Geomorphic principles of terrain organization and vegetation gradients

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

Keywords: Allometric equation; Dynamics; Geomorphology; Hill slope; Landscape ecology; Mixed-wood boreal forest; Moisture gradient; Nutrient gradient; Ordination; Toposequence.

Abbreviations: PCA = Principal Components Analysis; RDA = Redundancy Analysis.


Introduction

One of the goals of ecology is to predict the spatial distribution and composition of species over the landscape. Plant ecologists have been successful at defining the changes in species abundance along abstract environmental gradients at the scale of the stand (1 m to 1 km) (e.g. Swan & Dix 1966; Whittaker & Gauch 1973; Peet & Loucks 1977; Lieffers & Larkin-Lieffers 1987; Allen & Peet 1990) and in testing ideas about the organizing principles responsible for these gradients (e.g. MacNaughton & Wolf 1970; Tilman 1988). Moisture and nutrients have consistently been the two most important gradients in explaining variation in plant distribution and abundance (Chabot & Mooney 1985; Barbour & Billings 1988). These gradients are abstract in that stands (specific geographic locations) are arranged along continuously changing values of moisture and nutrients. However, stands next to each other on the gradient need not be next to each other geographically. The difficulty has been in relating the organization of species along these abstract environmental gradients to the organization of the terrain in terms of physical processes of geomorphology and climate. In cases where the vegetation composition has been related to topography (e.g. slope, aspect and elevation) it has either been directed largely at improving the shortcomings of remote-sensed image processing (e.g. Frank 1988; Franklin & Wilson 1991; Peddle & Franklin 1991; Franklin 1992, 1995) or else the relationships have been qualitative (e.g. between moisture and topographic position on slope) (e.g. Day & Monk 1974; Niering & Lowe 1984; Lieffers & Larkin-Lieffers 1987; Baldwin et al. 1990). The qualitative nature of these relationships has hindered our ability to model and predict the landscape scale spatial distribution of vegetation.

Geomorphologists and hydrologists, on the other hand, have focused on quantifying the spatial distribution of moisture and nutrients across the landscape as well as the general principles of hill-slope assembly (Hack & Goodlet 1960; Bull 1975; Anderson & Burt 1976; O'Loughlin 1981 and others). Using distributed hydrological modeling, they have found that the spatial distribution of moisture and nutrients is often determined primarily by topographic position on the hill slope (Anderson & Burt 1977; Sinai et al. 1981; O'Loughlin 1981; Wood et al. 1988; Dawes & Short 1994 and others) and only secondarily by variation in soil hydraulic conductivity and rainfall (O'Loughlin 1981; Wood et al. 1988; Dawes & Short 1994). Furthermore, hill slopes...
show 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). However, geomorphologists and hydrologists have focused on the physical processes controlling the subsurface movement of moisture and nutrients down hill slopes (e.g. Harr 1977; Band 1993; Famiglietti & Wood 1991) and not on the response of plant species to different levels of these resources. Thus, questions about the general patterns of the spatial distribution of vegetation have remained largely unexplored from this perspective as well.

This study attempts to bring the two perspectives of ecologists and geomorphologists closer together by linking abstract vegetation gradients to hill-slope geomorphology. We start by establishing the main physical environmental gradients that control vegetation distribution and abundance in our study area. This study was conducted in the boreal forest, where species recovery after large, high intensity wildfires is also viewed as an important process controlling the variation in vegetation distribution (e.g. Dix & Swan 1970; Binkley et al. 1993; Christensen 1993; Johnson et al. 1998). In order to avoid confounding the physical environment gradients, we remove variation in species abundance with time since fire from the gradient analysis (cf. Johnson 1981). We then use allometry to describe patterns of hill-slope form and to relate changes in gradient position to changes in position on hill slope. Hill slopes that are underlain by the same substrate and are down-wasting at a similar rate are often described by the same allometric equation (Hack & Goodlet 1960; Bull 1975). Given that moisture and nutrient fluxes are controlled primarily by slope position (e.g. Kleiss 1970; Malo et al. 1974; Anderson & Burt 1977; Harr 1977; Sinai et al. 1981; Ciha 1984; Quinn et al. 1992), it should be possible to quantitatively relate moisture and nutrient gradients to the allometric equations that characterize hill-slope form. In doing so we characterize the distribution of these resource gradients, and of vegetation, on all hill slopes across 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.
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) (Fig. 1). This 4000-km² Park has a gently rolling topography with elevations ranging from about 500 m to 800 m a.s.l. The surficial geology is composed primarily of glacial till, but also contains significant organic, glaciofluvial and glaciolacustrine deposits. Till in this region is at least 160 m thick (Padbury et al. 1978). 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 characterized 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 annual precipitation ranges from 400 to 500 mm, of which about 70% occurs as rain.

The major disturbance in this region is large, infrequent, high intensity, lightning-caused fires which kill most of the canopy trees and understory vegetation. Large fires are controlled primarily by weather variables while variation in topography, substrate and micro-climate has less influence on fire intensity (Bessie & Johnson 1995). Low intensity ground fires account for a small proportion of the total area burned, only ca. 5% of the land area within the Park (J.M.H. Weir pers. comm.).

Vegetation sampling

Stands were selected in order to obtain as much variation in upland vegetation composition as possible, subject to the following criteria:

1. stands were > 4 ha 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.;
4. stands had no evidence of significant anthropogenic disturbance in the lifetime of the canopy trees.

In total, 101 stands were sampled with 97 stands located inside the Park and four 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 Ø at the bole base (only trees capable of forming a forest canopy fit this criterion);
2. Understorey shrubs and saplings: woody stems < 10 cm Ø, but > 1 m;
3. Seedlings: tree species < 1 m;
4. Herbaceous - non-tree species including mosses < 1 m.

In each stand, vegetation was sampled along two parallel transects 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 each stand. At each sampling point, samples were taken using the point centered quarter method (Cottam & Curtis 1956). In each quarter, the distance from the center point to the nearest tree and its diameter at the bole base were measured as well as the distance to the nearest understory shrub or sapling.

The relative density, relative frequency and relative basal area for each tree species were calculated from all 15 sampling points and combined into a synthetic importance value for each tree species (Curtis & McIntosh 1951). Relative density was calculated for understory species. The average relative density of seedlings in the stand was calculated from two 1-m² quadrats at each point. These quadrats were placed on opposite sides of the center point at a distance of 1 m from the center 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 cm 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 center. Pilot studies of these techniques showed that densities calculated for both the plotless and quadrat techniques had a standard error < 10% of the mean density and that the most numerous herb and moss species had a frequency of ca. 90% (cf. Curtis & McIntosh 1951; Cottam et al. 1953; Cottam & Curtis 1956).

For all stands within the Park, the time since last fire was determined from a time-since-fire map of the Park (Weir 1996). Ages on this map were determined from increment bores and disks taken from all stands > 4 ha in the Park. The map is accurate to within 1 yr 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, and topographic position on slope for each stand were assessed from 1 : 50000 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, top-slope, mid-slope, foot-slope 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 of mineral soil. 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 CaCl₂ and measured colorimetrically by flow injection analysis; cation exchange capacity was determined with 1 N BaCl₂ at pH = 8. Available phosphate and potassium were extracted with a modified Kelowna extractant. Available phosphate was determined by reaction with ammonium molybdate and measured colorimetrically, while available potassium was determined by flame emission spectrometry. Available potassium was also determined with inductively coupled plasma emission spectrometry along with sulphate, calcium, magnesium, and sodium. Soil water retention capacity at 33 and 1500 kPa 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 abstract environmental gradients

Two types of processes may be responsible for much of the variation in vegetation data: spatial processes, which produce variation in physical environmental conditions, and temporal processes, which produce variation in the time since disturbance. Determining the abstract environmental gradients is broken down into three steps that try to separate the effects of these two processes.

The first step in the analysis was to partition the data into recovery after fire (i.e. temporal) and physical environment (i.e. spatial) components in order to avoid confounding the ordination. The starting matrix for this partitioning, \( Y \), is the original \( n \times s \) matrix of stands (n) by species (s) in which the species abundance scores are synthetic 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 yr 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 time since the last fire of each stand can be used as a concomitant variable to partition the total variance in the species abundance data into recovery after fire and physical environment components using the equation:

\[
Y = X\Gamma + R
\]  

(1)

where \( X \) is an \( n \times 1 \) vector of stand ages, \( \Gamma \) is a \( 1 \times s \) vector of regression coefficients and \( R \) is an \( n \times s \) matrix of deviations from the regression (i.e. residuals). 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 (\( X\Gamma \)) can then be subtracted from the original samples by species matrix (\( Y \)). A number of different polynomial regression functions were tried but third order functions that were linear in the parameters (cf. Neter et al. 1990) and were not forced through zero gave the best visual fit. 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 (cf. 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 (\( X\Gamma \)) from the original data matrix (\( Y \)). The matrix \( R \) is called the physical environment matrix.

The second step in the analysis was to hypothesize gradients that explained most of the variation in the physical environment matrix. Principal Components Analysis (PCA) 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. Despite the limitations of PCA (e.g. Whittaker & Gauch 1973; ter Braak 1987), the analysis should be robust as the two ends of the gradients share many species in common, suggesting that β-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 about 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 in the parameters.

A redundancy analysis (RDA) was also performed on the physical environment 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 (ter Braak 1988). The environmental variables were standardized 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 physical environment PCA using a Spearman rank correlation to confirm whether or not the hypothesized gradients also explain the most variation in the samples by species data.

The third step in the analysis was to produce a recovery after fire gradient. The unpartitioned matrix, \( Y \), contains variation due to both time-since-fire and differences in physical environment. The physical environment matrix, \( R \), however, has the expected variation due to time-since-fire removed. A recovery-after-fire gradient was produced by performing a PCA on the original unpartitioned data (matrix \( Y \)) and subtracting the species loadings from their compatriots in the rotated physical environment (matrix \( R \)) principal components analysis (Johnson 1981). It is not appropriate to simply ordinate the expected species abundances with time (matrix \( X \)) 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, stand scores were calculated as in PCA. That is, 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.

**Linking abstract environmental gradients to terrain organization**

The stratigraphic surfaces in the study area are a result of the most recent continental glaciations that occurred during the Pleistocene epoch. Undifferentiated glacial till surfaces occupy extensive areas throughout the Park, especially in the upland regions, while glaciofluvial surfaces occupy a much less total area than till. Glaciolacustrine surfaces occupy only a very small proportion of the Park (Padbury et al. 1978).

The coefficients of the hill-slope allocentric equations change when the underlying surficial material is different. Therefore, before proceeding with the allocentric analysis of hill slopes, areas of different surficial material were delineated on the landscape. The allocentric analysis then proceeded separately for each area.

The identification of stratigraphic 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, 1 : 12500 black and white panchromatic aerial photographs and a surficial deposit map (Padbury et al. 1978).

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 were a total of 72 stands on glacial till deposits and 29 stands on glaciofluvial deposits.

Once the landscape had been separated into stratigraphic surfaces, individual slope forms within these areas were analysed. The path running perpendicular to the contour lines from the ridgeline to the channel defines the hill-slope profile. Hill slopes on the same type of stratigraphic surface are often described by allometric equations with the same coefficients (Hack & Goodlet 1960). Hill-slope profiles from first, second and third order streams in each of the different surficial material types were examined to see if they conformed to this behavior. Within each area of homogeneous surficial material, hill-slope profiles were picked that were close to sampled stands and within the same watershed or in a neighboring watershed. Hill-slope profiles that crossed over from one stratigraphic 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 hill-slope profiles that do not cross onto another type of stratigraphic surface. Therefore, several additional hill-slope profiles were examined that were not close to a sampled stand, but did reside entirely on a glaciofluvial stratigraphic surface. Twenty-three hill slopes on glacial till deposits and six hill slopes on glaciofluvial deposits were examined. Hill slopes on glaciolacustrine materials were not analysed because they occupy a very small proportion of the study area.

Hill-slope profiles were examined by plotting paths on 1 : 50000 topographic maps of the area (Department of Energy, Mines and Resources, Canada) and graphing the log fall from the ridgeline on the ordinate versus the log horizontal distance from the ridgeline on the abscissa. Hill-slope profiles were only analysed if a ridgeline could be delineated with reasonable accuracy from the map. Because the topography can be quite flat in places, delineating ridgelines from 1 : 50000 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).

The gradient position of a stand is characterized by its score on the moisture and nutrient gradients. If the gradient position of a stand is related to the stand’s position on slope, then it should be possible to characterize changes in gradient position down a slope by relating this change to the allometric equations. This provides a quantitative model of vegetation change down hill slopes.

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. 74 hill-slope profiles on glacial till deposits were measured. Only nine hill-slope profiles on glaciofluvial deposits could be measured so the effects of horizontal curvature were not analysed 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 were compared using analysis of covariance.

**Results**

The variation in the vegetation data was first partitioned into a physical environment component (matrix R), caused by spatial processes which produce variation in physical environment conditions, and a recovery after fire component, caused by temporal processes which produce variation in recovery after fire. Here, we present only those results derived after the data were partitioned.

**The moisture and nutrient gradients**

The first component of the physical-environment PCA for species has high loadings for *Picea mariana*, *Hylocomium splendens*, *Pleurozium schreberi* 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 has high loadings for *Pinus banksiana*, *Vaccinium vitis-idaea* and *Vaccinium myrtillus* at one end and low loadings for *Picea glauca*, and *Abies balsamea* at the other (App. 1, see http://www.opuluspress.se/jvs/arch.htm*).

**Fig. 2.** The stand scores and species abundances on the first two gradients of the physical environment principal components analysis. Each figure shows the abundance of a given species in stands on the ordination - with larger circles indicating higher abundance. The broken curve running diagonally across the ordination separates stands residing on undifferentiated glacial till deposits on the left from stands residing on highly sorted glaciofluvial deposits on the right. 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.
Fig. 3. Stand loadings on the Redundancy Analysis of the physical environment 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: NO₃ = nitrate; CEC = cation exchange capacity; pH = pH; Ca = calcium; Mg = magnesium; OMD = organic matter depth; Cond = conductivity; 1 : 2 soil : water mS/cm. Cond₂ = conductivity (saturation extract mS/cm); Na = sodium; SO₄ = sulphate; %Slope = % slope; AMC = available moisture capacity; K (meq/100g) = potassium (meq/100g); Asp = aspect; FC = moisture capacity at 33 kPa; WP = moisture capacity at 1500 kPa; K (ppm) = potassium (ppm); PO₄ = phosphate. A forward selection of environmental variables showed that using fewer variables does not alter the ordination significantly, however, for ease of interpretation we have included all of the variables on the diagram.

Stands on the ordination can be divided into clearly defined groups based on the type of stratigraphic surface on which they reside (Fig. 2). The first axis of the redundancy analysis (RDA) was correlated with variables related to soil texture which strongly reflect the change from till surfaces on the left to glaciofluvial surfaces on the right (Fig. 3). In particular, the first axis was strongly related to soil texture with stands on the left having loamy soil while stands on the right have 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 stratigraphic surface. 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) (Table 1). However, within each surficial group there were no obvious trends between the soil moisture capacities and the stand positions on the gradients (Fig. 4). 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

Fig. 4. Soil moisture capacity (% dry weight) at (a) 33 kPa, (b) 1500 kPa and (c) available moisture capacity for stands on the physical-environment PCA. 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. Average percent moisture, dry mass basis, at 33 kPa, 1500 kPa and the available moisture capacity (difference between 33 kPa and 1500 kPa measurements) with standard errors for glacial till and glaciofluvial deposits.

<table>
<thead>
<tr>
<th></th>
<th>Glacial till</th>
<th>Glaciofluvial</th>
</tr>
</thead>
<tbody>
<tr>
<td>n=62</td>
<td>n=26</td>
<td></td>
</tr>
<tr>
<td>33 kPa *</td>
<td>14.0 ± 0.8</td>
<td>10.9 ± 1.1</td>
</tr>
<tr>
<td>1500 kPa</td>
<td>8.3 ± 0.7</td>
<td>6.5 ± 0.9</td>
</tr>
<tr>
<td>Available moisture capacity *</td>
<td>5.7 ± 0.4</td>
<td>4.5 ± 0.4</td>
</tr>
</tbody>
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*Significant difference at P < 0.05.
ents of moisture and nutrients do explain most of the variation in the species composition data. In addition, the RDA-eigenvalues (axis 1: $l = 0.20$, axis 2: $l = 0.13$) were only slightly smaller than the PCA-eigenvalues (axis 1: $l = 0.31$, axis 2: $l = 0.14$) indicating that the two techniques accounted for similar variation.

Within each surficial group, stand position on the first and second physical environment principal components was also strongly related to topographic position on slope (Fig. 5). Stands located in the top left portion of each group tended to be at the tops of hill slopes, while stands at the bottom right tended to be at the bottom of hill slopes. Given the commonly observed relationships between soil moisture and topographic position on slope, this suggests that within each surficial group, the first principal component represents a moisture gradient with stands on the left being drier than stands on the right.

**The recovery-after-fire gradient**

The recovery after fire gradient gives a one dimensional distribution on both the species loading and stand score ordinations (Figs. 6 and 7). Species at the top left of the species ordination (Fig. 6) have abundance patterns that recover quickly after fire. Species at the bottom right have abundance patterns that recover slowly after fire. Notice this does not show successional change, but simply the change in species abundance. All species are present more or less immediately after the fire.

A high correlation (Spearman's $r^2$; axis 1=0.99, axis 2=0.84) between both components of the unpartitioned
Fig. 7. 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 Fig. 6). The dots on the small figures are the species abundances for the stand being pointed to. 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.

species ordination (PCA) and the rotated species physical-environment 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 because physical environmental gradients show much greater change in species abundance than do recovery after fire gradients which only show marked change in abundance early in recovery.

Linking abstract environmental gradients to terrain organization

It was first necessary to determine if the 23 allometric equations for glacial till surfaces were sufficiently similar to pool the data and construct a single equation that adequately describes most hill slopes on this type of surficial material. It was found that there was no significant difference in either the slope or intercept among 22 of the 23 allometric equations that describe hill-slope form ($P > 0.05$). We performed the same test for the set of six allometric equations on glaciofluvial surfaces and found no significant difference in either the slope or intercept for five of the six hill slopes ($P > 0.05$). The one significantly different hill-slope profile on till had a ridgeline that was difficult to locate on the map but it was kept in the analysis because the profile went directly through one of the sampled stands. The significantly different hill-slope profile on glaciofluvial material was found to be on a rare veneer of glaciofluvial material overlying till. The slope data were pooled for each of the two stratigraphic surfaces to produce two hill-slope equations. The two equations did not have significantly different slopes ($P > 0.05$), but the intercepts were significantly different from one another ($P < 0.05$) (Fig. 8). In both cases, the slopes were significantly different from zero ($P < 0.05$).

Once it was determined that most hill slopes on the same surficial material were described by the same equation, then the relationship between a stand’s distance from the ridgeline and its position on the moisture and nutrient gradients could also be determined. But, first it was necessary to know whether horizontal slope
curvature played any role. An ANCOVA, using horizontal curvature as a concomitant variable, was used to examine these relationships on glacial till surfaces. It was found that, for the relationship between the stand position on the moisture gradient and the distance from the ridgeline, there was no significant difference (\(P > 0.05\)) in the regression slope or intercept between the horizontally convex (i.e., noses or spurs) and flat slopes, so these data were pooled. The pooled regression line showed a positive relationship (\(r^2 = 0.46, n = 34\)) that is significantly different from zero (\(P < 0.05\)) (Fig. 9). 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 (\(r^2 = 0.18, n = 47\)) (Fig. 9).

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 (moisture gradient: \(r^2 = 0.56\), nutrient gradient: \(r^2 = 0.65\)) (Fig. 9).

**Discussion**

Within each surficial type there is a strong relationship between qualitative measures of topographic position on slope and gradient position (Fig. 5). On hill slopes cut into homogeneous surficial material, the primary determinant of soil moisture flux and storage is usually topography (Quinn et al. 1992), while variability in soil hydraulic conductivity and rainfall play only a secondary role (O’Loughlin 1981, 1986; Selby 1982; Wood et al. 1988). The lack of any obvious trend in soil moisture capacities with topographic position or gradient position on each stratigraphic surface (Fig. 4) indicates that this is true here. This suggests that, within each surficial group, the first principal component represents a moisture gradient. This is consistent with studies in many other forested systems where vegetation composition reflects topographic control over moisture and nutrient gradients (e.g., Day & Monk 1974; Johnson 1981; Marks & Harcombe 1981; Allen & Peet 1990; Busing et al. 1992).

In this region, three different stratigraphic surfaces have been left on the landscape through the action of glacial ice and glaciofluvial and glaciolacustrine melt.
water (Padbury et al. 1978). On each of these different surfaces, the geomorphic processes produce hill slopes 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). We estimated the parameters for two allometric equations that describe hill slopes on glacial till and glaciofluvial surfaces (Fig. 8). The intercept, or coefficient of steepness (Hack & Goodlet 1960), was significantly higher for hill slopes on glacial till surfaces, meaning that these hill slopes are steeper for any given distance from the divide than are hill slopes on glaciofluvial surfaces.

On both stratigraphic surfaces, moisture and nutrients increased significantly as distance down-slope from the ridgeline increased (Fig. 9). Again, this is consistent with topography’s strong control over moisture and nutrient flux and storage (Kliess 1970; Malo et al. 1974; Selby 1982; Wood et al. 1988; O’Loughlin 1981; 1986; Litaor 1992; Quinn et al. 1992). 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. This may be because these slopes accumulate a lot of water from a large up-slope area and are quite wet all the time. However, all of our plots on horizontally concave sites were also within ca. 900 m of the ridgeline. This is less than half of the maximum distance from the ridgeline for plots on horizontally convex and flat slopes. This may have impeded our ability to adequately detect stand relationships to distance from the ridgeline.

The general pattern of gradient and vegetation composition change down most hill slopes for this region is depicted in Fig. 10. Unlike previous stylized figures of vegetation change on hill slopes (Day & Monk 1974; Niering & Lowe 1984; Lieffers & Larkin-Lieffers 1987; Baldwin et al. 1990), this figure is derived from the allometric equations and the relationships between the stand positions on the gradients and their distances down-slope from the ridgeline. Since the geomorphic processes form hill slopes in the same general way in many environments (Hack & Goodlet 1960; Troeh 1965; Bull 1975; Nash 1980), this approach to characterizing the landscape scale spatial patterns of vegetation in terms of geomorphic principles should be applicable in many places.

In previous studies, the allometric description of hill slopes and the distributed modeling of moisture have taken place on terrain with considerably more topographic relief than central Saskatchewan (e.g. Hack & Goodlet 1960; Bull 1975). It is noteworthy, then, that allometric measurements of hill slopes and the quantitative relationships between gradients and distance from the divide works so well in this relatively flat study area. This is an important point from this study. It is quite likely that these relationships will be even stronger in areas of greater relief, strengthening the suggestion that this approach to understanding landscape scale vegetation patterns may be applicable in many different environments. It also suggests a reason why moisture and nutrients, as opposed to other gradients, are so common as controls of variation in vegetation distribution. Since hill slopes are a universal feature of landscapes, variation in moisture and nutrient values across the landscape will always be high.

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. For instance, vegetation composition could be linked to a dimension-less wetness function.
(O'Loughlin 1986; see also 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 up-slope catchment area. Unfortunately, the available digital elevation data required for distributed hydrological modeling such as this was of insufficient quality to accurately model the spatial distribution of moisture flux and storage on the landscape in this region. Again, however, in areas of greater topographic relief, relating vegetation gradients to process oriented moisture variables should be feasible.

On any given stratigraphic surface species can only move to higher or lower topographic positions to find more suitable environmental conditions. Why then does the gradient analysis indicate that two gradients, moisture and nutrients, are the most important gradients controlling the variation in vegetation distribution rather than one gradient of topographic position on slope? The most likely explanation for this is that the rates of change of moisture and nutrients down the hill slope vary independently of one another over time. For example, climate change may alter the average amount of precipitation falling in the study area resulting in a different rate of change in moisture down the hill slope. However, the rate of change in nutrients down the hill slope, which depends upon weathering of the parent material and leaching, may be slower to react to the climate change. Thus, the old combinations of moisture and nutrients have not simply moved to higher or lower topographic positions on the hill slope, but instead, entirely new combinations of these gradients are presented. It is unlikely that moisture and nutrients are equally limiting at all times among different species, therefore, species continue to respond to both gradients independently in order to deal with these gradient changes over time.

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

In retrospect, it may have been preferable to identify the different stratigraphic surfaces first and then sample enough sites on each surface to analyse 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.

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

Recent work in surface hydrology has shown that the landscape can be divided up into a series of hill slopes (Band 1989; Wood et al. 1988; Band 1991). The hill slopes can then be related to the planimetric form of the river channels to predict the moisture and carbon flux and storage of watersheds (Wood et al. 1988; Band 1993). Similarly, by characterizing vegetation change down hill slopes and relating that change to the planimetric form of the channel network, it should be possible to derive a statistical description of the landscape scale vegetation distribution patterns. These patterns will be couched in the geomorphic processes that shape the landscape. A similar argument can be made for the relationship between the recovery after fire gradient and time and the pattern of time since last fire across the landscape.

Acknowledgements. This research was supported by Environment Canada’s Environmental Innovation Program, a Natural Sciences and Engineering Research Council operating grant and the NSERC Sustainable Forest Management Network of Centres of Excellence. We thank Prince Albert National Park, particularly Greg Fenton, Paul Tarlton and Jeff Weir, for their cooperation and logistical support in the field and we thank James Clark, Deborah Clark, Robert Knox, Kiyoko Miyaniishi, and Christian Lemay for their critical and useful comments on this manuscript. We also thank Sylvia Chipman, Caren Dymond, Monica Kidd, Madeleine Yarranton and Marlene Wong for their assistance in the field and the lab. S.R.J. Bridge also thanks Carolina Caceres for her support.
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Received 31 August 1998; Revision received 25 February 1999; Accepted 18 April 1999.
Coordinating Editor: P.S. White.