## EXPERIMENTAL HABITAT FRAGMENTATION AND SIMULATION OF LANDSCAPE DYNAMICS IN THE BOREAL MIXEDWOOD: A PILOT STUDY

1995

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### Abstract

Much of the boreal mixedwood forest of western Canada is now being managed for the production of hardwood pulp and softwood saw timber. The likely impacts of this development on the structure of the forest and on populations of resident and migratory wildlife are unknown. In 1991, we initiated an interdisciplinary study of the spatial dynamics of a large ( $\approx 73,000 \text{ km}^2$ ), mostly undisturbed study area within the mixedwood forest. This region includes the timber supply area for a large pulp mill and several saw mills. Based on forest inventory data, a study of the spatial distributions of stand populations indicates that forest composition of the region is not in a steady state and that no small representative areas exist. Patch level simulation models are being developed to predict forest stand dynamics as a function of local climate and site condition, and seed dispersal. A study of fire history records reveals that the annual area burned is influenced by factors other than ignition frequency, and that young deciduous forests inhibit fire. The forest landscape is structured both by episodic fire years, and by background levels of fire in intervening years. Results have provided parameter estimates needed for landscape-scale spatial fire models, including the effects of fire suppression. A spatial timber harvest scheduler has been developed. Preliminary simulations indicate that even after the first 70-year rotation, some large forested areas of study area remain unharvested, because of comparatively disadvantageous yields or hauling distances. These components will ultimately be linked into a landscape scale simulation of forest dynamics. A large scale forest fragmentation experiment has been designed and implemented near Calling Lake, Alberta. Three replicates each of 1 ha, 10 ha, 40ha, and 100ha rectangular patches have been isolated from the surrounding mature forest. The plots have fully matched controls, located within a contiguous 3, 5000 ha block of forest. This study will quantify habitat associations and habitat area requirements for many bird species. The first two years of data have been collected. Sixty-one species of forest songbirds or woodpeckers were encountered during dawn surveys, exhibiting the species richness (S) to area (A, in ha) relationship  $S = 0.57 A^{0.50}$ . Some effects of habitat composition and isolation on bird communities are described. A systematic comparison of three spatial forest inventory data sets has revealed potentially significant discrepancies in estimated forest composition, even at high levels of data aggregation. The ubiquitous legacy of wildfire as an agent of change, and the naturally fragmented nature of the forest mosaic, indicate that it may be possible to develop harvesting strategies that preserve many properties of the natural system over the long term.

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## 1 Introduction

## 1.1 Background

The majority of Canada's forest lands are boreal forest, which, in Western Canada, are only now being brought under management. For example, in Alberta, more than 200,000 km<sup>2</sup> of the boreal mixedwood, representing  $\approx 40\%$  of the total forested area under provincial jurisdiction, has, in recent years, been committed to industrial timber production. Developments of this kind can lead to conflict with other forest uses due to the speed with which large areas of natural forest can be harvested.

Alberta's boreal mixedwood has been structured by periodic large fires, resulting in a complex mosaic of stands with a mean age of  $\approx 80$  years. Under existing operating groundrules and land-use policies, harvesting will have three predictable consequences: (1) there will be a truncation of the natural age distribution of the forest; (2) partitioning of the landbase between coniferous sawlog and deciduous pulpwood production will result in a marked reduction of the region's characteristic mixed stands (Cumming *et al.*, 1994); and (3). as harvesting progresses, the landscape will become increasingly fragmented with areas of older forest becoming smaller and more isolated. To respond to public demands for integrated resource management, the forest industry requires the ability to design operating plans that minimise losses to non-timber values. An understanding of spatial dynamics is necessary to predict some ecosystem responses as natural disturbance regimes are replaced or augmented by timber harvesting.

## 1.2 Study Area

Our study area of  $\approx 74,000 \text{ km}^2$  is located in northeastern Alberta, mostly within the high and mid boreal mixedwood ecoregions, as defined by Strong (1992). It is largely coextensive with the the timber supply area for a large bleached kraft pulp mill which has been operating since September 1993. The area is bounded by the Saskatchewan border to the east and by agricultural land to the south. The east-west and north-south extents of the study area are roughly 300 km (Figure 1). Although a number of coniferous saw-timber operations exist, the vast majority of the forest has never been logged. Much of the area is inaccessible by road, although an extensive network of seismic cutlines and natural gas pipelines exists. The principal impact of European settlement on natural processes to date is generally believed to have been fire suppression.

The high and mid boreal mixedwood ecological regions cover  $\approx 240,000 \text{ km}^2$  of northern Alberta (Strong, 1992), more than 50% of the province's forested land. The most abundant tree species are trembling aspen (*Populus tremuloides* Michx.), white spruce (*Picea glauca* (Moench) Voss), jack pine (*Pinus banksiana* Lamb), black spruce (*Picea mariana* (Mill.) B.S.P.), and balsam poplar (*Populus balsamifera* L.). Paper birch (*Betula papyrifera* 

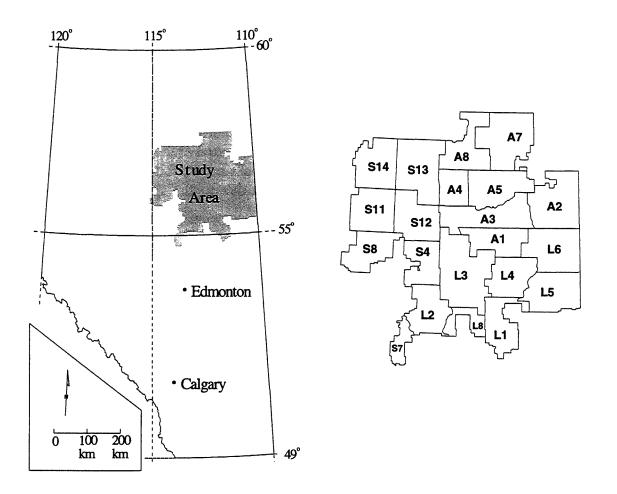


Figure 1: Location of the study area within Alberta, and enlargement of the study area showing forest management unit boundaries.

Marsh.), tamarack (*Larix laricina* (Du Roi) Koch) and balsam fir (*Abies balsamea* (L.) Mill) are widely distributed but seldom form mature stands. In northwesterly areas, lodgepole pine or lodgepole/jack pine hybrids are common. The predominant natural disturbance agent is fire (Rowe, 1961; Kabzems *et al.*, 1986; Johnson, 1992). Mono-specific or "pure" stands (those in which a single tree species comprises more than 80% of the canopy) account for 66% of the total forested area in the study area. Aspen (36%) and black spruce (17.6%) form the bulk of these "pure" stands. Mature mixed stands with high densities of both aspen and white spruce characterize the region (Kabzems *et al.*, 1986), although other varieties of multi-species stands, such as mixed black spruce and pine, exist in lower abundances.

The region has generally low relief, with limited variation in landforms and topography. On medium-textured, well-drained sites, aspen is the dominant species. Traditional views of regional stand dynamics assert that the aspen canopy is gradually replaced by white spruce, which is itself eventually replaced by the more shade-tolerant balsam fir in the absence of fire. On drier sites pines are found. Black spruce is the dominant coniferous species of poorly drained sites. Large areas of treeless wetlands or sparsely treed muskeg are also present, covering about 42% of the study area. For a more thorough description of the regional ecology see Moss (1932, 1955), Dix and Swan (1971), Kabzems *et al.* (1986) and Peterson and Peterson (1992). The region's physiography and climatology are outlined in D. A. Westworth and Associates Ltd. (1990) and Strong (1992).

The genesis of the characteristic mixed stands is not fully understood. Some reports indicate that aspen and spruce establish nearly simultaneously after a stand-initiating fire (Thorpe, 1992), with aspen dominating the canopy initially because of its higher juvenile growth rate. The gradual establishment of white spruce under an existing aspen canopy is less well documented, although high densities of young spruce under mature aspen canopies and spruce regeneration on decaying aspen logs (Nienstaedt and Zasada, 1990) are commonly seen. Mixed stand trajectories are probably determined in part by the availability of white spruce seed sources, which is itself dependent upon the size and severity of the stand-initiating disturbance events. Overall landscape pattern in the boreal mixedwood is therefore a consequence of three major factors: (1) physiography (*i.e.* landform and drainage); (2) fire; and (3) stand dynamics and succession.

## 1.3 Objectives

The main objective of this project is to acquire, synthesize and apply information on the response of the boreal mixedwood forest to broad-scale timber harvesting. We are developing landscape scale models of fire, stand dynamics and forest harvesting. One application of these models is to explore options for reserve systems within the working forest that will support populations of wildlife while allowing sustained timber harvesting. In order to develop the tools to compare the merits of alternative management practices, we need to understand the pre-management structure of the forest and its relation to the natural disturbance regime, trends in post-disturbance stand development and succession, and the relative affinities of different wildlife species to forest habitats of varying composition, size and spatial arrangement.

Work in progress at the University of British Columbia, includes three major components. Mr. S. G. Cumming and Dr. P. J. Burton (Department of Forest Sciences) are developing landscape-scale spatial simulations of the vegetation and disturbance dynamics of the boreal mixedwood forest. Mr. M. Joy and Dr. B. Klinkenberg (Department of Geography) are studying methods of characterising and tracking error and accuracy in GIS and spatial simulations, and are developing spatial error models for forest inventory data sets. Ms. F. Schmiegelow and Dr. J. Smith (Department of Zoology) have initiated a large scale experimental fragmentation of a  $\approx 100 \,\mathrm{km}^2$  region within the study area, and are now examining the consequences for bird communities. This document reports on the establishment of the fragmentation study and presents some preliminary results. It also constitutes a progress report on the simulation of landscape dynamics. Some of the linkages between project components are discussed. This pilot study was funded from September 1992 to April 1994.

## 2 Landscape Modelling

## 2.1 Landscape Pattern Analysis

This section presents an analysis of the spatial structure of the forest within the study area, based on low spatial resolution raster maps produced from Alberta Forest Service Phase 3 Inventory data sets (Alberta Forest Service, 1985a). The original data are 1:15,000 photointerpreted inventory maps, where each mapped polygon differs from its neighbours in species composition, age or canopy structure. We consider each forested polygon to be a "stand". Details of methods and additional results beyond the scope of this report are presented in Cumming *et al.* (1995). Three principal results of this study are:

- 1. Large scale patterns in species composition and age structure were identified.
- 2. Evidence for the shifting-mosaic steady state hypothesis (Bormann and Likens, 1979) was not found for the study area;
- 3. Phase 3 inventory data is shown, in many respects, to be consistent with what is known of the regional ecology, which partially justifies the extensive use we have made of it.

In addition, this work has provided some objective measures of natural landscape attributes, which could be maintained in a conservative approach to wildlife habitat protection in the managed landscape. They also constitute a partial set of phenomena which a landscape model must be able to predict.

#### 2.1.1 Species specific population attributes

The absolute and relative abundances of five common stand types (pine, deciduous, mixed deciduous and white spruce, white spruce and black spruce) within the study area are shown in Table 1. Each of these populations of stands has a distinctive age structure: under pairwise Kolmogorov-Smirnov (KS) tests, all age structures are different  $(p < 10^{-6})$ . Pine stands and deciduous stands (not shown) have a right-shifted negative exponential age structure (Figure 2a). This shift could be construed as a consequence of fire-suppression, but we argue in Section 2.3.1 that this is unlikely; a fortuitous absence of significant fire episodes in the 20 years preceding the inventory appears to be the best explanation. White spruce increases in abundance with age, peaking at 135 years. The mixed aspen/spruce stand population has three peaks, at 55, 115 and 135 years (Figure 2a); the first peak is common with pine and deciduous stands (not shown) and the latter two with white spruce. It is not certain whether the 115 and 135 year peaks are truly distinct, or result from a bias in the inventory data. However, studies of operational inventory data sets conducted in May 1995 indicate that Phase 3 age data may be sufficiently accurate to distinguish these age classes (S. G. Cumming, unpublished data). Furthermore, the oldest peak corresponds closely to a major fire event in 1858, documented by Moss (1932).

Table 1: Total and percent forested area within the study area, by stands species composition.	
The dominant unforested types are also shown.	

Stand Type	Total Area	% Forested Area	% Total Area
Deciduous	$1.27  imes 10^4 \ \mathrm{km^2}$	35.6	17.3
Black spruce	$6.17  imes 10^3  m km^2$	17.3	8.4
Pine	$3.06  imes 10^3  m km^2$	8.6	4.2
White spruce	$1.67  imes 10^3  ext{ km}^2$	4.7	2.3
White spruce / Aspen	$5.62  imes 10^3  m km^2$	15.8	7.7
Pine / Aspen	$2.40 imes10^3~{ m km}^2$	6.7	3.3
Black spruce / Pine	$2.01  imes 10^3  ext{ km}^2$	5.6	2.7
Other Forested	$1.94 imes10^3~{ m km}^2$	5.5	2.6
Total (Forested)	$3.56 imes10^4~{ m km}^2$	100	48.6
Wetlands	$3.10 imes10^4~{ m km}^2$		42.3
Burns and Clearcuts	$3.40 imes10^3~{ m km}^2$		4.6
Lakes	$2.93 imes10^3~{ m km}^2$		4.0

Stand population size structures are also distinctive. Figure 2b plots log-transformed stand sizes of deciduous, mixed and white spruce stands as probability density functions, indicating approximately log-normal distributions; this is also the case for pine and spruce stands. Pairwise KS tests show that all size distributions are different  $(p < 10^{-6})$ , while fitted log normal distributions show that either the means, the standard deviations or both are distinct. Large deciduous stands (>30ha) are more common than large mixed stands, suggesting that, in some instances, white spruce establishment is dispersal limited: further evidence of this is presented in Section 2.3.1, especially Figure 21. Most stand types exhibit a peak in the abundance of small ( $\approx .5$  ha) stands. This is at least in part a true feature of the landscape, and not a reporting bias. Numerous small isolated patches of mesic stands (the types shown in Figure 2b) exist within expanses of muskeg and black spruce dominated wetlands. It is not known if these exist because of topographic variability, or as a result of openings created by small fires. A similar phenomenon is seen in aspen dominated mesic sites, where small isolated patches of pine and black spruce stand by topographic variation.

The relationship between stand age and size is not uniform in these populations (Figure 3a). In pure white spruce stands, there is a trend to increased stand size with age, perhaps indicating a slow diffusion-like invasion process. The anomalous large size of young stands is attributable to clear-felling and artificial regeneration of this species: the abundance of these stands is low (Figure 2a). No such trend is evident for mixed stands, or for pine. For pure deciduous stands, mean area appears constant for stands older than 80 years. This is roughly the age at which a coniferous understory becomes conspicuous from the air. The steady decline in mean stand area from ages 20 to 80-100 years may be due to the

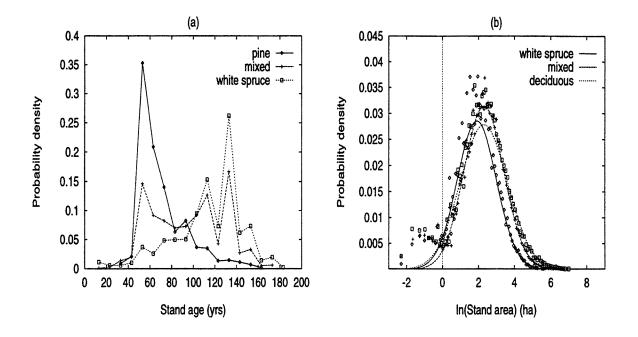


Figure 2: (a) Age and (b) size structures for several stand populations within the study area.

gradual fragmentation of large, fire origin deciduous stands because of local variations in site condition and coniferous seed availability. Misclassification of young stands having an undetected coniferous understory could contribute as well.

Black spruce stands exhibit a pronounced decline in mean area with age, shown for two age classes in Figure 3b. Both the mean and standard deviation decline over time, consistent with wildfire-induced fragmentation of large old stands.

The local correlation between stand types was assessed by computing Spearman rank correlations for proportional stand abundances in 825 townships ( $\leq 93.2 \text{ km}^2 \text{ each}$ ) within the study area (Table 2). The area appears to possess three partially overlapping (and by no means necessarily contiguous) habitat types: pine, black spruce and deciduous/mixed zones. This presumably reflects regional topography, and is consistent with the standard accounts of boreal mixedwood ecology. Despite having distinctive site preferences, pine and black spruce abundances are independent at this scale.

#### 2.1.2 The shifting mosaic hypothesis

In studying the dynamics of a large forested area, it is natural to inquire whether any small subregion can be said to be "representative" of the whole. If the shifting-mosaic steady state model of Bormann and Likens (1979) applies, then an equilibrium should exist, at some spatial scale, between the forest and its disturbance regime, whether dominated by gap-phase replacement, wind-storm, herbivory or wildfire. This equilibrium or "stable mosaic" (Baker, 1989) should be evident in the age structure and successional composition of the forest.

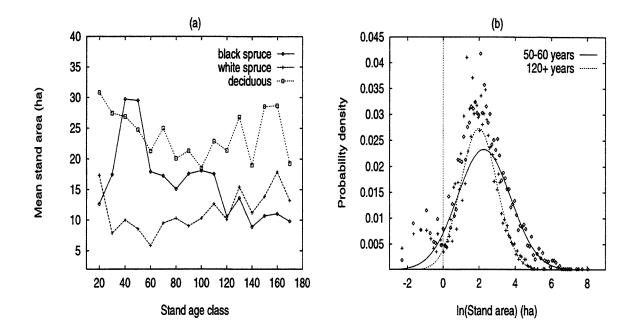


Figure 3: Most stand types have distinctive age-size relationships (a). Where a temporal trend in stand size is seen, as for black spruce, size distributions for different age classes are highly distinct (b).

Table 2: Spearman rank correlation coefficiants of proportional stand area of common stand types, within individual townships ( $\approx 92 \text{ km}^2$ ; n = 820.) Ignoring the effects of spatial autocorrelation (Cliff and Ord, 1981, Ch. 7,), all results are significant (p < 0.001) except those marked \*.

Stand type	Mixed	White spruce	Black spruce	Pine
Deciduous	0.317	0.171	-0.516	-0.264
Mixed		0.592	-0.204	-0.317
White Spruce			*-0.025	-0.280
Black Spruce				*0.103

This prediction follows also from the similar mosaic-cycle model advanced by Remmert (1991). Operationally, a "representative area" is a small part of a region constituting a stable mosaic, or, more generally, that is similar in composition to the entire region, under whatever structural measures are deemed important. Furthermore, such areas should not be unique. If there is a spatial scale at which a stable mosaic exists, any contiguous region of at least that size should also be a stable mosaic. This requirement is an elaboration of criteria set forth by Baker (1989). Evidence for stable mosaics has been reported for a number of ecosystems, however Turner and Romme (1994) have concluded that forests dominated by crown fires are unlikely to be in equilibrium.

According to Baker (1989), the "landscape age class structure" of a region, considered as a population of patches, is sufficient to test the shifting-mosaic steady state hypothesis in landscapes subject to large disturbances. Patch age, in this view, is a surrogate variable for any post-disturbance compositional changes. This test may be inadequate where, as in the boreal mixedwood, populations are spatially segregated by site preference, or where different patch types are subject to different disturbance regimes. The available data indicate that disturbance rates due to wildfire greatly across stand types (see Section 2.3.1). Moreover, to focus on age structure alone ignores an important feature of the events (fires) which are assumed to induce it. Fires vary greatly in size, and are not uniformly destructive across their extent (Eberhart and Woodard, 1987; Turner and Romme, 1994). As a result, the post-fire successional development and composition of stands is variable. Stands may also coalesce or fragment over time. For these reasons, we chose to consider the stand populations separately, and to characterise them by both age and size structure. We focus on five stand populations: pure stands of aspen, pine, black spruce and white spruce, and mixed aspen and white spruce stands.

To compare population structures between and across scales, we developed a quasi- two dimensional variant of the Anderson-Darling goodness-of-fit statistic  $A^2$  (Anderson and Darling, 1952; Kotz *et al.*, 1982). This statistic is the integral of the product of the squared difference between two cumulative probability density functions's (cdf's) and a weight factor sensitive to differences near the extrema of the two cdf's, where values for the squared difference are necessarily close to zero. Formally, to compare an empirical distribution f(x) against an empirical standard distribution g(x), first compute the cumulative density functions F(x)and G(x). Then

$$A^{2} = \int_{-\infty}^{\infty} \left[F(x) - G(x)\right]^{2} \psi(x) dx$$

where the weight factor  $\psi(x)$  is defined by

$$\psi(x) = [G(x) \{1 - G(x)\}]^{-1}$$

We compute  $A^2$  by numerical integration for age and size distributions separately, and adopt the euclidean norm of the two values,  $D_a^2$ , as a quasi-2-dimensional statistic measuring the overall similarity of two stand populations. Significance values for Anderson-Darling tests are known only for some underlying distributions (Kotz *et al.*, 1982); we did not attempt to derive them. The study area is divided into three administrative regions of roughly equal size (the Athabasca, Slave Lake and Lac La Biche Forests), which are subdivided into a total of 21 approximately rectangular sub-regions (Forest Management Units or FMUs), mostly between 3,000 km<sup>2</sup> and 4,000 km<sup>2</sup> in size (Figure 1). These units are one possible zonation of the study area. We also induced an alternate set of zonations by hierarchical (quadtree) decomposition, producing subzones ranging from  $\approx 24,000 \text{ km}^2$  to  $\approx 370 \text{ km}^2$  in size. Stand size and area distributions for each of the five stand types were generated at each scale of aggregation for both the administrative and the induced hierarchical zonations.

Using the  $D_a^2$  statistics, we performed pairwise cross-scale comparisons between subzonal distributions. Thus, each FMU was compared with all other FMUs, with the Forest containing it, and with the entire study area. By studying the distributions of test statistics that resulted, and comparing surface plots of stand age and size distributions between regions, we conducted an informal but quantitative assessment of representativeness.

Figure 4 compares the age and size structures of mixed stand populations between the entire study area and three large subregions defined by Forest boundaries. Distributions are represented as contour plots of probability density, or proportional abundance. Over the entire study area, this distribution exhibits three peaks at about ages 45, 100, and 125 years, of roughly equal amplitude. Both the Athabasca and Slave Lake Forests approximate the areal distribution rather closely, although Athabasca has fewer stands of intermediate age, while Slave Lake clearly has the largest proportion of younger stands. The Lac La Biche Forest is highly skewed towards older, larger stands. This general pattern of relative age of the three Forests is consistent across all five stand types.

Table 3 shows the values of  $D_a^2$  obtained by comparing each forest with the entire study area, for each of the five cover types. Statistic values of less than 2.0 generally indicate a high degree of similarity in stand distributions: this value is close to a .05 significance value, estimated from the distribution of the test statistic resulting from 1394 cross scale

Table 3: A comparison of the age/size distributions of the five common stand types in the boreal mixedwood, between each of three large contiguous subzones ("Forests") and the entire study area. Values shown are the 2-dimensional Anderson-Darling statistic  $D_a^2$ ; smaller values indicate greater degree of representativeness. No single Forest is most representive for all stand types.

			Star	nd Type	
Forest	Pine	Mixed	Deciduous	White Spruce	Black Spruce
Athabasca	1.38	1.82	3.35	7.38	3.75
Lac La Biche	1.95	4.28	4.88	3.23	3.93
Slave Lake	8.65	1.20	1.17	0.75	2.74

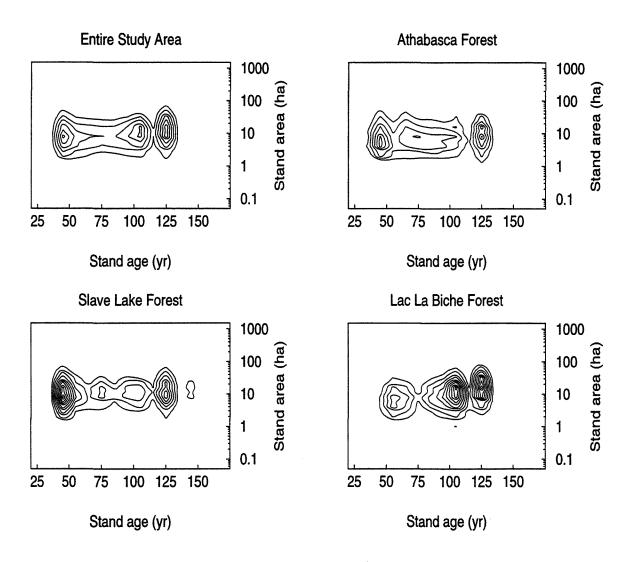


Figure 4: The age-size structures of mixed aspen/spruce stand populations for the entire study area and for three large subregions (Forests). Spline-smoothed contours represent probability density, in steps of 0.0025.

comparisons. Clearly, the Athabasca and Slave Lake forests are much more similar to the areal distributions of mixed stands than is the Lac La Biche forest. We adopt  $D_a^2 < 2.0$  as a criterion and henceforth consider a subregion "representative" of an area containing it, or a "good" fit, if comparing the two areas yields a  $D_a^2$  value of less than 2.0, and consider it highly unrepresentative or a "poor" fit if the measure is > 20.0, always with respect to a particular stand type. Although the Slave Lake Forest is, by this criterion, representative with respect to at least three stand types, it is very poorly representative with respect to pine stands, with stands older than 70 years almost absent. Black spruce stand attributes are not well represented in any of the three Forests. At a smaller spatial scale, no FMU is simultaneously most representative for all cover types, either within the entire study area, or when compared only to the Forest containing it.

Even for single stand types, considerable heterogeneity exists within large subregions of the study area. For example, the Athabasca Forest, most representative of the overall population of pine stands, contains highly unrepresentative FMUs (Figure 5). The  $D_a^2$  value for the FMU shown in Figure 5b (A7) is 19.5. Similar results are found for all cover types, across a wide range of spatial scales.

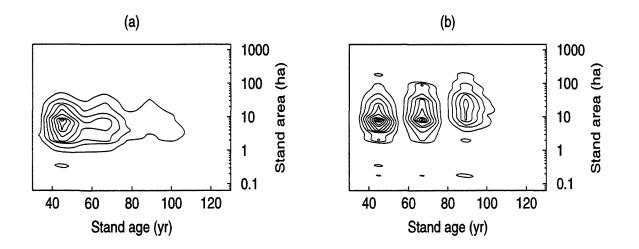


Figure 5: Contour plots of the age/size distribution of pine stands in (a) a large region of the study area (the Athabasca Forest) and (b), a highly dissimilar subregion (FMU A7) within the Athabasca Forest containing 18% of the Forest's pine stands. Spline-smoothed contours represent probability density in steps of 0.005.

The variability in age and size structures in mixedwood stands, as shown in Figure 4, is sufficient to reject the shifting mosaic steady state model for the study area. Since the study area comprises approximately 1/7 of the total area of the entire boreal mixedwood in North America, it appears likely that the region is not an equilibrial system. This means that there exists no unique long term stable state which is characteristic of the boreal mixedwood or of the study area. Nonetheless, other evidence suggests that changes in age structure and species composition are confined to certain limits. Simulations of some forest types which are regarded as exhibiting mosaic cycles predict oscillations in the abundance of older, late successional patch types (Wissel, 1992). The paleo-ecological record indicates that, at a spatial scale of  $\approx$  3,000 km<sup>2</sup>, relative tree species abundances and climatic conditions have remained constant in the southern parts of boreal mixedwood for the last 3000 years (MacDonald and Reid, 1987) and as long as 5000 years in more northerly areas (Hutton et al., 1994). Thus, fire regimes may also have remained relatively constant over this interval. We therefore still expect that the dynamics of the system can be predicted and modelled. An expanded version of these results (Cumming et al., 1995), which considers the problem of habitat reserve design in a heterogeneous, dynamic landscape, proposes alternatives to a fixed, contiguous reserve area (the "floating reserve system") and describes some applicable software tools.

#### 2.1.3 Broad scale landscape patterns

Maps of proportional forest cover abundance reveal a number of additional features of the landscape that may be of importance in model development. The large areas of wetland in the centre of the study area (Figure 6a) could influence landscape pattern by dividing the region into two distinct areas between which fires can not easily spread. Other geographic features may provide more direct explanations for species distributions. Figure 6b shows the spatial pattern in white spruce abundance. While seldom common, areas of concentration are evident. The roughly linear area of high white spruce abundance in the centre of the map corresponds closely with the Athabasca River valley, while the Christina River valley may also be apparent. White spruce abundance increases to the West, presumably due to increased precipitation. Pine stands (not shown), on the other hand, are most abundant in the south and northeast segments of the study area, which is as expected, given the climatological gradients described in Section 2.2.2.

The distribution of deciduous stands is less clearly related to precipitation or edaphic gradients. Figure 7 compares the spatial pattern in abundance of mature (40 to 70 years) and old (> 70 years) deciduous stands. There seems to be evidence of a spatial oscillation in forest age structure. This might be expected if there was a relationship between stand age and fire hazard, which appears to be the case (see Section 2.3.1).

**Further Work** Further studies of the spatial relationships between topography, fire history and forest cover will be conducted, using high spatial resolution data sets that were unavailable at the time of writing. This will assist in the parameterisation of a landscape scale

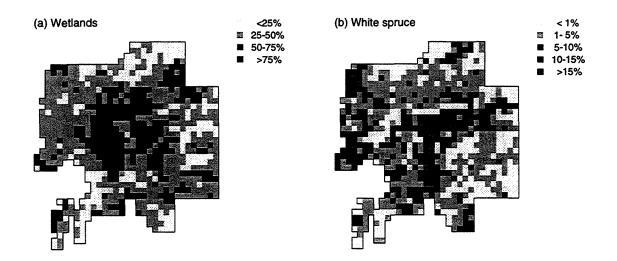


Figure 6: Density of (a) wetlands (bog and muskeg) and (b) white spruce dominated stands within the study area, represented as proportional township area.

vegetation model by quantifying the relative importance of climatological, physiographic and autogenic factors in the development of forest cover within the study area.

## 2.2 Model Development

A model of landscape dynamics must include components of vegetation zonation, successional change and disturbance regimes. Progress towards describing and simulating natural and artificial disturbances is described in Section 2.3. Our overall development plan for a landscape scale vegetation model consists of two parts. The goal of the first part is to enhance an existing model of forest stand dynamics such that it is capable of simulating actual patterns of stand development in the study area, given descriptions of site, climate and propagule input. In the second phase, this model will be used to generate a large suite of possible stand trajectories. These trajectories will be defined as parametric families of curves (functional forms whose shape is controlled by one or more parameters representing e.g. time) describing species specific stem density, age structure and size distributions. Each patch in the landscape will be assigned a trajectory based upon its location and surroundings. At any given time, a patch will be defined by which trajectory it is on, and a single state variable indicating the patch's location on the curves. In this way, a high spatial resolution and large spatial scale forest cover model will be defined which remains computationaly feasible. Patch trajectories will be, in effect, summarised results of detailed individual based simulation models.

## 2.2.1 Stand Dynamics Modelling

Individual-based forest stand models (gap or patch models) simulate the regeneration, mortality and growth of uneven-aged mixed-species stands of forest trees, based on competition for light and on site-imposed constraints of soil moisture, soil nutrients and temperature (Shugart and West, 1977). We have taken as our starting point the gap model Zelig 1.0 developed by Urban (1990), variants of which have been used in the study of forest dynamics in many parts of the world, including boreal forests (Shugart, 1984; Urban *et al.*, 1993; Sirois *et al.*, 1994).

When applying a generic gap model such as Zelig to a real ecosystem, some recalibration or additional features are necessary. This section describes the steps we have taken and are taking to produce a stand model capable of predicting and explaining fairly detailed features of small scale dynamics in the boreal mixedwood. At the same time, our research has partially overcome a long-standing limitation of this class of models. We have dubbed the resulting model Zelig++. It retains the ability to simulate many aspects of forest harvesting and silviculture (Cumming and Burton, 1993). We have found that the model enhancements described below have improved the model's ability to predict the composition of forest stands at a wide range of sites in British Columbia, when compared to the older, baseline version (Cumming and Burton, unpublished data). The greatest improvements were achieved in

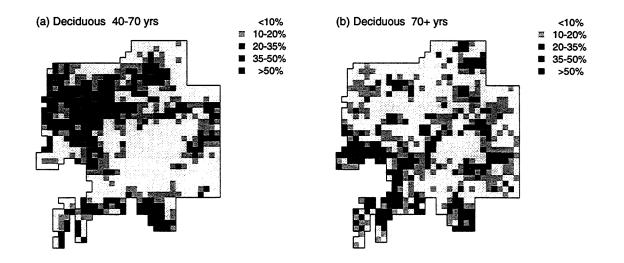


Figure 7: Density of (a) medium (40-70 year) and (b) old (70+ year) deciduous stands within the study area, represented as proportional township area.

high elevation conifer forests and in those forest types in BC similar to Alberta's boreal mixedwoods. A detailed description of model enhancements described below is given by Cumming and Burton (1994). Some applications of the new model are reported by Burton and Cumming (1995) and Cumming and Burton (1995).

**Temperature response and phenology** Gap models have been criticised for their treatment of whole plant temperature response. Many forest gap models, including Zelig 1.0, assume a plant temperature response function based on species range data. A growing season heat sum is computed annually for a site, dependent only upon simulated weather. This value is an argument to a species-specific parabolic function which is set to be zero at heat sum values corresponding to the elevational or latitudinal limits of a species range (Botkin et al., 1972). Thus, species have low or zero growth potential near the limits of their range, and achieve optimal growth potential at an intermediate point. There are many problems with this approach. Aside from its inability to explain observed range limits, it is well known to be false (see e.g. Urban et al., 1993; Sirois et al., 1994), especially at the warmer extremes of a species' distribution. Of the growth factors included in Zelig, it is both the least biologically interpretable, and can be the most important determinant of which species can potentially grow at a site. We have completely reformulated the temperature response function, which is now independent of range data. In principle, all factors in Zelig++ are now so independent, although, in practice, estimating them for species where they have not been measured may require an appeal to range data.

In Zelig++, tree phenology and growth follows the "degree growth stage model" of Fuchigami *et al.* (1982). A species-specific temperature *threshold* defines the annual interval of physiological activity. A supra-threshold heat sum is then required for spring *bud-break* (Worrall, 1983). These two values determine the length of the growing season at a site, which may

be different for each species. Temperate species generally require a period of cool temperatures near the end of the growing season to permit normal bud and shoot development the following spring: a *chilling requirement* (Lavender, 1991). During roughly the same interval a degree of *frost hardiness* is induced. Figure 8 illustrates the annual cycle as represented in Zelig++.

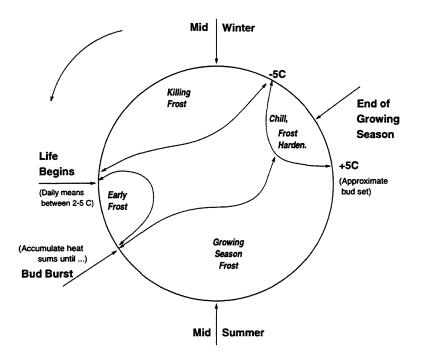


Figure 8: Phenology, as simulated by Zelig++.

Inadequate chilling reduces potential growth in the following year and limits realised frost hardiness. This can be caused by an insufficient interval of low temperatures, or if subzero temperatures are reached too quickly. If winter temperatures fall below realised frost hardiness, mortality occurs. Prior to bud-break in the spring, frost hardiness linearly declines to  $-2^{\circ}$  C (Sakai and Wesier, 1973). During this interval, *early frosts* can severely reduce growth (Cannell and Smith, 1986); growth potential may be further limited by growing season frosts. Direct effects of site temperature regime on growth are simulated by computing a species-specific growing season heat sum. The ratio of this value and the maximum heat sum over all species on a site is interpreted as a measure of relative growth potential, and captures some differences between evergreen and deciduous habits. Alternate formulations, based on relative growing season length, are being explored.

**Frost effects** Zelig++ introduces a new aspect of climate to stand modelling by its simulation of frost regime. As Figure 9 illustrates, many regions are as well characterised by

the distribution of low-temperature events throughout the year as by more usual attributes such as annual patterns of mean temperature and precipitation: the region's names in the figure refer to characteristic sites in two biogeoclimatic zones in British Columbia (Pojar *et al.*, 1987). Differential species tolerances for low temperatures at different times of the year may provide an explanation for some patterns of species distribution that do not seem to follow (at least in standard gap-models such as Zelig) from the usual abiotic factors, species tolerances and light competition during stand development.

Many aspects of the phenological model of Figure 8 are influenced by frost regime, specifically by the frequency and timing of extreme low temperature events. In Zelig++, a frost regime is defined by the conditional expectations and standard deviations of low-temperature event frequencies, given a mean monthly temperature range. The dependence upon mean monthly temperature comes from the fact that Zelig++ simulates weather on a monthly time step, although some quasi-daily values, interpolated from monthly means, are used in parts of the phenological submodels. To use this feature of the model long term records of daily mean and daily minimum temperatures are required. We have developed a number of tools to assist in the construction of frost regime descriptions from such data sets.

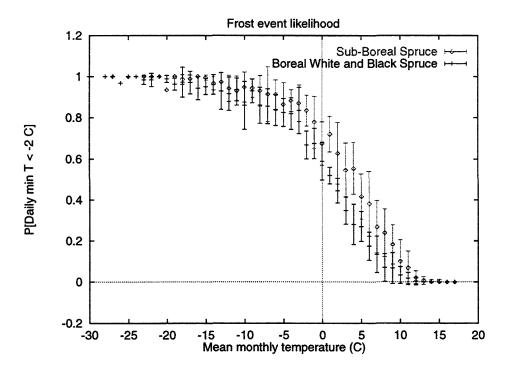


Figure 9: Frost event likelihood as a function of mean monthly temperature for two ecological regions in British Columbia which are comparable to the boreal mixedwood of Alberta. Likelihoods were estimated from more than 40 years of daily weather data. Feducial limits indicate  $\pm 1.0$  standard deviation.

Precipitation density estimation Gap models of the JABOWA lineage, including Zelig, have generally assumed that monthly precipitation is normally distributed. This assumption is invalid; a wide variety of more or less skewed distributions are used in the climatological/hydrological literature (Legates, 1991), although there is no agreement on which is most suitable. It seems likely that the "best" distribution to use as a precipitation model is site dependent; gamma functions have been used in some gap models for boreal regions (see Bonan, 1989, and references therein) and are used in Zelig 2.0. A possible difficulty with the assumption of normality is that, in regions with low monthly precipitation and high variance, the model may substantially underestimate mean annual precipitation, and hence overestimate the dominance of drought hardy species.

With Zelig++, it is possible to use a non-parametric density function estimation algorithm to generate a probability density function which fits the empirical data. The raw data required are only a list of historic monthly precipitation totals. For the theory and specific algorithms underlying this approach see Silverman (1986) and Sheather and Jones (1991). The implementation in Zelig++ is based on source code generously supplied by Dr. Upmanu Lall and Mr. Balaji Rajagopalan, of the Utah Water Research Laboratory, Utah State University.

Local inseeding and suppression mortality Collaboration with some workers from the Université du Quebec à Montréal led to some extensions to the regeneration submodel and to the simulation of stress induced mortality. These are preliminary steps towards some of the future developments discussed below.

In this extension, local, or plot-level, seed rain is dependent on the size of the largest tree of each species on the plot. Seed production follows a Michaelis-Menton dynamics controlled by species-specific parameters representing the "diameter to first reproduction", the half saturation constant and a maximum establishment rate. Some trials with real data, coupled with the improved mortality estimator described below, have led to realistic predictions of community dynamics in areas where the model had not previously done well.

Zelig assumes that individual trees have only a 1% chance of surviving for 10 years of continuous suppression, as measured by low growth rates. Since all stress factors are conflated in the growth rate computation, understory trees of shade tolerant species can suffer very high mortality in the presence of any additional growth limiting factor. This may not accurately reflect the resilience of some species with respect to light stress. A new tolerance parameter can be used to provide a species-specific estimate for the 1% survival time for stressed individuals. For a recent alternative approach to the simulation of local seed effects in boreal forest stands, see Sirois *et al.* (1994). For a critical appraisal of the evidence for a simple, general relationship between growth rates and survivorship under low-light conditions, see Pacala *et al.* (1993).

**Verification data sets** Only limited data are available against which to test model performance. We have obtained copies of Forest Service Permanent Sample Plot data and related

soils data. Unfortunately, in most cases, the data contain only two measurements 10 to 15 years apart. Their utility will probably be restricted to verifying model predictions regarding which species is locally dominant, *e.g.* pine or aspen. The Calling Lake fragmentation study (described in Section 3.1) has gathered extensive vegetation data for several hundred plots contained within older aspen and mixed stands. The data include tree species, height and diameter class, and snag size classes and downed log size and decomposition classes. These will serve as verification sets for more extended model simulations. Soils data for these plots are presently lacking.

Further Work Three principal enhancements are needed before this portion of the project is completed. These are: (1) the inclusion of propagule dispersal, (2) snag and downed log dynamics, and (3) an improved soil moisture model and/or whole tree drought-stress relationships. Once these three tasks are accomplished, the development of a set of patch trajectories will be straightforward.

The predominant mode of vegetation interaction between patches in the landscape model will be propagule dispersal. Probably the most important two aspects of this are vegetative reproduction by aspen, and white spruce inseeding. Sufficient data are available in the literature to quantify both of these phenomena in the context of a spatial patch model. The dynamics of snags and downed logs are crucial both for wildlife habitat considerations, and because of the role that downed logs may play as a regeneration substrate for white spruce. The Alberta Environment Centre has gathered sufficient data to formulate a version of this comparatively elementary submodel (Dr. Phil Lee, AEC, personal communication, 1994), which we will incorporate into our work.

Zelig++ is overly sensitive to soil moisture conditions in the study area. Preliminary runs under realistic climate regimes, using real soils data for locations within the study area, predict periodic dieback of most species due to episodic periods (over two or three years) of below-average precipitation and/or above-average summer temperature. Such drought events do occur in the historical record, but the model is over-reacting to them. This is probably a result of two model limitations. The soil moisture model inherited from Zelig 1.0 does not account for canopy induced attenuation of soil evaporation, and the mortality submodel over-reacts to short periods of drought stress. A more sophisticated soil moisture model will be adopted from Zelig 2.0 (Urban *et al.*, 1993) or from Bonan (1989). Discussion and references given by Coates *et al.* (1994) and Peterson and Peterson (1992) indicate that sufficient information exists in the literature regarding water relations of boreal tree species to permit a refined drought stress response function to be developed without recourse to field work.

## 2.2.2 Landscape Base Layers

The landscape model will require a number of spatial data sets to describe site and climate conditions, including elevation, soils, temperature and precipitation.

Elevation High resolution digital elevation models (DEMs) are available for parts of the study area, but a complete coverage does not exist. Furthermore, the spatial resolution ( $\approx 100 \text{ m}$ ) is higher than necessary for our present purposes, and the cost of obtaining an extensive coverage is prohibitive. However, it has proved possible to derive a coarse scale elevation model inexpensively, using Geodetic Survey Branch data obtained from Maps Alberta. Figure 10 illustrates a simple elevation model for the study area and surroundings that we have produced from this data source: elevation in m is shown on the z axis, as a function of latitude and longitude, plotted here at  $\approx 10 \text{ km}$  resolution. This map was produced using a fourth order polynomial distance weighted averaging scheme, from 3012 survey markers, mostly irregularly spaced. Significant landscape features are readily detectable, including the Pelican, Birch and Caribou Mountains, the Swan Hills, and the Athabasca Delta and adjacent lowlands. The primary use of this elevation model will be to improve the interpolated mean surface temperature model described below.

Climate The ecological land classification used in Alberta treats the study area as largely homogeneous with respect to climate Strong (1992), with the exception of some high elevation regions. However, our analysis of the available climatic data indicates that considerable spatial variability exists in both temperature and precipitation regimes. Figure 11a shows an interpolated precipitation map of the study area and surroundings. The rain shadow of some high elevation features may be clearly seen: the lack of features in the northwest portion of the map is due to the scarcity of long-term data in that part of Alberta. Figure 11b plots a number of climate stations according to their mean annual temperature and mean annual precipitation. The expected south to north temperature gradient is evident. There is also a general west to east decline in precipitation. These low resolution data sets appear sufficient to capture many features which may have ecological significance.

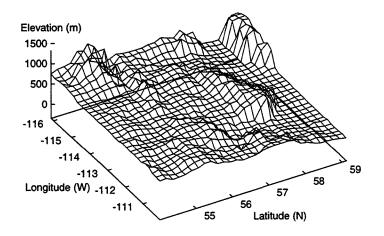


Figure 10: Low resolution digital elevation model for the study area and surroundings, based on 3012 geodetic survey markers. Vertical exaggeration is  $\approx 200$ .

The spatial variability in climatic conditions is enough to cause significant variations in forest composition and stand dynamics, as predicted by 2elig++. Figure 12 shows plots of simulated basal area for all species, for two 2elig++ runs conducted for sites at Fort Chipewyan and Whitecourt. The former is relatively cool and dry with a mean annual temperature (MAT) of  $-2.65^{\circ}$  C and mean annual precipitation (MAP) of 330 mm, while Whitecourt is relatively warm and moist, (MAT =  $1.15^{\circ}$  C and MAP = 540 mm) as shown in Figure 11b. The simulations were conducted assuming clayey soils, and with precipitation and temperature variance set to 0. Under a constant climatic regime, the failings of the soil moisture sub-model discussed in Section 2.2.1 are less apparent. It is clear that considerable differences in stand trajectories could be expected across the range of conditions prevailing within the study area.

**Soils** Although current Zelig++ simulations are largely insensitive to the variability in soil conditions, this reflects a weakness in the model which will be corrected. In reality, soil, and especially soil moisture regimes, are important determinants of vegetation in the study area (Lesko and Lindsay, 1973; Kabzems *et al.*, 1986).

High resolution soils maps are unavailable for the vast majority of the study area, and are not likely to become available in the foreseeable future. The data we have obtained include roughly 100 point samples, many of which are associated with Alberta Forest Service permanent sample plots, and some 1:126,000 scale soils maps for the Ft. McMurray region (Turchenek and Lindsay, 1982), portions of which we have digitised. The 1 : 1,000,000 digital version of the ecodistricts of Alberta Strong (1992) and a number of soil surveys at the same resolution may be adequate to designate the prevailing combination of site conditions within landscape units. We expect that the designation of four soils categories will suffice: coarse-textured or excessively drained locations; poorly drained organic terain, poorly drained or clayey mineral soils; and well-drained, loamy mesic sites.

Further work The elevation model (Figure 10) will be improved by sampling elevations from topographic maps along the major river systems in the study area, including the Athabasca and Christina Rivers. A superior interpolation method will be used to produce the final version. Maps of mean slope and aspect will then be produced. Samples of detailed slope, aspect and elevation obtained from 1:20,000 digital elevation models will be used to develop a spatial "noise" layer which will be overlaid on the low resolution maps, to generate a higher resolution pseudo-landscape. The precipitation map will be improved by incorporating growing season data from the network of fire towers in the area. The resulting maps will be used to produce elevation-corrected monthly mean temperature maps. Simulations of regional climate must preserve the spatial autocorrelation in temperature and precipitation anomalies, which has yet to be quantified.

Our stand modelling efforts to date have been concerned with replicating stand tree species composition on sites with known soil conditions. If resources permit, we hope to sample a number of soil profiles from the Calling Lake site vegetation plots, characterizing drainage,

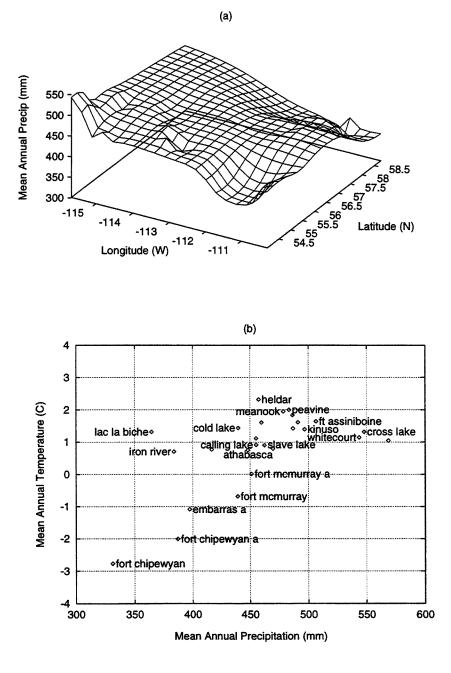


Figure 11: (a) Interpolated map of mean annual precipitation in the study area and surroundings, based on 23 long term climate station data sets. (b) Mean annual temperature and precipitation for a number of climate stations within the study area.

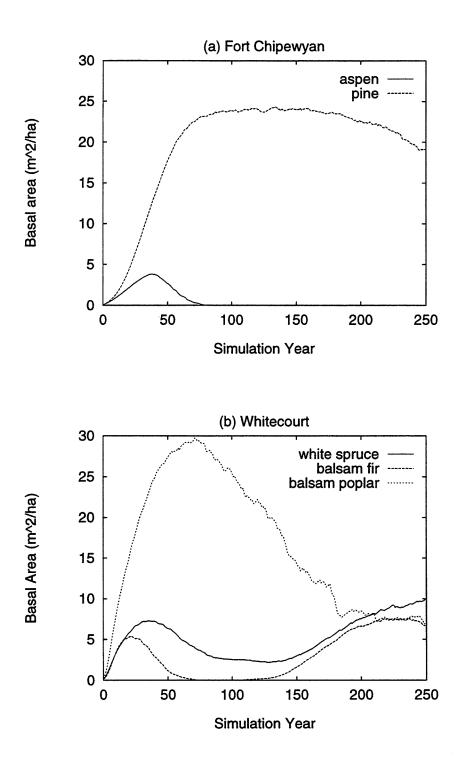


Figure 12: (a) Simulated stand dynamics for a cold dry site with clayey soils near Fort Chipeweyan, Alberta, to the northeast of the study area. (b) Simulated dynamics for a comparatively warm, moist site with clayey soils, near Whitecourt, Alberta to the southwest of the study area.

soil texture and coarse fragment content by horizon, and depth of rooting zone. This will extend our soils data base to include a variety of mature upland sites.

## 2.3 Disturbance Simulation

Our efforts have concentrated on the analysis and simulation of two predominant disturbance regimes in the study area, wildfire and logging. For current reviews of the role of fire in boreal forests, we refer the reader to Payette (1992). A more extensive treatment of fire behaviour, effects and ecology in the boreal forest is given by Johnson (1992). For an analysis of the implications of existing forest management policies in the study area, see Cumming *et al.* (1995). An overview of the general class of models described in this section (essentially area matrix wood-supply models) is given by Duinker *et al.* (1992). While insect defoliators, windstorm and tree pathogens may also influence landscape structure in the boreal mixedwood, we have not had the resources to explore these aspects of the regional ecology.

## 2.3.1 Fire

A number of spatial models of fire behaviour exist which are suitable for landscape modelling. Examples are described by Green (1989), Baker *et al.* (1991), and Baker (1993). The difficulties in developing landscape scale models of fire dynamics are not primarily technical, but lie in the estimation of model parameters describing the likelihood of fire ignition and spread. It is necessary to quantify the spatial pattern, frequency and timing of ignition events and the size distribution of the resulting fires. This is complicated by the possible existence of temporal trends in any or all of these properties, induced by climatic change, or (as is generally supposed) by fire suppression. Individual fire behaviour depends on many factors, including weather conditions prior to ignition and during the blaze, forest type, fuel loading and topography; the affects of some of these factors for Canadian forests are quantified (Anonymous, 1992). We aim to describe and simulate landscape patterns, not the behaviour of individual fires. Our goal is to develop simulations that capture the statistical properties of fire processes in the mixedwood.

This section describes empirical estimates of fire parameters, based on a study of 53 years of fire history data: data from 1961-1993 are described below, while a more limited data set covering 1940 to 1960 was obtained from Delisle and Hall (1987). We characterise certain spatial and temporal patterns of fire frequency, and estimate the impact of fire suppression on the natural fire regime. Two major fire events occurred during the study interval, enabling us to estimate the relative importance of extreme fire years and "background years" in structuring the landscape. Preliminary estimates of the relative impact of fire on different stand types are presented. A simple non-spatial fire model was then developed to explore the implications of our findings. The principal conclusions of this work are that the fire regime since 1940 is not consistent with forest age structure, as given by Phase 3 inventory data, and that this discrepancy is not a result of fire suppression. AFires database Most of the results described in this section are based upon an analysis of historical forest fire records, obtained from the Alberta Provincial Forest Fire Centre. The analysis of these records has been hampered by the variable format of the data sets, which cover five intervals: 1961 to 1982; 1982 to 1989; 1990 to 1991; and the individual years 1992 and 1993. The record formats, units of measurement, and data recorded are not consistent through time. We have developed a consistent data base for the entire interval 1961 to 1993. As many data elements as possible have been preserved or estimated for each fire for the entire period of record. All units of measurement are consistent, and fields have uniform meaning over time and have uniform default or null values that can be recognised by software. The database (dubbed AFires) contains 26,261 records. It is a flat text file, and is not restricted to any particular database software or operating system. We have developed an interactive extensible software tool, based on the awk scripting language (Aho et al., 1988), to interrogate AFires and to generate reports and output files suitable for external analysis or graphical display. Complete documentation of the methods used to derive AFires from its component parts, and documentation of the query tool, have been drafted. Pending authorisation from Provincial authorities, we will make the database and associated documentation and tools available as a service to the research community.

Spatial and temporal patterns in fire frequency Figure 13 summarises Provincial fire history data between 1961 and 1993. It shows the number of reported fires and the total area burned for the entire province and for a large ( $\approx 150,000 \text{ km}^2$ ) contiguous area of the boreal mixedwood, essentially that portion to the east and south of the Peace River (the "eastern mixedwood"). The mean annual number of fires has increased since 1979. This may be partly due to increased surveillance—although the present fire tower network was completed by 1968 (Murphy, 1985a)— or to more methodical record keeping. Mean annual area burned has declined significantly since 1983. This is presumably attributable to the efficacy of the pre-suppression preparedness system which went into effect in 1983 as a response to the large and destructive fires that occurred between 1980 and 1982 (Table 4). However, this apparent reduction may be in part an artefact of size-related biases in detection or recording in the 1960's and 1970's. Table 4 summarises these statistics.

Table 4: Mean fires per year  $(\hat{n})$ , mean annual area burned  $(\hat{A}, \text{ in } \text{km}^2)$  and mean fire size  $(\hat{s}, \text{ in } \text{ha})$  for the entire province, over various intervals between 1961-1993

Interval	ñ	$\hat{A}~{ m km^2}$	$\hat{s}$ ha
1961-1979	622	517	83
1980-1993	1056	2072	196
1983-1993	969	200	21
1980-1982	1374	8937	650

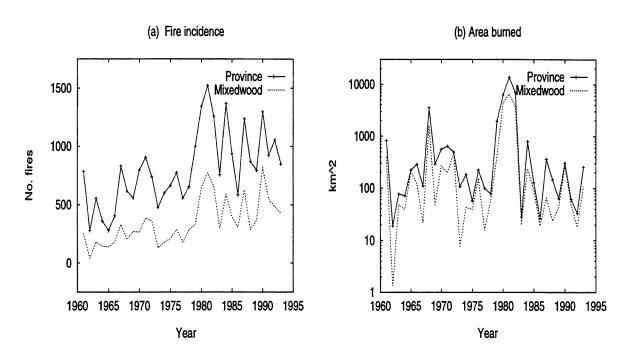


Figure 13: Overall trend in (a) number of fires and (b) area burned over the period of record. The graphs compare totals for the entire province with totals for that portion of the mixedwood ecoregion east of the Peace River.

Table 5 presents inter-regional correlations of annual area burned and of numbers of fires, between 1961 and 1993. Three regions are considered: the east and west portions of the eastern mixedwood (the east part is our study area) and the coniferous forests of the Rocky Mountains foothills south of  $55^{\circ} N$ . The two parts of the eastern mixedwood have essentially identical ignition regimes, while the foothills ignition regime is only weakly correlated with those of the mixedwood; the relatively strong relationship between lightning ignitions in the western mixedwood and the foothills may exist because these areas are contiguous, and hence likely to share storm events. Nonetheless, annual area burned in the western portion of the mixedwood, these statistics are strongly correlated. The correlation between annual area burned by lightning fires in the study area and in the foothills is puzzling; it is perhaps related to differences in precipitation regimes from west to east in the mixedwood region, or to a small number of years with unusual climatic conditions.

Table 6 shows the intra-regional correlations between area burned and numbers of fires. Clearly, annual area burned is influenced by factors other than ignition frequency. Johnson (1992) discusses some relevant climatic factors (*e.g.* his Figure 2.10) which might cause, for example, years with many small lightning fires. Such factors could well have large scale spatial variability, which would also explain why the correlations between area burned in the two parts of the mixedwood are far weaker than the correlations between numbers of fires.

The spatial distribution of fires throughout the study area is non-uniform and temporally variable. Figure 14 maps the abundances of lightning-caused fires for three 10 year intervals. The spatial distributions of the 1970's and 1980's are correlated (Pearson product moment,

Table 5: Relationships between area burned and fire frequency in the study area (EAST), that portion of mixedwood between the study area and the Peace River (WEST) and the Eastern slopes of the Rocky Mountains (SLOPES), from 1961-1993. Table entries are Spearman rank-order correlation coefficients, with significance values.

	Area Burned				
	WE	EST	SLOPES		
	All	Lightning	All	Lightning	
EAST	$.58 \ (p < 0.001)$	$.65 \ (p < 0.001)$	$.29 \ (p = 0.11)$	.45 $(p = 0.0083)$	
WEST			.16 $(p = 0.37)$	.16 $(p = 0.38)$	
		Number	r of Fires		
	WE	EST	SLC	OPES	
	All	Lightning	All	Lightning	
EAST	$.90 \ (p < 0.001)$	$.93 \ (p < 0.001)$	$.34 \ (p = 0.052)$	.45 $(p = 0.011)$	
WEST			$.37 \ (p = 0.034)$	.51 $(p = 0.0022)$	

Table 6: Regional correlations between area burned and numbers of fires from 1961-1993. Regions are as specified in Table 5. Table entries are Spearman rank-order correlation coefficients, with significance values.

Region	All	Lightning
EAST WEST SLOPES	$\begin{array}{c} .561 \ (p < 0.001) \\ .547 \ (p < 0.001) \\ .458 \ (p = 0.001) \end{array}$	.458 $(p = 0.007)$ .439 $(p = 0.01)$ .542 $(p = 0.001)$

r = .31); the correlations between the 1960's and 1970's (r = .17) and the 1960's and 1980's (r = .11) are much weaker (p < 0.001 in all cases). When non-lightning fires are included in the analysis, inter-decadal correlations are higher, which is probably due to a relatively constant spatial pattern in human caused ignitions.

There is evidence that inter-decadal variability in the spatial pattern of lightning fires is partly controlled by vegetation dynamics, at the township scale. Lightning fires incidence between 1981-1991 (Figure 14c) is negatively correlated with the abundance of 40–70 year old deciduous stands (Spearman rank-order coefficient (s = -.38) and positively correlated with the abundance of black spruce (s = .35) and white spruce (s = .16). All correlations are significant (p < .001). There is no correlation with pine, mixed aspen/white-spruce, or deciduous stands over 70 years of age. Assuming that lightning strike patterns are independent of forest cover, we conclude that presence of abundant deciduous forest temporarily inhibits fire. Once the stands either age, or become increasingly dominated by conifers, this effect declines, or even reverses. Further data on the spatial relationships between fire frequency and forest composition are reported in Cumming and Pelletier (1995).

The different spatial relationships between lightning and human caused fires are illustrated by Figure 15, which maps the approximate location, size, decade of occurrence and cause of all fires in an  $\approx 15,000 \text{ km}^2$  region bounded by 55° N 114° W and 56° N 112° W. The large human caused fires during the 1960's are probably due indirectly to agricultural expansion at the southern edge of the mixedwood region. The concentration of small anthropogenic fires in the northwest corner of the map is due to settlements adjacent to the Wabasca Lakes. Generally, in the study area, human caused fires are small, and are associated with settlements or transportation corridors.

From 1983 to 1993, 93% of the area burned within the study area was due to lightning caused fires, as opposed to 72% for the western portion of the mixedwood region, and only 4.7% in

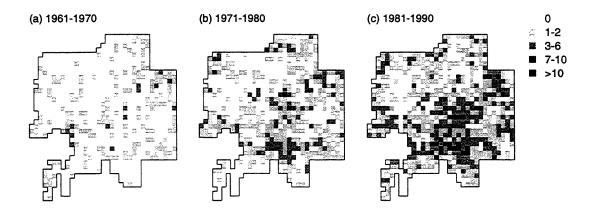


Figure 14: Spatial distribution of reported lightning caused fires within the study area during the intervals 1961-70 (a, 281 fires), 1971-80 (b, 477 fires) and 1981-91 (c, 607 fires).

the foothills slopes. Over the entire period from 1961-1993, the proportions are 68%, 71% and 65%, respectively. However, in the study area, almost all (> 95%) of the remaining 32% of burned area was due to a single human caused fire, in 1980. Of all fires larger than 1000ha, 20% on the eastern slopes were caused by lightning, as opposed to 76% in the western portion of the mixedwood, and 83% in the study area. The other regionally important causes of fire have been recreational activities in the study area, industrial activity in the remainder of the mixedwood, and local inhabitants in the foothills. These facts suggest that, as timber harvesting and related road building proceed in the study area, access control should play an increasingly important role in forest protection.

A marked and well-known feature of the temporal pattern in total area burned is the existence of fire years, or fire episodes in which unusual numbers of large, destructive fires occur, as in 1980-1982 in Figure 13. The longer term data sets assembled by Delisle and Hall (1987) (Figure 16) reveal another major event in the study area, in 1940 and 1941. Murphy (1985a) documents a major event in 1919, while evidence of repeated fire episodes as far back as 1860 led Moss (1932) to propose that major fire events followed a 20 year cycle: the spatial extent of these early episodes seems unknown, however. Inter-decadal variability has also been documented in Wood Buffalo National Park (Larsen, 1995). The phenomenon is general in boreal forests (Antonovski *et al.*, 1992), and it might be concluded that these infrequent episodes are the major factor structuring the boreal landscape. Note, however, that the impact of fire episodes is spatially variable. For example, 1979 was relatively severe on a provincial scale, but negligible in the eastern mixedwood, as were several years during the 1950's. On the other hand, most of the area known to have burned in the Province in 1940 was in the study area.

The relative impact of fire episodes and "background years" obviously depends on the interval sampled. From 1940 to 1993, which includes two major episodes (5 of 54 years), background years accounted for 37% of the area burned; from 1942 to 1982 (after one interval, but including the next), they accounted for 49% of the area burned. We therefore conclude that background years are not negligeable in their effects on forest age structure.

Quantifying the impact of fire suppression According to Murphy (1985b), approximately 2% of Alberta's forests burned each year, prior to the initiation of fire suppression. If so, then the average time between fires, and hence the mean age of forest stands, should be about 50 years. The 54 years of fire history data summarised in Figure 16 should therefore be sufficient to characterise the fire regime in the study area, except for the confounding effects of fire suppression. Here we describe some indirect methods of estimating the effectiveness of fire suppression efforts, and how they could be used to estimate the "natural" fire regime. Our methods assume that (1) in an area where most fires are caused by lightning, fire suppression can influence only the size of fires, not their number; and (2) any size-dependent bias in the recording of fires has been constant over time. Then changes in fire size distributions may be taken as a measure of the influence of fire suppression.

Figure 17 contrasts the size distributions of fires > 1 ha in the eastern mixedwood over four intervals, including the major fire event 1980-82. The numerous smaller fires (< 1 ha) were

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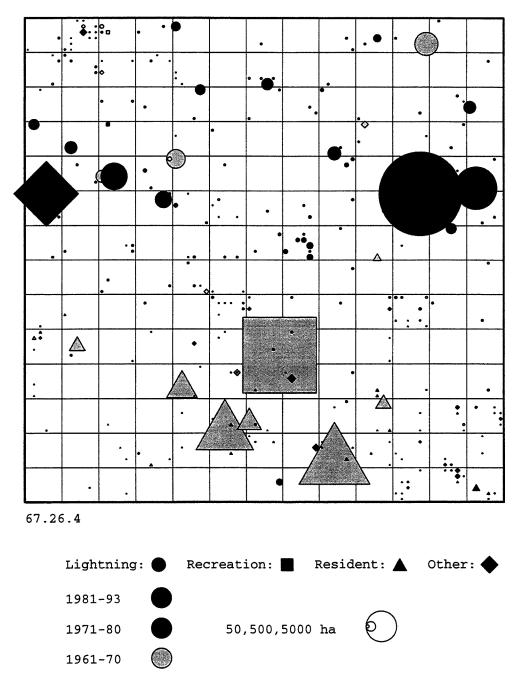


Figure 15: Size, cause, decade of occurance and approximate location of all reported fires between 1961 and 1993, in a  $\approx 17,000 \text{ km}^2$  region, approximately the southwest corner of the study area.

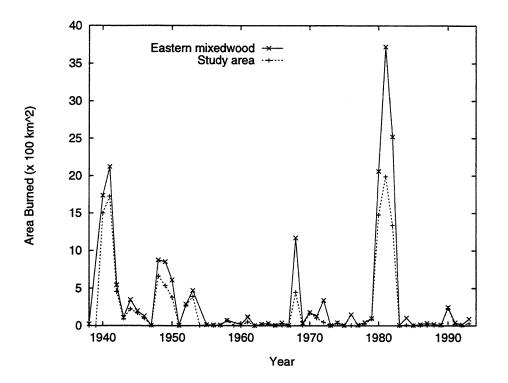


Figure 16: Fire history in the study area and the entire eastern mixedwood, 1940-1993.

removed, to partially correct for observational bias and changing reporting standards. All pairs of distributions are different under K-S tests at the p < 0.05 level, except 1961-1970 and 1980-82. The overall shapes of the distributions for the 1960's, 1970's and post-1982 are consistent with increasingly effective fire suppression, as are changes in mean fire sizes: 357 ha in 1961-1970, 233 ha in 1971-1979 and 145 ha in 1983-1993. The mean size of fires > 1 ha during the 1980-1982 episode was 2923 ha. There are. in fact, important differences between the 1961-1970 distribution and that of 1980-82, as is evident from the shape of the curves. When the samples are restricted to large fires (< 200 ha), the 1980-1982 size distribution is different from that of all other intervals, including 1961-1970, at a p = 0.0001 significance level. Fire episodes clearly differ from background years not only in that fires are more numerous, but also in that the fires are much larger. This is evident in the extended tail of the 1980-82 distribution in Figure 17.

Data prior to the 1960's exist only for fires > 200ha (Delisle and Hall, 1987) and, in the study area, only since 1940. There is no significant difference between the distributions of these large fires during the 1940's, 1950's or 1960's. However, the mean annual area burned in the 1960's was less than in the two previous decades (not counting the 1940-41 fire event), by a factor of 2.3 Provincially, 1.9 in the eastern mixedwood, and 2.6 in the study area. (Figure 16). Was this because of fire suppression? According to Murphy (1985a), fire suppression in northern areas of Alberta was, as a matter of policy, negligible prior to 1952, while the physical resources available for detecting or fighting fires were very limited until at least 1958. A network of fire towers was not completed in the area until 1968, and organised fire suppression extended to the northern boundary of the province by 1971, at which time a

Trends in fire size distributions

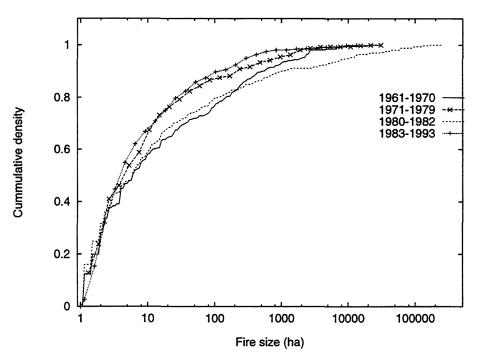


Figure 17: Trends in fire size distributions from 1961 to the present, for lightning caused fires > 1 ha within the boreal mixedwood region of Alberta

policy of total suppression of all fires was in effect. The ability of fire suppression to influence events in the eastern mixedwood was clearly minimal before 1960, and may have remained so as late as 1970. It seems probable, therefore, that the generally low burn rates of the 1960's are attributable to an interval of favourable climatic conditions, rather than to the early effects of suppression; this requires further investigation.

To reconstruct a possible "natural" fire regime in the study area since 1940, we need to estimate the area that would have burned, had no suppression been attempted. For the background fire years since 1940 (ignoring 1940-41 and 1980-82), we have attempted to do this with resampling. Using filter kernel methods (Silverman, 1986), we constructed empirical probability density functions of fire size for the three intervals 1961-1970 (260 fires, 24 886ha), 1971-1979 (592 fires, 22 252ha) and 1983-1993 (1467 fires, 29 778ha). An estimate of the area that would have burned in the 1983-1993 interval under a 1960's fire regime, for example, was then obtained by repeatedly resampling from the 1960's distribution. All reported fires were used in the resampling: fires with a recorded size of 0 ha were assigned an size of .05 ha, one half the smallest recorded non-zero value. This analysis assumes that average fire weather conditions were similar during the three intervals. Results for the study area are given in Table 7; for example, had the post 1983 fires followed the size distribution of 1961-70, the area burned would have been 4.84 times greater than it in fact was. Similar results are obtained when the entire eastern mixedwood is considered.

Note that the figures employed have excluded the extreme fire years of 1980-1982. This event can only be compared to the 1940-41 event. The two size distributions for large fires > 200 ha are not distinguishable by K-S tests. However, resampling indicates that the 1980's event was for more severe than 1940-41. The expected total area burned in 1980-82, given the 1940-41 size distribution, is 196 000 ha with approximate 95% confidence limits of 95 000 ha to 312 000 ha. The actual area burned in the study area during 1980-82 was  $\approx$  480 000 ha. The 1980's fire event was apparently far more severe than the only known, similar event. It seems impossible to estimate the impact of fire suppression on that event in any simple way. It is possible that predictive statistical models, incorporating fire weather parameters, could be used to provide superior estimates of changing fire suppression effectiveness; for some examples of such models, see Harrington *et al.* (1983); Antonovski *et al.* (1992). To develop and validate such models is not trivial, and outside the scope of this pilot study.

According to the fire history database, the total value of merchantable timber lost due to wildfire in the eastern mixedwood between 1983 and 1993 is estimated to be \$27, 400, 000. These estimates are probably biased towards conifer timber. Based on resampling methods, and the mean value lost per ha in several fire size classes, the 1970's fire size distribution would have entailed a loss of \$56, 690, 000 during 1983-93, while the 1960's distribution would have entailed a loss of \$125, 000, 000. These values are conservative because mean loss per fire appears to be an increasing function of fire size. It is difficult to fit a good empirical curve, however, both because the largest 1% of the fires inflicted 66% of the damage, and because some large fires evidently burn no merchantable stands at all. Another possible source of underestimation is in the valuation of deciduous stands, which may have been neglected in at least part of the interval.

We conclude that fire suppression effectiveness has increased steadily since the 1960's. Assuming that changes in fire size distributions are the result of suppression activities alone, the mean annual area burned in the mixedwood has declined by a factor of  $\approx 4.8$  since the 1960's. Pre-suppression values can be at most a further factor of two greater, depending upon the effectiveness of fire suppression during the 1960's. We have so far been unable to estimate the effect of fire suppression on extreme events such as the 1980-82 fire years.

Interval	Resampled	Factor	CI
1983-1993	1961-1970	4.84	(3.4, 5.9)
1983-1993	1971-1979	1.83	(1.25, 2.35)
1971-1979	1961-1970	2.61	(1.4, 3.6)

Table 7: Estimated fire suppression factors (Factor) with 95% confidence intervals (CI) based on changes in fire size distributions since 1961.

Estimating the "natural" age structure A notable feature of the forest age structure in the study area is the shortage of stands aged 1950 to 1979 (see Figure 2a). Only 6% of the forested area appears to be in this age class. This does not agree with the usual negative exponential age structure models (Van Wagner, 1978; Johnson and Van Wagner, 1984), which generally predict the existence of substantial areas of young stands. For example, if an average of 2.2% of northern Alberta burned every year (see below), 48% of the forest should have been less than 30 years old when the inventory was completed, about 1980. Assuming the 1% annual burn rate advanced by Johnson (1992) as average for boreal forests, 26% of the forest should have been younger than 30 years. This discrepancy is sometimes claimed to be a consequence of fire suppression. The results of the previous section allow us to evaluate this possibility.

Known fires in the study area from 1950 to 1979 have a total reported size of  $\approx 215,000$  hay or 2.9% of the area. This is less than the 6% of forested area in the give age class. Possible reasons for this include undetected fires, mis-classification of stands originating in 1948 or 1949 fires, and the effects of clear-cut logging. Using values from Table 7, with an additional factor of 2 to allow for possible early effects of fire suppression in the 1960's, we estimated the area that would have burned, in the absence of fire suppression. We applied these corrections both to reported fires, and to the aggregate area of stands in 1960's and 1970's age class, conservatively assuming they were all of fire origin. We found that between 6.3% and 12% of the forest would then have been less than 30 years old in 1980; the forest would still be skewed towards older age classes. We conclude that the scarcity of young stands revealed in the inventory data is not a consequence of fire suppression.

Estimation of the long term mean annual area burned (b) is sensitive to the time interval selected, because of the disproportionate impact of the two major fire episodes. Here, we estimate this value over the entire interval from 1940 to 1993, correcting for fire suppression effect using the factors contained in Table 7. Rates are obtained by summing over all fire sizes, scaling by the total size of the study area excluding water bodies (see Table 1), and dividing by the length of the interval (53 years). The uncorrected value of b obtained in this way is 0.0034, or 0.34% of the area burned per year. Using the values of Table 1, assuming that suppression had no effect prior to 1960 and that the 1970's factor applies to the 1980-82 fire years yields b = 0.00492. Applying an additional factor of 2 to allow for the possible impact of 1960's fire suppression yields b = 0.00806.

Figure 18 shows the predicted pre-suppression landscape age structures for the study area, given these two values, assuming the negative exponential models of Van Wagner (1978). It also shows the Phase 3 age structure of all stands in the landscape, considered as a population of patches. Under the hypothesis (refuted above) that the lack of young stands is due to fire suppression, the population was, for the sake of argument, shifted to the origin (see (Murphy, 1985b)). A fitted negative exponential curve is plotted against this age structure, with b = 0.022, very close to that obtained by Murphy's far more careful application of the methods of Van Wagner (1978); this corresponds to a mean stand age of 46 years. The values of b we have estimated correspond to mean stand ages of 124 and 203 years. According to the Phase 3 data, the mean age of the forested study area is 78 years. The expected age of

the forest based on our reconstruction of the natural fire regime is much greater than that given by the inventory data.

The management implications of this disagreement are considerable. For example, suppose these hypothetical age distributions apply to the commercial forest, which is to be managed at a rotation age of about 70 years. Then, if b = 0.22, only 22% of the forest would be expected to be older than rotation age. Our estimated values imply that between 56% and 71% of the forest would be older than rotation age.

We suggest four hypotheses to account for this discrepancy: (1) historic burn rates may have been higher than the available evidence suggests; (2) fires in the study area are significantly under-reported; (3) other agents of stand-level mortality (e.g. insect herbivory) may be operating; and (4) there exist substantial areas of stable, self-replacing stands which are older than their component trees, and whose ages (as time since fire) are underestimated in the inventory data.

Hypothesis (1) is not supported by a detailed study of fire history in Wood Buffalo National Park. Larsen (1995) found evidence of considerable inter-decadal variability in annual area burned, but it is not obvious from his results that the interval from 1850 to 1940 had significantly more fires than the interval since 1940, especially when fire suppression factors are considered. Hypothesis (3) certainly not be rejected. However, to reconcile the Phase 3 age structure with the fire regime we have reconstructed, other stand killing processes would have to operate at rates similar to that of fire. Hypothesis (4) has some plausibility, since many stand types in the study area are known to be capable of developing into potentially self-replacing, uneven-aged communities under some circumstances, including black spruce (Dr. J. Beck, 1993, personal communication), pine (Gauthrier et al., 1993), and aspen (Peterson and Peterson, 1992). Studies in Scandinavia indicate that self-replacing spruce stands may exist, with windthrow as the gap-generating disturbance agent (Jonsson, 1990; Hytteborn et al., 1991). The persistence of aspen in presumptive successional coniferous stands (Bergeron and Dubuc, 1989) and their ability to produce viable suckers in large numbers even in 200 year old stands (Lavertu et al., 1992) suggests that even mixed aspen-spruce stands could persist for long intervals. Kabzems et al. (1986) describe such an "extended mixedwood phase" for the Saskatchewan mixedwood, but do not indicate how common it may be.

Fuel type specific fire characteristics Serious fire years may have variable effects on the landscape depending on why they occurred. For example, the fire years of 1980 and 1981 were evidently caused by quite different climatic events, that resulted in a severe spring fire season in 1980, and a severe late-summer fire season in 1981 (Harvey *et al.*, 1986). According to AFires, 97% of the area burned in the study area in 1980 resulted from fires initiated in pine stands, while 86% of the area burned in 1981 resulted from fires originating in stands described as "spruce," almost certainly black spruce. These stand types tend to occur together in the southeast portion of the study area, where many of the large fires in this interval burned. However, this fact emphasises that different stand types may have

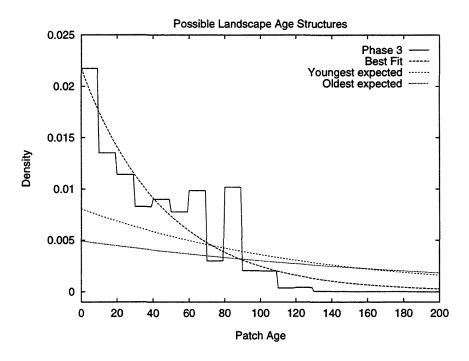


Figure 18: A possible landscape age structure circa 1940, compared to some predictions of a negative exponential fire history model, parameterised as explained in the text.

characteristic fire seasonality and fire size distributions, and may respond to extreme fire years in different ways.

Figure 19a contrasts the fire size distributions of several stand populations, for lightning caused fires in the eastern mixedwood region during the interval 1983 to 1992. Unfortunately, fuel type codes prior to 1983 can not be compared with those after 1983. Fires originating in black spruce stands are larger on average than are pine fires, which appear to be larger than fires starting in mixed stands, although the difference is not statistically significant. Table 8 summarises pairwise KS tests on fire size distributions of five common stand types same interval. Black spruce fires are quite different from any other type. Fires originating on mesic sites (deciduous, white spruce and mixed stands) can not be distinguished on the basis of their size distributions, mostly because of the small sample size for deciduous and pure white spruce fires. However, another view of the data is more illuminating. Figure 19b contrasts fire impact for these five types, plotting proportional total area burned as a function of fire size. Fires in pure aspen and white spruce stands are few, and almost all very small. Fires in mixed stands are more numerous, but the total impact is due almost entirely to a very small number of large fires (> 100 ha). A similar, but less marked effect is seen with black spruce fires, which have the most even size distribution. Analysis of AFires records since 1982 confirms some well known fire seasonality effects (Kabzems et al., 1986; Quintilio et al., 1991). Different fuel types are susceptible to ignition by lightning at different times of the year. Most of the area burned in deciduous origin fires is in the months of May or September, while fires in black spruce, pine and mixed stands are most severe in July.

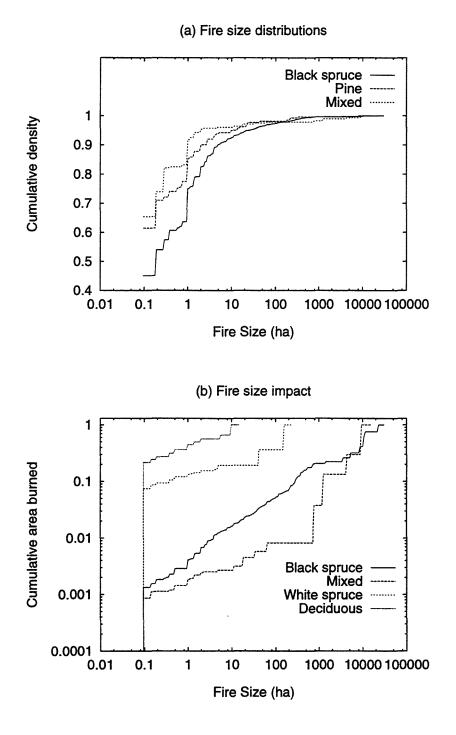


Figure 19: (a) Cumulative probability distribution of sizes of lightning caused fires in the boreal mixedwood east of the Peace River for the years 1983-1992, by fuel type. (b) Cumulative proportional area burned as a function of fire size for the same region and interval.

Table 8: Results of pairwise Kolmogorov-Smirnov tests on the fire size distributions for several fuel types; values denote the probability that differences are due to chance alone. Note that White Spruce, Deciduous and Mixed types are indistinguishable under this test.

	Pine	Mixed	White Spruce	Deciduous
Black Spruce Pine Mixed White Spruce	$2.3 \times 10^{-6}$	$< 1 \times 10^{-7}$ 0.125	$< 1 \times 10^{-7}$ 0.0008 0.17	$< 1 \times 10^{-7}$ 0.115 0.62 0.99

Table 9 contains very preliminary estimates of mean annual proportional area burned (burn rates) for several stand types within the study area, from 1983-93. Values were estimated using the total area burned by lightning fires starting in stands of various types, and the total area of each type available to be burned. The most significant facts revealed by this table are that different fuel types have vastly different ignition hazards, and that the annual burn rates for deciduous and mixedwood stands are too low to explain their Phase 3 age structures, even when the values of Table 9 are multiplied by the correction factors derived above. For example, if the burn rate for the aggregated mesic category (0.041% per year) is corrected to a 1960's fire regime, multiplied by 2 to allow for fire suppression in the 1960's, and another factor of 2 to allow for the long term average effect of extreme fire years, the mean annual burn rate is 0.79%. We may also conclude that if indeed most aspen stands are of fire origin, then either the pre-fire stand was not a pure aspen stand, or the fire originated in a different stand type.

Table 9: Total area burned by lightning fires (1983-93) within the study area for each major forested type, total area of that type, and their ratio, the mean annual proportional area burned, or annual burn rate. "Mesic" stands include all white spruce, mixed and pure aspen stands.

Fuel Type	Area Burned (ha)	Available Area (ha)	Burn Rate
Pine	330	$3.09  imes 10^5$	$9.7  imes 10^{-5}$
Black Spruce	15480	$6.19 imes10^5$	
White Spruce	19	$1.68 imes10^5$	$1.0  imes 10^{-5}$
Deciduous	8	$1.27 imes10^6$	$5.4  imes 10^{-7}$
Mixed	10935	$9.74 imes10^5$	$1.0  imes 10^{-3}$
Mesic	10962	$2.41 imes10^6$	$4.1  imes 10^{-4}$
Total	26771	$3.34 imes10^{6}$	$7.3 imes10^{-4}$

It must be noted that this analysis is based on the recorded fuel type at initial assessment, when the fires are usually small. In fact, large fires are not homogeneous. Where a fire starts may be a poor predictor of the final stand composition of the fire. A quantitative, map-based study of this effect is underway at the time of writing, which will include many of the large fires of 1980-82, and most of the large fires from 1940-1955. This should yield far more refined and reliable estimates of stand type specific fire hazard.

A new, non-spatial fire history model Although the ultimate goal of the present study is to obtain empirical parameters for a spatial model of fire incidence and spread, the data obtained have been used to develop a simpler, non-spatial model, which incorporates certain aspects of species-specific fire hazard and succession. The model has been used to explore the implications of the results of this section, including the estimated effects of fire suppression. It has also been incorporated into a low resolution spatial model of harvest scheduling, as described in Section 2.3.2.

The discussion in Section 2.1 (see especially Table 2) argues that the five common stand types break down into three independent ecological complexes, of which only the "mesic complex," composed of aspen, white spruce and mixed stands, is commercially significant. Figure 19 and Table 8 demonstrate that this complex experiences a distinct fire regime, so far as size distributions are concerned. However, Table 9 shows that the three stand types have vastly different burn rates. In addition, these types are successionally related. These facts suggest a straightforward generalisation of the traditional fire-frequency models, which assume either a constant or age-dependent rate of combustion (Van Wagner, 1978; Johnson and Van Wagner, 1984). Figure 20 illustrates the structure of such a generalised population level fire model, summarised as follows:

- Aspen, white spruce and mixed stands are stratified into a forest matrix by stand age (i) and % conifer content (j). Each matrix element represents the total area of stands of that age and conifer content.
- At each time step, a proportion B(i, j) of each matrix element burns, and regenerates to age class 0, with initial conifer content drawn from an estimated distribution.
- A proportion C(i, j) of unburned stands increases in conifer content at the next time step; the balance just ages.
- Intermittent (Poisson) "Fire Years" can occur, where the burn rate is a multiple of the background B(i, j).

By contrast, the usual negative exponential fire return models represent a stratification by age (i) only, with constant B(i) and no "fire years". The parameters B(i, j) are estimated from fire frequency data, and are here assumed to depend only on conifer content. No age-specific fire hazard data are presently available for the study area. Burn rates are interpolated from the values given in Table 9, assuming that flammability increases linearly until conifer content is 65%. The apparently low burn rates for pure white spruce stands may be a

consequence of their small size and dispersion. In the example simulations presented below, burn rates are assumed to be the same for all stands containing 65% or more conifer.

The frequency and intensity of fire years can in principle be estimated from the fire record, or, as here, be set to arbitrary values to explore model behaviour. The assumption that an individual large fire burns solely or mostly in stands of the same type in which ignition occurred is untenable. In a spatially explicit model, adjacency to a high hazard site may prove more important to stand susceptibility than age or conifer content. Thus, in modelling fire years, it is unclear whether the relative fuel-type specific combustion rates should be constant, or if one should assume that a fixed proportion of every stand type burns. At present, we have no empirical data to justify one assumption over the other. The simulations discussed below assume the latter option, using as a burn rate (during fire years) a constant multiple of the areal mean value shown in Table 9. That is, fire years are simulated as if large, intense fires that overwhelm any differences in relative flammability among stand types.

The remaining parameter, C(i, j) is crucial. We derived an empirical estimate for it by examining the relationship between stand age and white spruce content for all stands in the mesic complex, using Phase 3 inventory data. Figure 21a shows the resultant mean and standard deviations of conifer content by 10 year age class. The rather high mean conifer content of the two youngest age classes appears to result from an a relative abundance of large young white spruce stands, which may originate as planted clear cuts; these stands comprise only 0.26% of the total area. The straight line shows the results of a least squares

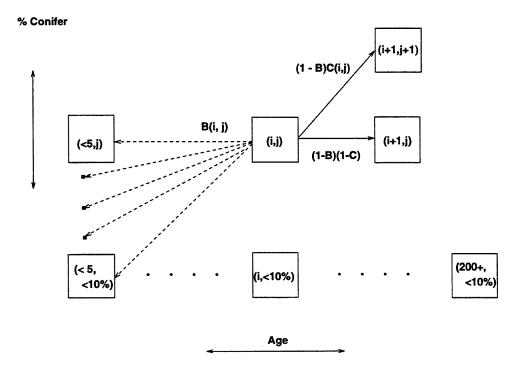


Figure 20: Structure of a new non-spatial fire-history model based on empirical data.

regression on the entire data set, ignoring stands of origin later than 1970; the slope is 0.00375 with y-intercept 0.126. This indicates that the mean conifer content of young, naturally regenerating stands is very low. We estimated the probability density function for the initial coniferous content of regenerating stands by correcting the conifer content values for 3,520 1960's origin stands, using the slope determined above. Regenerating areas in the model are assigned an initial conifer content by sampling from the estimated empirical distribution. These values may be biased downwards, if the conifer composition of young mixed stands is underestimated because of initial height differences between spruce and aspen. It is noteworthy that the relationship shown in Figure 21a is sensitive to stand area. When the population is stratified by stand size, conifer invasion in large stands (*e.g.* > 64 ha) is detectably inhibited for almost 100 years (Figure 21b). This result is consistent with dispersal limited recruitment of white spruce into large, fire-origin deciduous stands. This fact, together with the observed abundances of large deciduous stands in the study area, was used to estimate realistic values of C(i, j) for younger stands of low conifer content.

Figure 22 illustrates the current state of the study area when stratified as described above (Figure 22a), and the results of a number of simulations of the fire model. These simulations use C(i, j) obtained as described above, and using background burn rates and frequency and intensity of fire years roughly as given in Table 9 and Figure 13. Pre-suppression burn rates of 1.0% per year were assumed, and one half of the total fire effect is assumed to occur in fire years. Figure 22b shows that, given differential fuel type flammability, burn rates in the range supported by the available data lead to highly implausible age structures and species compositions. When the model is run with a background burn rate in the range supported by the data (1%) together with severe fire years at a mean interval of 40 years, some of the qualitative features of the existing landscape emerge (Figure 22c). However, substantial area of very old mixed and coniferous stands are still predicted. In Figure 22d the "natural forest" shown in (c) experiences increasingly effective fire suppression applied over 70 years, culminating in 10 years of burn rates shown in Table 9. Fire years continue to occur, but at reduced intensities, as the background rate declines. The changes are minor; because fire years are stochastic events, instances of the process which generated (c) exist which could not easily be distinguished from the results of fire suppression. It might be impossible to tell from age structural and species compositional data alone whether fire suppression had had any effect on the forest, because of the masking effect of severe fire years. Figure 22e is as 22c, except that the mean fire year frequency was 20 years. Although the amount of coniferous and older mixed stands is overestimated, the age structure of aspen resembles that given in Phase 3 inventory data, if one allows that adjacent peaks could be "smoothed" from slight errors in stand age estimates. In Figure 22f, the state shown in (e) is again subject to 70 years of simulated fire suppression, again yielding a final state which would be difficult to distinguish from the "natural" processes as simulated in (e).

**Further Work** A number of additional related projects are pending, which we briefly describe here. The modelling work to date suggests that fires which start in in black spruce or pine stands may have large effects on nearby deciduous and mixed stands. A study of the original stand composition of 36 mapped fires (which burned a total of 29,000ha) is underway

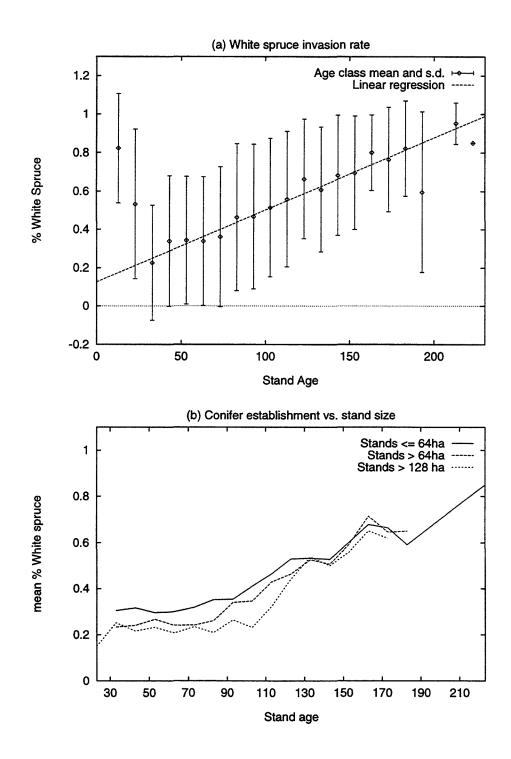


Figure 21: (a) White spruce invasion rate estimated from the relationship between stand age and conifer content, according to Phase 3 inventory data. (b) Mean white spruce content as a function of stand age, for several stand size classes.

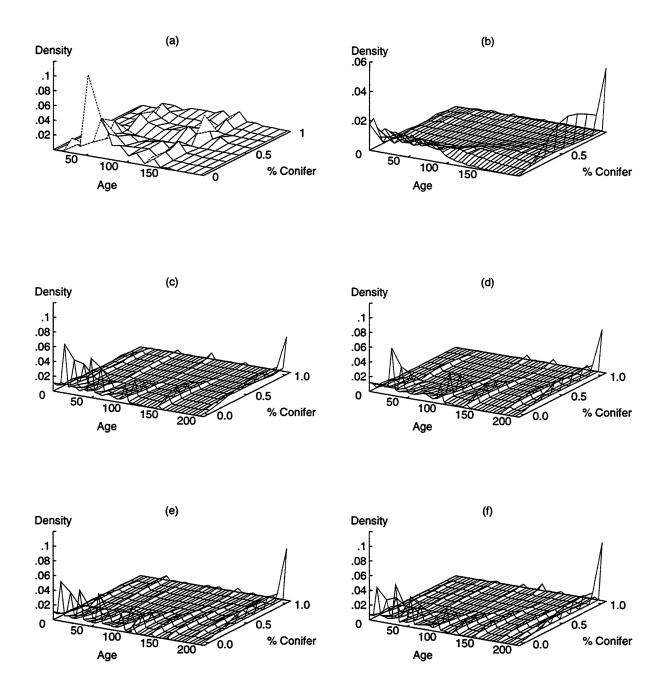


Figure 22: (a) Present structure of the aspen, mixed and white spruce components of the study area, based on Alberta Phase III inventory data. (b) Simulated long-run structure, assuming long run average annual burn rate of 1%. (c) Simulated structure assuming a background burn rate of 1% and fire years of 20x background intensity at 40 year mean intervals. (d) Starting from the state shown in (c), the background burn rate declines linearly to 0.15% over a 70 year period. Fire years as with scenario (c). (e) As (c), but with fire years at 20 year intervals. (f) Starting from the state shown in (e), the background burn rate declines rate declines linearly to 0.15% over a 70 year period. Fire years as with scenario (c).

at the time of writing. A systematic study of the composition of the large fires of 1980-1982 and 1940-41 was also initiated. This should permit at least a preliminary quantification of these effects, and lead to much superior model parameter estimates. The model presented in this section will be a more valuable tool when some of the present uncertainties are reduced by these studies.

Not all fires are stand-replacing fires. Also, fires in Alberta are heterogeneous in their effects (Eberhart and Woodard, 1987). The impact of fires on forest age structure could be overestimated if fire area statistics are accepted uncritically. We studied the relationship between fire size as reported in provincial records and fire effect, by looking for evidence of stand-replacing fire in forest inventory maps. One hundred and sixty recorded fires in 40 townships were studied. The results of this study have not yet been quantified.

For 19 large fires whose boundaries are overlaid on forest inventory map sheets, we sampled the stand boundaries which the fire crossed, and the stand type at the perimeter of the fire. Close to 3000 samples were obtained. We hope to use these data to estimate the likelihood of fire spread as a function of stand type. Some issues regarding spatial pattern of flammability and ignition could perhaps be settled by studying lightning strike data. We are endeavouring to obtain a copy of the available data from Provincial authorities.

#### 2.3.2 Logging

To simulate the effects of logging in the study area we have developed TARDIS, a spatial harvest schedule simulator. The underlying software technology will support the spatial models of vegetation dynamics and of fire. In its present form, however, it is strictly a timber harvest scheduler, operating at township resolution. This is the spatial resolution of currently available extensive forest inventory data sets, and the scale at which cut-block level harvest plans are presently developed in the study area. With the exception of the spatial component, the overall modelling framework is as described by Cumming *et al.* (1994).

Model structure The model treats the study area as a rectangular grid of equal sized areas (townships). Stands defined by Alberta Phase 3 inventory data (Alberta Forest Service, 1985a), as contained in the Province's AFORISM database, are stratified by age and conifer content. A township is defined by a matrix whose elements are the total area (ha) of stands of a given age class and conifer content; stands are stratified by 5 year age classes and 10% conifer content classes. Stands dominated by black spruce, pine or balsam fir are ignored, as these species are presently subject only to incidental harvest in the study area (Bamsey, 1993). Wetland and brush areas are not considered. Natural disturbance, regeneration, succession, and silviculture are simulated by specifying age- and composition-specific mortality and regeneration rates, using, for example, the semi-empirical values described in Section 2.3.1. There are no explicit spatial interactions between townships.

The principal spatial component in the model is the effect of geographic location on hauling cost. These costs are defined by a subsidiary input map (which may be produced, e.g., by a

Geographic Information System) defined using the provincial township grid, and existing or planned road corridors. However, a simple map of estimated distances to a specified point (e.g. a large pulp mill immediately to the south of the study area, near Grassland, Alberta) is sufficient to produce meaningful results: this is the default cost function used.

Spatially variable harvesting policies may be specified, determining operability (harvestable stand types by age and/or conifer content), number of passes, and green-up time for arbitrary geographic regions. Target annual volumes can be set independently for arbitrary regions. During each five year model time step, a number of townships are selected for logging, based on the amount of available operable area in the township and hauling costs from the township to the mill. At present, the scheduler tries to find a small number of townships as close to the mill as possible.

For each township selected in a time step, the model simulates a total chance harvesting plan, from first entry to the final pass. The area matrix is divided into components based on operable age, as a surrogate for yield classes. The number of components depends upon the number of passes. The older component is logged first. In subsequent passes, the (aged) remaining portions are taken, in order. After the last pass, the township is regarded as being in rotation. The next time that township is scheduled, a new plan is developed.

The effects of different volume yield assumptions may be studied by incorporating either interpolated Alberta Phase 3 yield tables (Alberta Forest Service, 1985b), or the results of computer simulations using stand yield models. By default, a mean yield of  $150 \text{ m}^3 \text{ ha}^{-1}$  is assumed. The effect of uncertainty in inventory data may be explored by specifying "confusion matrices" which alter the stratification of AFORISM stands. We are now conducting a study of the possible consequences of uncertainties in yield predictions and classification error, using the results of the error analysis described in Section 4.2. Another interesting feature of the model is that it permits the study of the interacting effects of number of passes and greenup time upon spatial and temporal patterns in harvest effort.

The results of habitat association analyses, such as those described in Section 3.3.1 or Section 3.4 may be used to derive low-resolution habitat models. This permits some evaluation of the effects of harvesting on the spatial distribution of breeding habitat for many bird species. The background disturbance, succession and regeneration modules of TARDIS have not yet been calibrated to reflect the best available data, so presentation of such results would be inappropriate at this time. TARDIS may be applied directly to any region in Alberta for which inventory data are available. It could easily be applied to most forested areas in western North America by revising the module that interprets and stratifies inventory data. TARDIS is written in C, and has been run on Silicon Graphics and Sun Microsystems workstations.

**Sample simulation** Figure 23 illustrates a TARDIS simulation, in which the study area was divided into three zones based upon the abundance of deciduous stands in each township, as shown in Figure 23a. The total deciduous pulpwood demand, assumed to be  $2.5 \times 10^6 \text{ m}^3 \text{ yr}^{-1}$ , is distributed so that 5% comes from the low abundance zone, 45% from the medium zone, and the remaining 55% from the high abundance zone. A uniform 2-pass harvesting schedule

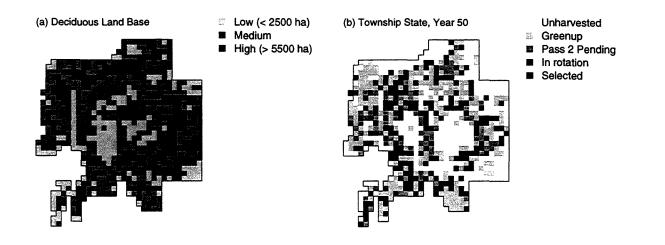


Figure 23: (a) Distribution of deciduous stands in the study area. (b) State of the study area after 50 years, under a harvesting scenario explained in the text. Areas marked "In rotation" have completed both passes of the simulated two pass plan, and will be re-evaluated prior to further logging activity. Areas marked "Selected" were logged during years 46 to 50.

is used, with a greenup interval between passes of 10 years. All ages classes greater than 40 years with a conifer content of less than 60% are considered operable. Harvested areas containing more than 50% conifer are regenerated as white spruce. Townships containing fewer than 200 operable ha are not scheduled for logging.

Figure 23b shows the resulting spatial distribution of unharvested, active, and greening-up townships after 50 years. In this simulation, the number of townships entered per year rises from 5 to 30, as high density areas are logged first. By year 50 about 40% of harvested townships are still being entered for the first time. 330 (40%) of the townships are still unharvested. Of these, more than 200 are high or medium productivity areas. No township has yet entered the second rotation, although 58 (those marked "In rotation" in the figure) are eligible to do so, having completed green-up time after the second pass. After year 35, the low productivity zone is unable to meet the volume demand placed upon it, as many townships in this zone have fewer than the minimum 200 ha of operable deciduous stands.

Under a three pass system, the number of high productivity townships which remain unlogged after 50 years is much reduced. This is partly because increased numbers of townships are unharvestable at any one time, due to greenup requirements, and partly because the volume harvestable from any one township during a single entry is lower. This necessitates the entry of a much higher proportion of the townships over the long run.

**Further Work** Work now underway to improve the realism of TARDIS includes representing the activity of coniferous quota holders and the exchange of coniferous saw logs and coniferous chip supply between deciduous and coniferous operators. Improved cost maps based on hauling distances and road classes are being developed. It may be necessary to add a haul

cost balancing component to the model. A disturbance and succession model based on the fire model described in Section 2.3.1 will be added when analysis of the fire history data is completed. The model has also been used to explore the consequences of the uncertainty in inventory and yield data (described in Section 4) on harvesting operations (Joy, 1995).

Linkages to the habitat reserve design system mentioned in Section 2.1.2 (see also Cumming *et al.* (1995)) will be implemented. A model subsystem will select zones which capture the regional variability in age structure and species composition, within which little or no harvesting will be done for a period of time. The zones will be re-evaluated at twenty-year intervals.

These enhancements will largely exhaust the potential of the system as it presently stands. In the longer term, a revised model based on higher resolution spatial data with little or no aggregation of stands into larger spatial units will be developed. Harvest scheduling will then run in tandem with high-resolution models of stand dynamics and disturbance described in Sections 2.2 and 2.3.1.

# 3 Effects of broad-scale forest harvesting on wildlife

#### 3.1 Establishment of a Forest Fragmentation Experiment

The focus of the wildlife sub-project is an experimental study of how forest fragmentation induced by timber harvesting affects the community and population dynamics of non-game birds in aspen-dominated forest. Birds as a group are known to be sensitive to the effects of forest fragmentation (Morton, 1992; Reed, 1992) and have been used as indicators of forest condition in the eastern boreal forest of Canada (Welsh, 1987). Neotropical migrants are thought to be particularly sensitive to fragmentation, especially in eastern deciduous forests where numbers of some species are declining due to loss of area and habitat, isolation effects, and edge effects (Robbins *et al.*, 1989a, 1989b). Cavity-nesting birds and those requiring large trees for nesting also will suffer from harvesting if snag or live tree retention is not adequate, because recurrent timber harvest will substantially reduce the availability of large, old trees. Birds are good indicators of the effects of forest fragmentation because they are ecologically versatile, function at a variety of scales, are relatively conspicuous, and easy to census (Koskomies, 1989). They are also the richest vertebrate taxon in the boreal mixedwood forest.

We focused on older stands for the experiment as there are no current provisions for retention of areas of forest older than 70 years, except along riparian buffer strips and in other reserve lands. All study sites were selected to be similar in age, canopy hight, canopy closure, tree species composition and understory features. This information was obtained from forest stand maps conforming to Alberta Vegetation Inventory (AVI) specifications, and confirmed by extensive ground truthing in the spring and summer of 1992. The study site is located in Township 72, Range 23, west of the 4th meridian, just east of Calling Lake, Alberta.

Harvesting plans for this study were approved by the Alberta Forest Service and Alberta Pacific Forest Industries in August 1992. During the winter of 1993-94, fragments of old mixedwood forest, 1, 10, 40 and 100 ha in size, with a consistent rectangular shape, were isolated from adjacent forest by cutblocks at least 200 meters wide on all four sides. Each size class is replicated three times, as determined by a priori power analyses (Schmiegelow and Hannon, 1993), and an equal number of controls (three replicates of each of the four size classes) have been established within an adjacent > 3500 ha area of continuous forest which will not be harvested. The experimental layout is shown in Figure 24. Fragment size classes over the 1, 10 and 100 ha plots should result in animals perceiving each size class as a different type of habitat (Hunter, 1987), and it provides species/area data over three logarithmic scales. The isolation distance of 200 m approximates some effects of expected forestry practices; isolation by 100 m or less can act as a barrier to fragmentation-sensitive bird species (Soule *et al.*, 1988; Bierregaard and Lovejoy, 1989).

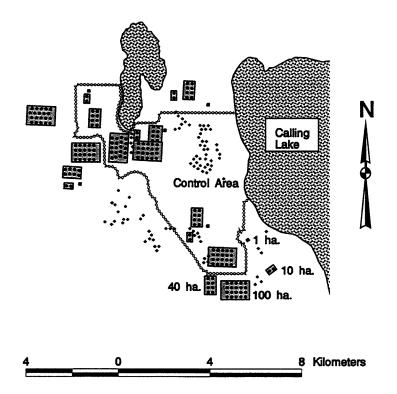


Figure 24: Experimental design of the Calling Lake forest fragmentation study, in township 72-23-4, Alberta. Location of point count stations in the fragments and in additional conifer plots are shown.

The experimental area was selected to be representative of the composition of older, deciduous dominated portions of the boreal mixedwood ecoregion, for it's similarity to sites selected for the Alberta Environment Centre's Aspen Biodiversity Study, and for it's spatial context. The landscape to the south of the Calling Lake Fragmentation Study Area is already fragmented by agricultural and forestry land uses. Townships to the west and north of the study area are slated for harvesting over the next two years. Immediately to the east is the large Calling Lake ( $\approx 140 \text{ km}^2$ ). Because of its location, this region will rapidly experience large-scale fragmentation, and will therefore approximate longer-term patterns anticipated throughout the boreal mixedwood forest as harvesting proceeds.

Subsequent to our initiating the fragmentation experiment, the study has expanded to include several other researchers. Mr. C. Machtans, a masters student with Dr. S. Hannon, from the University of Alberta, is studying forest fragments connected via 100 m wide riparian buffer strips, to test if these travel corridors increase conservation potential for birds. Dr. M. A. Villard, also with Dr. S. Hannon, is engaged in a detailed population-level study of the neotropical migrant American Redstart (*Setophaga ruticilla*). Our work provides baseline information for these endeavors. Students with Drs. F. Bunnell and A. Chan-McLeod, from the Centre for Applied Conservation Biology, University of British Columbia, are studying community-level patterns of small mammal and amphibian response in the Calling Lake study area, using the existing experimental design. All of these studies are fully integrated, with common sampling methods being employed where possible.

## 3.2 Preliminary Avifauna Habitat Affinities

#### 3.2.1 Methods

Point counts provide species richness and evenness measures within the breeding season. We conduct five surveys each year, between the last week of May and the first week of July (Ralph et al., 1992). In the winter, when birds occur mainly in flocks, transect counts are used to measure bird activity (Robbins, 1981). Permanent sampling stations have been established along transect lines on a 200 by 200 meter grid. Observer and diurnal variation, as well as order of surveying, are standardized across all areas and seasons, in each year. Because presence/absence and relative abundance data alone can be misleading indicators of habitat quality (Van Horne, 1983; Pulliam, 1988; Martin, 1992b), we are also conducting more detailed studies to distinguish "source" from "sink" areas. Breeding status and success of individuals and species are being monitored through territory mapping, nest searches, and other observational methods. Although the relative abundances of some species in recently fragmented areas may increase due to displacements caused by cutting, we predict that birds in small fragments will have lower pairing success, higher reproductive failure, and higher turnover rates than those in large fragments or continuous areas. Detailed measurements of habitat structure and composition are also being collected at all stations within each site to determine the effect of local habitat heterogeneity on bird communities and populations. Sampling protocols for these studies follow North American standards (e.g. Ralph et al. (1992); Martin (1992a)) to allow direct comparisons to other studies. Finally, the characteristics of neighbouring areas around each fragment (e.q. Lauga and Joachim, 1992) will be used to assess landscape heterogeneity.

Harvesting of the boreal mixedwood forest will reduce the area of older forest, and simultaneously increase the area of younger stands. The landscape matrix within which patches of older forest occur may influence population dynamics within these fragments due to isolation and edge effects, such as increased predation, competition and nest parasitism (Robbins *et al.*, 1989b; Robinson, 1992). We have been monitoring avian community composition in a ten-year-old cutover site within our study area, as this regenerating forest resembles what a first pass area will look like when the second pass takes place. Movement patterns of birds between this area and areas of older forest are being studied. We are also monitoring community composition and movement patterns in the recently harvested areas surrounding our study sites.

A study of old, aspen-dominated stands which are surrounded by black spruce has also been initiated, in collaboration with Dr. S. Hannon. Because bird communities in black spruce and mature aspen differ strongly, these areas represent natural isolates, and serve as temporal analogues for our shorter-term studies. We sampled bird community composition (richness and relative abundance) in a small sample of these areas in 1993, and a larger sample in 1994 with a greater range of fragment sizes. These areas are interesting ecologically, and are candidate habitat reserves, because they are operationally undesirable.

A final complement to the community-level work is the addition of study plots in coniferousdominated stands within the Calling Lake area. There is concern that partitioning of the mixedwood land-base in Alberta between coniferous sawlog exploitation and deciduous pulpwood production may virtually eliminate the region's characteristic mixed stands (Cumming *et al.*, 1995; Lieffers and Beck, 1994). This research will document avian community composition in old mixedwood stands with varying amounts of white spruce in the canopy. A manuscript detailing this work is in preparation.

Collection of pre-fragmentation data on wildlife occurrence and habitat use has been completed. These data document the natural patterns of habitat occupancy and productivity, both within the breeding season and in the winter, prior to disturbance by forest harvesting. The area was harvested in the autumn and winter of 1993/94.

#### **3.3 Preliminary Results**

Sixty-one species of forest songbirds and woodpeckers, represented by over 9,000 observations, were recorded in the upland deciduous experimental and control sites during dawn counts in 1993. Six additional species of songbirds and woodpeckers were recorded only during the first count. These were considered transients and were removed from subsequent analyses. Other birds, such as hawks, owls and grouse, were not adequately sampled during dawn point counts and so were also excluded from the analyses. Species counts for the treatment and control areas are shown in Figure 25. The smaller study sites (1 and 10 ha) exhibited the greatest variation in species number, and the highest number of species in any single site was recorded in one of the 100 ha control sites. However, there was no significant difference in the pre-fragmentation species-area relationship between experimental and control areas. Further, there is no significant difference among replicate groups (1, 2 and 3 in both experimental and control sites) (Figure 26). The overall species-area relationship (Figure 26) is significant (p < 0.001,  $R^2 = 0.90$ ), and is described by the following equation:

 $S = 0.57 A^{0.50}$ 

where S represents species number and A represents area, in ha.

There are several interesting aspects to this baseline community description. First, even the largest study sites (100 ha) did not completely represent the species richness of the avian community in the area. Second, the slope of the pre-fragmentation species-area relationship (0.55) is extremely high compared to those documented for other contiguous areas (e.g. 0.12 for the Great Lakes-St. Lawrence forest region in Ontario), approximating more closely values seen in severely fragmented systems (Schmiegelow and Nudds, 1987; Schmiegelow, 1990). This suggests that the spatial and temporal patchiness of the boreal forest represents natural fragmentation. Finally, the variance about the pre-fragmentation species-area relationship (0.0013) is significantly less than that used in the initial power analyses. We should therefore be able to detect much smaller changes in species richness due to fragmentation, than previously suggested (Schmiegelow and Hannon, 1993).

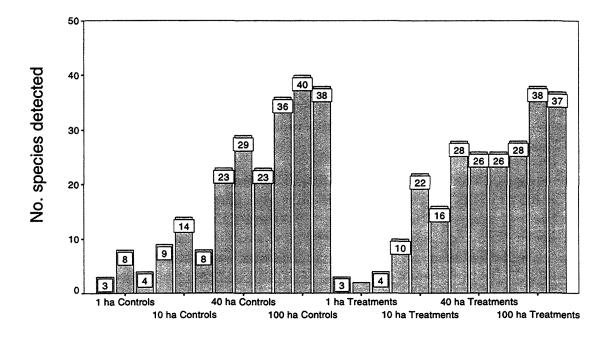


Figure 25: Pre-fragmentation bird species totals for experimental and control sites, 1993.

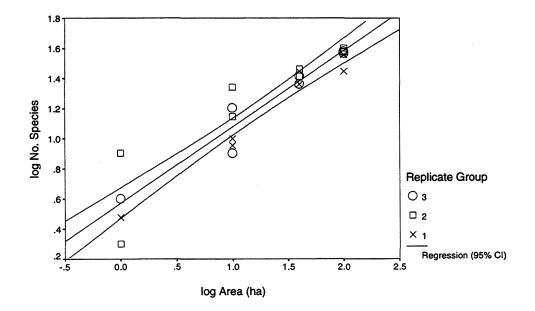


Figure 26: Pre-fragmentation species-area relationships for the replicates, with overall species-area relationship and 95% confidence intervals (1993 data).

A summary of descriptive statistics from upland aspen-dominated sites, naturally isolated aspen-dominated sites, and white spruce-dominated sites is given in Table 10. Upland deciduous sites had significantly more bird records per sampling station than either coniferous sites or natural isolates (p = 0.003, p < 0.001, respectively), and coniferous sites had more records than natural isolates (p < 0.001). There was no significant difference in number of species per sampling station between upland deciduous and coniferous sites (p = 0.145), but both had significantly more species than the natural isolates (p = 0.003, respectively). Similarly, there was a decline in overall species richness and uniqueness, defined as species found exclusively in a given site type, from upland deciduous to coniferous to naturally isolated deciduous sites.

Species-area regressions for coniferous and naturally isolated sites were also significant (p = 0.0162,  $R^2 = 0.54$ ; p = 0.0095,  $R^2 = 0.77$ , respectively) (Figure 27). The coniferous sites exhibited a shallower slope and higher intercept (0.30 and 1.17, respectively) than either the upland deciduous (0.45 and 1.06) or naturally isolated sites (0.52 and 1.02). The differences between the upland deciduous and isolated deciduous sites were not significant, but this was not a powerful test due to the small sample size of natural isolates (n = 6, number of stations = 12). Species composition among sites differed, with natural isolates sharing properties of both upland deciduous and coniferous sites (Table 11).

Black-throated Green Warblers were notably absent from all natural isolates, but were relatively common at all other sites. There was an overall paucity of warblers in the natural isolates, suggesting that these are effectively habitat islands. As well, species composition is nested across sites. This means that the species found in small sites are not random samples of those found in larger sites; small sites tend to share the same small group of species, which accounts for the lower number of species overall. This is further evidence that the surrounding matrix of black spruce is influencing these stands, by effectively isolating them from communities in nearby upland areas.

We examined relationships with vegetation structure and composition in more detail. Relative abundances of each bird species at 116 stations were calculated from the point count

	Aspen dominated	White spruce dominated	Natural isolates
No. of Sites	24	10	6
No. of Stations)	186	67	12
Total species	61	46	31
Unique species	18	. 3	0
Mean Species/Station	$14.2(\pm 3.6)$	$13.7(\pm 2.3)$	$11.4(\pm 2.5)$
Mean Records/Station	$37.7(\pm 9.6)$	$34.4(\pm 6.9)$	$23.2(\pm 5.0)$

Table 10: Summary statistics for all site types, 1993. Mean counts per station are given with standard errors.

Table 11: The ten most common species detected during point counts, in descending order of relative abundance, in upland deciduous, naturally-isolated deciduous, and coniferous sites, at Calling Lake, Alberta, 1993. Species occurring in multiple site types are marked.

UPLAND DECIDUOUS	ISOLATED DECIDUOUS	UPLAND CONIFEROUS
White-throated Sparrow	White-winged Crossbill	Yellow-rumped Warbler
Ovenbird	Yellow-rumped Warbler	White-winged Crossbill
Yellow-rumped Warbler	Swainson's Thrush	Ovenbird
Least Flycatcher	Least Flycatcher	Swainson's Thrush
Black-throated Green Warbler	Ovenbird	Black-throated Green Warbler
Red-eyed Vireo	Pine Siskin	White-throated Sparrow
Yellow-bellied Sapsucker	Red-eyed Vireo	Western Tanager
Mourning Warbler	Gray Jay	Golden-crowned Kinglet
Chipping Sparrow	Western Tanager	Pine Siskin
Western Tanager	Ruby-crowned Kinglet	Red-breasted Nuthatch

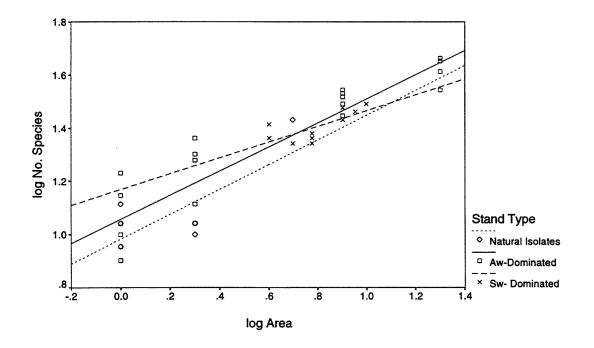


Figure 27: Species-area relationships for all sites, Calling Lake, Alberta, 1993. Aw=Aspen; Sw=White spruce.

data (Bibby et al., 1992). Two-tailed t-tests revealed 14 species that occurred at significantly higher (p < 0.05) abundances in deciduous stands, while 14 species seemed to prefer coniferous stands (Table 12). The remaining 24 species for which there were 10 or more records showed no significant preferences based on site type. These broad associations were explored further using detailed habitat measurements from 140 vegetation plots throughout the sites. Within a 5 m radius of each plot, we measured percent coverage of 6 classes of ground vegetation and leaf litter cover, leaf litter depth, the density and species composition of shrubs, tree saplings and poles, canopy cover, slope and aspect. Within an 11.3 m radius of each plot, density and composition of trees in four size classes, the height, species and percent bark of all snags, and the height of all major vegetation strata were measured. Downed woody debris (DWD) was sampled along transects between the 5 and 11.3 m radii (total 25.2 m per plot). For all DWD intersecting the transects with diameter < 11 cm, numbers were tallied for three size classes. For all larger DWD, actual diameters, length, rot class and, where possible, species were recorded. Principal Components Analysis (PCA) of 63 habitat variables revealed that three factors accounted for approximately fifty percent of the variation in the vegetation data set. Factor 1 was defined by the presence of large deciduous trees (r = 0.85), a well-developed sapling and pole layer (r = 0.87), extensive ground cover (r = 0.77) and depth of leaf litter (r = 0.77), and an absence of white spruce or other coniferous tree species (r = -0.92). Factor 2 exhibited a strong association with balsam fir (r = 0.98) and the presence of a coniferous sapling layer (r = 0.94). The abundance of black spruce (r = 0.98) and bare ground (r = 0.98) defined Factor 3.

Table 12: Habitat preference of bird species, based on significantly different abundance measures, at Calling Lake, Alberta, 1993.

DECIDUOUS	CONIFEROUS				
American Redstart	Bay-breasted Warbler				
Black-capped Chickadee	Boreal Chickadee				
Brown-headed Cowbird	Chipping Sparrow				
Brown Creeper	Dark-eyed Junco				
Least Flycatcher	Golden-crowned Kinglet				
Magnolia Warbler	Gray Jay				
Mourning Warbler	Ovenbird				
Rose-breasted Grosbeak	<b>Red-breasted Nuthatch</b>				
Red-eyed Vireo	Solitary Vireo				
Warbling Vireo	Swainson's Thrush				
White-throated Sparrow	Western Tanager				
Western Wood Peewee	Winter Wren				
Yellow-bellied Sapsucker	White-winged Crossbill				
Yellow Warbler	Yellow-rumped Warbler				

A correlation matrix of all bird species densities and habitat variables revealed a correspondence of significant relationships (p < 0.05) with the variables that defined Factor 1. Exceptions to this generalization are the strong associations of many bird species with large balsam poplar trees, large snags and white birch. These did not appear as significant explanatory variables in the PCA. Next, we shall plot the bird species habitat distributions within the variable space defined by the PCA, and look for overlapping or exclusive domains. The results of the correlation analyses provide a subset of variables which can be used to build species-habitat regression models. Non-linear relationships in the data set are also being explored. Models derived from 1993 data must be tested against data from subsequent years and other sites. Also, these analyses are strictly descriptive, and future work will be directed towards the processes involved.

#### 3.3.1 Ongoing Research

An additional year of post-treatment data was collected in the winter and summer of 1994, with final winter and summer field seasons planned for 1995. By the end of 1995, we will have three years of data from our control areas. These will be used to estimate the natural annual variation in species abundances, independent of harvesting-induced perturbations. We shall also have two years of post-treatment data from the newly fragmented areas, three years of data from the second growth areas, and two years from the recent cutovers. These data will provide quantitative measures of the suitability of habitat patches for many species, as a function of patch structure, composition, size and adjacency. Those species, if any, sensitive to forest harvesting will be identified. This information will then be used to develop predictive models of bird species occurrence and abundance within the landscape model.

We will also continue to document patterns of habitat occupancy in coniferous-dominated forest and natural deciduous isolates. We shall expand this work to include more natural isolates, of a greater range of sizes, and more mixed stands. Community-level reproductive success, as an indicator of habitat productivity, will be measured in some of these areas. This information will be used in landscape level models, both to simulate the effect of combined pulp and saw-log operations, and to explore reserve options.

Other initiatives are also underway. We now have broad-scale distributional data for furbearers and birds over much of northeastern Alberta, from long-term trapline records and the survey data used to produce the Atlas of Breeding Birds of Alberta (Semenchuk, 1992). We will use these data to test if existing forest inventory data can predict broad-scale distribution patterns of wildlife, and serve as a basis for extrapolation from our more localized intensive studies. The detailed habitat inventory data collected in conjunction with the fragmentation experiment and the coniferous forest study will be used to assess the comparative accuracy of different forest inventories (see Section 4.2).

### 3.4 Wildlife Habitat Suitability Modelling

We eventually will develop bird habitat models which relate breeding density to stand age, composition, size and the surrounding matrix. These, however, must await completion of the studies described in Section 3.3.1. Here we present some preliminary models based on a simple non-spatial representation of a patch of forest (Table 13). The models are expressed by suitability indices which relate reported species abundances, or, in some cases, breeding activity to structural features of a patch. "Suitability" is scaled from 1 (unsuitable) to 6 (most suitable) to allow qualitative comparisons of species responses to changes in a landscape, considered as a non-interacting population of patches. A patch is defined by its dominant tree species and its habitat "stage" which divides the life-history of a stand into temporal stages where particular structural or compositional features (high stem density, crown closure, the presence of snags) predominate. We considered five distinct patch types, namely pine, black spruce, white spruce, aspen and mixed stands. Six habitat stages are recognised for all patch types (Cumming *et al.*, 1994).

Aspen stands are defined to have six stages, namely establishment (0-5 years), an interval to maximum stem density (5-15 years), an interval to maximum crown closure (15-30 years), an interval to maximum basal area (30-60 years), an interval of maturity (60-80 years) and a final old-growth stage, characterised by canopy gaps, large snags, downed logs, and changes

Table 13: Some preliminary habitat suitability values, based on literature reviews. Habitat stages are defined in the text. Patch types and stages not mentioned, or blank, indicate suitability scores of "1".

Species	Patch Type	Habitat Stage					
		1	2	3	4	5	6
Pine Marten	Pine			2	2	2	2
	White Spruce			2	3	4	6
	Mixed				2	3	4
Meadow Vole	Pine	3	2				
	Spruce	6	3				
	Åspen	6	3				
	Mixed	6	3				
	Black Spruce	3	2				
Broad-winged Hawk	Aspen					4	6
-	Mixed				4	5	4
Three-toed Woodpecker	Pine	4			2	4	5
-	White Spruce				3	4	6
	Mixed				2	3	4
	Black Spruce	3			2	4	6
Black-throated Green Warbler	White Spruce			2	4	5	4
	Mixed			2	4	6	6

in the shrub layers (Westworth *et al.*, 1984). For all other cover types, these stages are assigned the age intervals of (0-5), (5-25), (25-60), (60-100), (100-150) and 150+ years. In these cases, the mature stage beginning at age 100 corresponds roughly to the period when stand volume increment begins to decline. Justification of the model values shown in Table 13 is given in Cumming *et al.* (1994). In that paper, the consequences of a number of alternative forest management policies in the boreal mixedwood are explored in terms of their effects on wildlife habitat availability. Models of this kind, whether based on literature reviews or empirical studies, may easily be linked into the harvest schedule simulations described in Section 2.3.2, to explore some spatial implications of management policies on the abundance of habitat for various species. Some preliminary trials have been made, using the values given in Table 13, but are not reported here.

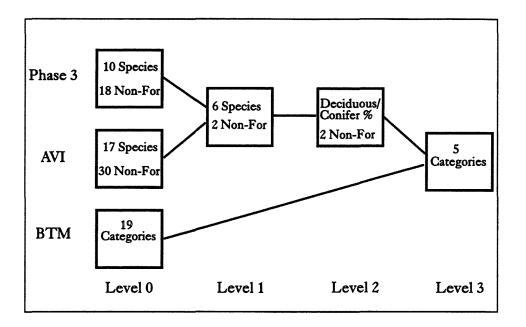


Figure 30: Thematic aggregations used to compare inventory datasets

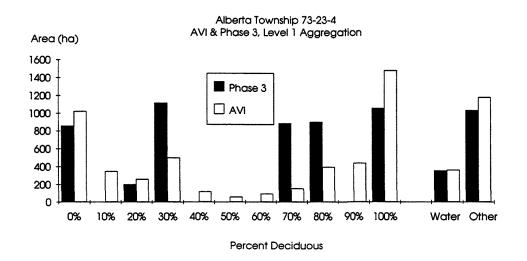


Figure 31: Level 2 thematic aggregations: area by category

Phase 3 shows a greater area in the 30% and 70-80% range. It is also interesting to note the small area Classified between 40% and 60% deciduous content in AVI, and the total absence of such areas in Phase 3. This may be partly an artefact of the species composition scheme used in Phase 3 data.

The purpose of Level 3 aggregation is to enable the comparison of all three datasets. This required a high level of aggregation, using the following five categories: Deciduous (70-100%), Coniferous (70-100%), Mixed (40-60% each of conifer and deciduous), Water and Other. Figure 32 shows a bar chart for the Level 3 aggregation level. AVI shows less deciduous area and marginally less coniferous area, compared to Phase 3. These figures do not lend any support to the possibility of a conifer bias (over-estimated conifer species composition) in the Phase 3 data. Also shown on this graph are the BTM pilot study and the BTM production phase datasets. A striking feature of this graph is the large discrepancy between the BTM pilot and BTM production phase datasets, and the discrepancy between the BTM datasets and the two higher resolution datasets (Phase 3 and AVI).

Figure 33 compares the spatial distribution of forest cover at Level 3 aggregation; the figure may also be viewed as a "map of uncertainty". Table 14 compares the areal agreement between the three data sets; generally, BTM data is in poor agreement with the other two sources. All three data sets are in agreement for 41% of the total area; for 48% of the area, 2 out of three datasets are in agreement, while all three data sets yield different classifications for 11% of the total area. The areas where all three datasets agree are perhaps smaller than expected, given the high level of aggregation present. For a significant proportion of the area, all three datasets disagree. In general, there appear to be large areas in a particular agreement class, rather than many small areas. This implies that positional inaccuracy and boundary effects account for only a small proportion of discrepancies, compared with differences in category definition. The effects of temporal change due to stand dynamics are not accounted for on this map, and are currently under study (see below). Note that white areas on the map denote areas for which one or more datasets have no data.

Table 14: Pairwise areal agreement among the three vegetation data sets, at Level 3 aggregation.

	Phase 3	AVI	BTM
Phase 3 AVI BTM	100% 73% 49%	100% 48%	100%

#### 4.2.2 Future Research

**Temporal change and stand dynamics** The results reported here contain no analysis of temporal change and stand dynamics, particularly with reference to the Level 1 and Level

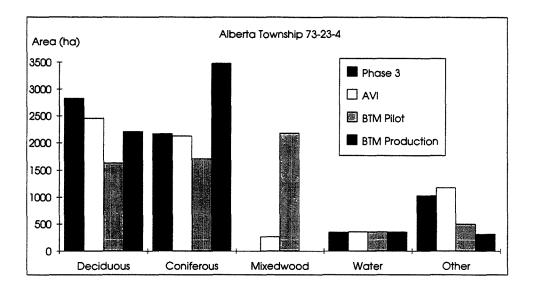


Figure 32: Level 3 thematic aggregation: area by category.

2 Phase 3/AVI comparisons. We are currently analyzing the change in species composition between Phase 3 and AVI (using Level 1 aggregation, as described in Section 3), and comparing the observed differences with likely changes due to stand dynamics. In order to determine the expected changes in stand composition, we are investigating the results of stand simulators (including Zelig and the Stand Projection System (SPS; Arney, 1993), provincial Forest Service permanent sample plot data and other published descriptions of stand dynamics relevant to the area. We are including SPS predictions because it appears to be the model of choice for consulting foresters in the study area.

Applying the methodology to different townships The GIS procedures developed to implement the methodology outlined herein have now been automated and can be carried out rapidly when township data become available. We have 6 digitized Phase 3 maps available for this analysis, and have recently received BTM data for the entire area, courtesy of Pearson Timberline Forestry Consultants (Edmonton) and Alberta Pacific Forest Industries Inc. A more complete analysis, extended to four townships for which all three data sets were available as of January 1995, was completed after the conclusion of the pilot study: see Joy (1995). More extensive studies could easily be conducted if necessary.

Incorporating ground-based data We hope to use ground-based data in the analysis, wherever this information is available. These data will include the extensive vegetation data collected by Ms. Fiona Schmiegelow and others, as described in Section 3.3. BTM ground truth data and AVI ground samples may also be available. Another potential source of point data are "air calls," direct estimates of forest cover at a particular point made in the course

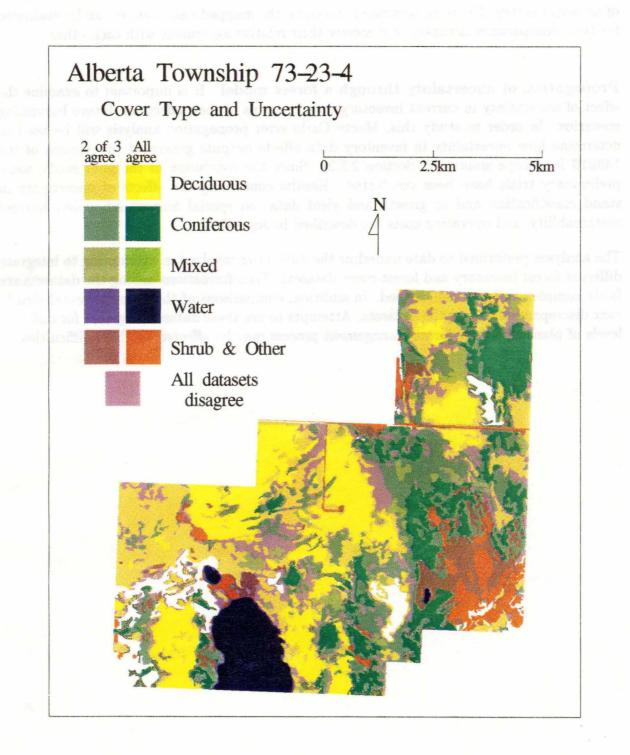


Figure 33: Uncertainty in forest cover based on the third level aggregation.

of an aerial survey. By using accurate point data, the mapped data sources can be evaluated for their comparative accuracy, not merely their relative agreement with each other.

**Propagation of uncertainty through a forest model** It is important to examine the effect of uncertainty in current inventory data in terms of their effects on future harvesting scenarios. In order to study this, Monte Carlo error propagation analysis will be used to determine how uncertainty in inventory data affects outputs generated by versions of the TARDIS landscape simulator (Section 2.3.2). Since the conclusion of the pilot study, some preliminary trials have been conducted. Results concerning the effects of uncertainty in stand classification and in growth and yield data, on spatial harvest schedules, harvest sustainability, and operating costs are described in Joy (1995).

The analyses performed to date underline the difficulties involved in attempting to integrate different forest inventory and forest cover datasets. Transformations among the datasets are fairly complex and not well defined. In addition, comparisons of the datasets reveal significant discrepancies among the datasets. Attempts to use these datasets together for different levels of planning in the forest management process may be affected by these difficulties.

## 5 Overview

The first  $2\frac{1}{2}$  years of work on this project have initiated several studies of the ecology of the boreal mixedwood ecoregion in northern Alberta. The analysis of large scale patterns and fire history are largely complete. These studies were essential preliminaries to the development of a spatial model of the ecological dynamics of the region. A large scale controlled forest fragmentation experiment was initiated, and two years of field data have been collected. Considerable progress has been made in stand development modelling and disturbance simulation. A systematic exploration of the uncertainties in spatial forest inventory datasets has been completed. We have begun to develop predictive models of forest bird habitat use, based on extensive field work.

These studies will help assess if widespread forest harvesting will have serious negative effects on animal communities and impair the function of forested landscapes. The ubiquitous legacy of wildfire as an agent of change, and the naturally fragmented nature of the forest mosaic, suggest that it may be possible to develop harvesting strategies that preserve many properties of the natural system over the long term. To determine to what extent this is possible, we identified the following tasks to be accomplished:

- 1. Document and quantify the "natural" pattern of forested habitats on the landscape;
- 2. Develop biologically realistic simulations of forest stand dynamics including their timber and wildlife habitat values;
- 3. Develop flexible simulations of both natural and anthropogenic disturbance regimes, including wildfire and timber harvesting;
- 4. Determine wildlife affinities to different stand compositions, stand structures, and landscape features such as fragment size, isolation or proximity to edge;
- 5. Develop or adopt methods for the seamless use and visualisation of spatial data and spatial model output; and
- 6. Quantify the effects of uncertainty and error in spatial databases, particularly with respect to error propagation in simulations.

Forest stand age and size structures, and the spatial distributions of five important forest cover types in the study area were determined from Alberta Forest Service Phase 3 inventory data. Spatial models must be able to predict the development of these landscape patterns. These patterns also suggest targets for emulation by management strategies. Other important landscape features include the topological arrangement of patches; data suitable for their analysis have only recently become available.

The apparent age structure of natural forest patches in some ways exhibits the negative exponential form expected of fire-dominated forests with age-independent fire hazard, but punctuated by a few extreme fire years. However, there are very few stands younger than 30 years, apparently due to a lack of fire episodes in the decades prior to the inventory. It remains unclear whether the historical fire regime can explain the given age structure. The size structure of some stand populations shows the influence of gradual fragmentation; older stands of fire prone species (such as black spruce) tend to be smaller. Great spatial variability in species composition and in stand age and size structures indicates that no "representative" subareas exist within the study area. There is no evidence that these patterns are in equilibrium with the prevailing climate and disturbance regime.

We are using the patch model Zelig++ as the basis for projecting forest stand development after disturbance, because it can model multi-species, uneven-aged stands with natural regeneration. Model enhancement has included the consideration of biologically realistic temperature responses based on species-specific temperature thresholds, chilling requirements, and frost hardiness as well as the more traditional heat sums. Coupled with the ability to simulate the occurrence of frosts, these enhancements have improved the ability to predict realistic tree species distributions. Additional improvements have included a dynamic, local seed rain (which appears to be important in explaining the spotty occurrence of white spruce), and species-specific abilities to withstand understory suppression (important to balsam fir, and perhaps white spruce). Improved soil moisture simulation and a reliable means of deriving the soil moisture regime from such mapped data as is available remain to be accomplished. When this is done, simulations can be run to project the successional development of each forest cover polygon as a function of site, climate and seed availability.

Historical fire records confirm the incidence of fire episodes in which many large destructive fires occur; however, the more numerous average years are also important. While the average size of fires has decreased over the last three decades, the number and maximum size of fires seems to have increased. Fires in pure aspen and pure white spruce stands have been few and very small, while fires in mixed aspen/spruce stands and in black spruce stands have been more numerous. A very small number of large fires are responsible for most of the area burned. Different forest types typically burn in different seasons (e.g. black spruce primarily in July, aspen stands in May and September). A simple non-spatial fire model has been developed, that can reproduce some of the observed patterns of stand age structure and species composition found in the natural landscape. Model simulations indicate that fire episodes are a principal determinant of landscape age structure.

The study of anthropogenic disturbance has concentrated on low-spatial resolution harvest scheduling. The prototype harvest scheduling model, TARDIS, selects suitable townships for development on the basis of crop tree abundance and haul costs. Simulations indicate that, under a two-pass or three-pass system, many townships might never be harvested because of their remoteness, and the greater productivity of stands located closer to the mill site. Zelig output and fire simulations remain to be incorporated into the TARDIS framework. While we have not yet compared simulated forest structures and patterns with those of natural or developed forests, a preliminary aspatial model suggests that much prime habitat for many vertebrate species will decline as a result of forest development, and that strategies which might favour some wildlife species are likely to penalize others. The development of cut-block or patch level harvesting simulations has not yet been attempted.

Alternative forest development policies may be compared by their relative impacts on wildlife populations. Multiple passes of clear-cut harvesting within relatively uniform townships is likely to result in the fragmentation and isolation of mature forest habitats. Little is known about the sensitivities of most boreal vertebrates to the combined influences of stand size. composition, successional stage and landscape position. A replicated forest fragmentation experiment was initiated to fill these information gaps with regard to birds. Samples of 1, 10, 40 and 100 ha mixedwood fragments were isolated by > 200 m from adjacent forest during the winter of 1993/94. A  $\approx$  3500 ha unlogged area contains compositionally matched control areas. One season of pre-treatment sampling was conducted in 1993; the first posttreatment data were collected in the summer of 1994. Preliminary results have provided an overall species-area relationship of  $S = 0.57 A^{0.50}$ , where A is the area sampled in hectares, and S is the number of bird species likely to be encountered. Pre-fragmentation data have also identified characteristic bird communities of upland deciduous, isolated deciduous and upland coniferous forest stands. Bird community composition is evidently very sensitive to the relative abundance of coniferous trees in the stand. The simulation of stand trajectories, and compositional changes in particular, is one of the principal objectives of the stand modelling component of this project. The results of the fragmentation study, in conjunction with information gleaned from the literature, will allow the definition of habitat suitability criteria that can be linked directly to a landscape scale model.

It is important to examine the effect of uncertainty in inventory data on harvesting and habitat scenarios. Preliminary comparisons of Alberta Phase 3 Forest Inventory, Alberta Vegetation Inventory (AVI), and remotely sensed forest cover type (BTM) data have been made, at various levels of thematic aggregation. There is some consistency between Phase 3 and AVI data at high levels of aggregation, but rather poor agreement between BTM data and the other two data sets. This is somewhat surprising given the degree of aggregation we used. Comparisons with vegetation data collected in conjunction with the fragmentation study should ascertain the absolute validity of these different coverages, at least for portions of the study area similar to the Calling Lake experimental site.

This project provides a framework for the integration of a number of interrelated studies of the landscape ecology of a large area within the boreal mixedwood. Many results stand on their own and may apply to other parts of the boreal forest; other results are specific to the development and assessment of land-use scenarios in northeastern Alberta. Sub-project integration is only now becoming a predominant activity. Integration of stand development and disturbance models into the TARDIS framework constitutes one major task remaining. Data collection from our component of the Calling Lake forest fragmentation experiment will continue at least until 1995. Preliminary results have yet to be integrated into habitat suitability submodels which could be used in the TARDIS framework, or as components of other stand and landscape simulators.

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