glacial till surfaces, meaning that these hillslopes are steeper for any given distance from the divide than are hillslopes on glaciofluvial surfaces.

Linking the Abstract Environmental Gradients to Terrain Organization

New slope profiles were plotted to determine distance from the ridgeline for 47 stands on till surfaces and nine on glaciofluvial surfaces. These distances were then plotted against the stands' gradient position. On both geomorphic surfaces, moisture and nutrients increased significantly as distance down slope from the ridgeline increased (Figure 5).

Again, this is consistent with the strong control of topography over moisture and nutrient flux and storage (Kliess 1970; Malo et al. 1974; Selby 1982; Wood et al. 1988; O'Loughlin 1981, 1986; Litaor 1992; Quinn et al. 1992). As moisture and nutrients change down slope so does the vegetation composition. This quantitative linkage between the moisture and nutrient gradients and the allometric equations of hillslope profile form provide a way to characterize the general pattern of gradient and vegetation composition change down most hillslopes for this region. This general pattern is depicted in Figure 6 which, unlike stylized figures of vegetation change on hillslopes (Day and Monk 1974; Niering and Lowe 1984; Lieffers and Larkin-Lieffers 1987; Baldwin et al. 1990), is derived from the allometric equations and the relationships between the stand positions on the gradients and their distances down slope from the ridgeline. Since the geomorphic processes form hillslopes in the same general way in many environments (Hack and Goodlet 1960; Troeh 1965; Bull 1975; Nash 1980), this approach to characterizing the landscape scale spatial patterns of vegetation in terms of geomorphic principles should be applicable in many places.

In previous studies, the allometric description of hillslopes and the distributed modeling of moisture have taken place on terrain with considerably more topographic relief than central Saskatchewan. It is noteworthy, then, that allometric measurements of hillslopes and the quantitative relationships between gradients and distance from the divide work so well in this relatively flat study area. This is an important point from this study. It is quite likely that these relationships will be even stronger in areas of greater relief, strengthening the suggestion that this approach to understanding landscape scale vegetation patterns may be applicable in many different environments. It also suggests a reason why moisture and nutrients, as opposed to other gradients, are so common as controls of variation in vegetation distribution. Since hillslopes are a universal feature of landscapes, variation in moisture and nutrient values across the landscape will always be high.

On any given geomorphic surface species can only move to higher or lower topographic positions to find more suitable environmental conditions. Why then does the gradient analysis indicate that two gradients, moisture and nutrients, are the most important gradients controlling

Figure 5

Relationship between stand position on the moisture gradient (PCA 1), or the nutrient gradient (PCA 2), and the distance from the ridgeline for slopes on: (*a*) glacial till deposits that are either horizontally flat or convex, (*b*) glacial till deposits that are either horizontally flat, convex or concave, (*c* and *d*) glaciofluvial deposits.

Figure 6

General landscape patterns of vegetation composition. The shape of the hillslopes is derived from the allometric equations for hillslopes on glacial till and glaciofluvial surfaces. The tree symbols depict the general change in dominant canopy species down the hillslope which is based on the relationship between the stand positions on the moisture and nutrient gradients and the stand distances from the ridgeline.

the variation in vegetation distribution rather than one gradient of topographic position on slope? The most likely explanation for this is that the rates of change of moisture and nutrients down the hillslope vary independently of one another over time. For example, climate change may alter the average amount of precipitation falling in the study area resulting in a different rate of change in moisture down the hillslope. However, the rate of change in nutrients down the hillslope, which depends upon weathering of the parent material and leaching, may be slower to react to the climate change. Thus, the old combinations of moisture and nutrients have not simply moved to higher or lower topographic positions on the hillslope, but instead, entirely new combinations of these gradients are presented. The species must, therefore, continue to respond to both gradients independently if they are to deal with these gradient changes over time.

MANAGEMENT APPLICATIONS

Recognition that hillslopes are the predominant geomorphic form on erosional landscapes and, consequently, that the environmental gradients down these slopes have been a principal selection force on plants provides the link between the physical environment and the ecology needed for biophysical land classification. The variation in vegetation composition on the landscape is determined in part by the proportions of hillslopes which are made up of different substrates and resistance-erosional environments. In the mixedwood, these proportions were determined by glacial and postglacial events.

CONCLUSIONS

We have shown that, in the mixedwood boreal forest, the upland vegetation composition can be quantitatively linked to topographic position on slope. In this region, hillslope geomorphology seems to be a unifying explanation for upland gradients; however, this hypothesis needs further testing in areas with different vegetation and stratigraphic histories. The fact that hillslopes are assembled in the same fashion in many environments suggests that quantitative linkages between vegetation change and hillslope position should occur elsewhere. Any attempt to understand the landscape patterns of vegetation distribution and abundance must, therefore, focus on the processes that distribute these gradients across the landscape. By understanding the processes involved, more accurate predictions about landscape scale vegetation patterns may be made.

Recent work in surface hydrology has shown that the landscape can be divided up into a series of hillslopes where the parameters of the water flux and storage processes are assumed to be spatially homogeneous (Wood et al. 1988; Band 1989, 1991). Extending the statistical descriptions of the planimetric form of the river channels to their associated hillslopes has met with some success in predicting the moisture and carbon flux and storage of watersheds (Wood et al. 1988; Band 1993). We have been able to characterize the change in vegetation down hillslopes. It should, therefore, also be possible to extend the statistical description of planimetric form of the channels to their associated hillslopes to derive a statistical description of landscape scale vegetation distribution patterns. These patterns will be couched in the geomorphic processes that shape the landscape. A similar argument can be made for the relationship between the recovery after fire gradient and time and the pattern of time since last fire across the landscape.

Although two physical environmental gradients, moisture and nutrients, are shown to be important in controlling variation in vegetation distribution, the species on a given stratigraphic surface can only respond to the gradients by changing topographic position on slope. Species still respond to both moisture and nutrient gradients though, as the rate of change of moisture and nutrients down a hillslope may vary independently of one another with time.

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Fire frequency and the spatial age mosaic of the mixedwood boreal forest of Saskatchewan.

SFM Network Project:

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

by

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EXECUTIVE SUMMARY

One approach to ecosystem management is to emulate the effects of natural disturbance in producing landscape patterns. This approach requires a spatial analysis of the pattern and an understanding of the processes producing the pattern. Forested landscapes exhibit mosaic patterns of both stand types and ages. This study investigates the spatial mosaic of stand ages produced by high intensity, stand-replacing fires in the mixedwood boreal forest of western Canada.

A high resolution, accurately dated time-since-fire map for a large (3,461 km^2) contiguous area is used to produce the landscape survivorship distribution in which both spatial and temporal changes in fire cycle are statistically tested. Spatial multivariate analysis of the time-since-fire map is also used to investigate the spatial assembly of the age mosaic.

Significant changes in fire cycle can be explained by climatic change as well as by land use change in the surrounding area. The shift from a short (15 year) fire cycle to a longer (75 year) cycle after 1890 in the northern half of the study area coincides with climatic change at the end of the Little Ice Age. In the southern half of the study area, the short fire cycle continues after 1890 due to the spread of human-caused fires from the adjacent area which was settled and cleared for agriculture during the first half of this century. Upon completion of settlement in 1945, the fire cycle becomes significantly longer due to the fragmentation of the once continuous forest that surrounded the study area and from which the majority of large fires propagated in the past.

The different fire cycle histories of the two regions within the study area also explains the spatial mosaic pattern of stand ages, sizes and shapes. The extended period of the short fire cycle through the first half of this century in the southern region results in it being dominated by larger oblong-shaped polygons with irregular edges that are younger in age. These are characteristics that describe the pattern of large burns. The northern region generally has circular-shaped compact polygons that are older and are the remnants of larger, much earlier burns that have since been overburned. The polygons in the northern region are more similar in size and shape to adjacent polygons, but less similar in age, than are those in the southern region. Thus, this study shows how spatial heterogeneity in the landscape mosaic pattern can be characterized and related to the disturbance history of an area. Furthermore, it provides evidence of the impacts on the age mosaic due to forest fragmentation in surrounding areas.

INTRODUCTION

Ecosystem management has suggested the hypothesis that by emulating the effects of natural disturbances, we will be able to develop a more ecologically sound basis for resource management. In order to test this approach, we must first gain an understanding of the ecosystem patterns and how these patterns come about.

Vegetation landscape patterns are determined by both terrain and forest fires. For the mixedwood boreal forest in Western Canada, Bridge and Johnson (1999) have demonstrated the role of surficial geology and geomorphic processes in producing the upland mosaic pattern of species composition across the landscape. They found that species sorted themselves according to moisture and nutrient gradients, which in turn are related to hillslope position and surficial geology. These processes could be used to predict that part of the landscape pattern usually described in biophysical classification.

In this paper, we will address the second mosaic pattern: the time since the last fire or forest landscape age. The time-since-fire mosaic is the pattern that the natural disturbance hypothesis wishes to emulate. We will analyze two aspects of this pattern: the pattern created by the over-burning of past fires (i.e. the fire frequency) and the spatial assembly of the age mosaic.

A time-since-fire map was constructed using the methods of Johnson and Gutsell (1994) for a 3,461 km^2 area in the mixedwood boreal forest of Prince Albert National Park. This area was chosen because it was relatively undisturbed in the last 75 years by logging. The 1:50,000 scale time-since-fire map contained 1,249 polygons whose boundaries were verified and whose fire dates were determined by visiting each polygon and dating trees. No successional arguments, tree composition or height from air photos were used to infer ages. Fire dates after 1700 are accurate to the year, while those before 1700 are accurate to within 5 years. Fire frequency was analyzed using the methods of Johnson and Gutsell (1994), Reed 1994, and Reed et al. (1998). The spatial mosaic was analyzed by spatial multivariate analysis using spatial correlation of polygon's age, size and shape (Wartenberg 1985).

This study was carried out with the significant support of Prince Albert National Park and modest support from SFMN funding. However, it plays an important part in our understanding of the SFMN's objectives. At the present time, this is the only fire frequency study based on a large, detailed fine resolution time-since-fire map of the mixedwood boreal forest (Weir et al., in press).

Figure 1

The time-since-fire distribution for Prince Albert National Park: north and south regions. Data were grouped into 5-year age classes.

SUMMARY OF DATA ANALYSIS

During the last 235 years, all of the study area burned at least once. Less than 5% of the study area is older than 125 years. The negative exponential time-since-fire distribution is mixed both spatially and temporally. The only spatially significant division (Figure 1) was along the 57th township line in the Park, dividing the area into a north (1,563 km^2) and a south (1,898 km^2) region. The time-since-fire distribution of the north region consists of three epochs with statistically different ($P<0.0005$) fire cycles (the parameter of the negative exponential and the time required to burn an area equal to the study area). Prior to 1890, the fire cycle was shorter (15 years, CI = 45-150 years) than between 1890 and 1945 (75 years, CI=45-150 years). Since 1945, the fire cycle has increased to 1,745 years (CI=285-127,225 years). This later period is clearly not long enough to get a precise estimate. The time-since-fire distribution of the south region had only two statistically different epochs. Prior to 1945, the fire cycle was 25 years (CI=40 years), while after 1945 the fire cycle was 645 years (CI=200-4,270 years). The change in fire cycle in 1890 is coincident with the end of the Little Ice Age and has been found in a number of other fire frequency studies in coniferous forests across North America (Heinselman 1973; Johnson 1979; Yarie 1981; Suffling et al. 1982; Masters 1990; Bergeron 1991; Johnson and Larsen 1991; Larsen 1997).

The shorter fire cycle in the Little Ice Age is not what would be expected in a period of cooler moister weather. However, Bergeron and Archambault (1993) have shown that this result was common in the southern boreal forest during the final part of the Little Ice Age. They suggest that the decreased frequency of persistent blocking high pressure systems since the end of the Little Ice Age may explain the decreased fire frequency. Persistent blocking high pressure systems are strongly correlated with the development of large area burn years (Stocks and Street 1983; Flannigan and Harrington 1988; Johnson and Wowchuk 1993; Nash and Johnson 1996).

The difference between the time-since-fire distributions of the north and south between 1890 and 1945 are hypothesized to be due to land use changes in the areas adjacent to the south half of the Park. Prior to settlement in the 1890’s, the area south of the Park was covered by closed canopy mixedwood boreal forest. Between 1900 and 1940, homestead clearance progressed along a relatively uniform front from the south and southwest towards the north and northeast (Weir and Johnson 1998). This conversion of forest to agriculture occurred by cutting of the forest, then piling and burning of the debris. These debris fires frequently escaped control and burned northward into the adjacent forest (MacMillan and Gutches 1909; Mitchell 1910). These fires extended as far as 40 km into the southern region of the Park. The increased area burned during the period of settlement offset the increase in fire cycles due to climate (as seen in the north region). As a result, the fire cycle of the south region remained unchanged during the 1890-1945 period. The escaped fires stopped once settlement was complete, and the largely unforested area now acts as a firebreak.

Simple observation of the time-since-fire map suggests a pattern of smaller, rounder, older polygons embedded within larger, oblong, younger polygons. Spatial multivariate analysis supports this observation that the mosaic pattern in the north part of the Park consists of relatively smaller, older, more circular and compact polygons that are less similar in age but more similar in size and shape to adjacent polygons. The south part of the Park has relatively larger, younger, more oblong polygons with more irregular boundaries that are more similar in age but less similar in size and shape to adjacent polygons. From the spatial analysis of the time-since-fire map, it appears that the assembly of the spatial age mosaic reflects the differences in the fire cycle history.

MANAGEMENT APPLICATIONS

The preoccupation of resource managers with determining the natural disturbance regime and the resulting natural mosaic pattern of time-since-last-disturbance and composition implies a long-term equilibrium of the disturbance regimes. In this study, we provide a clear definition of equilibrium as that period when the fire cycle is constant. We conclude that the spatial mosaic of vegetation would rarely, if ever, be in equilibrium with the disturbance regime, a conclusion already well supported (see Johnson et al. 1998).

In the past, the natural variation of the fire disturbance in the mixedwood boreal forest was driven primarily by large-scale climate change. More recently it is being driven by fire spreading from adjacent agricultural settlement (Weir and Johnson 1998). In this study, the variation in the fire cycles between the epochs of change was two orders of magnitude. This variation in fire frequency demonstrates not only that the changes are frequent, but also that the forested landscape carries a record of several of these changes. Although this variation in fire cycle between epochs can be large, in recent centuries it has been relatively small. The absolute magnitude of the fire cycles in recent centuries has been short and consequently the forested landscape is generally young. Thus, the “old growth” forests in this landscape are only between 156-276 years of age and account for about 5% of the landscape (Johnson et al. 1995, Lesica 1996).

The assembly of the age mosaic of the landscape is of considerable importance if one wishes to emulate this pattern. The spatial arrangement of the age mosaic appears to be controlled by the fire cycle in a relatively logical fashion. Shorter fire cycles produce a younger landscape with larger, more oblong polygons with more irregular boundaries that are more similar in age but less similar in size and shape to adjacent polygons. Longer fire cycles produce a landscape of opposing characteristics.

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The Relative Importance of Terrain and Forest Fire in Determining Understory Vascular Plant Diversity

SFM Network Project:

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

by

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EXECUTIVE SUMMARY

To preserve the natural patterns of plant species diversity, forest managers in the boreal forest attempt to imitate disturbance conditions associated with high intensity, stand replacing fires. However, fire is not the only determinant of plant species diversity and may not even be the most important factor. Therefore, this study examined 1) the relative contribution of three gradients, temporal (time-since-disturbance), moisture and nutrients and light availability, in determining understory plant species richness in the southern mixedwood boreal forest of Saskatchewan, 2) the resulting patterns of richness on the landscape and 3) whether current forestry practices result in the same patterns of richness and composition as burned stands. Species composition and richness were sampled in 159 upland stands in the southern mixedwood boreal forest of Saskatchewan. One hundred and twenty-one of these stands ranged in age from 1 to 234 years and had no evidence of anthropogenic disturbance while the other 38 stands were harvested and ranged in age from 0-11 years since Weyerhaeuser only began clearcutting in 1986.

Light availability is the principal determinant of species richness while moisture and nutrients are secondary. The hillslope pattern of species richness is related to the dominant canopy species which, in turn, is related to both substrate material and topographic position on the hillslope. Therefore, on glacial till, trembling aspen stands are found near the tops of hillslopes and are species rich, while mixedwood stands are found further downslope and are species poor. On glaciofluvial substrate, jack pine dominated stands are found on the tops of hillslopes and are species rich, while black spruce stands are found further downslope and are species poor. The landscape pattern of species richness is related to the hillslope pattern of richness as well as to the temporal gradient of time-since-fire where young, trembling aspen stands have the highest species richness while old black spruce stands have the poorest species richness. Finally, current harvesting practices do not change species richness (with the exception of white spruce stands), but do alter species composition. For example, harvested stands tend to support more grass species.

The results suggest that manipulating species richness will involve changing light regimes through such techniques as planting and stand thinning. However, the landscape pattern of richness is composed of a variety of diversities and preserving this variety seems more appropriate. Secondly, species composition and not species richness is affected by current harvesting practices. Forest managers really have two goals 1) preserving species diversity / composition and 2) promoting tree regeneration. In harvested stands there is a compromise between the cover of competing vegetation and the establishment and growth of tree seedlings not seen in burned stands. Part of this dichotomy is due to residual patches of vegetation, less exposure of suitable seedbeds and the potential spreading of clonal species due to scarification in harvested stands. With few exceptions, information in the literature comparing these characteristics between harvested and burned stands of similar ages is lacking.

INTRODUCTION

To preserve the natural patterns of plant species diversity, forest managers in the boreal forest attempt to imitate disturbance conditions associated with high intensity, stand replacing fires in the hopes of mimicking the ecological processes operating in the forest ecosystem. However, fire is not the only determinant of plant species diversity and may not even be the most important factor. Plant diversity patterns are dictated by the patterns of species distribution and abundance. These, in turn, are affected by gradients of time (e.g. Lawton 1978; Roberts and Christensen 1988; Richardson et al. 1995), moisture and nutrients (e.g. Whittaker and Neiring 1975; Marks and Harcombe 1981; Day, Jr. and Monk 1974; Roberts and Christensen 1988; Host and Pregitzer 1992) and light availability (Kull and Zobel 1991; Uemura 1994). Species richness is variable with time since the last disturbance and this is likely due to the frequency and types of disturbances in the region. Species richness can peak in the first year following fire and then decline with time (McConnell and Smith 1970; Russell and Parsons 1978; Specht et al. 1958), it can increase over time (Holland 1971; Nicholson and Monk 1974; Halpern and Spies 1995) or follow a unimodal pattern with time (Auclair and Goff 1971; Shafi and Yarranton 1973; Schoonmaker and McKee 1988). In most upland forests, moisture and nutrient gradients are the principal environmental gradients (Chabot and Mooney 1985; Barbour and Billings 1988) and generally, richness decreases with increasing moisture or nutrients (Zobel et al. 1976; Huston 1994; Kull and Zobel 1991). Species richness also decreases with decreasing light availability (Kull and Zobel 1991; Uemura 1994) and light availability decreases with increasing canopy stem density (Bartelink 1998). Therefore, as canopy density increases ground cover diversity decreases (Taft et al. 1995).

There have been numerous studies relating plant species composition to temporal and moisture and nutrient gradients (e.g. Romme 1982; Foster and King 1986; Host et al. 1987; Host and Pregitzer 1992) but few that have related plant diversity to light availability (Kull and Zobel 1991; Uemura 1994). No studies have related plant diversity to all three gradients. Therefore, the **first objective** was to determine the relative contributions of three gradients, temporal, moisture and nutrient, and light availability, in determining understory plant species richness in the southern mixedwood boreal forest. Due to the importance of light for photosynthetic processes, it is expected that light availability will be the primary determinant of species richness and that moisture and nutrient gradients will be secondary.

The **second objective** was to use the relative contributions of the different gradients to predict the pattern of species richness on the landscape. If light availability is the primary determinant of species richness, then the pattern of richness will be related to canopy species since the percent of incoming light transmitted to the forest floor depends on canopy species. For example, aspen dominated canopies transmit 14-40% while white spruce dominated canopies transmit only 5-11% of incoming light (Lieffers and Stadt 1994). Pine stands transmit intermediate levels of light.

Moisture and nutrient gradients also influence species diversity and typically, moisture and nutrient gradients are related to the topographic position on the hillslope (e.g. Kleiss 1970; Day, Jr. and Monk 1974; Malo et al; 1974; Anderson and Burt 1977; Harr 1977; Johnson 1981; Marks and Harcombe 1981; Ciha 1984; Bridge and Johnson 1999). That is, soil moisture and nutrient gradients increase down hillslopes in a predictable manner depending on the shape of the hillslope, and, based on these gradients, the distribution of vegetation can be predicted (Bridge and Johnson 1999). The shape of the hillslope depends on the surficial material, which affects the geomorphic processes of erosion and resistance (Hack and Goodlet 1960; Bull 1975). In turn, soil moisture flux rates and storage capacities, which are primarily dependent on topographic form, are affected (O'Loughlin 1981; Wood et al. 1988; Dawes and Short 1994). Thus, we see similar patterns of moisture and nutrient gradients and vegetation down hillslopes and across the landscape (Bridge and Johnson 1999). The repeatability of these patterns is attributed to plant tolerances (Wentworth 1981). Therefore, since low moisture and nutrients characterize hilltops, species diversity should be high. Further downslope, where moisture and nutrients are higher, species diversity should be lower.

Since canopy trees are organized on the hillslope according to moisture and nutrient gradients (Bridge and Johnson 1999), the pattern of light availability will be correlated to the pattern of moisture and nutrient gradients. Where moisture and nutrients are high, mixedwood stands dominate on glacial till substrate and black spruce stands dominate on glaciofluvial material. Where moisture and nutrients are low, aspen and jack pine dominate on glacial till and glaciofluvial substrate, respectively.

Although the landscape pattern of species richness is related to the hillslope pattern of richness, these hillslope gradients are abstract and do not necessarily reflect the spatial organization of the vegetation on the landscape. For example, hillslopes can be composed of both glaciofluvial and glacial till substrates so that black spruce may not always be found downslope of jack pine. How the hillslopes comprise the landscape will determine whether glaciofluvial substrates are adjacent to glaciofluvial substrates or glacial till. As well, landscape patterns are complicated by the temporal gradient of time-since-fire. For example, young stands, irrespective of species, will be characterized by high light and thus be relatively species rich while old stands will have low light availability and be species poor.

Since forest managers are attempting to mimic natural patterns of diversity the **third objective** was to determine whether current harvesting practices produce the same patterns of species richness and species composition as burned stands. Some studies have reported a loss of species diversity in harvested stands compared with undisturbed stands (Meier et al. 1995). However, the real issue is whether species composition is being altered. If light availability and moisture and nutrient gradients are the principal controls of species richness, then species richness patterns in harvested areas are likely to be the same as those in burned areas. This is because initially, light availability is unlikely to be much different between burned and harvested sites and because moisture and nutrient gradients are generally fixed on the landscape. Therefore, species diversity should be similar. However, species composition may be altered since stand characteristics that affect regeneration, such as the amount of exposed mineral soil, differ between harvested and burned stands (Fleming et al. 1987). Alternatively, current harvesting practices may have no effect on diversity or composition. For example, Reich et al. (1999) detected no differences in species diversity or composition in post-fire and post-logged stands of comparable age (1-100 years) in the boreal forest. They suggest that this is because, in terms of disturbance severity, both crown fires and logging are comparable.

SUMMARY OF DATA ANALYSIS

Study Area

The study area is located in central Saskatchewan and covers a total area of approximately 8000 km^2, including Prince Albert National Park (PANP) and the surrounding Forest Management License Area (FMLA) leased by Weyerhaeuser Canada Ltd. This area is part of the southern mixedwood boreal forest (Rowe 1972). It has a gentle relief with elevation ranging from 450 m to 900 m a.s.l., and is dominated by undulating hummocky morainal deposits. There are eight tree species in the study area including white spruce (*Picea glauca* (Moench) Voss.), black spruce (*Picea mariana* (mill) B.S.P.), jack pine (*Pinus banksiana* Lamb.), balsam fir (*Abies balsamea* (L.) Mill.), tamarack (*Larix laricina* (Du Roi) K. Koch), trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.) and white birch (*Betula papyrifera* Marsh.).

Sampling Regime

Sampled stands were greater than 4 hectares in size, had vegetation rooted in the mineral soil with no evidence of water in the top 30 cm of the mineral soil and were visually homogeneous with respect to stand age, structure and species composition. One hundred and twenty-one stands with no evidence of significant anthropogenic disturbance were sampled in and around Prince Albert National Park. Thirty-eight harvested stands were sampled in Weyerhaeuser's FMLA. To reduce variation in the data, only stands that underwent the same post-harvest treatments with similar pre-harvest compositions were selected. For example, all harvested trembling aspen stands were left to naturally regenerate, jack pine stands and black spruce stands were either left to naturally regenerate or were site prepared with anchor chains and white spruce stands were site prepared with disc trenchers, planted with white spruce and thinned of aspen as they matured. Stands ranged in age from 0-11 years, since Weyerhaeuser only began clearcutting in 1986.

In each stand, presence or absence of vascular herbaceous species was recorded in thirty 25 cm^2 quadrats. Species diversity was measured as species richness, where species richness is simply the number of species summed over all 30 quadrats. Only herbaceous species were used to estimate species richness since there are only 8 tree species in the boreal forest.

Disturbance was measured as time since the last fire, moisture and nutrient gradients as distance from the ridgeline and light availability as canopy stem density. Time-since-fire was established by Weir et al. (1999). Distance from the ridgeline was established by Bridge and Johnson (1999). Canopy stem density, as well as understory and shrub species, were sampled using the point centred quarter method (Cottam and Curtis 1956).

Objective 1: What Is The Relative Contribution Of The Temporal, Moisture And Nutrient And Light Availability Gradients, In Determining Species Richness?

Light availability was the primary determinant of species richness since only canopy stem density and canopy species showed a significant relationship with species richness in the standard least squares model ($p<0.0001$) (Figure 1). The variables of time-since-fire and distance from the ridgeline increased the amount of variation explained (72%) but did not show significant relationships with species richness. However, light availability is not the sole determinant of species richness. Remember that distance from the ridgeline is correlated to canopy species (Bridge and Johnson 1999) and thus the significance of canopy species reflects the importance of moisture and nutrient gradients as well as light availability in determining species richness.

Objective 2: What Is The Pattern of Species Richness?

Hillslope:

The pattern of species composition is related to topographic position on the hillslope, dominant canopy species and substrate material. This pattern of composition was derived from a Principal Component Analysis. Principal Component Analysis reduces the dimensionality of the species abundance data set so that fewer axes explain most of the variation. Stand positions on the first two principal components could be grouped into classes that correspond to the dominant canopy species as well as to the substrate. These include classes dominated by jack pine and black spruce on glaciofluvial substrate and trembling aspen and a mixedwood class comprised of trembling aspen, white spruce and balsam fir on glacial till. In addition, stand positions on the first two principal components were also strongly related to topographic position on the hillslope.

Since the pattern of species composition was related to dominant canopy species and substrate, the pattern of species richness was determined by comparing mean species richness of the herbaceous stratum within substrate but between the dominant canopy classes using t-tests (two-tailed, $p<0.05$). Species richness was significantly different between jack pine and black spruce dominated stands ($t= 2.40$, $p<0.05$) and between trembling aspen and mixedwood stands ($t= 4.91$, $p<0.001$). Therefore, on glacial till substrate, aspen dominated stands are found near the tops of hillslopes and are species rich (Figure 2). Mixedwood stands of aspen, white spruce, and balsam fir are found further downslope and are species poor. On glaciofluvial substrate, jack pine dominated stands occupy hilltops and are relatively species rich. Stands dominated by black spruce are found further downslope and are species poor.

Figure 1. Results of the standard linear regression model where canopy stem density and canopy species show significant relationships with species richness.

Figure 2. General landscape patterns of vegetation composition in Prince Albert National Park. The shapes of the hillslopes depict the profile of most hillslopes in Prince Albert National Park. The tree symbols depict the general change in dominant canopy species down the hillslope, which is based on the relationship between stand positions on the abstract moisture and nutrient gradients, and the stand distances from the ridgeline (Bridge and Johnson 1999).

Landscape:

We know that the hillslope pattern of species richness is related to canopy species. Therefore, we should be able to predict species richness using a LANDSAT TM image since it is produced from reflectances of the canopy vegetation in 6 spectral bands and 1 thermal band. We also know that species richness is related to distance from the ridgeline and that the pattern of time since the last fire should also affect species richness. Therefore, the addition of a Digital Elevation Model and a digitized time-since-fire map (Weir et al. 1999) should improve the accuracy of the prediction. The predicted species richness map using LANDSAT TM image, a digitized image of a time-since-fire map and a Digital Elevation Model (DEM), had an overall accuracy of 76% (Figure 3).

Therefore, the landscape pattern of species richness is related to both the hillslope pattern of species richness (which is related to the gradients of light availability and moisture and nutrients) and the temporal gradient of time-since-fire. Young, trembling aspen stands have the highest species richness, while old black spruce stands have the poorest species richness.

Objective 3: Do Current Harvesting Practices Produce The Same Patterns Of Species Richness And Composition As Burned Stands?

Current harvesting practices do not change species richness (with the exception of white spruce stands), but do alter species composition. We compared mean species richness between harvested and burned stands of similar pre-disturbance dominant canopy species and only the harvested white spruce stands had significantly higher species richness than burned white spruce stands ($t=3.22$, $p<0.011$).

However, species composition differs between harvested and burned stands. Linear discriminant analysis was performed on harvested and burned stands of similar pre-disturbance canopy composition (Wilks' Lambda, $p<0.05$). Species abundances were transformed with the logistic transformation for multinormality. Accuracies ranged from 87 - 100%. Therefore, using the abundances of the species in Table 1, we can determine whether a stand was harvested or burned. Understandably, certain species are encouraged or discouraged depending on the disturbance type. For example, *Calamagrostis canadensis* is typically found in high abundances in harvested mixedwood stands but not in burned stands of similar canopy composition (Table 1).

MANAGEMENT APPLICATIONS

It is commonly believed that fire is more important in determining species richness than other factors and so the suggested strategy for preserving species diversity in the boreal forest is to imitate disturbance conditions associated with high intensity, stand replacing fires. We tested this hypothesis using a standard least squares model that indicates which variables have significant relationships with species richness as well as the relative importance of each variable. Light availability was the principal determinant of species richness followed by canopy species.

Figure 3. Actual distribution of plant species richness in Prince Albert National Park. A supervised classification of a LANDSAT TM image, using a digitized image of a time-since-fire map and a Digital Elevation Model (DEM), was performed using the image analysis software PCI^{TM} version 5.2. The image was taken on July 12, 1990 under cloud free conditions.

Table 1. species that discriminate between harvested and burned stands of the same pre-disturbance canopy species. Using the discriminating species, stands can be classified as burned or harvested with a percent accuracy. Wilks' Lambda tests significance of the discriminating function and has an associated probability.

However, moisture and nutrients are also related to canopy species. Therefore, moisture and nutrients also determine richness. That is, species richness is determined by the topographic position on the hillslope. The position plus the substrate determine the moisture and nutrients, and moisture and nutrient gradients organize the canopy trees on the hillslope, thereby establishing light availability. If forest managers wish to promote species richness, they need to increase light availability since moisture and nutrients are not easily manipulated.

Recall that time-since-fire was not a significant determinant of species richness. This is due, in part, to the fact that there is only a small proportion of the landscape in the younger age classes so their effect on species richness is minimal. Also, time-since-fire does not have a significant relationship with species richness under the current fire cycle of 25 to 75 years (Weir et al., this report). If the fire cycle decreased to less than 25 years, the relative importance of the temporal gradient compared with light availability and moisture and nutrients would likely increase. This is because, at shorter fire cycles, canopy closure will not have occurred and many light requiring herbaceous species will be present. It is unlikely that the fire cycle or the rotation age in harvested stands will decrease below 25 years. It takes about 70 years for trees to reach a diameter that is economically feasible to harvest.

Therefore, the real issue is not species richness, but rather changes in species composition. Since topographic position cannot be easily manipulated, forest managers need to focus their attention on the factors that cause differences in species composition between harvested and burned stands. Forest managers really have two goals 1) preserving species diversity / composition and 2) promoting tree regeneration. In stands burned by fire, tree regeneration is generally not a problem. Otherwise, we would see large tracts of land deforested and not recovering following fire. Greene and Charron (this report) have shown that seedling survival of jack pine, black spruce, white spruce and trembling aspen is much higher on mineral soil and humus seedbeds where the duff has been consumed by fire. Therefore, forest managers may want to imitate the patterns of duff consumption found in stands burned by fire (Miyanishi and Bajtala, this report) in an attempt to retain similar patterns of tree regeneration.

Preserving species diversity / composition and promoting tree regeneration are not mutually exclusive issues. In harvested stands, there is a compromise between the cover of competing vegetation and the establishment and height / diameter growth of tree seedlings that is not seen in burned stands. *Calamagrostis canadensis* can seriously inhibit the establishment of white spruce seedlings (Eis 1981; Lieffers et al. 1993) and in mixedwood stands of the southern mixedwood boreal forest, *C. canadensis* is characteristic of harvested but not burned stands (Table 2). Lieffers and Stadt (1994) demonstrated that, at 40% light transmission, the cover of *C. canadensis* is well below that attained in open sites and the height growth of *Picea glauca* is near maximum. Part of the problem is that harvested stands tend to have more types of seedbeds than burned stands. In addition to mineral soil and humus and organic layer seedbeds (Greene and Charron in this report), harvested stands also have litter, slash, and residual patches of intact vegetation such as moss and grass seedbeds, not found in burned sites (unpublished data). The residual patches of vegetation are the problem. For example, if *C. canadensis* is found in nearly every square meter in pre-harvest understory it will rapidly spread post-harvest and decrease white spruce establishment (Lieffers et al. 1993).

Site preparation techniques also affect the cover of competing vegetation. In the stands sampled in Weyerhaeuser's FMLA, jack pine and black spruce stands were anchor chain scarified and white spruce stands were disc trenched. In northwestern Ontario, scarification resulted in four times less exposure of mineral soil and humus than wildfires (Fleming et al. 1987). With less exposure of the mineral soil, potential seedbeds for tree regeneration are lost (Greene and Charron this report). Anchor chain scarification and disc trenching also potentially spread clonal species by cutting their rhizomes (Lieffers et al. 1993). In fact, *C. canadensis*, *Elymus innovatus* and *Fragaria virginiana* are characteristic of, and found in high abundance in, harvested jack pine and mixedwood stands and not in the burned counterparts (Table 1). This dichotomy between the cover of competing vegetation and tree regeneration between harvested and burned stands is another reason forest managers may wish to imitate the patterns of duff consumption in burned stands (Miyanishi and Bajtala, this report).

CONCLUSIONS

Light availability is the principal determinant of species richness while moisture and nutrients are secondarily involved. Disturbance processes may not be a very important determinant of species diversity patterns in the boreal forest due to the type and frequency of disturbance. For example, the main disturbance in the southern mixedwood boreal forest is large, high intensity, stand replacing fires. In the Pacific Northwest, there are a variety of disturbances including large wildfires, low intensity underburns, windstorms and pathogens (Halpern and Spies 1995). These disturbances affect forest structure in different ways. Therefore, plants adopt many strategies to be successful. In Prince Albert National Park, the fire cycle has changed three times since 1700 (Weir et al. 1999). Therefore, in the boreal forest, plants can adopt a strategy of recolonization within the first few years following fire. In fact, this has been demonstrated for tree species in the southern mixedwood boreal forest (Greene and Charron this report). Herbaceous plants may follow the same strategy since, given the variable fire cycle, plants that adopt a strategy of establishing a long time after fire may never get the opportunity.

The hillslope pattern of species richness is related to the dominant canopy species which is, in turn, related to substrate material and topographic position on the hillslope. Therefore, on glacial till, trembling aspen stands are found near the tops of hillslopes and are species rich while mixedwood stands, further downslope, are species poor. On glaciofluvial substrates, jack pine dominated stands on the tops of hillslopes are species rich while further downslope black spruce stands are species poor. The landscape pattern of species richness is related to the hillslope pattern of species richness as well as to the temporal gradient of time-since-fire. Young, trembling aspen stands have the highest species richness, while old black spruce stands have the poorest species richness.

Current harvesting practices do not change species richness (with the exception of white spruce stands), although they do alter species composition. If the goal is to imitate the forest ecosystem processes, then forest managers should be examining the change in species composition caused by harvesting and not changes in species richness. Forest managers really have two goals: 1) preserving species diversity / composition and 2) promoting tree regeneration. In harvested stands there is a compromise between the cover of competing vegetation and the establishment and growth of tree seedlings not seen in burned stands. Part of this dichotomy is due to residual patches of vegetation, less exposure of suitable seedbeds and the potential spreading of clonal species due to scarification in harvested stands.

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A model of fragmentation resulting from human settlement in the mixedwood boreal forest of Saskatchewan.

SFM Network Project:

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

by

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EXECUTIVE SUMMARY

One of the objectives of the SFM has been to use forestry practices to mimic the effects of natural disturbances on the landscape. To ensure that forestry practices are mimicking natural disturbance processes rather than other anthropogenic disturbance processes, it is important to determine what effects both natural and man-made disturbance processes have on the landscape. Natural disturbance processes temporarily fragment the forest, leaving a mosaic of age classes and forest types, while agricultural practices leave different patterns and are more persistent in altering the landscape by converting forest to agriculture. Therefore, we define fragmentation as a continuum, with natural disturbance occupying one extreme and agricultural disturbance on the other. The **objective** of this study was to model fragmentation resulting from agricultural practices, since models of fire frequency have already been developed by Weir et al. (elsewhere in this project report) to determine the fragmentation patterns resulting from natural disturbance. The next step will be to modify the agricultural fragmentation model to determine what patterns forestry activities will leave on the landscape and to place fragmentation due to logging along the disturbance continuum.

Fragmentation resulting from human activities, whether it is permanent or temporary, also concerns ecosystem managers because of its widespread occurrence and effect on ecosystem processes. The conversion of much of the eastern half of the North American continent to a productive agricultural landscape, and the recent conversion of the southern edge of the western boreal forest to mixed agriculture, have significantly altered the structure of the North American forest. Forests to the immediate north of the agricultural fringe have also experienced human disturbance from logging or pulpwood cutting activities, and locating a forested area that is not influenced to some degree by human activities is unlikely. A mechanistic understanding of fragmentation is needed to understand the implications of these widespread human disturbances on ecosystem processes such as animal and seed dispersal, habitat loss, vegetation composition and natural disturbance.

Previous studies in landscape ecology have attempted to quantify fragmentation based on the patterns created. Unfortunately, this descriptive approach lacks generality since it does not define the underlying mechanisms of the fragmentation process. As a result, patterns produced by similar mechanisms (processes) can appear different on different landscapes. Since settlement is a decision-based process based on maximizing the ratio of economic return to energy investment, a decision-based model of the fragmentation process will be used to determine which parts of the landscape are more likely to experience human disturbance, through settlement and agricultural activities, and which are more likely to be left as forested remnants. The decision rules used to determine where to settle are based on biophysical and socioeconomic attributes such as nearness to neighbors and transportation networks, as well as moisture and nutrient gradients.

Empirical maps (1890-1960) of land use change in the mixedwood boreal forest south of Prince Albert National Park, Saskatchewan, were compared to simulations of land use change

from a decision-based fragmentation model to determine which decision rules were driving the settlement process. Amount of stoniness, soil formation and soil texture govern the fragmentation that occurs as a result of agricultural practices, highlighting the importance of terrain structure on forest fragmentation. Areas of lacustrine origin with fine textured soils and few stones were most influential, followed by soils of glaciofluvial and glacial till origin. Other biophysical and socioeconomic attributes did not seem to be very important in influencing the settlement decision rules.

Our fragmentation model can be used as part of a **tool kit** to predict which parts of the terrain are most likely to experience settlement. The predictive ability of this model has many applications. For example, this model of fragmentation can be combined with information on dispersal mechanisms, migration patterns and habitat preferences of birds and other wildlife to determine how a change in landscape or a change in decision rules will affect these species. In forests that have been fragmented this model can also be used to predict the behavior of natural disturbance processes (e.g. fire, insects), which follow certain rules of spread.

Since the decision rules of logging are similar to the decision rules of settlement, the next step will be to modify the fragmentation model to determine what patterns cutting and regeneration will leave on the landscape. The fragmentation patterns resulting from the model of forestry activities will then be compared to patterns resulting from the settlement model, as well as to patterns resulting from existing models of fire frequency, to determine how forestry practices should operate to best mimic the effects of natural disturbances on the landscape.

INTRODUCTION

The physical manifestation of both natural and man-made disturbance processes, defined here as fragmentation, can have both permanent and temporary effects on the landscape. Natural disturbance processes temporarily fragment the forest, leaving a mosaic of both age classes and forest types that are different than the patterns created by the long-lasting removal of forest sections by agricultural activities. However, abandonment of farmsteads and shifting agricultural practices may leave fragmentation patterns more similar to the patterns left by natural disturbance processes than to the patterns normally associated with persistent agricultural activities. Ecosystem managers are interested in using forestry practices to mimic the effects of natural disturbance processes on the landscape. To ensure that forestry practices are mimicking natural disturbance processes rather than other man-made disturbance processes, it is important to determine what effects both natural and man-made disturbance processes have on the landscape.

Fragmentation operates within a continuum of disturbance. Occupying one end are natural disturbance processes with regrowth of the forest, while at the other extreme are agricultural practices with little or no regrowth of the forest. Other fragmentation processes (i.e. logging, shifting agriculture, homestead abandonment) lie somewhere between these two endpoints. Since models of fire frequency have already been developed to determine fragmentation patterns resulting from natural disturbance (Weir et al. elsewhere in this project report), the objective of this study is to model the fragmentation resulting from agricultural practices. Once the two endpoints on the disturbance continuum have been defined, the next step will be to modify the fragmentation model by incorporating cutting and regeneration to determine where the fragmentation resulting from logging activities lies along the disturbance continuum. It is unknown whether forestry practices result in landscape patterns that are more similar to those patterns created by natural disturbance processes, to those created by temporary agricultural practices or to those created by enduring agricultural practices.

Fragmentation resulting from agriculture, whether permanent or temporary, also concerns ecosystem managers because of its widespread occurrence and effect on animal and seed dispersal, habitat loss, natural disturbance and other ecosystem processes (Burgess and Sharpe 1981; Noss 1987; Saunders et al. 1991; Wilcove et al. 1986). Although human disturbance processes operate at small spatial scales, their effects are widespread throughout the mixedwood boreal forest and include the valleys of interior British Columbia, the wooded plains of central Saskatchewan and Manitoba, the Peace River District of Alberta and the Claybelts of Ontario (Figure 1). Logging practices for saw timber and pulp occur in the northern region of this area, while the southern region has either been fragmented by settlement or completely converted to agriculture (Weir and Johnson 1998). The widespread prevalence of agriculture at the landscape scale means that many forested areas are either adjacent to, or influenced by, this man-made

Figure 1. The agricultural fringe in the southern boreal forest in Western Canada (modified from Vanderhill 1958).

disturbance. For this reason it is important to understand the underlying mechanisms of this disturbance process.

Previous studies in landscape ecology have focused exclusively on singular landscapes, classifying the change in spatial patterns from settlement processes and quantifying fragmentation based on the patterns created (Moran 1990; Leemans 1992). Unfortunately, this descriptive approach lacks generality, since it does not define the underlying mechanisms of the fragmentation process. For example, patterns produced by similar mechanisms (processes) can appear different on different landscapes. In the same way, different processes may produce similar patterns on different landscapes. Pattern analysis would be unable to discern whether the differences in pattern are due to different topographies or to different process mechanisms. Our approach is to study fragmentation as a disturbance process and to define the underlying mechanisms. The generality of this approach is more desirable since the fragmentation model can be applied to any landscape defined by those mechanisms.

Settlement is not haphazard or random, but is instead a decision-based process with orderly mechanical movements operating in response to predictable laws and landscape patterns (Lloyd and Dicken 1972; Meinig 1979). Humans settle in specific areas to maximize the agricultural return per energy investment (Hall et al. 1986; Odum 1983). In general, population growth and land use policy influence the amount of land use change, while physical features fundamentally determine the pattern of land use change (Hall et al. 1995). Although basic settlement patterns should reveal man's conscious selection of cultural and physical elements (Bylund 1960; Birch 1967; Meinig 1979; Robinson 1982), settlers were privy to only a limited amount of knowledge with respect to landscape attributes. Therefore, the decision rules used to determine where to settle are few and are based on biophysical and socioeconomic attributes (e.g. nearness to neighbours and transportation networks, moisture and nutrient gradients). This study has determined which of these attributes were most influential in deciding where settlement should occur. A decision-based model using statistical deduction was used for a first approximation of the best fitting attributes, and these attributes were used to determine which parts of the landscape are more likely to be settled and which are more likely to be left as forest remnants. Although the spatial pattern of the simulated landscape will more closely approach the actual landscape pattern as more attribute information is added, certain attributes were more important than others in determining settlement patterns.

SUMMARY OF DATA ANALYSIS

The study area is a 3260 km^2 agricultural region located just north of Prince Albert in central Saskatchewan, Canada. Although the forest cover of the study area has been modified and today is primarily composed of small isolated fragments of forest surrounded by agricultural land, it was originally covered by continuous mixedwood boreal forest (Rowe 1972). The topography of the study area ranges in elevation from 510 to 580 m above MSL. Glacial meltwater sorted the glacial debris, producing undulating glacial till deposits, fluvial plains of sandy outwash and finer textured lacustrine deposits. Forest Reserves were established on the sandy outwash plains (Ellis and Clayton 1970) while dark gray chernozemic and luvisolic soils dominate the rest of the region.

Timber and agricultural exploitation of this area began in 1890 (Weir and Johnson 1998). Between 1890 and 1920, white spruce sawlogs were extracted from berths located throughout the area. After the timber was removed, the berths were canceled and the land was opened to settlement. Organized settlement began in the 1890's after lands in the southern part of the province were largely occupied and most of the homesteads in this region were claimed for settlement. Between 1890 and 1920, the only areas that were not open to settlement were the Indian and Forest Reserves. The majority of the remaining homesteads were claimed in the 1930's, when homesteads in southern Saskatchewan were abandoned because of drought (Fitzgerald 1965). Agriculture consisted primarily of grain (wheat and oats) and livestock operations (Stutt and Van Vliet 1945).

The first step of this study was to develop a model of fragmentation based on the decision rules driving the settlement process. Digital attribute maps of soil texture, soil formation, slope, stoniness, distance to railroad and distance to roads were first reclassified as percent disturbed maps by comparing the categories in each attribute map to empirical land use maps of the mixedwood boreal forest south of Prince Albert National Park, Saskatchewan. To determine which biophysical and socioeconomic attributes were most important in governing the fragmentation process of settlement, a statistical deduction approach (Principal Components Analysis) assigned weights to the digital attribute maps. Attributes highly correlated to disturbance received large weights and were more important in influencing land use change, while attributes less correlated to disturbance received smaller weights. Principal Components Analysis was an appropriate method since the interrelations among factors affecting land use change are unknown. Other statistical methods require that the dependence or independence among variables be known.

Six Principal Components Analyses were carried out for each of the six decades from 1900-1960 on the percent disturbed maps and weights proportional to the attribute’s coefficient in the first principal component were assigned to each percent disturbed map. The first principal component accounted for 48% - 61% of the variation and was defined consistently in all analyses by large positive weights for amount of stoniness, soil formation and soil texture. The second principal component accounted for an additional 17% - 30% of the variation and was defined by a large positive weight for nearness to railroads.

The results confirm that terrain structure fundamentally determines the pattern of land use change. Since settlement is a decision-based process operating at the scale of the individual settler, the ability to recognize different vegetation zones and soil types was reflected in the settlement pattern. That is, a map cell was more likely to experience disturbance if it had few stones, was classified as either a lacustrine, glaciofluvial or glacial till site and if its soil was a fine textured silty loam, clay or clay loam. These soil characteristics are conducive to the successful harvesting of wheat crops and to livestock operations. Agricultural disturbance rarely occurred on sites with large amounts of stones, on steep slopes or in depressions, on organic soils or on very coarse soils such as gravel or sand.

To confirm that the weights correctly identified the attributes driving the settlement process, simulations were run incorporating the attribute weights in a spatially explicit, GIS based computer program. The settlement process was simulated by searching the landscape for locations with the highest percent disturbed on the heavily weighted attributes. The model of fragmentation was then validated by comparing the settlement simulations to empirical settlement data. The Kappa parameter was used to compare the percent success of the simulation to the expected percent success due to chance alone. Success occurred when a grid cell in the simulated map matched the corresponding grid cell in the empirical map of land use. A Kappa equal to 1 indicates that the simulation is perfect, while a Kappa equal to 0 indicates that the simulation is only as successful as would be expected by chance alone. The Kappa for the undisturbed cells ranged in values from 0.1384 to 0.6925 while the Kappa for the disturbed cells ranged in values from 0.3742 to 0.6993. Overall Kappa values ranged from 0.7282 to 0.7903. The percent of total cells classified correctly by the model ranged from 70% - 89%. These results indicate that the fragmentation model performed well in predicting the locations of settlement and in determining the decision rules used to settle the landscape (Figure 2a and b).

MANAGEMENT APPLICATIONS

The simplification of the settlement process into a general model has several applications. Our mechanistic approach provides inherent understanding of the spatial organization of the patterns on the landscape. Unlike many pattern analysis studies which only provide a description of the pattern and then attempt to correlate this pattern to an ecosystem process (e.g. fractal dimension, amount of edge, fragmentation indices, etc.), we can use our model as part of a **tool kit** to predict where and why fragmentation occurs. This approach is more powerful because it allows us to determine the mechanisms controlling fragmentation and how those mechanisms influence other ecosystem processes.

This model has shown that fragmentation is not a random process, but that the spatial arrangement of forested remnants across the landscape reflect the spatial arrangement of productive and unproductive land. Land use policy makers who must decide how to optimally partition the land into various uses can apply this model in predicting what effects their decisions will have on the landscape. The ability to predict areas that are susceptible to fragmentation is

Figure 2a. 1963 map of simulated land use change of the mixedwood boreal forest south of Prince Albert National Park, Saskatchewan.

Figure 2b. 1963 map of empirical land use change of the mixedwood boreal forest south of Prince Albert National Park, Saskatchewan.

also of practical use to the forestry industry. Large forestry operations, as well as small logging companies, may want to predict the location and distribution of remnant forest stands across the landscape to increase their economic productivity. For example, the ability to predict the type of forests remaining on the landscape can influence decisions regarding what proportion of the operation should be devoted to hardwoods and what proportion to softwoods. As well, this model can be used to predict the distance or connectivity between remnant stands to reduce transportation costs and to debate the merits of one land use policy to that of another.

Another application of this tool is to alter the decision rules driving the fragmentation model and analyze the change in fragmentation patterns across the landscape. Each rule could be manipulated separately to compare the resulting landscape patterns to those found by the original settlement rules. Ecosystem managers may find this useful when predicting the landscape effects of a particular land use policy on a singular landscape or in determining how topography alters the fragmentation pattern. Our plan is to incorporate the decision rules used in logging (i.e. a particular slope angle, nearness to roads, etc.) and use the model to predict what patterns cutting and regeneration will leave on the landscape. The patterns resulting from forestry activities can then be compared to patterns resulting from the settlement model and those from existing models of fire frequency to determine how forestry practices should operate to best mimic the effects of natural disturbances.

This model can also be used to study the effects of fragmentation on ecosystem processes by predicting changes in connectivity of forested remnants. For example, birds and wildlife are often restricted in their distributions by habitat type and by the amount of continuous forest. We can use this model to predict the spatial distribution of specific stand types across the landscape to determine the importance of the connectivity of forested remnants to their dispersal and migration patterns. Another process that fragmentation also affects is the fire cycle. The spatial continuity of forest stands (i.e. fuel) is essential for fire to propagate across the landscape. There exists a critical point at which the forest becomes so fragmented that the individual fires along the flaming front can no longer connect and begin behaving independently of each other. We can use this fragmentation model and our knowledge of fire spread to determine this critical fragmentation value and develop a causal mechanism linking the effects of forest fragmentation to the spread of fires.

CONCLUSION

To ensure that forestry practices are mimicking the effects of natural disturbances on the landscape and not other man-made disturbance processes, it is important to study the effects of both natural and man-made disturbances. The first step of the study was to characterize fragmentation effects on the landscape based on a continuum of disturbance. Since fire frequency models have already been developed (Weir et al. elsewhere in this project report) to define one end of the continuum, empirical data were used in this study to develop a fragmentation model based on the decision rules of settlers to determine the other extreme of the continuum. It was found that terrain structure governed the forest fragmentation resulting from human settlement since areas of lacustrine origin with fine textured soils and few stones were preferred, followed by areas of glaciofluvial and glacial till origin. The importance of this study is that the settlement process has been simplified into a general model which can be applied to other landscapes. This model can be used to provide insight into how agricultural settlement can change the pattern on the landscape.

What remains to be determined is where forestry practices fit on the disturbance continuum. To answer this question, records of logging activities will be combined with management policies and goals to determine the decision rules employed by forestry companies to fragment the forest. Since forestry managers incorporate the effect of terrain when choosing the type and age of stand to harvest, we should be able to easily modify the settlement model to determine what patterns cutting and regeneration will leave on the landscape. The fragmentation patterns resulting from the model of forestry activities can then be compared to patterns resulting from the settlement model and from existing models of fire to provide insight into how landscape patterns change with respect to changes in land use.

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Patterns of 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.

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EXECUTIVE SUMMARY

Post-fire regeneration of *Pinus banksiana* (jack pine) and *Picea mariana* (black spruce) is generally limited more by the availability of appropriate seedbed than of seeds, due to their in situ aerial seedbanks. Successful recruitment of these species is largely restricted to areas from which duff (the organic layer above the mineral soil) has been removed. Studies have shown that duff consumption in boreal forest fires exhibits extreme patchiness within stands. Since successful seedling establishment appears to occur primarily within burned patches from which the duff has been consumed, the ability to predict the total area as well as the spatial distribution of these burned patches would help in predicting the density and spatial distribution of post-fire seedling regeneration. Therefore, the objective of this study was to describe and explain the spatial pattern of duff consumption within and between *P. banksiana* and *P. mariana* dominated stands. The burned patches were found to be significantly spatially correlated to the standing boles of fire-killed trees. A major factor explaining this relationship appears to be the significantly lower duff moisture found directly beneath tree crowns since propagation of smoldering combustion (the process by which duff is consumed) is limited by duff moisture. This within stand spatial variation in duff moisture can be explained by the interception of precipitation by tree crowns as well as inhibition of dew formation beneath tree crowns. The large within-stand variability in duff moisture and in duff consumption by fire raises questions about the usefulness of mean estimates of either measure, especially for predicting post-fire seedbed conditions.

The results from this study also found significant differences between the two stand types in their patterns of duff consumption; *P. banksiana* stands had a greater number of burned holes in the duff than *P. mariana* stands, but these holes were significantly smaller and the total area covered by these holes was significantly less than in *P. mariana* stands. These differences were explained by the more clustered distribution of trees in *P. mariana* stands compared with *P. banksiana* stands, resulting in larger continuous areas of dry duff. The implications of these results are that the density and spatial distribution of trees in the post-fire stand may be the result of the density and spatial distribution of trees in the pre-fire stand. In other words, a high density stand with clustered trees would result in a few large areas of duff consumption within which successful seedling recruitment is likely to occur. Thus, the trees in the regenerating stand after the fire are likely to be clustered within these burned patches of duff. The results of this study together with those from the Greene and Charron study (this report) could help provide a guide to the types of burned stands that may require some post-fire treatment (e.g. surface scarification) for the desired regeneration.

ACKNOWLEDGEMENT

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INTRODUCTION

It has long been recognized that boreal forest trees such as *Pinus banksiana* (jack pine) and *Picea mariana* (black spruce) establish best on exposed mineral soil (Van Wagner 1972; Chrosciewicz, 1970, 1974, 1976). Overlying the mineral soil in unburned boreal stands is a layer of litter and duff. Duff (the O soil horizon) is composed of a top O_f layer of partially decomposed material whose origins can still be recognized and a bottom O_h layer of decomposed material whose origins cannot be identified (Van Wagner 1972). Greene and Charron (this report) show that seedling survivorship is similar on mineral soil and the O_h layer but low enough on the O_f layer to virtually preclude successful seedling recruitment on this latter seedbed. Thus, anyone interested in post-fire seedling regeneration must be concerned with the consumption/removal of the O_f layer by fire. Duff is consumed primarily by smoldering combustion which occurs after passage of the flaming front.

Duff consumption has generally been measured by the mean difference between pre- and post-fire duff depths or mass. However, a number of studies (e.g., Van Wagner 1972; Chrosciewicz 1976; Dyrness and Norum 1983; Zasada et al. 1983) have commented on the large within-stand variability in duff consumption. As described by Dyrness and Norum (1983), burned sites in the boreal forest appear to be characterized by “many deeply burned holes scattered among broad areas of unburned or scarcely burned forest floor”. This observed discontinuous pattern of duff consumption raises questions concerning the usefulness of *mean* measures of post-fire duff depth or duff reduction as an indication of the availability of suitable seedbed for tree seedling regeneration. Furthermore, since successful seedling regeneration appears to be primarily restricted to these burned holes in the duff (Greene and Charron, this report), we should be more concerned with the areal extent and spatial distribution of these burned holes rather than with mean estimates of either duff consumption or post-fire duff depths.

Therefore, the **objective** of this study was to describe and explain spatial patterns of duff consumption (i.e. burned holes in the duff) in order to develop some understanding of the process by which duff is consumed in a fire and the major factor(s) influencing this process. Our study site was a 900 ha burn near Bittern Creek, located in the Weyerhaeuser FMLA in the mixedwood boreal zone of central Saskatchewan. This stand-replacing fire was ignited by lightning on June 5, 1996 and burned for 3 days. Data were collected from this site 3 months after the fire. We sampled 20 upland mature stands dominated by either *Pinus banksiana* or *Picea mariana*, mapping and measuring standing and fallen trees as well as measuring spatial variation in duff depth. The burned holes in the duff were very distinct. Therefore, these holes were mapped and their areas were visually estimated. The data were used to describe the extent and patterns of duff consumption within and between stand types as well as to attempt to relate the patterns to stand characteristics.

In 1997, data on spatial variation in duff characteristics (moisture, depth and bulk density) were collected from unburned stands comparable to the burned stands in age, density and species composition. Also, the influence of tree crowns on precipitation interception, duff moisture, depth and bulk density was investigated.

A detailed description of the methods and results can be obtained in Bajtala (1999).

SUMMARY OF DATA ANALYSIS

Overall, we found that the mean percent of burned area was significantly greater in *P. mariana* stands (24.4%) than in *P. banksiana* stands (8.6%). Furthermore, the *P. banksiana* plots had on average three times the number of patches as the *P. mariana* stands, while those fewer holes in the *P. mariana* stands were significantly larger (by an order of magnitude) than the holes in the *P. banksiana* stands. Since each burned patch had to be initiated by at least one ignition point, the fact that the *P. banksiana* stands had significantly more patches but significantly less area in burned patches than the *P. mariana* stands indicates that the area of burned duff is not limited by duff ignition points but rather by whether or not smoldering is propagated or extinguished once the duff has been ignited.

The next step was to explain why smoldering would be preferentially propagated in the *P. mariana* stands, creating these large burned holes, and not in the *P. banksiana* stands. Examination of the maps showing the location of the burned patches and standing stems suggested that the burned patches may be spatially related to the standing boles of the fire-killed trees. Chi-square analyses confirmed that, for all but two of the stands, this spatial relationship was significant. The most obvious explanation for this relationship is the interception of precipitation by the tree canopy, decreasing moisture input to the duff directly beneath trees. Measures of precipitation throughfall for a sample of isolated trees in unburned stands found generally significantly increasing throughfall with distance from the stems although the degree of interception varied between rainfall events, even for the same trees. Thus, from precipitation inputs alone, we should expect drier patches of duff around the bases of trees. Furthermore, re-radiation from the canopy to the ground at night would inhibit surface cooling and dew formation directly beneath the canopy, thus influencing duff moisture even in the absence of rain. Actual measures of duff moisture obtained from beneath and beyond the canopy of *P. mariana* trees in unburned stands confirmed this pattern of significantly drier duff around the bases of trees. No significant differences were found in depth or bulk density of the duff beneath and beyond the canopy. Thus, within stand variation in duff moisture alone appears to be a reasonable explanation for within stand variation in duff consumption. Fuel moisture is a critical factor in the extinguishment of smoldering combustion (Ohlemiller 1985).

To use precipitation interception by tree crowns to explain the spatial patterns of duff consumption and their differences between stand types, we then looked at the density and spatial distribution of standing stems in the burned stands to obtain an idea of the distribution of the pre-fire tree crowns. First, the two stand types differed significantly in density of standing stems with the *P. mariana* stands having a significantly higher density of stems than the *P. banksiana* stands. Second, using nearest neighbour analysis, we found that the stems were significantly more clustered in the *P. mariana* stands than in the *P. banksiana* stands. The more clustered the stems and the higher the density of stems, the more likely it is that there would be both larger continuous patches of dry duff and a greater total area of dry duff.

Therefore, given the same weather conditions and the same precipitation in both types of stands, we would expect to find greater spatial discontinuity in duff moisture within *P. mariana* stands than within *P. banksiana* stands. This spatial discontinuity in duff moisture would be spatially correlated with the tree crowns. In turn we find that the burned holes in duff are spatially correlated with the trees. Continued propagation of smoldering is dependent on sufficient heat being transferred from the exothermic oxidation zone to the unburned duff to cause pyrolysis or heat degradation, resulting in the formation of char which is the first stage in the process of smoldering. The presence of moisture means that heat being generated from the oxidation of the char would be converted to latent heat in evaporating the water. The evaporation process thus acts as a heat sink and, if enough heat from the oxidation zone is used up in latent heat, there would not be sufficient heat to pyrolyze the unburned duff. This would result in the extinguishment of smoldering.

MANAGEMENT APPLICATIONS

There are several findings from this study that should be of interest to forest managers. The first is the recognition of the discontinuous nature of duff consumption. Since Greene and Charron (this report) found that the key factor in first year seedling survivorship is the seedbed type (i.e. humus (O_h) or mineral soil vs O_f), the success of post-fire regeneration is dependent not on the mean decrease in duff depth nor on the mean mass of duff consumed by fire (measures used in most previous studies of post-fire regeneration) but on the **area** over which the O_f layer is totally removed. If stands differ in pre-fire duff depth, a similar percentage loss of duff mass or mean duff depth can represent a significantly different availability of suitable seedbed for seedling regeneration.

The second is that, even in a stand-replacing crown fire such as the one occurring at Bittern Creek in 1996, removal of the Of layer occurred on only about 9% of the forest floor in *P. banksiana* stands and about 25% in *P. mariana* stands. Greene and Charron’s (this report) study of the post-fire seedfall in these stands indicates that the in situ aerial seedbank is depleted after the first couple of years and that the majority of seedling mortality occurs within the first year. Furthermore, Gutsell and Johnson’s (this report) study of stand dynamics indicates that recruitment of canopy trees is restricted to the first few years after fire. Thus, the condition of the forest floor immediately after the fire is critical in determining the density of trees in the post-fire stand. This would suggest that seedbed preparation (e.g. scarification of the forest floor) within the first year following fire would significantly increase the density of the post-fire regenerating stand. It also suggests that disturbance of the duff during salvage logging may have a beneficial side effect.

A third result of this study is a recognition of the patchiness of the post-fire surface in terms of available seedbed. This patchiness has important implications for the spatial distribution of the trees in the stand regenerating after a wildfire. Numerous small patches of suitable seedbed scattered throughout the stand (as we found in *P. banksiana* stands) would be expected to result in more regularly spaced small groupings of seedlings among which self-thinning would occur, resulting in a potentially lower density stand of trees that are more regularly or randomly distributed. On the other hand, a few very large patches of suitable seedbed covering a greater proportion of the stand surface (as we found in *P. mariana* stands) would be expected to result in stands with a higher density of trees that are clustered. Our study of unburned upland stands dominated by *Pinus banksiana* and *Picea mariana* found significantly higher densities of trees in *P. mariana* dominated stands with trees that were significantly more clustered in their spatial distribution. Although these may often be the natural types of stands regenerating after wildfires, they may not necessarily be the desirable types of stands in terms of fiber production. The explanation provided for the spatial distribution of trees found in these stands allows managers the opportunity to influence the post-fire stand through seedbed treatments.

CONCLUSIONS

In conclusion, we can make two points. The first is that the discontinuous nature of duff consumption points out the limitations of using mean measures of duff consumption or post-fire duff depth to predict post-fire seedbed availability and potential post-fire seedling regeneration. Second, we can speculate on the consequences of the patterns and stand type differences we found in the areal extent and spatial distribution of these burned patches of duff. A reasonable explanation for the higher stem densities and more clustered distribution of stems that we tend to find in *P. mariana* stands compared with *P. banksiana* stands lies in the greater area of burned duff and the fewer larger patches of burned duff occurring at the time of initiation of the stand after a fire. If this is the case, it may be that, not only is the species composition of the pre-fire stands likely to be repeated in the post-fire stands due to seed availability (see Greene and Charron’s report) but perhaps also the densities and spatial distribution of stems.

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Recruitment models: seed production, dispersal and juvenile mortality after fire and cutting

SFM Project:

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

by

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EXECUTIVE SUMMARY

Foresters are hopeful that they will be able to better regenerate clearcut sites if they are capable of mimicking natural disturbances. It is therefore important to understand processes influencing natural regeneration after disturbances. Models of tree regeneration that include seed production, seed dispersal, sprout production, and juvenile mortality have been developed for eight boreal tree species. The models have been divided into three groups depending on the mode of reproduction of the species of interest. The models are applicable to both fires and clear-cuts.

The first model is derived for species that disperse from aerial seedbanks like jack pine and black spruce, and therefore does not include a dispersal term. The second model derived for aspen and balsam poplar also lacks a dispersal term since the species recruit from root suckers. The third model derived for white spruce, balsam fir, and larch includes a dispersal term since the species must disperse from living sources.

The models demonstrate that both sprout and seed production are dependent on tree size (basal area) and seed size; that seed dispersal by wind is dependent on seed size (terminal velocity) and release height; and that germinant mortality is dependent on organic layer thickness and seed size.

In essence, the theory of the models is based on four easily measured parameters: two of them biotic (seed size and tree size) and two controlled by disturbances (distance-to-source and organic layer thickness). Thus, this study now provides foresters with tools to predict regeneration densities following disturbances such as burns and large clearcuts.

INTRODUCTION

Studies of population dynamics of boreal forest trees have found that recruitment of individuals which will eventually make up the canopy does not occur throughout the history of the stand but only during the first few years after large disturbances (Johnson 1992, Gutsell and Johnson in this report). Consequently the recruitment processes during this post-disturbance period are critical to the future growth and composition of a stand.

In the last 4 years we have developed models of tree regeneration (seed production, dispersal, and juvenile mortality) following large-scale disturbances. Although the theory is at present not general; it applies only to burns, we do have some data to indicate that it is applicable for any large clearing (stripcuts, clearcuts) where light is not limiting. We divide the eight boreal tree species into three functional groups. The first group includes the three hardwoods (aspen, paper birch, balsam poplar) that can regenerate asexually after a severe disturbance. The second group consists of jack pine and black spruce, which can also recruit from within the disturbance, but do so via an aerial seedbank rather than asexually. The final group involves the three species that must disperse into the disturbance via seed from living sources (white spruce, larch, and balsam fir). Of course the previous five species are also capable of colonizing sexually from disturbance edges. The **objective** of this study is to provide a series of simple tools for foresters to predict the regeneration following large disturbances. These are cohort models in that the density being predicted is for the initial group of seedlings that started in the first years following the disturbance.

The Asexual Recruitment Model

Root suckers

Drawing on published data sets for clearcuts and burns from Alaska, Saskatchewan, Minnesota, Ontario, and Quebec, Greene and Johnson (1999) have shown that aspen and balsam poplar root sucker density (F_D) is a function of pre-disturbance basal area density (the dimensionless B_D (m^2/m^2)) and time since disturbance (t in years):

$$F_D = 11600\, B_D^{\,0.79} (t+1)^{-1.64} \qquad (1)$$

This equation is expected to hold at least until 100 years after a disturbance (cf. yield tables such as those of Jarvis 1968). Unlike the equations for sexual recruitment below, we include time- since-fire because the clonal stems almost immediately begin to self-thin. We see no need to make equation (1) spatially realistic as poplar suckers typically recruit within about 10 m of the nearby boles and it is rare to find conspecific boles isolated by more than 10 m (except in cases where the poplars comprise such a small proportion of the basal area that they are of little interest to foresters).

Basal suckers

We have no model for basal suckering for poplars and birch but it seems reasonable to imagine that,

$$F_D=N_D \tag{2}$$

where N_D is pre-disturbance stem density (stems/m^2). That is, we picture the large number of rapidly thinning, asexual recruits as, in effect, a single self-replacing stem. An unpublished data set from Saskatchewan indicates that asexual stem number in birch is unrelated to the basal area of the parent bole while total basal area of the asexual stems (summed) is strongly correlated with parent basal area. We see, however, no practical significance for this.

THE SEXUAL RECRUITMENT MODELS

The basic model for sexual recruitment density (F_{Dx}) at distance x a decade after a severe disturbance is

$$F_{dx}=Q_D ST f(x) \tag{3}$$

where Q_D is seed density (seeds/m^2) within an area source (array of conspecific sources), S is juvenile survivorship, T is the number of years available for colonization before shading and seedbed deterioration dramatically reduce the initially high survivorship, and $f(x)$ is the dispersal term.

In what follows we will develop two varieties of the model. In the first version, appropriate for any wind-dispersed species, we deal with an area source adjacent to a burn or clearcut. In the second version, we deal with the two aerial seedbank species (jack pine and black spruce) that can colonize the clearing in situ (from standing dead trees or scattered slash).

Seed Production

Following Greene and Johnson (1994), the seed production equation is

$$Q=3067B^{0.92}m^{-0.58} \tag{4}$$

where Q is the mean annual seed production of a single seed tree, B is the basal area (m^2) of a single tree, and m is seed mass (in grams). We will assume that averaging across T years (the colonization period) will reduce the enormous temporal variation due to masting.

Let us translate Q in equation (4) to seed density, Q_D (seeds/m^2), the more appropriate measure for an area source, as

$$Q_D=3067B_D m^{-0.58} \tag{5}$$

where the exponent on B (0.92) can be ignored as we switch to B_D because it is sufficiently close to 1.0 that there is less than a 50% overestimate of the seed density given the relatively low coefficient of variation of conspecific seed producer (canopy tree) basal area.

Greene and Johnson (1999) examined the stored seed production in jack pine and black spruce and found that equation (5) is a good predictor of the accumulated seed bank; i.e. they behave as if they had a single mean year's crop.

Juvenile Survivorship

The great majority of mortality within a conifer cohort in the first decade occurs in the first summer, about 85% of the total mortality on mineral soil and burned humus, and about 99% of the total mortality on burnt O_f (Charron and Greene, unpubl. report; Greene et al. 1999). Subsequently, for a cohort, annual mortality is near zero until the onset of thinning. As argued by Greene and Johnson (1999) and Charron (1998), this juvenile mortality is greatly dependent upon seedbed quality, and, further, seedbeds in upland sites can be reasonably dichotomized as optimal (mineral soil, fresh or burnt humus, well rotted logs, fresh Sphagnum) or poor (fresh or burnt duff, non-Sphagnum mosses, undecomposed logs). Note that, with the exception of Sphagnum, these categories correspond to high or low porosity, respectively. That is, they represent a dichotomy in microenvironmental water availability at the scale of a boreal germinant (less than 4 cm in length: Charron 1998).

Relying on direct seeding results, Greene and Johnson (1998) have written the equation for juvenile survivorship (S) by the third year for a cohort averaged across all seedbeds as

$$S=0.43\ (pS_1+(1-p)S_2) \tag{6}$$

where the subscripts 1 and 2 refer to the optimal or poor seedbeds, respectively, and p is the fraction of the post-disturbance forest floor composed of the optimal seedbeds and

$$S_1=1-\exp(-1.83m^{0.43}) \tag{7}$$

$$S_2=1-\exp(-0.33m^{0.77}). \tag{8}$$

The survivorship for either seedbed category is a function of seed mass (m in grams), as this quantity controls germinant length. Charron (1998) showed that length was proportional to mass raised to the power 0.33 as expected from allometric reasoning.

Equations (7) and (8) apply only to recent disturbances sufficiently severe that light is ample for the first decade.

A simpler formula (with the assumption p=0.17) for burns and clearcuts is

$$S=0.28m^{0.52} \tag{9}$$

The initial value of p varies widely at the scale of the 30 x 2 m transects used by Charron (1998) ($0.05<p<0.7$). Consequently, even if seed deposition were uniform across an area, we would expect wide variation in seedling density. In addition, Charron (1998) found marked spatial segregation of seedbeds at the scale of inter-bole distances of 1-3 m with the areas at the bases of boles being effectively 100% mineral soil or humus, while the inter-bole areas was comprised of thick burnt O_f. Thus, there is, at this small scale, almost perfect self-replacement of vegetation types with conifers colonizing exactly the same sites as before while herbs, mosses, and shrubs resume their cover of the intervening areas (see also Miyanishi and Bajtala this report).

The value of p must decline with time-since-fire but the rate of decline is unclear. Charron and Greene (unpubl. report) report that mineral soil and humus were exceedingly rare in an 8-year-old fire with the predominant seedbed being leaf litter or pioneer mosses. By contrast, in more recent fires (two or three years after burning) mineral soil was still an appreciable component of the substrate. It would appear then that the great decline in p occurs in the interval 4 to 8 years after burning (the period of rapid increase in the herb/hardwood leaf area index). In a few more years our permanent plots at recent burns will permit us to clarify this issue.

As reviewed in Greene et al (1999), the time frame for the relatively high survivorship in equations (6) through (9) is short. After a few years, litter accrual and rapidly increasing leaf area indices begin to dramatically increase the first year mortality for a new cohort. This means that the period of actual recruitment after disturbance is short. No quantification has yet been carried out for this change in cohort mortality. However, we have permanent plots that we have monitored for four years in which each year we sow seeds. At present, we believe the recruitment period to be about four years. During this interval, S is given by equations (6) or (9) and after the fourth year, S=0 for a new cohort. Thus,

$$T=4 \tag{10}$$

For the aerial seedbanks of jack pine and black spruce, the colonization period is limited by seedbank depletion rather than seedbed deterioration, with the aerial cones effectively emptied of seeds by the second or third year, respectively, following fire.

Dispersal

As in Greene and Johnson (1996), we idealize the area source as an orchard-like array of conspecifics, with a source strength of Q_D (seed/m^2) experiencing a uniform distribution of horizontal wind azimuths. With x=0 defined as the forest edge, the amount of seeds (Q_{DX}=seeds/m^2/distance) in the clearing is given as

$$Q_{DX}=0.5Q_D\exp(-0.15(xf)^{0.5}) \tag{11}$$

where f is the mean terminal velocity (m/sec) of the seeds, and the empirical coefficients in the exponential term result from default parameters for the distributions of horizontal and vertical wind speeds for a forest 25 m in height. We have measured the terminal velocities of all the boreal tree species and arrived at the equation (r^2=0.87, N=8 species):

$$f=1.9m^{0.17} \tag{12}$$

Note that the exponent 0.17 is expected from dimensional considerations of the aerodynamics of lift (as in Greene and Johnson 1992).

Sexual Recruitment from a Forest Edge

Coupling equations (5), (9), (10), and (11) we write the equation for F_{Dx} (stems/m^2/distance) by about the tenth year following disturbance (with T = 4 years only) as

$$F_{Dx}=1717B_D\ m^{-0.06}\exp(-0.15(xf)^{0.5}) \tag{13}$$

Greene and Johnson (unpubl. report) have evidence that this argument applies fairly well to white spruce, balsam fir, larch, and balsam poplar in both clearcuts and burns. Note that in equation (13) the role of seed mass in production and survivorship has, essentially, canceled out and could be ignored.

Sexual Recruitment from Aerial Seedbanks

For jack pine and black spruce, the colonization term, T, can be ignored as the aerial seedbanks are essentially depleted by the third year following the death of the seed sources (Charron 1998). Thus, ignoring the dispersal term, we can write the recruitment density of these two species as

$$F_D=429B_D\ m^{-0.06} \tag{14}$$

Greene and Johnson (1999) have shown that equation (14) is a good approximation of recruit density following fire in Quebec, Saskatchewan, and Ontario. How well it might apply to clearcuts where cone-laden slash has been scattered is not known.

Residual Stands and Distance to Living Sources

Using color air photos of recent burns in central Saskatchewan, we have arrived at the following conclusions regarding the role of residual (unburnt) stands in post-fire recruitment.

First, the proportion of residual stands increases with burn area. Our largest burns (10,000 ha) have about 5% of the nominal area in residual stands. Nonetheless, the residual stands themselves have a log-normal distribution of sizes (median size around 0.1 ha); the great majority of the summed residual area is "wasted" in a few very large residual stands where the majority of the seed production falls within the stand.

Second, the distribution of distance-to-nearest-living-source is an extreme value distribution. The median distance is only about 100 m (around the maximum effective seeding distance for spruce, fir, and larch where we might expect adequate stocking from a large area source) but around 30% of the burn is farther than 250 m from any source. Consequently, much of the burn, as with a large clearcut, is poorly stocked by these three species. Further, the main reason the median distance in large fires is so small is not because of the residual stands but rather primarily because of the strong invagination of the nominal burn perimeter. In conclusion, residual stands certainly aid in the stocking of burns by the three obligatory dispersing species, but they are less important than the convolution of the main burn edge. In any case, the distance-to-source distribution makes clear that large burns can never be adequately stocked by these three species.

The final conclusion is that there is no strong tendency for one species to dominate the composition of residual stands as one might expect if there were marked differences in flammability. In the larger burns, aspen and white spruce had a 6% chance of being in a residual stand while black spruce and jack pine had a 4% chance. With a large enough sample size, such differences become statistically significant but it is not clear whether they are significant ecologically or silviculturally.

MANAGEMENT APPLICATIONS

We can draw from this research a number of conclusions of interest to managers. Keep in mind these conclusions apply only to burns and large man-made clearings in upland sites.

Poplar density can be tolerably well predicted from 1 to 100 years following disturbance as a simple function of pre-disturbance basal area per area and time-since-disturbance. Indeed, stand density of the poplar is the least variable phenomenon in boreal forest recruitment. Therefore, pre-harvest inventory data will allow prediction of post-harvest stem density. Despite what is sometimes said (largely anecdotally) in the forestry literature, we see no evidence that a small number of poplars per hectare can give rise to a well-stocked post-harvest stand.

The recruitment of white spruce, fir, and larch in burns and clearcuts is predictable but there is a large amount of variation. At the scale of a harvest block, this variation is primarily due to the percentage of mineral soil exposed by the fire or site preparation, and to the clumping of seed sources at the edges of the disturbance. The essentials of the management prescription for adequate natural regeneration are as follows. The cut requires a percentage mineral soil exposure that must rise as the basal area per area of the target species declines. For example, in an area where white spruce comprises a small fraction of the basal area, the amount of optimal seedbed must increase. Indeed, we can show that where white spruce basal area per area is less than 5 m^2/ha, even 100% mineral soil exposure (an impossible task) would give you adequately stocked stands in only about 20% of such harvest blocks.

One thing foresters can do to increase the likelihood of adequate stocking is to increase the ratio of edge to harvested area (thus increasing the mean number of seeds per area). This can be done most economically by strip cuts with very narrow residual strips. Nonetheless, we hasten to point out that even this measure cannot provide a highly reliable stocking if the source basal area per area is small.

We can also mention a public relations issue. Environmentalists have made much of the fact that natural recruitment of white spruce and fir in clearcuts is rather poor and, further, that the proportion of hardwoods (i.e. primarily aspen and paper birch) relative to conifers rises greatly following cutting. Thus, it has been argued that there is proof that the cuts are “unnatural”. We have shown that white spruce, fir, and larch colonize natural burns just as poorly as they colonize clearcuts. They never satisfactorily stock large burns. The reason is the dispersal constraint. The three hardwood species have in situ recruitment mechanisms and fast growth rates and thus their proportion of the recruitment (measured as either stem number or basal area) at, say, the tenth year following a fire is much higher than before the fire. Nonetheless, the sustained mortality of these asexual stems (in contrast to the conifers with their brief initial mortality) means that the difference in numbers will decline with time.

Managers are usually required to establish a post-harvest forest that is, more or less, similar in species composition to the pre-harvest forest. Our results argue that managers could best ‘imitate’ nature if they were permitted to maintain species proportions at the scale of the landscape rather than the harvest block. White spruce, fir, and larch shift around the landscape from one fire cycle to the next. Adequate stocking is only found within about 100 m of burn edges that contain a suitably large source strength. Given the inherent unreliability of sexual recruitment by these species (due primarily to temporal variation in seed production-masting-and the short lifetime of optimal seedbeds) the manager could argue for flexibility in the legislative stocking standards as a necessary pre-requisite of a shift toward reliance on natural regeneration as well as an attempt to ‘imitate nature’.

Jack pine, black spruce, and aspen essentially replace themselves following fire. Given that the bulk of jack pine seeds are released in the first few months following fire, adequate stocking is assured as long as salvage is delayed until the late autumn, and the machinery that crushes germinants/seedlings and churns seeds deep into the soil is limited to about 30% of the total surface area. The same reasoning applies to the asexual stems of aspen where the great majority will appear in the first summer. Black spruce is more problematic because its seed abscission schedule is staggered across the first three summers. We recommend that the black spruce portions of burns should have salvage delayed to at least the second autumn, where about 70% of the seeds have abscised.

CONCLUSION

The foregoing models have been adequately tested and the variables can be easily obtained. These models include functions for life history processes, and it is of some interest that seed mass and tree size figure repeatedly in the equations. Seed mass is inversely correlated with both seed production and dispersal and positively correlated with juvenile survivorship. As we saw, however, the roles of seed mass in production and survivorship tend to cancel out. Larger trees produce more seeds or asexual stems. Further, although it was embedded in the coefficients in equation (11), taller trees have more effective dispersal than shorter trees. The median dispersal distance of a single tree is proportional to the height of the tree.

Seed mass can be taken as default value from Schopmeyer (1974) as in Greene and Johnson (1994, 1996, 1999). Basal area density is a standard inventory measurement. In short, the models advanced here can be readily applied to burns and clearcuts.

Another conclusion from our research is that jack pine, black spruce, and the three hardwood species tend to simply self-replace at almost any spatial scale we might examine (Greene and Johnson 1999). There is no succession (see Gutsell and Johnson in this report). By contrast, fir, white spruce, and larch shift around the landscape from one fire cycle to the next. A burnt white spruce stand, for example, will not have white spruce recruitment unless unburnt seed sources are nearby. Most of the time there will be no nearby sources as over 50% of the burn area is farther than adequate seeding distance from the nominal burn edge or residual edges.

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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

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EXECUTIVE SUMMARY

The proposal that forest management practises 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 have challenged our strong 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 static diameter and static age distributions, have led to questionable conclusions. Since the conclusions reached by these studies have guided forest management practises, 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 wildfire. 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 our study area, particularly because of the slow growth rates of tree species and the relatively short fire cycle.

INTRODUCTION

It has been proposed that sustainable forest management practises 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 produce 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. in this report), 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 in this report). 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 between fires, affects 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 approaches, each of which relies on one or more critical assumptions. In most studies this involves stand level arguments about tree species replacement through time, i.e. **succession**. Although most studies acknowledge that the assumptions 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 approach 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. Such diameter data are most commonly presented as a **static diameter distribution** (e.g. Stewart 1986; Platt et al. 1988; Kuuluvainen et al. 1998), which is simply a frequency histogram of live individuals in diameter classes representing a single stand at one point in time. In a static diameter distribution it is assumed that the larger individuals represent the early stages of succession and the smaller individuals represent a future successional stage, i.e. the larger individuals will eventually be replaced by the smaller individuals.

Another approach has been to record individuals by their age. By coring at breast height or at the base of all live individuals within a stand 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), or as a **chronosequence** (e.g. Huff 1995; Frenot et al. 1998). A static age distribution is simply a frequency histogram of live individuals in age classes from a single stand at one point in time. A chronosequence is a series of stands (static age distributions) of different ages. In a static age distribution 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, i.e. the older individuals will eventually be replaced by the younger individuals. In a chronosequence, the assumption is that younger stands, representing the earlier stages of succession, will later have a species composition identical to that of the older stands.

An alternative approach called stand reconstruction tracks changes in a given stand over time by reconstructing the recruitment and mortality of individuals at different times in a stand's history (Johnson and Fryer 1989; Johnson et al. 1994). It requires the ability to detect and date trees that have died in the past. By aging at the root collar all live and dead individuals (standing, fallen and buried) within each stand, patterns of recruitment and mortality are observed rather than inferred.

The **objective** of this study has been to use stand reconstructions to test the critical assumptions underlying the most common approaches to studying patterns of forest dynamics: the static diameter distribution, the static age distribution and chronosequences. Using evidence from 42 stand reconstructions, our study demonstrates that the assumptions made using these methods are questionable and can lead to inaccurate conclusions regarding patterns of forest succession. As we will demonstrate, many of our strongly held beliefs about forest succession are misconceptions stemming from studies which have made, but not validated, these 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.

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 based on the distributions of the five dominant upland tree species along the moisture and nutrient gradients (see Bridge and Johnson in this report), and the time-since-fire map by Weir et al. (in this report). Twenty five stands were sampled on glaciofluvial hillslopes, and seventeen stands on glacial till hillslopes (Figure 1). For each hillslope position (top-mid, and bottom), 8-15 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 age 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 establishment. Finally, the forest floor was excavated to locate and sample all dead buried boles. In the laboratory all discs were sanded and rings counted. A master chronology was constructed for each species in each stand to determine the date of recruitment and death of each dead tree. All stumps were cross-sectioned and cross-dated to locate any missing rings and determine the date of establishment

Figure 1. General landscape patterns of vegetation distribution. Locations of dominant canopy species is based on the relationship between stand position on the moisture and nutrient gradients and the stand distance from the ridgeline (Bridge and Johnson in this report).

(DesRochers and Gagnon 1997). For brevity in this report, we will only discuss our tests of the assumptions of the static diameter and static age distributions.

Within each of our stands we constructed a static diameter distribution by dividing all live individuals into size classes based on basal diameter. The static diameter distribution method makes at least two key assumptions: 1) there is a good correlation between diameter and age, i.e. larger diameter individuals are older than smaller diameter individuals; and 2) within a stand, the larger diameter individuals represent the early stages of succession, whereas the smaller diameter individuals represent a future successional stage, i.e. the larger individuals will eventually be replaced by the smaller individuals.

We tested the first assumption of the static diameter distribution by examining the correlation between basal diameter and age for all species within each stand. In all of our stands the same pattern was evident: despite a wide range in the basal diameter of individuals, most individuals are very close in age. For example, Figure 2 shows the static diameter distribution of a 126 year old jack pine-black spruce stand. The basal diameter of jack pine individuals ranges from 13-35 cm, however, all are about 124 years of age (Figure 3). The basal diameter of the oldest group of black spruce individuals ranges from 12-26 cm, however, they are also about 124 years of age. In addition, notice that the basal diameter of the youngest group of black spruce individuals are all 1 cm, however, they range in age from 5-30 years. Since data from our stands shows that despite a wide range in diameter, larger diameter individuals are no older than the smaller diameter individuals, it follows that we should not expect a replacement in time of the larger with the smaller individuals (i.e. assumption 2). We will address the question of a replacement of the oldest individuals of jack pine and black spruce with the youngest individuals of black spruce later, within the section discussing static age distributions. Consequently, we conclude that unless diameter and age are very well correlated, we must question the conclusions reached by studies that use the diameter distribution method to infer patterns of succession.

Within each of our stands we constructed a static age distribution by dividing all live individuals into age classes based on age at 30 cm above ground level, the typical height at which trees are cored. The static age distribution method makes at least two key assumptions: 1) the number of annual growth rings counted on each tree core or basal 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.

We tested the first assumption of the static age distribution by examining whether the number of annual growth rings counted on each tree core or basal disk taken 30 cm from ground level matches the number of rings counted at the root collar. As shown recently by DesRochers and Gagnon (1997), the only accurate way to determine the age of a tree is to locate the root collar (the transition zone between stem and root) and use dendrochronology to account for missing rings. In all of our stands, we found that aging a tree by counting rings at 30 cm will almost always underestimate the actual age of a tree. This age underestimate increases as tree growth rate decreases. In addition, the number of locally missing rings increases as growth rate

Figure 2. The static diameter distribution of individuals within a 126 year old jack pine – black spruce stand.

Figure 3. The correlation between basal diameter and age of individuals within a 126 year old jack pine – black spruce stand.

decreases. For example, Figure 4 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 the faster growing jack pine and ten years for the slower growing 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 five years after fire. This pattern of recruitment is consistent among all of our stands dominated by jack pine and black spruce (also see Greene and Charron in this report). In our stands dominated by trembling aspen, white spruce and balsam fir, most individuals recruit within the first 7 years after fire. Very little successful recruitment occurs after this period as most individuals suffer very high rates of mortality. 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).

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, leading one to infer in a static age distribution that there will be a replacement of early recruiting species with later recruiting species. In mixed species stands there is often a conspicuous change in the 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 5), shows that while both species recruit within the first five years after fire, jack pine grows much faster within the first 25-30 years. 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 any conclusions of studies that are based on trees aged by coring or cutting above the root collar.

We tested the second assumption of the static age distribution, that older individuals would eventually be replaced by younger individuals, by examining the possibility that a second cohort of individuals will eventually make it into the canopy. To establish this, we looked at the height growth rates of individuals within each stand using our stem analysis data. In all stands the likelihood of a second cohort making it into the canopy was very low, simply because of the slow growth rates of most tree species and the relatively short fire cycle. 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 5). Given that the 2nd small cohort of black spruce established 110 years post-fire, the chance of the stand surviving another 65 years, to 190 years, is about 1% (i.e. 1% of the study area is older than 190 years, see Weir et al. in this report). Consequently, our tests of both assumptions for the static age distribution demonstrate that we must question the conclusions reached by studies that use a static age distribution to infer patterns of succession.

Figure 4. The static age distribution of individuals within a 126 year old jack pine – black spruce stand, showing individuals aged at 30 cm from ground level and at the root collar.

Recent studies have also indicated that gap-phase replacement, that is, the replacement of canopy individuals who die and leave a canopy gap, with individuals from successive cohorts, 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 subsequent cohorts, there is little chance that they will make it into the canopy to fill in the gap. If however, individuals within subsequent cohorts are capable of releasing, that is, increasing their growth rates once a gap forms, then gap replacement may be possible. We tested this hypothesis by examining whether the mortality of canopy individuals within old stands is followed by an increase in the height growth rate of understorey 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 understorey individuals releasing such that they fill in the gap (see for example Figure 5). Consequently, it does not appear likely that gap phase replacement plays an important role in the forest dynamics within our study area.

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 static diameter distribution or static age distribution, both of which are based on a number of untested assumptions. We found no evidence to support the assumptions of these methods, bringing into question conclusions reached by studies using static diameter or age distributions. Since the conclusions drawn by such studies have been important, at least in part, in guiding forest management practises, 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. As our results have shown, the recruitment of individuals that successfully make it into the canopy occurs within the first few years after wildfire, except balsam fir that is capable of recruiting for longer periods. 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 in this report), 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). With an understanding of how fire creates patterns of appropriate seedbeds (Miyanishi and Bajtala 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 (but old) 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, the static diameter and static age distributions. We found no evidence to support the assumptions underlying these methods which raise serious questions about the conclusions of studies using these methods. Our results challenge some of our strong beliefs regarding patterns of species replacement through time, i.e. succession, and gap-phase replacement. Since the conclusions reached by other studies have, at least in part, guided forest management practises, our results have important implications for forest management.

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Figure 5. The height growth of individuals within a 126 year old jack pine – black spruce stand. Note the slower growth rate of black spruce (grey lines) compared to the jack pine (black lines) within the first 25-30 years.

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