

**THE UNIVERSITY OF CALGARY**

**The landscape scale spatial distribution of vegetation gradients in a mixedwood boreal  
forest: linking ecological patterns to geomorphic processes across scales.**

**by**

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## ABSTRACT

This study shows how geomorphic processes operating at two scales provide an explanation for landscape scale ( $10^1$  to  $10^3$  km) spatial patterns of vegetation distribution and abundance. These processes work in a similar fashion in many environments so these patterns should be general. Moisture and nutrient gradients often control upland forest composition. This study uses allometric equations of hillslope profile shape to link vegetation gradients in the mixedwood boreal forest to geomorphic principles of hillslope form. This provides a model of vegetation composition change down hillslopes. The study then uses geomorphic principles of hillslope assembly into drainage basins to show that the proportions of different vegetation types in basins remains fairly constant. Finally, the deviations between landscape vegetation patterns predicted by geomorphic principles and actual vegetation patterns are examined. This shows landscape scale changes in forest composition from *Picea glauca* to *Populus tremuloides* dominated forests caused by logging and an increased fire cycle.

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## TABLE OF CONTENTS

<b>APPROVAL PAGE</b>	<b>ii</b>
<b>ABSTRACT</b>	<b>iii</b>
<b>ACKNOWLEDGMENTS</b>	<b>iv</b>
<b>TABLE OF CONTENTS</b>	<b>v</b>
<b>LIST OF TABLES</b>	<b>vii</b>
<b>LIST OF FIGURES</b>	<b>viii</b>
<b>INTRODUCTION</b>	<b>1</b>
<b>CHAPTER 1: Why are moisture and nutrient gradients so common as controls of variation in vegetation composition?</b>	<b>3</b>
<b>INTRODUCTION</b>	<b>3</b>
<b>METHODS</b>	<b>7</b>
Study area	7
Vegetation sampling	8
Environmental sampling	10
Determining the moisture and nutrient gradients	11
Characterising gradient change down a hillslope	15
<b>RESULTS</b>	<b>18</b>
The moisture and nutrient gradients	18
Relating environmental gradients to geomorphic processes	39
<b>DISCUSSION</b>	<b>44</b>
Recovery after fire gradient	52
Conclusion	55
<b>CHAPTER 2: Linking landscape scale vegetation patterns to geomorphic processes operating at two scales</b>	<b>57</b>
<b>INTRODUCTION</b>	<b>57</b>
<b>METHODS</b>	<b>63</b>
Study area	63
Drainage basin delineation	63
Determining allometric relationships of basin area and length	65
Mapping the actual distribution of vegetation on the landscape	66
Predicting the upland vegetation distribution on the landscape	68
Detecting pattern deviations between the actual and predicted vegetation	71

<b>RESULTS</b>	75
Allometric relationships of basins	75
Classification of LANDSAT TM image	75
Predicting the Vegetation Distribution on the Landscape	75
Vegetation Distribution in Watersheds	82
<b>DISCUSSION</b>	89
Linking geomorphic processes to landscape vegetation patterns	89
Defining the role of other processes on landscape vegetation patterns	93
Conclusion	95
<b>CONCLUSION</b>	98
<b>LITERATURE CITED</b>	100

## LIST OF TABLES

TABLE 1.1: Average percent moisture, dry mass basis, at 33 kPa, 1500 kPa and the available moisture capacity (difference between 33 kPa and 1500 kPa measurements) for glacial till and glaciofluvial deposits. ....	29
TABLE 2.1: The vegetation classes found on glacial till and glaciofluvial geomorphic surfaces and their corresponding distances from the ridgeline used in predicting the vegetation from the digital elevation model (DEM). ....	72
TABLE 2.2: Distances from the ridgeline used for reconstructing vegetation in conjunction with time-since-fire date for glacial till stands. ....	74
TABLE 2.3: Percent omission/commission error patterns for supervised classification of Prince Albert National Park using the first four principal components of the LANDSAT TM image and the Time-Since-Fire map. ....	76
TABLE 2.4: Percent of test pixels classified into each class of the predicted vegetation map constructed without using time-since-fire information. Only upland forest classes are considered. Class numbers are the same as Table 2.3. ....	77
TABLE 2.5: Percent of test pixels classified into each class of the predicted vegetation map constructed using time-since-fire information. Only upland forest classes are considered. Class numbers are the same as table 2.3. ....	83

## LIST OF FIGURES

FIGURE 1.1: The species loadings on the habitat principal components analysis.

The loadings are determined by differences in variation among species due to the habitat and not variation related to interval between fires. Numbers correspond to the following species: (1) *Abies balsamea* (L.) Mill., (2) *Betula papyrifera* Marsh., (3) *Picea glauca* (Moench) Voss, (4) *Picea mariana* (Mill.) BSP., (5) *Pinus banksiana* Lamb., (6) *Populus balsamifera* L., (7) *Populus tremuloides* Michx., (8) *Abies balsamea* (L.) Mill. (sapling), (9) *Alnus crispa* (Ait.) Pursh, (10) *Amelanchier spp.*, (11) *Betula papyrifera* Marsh. (sapling), (12) *Picea glauca* (Moench) Voss (sapling), (13) *Picea mariana* (Mill.) BSP. (sapling), (14) *Populus tremuloides* Michx. (sapling), (15) *Rosa acicularis* Lindl. (shrub), (16) *Aralia nudicaulis* L., (17) *Aster ciliolatus* Lindl., (18) *Cornus canadensis* L., (19) *Fragaria virginiana* Duchesne, (20) *Galium boreale* L., (21) *Hylocomium splendens* (Hedw.) B.S.G., (22) *Lathyrus ochroleucus* Hook., (23) *Linnaea borealis* L., (24) *Mertensia paniculata* (Ait.) G. Don., (25) *Maianthemum canadense* Desf., (26) *Mitella nuda* L. (27) *Petasites palmatus* (Ait.) A. Gray., (28) *Pohlia nutans* (Hedw.) Lindb. (29) *Pleurozium schreberi* (Brid.) Mitt. (30) *Ptilium crista-castrensis* (Hedw.) De Not. (31) *Pyrola asarifolia* Michx., (32) *Pyrola secunda* L., (33) *Rosa acicularis* Lindl., (34) *Rubus idaeus* L., (35) *Rubus pubescens* Raf., (36) *Trientalis borealis* Raf., (37) *Vaccinium myrtilloides* Michx., (38) *Vaccinium vitis-idaea* L., (39) *Viburnum edule* (Michx.) Raf., (40) *Viola canadensis* L. var. *rugulosa* (Greene) C.L. Hitchc., (41) *Abies balsamea* (L.) Mill. (seedling), (42) *Populus tremuloides* Michx. (seedling). . . . . 20

FIGURE 1.2: The stand scores on the first two gradients of the habitat principal components analysis. The classification is an arbitrary means of breaking the gradients up for ease of discussion based on the abundant canopy species. The broken curve running diagonally across the ordination separates stands residing on undifferentiated glacial till deposits from stands residing on highly sorted glaciofluvial deposits. Two of the stands depicted on the glacial till side of the ordination (□) actually reside on glaciofluvial deposits and one stand on the glaciofluvial side of the ordination (○) actually resides on a glacial till deposit. . . . . 22

FIGURE 1.3: Stand loadings on the Redundancy Analysis of the habitat matrix. The centroids of the categorical variable soil texture are indicated by open symbols. Centroids give the mean gradient position for stands possessing a given soil texture. The vectors point in the direction of maximum change of the specified site variables, and the vector lengths indicate the degree of correlation between variables and axes. The variables indicated by the



vectors are: (a) nitrate, (b) cation exchange capacity, (c) pH, (d) calcium, (e) magnesium, (f) organic matter depth, (g) conductivity (1:2 soil:water), (h) conductivity (saturation extract), (i) sodium, (j) sulphate, (k) % slope, (l) available moisture capacity, (m) potassium (meq/100g), (n) aspect, (o) moisture capacity at 33 kPa, (p) moisture capacity at 1500 kPa, (q) potassium (ppm), (r) phosphate. . . . . 24

FIGURE 1.4: Soil moisture capacity (% dry weight) at (a) 33 kPa, (b) 1500 kPa and (c) available moisture capacity for stands on the habitat principal components analysis. The curve running diagonally across the figures divides the ordination into stands on glacial till deposits on the left and glaciofluvial deposits on the right. . . . . 27

FIGURE 1.5: Centroids for topographic position on slope with the stand loadings on the first two habitat principal components. The centroids for topographic position on slope are indicated separately for the two types of surficial deposits. The curve running diagonally across the ordination divides the stands into two groups based on the geomorphic surface. . . . . 31

FIGURE 1.6: Stand loadings on the unpartitioned principal components. Dominant species are defined as in Figure 1.2. Arrows show movement of points when effect of time is removed. . . . . 33

FIGURE 1.7: The species loadings on the recovery after fire principal components analysis, calculated from the differences between the principal components analysis in which the variation due to the age of the stand has been removed (habitat ordination) and the principal components analysis in which differences due to stand ages are still present (unpartitioned data). Species on the upper left side of the diagram are species adapted to fast recovery after fire while species on the lower right are species adapted to slower recovery after fire. Numbers correspond to the species in Figure 1.1. . . . . 35

FIGURE 1.8: The stand scores on the recovery after fire principal components analysis. The stand scores are a characterization of species of each recovery strategy present in the stand. The small figures display this abundance distribution for species ordered (on the abscissa) by their different recovery strategies (i.e., species loadings along a rotated axis that is the best fit line through the species points in Figure 1.7). The dots are the stand abundances of the species. Points on the left of the abscissas of the small figures represent species adapted for fast recovery after fire while those on the right are species that recover more slowly. . . . . 37

<b>FIGURE 1.9: Allometric relationships for hillslope profiles on glacial till deposits and glaciofluvial deposits. . . . .</b>	<b>40</b>
<b>FIGURE 1.10: Relationship between stand position on the moisture gradient (PCA 1) or the nutrient gradient (PCA 2) and the distance from the ridgeline for slopes on (a) glacial till deposits that are either horizontally flat or convex, (b) glacial till deposits that are either horizontally flat, convex or concave, (c and d) glaciofluvial deposits. . . . .</b>	<b>42</b>
<b>FIGURE 1.11: General landscape patterns of vegetation composition. The shape of the hillslopes is derived from the allometric equations for hillslopes on glacial till and glaciofluvial surfaces. The tree symbols depict the general change in dominant canopy species down the hillslope which is based on the relationship between the stand positions on the moisture and nutrient gradients and the stand distances from the ridgeline. . . . .</b>	<b>50</b>
<b>FIGURE 2.1: Hack's (1957) allometric relationship between drainage basin length and area with three examples of drainage basins in Prince Albert National Park that conform to the relationship. . . . .</b>	<b>60</b>
<b>FIGURE 2.2: Principal Components Analysis of stands showing arbitrary division into vegetation classes based on the canopy species with the highest importance value. . . . .</b>	<b>69</b>
<b>FIGURE 2.3: The relationship between drainage basin length and area for glacial till watersheds. Also shown is the geometric mean regression line (GMR) for the data and Hack's (1957) relationship. The GMR is least squares fit that assumes both length and area are subject to error. . . . .</b>	<b>78</b>
<b>FIGURE 2.4: The relationship between drainage basin length and area for glaciofluvial watersheds. Also shown is the geometric mean regression for the data and Hack's (1957) relationship. The GMR is a least squares fit that assumes both length and area are subject to error. . . . .</b>	<b>80</b>
<b>FIGURE 2.5: The average proportion of actual vegetation, predicted vegetation without time-since-fire and predicted vegetation using time-since-fire as a concomitant variable for upland forest classes in glacial till watersheds for (a) the entire Park, (b) the northern portion of the Park and (c) the southern portion of the Park. Standard error bars are too small to be shown. . . . .</b>	<b>84</b>
<b>FIGURE 2.6: The average proportion of actual vegetation and predicted vegetation for upland forest classes in glaciofluvial drainage basins for the</b>	

entire Park. Only one line is shown for the predicted vegetation as there is no difference between the predicted proportions with and without time-since-fire. Similar lines are not shown for the northern and southern portions of the Park as there is no difference in the proportions between the north and south portions and the Park as a whole. Standard error bars are too small to be shown. . . . . 86

## INTRODUCTION

Plant ecologists have long sought to explain the spatial distribution of species abundance across the landscape. Previous research has focussed on variation in vegetation structure and composition at the stand scale ( $10^{-3}$  to  $10^1$  km) (cf. Whittaker and Gauch 1973). To this end, gradient analysis has been helpful in determining the main physical environmental gradients controlling the distribution of vegetation. Moisture and nutrients have been found to be the most common gradients in upland forest systems (Chabot and Mooney 1985, Barbour and Billings 1988). However, these gradients are abstract and they only tell us the species composition given a certain level of resources. The spatial distribution of resources across the landscape and how these distributions affect landscape scale ( $10^1$  to  $10^3$  km) spatial vegetation patterns has not previously been examined.

Likewise, geomorphologists and hydrologists have long sought to explain the spatial distribution of moisture across the landscape as well as the spatial assembly of landscape units like hillslopes, watersheds and sub-watersheds (basins). To this end, spatially explicit models of sub-surface moisture flow have helped determine that soil moisture and nutrients are controlled by hillslope position (e.g., Kleiss 1970, Malo et al. 1974, Anderson & Burt 1977, Harr 1977, Sinia et al. 1981, Cihra 1984). Soil moisture depends on upslope catchment area, slope and soil hydraulic conductivity (Quinn et al. 1992, O'Loughlin 1981, Wood et al. 1988, Dawes & Short 1994). Furthermore, allometric equations describing hillslope profiles and basin shape have shown that these landscape units are highly organized (Hack and Goodlet 1960, Bull 1975). Hillslopes on

the same surficial material often have the same slope profile and drainage basins become longer and narrower at larger sizes, maintaining a constant hillslope length. Hillslopes are produced by the divergent processes of rain splash, soil creep and mass wasting while basins are formed by the concentrative processes of overland flow (Schumm et al. 1987, Rinaldo et al. 1995).

What has been missing up to now is the linkage between the abstract vegetation gradients and the geomorphic principles of moisture and nutrient spatial distribution across the landscape. This thesis develops that linkage and shows that substrate, hillslope allometry and basin allometry provide a basis for explaining the landscape scale patterns of vegetation distribution. The allometric approach also defines the scaling relationships at which vegetation is organized: the hillslope scale and the basin scale.

The thesis is divided into two chapters. The first chapter explains why moisture and nutrient gradients are so common in upland forests by relating moisture and nutrient gradients in a southern mixedwood boreal forest to allometric equations that describe hillslope profile form. The second chapter examines the landscape scale spatial patterns of vegetation distribution by linking the gradient distributions down hillslopes to geomorphic principles of hillslope assembly into basins. This will link different geomorphic processes occurring at two different scales

## **CHAPTER 1**

### **Why are moisture and nutrient gradients so common as controls of variation in vegetation composition?**

#### **INTRODUCTION**

Much of the research to date on vegetation distribution and abundance has found that moisture and nutrient gradients are very important in determining changes in vegetation composition (e.g., Chabot & Mooney 1985, Barbour & Billings 1988). In cases where elevation is found to be an important gradient, it is often interpreted primarily as a function of moisture (Day & Monk 1974, Busing et al. 1992).

Why are moisture and nutrient gradients so common? The answer lies in understanding the importance of geomorphic processes in arranging hillslopes across the landscape and in controlling moisture and nutrient storage capacities and flux rates down these hillslopes. A landscape can be viewed as a framework of ridges and valleys on which hillslopes are hung. The valleys are arranged by geomorphic processes into organized channel networks and thus, provide the basis for the landscape scale ( $10^1$  to  $10^3$  km) spatial patterns of hillslope assembly. It should, therefore, be possible to use geomorphic principles of landform organization and composition to aid in the explanation of why moisture and nutrient gradients are so common in determining vegetation composition. This may also provide insight into the patterns of moisture and nutrients across the landscape and may help explain the landscape scale patterns of vegetation distribution and the processes involved.

The main focus of this chapter is on the geomorphic assembly of individual hillslopes and the distribution of gradients down those hillslopes. The focus is not the landscape scale spatial arrangement of hillslopes around the channel framework, which is the subject of the second chapter. However, a limited discussion of channel networks is given here to place the hillslopes in the context of the landscape and to give an intuitive feel for how the processes that govern vegetation distribution at the stand scale can be developed to explain patterns of vegetation distribution at the landscape scale. The assembly of individual hillslopes can be separated from their arrangement around the channel framework because the two patterns tend to be governed by different processes. Hillslopes tend to be shaped by processes such as rain splash, soil creep and mass wasting, which are different from the framework of the channel network which tends to be shaped by processes associated with concentrated overland flow (Schumm et al. 1987, Rinaldo et al. 1995). Also, it is helpful to establish the patterns at the scale of the hillslope first before working up to the scale of the landscape.

Channels are formed as runoff is concentrated into distinct flow lines and the erosive force of the runoff is enhanced. Flow lines suffer greater erosion than neighbouring areas upon which sheetflow or subsurface flow occurs and channels are incised below the level of the initial soil surface. The various channels then join downstream to form a network. Channel networks can be viewed as an assembly of randomly merging stream channels in which all topologically distinct networks with the same number of first order streams are equally likely to occur (Shreve 1966, 1967). This model, known as the random model of channel networks, predicts a number of statistics

that describe the orientation-free planimetric properties of channel networks and their drainage basins in uniform environments. Predictions by the random model are in close agreement with empirically observed statistical regularities (Smart 1974, Shreve 1975)

Hillslopes also show surprising regularity in form which can be examined by using allometric equations that relate the vertical fall to the horizontal distance from the ridgeline (Hack & Goodlet 1960, Troeh 1965, Bull 1975, Nash 1980). Allometry relates part of a system to change in some other part of the system. In geomorphology, this relationship summarizes the interrelations of materials, processes and landforms, although it does not show process itself. Hillslopes that are underlain by the same material and are downwasting at a similar rate are often described by allometric equations with the same parameters (Hack & Goodlet 1960, Bull 1975). Consequently, all of the hillslopes in an area can be described by an equation with just one or a few parameters. For example, the hillslopes that drained into first order streams in Hack & Goodlet's (1960) study area were described by an allometric equation with just two sets of parameters. Thus, allometry provides the power to summarize hillslope characteristics across the landscape.

The physical state of each point on the surface is not formed independent of other points on the surface, but is coupled to those points upslope from it that contribute drainage. For example, the temporal response of soil moisture for a point at the base of a slope will be considerably different from a point at the ridge due to convergent drainage from upslope areas. Soil and vegetation properties often depend upon position on slope. Both moisture and factors related to soil nutrient regime have been shown to be controlled by topography (e.g., Kleiss 1970, Malo et al. 1974, Anderson & Burt 1977, Harr 1977,



Sinia et al. 1981, Cihra 1984). Furthermore, work in surface hydrology suggests that, in most cases, topography is the principal factor controlling surface moisture flux (Quinn et al. 1992) and that variation in soils and rainfall plays only a secondary role at the scale of hillslopes (O'Loughlin 1981, Wood et al. 1988, Dawes & Short 1994). Vegetation also reflects these patterns of topographic control over moisture and nutrients, showing consistent relationships between floristic composition and position on slope (Day & Monk 1974, Johnson 1981, Marks & Harcombe 1981, Allen & Peet 1990, Busing et al. 1992). Given the dependence of moisture and nutrient fluxes on position on slope, it should be possible to relate moisture and nutrient gradients to the allometric equations that characterize hillslope form. In doing so we characterize the distribution of gradients on all hillslopes across the landscape.

By specifying or estimating the assemblage of hillslopes and the expected covariance of environmental gradients and vegetation with topographic position, it is possible to synthesize the pattern of vegetation distribution for part of the landscape. This may form the basis for a succinct and efficient method of parameterizing the spatial patterns of vegetation distribution and abundance with only limited knowledge of the land surface structure.

The purpose of this study is to link the spatial distribution of vegetation to geomorphic principles of hillslope formation in order to explain why moisture and nutrient gradients are so common as controls of variation in vegetation composition. I start by establishing the main environmental gradients which control vegetation distribution and abundance in the study area. I then use allometry to describe the patterns of hillslope form

and to relate changes in gradient position to changes in position on slope. Finally, I discuss how the similar ways in which geomorphic processes assemble hillslopes suggest that moisture and nutrient gradients are always prevalent across the landscape.

Adaptation by plants to gradients that are consistently present may explain the importance of moisture and nutrient gradients in many studies.

## METHODS

### *Study area*

The study area is located in Prince Albert National Park, Saskatchewan (53° 35' N to 54° 20' N and from 106° 0' W to 106° 47' W). This 4000 km<sup>2</sup> Park has a gently rolling topography with an elevation range from about 500 metres to 800 metres a.s.l. The Park occurs in the northern part of the Saskatchewan Plain and is dominated by the Waskesiu Hills Uplands. These hills are composed primarily of glacial till, but also contain significant organic, glaciofluvial and glaciolacustrine deposits. Till in this region is at least 160 m thick. The surficial material is composed of grey, non-calcareous silt and clay. Most of the area is covered by Luvisolic order soils (Padbury et al. 1978).

The climate is characterised by long, cold winters and short, cool summers. The frost free period is usually less than 80 days and freezing may be expected during any month. July and August are the warmest part of the year with average maximum temperature exceeding 20°C three days out of four. The average annual precipitation ranges from 400 to 500 mm, of which about 70% occurs as rain.

The major disturbance in this region is large, high intensity, lightning caused fires which kill most of the canopy trees and understorey vegetation. Large fires are controlled primarily by weather variables and variation in topography, substrate and micro-climate has relatively little influence on fire intensity (Bessie & Johnson 1995). Low intensity ground fires account for a very small proportion of the total area burned; only about 5% of the land area within the Park (Jeff Weir *personal communication*). Insect outbreaks do not seem to have been a major source of disturbance in this century. The study area is part of the Boreal Mixedwood Forest (Rowe 1972), so called because of the dominance of both the coniferous species *Picea glauca* (Moench) Voss, *Picea mariana* (Mill.) B.S.P., *Pinus banksiana* Lamb., *Abies balsamea* (L.) Mill. and *Larix laricina* (DuRoi) K. Koch., and the broadleaf deciduous species *Populus tremuloides* Michx., *Populus balsamifera* L. and *Betula papyrifera* Marsh.

#### *Vegetation sampling*

Stands were selected in order to obtain as much variation in upland vegetation composition as possible. The selection criteria were as follows: (1) stands were > 4 hectares in size (as determined from aerial photographs), (2) the vegetation was rooted in the mineral soil with no evidence of standing water in the top 30 cm of mineral soil, (3) stands were visually homogeneous with respect to stand age, structure, species composition, etc., and (4) stands had no evidence of significant anthropogenic disturbance in the lifetime of the canopy trees. One hundred and one stands were sampled over the summers of 1993 and 1994 with 97 stands located inside the Park and 4 located just outside the Park.

For each stand, information was collected on vegetation composition and structure, physical environment, stand age and fire history. The vegetation was divided into the following strata: (1) trees - stems > 10 cm diameter at the bole base (only trees capable of forming a forest canopy fit this criterion), (2) understorey shrubs and saplings - woody stems < 10 cm in diameter, but taller than one metre, (3) seedlings - tree species < 1 metre tall, (4) herbaceous - non-tree species including mosses < 1 metre tall.

In each stand, vegetation was sampled along two parallel transects that were placed side by side and 30 m apart. The first transect had eight sampling points and the second had seven with 15 m between points on a transect. The transects ran parallel to the contour lines and were randomly positioned near the middle of the stand. At each sampling point, samples were taken using the point centered quarter method (Cottam and Curtis 1956). In each quarter, the distance to the nearest tree and its diameter at the bole base were measured as well as the distance from the centre to the nearest understorey shrub or sapling. The relative density, relative frequency and relative basal area for each tree species was calculated from all 15 sampling points and combined into an importance value for each tree species. (Goff and Cottam 1967). Relative density was calculated for understorey species. The average relative density of seedlings in the stand was calculated from two 1 m<sup>2</sup> quadrats at each point. These quadrats were placed in quarters two and four at a distance of 1 m from the centre with one side of the quadrat on the transect line. The frequency of herbaceous species and mosses was calculated from a total of 30 quadrats measuring 25 X 25 cm each. Two such quadrats were placed at each sampling point, nested within the seedling density quadrats at a distance of 1 m from the centre.

Pilot studies of these techniques showed that densities calculated for both the plotless and quadrat techniques had a standard error less than 10% of the mean density and that the most numerous herb and moss species had a frequency of about 90% (cf. Curtis and McIntosh 1950, Cottam, Curtis and Hale 1953, Cottam and Curtis 1956). Nomenclature for species follows Moss (1983).

For all stands within the Park, the time since last fire was determined from a time since fire map of the Park (Weir 1996). This map gives the time since last fire for all stands > 4 ha in the Park and is accurate to within 1 year for most stands. For the four stands outside of the Park the time since last fire was determined from fire records provided by Parks Canada and Saskatchewan Environment and Resource Management.

#### *Environmental sampling*

The overall slope steepness, aspect, topographic position on slope for each stand was assessed from 1:50 000 topographic maps. Slope steepness was calculated from the distance between contour lines on either side of the transects. Topographic position on slope was arbitrarily assigned as either crest, topslope, midslope, footslope or flat. A sample of the top 15 cm of mineral soil was taken from three soil pits spaced evenly along the first transect in each stand. The three samples were homogenized and a sub-sample was removed and air dried. The average depth of organic matter was also assessed from these three soil pits and each pit was examined for the presence of mottling or gleying in the top 30 cm. Soil analysis was carried out on 40 stands, arbitrarily selected to represent as much variation in species composition as possible, by Plains Innovative Laboratory Services, Saskatoon, Saskatchewan. Soil texture was determined by the feel method and

pH and electrical conductivity were determined in a 1:2 soil:water suspension. Available nitrate was extracted with 0.001 M  $\text{CaCl}_2$ , cation exchange capacity was determined with 1 N  $\text{BaCl}_2$  at pH = 8 and extractable phosphate and potassium were determined with a modified Kelowna extractant. Extractable potassium was also determined with inductively couple plasma emission spectrometry along with sulphate, calcium, magnesium, and sodium. Soil water retention capacity at 33 (ie. field capacity) and 1500 kPa (ie. wilting point) was determined for 88 of the 101 samples using a ceramic pressure plate apparatus. The 13 remaining samples were not tested due to insufficient soil.

#### *Determining the moisture and nutrient gradients*

Two types of processes may be responsible for much of the variation in vegetation data: temporal processes which produce variation in the time since disturbance, and spatial processes which produce variation in physical environmental conditions. The first step in the analysis is to partition the data into temporal and spatial components in order to avoid confounding the ordination.

The starting matrix,  $Y$ , is the  $n \times s$  matrix of stands ( $n$ ) by species ( $s$ ) in which the species abundance scores are importance values for trees, relative density for shrubs, saplings and seedlings and frequency for herbs and mosses. Stands range in age from 8 to 220 years old. The effect of time since fire was factored out of the data by removing the covariance in species abundance change with time using a modification of Johnson's (1981) methodology. The age of each stand since the last fire can be used as a concomitant variable to partition the total variance in the species abundance data into spatial and temporal components using the equation:

$$Y = X\Gamma + R$$

where  $X$  is a  $n \times 1$  vector of stand ages,  $\Gamma$  is a  $1 \times s$  vector of regression coefficients and  $R$  is a  $n \times s$  matrix of deviations from the regression. This technique removes temporal variation from the species data by fitting regression functions to the species abundance data using stand time since the last fire as the independent variable and the species abundance in each stand as the dependent variable. A separate regression is fit to each species. The expected variation due to time for each species can then be subtracted from the original samples by species matrix. A number of different polynomial regression functions were tried but third order functions that were linear in the independent variables and were not forced through zero gave the best visual fit ( $r^2$  ranges from 0.02 to 0.66). In this case the deviation from the mean age, the deviation squared and the deviation cubed are the independent variables in the regression instead of using time since fire directly. The deviation from the mean age was used in order to reduce correlation between the independent variables in the regression (Neter et al. 1990).

The result is two data matrices. The original, or unpartitioned, matrix  $Y$ , and a matrix  $R$  of residuals formed by removing the expected variation in species abundance due to time from the original data matrix. The matrix  $R$  is called the habitat matrix.

The second step in the analysis was to hypothesize gradients that explained most of the variation in the habitat matrix. Principal components analysis (PCA) reduces the dimensionality of the data while explaining most of the variation in the data. The axes of PCA can then be interpreted as gradients. Principal components analysis was used because it is an objective technique that is mathematically understood and it gives both

species and stand ordinations that are mathematically relatable to one another. The limitations of principal components analysis are well known (Whittaker & Gauch 1973, ter Braak 1987); however, the analysis should be robust as the ends of the gradients share many species in common, suggesting that beta diversity along the gradients is low, and most zero abundance scores were removed by excluding species present in less than 25% of the stands. Redundancy inherent in the species composition data ensures that very little information is lost by doing this. The PCA appeared robust to the use of third order regressions to remove variation due to time as almost half of the regressions were either monotonic or very close to monotonic which is consistent with PCA's assumption that species responses be monotonic and linear. The most important environmental gradients were hypothesized from a PCA performed on the habitat matrix R.

The third step in the analysis is to produce a recovery after fire gradient. The unpartitioned matrix, Y, contains variation due to both time since fire and differences in habitat. The habitat matrix, R, however, has the expected variation due to time since fire removed. The simplest way to produce a recovery after fire gradient, therefore, is to perform a principal components analysis on the original unpartitioned data (matrix Y) and subtract the species loadings or stand scores from their compatriots in the rotated habitat (matrix R) principal components analysis (Johnson 1981). It is not appropriate to simply ordinate the expected species abundances with time (matrix XT) since fitted linear, monotonic data have species loadings of either 1 or -1 in PCA. This would tell us very little about the recovery of species after fire. Once the species loadings on the recovery after fire gradient were produced, each stand's score on the gradient was calculated using



the same technique that PCA uses to calculate stand scores. Each species abundance within a stand (i.e. from matrix Y) was multiplied by its species loading on the recovery after fire gradient. These products were then summed for each stand to produce that stand's gradient score.

Principal components analysis summarizes the variation in the stands by species data by reducing the dimensionality of the data set so that fewer axes explain the most variation. In this type of analysis, called an indirect gradient analysis, the stands are ordered along the axes independently of the environmental information. Other techniques, known as direct gradient analysis (e.g. redundancy analysis), order stands or species along the axes in a way that is dependent on the environmental information. A comparison of the order of stands between the indirect and direct analyses confirms whether or not the environmental axes chosen also explain the most variation in the samples by species data and, hence, represent important gradients for explaining variation in vegetation composition.

Redundancy analysis (RDA) is a linear eigenvalue technique similar to principal components analysis except that the axes are constrained to being linear combinations of the environmental variables (Ter Braak 1988). For the direct gradient analysis, redundancy analysis was performed on the habitat matrix, R. The 40 samples for which full environmental data were available were used as active samples in the analysis, while the rest were passive. Active samples are the only samples the RDA uses to derive the eigenvalues. The passive samples are then placed on the ordination by multiplying their species abundances by the species loadings derived from the active samples. The

environmental variables were standardised to unit variance to ensure that no single variable dominated the ordination. The first two axes of the RDA were compared to the first two axes of the habitat PCA using a Spearman rank correlation.

### *Characterising gradient change down a hillslope*

A geomorphic surface is an area of land formed by deposition or erosion during a defined time period (Daniels & Hammer 1992). The geomorphic surfaces in the study area are a result of continental glaciations that occurred during the Pleistocene Epoch, roughly 10 000 to 1 000 000 years ago. The surficial materials deposited as a result of the glaciations can be divided into two distinctive groups: those deposited by glacial ice and those deposited by glacial meltwaters. The former includes glacial till deposits, the latter glaciofluvial and glaciolacustrine deposits. Undifferentiated till occupies extensive areas throughout the Park, especially in the upland regions while glaciofluvial surfaces may be large, although they are not as extensive as till areas. Glaciolacustrine surfaces occupy only a small proportion of the Park, predominantly in remote locations (Padbury 1978).

The coefficients of the hillslope allometric equations change when the underlying surficial material is different. Therefore, before proceeding with the allometric analysis of hillslopes, areas of different surficial material were delineated on the landscape. The allometric analysis then proceeded separately for each area.

The identification of geomorphic surfaces was accomplished through field reconnaissance, observations of soil profiles, and soil texture analysis at each site. It was further augmented by 1:50000 topographic maps and 1:12500 black and white panchromatic areal photographs and a surficial deposit map (Padbury et al. 1978).

The geomorphic surfaces were delineated by identifying areas with distinct surface expression and from the soil profiles within each stand. The mean soil moisture capacities at 33 kPa and 1500 kPa and the available soil moisture capacity (33 kPa moisture capacity *minus* 1500 kPa moisture capacity) were also compared between the differentiated surficial types. There was a total of 72 stands on glacial till deposits and 29 stands on glaciofluvial deposits.

Once the landscape had been separated into geomorphic surfaces, individual slope forms within these areas were analyzed. The path running perpendicular to the contour lines from the ridgeline to the channel is defined as the side slope. Side slopes on the same type of geomorphic surface that flow into streams of the same order are often described by allometric equations with the same coefficients (Hack and Goodlet 1960). Side slopes from first, second and third order streams in each of the different surficial material types were examined to see if they conformed to this behaviour. Within each area of homogeneous surficial material, side slopes were picked that were close to sampled stands and within the same watershed or in a neighbouring watershed. Side slopes were analyzed only if they resided on one geomorphic surface. Side slope profiles that crossed over from one geomorphic surface to another were not included in the analysis. Because glaciofluvial landforms occupy only a small portion of the study area and tend to be long, narrow outwash channels, it was difficult to find side slope profiles that do not cross onto another type of geomorphic surface. Therefore, several additional side slope profiles were examined that were not close to a sampled stand, but did reside entirely on a glaciofluvial geomorphic surface. Twenty-three sideslopes on glacial till deposits and six

sideslopes on glaciofluvial deposits were sampled. Hillslopes on glaciolacustrine materials were not analyzed because they occupy a very small proportion of the area and access was difficult.

Side slope forms were examined by plotting paths on 1:50 000 topographic maps of the area (*Department of Energy, Mines and Resources, Canada*) and graphing the log fall from the ridge line on the ordinate versus the log horizontal distance from the ridgeline on the abscissa. Side slope profiles were only analyzed if a ridgeline could be delineated with reasonable accuracy from the map. Because the topography can be quite flat in places, delineating ridelines from 1:50 000 maps can sometimes be difficult. Simple linear functions were fit to each log transformed slope profile using a least squares fit. The slope profile equations within each homogeneous area were compared using an analysis of covariance (ANCOVA). While a model II regression would be more suitable for these data, the  $r^2$  values for all slopes were high ( $> 0.95$ ) and therefore the difference between the two types of regression was negligible. Using a model I regression allows for a more rigorous statistical test to be used to compare slopes.

The gradient position of a stand is characterized by its stand loadings on the moisture and nutrient gradients. If the gradient position of a stand is related to its position on slope, then it should be possible to characterize the change in gradient position down a slope by relating this change to the allometric equations. The relationship between the moisture and nutrient characteristics and the topographic position on slope may be influenced by the curvature of the surface in the horizontal direction. Horizontally concave sites, such as valleys, will likely experience convergent subsurface flow whereas

horizontally convex slopes, such as spurs or noses, will likely experience divergent subsurface flow. Each stand on a glacial till deposit was assigned to either a convex, linear, or concave class depending on the shape of the map contour line closest to the transect lines. A slope profile path was then plotted from the ridgeline to the stand and the distance measured. Although fall from the ridgeline could also be used it is much easier to measure horizontal distance. Forty-seven side slope profiles on glacial till deposits were measured. Only nine side slope profiles on glaciofluvial deposits could be measured so the effects of horizontal curvature were not analyzed for these stands. Treating each gradient separately, the stand loadings on the gradient were regressed onto the stand distances from the ridgeline. For stands on glacial till deposits, the three classes of horizontal contour curvature were used as concomitant variables. For each gradient, the relationships between the three regression lines was compared using analysis of covariance.

## RESULTS

### *The moisture and nutrient gradients*

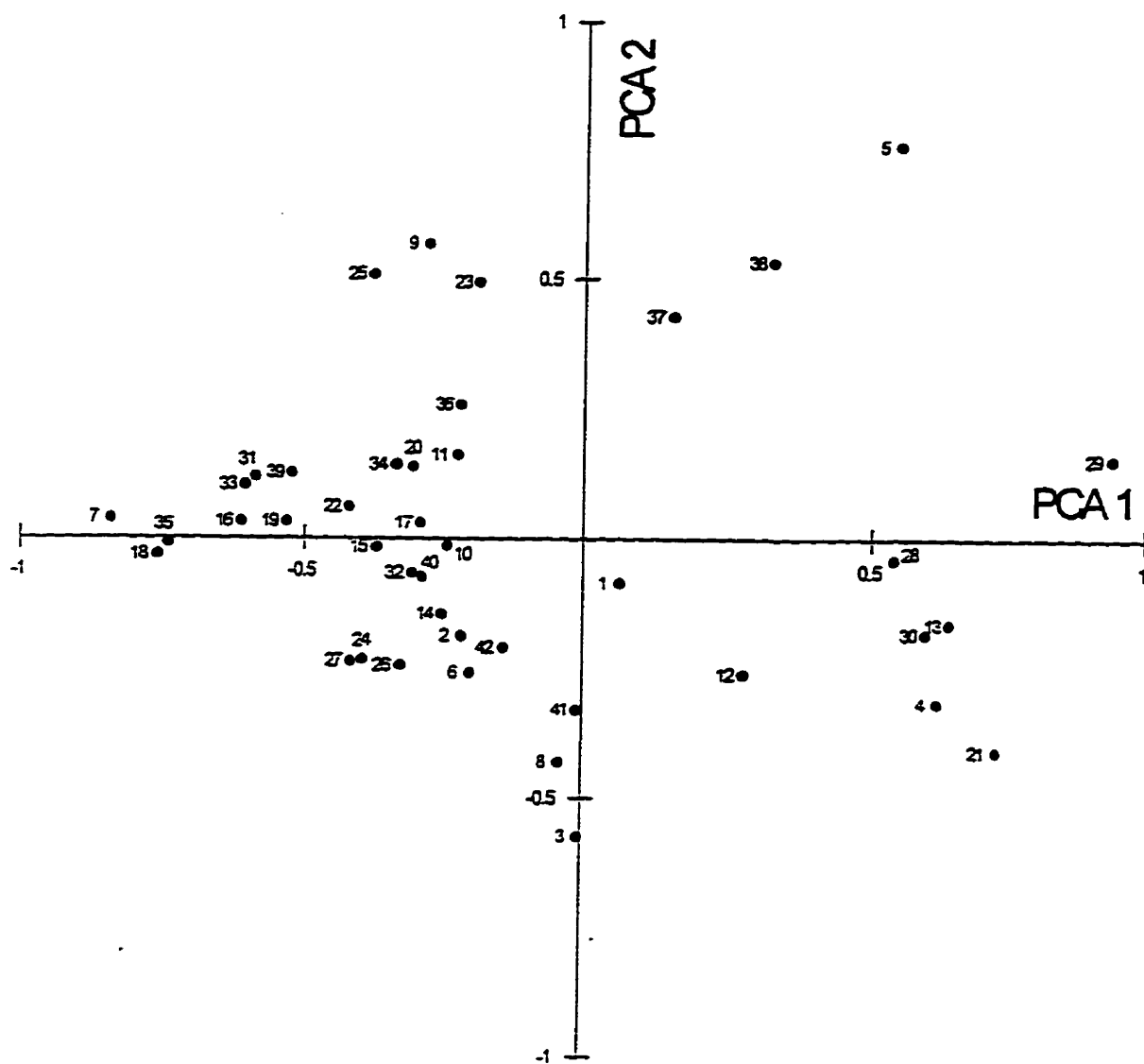
The first component of the habitat principal components analysis for species had high loadings for *Picea mariana*, *Hylocomium splendens*, *Pleurozium shreberi* and *Ptilium crista-castrensis* at one end and low loadings for *Populus tremuloides*, *Cornus canadensis* and *Rubus pubescens* at the other end. The second component had high loadings for *Pinus banksiana*, *Vaccinium vitis-idea* and *Vaccinium myrtilloides* at one end and low loadings for *Picea glauca* and *Abies balsamea* at the other (Figure 1.1).

Figure 1.2 shows the habitat PCA for stands. Stands were classified based on the dominant canopy species. The first component had negative loadings for stands dominated by *Populus tremuloides* and *Cornus canadensis* at one end and positive loadings for *Picea mariana* and *Ptilium crista-castrensis* dominated stands at the other. The second component had negative loadings for *Picea glauca*, *Picea mariana* and *Mitella nuda* dominated stands at one end and positive loadings for *Pinus banksiana* and *Vaccinium vitis-idaea* dominated stands at the other. The vegetation shows remarkably strong affinities for the different types of geomorphic surfaces. Stands on the habitat ordination can be divided into clearly defined groups based on the type of geomorphic surface on which they reside (Figure 1.2). Stands on glacial till are dominated by *Populus tremuloides*, *Picea glauca* and *Abies balsamea*, while stands on glaciofluvial sediments are dominated by *Pinus banksiana* and *Picea mariana*.

The PCA appeared robust to the use of third order regressions to remove variation due to time as almost half of the regressions were either monotonic or very close to monotonic which is consistent with PCA's assumptions.

Stand scores and environmental vectors for the RDA are shown in Figure 1.3. The vectors point in the direction of maximum change of the specified site variables, and the vector lengths indicate the degree of correlation between variables and axes (Ter Braak 1988). The centroids of categorical variables are indicated by diamonds. Centroids give the mean gradient positions for stands possessing the categorical variable. A forward selection of environmental variables showed that using fewer variables does not alter the

FIGURE 1.1: The species loadings on the habitat principal components analysis. The loadings are determined by differences in variation among species due to the habitat and not variation related to interval between fires. Numbers correspond to the following species: (1) *Abies balsamea* (L.) Mill., (2) *Betula papyrifera* Marsh., (3) *Picea glauca* (Moench) Voss, (4) *Picea mariana* (Mill.) BSP., (5) *Pinus banksiana* Lamb., (6) *Populus balsamifera* L., (7) *Populus tremuloides* Michx. (8) *Abies balsamea* (L.) Mill. (sapling), (9) *Alnus crispa* (Ait.) Pursh, (10) *Amelanchier spp.*, (11) *Betula papyrifera* Marsh. (sapling), (12) *Picea glauca* (Moench) Voss (sapling), (13) *Picea mariana* (Mill.) BSP. (sapling), (14) *Populus tremuloides* Michx. (sapling), (15) *Rosa acicularis* Lindl. (shrub), (16) *Aralia nudicaulis* L., (17) *Aster ciliolatus* Lindl., (18) *Cornus canadensis* L. (19) *Fragaria virginiana* Duchesne, (20) *Galium boreale* L., (21) *Hylocomium splendens* (Hedw.) B.S.G., (22) *Lathyrus ochroleucus* Hook., (23) *Linnaea borealis* L., (24) *Mertensia paniculata* (Ait.) G. Don., (25) *Maianthemum canadense* Desf., (26) *Mitella nuda* L. (27) *Petasites palmatus* (Ait.) A. Gray., (28) *Pohlia nutans* (Hedw.) Lindb. (29) *Pleurozium schreberi* (Brid.) Mitt. (30) *Ptilium crista-castrensis* (Hedw.) De Not. (31) *Pyrola asarifolia* Michx., (32) *Pyrola secunda* L., (33) *Rosa acicularis* Lindl., (34) *Rubus idaeus* L., (35) *Rubus pubescens* Raf., (36) *Trientalis borealis* Raf., (37) *Vaccinium myrtilloides* Michx., (38) *Vaccinium vitis-idaea* L., (39) *Viburnum edule* (Michx.) Raf., (40) *Viola canadensis* L. var. *rugulosa* (Greene) C.L. Hitchc., (41) *Abies balsamea* (L.) Mill. (seedling), (42) *Populus tremuloides* Michx. (seedling).





**FIGURE 1.2:** The stand scores on the first two gradients of the habitat principal components analysis. The classification is an arbitrary means of breaking the gradients up for ease of discussion based on the abundant canopy species. The broken curve running diagonally across the ordination separates stands residing on undifferentiated glacial till deposits from stands residing on highly sorted glaciofluvial deposits. Two of the stands depicted on the glacial till side of the ordination ( $\square$ ) actually reside on glaciofluvial deposits and one stand on the glaciofluvial side of the ordination ( $\circ$ ) actually resides on a glacial till deposit.

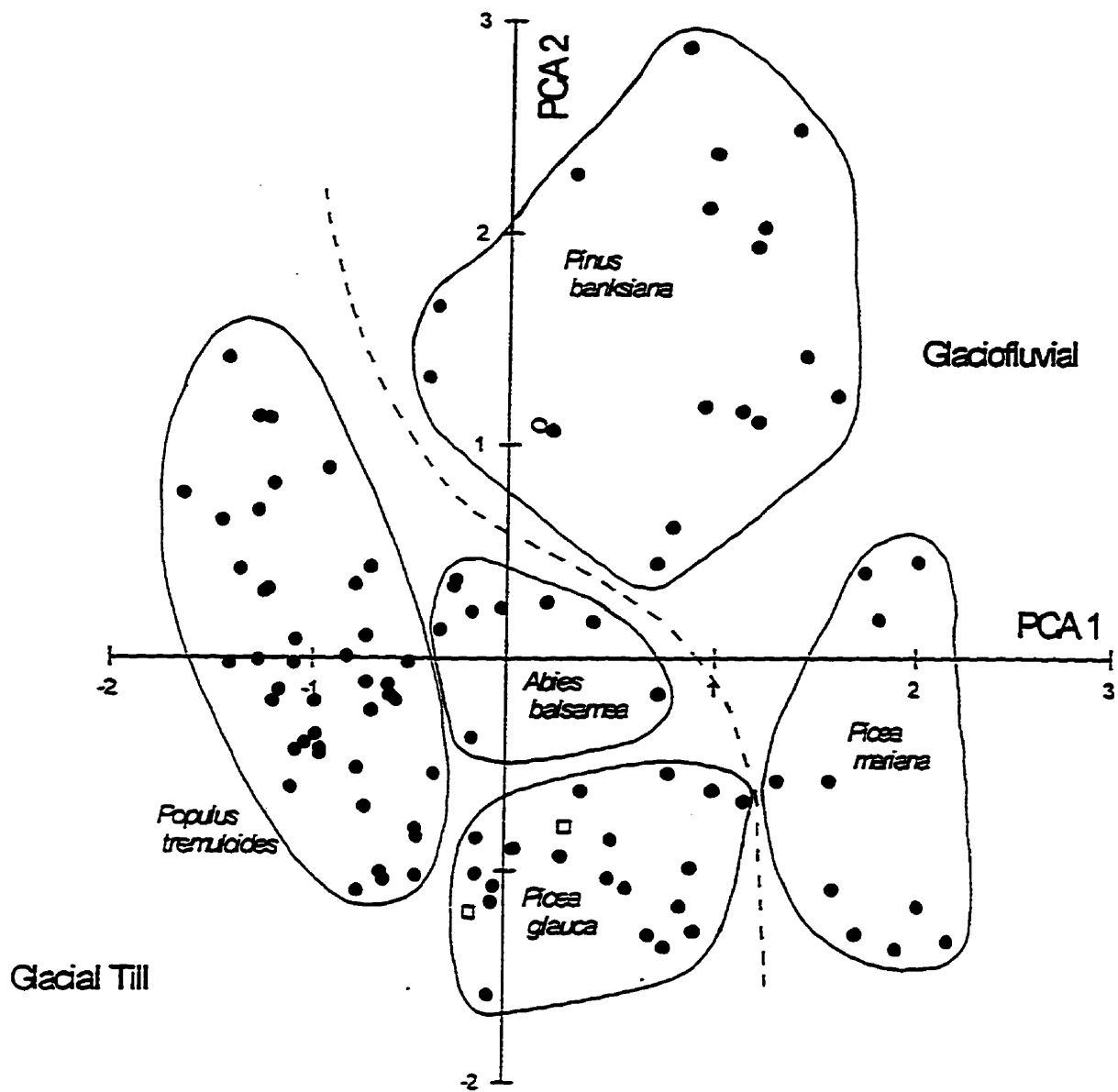
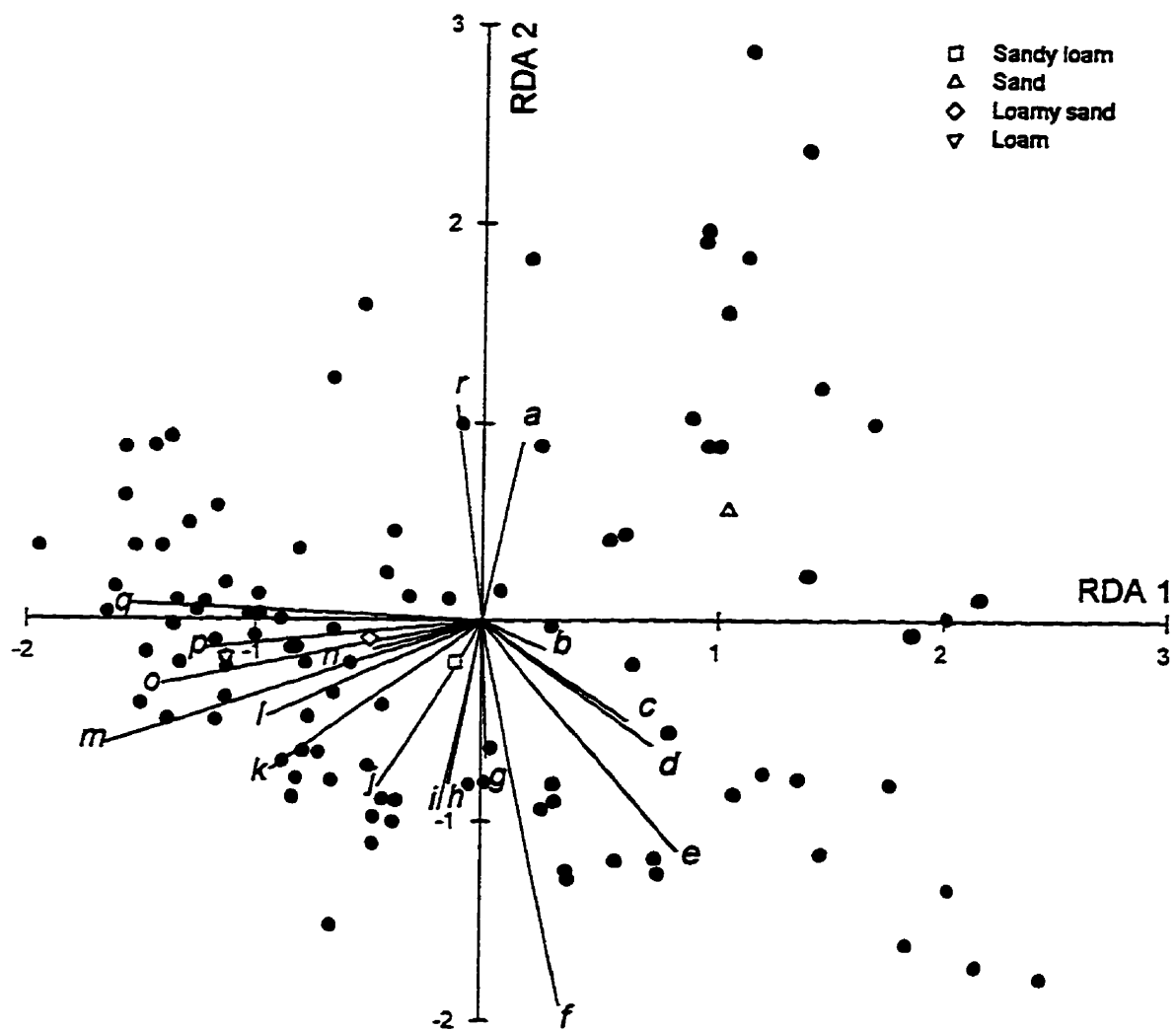


FIGURE 1.3: Stand loadings on the Redundancy Analysis of the habitat matrix. The centroids of the categorical variable soil texture are indicated by open symbols. Centroids give the mean gradient position for stands possessing a given soil texture. The vectors point in the direction of maximum change of the specified site variables, and the vector lengths indicate the degree of correlation between variables and axes. The variables indicated by the vectors are: (a) nitrate, (b) cation exchange capacity, (c) pH, (d) calcium, (e) magnesium, (f) organic matter depth, (g) conductivity (1:2 soil:water), (h) conductivity (saturation extract), (i) sodium, (j) sulphate, (k) % slope, (l) available moisture capacity, (m) potassium (meq/100g), (n) aspect, (o) moisture capacity at 33 kPa, (p) moisture capacity at 1500 kPa, (q) potassium (ppm), (r) phosphate.



ordination significantly; however, for ease of interpretation I have included all of the variables on the diagram.

The first axis was correlated with variables related to moisture status which strongly reflect the change from till surfaces on the left to glaciofluvial surfaces on the right. In particular, the first axis was strongly related to soil texture with stands on the left having loamy soil and stands on the right having sandy soils. Soil moisture capacities at 33 kPa, 1500 kPa and the available soil moisture capacity were also negatively correlated to the first axis, further reflecting the change in geomorphic surface. There were no obvious trends between the soil moisture capacities and the stand positions on the PCA within each surficial deposit group (Figure 1.4). However, the mean soil moisture capacity at 33 kPa and the available soil moisture capacity were both significantly higher in glacial till deposits than in glaciofluvial deposits ( $P < 0.05$ ). There was no significant difference in the mean soil moisture capacity at 1500 kPa between the two surficial deposits (Table 1.1). The first axis was also negatively correlated with slope and potassium levels in the soil.

The second RDA axis was most strongly correlated with nutrient variables. Organic matter depth, magnesium, sodium, sulphate, calcium, pH, electrical conductivity and cation exchange capacity were all negatively correlated with the second axis. Only nitrate and phosphate were positively correlated with the second axis.

The PCA and RDA, both with only 40 active samples, were extremely similar (axis 1  $r^2 = 0.99$ , axis 2  $r^2 = 0.97$ ) indicating that the physical environmental gradients of

FIGURE 1.4: Soil moisture capacity (% dry weight) at (a) 33 kPa, (b) 1500 kPa and (c) available moisture capacity for stands on the habitat principal components analysis. The curve running diagonally across the figures divides the ordination into stands on glacial till deposits on the left and glaciofluvial deposits on the right.

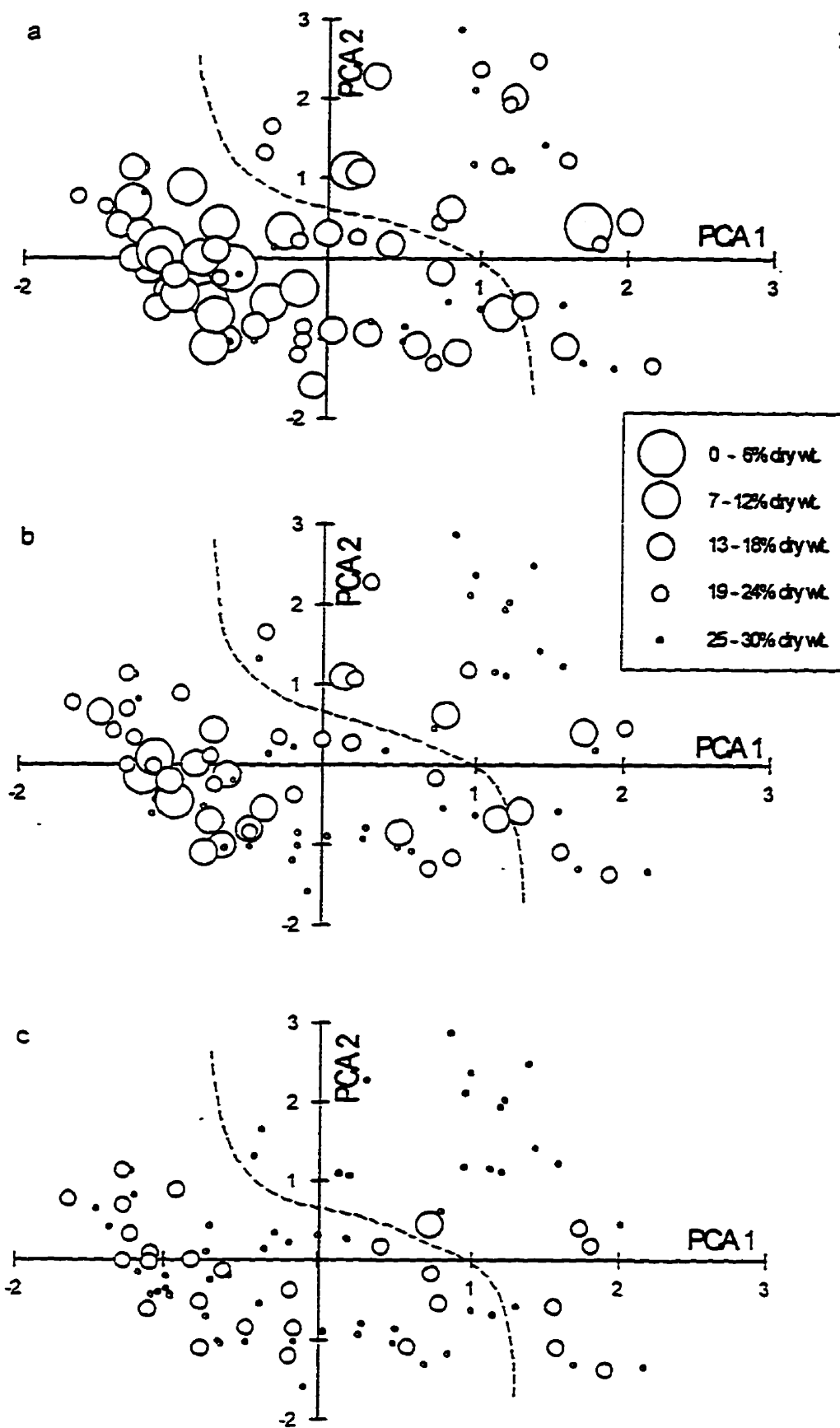


TABLE 1.1: Average percent moisture, dry mass basis, at 33 kPa, 1500 kPa and the available moisture capacity (difference between 33 kPa and 1500 kPa measurements) for glacial till and glaciofluvial deposits.

	% Moisture	
	Glacial Till	Glaciofluvial
	<i>n</i> =62	<i>n</i> =26
33 kPa *	14.0 (0.8)	10.9 (1.1)
1500 kPa	8.3 (0.7)	6.5 (0.9)
Available moisture capacity *	5.7 (0.4)	4.5 (0.4)

\* Significant difference at  $P < 0.05$ .



moisture and nutrients do explain most of the variation in the species composition data. In addition, the RDA eigenvalues (axis 1  $\lambda = 0.20$ , axis 2  $\lambda = 0.13$ ) were only slightly smaller than the PCA eigenvalues (axis 1  $\lambda = 0.31$ , axis 2  $\lambda = 0.14$ ) indicating that the two techniques accounted for similar variation. There was almost no difference between the habitat PCA with all samples active and the habitat PCA with only 40 samples active (axis 1  $r = 1.0$ , axis 2  $r = 1.0$ ). As expected, correlations between the RDA and the PCA with all samples active were only slightly lower (axis 1  $r = 0.98$ , axis 2  $r = 0.95$ ) than the correlations between the RDA and the PCA with only 40 active samples.

Stand position on the first and second habitat principal components was also strongly related to topographic position on slope (Figure 1.5). This relationship does not clearly distinguish between the two geomorphic surfaces like soil texture and moisture capacity do, although the relationship is clearer when the centroids for the stand position are shown separately for the two surfaces. Stands at the crests and tops of slopes tend to be at the left of the habitat ordination while stands at the bottom of slopes tend to be at the lower right of the ordination. There are also several stands on glaciofluvial surfaces at the top of the ordination that are located on very flat areas.

The effect of removing temporal variation from the data is best seen by comparing the unpartitioned (Figure 1.6) and habitat stand ordinations (Figure 1.2). Most stands did not have marked changes in their position; however, older stands dominated by *Abies balsamea* in the canopy had large changes in position. *A. balsamea* stands moved along the second component from low loadings to mid loadings, placing them in the centre of the ordination. Their position along the first component did not change appreciably.

FIGURE 1.5: Centroids for topographic position on slope with the stand loadings on the first two habitat principal components. The centroids for topographic position on slope are indicated separately for the two types of surficial deposits. The curve running diagonally across the ordination divides the stands into two groups based on the geomorphic surface.

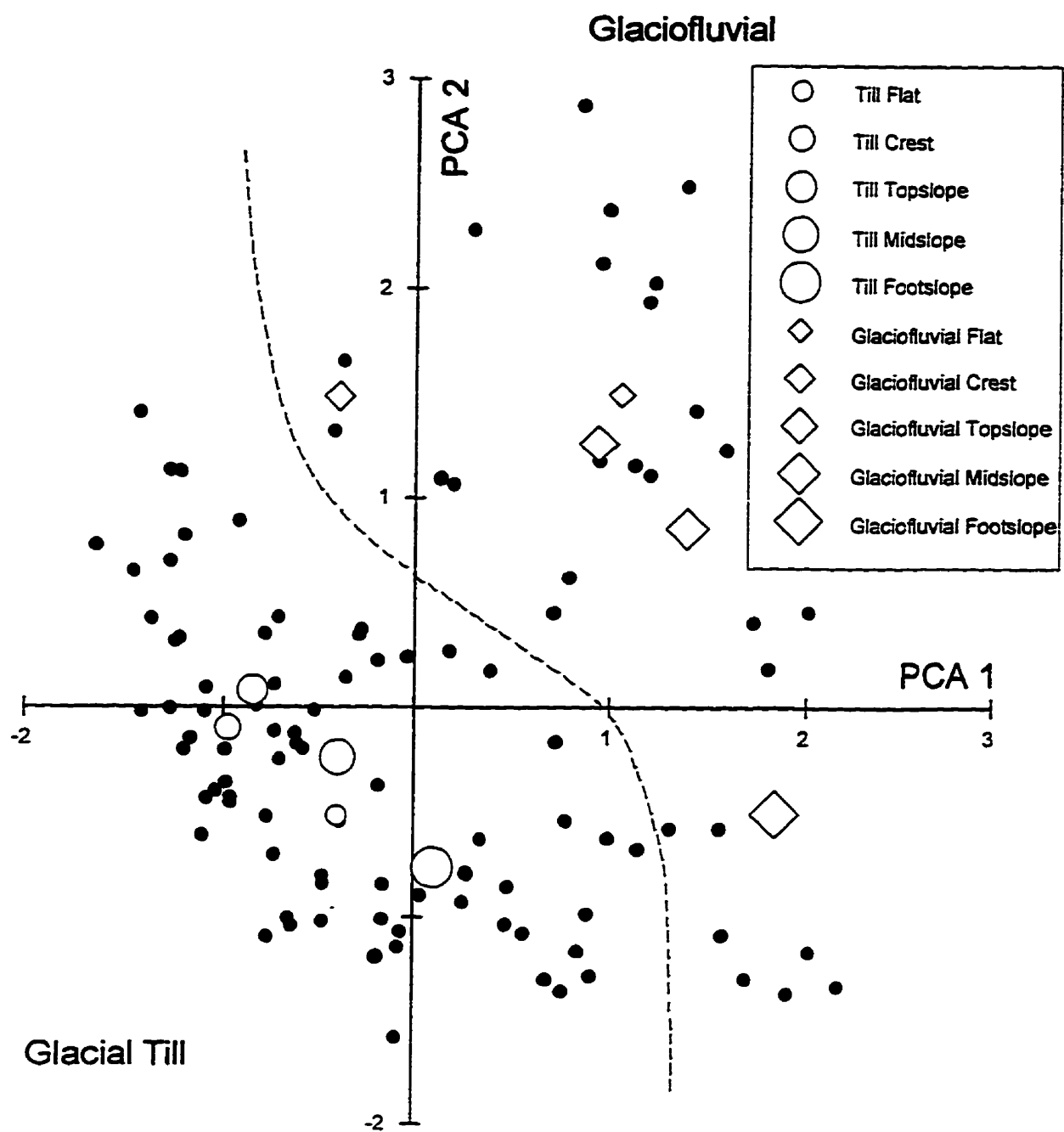
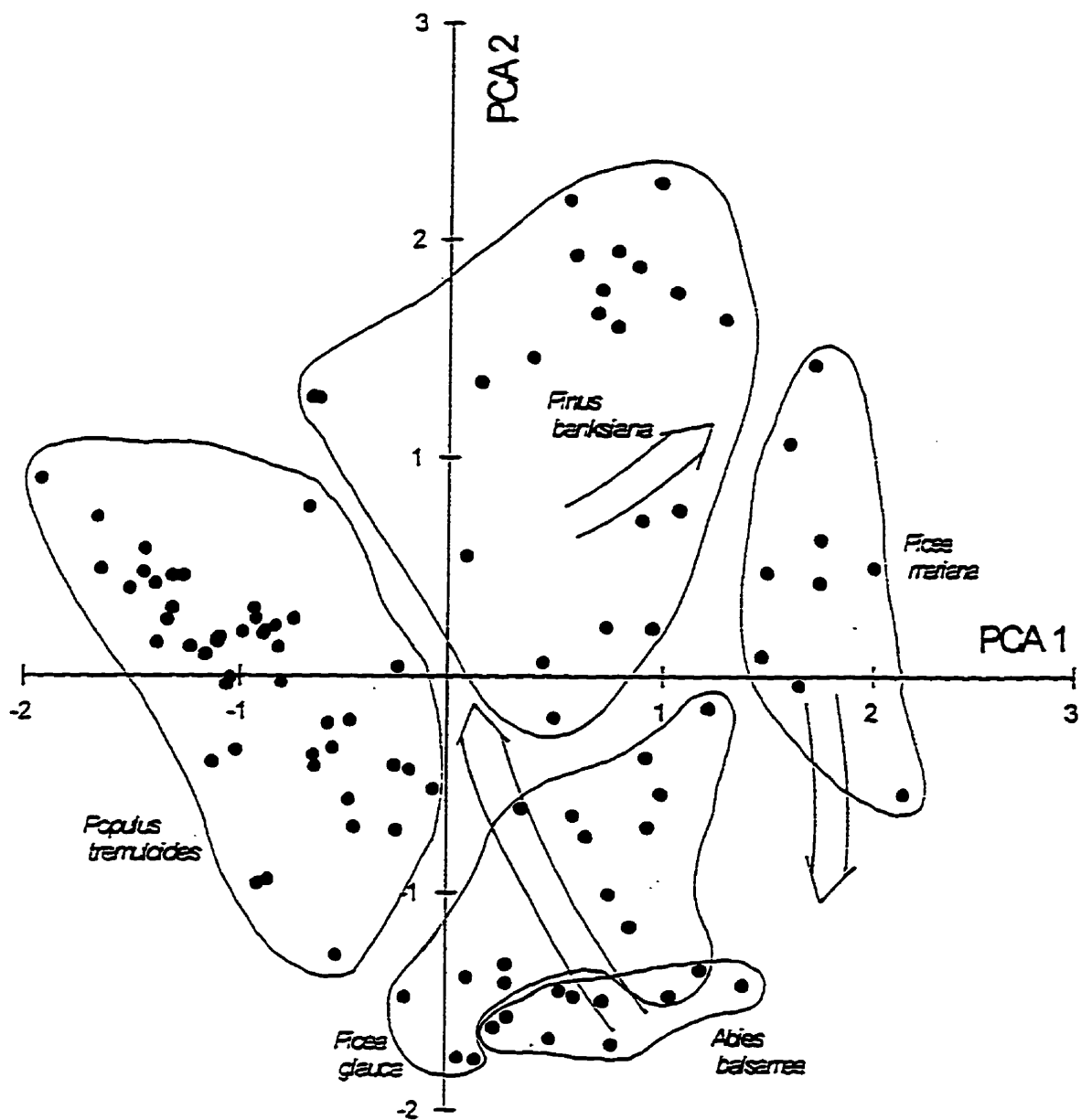
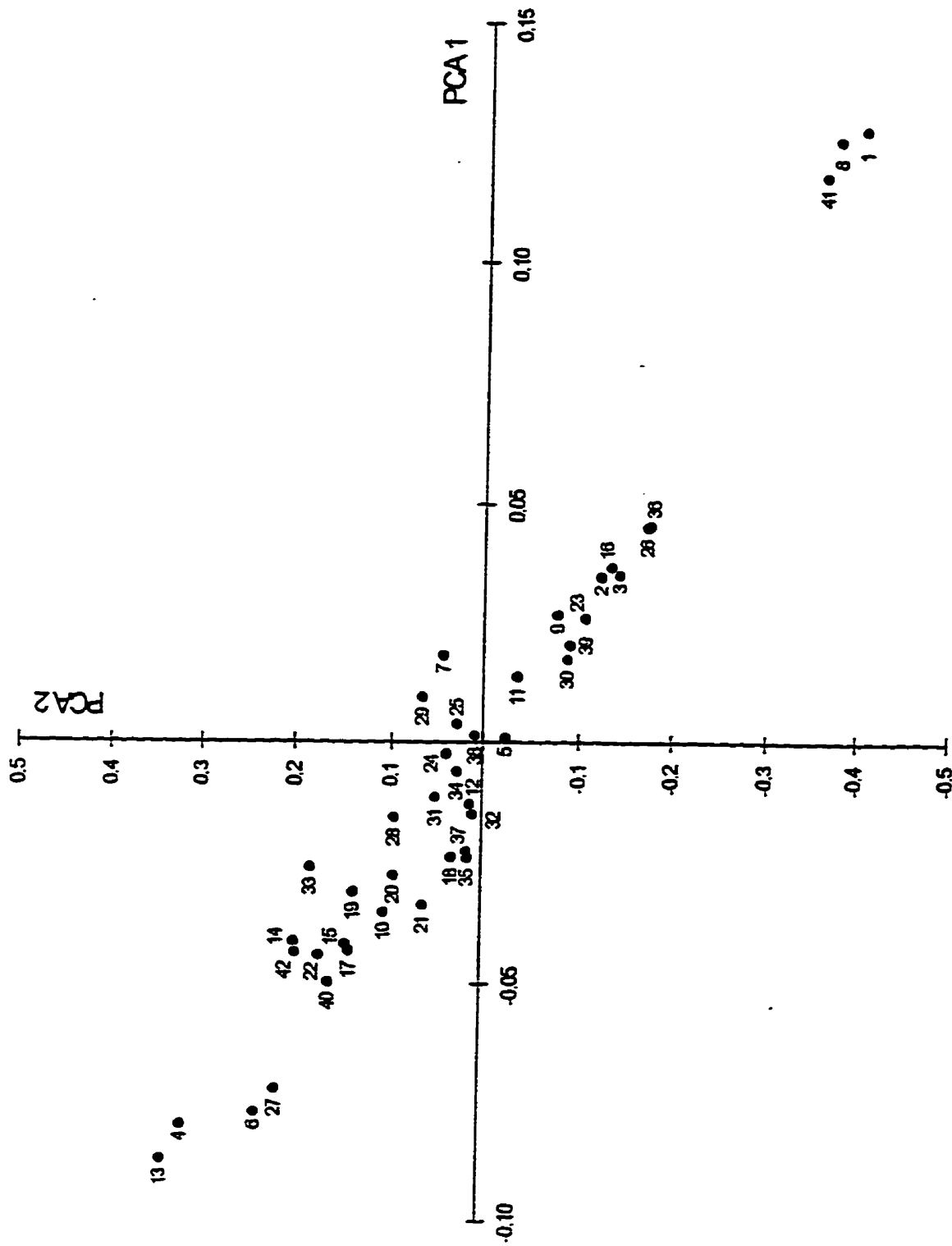


FIGURE 1.6: Stand loadings on the unpartitioned principal components. Dominant species are defined as in Figure 1.2. Arrows show movement of points when effect of time is removed.



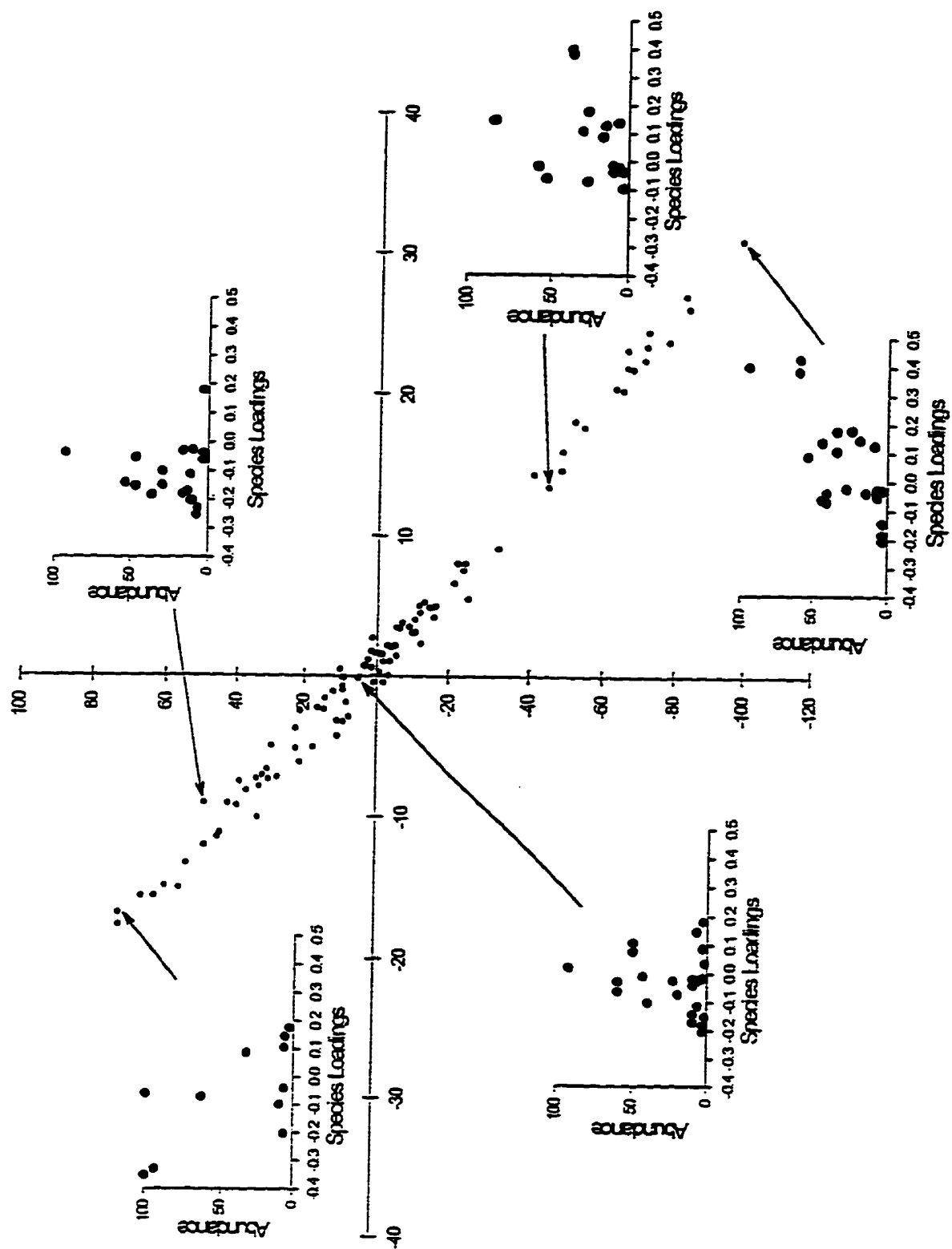
**FIGURE 1.7: The species loadings on the recovery after fire principal components analysis, calculated from the differences between the principal components analysis in which the variation due to the age of the stand has been removed (habitat ordination) and the principal components analysis in which differences due to stand ages are still present (unpartitioned data). Species on the upper left side of the diagram are species adapted to fast recovery after fire while species on the lower right are species adapted to slower recovery after fire. Numbers correspond to the species in Figure 1.1.**



**FIGURE 1.8: The stand scores on the recovery after fire principal components analysis.**

The stand scores are a characterization of species of each recovery strategy present in the stand. The small figures display this abundance distribution for species ordered (on the abscissa) by their different recovery strategies (i.e., species loadings along a rotated axis that is the best fit line through the species points in Figure 1.7). The dots are the stand abundances of the species. Points on the left of the abscissas of the small figures represent species adapted for fast recovery after fire while those on the right are species that recover more slowly.





The recovery after fire gradient gives a one dimensional distribution of both species loadings and stand scores (Figures 1.7 & 1.8). Species at the top left of Figure 1.7 have abundance patterns that recover quickly after fire. Species at the bottom right have abundance patterns that recover slowly after fire.

The stand ordination gives the relative position of stands determined by the sum of the species abundance in the stand multiplied by their loadings (Figure 1.8). Stands at the top left of the gradient are dominated by species that recover quickly after fire. Stands at the bottom right are dominated by species that recover slowly after fire.

#### *Relating environmental gradients to geomorphic processes*

For glacial till surfaces, there was no significant difference in either the slope or intercept between 22 of the allometric equations that describe hillslope form ( $P > 0.05$ ). On glaciofluvial surfaces, only one side slope showed a significantly different slope and intercept from the rest ( $P < 0.05$ ).

The slope data were pooled for each of the two geomorphic surfaces to produce two side slope equations. The two equations had similar slopes ( $P > 0.05$ ), but the intercepts were significantly different from one another ( $P < 0.05$ ) (Figure 1.9). In both cases, the slopes were significantly different from zero ( $P < 0.05$ ).

For stands on glacial till surfaces, the stand position on the moisture gradient was related to the stand distance from the ridgeline. There was no significant difference ( $P < 0.05$ ) in the slope or intercept between the horizontally convex (i.e., noses or spurs) and flat slopes, so these data were pooled. The pooled data showed a positive linear relationship ( $r^2 = 0.46$ ) that is significantly different from zero ( $P < 0.05$ ) (Figure 1.10a).

**FIGURE 1.9:** Allometric relationships for hillslope profiles on glacial till deposits and glaciofluvial deposits.

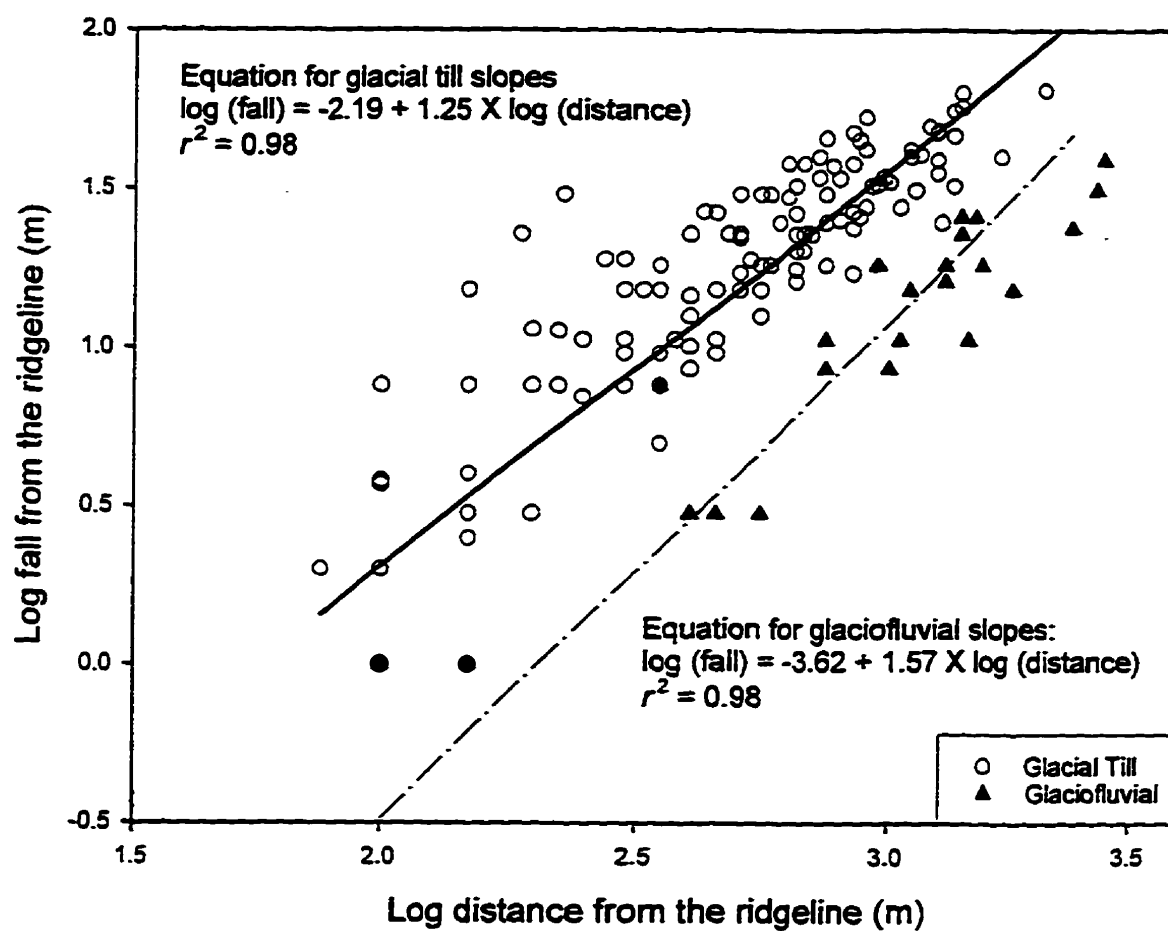
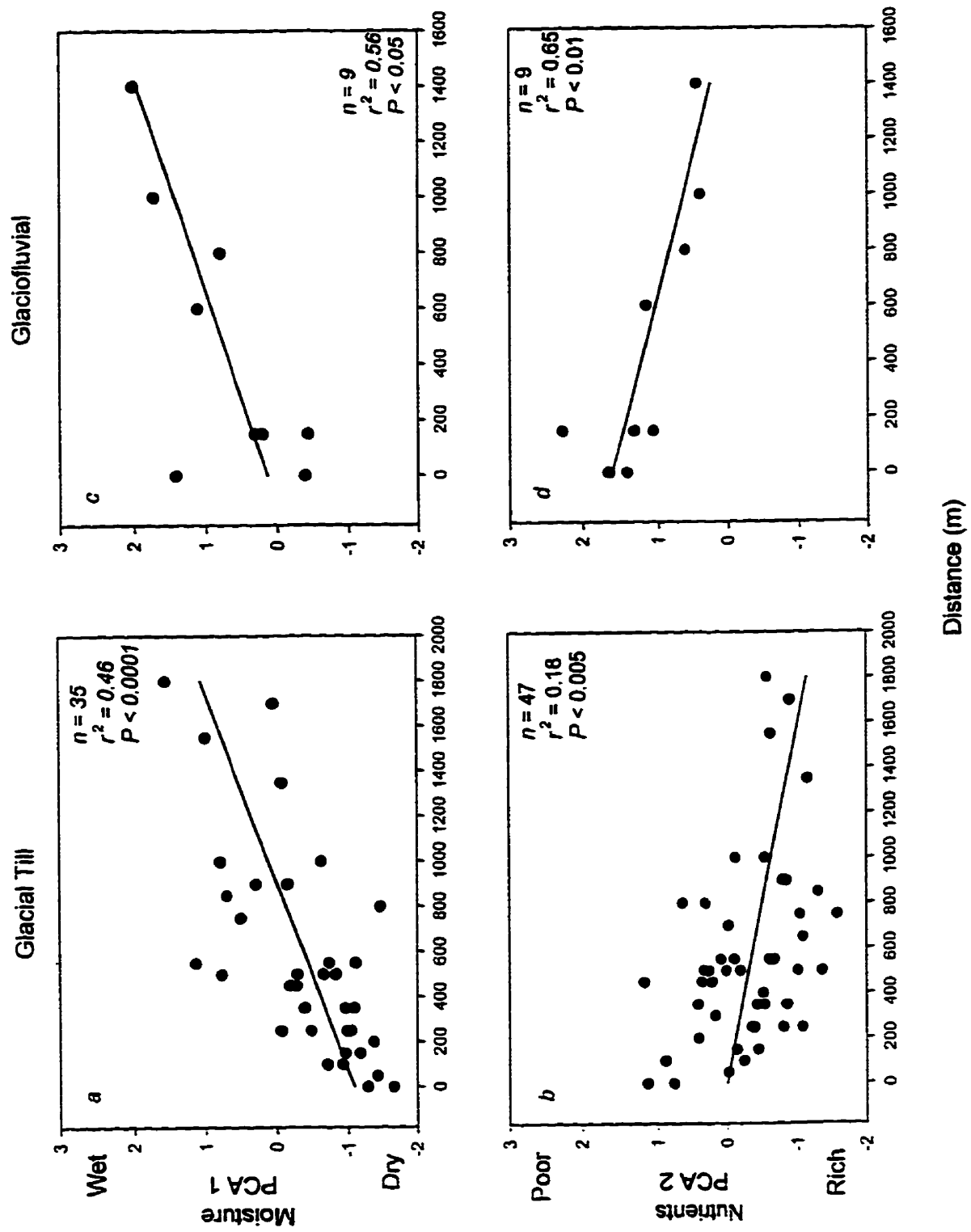


FIGURE 1.10: Relationship between stand position on the moisture gradient (PCA 1) or the nutrient gradient (PCA 2) and the distance from the ridgeline for slopes on (*a*) glacial till deposits that are either horizontally flat or convex, (*b*) glacial till deposits that are either horizontally flat, convex or concave, (*c* and *d*) glaciofluvial deposits.



Horizontally concave slopes did not show any relationship between distance from the ridgeline and position on the moisture gradient. On the nutrient gradient, the three different types of slopes were not significantly different from one another so the data were pooled. After pooling the data, a significant relationship ( $P < 0.005$ ) was found between distance from the ridgeline and nutrient status with sites further from the ridgeline having richer nutrient status ( $r^2 = 0.18$ ) (Figure 1.10*b*).

On glaciofluvial deposits, both moisture and nutrient gradients showed a significant ( $P < 0.05$ ) relationship between distance from the divide and position on the gradient with stands more distant from the divide being both moister and more nutritionally rich (moisture gradient  $r^2 = 0.56$ , nutrient gradient  $r^2 = 0.65$ ) (Figure 1.10*c* and *d*).

## DISCUSSION

In the southern mixedwood boreal forest, moisture and nutrient gradients explain most of the variation in species composition across the landscape. This is similar not only to other studies in the southern mixedwood boreal forest (La Roi 1991), but also to gradient analyses in many other forested regions in North America (e.g., Chabot & Mooney 1985, Barbour & Billings 1988). An important study close to Prince Albert National Park by Swan and Dix (1966) also corroborates this study's results upon re-examination of their evidence. Their stand ordination based on only the eight main canopy species led them to conclude that a soil texture gradient, but not a moisture gradient, explained most of the variation in species composition. However, their ordination based

on 84 understorey species revealed not only a strong texture gradient, but also a moisture gradient very similar to ours.

Why are moisture and nutrient gradients so common in a wide variety of vegetation types? The answer lies in understanding the importance of the geomorphic processes in sculpting the landscape, the importance of landscape form in influencing moisture and nutrient variation, and how plants may have adapted to this environmental variation.

The stands on the habitat ordination form two groups based on the geomorphic surface on which they reside. Stands dominated by the canopy species *Populus tremuloides*, *Picea glauca* and *Abies balsamea* reside almost exclusively on unstratified till deposits laid down directly by the glaciers, while stands dominated by *Pinus banksiana* and *Picea mariana* reside almost exclusively on glaciofluvial surfaces produced by flowing glacial meltwater.

In retrospect, it may have been preferable to identify the different geomorphic surfaces first and then sample enough sites on each surface to analyze the data separately. Partitioning the current data set into two separate ordinations would be inefficient here, however, because of the small number of samples in each group.

In this region, three different geomorphic surfaces have been left on the landscape through the action of glacial ice and glaciofluvial and glaciolacustrine meltwaters (Padbury et al. 1978). The different surfaces have different textural properties, resistive capabilities and soil transmissivities which affect the slope forms (Hack & Goodlet 1960, Bull 1975) and the soil water storage capacities and flux rates (O'Loughlin 1981, Wood et al. 1988).



The correlation between soil texture and moisture holding capacities and the first principal component reflects the change in geomorphic surface from glacial till on the left to glaciofluvial on the right. Till deposits have more finely textured soils and thus better moisture holding capacity than do glaciofluvial deposits and they may also have reduced nutrient leaching because of reduced soil water flux rates (Bower et al. 1957, Lai & Jurinak 1972).

Surfaces with different geomorphic histories often support different vegetation (e.g., Whittaker 1960, Marks & Harcombe 1981, Wentworth 1981 and McAullife 1994). This is usually attributed, in part, to the species' physiological characteristics which adapt them to deal more efficiently with the moisture and nutrient regime of a particular surface (e.g., Whittaker 1960, Marks & Harcombe 1981, Wentworth 1981). For example, in this region *Pinus banksiana*, through the use of tap roots and better control of water loss through stomata, is more drought resistant than *Picea glauca* and may be better suited to growth on the drier glaciofluvial surfaces (Anderson 1976). Changes in species distributions along textural gradients from other studies in the southern mixedwood boreal forest (Swan & Dix 1966, La Roi 1991) also probably reflect changes to different geomorphic surfaces, although different surfaces were not recognized in those studies.

On each of the different surfaces, the geomorphic processes produce hillslopes which can be described by allometric equations that summarize the relationship between the processes, the surficial material and the climate (Hack & Goodlet 1960, Bull 1975). I estimated the parameters for two allometric equations that describe hillslopes on glacial till and glaciofluvial surfaces. The intercept, or coefficient of steepness (Hack & Goodlet

1960), was significantly higher for hillslopes on glacial till surfaces, meaning that these hillslopes are steeper for any given distance from the divide than are hillslopes on glaciofluvial surfaces. This may be due to increased overland flow on glacial till surfaces because their loamy-sand soils typically have lower transmissivity and more surface saturation than do the coarser soils of glaciofluvial surfaces (Heath 1983, O'Loughlin 1986). Overland flow is concentrated into distinct flow lines which suffer greater erosion than neighbouring areas and channels are incised below the level of the initial soil surface (Schumm et al. 1987). The greater overland flow and erosion at shorter distances from the divide could lead to steeper hillslopes on glacial till surfaces. The greater surface saturation on glacial till surfaces could also enhance other erosive processes such as soil creep or solifluction (Carson & Kirkby 1972, Allen 1985) which could also contribute to steeper slopes.

On hillslopes cut into homogeneous surficial material, the primary determinant of soil moisture flux and storage is usually topography (Quinn et al. 1992), while variability in soils and rain play only a secondary role (O'Loughlin 1981, 1986, Selby 1982, Wood et al. 1988). The lack of any obvious trend in soil moisture capacities with topographic position or gradient position on each geomorphic surface (Figure 1.4) suggests that this is true here. Subsurface water diverges on nose slopes and converges on foot slopes (Anderson & Burt 1977, Harr 1977, Sinia et al. 1981, O'Loughlin 1981, 1986) carrying with it nutrients that are leached from higher positions on the landscape and accumulate in lower ones (Trudgill 1988, Litaor 1992, Tsuboyama et al. 1994). Consequently, top slopes are dry and nutrient poor, whereas bottom slopes are wet and nutrient rich (e.g.,

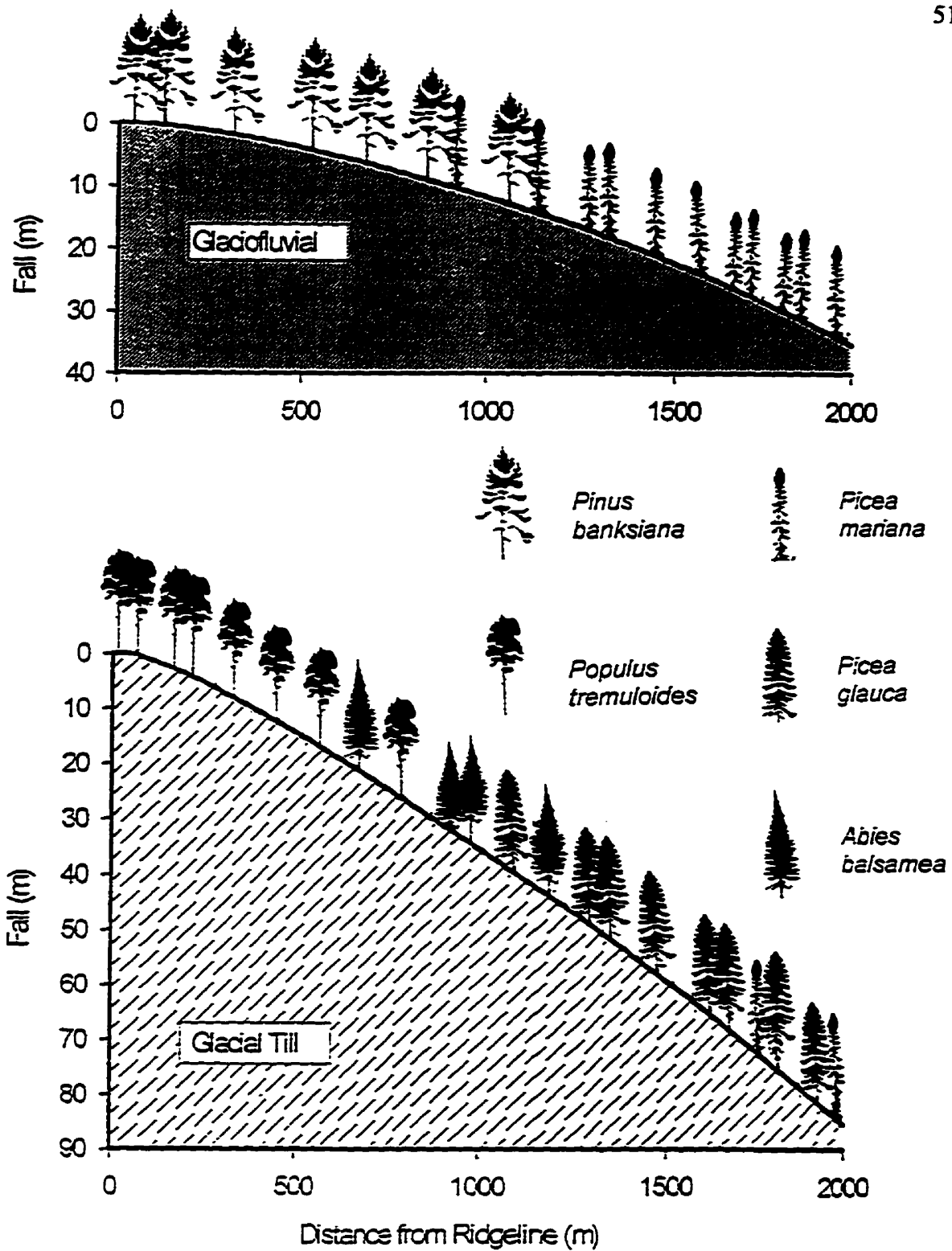
Malo et al. 1974, Harr 1977, Anderson & Burt 1977, Johnson 1981, O'Loughlin 1981, Sinia et al. 1981, Ciha 1984). Horizontal slope curvature had little effect on the relationship between a stand's gradient position and its distance from the divide. Only horizontally concave slopes on glacial till surfaces showed no relationship between the position on the moisture gradient and distance from the divide, likely because these slopes accumulate a lot of water from a large upslope area and are quite wet all the time.

Only nitrate and phosphate varied along the nutrient gradient opposite to other indicators of nutrient status. The results for nitrate, however, may be erroneous due to biological transformations which can change the amount or forms of inorganic nitrogen in the samples before analysis (Nelson and Bremner 1972, Page et al. 1982). Phosphate trends, on the other hand, may be due to the phosphorus recycling mechanism in these systems. Plant litterfall and precipitation leachate from the canopy are the dominant pathways for the return of phosphate back to the forest floor (Ugolini et al. 1977, Schlesinger 1991). In this region, stands that are moist and nutrient rich usually have an understorey dominated by feather mosses which act like a sponge, quickly absorbing any nutrients that fall on them and preventing nutrients like phosphate from reaching the mineral soil (Oechel & Van Cleve 1986). This may result in nutrient rich stands being depauperate in phosphorus relative to the nutrient poor stands which have few feather mosses. Occlusion of phosphate by secondary minerals in finer textured soils does not seem likely since the vector for phosphate on the RDA (Figure 1.3) is not well correlated with the first axis. Also, the pH range of these soils is close to the optimum for phosphate availability (Schlesinger 1991).

Potassium's strong negative correlation with the moisture gradient may be a result of the mineralogy of glacial till and glaciofluvial surfaces. Montmorillonite has generally been found to be the predominant clay mineral in this region with illite usually a major constituent (Renie & Ellis 1978). Potassium held by illite is generally not exchangeable under normal conditions (Drever 1982), however, weathered illite is often a source of potassium in soils (Rankama & Sahama 1968, Drever 1982). Because it is highly soluble, potassium has the potential to be leached quickly away from the site of weathering. However, montmorillonite often adsorbs potassium cations onto its surface thereby reducing this loss (Rankama & Sahama 1968, Drever 1982). Glaciofluvial surfaces have very little clay relative to glacial till surfaces, thus, they possess neither a good potassium source, nor the ability to hold the highly soluble cation in the soil. The strong negative correlation of potassium with the moisture gradient may simply be reflecting large differences in the ability of the two geomorphic surfaces to produce available potassium and hold on to it.

Since the geomorphic processes form hillslopes in the same general way in many places (Hack & Goodlet 1960, Troeh 1965, Bull 1975, Nash 1980) and moisture and nutrient flux and storage can be linked primarily to topographic form (Hack & Goodlet 1960, O'Loughlin 1981, 1986, Selby 1982, Wood et al. 1988), it seems likely that variation in moisture and nutrient status should be prevalent. If plants have adapted to take advantage of this large variation, it could explain why moisture and nutrient gradients often explain most of the variation in vegetation composition. Furthermore, since vegetation composition often reflects topographic control (e.g., Day & Monk 1974,

**FIGURE 1.11: General landscape patterns of vegetation composition. The shape of the hillslopes is derived from the allometric equations for hillslopes on glacial till and glaciofluvial surfaces. The tree symbols depict the general change in dominant canopy species down the hillslope which is based on the relationship between the stand positions on the moisture and nutrient gradients and the stand distances from the ridgeline.**



Johnson 1981, Marks & Harcombe 1981, Allen & Peet 1990, Busing et al. 1992), it suggests that the landscape scale spatial patterns of vegetation composition are dictated by the way the geomorphic processes shape the landscape.

The general landscape pattern of vegetation composition is depicted in Figure 1.11 which, unlike stylized figures of vegetation change on hillslopes (Day & Monk 1974, Niering & Lowe 1984, Lieffers & Larkin-Lieffers 1987 and Baldwin et al. 1990), is derived from the allometric equations and the relationships between the stand positions on the gradients and their distances downslope from the ridgeline. Thus, this figure shows the general pattern of vegetation composition change down most hillslopes in the study area. Clearly the analysis would be more elegant if the allometric equations were used to construct a driving variable rather than relating vegetation composition to distance which is obviously a proxy for more fundamental processes of moisture and nutrient horizontal, subsurface movement. However, the derivation of this driving variable has proven to be elusive thus far.

#### *Recovery after fire gradient*

A high correlation (Spearman's  $r$ ; axis 1 = 0.99, axis 2 = 0.84) between both components of the unpartitioned species ordination (PCA) and the rotated species habitat ordination (PCA) (significant at  $P < 0.001$ ) indicates the greater importance, in accounting for variation in species abundance, of the physical environmental gradients than of the temporal recovery after fire gradients. This is likely because only a few young (< 30 years old) stands could be sampled. However, other studies, with many more young stands, have shown a much larger effect due to temporal variation (e.g., Johnson 1981)

and many have recognized the need to examine species composition change with time since the last disturbance (e.g., Dix & Swan 1970, Peet & Loucks 1977, Johnson 1981).

Species recover at different rates after a disturbance. Of the species that recover quickly after fire (top left of Figure 1.7) most are herbaceous species producing light fruits that are easily dispersed by wind (e.g., *Petasites palmatus*, *Aster ciliolatus*) or fruits that provide important forage or have barbs and are easily dispersed by animals (e.g., *Cornus canadensis*, *Galium boreale*). These species quickly become conspicuous in areas where there is no tree canopy shading them. Most of the few remaining fast recovery species are deciduous woody shrubs (e.g., *Rosa acicularis*, *Rubus idaeus*), many of which possess vegetative methods of recovery and may recover more quickly from above ground disturbance than evergreen shrubs due to a greater amount of below ground storage (Archer and Tieszen 1980, Chapin 1980, Bryant et al. 1983). There are also a few tree species which possess fast recovery strategies. For example, *Populus tremuloides* aggressively recruits after disturbance by rapid vegetative propagation of root suckers (Brown & DeByle 1987). Combined with its fast growth rate, *Populus tremuloides* can quickly dominate a stand, explaining why it appears in the canopy stage at the fast recovery end of the recovery gradient along with its seedling and understory stages.

*Picea mariana* and *Populus balsamifera* also appear as very fast recovery species. This seems odd considering it takes several years for trees to reach the canopy. However, both *Picea mariana* and *Populus balsamifera* often grow in wet conditions and these species rarely grow together with any of the upland species studied here. In fact, most upland *Picea mariana* stands consist of *Picea mariana*, a few select mosses and very little



else. Other herbaceous and woody species in these areas are generally rare. Because of this, *Picea mariana* and *Populus balsamifera* appear to arrive early in disturbed sites and quickly dominate the stand. Both species are adapted to early arrival in newly disturbed sites. *Picea mariana* possesses some serotinous cones that release seeds after a fire and *Populus balsamifera* can reproduce both by light, easily dispersed seeds and by suckering. It is extremely unlikely that the results represent the recovery of these species in partial burns due to wetter microsites since approximately 95% of the park has been burned by stand replacing fires (Jeff Weir, *unpublished data*).

The species that recover slowly after fire (bottom right of Figure 1.7) are mostly tree species, many of them in the canopy. Herbaceous and woody shrubs occupy a much smaller proportion of the species at this end of the recovery gradient compared with the fast recovery end. Those tree species that reproduce by suckering (*Populus tremuloides* and *Betula papyrifera*) or have serotinous cones (*Pinus banksiana*, *Picea mariana*) recover faster in newly disturbed areas than those species that must disperse into the area by seed. Of the species that must disperse by seed (*Picea glauca* and *Abies balsamea*) *Abies balsamea* has the slowest growth rate and is the only species to recruit well on slightly shaded sites which have an accumulation of duff (Johnson 1992).

The tree species that are present in a stand just before a fire are also often present just after a fire (Did & Swan 1970, Ohmann & Grigal 1979, Johnson 1981, David Greene *personal communication*), as are many understorey species (Ohmann & Grigal 1979, Johnson 1981). Different species dominate the stands at different times. Early after a fire, the open spaces are invaded by herbaceous plants and by woody shrubs that can reproduce

vegetatively. Although trees are present, they are too small to shade out the herbs and shrubs. As the trees and larger shrubs, like *Alnus crispa*, grow they compete more effectively for resources and the abundance of herbs and shrubs declines. It is unlikely that the forest moves through a series of successional stages. Age distributions of stands within the study area show that most stands are even aged and that almost all of the trees in the canopy are recruited within a very narrow span of about 10 to 20 years.

A positive linear relationship exists between position on the recovery gradient and the time since the last fire ( $r^2 = 0.37$ , significant at  $P < 0.001$ ). If one can specify or estimate the spatial pattern of time since fire on the landscape and one knows the covariance of the recovery after fire gradient with the time since the last fire, it should be possible to synthesize a model that explains part of the variation in landscape patterns of vegetation distribution.

### *Conclusion*

This study has shown that in the mixedwood boreal forest, the upland vegetation composition at any given point on the landscape is controlled by the overlap of the moisture, nutrient and recovery after fire gradients. Any attempt to understand the landscape patterns of vegetation distribution and abundance must, therefore, focus on the processes that distribute these gradients across the landscape. In this region, hillslope geomorphology seems to be a unifying explanation for upland gradients; however, this hypothesis needs further testing in areas with different vegetation and geomorphic histories. By understanding the processes involved, more accurate predictions about future vegetation patterns due to environmental change may be made.

Recent work in surface hydrology has shown that the landscape can be divided up into a series of hillslopes where the parameters of the water flux and storage processes are assumed to be spatially homogeneous (Wood et al. 1988, Band 1989, Band 1991).

Extending the statistical descriptions of planimetric form of the river channels to their associated hillslopes has met with some success in predicting the moisture flux and storage of watersheds (Wood et al. 1988, Band 1993). This study has characterized the change in vegetation down hillslopes. It should, therefore, also be possible to extend the statistical description of planimetric form of the channels to their associated hillslopes to derive a statistical description of landscape scale vegetation distribution patterns. These patterns will be coupled in the geomorphic processes that shape the landscape. A similar argument can be made for the relationship between the recovery after fire gradient and time and the pattern of time since last fire across the landscape.

This has far reaching implications in ecology. For instance, many predict that climate change will have a significant impact on future vegetation patterns, however, the nature of that change is still very unclear. By understanding how climate change may influence the relationships between the environmental gradients and the hillslopes or the frequency of fires, it may be possible to make more accurate predictions about those future patterns. By relating vegetation patterns to large scale geomorphic and meteorological processes, it may be possible to produce general rules of habitat organization on the landscape. This may also lead to a better understanding of landscape patterns of biodiversity.

## **CHAPTER 2**

### **Linking landscape scale patterns of vegetation distribution and abundance to geomorphic processes operating at two scales.**

#### **INTRODUCTION**

The processes controlling the landscape scale ( $10^1$  to  $10^3$  km) spatial distribution of vegetation are poorly understood (Forman and Gordon 1986, Turner 1989). Indeed, many studies tend to concentrate on statistical descriptions of the spatial patterns and avoid discussion of how the patterns may have come about (Hall et al. 1991, Ripple et al. 1991, Mladenoff et al. 1993, Vogelmann 1995 and others). Chapter 1 showed that hillslope geomorphology plays an important part in controlling the principal vegetation gradients down most hillslopes. In turn, then, geomorphic principles of hillslope assembly into drainage basins must offer a further landscape scale process.

Moisture and nutrients are common gradients governing vegetation distribution and abundance in a wide variety of vegetation types (e.g., Chabot and Mooney 1985, Barbour and Billings 1988). This is due in part to the way geomorphic processes control hillslope profile shape and sub-surface moisture and nutrient flux rates and storage capacities down these hillslopes. The available moisture and nutrients at each point on a hillslope are not formed independently of other points on the hillslope, but are coupled to those points upslope that contribute drainage. Both moisture and factors related to nutrient status have been shown to be controlled principally by topography (e.g., Kleiss 1970, Malo et al. 1974, Anderson and Burt 1977, Harr 1977, Sinia et al. 1981, Cihra 1984, Quinn 1992) and only secondarily by such things as variation in rainfall and soil hydraulic

conductivity (O'Loughlin 1981, Wood et al. 1988, Dawes and Short 1994). Vegetation also reflects these patterns of topographic control over moisture and nutrients, showing consistent relationships between floristic composition and topographic position on slope (Day and Monk 1974, Johnson 1981, Marks and Harcombe 1981, Allen and Peet 1990, Busing et al. 1992 and others). Hillslopes on the same substrate tend to have the same slope profile. These profiles can be summarized with allometric equations that relate the vertical drop from the ridgeline to the horizontal distance from the ridgeline (e.g., Hack and Goodlet 1960, Bull 1975). Relating the moisture and nutrient gradients to the allometric equations characterizes the distribution of moisture and nutrients as well as vegetation down all hillslopes on the landscape. Thus, the general pattern of vegetation change down hillslopes is related to horizontal distance from the ridgeline (chapter 1).

Landscapes can be thought of as a framework of ridges and channels upon which hillslopes are hung. The valleys are arranged into organized channel networks around which the hillslopes form organized drainage basins. Hack (1957) showed that, in drainage basins ranging up to about  $10^4 \text{ km}^2$  in Virginia, the mainstream length is related to the basin area by the relation:

$$\text{Length} = 1.4\text{Area}^{0.6}$$

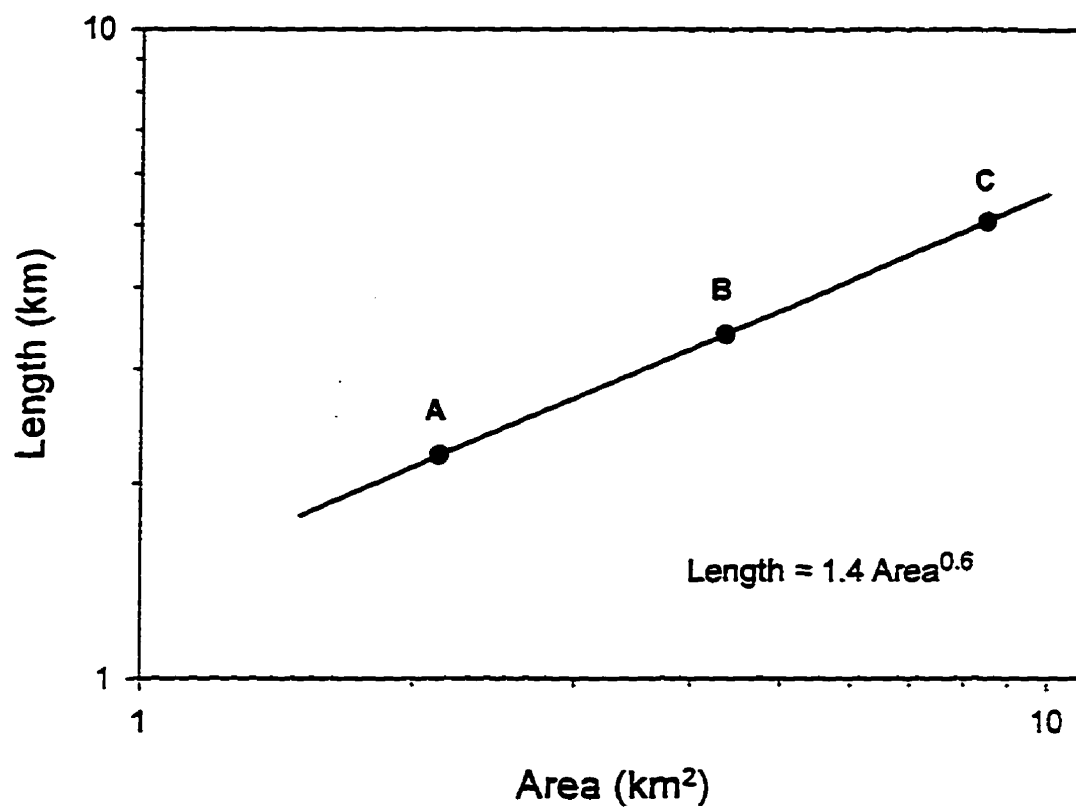
This relationship has subsequently been shown to hold for many drainage basins around the world in many diverse environments including some of the world's largest basins such as the Amazon and the Nile ( $\sim 10^6$  to  $10^7 \text{ km}^2$ ) (Gray 1961, Eagleson 1970, Mueller 1973, Shreve 1974, Newson 1978). In fact, almost all basins examined in this way have shown a similar relationship with the coefficient ranging between 1 and 2.5 and the exponent

usually ranging between 0.5 and 0.8. Note that when the exponent is greater than 0.5, the length of the basin increases at a disproportionately greater rate than its width as the basin size increases (Hack 1957). In other words, larger basins tend to be longer and narrower than smaller basins and thus the average distance from the ridgeline to the channelway tends to remain constant or to increase very slowly with increasing basin size (Figure 2.1).

Hack's (1957) work was based upon measuring the actual stream length from some point on the network all the way up the longest stream until a divide was finally reached (e.g., for a 3<sup>rd</sup> order stream, the longest stream distance would include the distance along the 2<sup>nd</sup> and 1<sup>st</sup> order streams upstream from the measuring point). Later, Shreve (1969, 1974), working with link lengths (the shortest distance between two stream forks), showed that this relationship is also true for the most probable topologically random stream networks. Furthermore, not only do the drainage areas of mainstream lengths conform to this relationship, but so do the drainage areas of all the individual interior and exterior stream link lengths of a random topological network (Shreve 1974). In other words, the relationship between the interior or exterior link length and the immediate contributing area that drains directly overland into that link is described by Hack's equation.

Irrespective of whether mainstream lengths or link lengths are considered, the relationship between basin area and length implies that the average distance of overland flow to the channelway remains fairly constant or increases slowly with increasing basin size. Chapter 1 showed that general patterns of vegetation change down hillslopes are related to distance from the divide. Consequently, the average proportions of different

**FIGURE 2.1: Hack's (1957) allometric relationship between drainage basin length and area with three examples of drainage basins in Prince Albert National Park that conform to the relationship.**



A



B



C



vegetation types should remain fairly constant within basins regardless of basin size.

Furthermore, this should be a general pattern of landscape vegetation assembly since basins seem to be assembled in the same fashion in different environments.

It is clear that geomorphic principles of hillslope and drainage basin assembly may explain a large proportion of the variance in landscape scale patterns of vegetation distribution and abundance. However, other processes must also be playing a role in controlling these patterns. By using the relationships between vegetation type and distance from the divide and knowledge of how hillslopes are assembled into drainage basins, it should be possible to predict part of the landscape pattern of vegetation distribution due to geomorphic processes. By examining deviations between the actual pattern of vegetation within basins and the predicted vegetation from the hillslopes and basins it may be possible to see the effects of other processes on the spatial patterns of vegetation.

The purpose of this study is, firstly, to explain some of the landscape scale patterns of vegetation distribution by linking the mechanisms of vegetation change down hillslopes to geomorphic principles of hillslope arrangement into drainage basins and, secondly, to define the role of other processes in controlling vegetation distribution by examining the deviations between the actual vegetation and the vegetation predicted by geomorphic processes .

I begin by building a map of drainage basins from a digital elevation model (DEM) of Prince Albert National Park, Saskatchewan, Canada. I then compare length-area relationships of basins in the study area to Hack's (1957) allometric relationship. Then I

use a supervised classification of a LANDSAT TM image of the Park to determine the actual vegetation. Using relationships between vegetation type and distance from the divide (chapter 1), I build a map of predicted vegetation types. By comparing these two maps, deviations between the predicted and the actual proportions of vegetation in drainage basins can be seen. If the length-area relationships in the study area are similar to Hack's (1957) and the predicted proportions of vegetation are similar to the actual proportions, then landscape scale vegetation patterns are in part controlled by geomorphic principles of drainage basin assembly. Deviations between the predicted and the actual proportions then allow the roles of other processes, such as disturbance, to be defined.

## METHODS

### *Study area*

The study area is located in Prince Albert National Park, Saskatchewan (53° 35' N to 54° 20' N and from 106° 0' W to 106° 47' W). This 4000 km<sup>2</sup> Park has gently rolling topography with an elevation range from about 500 to 800 metres a.s.l. The study area is part of the boreal mixedwood forest (Rowe 1972) with predominantly glacial till and glaciofluvial surficial materials (Padbury 1978). The climate is characterized by long, cold winters and short, cool summers with annual precipitation ranging from 400 to 500 mm of which approximately 70% occurs as rain. For a more complete description of the study area see chapter 1.

### *Drainage basin delineation*

Drainage basins were delineated from a digital elevation model (DEM) of the study area. The source data for the DEM were supplied by Prince Albert National Park and

consisted of digitized contour lines from 1:50 000 topographic maps. The vector image was imported into the remote sensing analysis package PCI version 5.2 (*PCI Inc., 50 West Wilmot St., Richmond Hill, Ontario, Canada*) and interpolated to a raster image using a conical search interpolation routine (cf. Carrara 1988).

Drainage basins were then delineated using the terrain analysis modules in PCI (cf. Jenson and Dominique 1988). The first step in the terrain analysis was to produce a "depressionless" DEM. DEMs almost always contain depressions that hinder flow routing. The object of this first step was to create an adjusted DEM in which the cells contained within depressions were raised to the lowest elevation value on the rim of the depression. In this way, each cell in the depressionless DEM was part of at least one path of cells monotonically decreasing in elevation and leading to an edge of the data set. A flow direction map was then produced from the depressionless DEM by comparing the elevation of each pixel to the elevation of its eight adjacent neighbours and calculating the most likely direction of water flow out of the pixel, or, in other words, the downstream direction. Using the flow direction map, a flow accumulation map was produced by assigning to each pixel a value equal to the total number of upstream pixels. Water in any of the upstream pixels will eventually flow through the pixel in question.

In the terrain analysis modules, drainage basins are delineated on the landscape by assigning one pixel on the image as a "seed point". All pixels upstream from the seed point are found and these pixels are then assigned to the seed point's drainage basin. For large landscapes seed points must be picked automatically. Seed points were assigned on the depressionless DEM wherever the flow accumulation value exceeded a threshold of

3000. This threshold produced drainage basins that were similar in size and location to several first order drainage basins delineated manually from 1:50 000 topographic maps of the study area. Seed points were also placed in pixels where the change in flow accumulation between the pixel and its downstream neighbour exceeded a threshold value of 3000. This usually occurred at the pixel above the fork between two channels large enough to be depicted on a 1:50 000 topographic map. In this case, all pixels upstream of the seed point, but not beyond any upstream seed points, were assigned to the new drainage basin. Thus, the drainage basins that were produced delineated an area of land where water flows directly overland into the channel between the forks of tributaries or between a fork and the drainage divide. In this way the drainage areas are analogous to the drainage areas of interior and exterior stream links. This technique has been used to successfully delineate drainage networks and basins elsewhere (Jenson and Domingue 1988). The drainage basin boundaries were then vectorized and the vectors used to produce a new raster image of drainage basin boundaries.

*Determining allometric relationships of basin area and length*

The relationship between area and length of basins was evaluated for basins within the Park. In order to avoid confounding this and other analyses with basins that were mixes of glacial till and glaciofluvial deposits, the basins were divided into those dominated by glacial till materials versus those dominated by glaciofluvial materials based on a surficial geology map of the area (Padbury 1978). A total of 89 glacial till basins (12% of the Park land area) and 91 glaciofluvial basins (14% of the Park land area) were examined.

In order to measure basin length, a vector image of the digitized stream channel network was first overlaid on the image of drainage basins. Length was defined as the straight line distance from the point where the stream flowed out of the basin to the most distant point in the basin (Morisawa 1958). Using this technique, measurements are not only simple to perform, but, for exterior links, are consistent with Hack's (1957) procedure of measuring all the way to the divide and, for interior links, are usually consistent with Shreve's (1969, 1974) procedure of measuring the shortest distance between two forks. In addition, the area-length relationships of basins are unaffected by the choice of measurement technique (e.g., Schumm 1956, Hack 1957, Shreve 1969, 1974, Smart 1969).

Allometric relationships between basin length and area were derived by regressing the log basin length onto the log basin area using a geometric mean regression. The regressions were performed separately for glacial till and glaciofluvial basins.

#### *Mapping the actual distribution of vegetation on the landscape*

The upland vegetation on the landscape was mapped via a supervised classification of a LANDSAT Thematic Mapper image acquired under cloud free conditions on July 12, 1990. In addition to TM bands 1-7, a digitized version of the time-since-fire map of the Park (Weir 1996) was used as ancillary information in the classification. Both the TM image and the time-since-fire map were co-registered in Universal Transverse Mercator (UTM) projection to the DEM.

For upland forest vegetation, training and accuracy assessment sites were taken from 101 forest stands sampled during the summers of 1993 and 1994 (chapter 1). Each

forest stand consisted of two parallel transects (see chapter 1) located using a Differential Global Positioning System in conjunction with a base station (accurate to within 1 metre 50% of the time). The exact pixels that the transect passed through, as well as all adjacent pixels, were used in the analysis, giving about 40 pixels per stand. The stands were arbitrarily divided into six vegetation classes identified by the highest importance value canopy species (Figure 2.2). These classes were named by the dominant canopy tree's common name. This prevents confusion in discussions of the actual species, which are referred to by their genus and species name. Half of the pixels from each sample were randomly selected to be used as training sites in classification and the other half were used for accuracy assessment.

For non-upland forest vegetation types and water, training and accuracy assessment sites were chosen by locating large homogeneous areas in the image data. Several hundred to several thousand pixels were obtained for each class using interpretational aids such as 1:12 500 aerial photographs, 1:50 000 forest cover maps as well as site visits. Pixels for training and accuracy assessment were then randomly and equally assigned from these sites.

A maximum likelihood classification (cf. Haralick and Fu 1983) was performed on the first four eigen channels of a principal components analysis of TM bands 1-7 (cf. Franklin 1992) and the time-since-fire image using the image analysis software PCI. A table showing the field class membership of the pixels in the test data set compared to the predicted class membership for each classification attempt (called the map accuracy) was also produced.

*Predicting the upland vegetation distribution on the landscape*

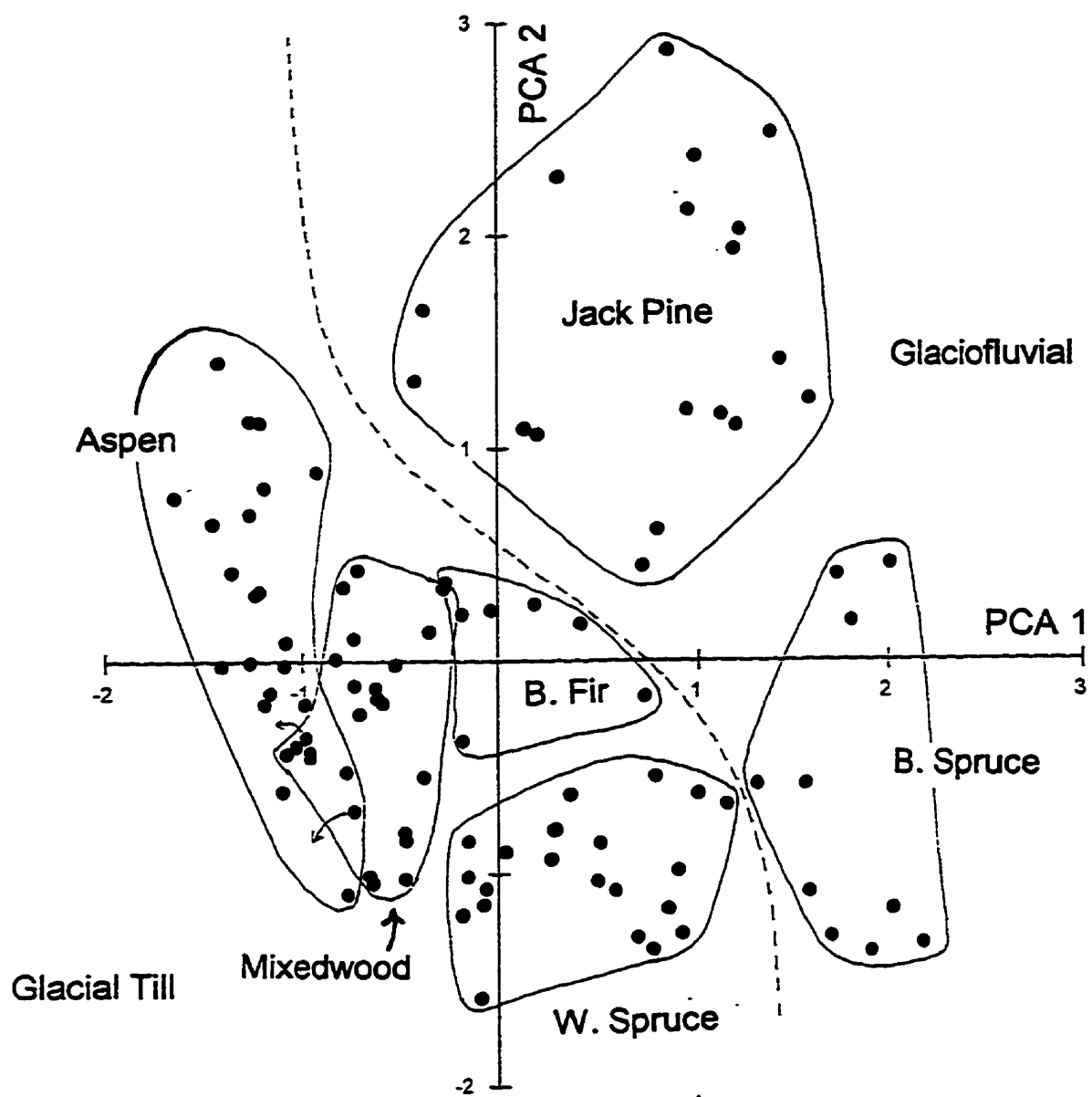
A map of predicted upland vegetation classes on the landscape was produced using the raster drainage basin boundary map and the relationships between vegetation type and distance from the ridgeline found in chapter 1. To begin with, a proximity to ridgeline image was produced in which the distance to the nearest drainage basin boundary, or ridgeline, was recorded for each pixel. Next, the proximity image was divided into areas of upland forest and non-upland forest. The upland forest areas were then further subdivided into areas with glacial till and with glaciofluvial surficial materials using a surficial geology map of the Park (Padbury 1978). Non-upland forest areas were not divided into areas of different surficial materials.

Next, each pixel in the till and glaciofluvial sub-divisions was classified into one of the vegetation types based upon the relationships between vegetation type and distance from the ridgeline found in chapter 1 (Table 2.1). Areas of non-upland forest vegetation type were left unclassified. The three sub-divisions were then reassembled into one map of predicted vegetation types on the landscape. Finally, the upland forest accuracy assessment sites used in the supervised classification of the TM image were used to produce a table showing which classes pixels were classified into so that the accuracy of the predicted vegetation image could be assessed.

In this region, *Abies balsamea* (L.) Mill. often grows with *Picea glauca* (Moench) Voss and sometimes with a mix of *Populus tremuloides* Michx. and *P. glauca*, but

**FIGURE 2.2: Principal Components Analysis of stands showing arbitrary division into vegetation classes based on the canopy species with the highest importance value.**





because *A. balsamea* often grows very slowly relative to the other tree species (Dix and Swan 1971, chapter 1), stand canopies are typically not dominated by *A. balsamea* until the stand is older. In younger stands where *A. balsamea* is present, the trees are usually shorter and of smaller diameter than the *P. glauca* or *P. tremuloides* trees (S.R.J. Bridge, *personal observation*). Because these stands are quite dense (mean = 970 trees/ha), variation in the satellite imagery should be most strongly correlated with variation in the tallest canopy vegetation. Consequently, areas that are fir stands on the ordination and in the predicted map may be classified as white spruce or aspen/white spruce mixedwood on the supervised vegetation classification of the TM image. This creates problems when comparing the predicted vegetation to the actual vegetation. To rectify this problem, a second predicted vegetation map was produced using the time-since-fire map as ancillary information in which young balsam fir stands (< 105 years) were classified as either white spruce or mixedwood forest types (Table 2.2). The cutoff age of 105 years was determined by simply using the youngest age of all stands dominated (importance value > 40) by *A. balsamea*.

*Detecting pattern deviations between the actual and predicted vegetation*

The proportion of the basin area occupied by each vegetation class was calculated for the drainage basins used to determine the allometric relationships between basin length and area. This was done for both the actual vegetation derived from the TM image and for the two predicted vegetation maps derived from the DEM. In all of the till basins examined, the proportion of non-upland forest area (i.e., grasslands, marshes and water) was less than 50% and the combined proportion of non-upland forest and upland glacial

TABLE 2.1: The vegetation classes found on glacial till and glaciofluvial geomorphic surfaces and their corresponding distances from the ridgeline used in predicting the vegetation from the digital elevation model (DEM).

	Distance From Ridgeline (m)	Vegetation Class
Glacial Till	0 - 108	Aspen
	108 - 400	Mixedwood
	400 - 800	Fir
	> 800	White Spruce
Glaciofluvial	0 - 975	Jack Pine
	> 975	Black Spruce

till type forest exceeded 80%. Likewise, in glaciofluvial basins the proportion of non-upland forest area was less than 50% and the combined proportion of non-upland forest and upland glaciofluvial type forest exceeded 80%. PCI was used to determine the area covered by each vegetation class in each basin as well as the total basin area from which the proportions were derived. The proportion of each vegetation type in a basin was also regressed onto basin size to check for any relationships. This analysis was performed on both the actual vegetation and the predicted vegetation.

Because human disturbances are known to have had an impact on vegetation in the southern half of the study area (Weir 1996), the above analysis was also conducted on basins in the north and south portions of the study area separately. The study area was divided into northern and southern portions by a line that runs roughly along the 52nd parallel and which separates the Park into areas of different disturbance regimes (Weir 1996). European settlement around the southern boundary of the Park resulted in settlement fires spreading north into the Park from 1890 to 1945, shortening the fire cycle (the time required to burn an area the size of the study area) in the southern portion of the Park. In addition, several timber berths existed in the southern portion of the Park around the turn of the century which were selectively logged for *P. glauca*. The northern portion, on the other hand, is still surrounded by mostly continuous forest and has never been logged.

TABLE 2.2: Distances from the ridgeline used for reconstructing vegetation in conjunction with time-since-fire date for glacial till stands.

	Distance From Ridgeline (m)	Age	Vegetation Class
Glacial Till	0 - 108	any	Aspen
	108 - 400	any	Mixedwood
	400 - 470	< 105	Mixedwood
	400 - 470	> 105	Fir
	470 - 800	> 105	Fir
	470 - 800	< 105	Spruce
	> 800	any	Spruce

## RESULTS

### *Allometric relationships of basins*

For both glacial till and glaciofluvial drainage basins, the exponents of the allometric equations fitted to the data were both greater than 0.5 (till  $r^2 = 0.47$ , fluvial  $r^2 = 0.59$ ). As well, the equation parameters (Figure 2.3 and 2.4) were very similar to Hack's (1957).

### *Classification of LANDSAT TM image*

The supervised classification of the LANDSAT TM image with the time-since-fire information had an overall accuracy of 74.1% (Table 2.3). Most of the misclassification was between similar vegetation types. All of the water classes tended to be very accurate, except for shallow lakes, which were sometimes confused with deep lakes. Treed and shrub marsh classes tended only to be confused with each other or with treed grassland. Forest class pixels were sometimes confused with other forest classes, but were rarely misclassified into non-forest classes. Jack pine and black spruce both showed some confusion with white spruce. Trembling aspen and white spruce/aspen mixedwood were mostly confused with each other and white spruce was also confused primarily with mixedwood.

### *Predicting the Vegetation Distribution on the Landscape*

The map of predicted vegetation on the landscape using the DEM resulted in a map that had an overall accuracy of 35.8% (Table 2.4). Most of the misclassification was between upland forest types that occupy adjacent positions on the hillslope. For example,

**TABLE 2.3: Percent omission/commission error patterns for supervised classification of Prince Albert National Park using the first four principal components of the LANDSAT TM image and the Time-Since-Fire map.**

Class	Percent Classified Correctly Into Class												
	1	2	3	4	5	6	7	8	9	10	11	12	13
<b>Pixels</b>	2269	2136	2843	281	874	1819	2353	316	172	370	306	127	359
<b>%</b>	11/34	14/3	39/2	14/2	35/44	39/12	26/21	77/70	39/33	35/46	51/52	24/15	40/59
<b>Overall accuracy = 74.1%; Average accuracy = 70.4%</b>													

**Class 1 = Deep Lakes; 2 = Intermittent Lakes; 3 = Shallow Lakes; 4 = Grassland; 5 = Treed Grassland; 6 = Shrub Marsh; 7 = Treed Marsh; 8 = Jack Pine; 9 = Black Spruce; 10 = Aspen; 11 = Spruce/Aspen Mixedwood; 12 = Fir; 13 = White Spruce.**

TABLE 2.4: Percent of test pixels classified into each class of the predicted vegetation map constructed without using time-since-fire information. Only upland forest classes are considered. Class numbers are the same as Table 2.3.

Class	Pixels	Percent Classified Into Class					
		8	9	10	11	12	13
8	316	55.7	15.8	14.2	2.2	0.9	0.0
9	172	72.6	7.2	0.5	0.0	2.9	9.1
10	370	2.9	0.0	37.0	27.3	13.3	13.0
11	306	0.0	4.6	21.9	41.8	12.7	14.7
12	127	0.0	0.0	11.8	25.2	50.4	5.5
13	359	4.2	0.3	15.7	25.7	22.7	22.1

Overall accuracy = 35.8%, Average accuracy = 35.7%.



**FIGURE 2.3:** The relationship between drainage basin length and area for glacial till watersheds. Also shown is the geometric mean regression line (GMR) for the data and Hack's (1957) relationship. The GMR is least squares fit that assumes both length and area are subject to error.

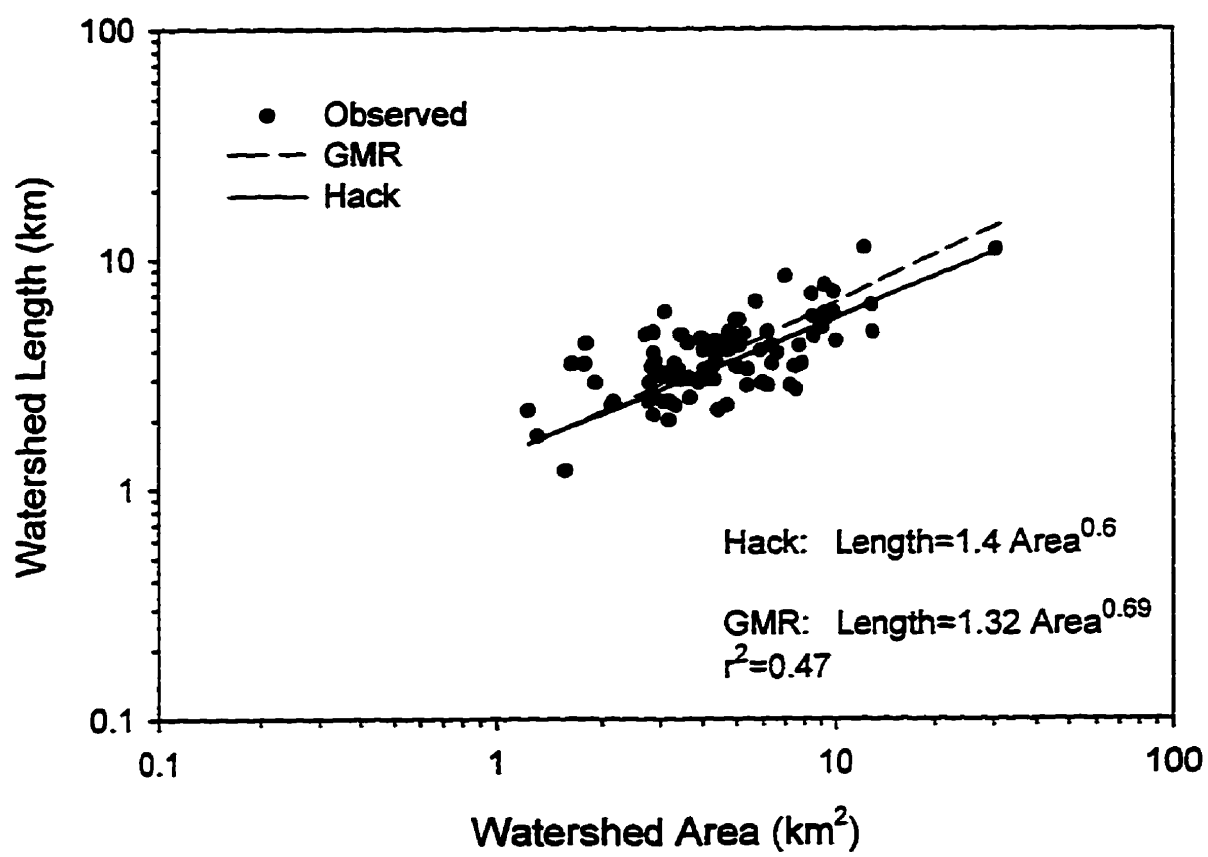
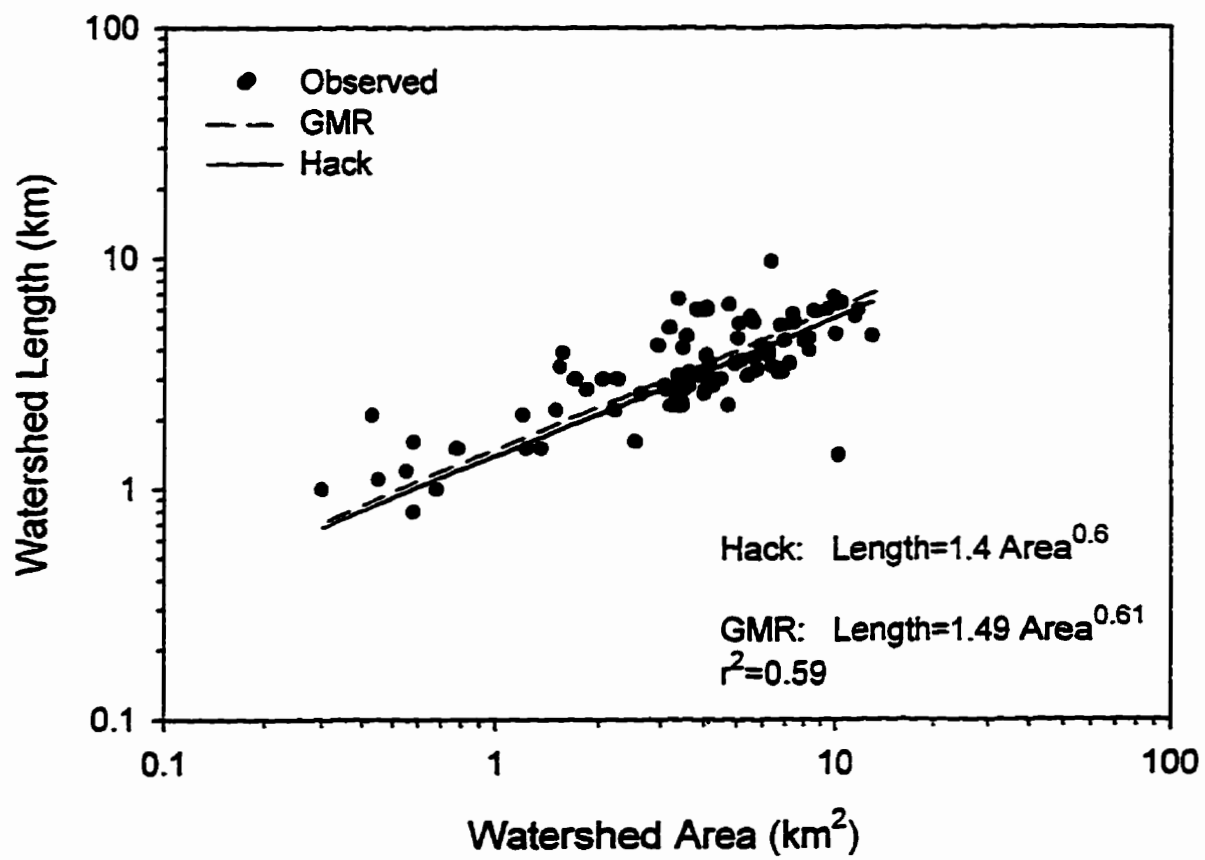


FIGURE 2.4: The relationship between drainage basin length and area for glaciofluvial watersheds. Also shown is the geometric mean regression for the data and Hack's (1957) relationship. The GMR is a least squares fit that assumes both length and area are subject to error.



black spruce had a high misclassification error and was most commonly misclassified as jack pine while trembling aspen and balsam fir were mostly confused with mixedwood.

Incorporating the time-since-fire map into the predicted vegetation map improved the overall accuracy by 2.2% to 39.0% with mixedwood and white spruce forest classes showing the greatest improvement. Other classes were relatively unaffected by the inclusion of time-since-fire information (Table 2.5).

### *Vegetation Distribution in Watersheds*

Linear regression was used to examine the relationship between basin size and the proportion of each vegetation class in the basin, but no significant ( $P < 0.05$ ) relationship was found for either the actual vegetation or the predicted vegetation.

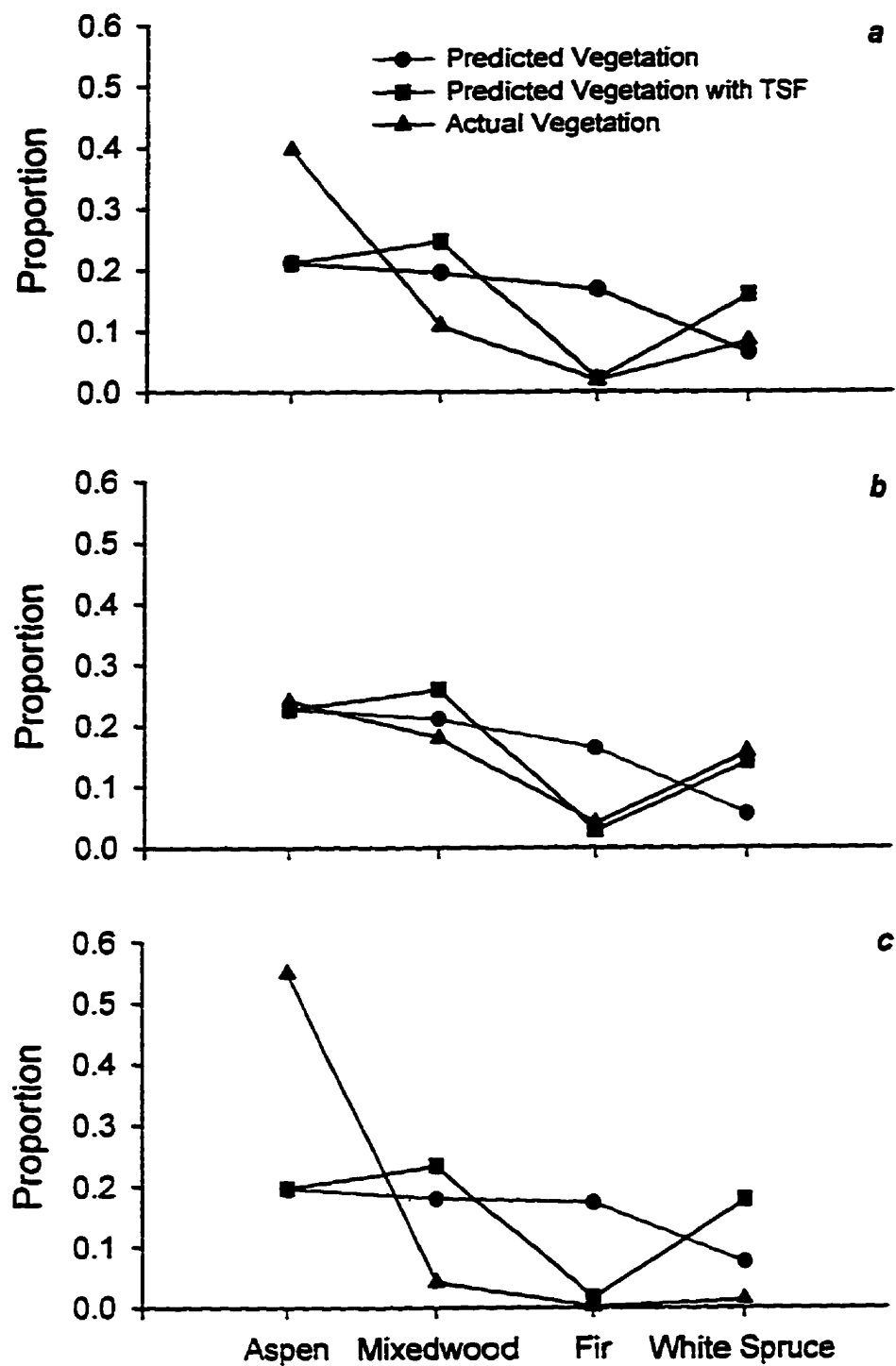
The average proportions of trembling aspen, mixedwood, balsam fir and white spruce forest types were calculated for all glacial till basins examined in the Park and, likewise, the average proportions of black spruce and jack pine forest types were calculated for all glaciofluvial basins examined in the Park. In addition, these average proportions were compared with the average proportions for basins in the northern part of the Park as well as with those in the south.

For each individual forest class, there was no significant ( $P < 0.05$ ) difference in the average proportions calculated from the two predicted vegetation maps between the entire Park, the northern portion or the southern portion for either surficial material. For the average proportions calculated for glacial till basins from the actual vegetation, the proportions differed significantly ( $P < 0.05$ ) between the northern portion, southern portion and entire park. The actual proportions were most similar to the

Class	Pixels	Percent Classified Into Class					
		8	9	10	11	12	13
8	316	55.7	15.8	14.2	2.2	0.0	0.9
9	172	72.6	7.2	0.5	1.0	0.0	11.1
10	370	2.9	0.0	37.0	30.5	4.2	19.0
11	306	0.0	4.6	21.9	49.0	0.0	20.3
12	127	0.0	0.0	11.8	25.2	50.4	5.5
13	359	4.2	0.3	15.7	31.7	3.6	35.0

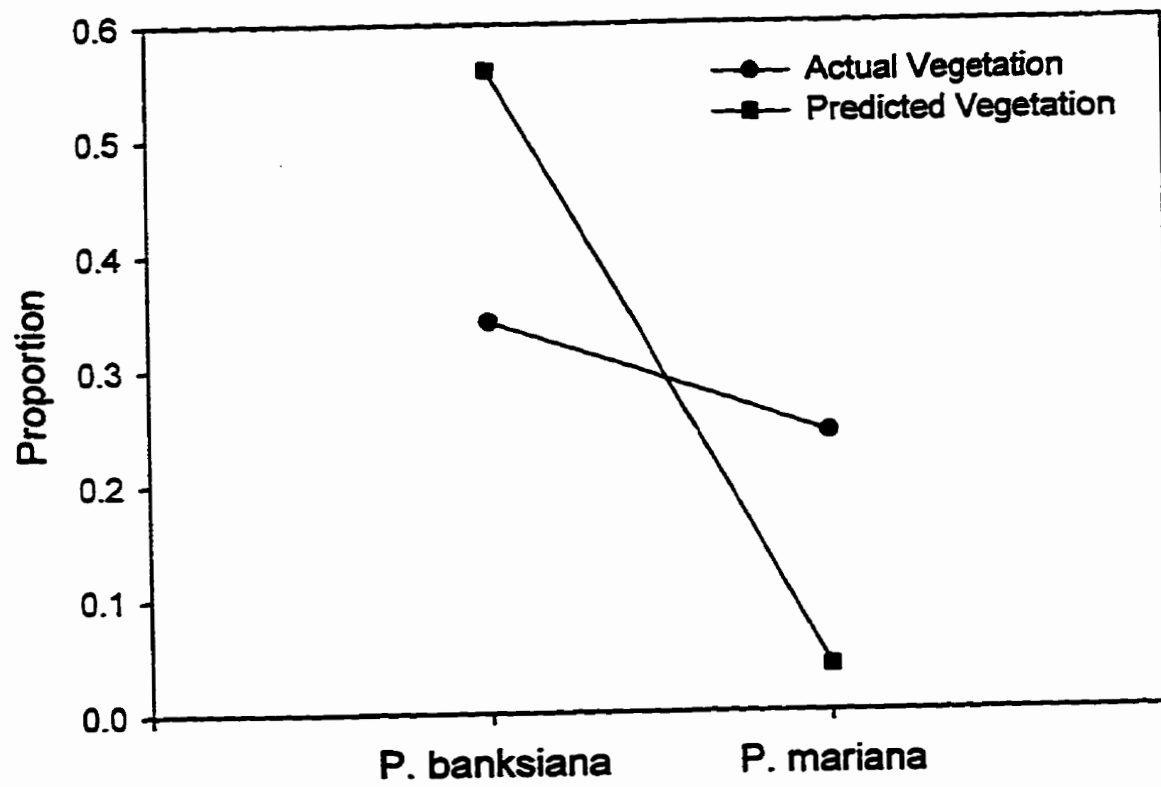
Overall accuracy = 39.0%, Average accuracy = 38.5%.

FIGURE 2.5: The average proportion of actual vegetation, predicted vegetation without time-since-fire and predicted vegetation using time-since-fire as a concomitant variable for upland forest classes in glacial till watersheds for (a) the entire Park, (b) the northern portion of the Park and (c) the southern portion of the Park. Standard error bars are too small to be shown.





**FIGURE 2.6:** The average proportion of actual vegetation and predicted vegetation for upland forest classes in glaciofluvial drainage basins for the entire Park. Only one line is shown for the predicted vegetation as there is no difference between the predicted proportions with and without time-since-fire. Similar lines are not shown for the northern and southern portions of the Park as there is no difference in the proportions between the north and south portions and the Park as a whole. Standard error bars are too small to be shown.



predicted vegetation in the northern part of the Park (Figure 2.5b) where there was often no significant ( $P < 0.05$ ) differences between the actual and predicted vegetation types. However, the actual vegetation proportions for the southern portion and the Park as a whole were often significantly ( $P < 0.05$ ) different from the proportions calculated from the predicted vegetation (Figure 2.5c). For the average proportions calculated for glaciofluvial basins from the actual vegetation, the proportions did not differ significantly ( $P < 0.05$ ) between the entire Park, the northern or the southern parts. The average proportions calculated from the actual vegetation did, however, differ significantly ( $P < 0.05$ ) from those calculated from the predicted vegetation maps (Figure 2.6).

For all glacial till basins examined in the whole study area (Figure 2.5a), the predicted vegetation without time-since-fire significantly ( $P < 0.05$ ) underpredicted the proportion of trembling aspen forest and significantly ( $P < 0.05$ ) overpredicted the proportions of mixedwood and balsam fir forest. There was no significant ( $P < 0.05$ ) difference in the proportion of white spruce between the predicted and the actual vegetation. For the predicted vegetation with time-since-fire, aspen was again underpredicted ( $P < 0.05$ ) and mixedwood was again overpredicted ( $P < 0.05$ ). However, balsam fir was not significantly different ( $P < 0.05$ ) from the actual proportion found, and white spruce was significantly ( $P < 0.05$ ) over predicted.

Examination of glacial till basins in only the northern half of the study area (Figure 2.5b) revealed significant differences ( $P < 0.05$ ) between the proportions of mixedwood, balsam fir and white spruce forest types predicted without time-since-fire and the proportions calculated from the actual vegetation. The predicted vegetation with time-

since-fire was much more similar to the actual vegetation. There was no significant difference ( $P < 0.05$ ) between the predicted proportions of aspen, balsam fir or white spruce forest types and the proportions calculated from the actual vegetation for these forest types.

For glacial till basins in the southern half of the study area (Figure 2.5c), the average proportion of aspen forest calculated from the actual vegetation was significantly ( $P < 0.05$ ) higher than what was predicted without time-since-fire. Also, the proportions of mixedwood, balsam fir and white spruce forest classes were significantly ( $P < 0.05$ ) lower in the actual vegetation than was predicted. Similar results were seen for the predicted vegetation with time-since-fire except for fir forest types which showed no significant difference ( $P < 0.05$ ) from the proportion calculated from the actual vegetation.

For glaciofluvial basins time-since-fire did not affect the proportions of jack pine or black spruce forest types so there was no significant ( $P < 0.05$ ) difference between the two types of predicted vegetation maps. Also, there was no significant differences ( $P < 0.05$ ) in the proportions of the two vegetation types for either the whole park or the north or south regions. In all cases the predicted vegetation significantly ( $P < 0.05$ ) overpredicted the proportion of jack pine forest and underpredicted the proportion of black spruce forest compared to the actual proportions of these types.

## DISCUSSION

### *Linking geomorphic processes to landscape vegetation patterns*

In the southern mixedwood boreal forest, two scales exist at which geomorphic processes operate on vegetation patterns and each scale is dominated by a different set of

processes. Furthermore, the geomorphic processes at both scales seem to operate in the same fashion in many different environments, suggesting that the vegetation patterns they produce should be prevalent in many places.

At the hillslope scale, divergent erosive processes such as rain splash, soil creep and mass wasting acting against the resistive properties of the surficial material govern the form of the hillslope profile (Schumm et al. 1987, Rinaldo et al. 1995). Hillslopes underlain by the same surficial material are often downwasting at a similar rate and can be described by allometric equations with the same parameters (Hack and Goodlet 1960, Bull 1975). Although the allometric equations do not show processes themselves, they do summarize the interrelations of materials, processes and landforms. Vegetation distribution and abundance are governed primarily by the distribution of moisture and nutrients down hillslopes. The available moisture and nutrients at each point on the hillslope are coupled to topographic position on slope and the sub-surface moisture and nutrient flux rates and storage capacities. The similarity in hillslope profile form and the relationship between moisture and nutrients and topographic position on slope lead to the consistent patterns of vegetation change down hillslopes (chapter 1).

At the drainage basin scale, the hillslopes are assembled around the channelways into drainage basins. The length of the hillslopes and the formation of channels are governed primarily by the location of surface saturation and concentrated overland flow which, in turn, are influenced mostly by the amount of upslope catchment area, the slope of the hill and type of surficial material (O'Loughlin 1981, 1986). Channels are formed as runoff is concentrated into distinct flow lines and the erosive force of the runoff is

enhanced. Flow lines suffer greater erosion than neighbouring areas upon which sheetflow or subsurface flow occurs and channels are incised below the level of the initial soil surface (Schumm et al. 1987, Rinaldo et al. 1995). The similarity in slope shape, soil transmissivities and moisture flux rates and storage capacities between slopes underlain by the same surficial material leads to surface saturation at roughly the same distance from the divide. This produces the roughly constant hillslope lengths and drainage basins that tend to be longer rather than wider at larger sizes (Figures 2.3 and 2.4). The consistency of slope length and the relationship between vegetation and distance from the divide ensure that the proportions of the different vegetation types remain roughly constant within basins. Furthermore, drainage basins seem to be assembled in the same fashion in many different environments (Gray 1961, Eagleson 1970, Mueller 1973, Shreve 1974, Newson 1978), so this should be a common pattern of vegetation distribution.

Clearly, this analysis would be more elegant if the change in vegetation composition down hillslopes were related to a process driven variable rather than to distance from the divide. Distance from the divide is a proxy for more fundamental processes of moisture and nutrient horizontal, subsurface movement. For instance, vegetation composition could be linked to a dimensionless wetness function (O'Loughlin 1986, also see Band 1985). Such a function entombs the processes of subsurface moisture horizontal movement in a dimensionless form by relating surface saturation to soil transmissivity, hydraulic conductivity, slope gradient and upslope catchment area. Unfortunately, the DEM is of insufficient quality to accurately estimate slope gradient and upslope catchment area so this relationship cannot be developed further here.

Relating the vegetation change down hillslopes to a process driven variable alleviates problems associated with changes in surficial material down hillslopes. This problem presents itself in this region in glaciofluvial drainage basins. Glaciofluvial drainage basins are usually formed as outwash channels by fast moving glacial meltwater. Consequently, these basins usually consist of glaciofluvial material around the channel way and the lower parts of the basin, while the ridgelines and higher parts are glacial till material. However, the original relationships between vegetation type and distance from the ridgeline were derived for homogeneous surfaces only (chapter 1). The reconstruction cannot account for downslope changes in moisture and nutrients that are related to changes in surficial material.

In basins with glacial till ridgelines and glaciofluvial channelways, *P. mariana* is growing closer to the ridgeline than it would in basins with glaciofluvial material all the way up to the ridgeline. This may be related to the nutrient status of hillslopes in basins with glacial till ridgelines. Glacial till materials contain much more clay than glaciofluvial materials (chapter 1), and weathered clay is often a source of nutrients (Rankama and Sahama 1968, Drever 1982). Nutrients are leached from the glacial till ridgelines and carried by subsurface moisture flow downslope (Anderson and Burt 1977, Harr 1977, Sinia et al. 1981, O'Loughlin 1981, 1986, Trudgill 1988, Litaor 1992, Tsuboyama et al. 1994) into the glaciofluvial material. In addition, the presence of clay can increase the soil cation exchange capacity (Rankama and Sahama 1968, Drever 1982). If some of the clay from the glacial till material has moved downslope into the glaciofluvial material, it could improve the retention of nutrients in the glaciofluvial material. This may mean that for any

given distance from the divide, glaciofluvial hillslopes with glacial till ridgelines are more nutrient rich than homogeneous glaciofluvial hillslopes. This may allow *P. mariana* to grow closer to the ridgeline on heterogeneous hillslopes than on homogeneous glaciofluvial hillslopes.

*Defining the role of other processes on landscape vegetation patterns*

A large proportion of the variance in vegetation distribution can be explained by geomorphic principles, such as hillslope shape, the flux rates and storage capacities of moisture and nutrients down hillslopes and the spatial arrangement of hillslopes around channel networks into drainage basins. However, it is clear that other processes also control the landscape scale spatial pattern of vegetation distribution and abundance. It is possible to see the effect of other processes on the landscape patterns of vegetation by examining the deviations between the actual vegetation and the predicted vegetation proportions within basins. In Prince Albert National Park, the effect of two disturbance processes (an increased fire frequency and selective logging for white spruce) can be seen on the vegetation patterns of the southern portion of the Park.

When the proportions of actual vegetation in glacial till basins were compared with the predicted proportions, large deviations existed in the southern half of the study area that did not exist in the north (Figure 2.5*b* and *c*). These differences seem to be a result of human disturbance in and around the southern half of the Park during the late 1800's and early 1900's. During this period, two principal factors conspired to produce large vegetation changes in the southern half of the Park. Firstly, several large timber berths existed in the area which were selectively logged for white spruce. Up to 1 million mature



white spruce trees were cut during this time, removing up to 211 mature trees per hectare (Weir 1996). Thus, a large proportion of the white spruce seed source was removed. Secondly, settlement during this period around the southern border of the Park resulted in an increased fire frequency within the Park (Weir 1996). Settlers moving into the area often used fires to clear their land. A large number of fires escaped from their land clearing operations and spread north into the Park. The more frequent fires within the Park made it difficult for the fewer recruiting white spruce trees to survive to maturity. The net result of the logging and more frequent fires was a significant loss of white spruce from the southern half of the Park and a change in the species composition of the south to a landscape dominated by trembling aspen forests (Weir 1996). In the northern half of the study area, which has never been logged and is surrounded on all sides by mostly uninterrupted forest, the actual proportions of upland forest types in glacial till drainage basins did not deviate from the predicted proportions (Figure 2.5b).

Vegetation patterns in glaciofluvial basins seemed unaffected by the two disturbance processes operating in the southern portion of the Park. This is likely because neither jack pine nor black spruce forest types were logged and both possess serotinous cones so their seeds do not have to disperse into burns from surviving patches.

Calculations of the actual proportions of upland forest types in glacial till basins was confused by the fact that variation in satellite imagery is correlated primarily with variation in the tallest canopy vegetation. This creates problems when dealing with slower growing species. In this region, *A. balsamea* grows slowly relative to the other tree species (Did and Swan 1971, chapter 1). Younger stands in hillslope positions suitable for

*A. balsamea* tend to have canopies dominated by *P. glauca* or, less frequently, *P. tremuloides*, while *A. balsamea* trees are smaller diameter and shorter. It is unlikely that this represents a series of successional stages. Age distributions of stands within the study area show that most stands are even aged and that almost all of the trees in the canopy are recruited within a very narrow span of about 10 to 20 years after the last fire (Did and Swan 1971, chapter 1). However, it does suggest that younger stands growing in hillslope positions suitable for *A. balsamea* will look like white spruce or aspen/spruce mixedwood stands, particularly in satellite imagery. This could result in an underestimate of the amount of balsam fir forest and an overestimate of the amount of white spruce forest in the basin and may explain the differences seen between the actual vegetation and the vegetation predicted solely from the DEM. Incorporating time-since-fire into the predicted vegetation map corrected this problem by making areas predicted to be suitable for fir appear to be white spruce or aspen/white spruce mixedwood forest types.

The remaining confusion between the upland forest types in the actual and the predicted vegetation maps (Figure 2.5) is a result of the species compositions of adjacent classes blending into one another. Combinations of species abundances are a continuum rather than distinct communities (Whittaker 1967) as the classification implies.

### *Conclusion*

Moisture and nutrients are common gradients governing the distribution and abundance of vegetation in many upland vegetation types (Chabot and Mooney 1985, Barbour and Billings 1988). This study shows that, in the southern mixedwood boreal forest, two sets of geomorphic processes operating at different scales are the principal

processes controlling the spatial distribution of moisture, nutrients and vegetation across the landscape. Any attempt to understand the landscape patterns of vegetation must, therefore, address these processes. The generality of this finding needs confirming in areas of different geomorphic history and vegetation, but the fact that moisture and nutrient gradients are so common (Chabot and Mooney 1985, Barbour and Billings 1988) and that hillslopes and drainage basins are assembled in the same general way in many places (Hack and Goodlet 1960, Bull 1975, Shreve 1974) strongly suggests that this is a general relationship.

Hillslopes are assembled around channelways into drainage basins and the channelways, in turn, are assembled into highly organized channel networks. A substantial body of literature exists on the organization of channel networks on the landscape (see Abrahams' 1984 review). From this, it is apparent that the length of interior links in uniform environments and, hence, some of the spatial characteristics of basins are governed by two space filling considerations: (1) the tendency for channel networks to develop a uniform drainage density and (2) the requirement that their drainage basins fit together in space (Abrahams 1984). The space filling configuration of basins, it seems, is largely determined by the slopes of channels and valley sides. For example, in valleys where the side slopes are equal, both mean link length and the angle between the link and the divide have been correlated to the magnitude of the link and the magnitude of the downstream link it joins (Flint 1974, Abrahams 1980, Smart 1981). By linking the patterns of vegetation within drainage basins to geomorphic principles of space filling by

basins it may be possible to predict further landscape scale patterns of vegetation distribution and abundance.

A good understanding of the processes controlling the vegetation patterns puts us in a much better position to make predictions about vegetation change due to such things as climate change than does a statistical description of the past trends. It also allows us to see the impact of other processes, such as human disturbance, on specific systems.

## CONCLUSION

Ecologists have argued that an understanding of ecological processes and the ability to make predictions depend crucially upon studying the system at an appropriate scale (May 1993, Schneider 1994, Forman 1995). However, the issue of scale is seldom explicitly dealt with and many studies of landscape patterns of vegetation distribution instead concentrate only on the statistical description of the patterns (Hall et al. 1991, Ripple et al. 1991, Mladenoff et al. 1993, Vogelmann 1995 and others). This study reveals two scales at which landscape patterns of vegetation distribution are organized: the hillslope scale and the basin scale. Linking vegetation gradients to geomorphic processes of hillslope assembly provides a general explanation of why moisture and nutrient gradients are so prevalent in upland forests. Linking patterns of vegetation distribution down hillslopes to geomorphic principles of hillslope assembly into drainage basins shows that the proportion of vegetation types within basins tends to remain constant. Since the geomorphic processes that assemble hillslopes and basins seem to work in a similar fashion in many different environments, the vegetation patterns found here should be common patterns in many places. By examining the space filling considerations of drainage basins it may be possible to develop general geomorphic principles of how basins are laid out together across the landscape.. This may provide the basis for a succinct and efficient method of describing landscape patterns of vegetation distribution and abundance with only a limited knowledge of the land surface structure.

Knowing the general principles behind the spatial distribution of gradients on the landscape has far reaching applications in many branches of ecology. For instance, in

meta-population biology the spatial arrangement of patches of suitable habitat affects the dispersal of individuals between patches and, hence, the overall population dynamics (e.g., Hastings 1990, Taylor 1990, Murdoch et al. 1992, Kareiva and Wennergren 1995 and others). One of the main sources of mortality of boreal trees is large, stand replacing fires. Since some species must disperse into the burn from surviving patches of individuals, dispersal distance is of considerable interest. Linking the spatial distribution of suitable habitat to geomorphic processes may be useful in determining dispersal rates and may help explain the spatial and temporal patterns of dynamics observed. Furthermore, most applied research regarding the dynamics of a single species in complex landscapes entails detailed simulations that move individuals around in landscapes drawn from actual maps of habitat (e.g., Noon and McKelvey 1992, McKelvey et al 1993). Linking the spatial arrangement of habitat patches to geomorphic processes has the appeal that it offers general rules of habitat organization that should be common in many places.

Disturbance processes must also play a role in determining the landscape patterns of vegetation distribution and abundance. However, the relative contribution of each process is unknown. This study suggests that geomorphic processes are more important than disturbance processes in determining these spatial patterns. Techniques that partition the variation in species abundance data into independent components (e.g., spatial, environmental and undetermined) may be helpful in determining the relative contribution of disturbance and geomorphic processes in the future (cf. Bocard et al. 1992, Legendre 1993).

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