THE UNIVERSITY OF CALGARY

Redefining species tolerances in a subalpine forest by using energy and moisture processes

by

Caren Dymond

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE

DEGREE OF MASTER OF SCIENCE

DEPARTMENT OF BIOLOGICAL SCIENCES

CALGARY, ALBERTA

JUNE, 1998

0-612-34958-6

Abstract

Physical process models define species tolerances based on resources that plants use. Energy available (e_a) and moisture available (m_a) models defined two gradients in the southern Canadian Rockies. I estimated e_a using temperature and solar radiation variation on the terrain, as input to photosynthesis. I estimated m_a using climate water flux due to elevation as input to hillslope drainage. These physical gradients correlated to Correspondence Analysis axes (r^2=0.45 for e_a and axis 1, r^2=0.27 for m_a and axis 2). The advantage of tolerances defined by resources plants use, is that it is possible to identify the separate niches of species that co-occur. For example, trembling aspen tolerances are indistinguishable from many other tree species in ordination studies, but on the physical gradients trembling aspen clearly occupies the highest e_a sites. On the terrain, these sites have no, or a SE aspect and are at low elevations. The spatial heterogeneity of the landscape is defined by the range of e_a and m_a gradients. The spatial heterogeneity of m_a is greater, 8.47 to 13.11 $m^2.y^{-1}$, at lower elevations compared to 15.9 to 17.5 $m^2.y^{-1}$ at higher elevations because of the greater variety of hillslope shapes and lengths. The higher elevation hillslopes are wetter because of greater climate input. Tree diversity increased as a result of this increased spatial heterogeneity of moisture. The e_a and m_a defined tolerances are also used to predict the spatial patterns of vegetation in a map, (66% accuracy) and link that pattern to the structure of the terrain. Ecosite systems that use the gradients of e_a and m_a are shown to be more useful for management than ordination studies based on judgement and categorical environmental variables.

Acknowledgements

I would like to acknowledge Ed Johnson for his powerful guidance and support. I would also like to acknowledge Kara Webster and Tara Tchir for their substantial contributions to my data set, and helping me improve my writing, and my running. My other lab mates, namely Garland Jonker, (the best office mate I could ask for), Simon Bridge, Sheri Gutsell, Sylvia Chipman, and Ceddy Nash were also very helpful and supportive. James Thomson has been a wonderful friend helping me grow and calm the stress in my life. Jason Snider has gifted me with countless walks to contemplate life, the universe and everything. Its been fun and challenging to travel through my masters parrallel with my sister Pam Reece. I have treasured the support from Shelley Dayman, Ian Hamilton and Sarah Shima.

I would like to thank the Kananaskis Field Stations, Challenge Grants in Biodiversity and NSERC for supporting my research. I would also like to thank the Department of Biological Sciences for their personal financial support through GTAs.

Dedication

To my parents, thank you for your love.

My Mom's passion for life inspires me still.

My Dad's committment to education helped focus my drive.

Table of Contents

List of Figures

List of Tables

Introduction

Geomorphic and climate processes control the distribution of temperature, solar radiation, and water on the landscape (Carson and Kirkby 1972). These, in turn, affect plant growth and survival (Jarvis and Leverenz 1983, Stephenson 1990, Larcher 1995). Energy and moisture process models allow us to redefine the common mountain gradients of climate (elevation) and moisture (Whittaker 1973, La Roi and Hnatiuk 1980, Wentworth 1981). The result is a mechanistic link between the structure of the terrain and species tolerances. As a result, redefining species tolerances in terms of energy and moisture processes leads to a better understanding of patterns of species composition, spatial heterogeneity and diversity.

The definition of a species tolerance curve hinges on the definition of the resource gradient (Hutchinson 1957). Traditionally, mountain plant distributions have been correlated to elevation and topographic indices (Whittaker 1973, La Roi and Hnatiuk 1980, Wentworth 1981, Peet 1981, Allen and Peet 1990). The nature of elevation and topographic indices means that they cannot answer questions about how terrain controls the spatial heterogeneity of resources and the community patterns. Elevation is not seen as affecting plants directly, but rather as correlated to climate processes (Whittaker et al. 1968, Zobel et al. 1976, Wentworth 1981). As well, topographic indices have two limiting characteristics. They are categorical and should not be used to calculate rates of species turnover (beta diversity), since a moisture ranking of 4 is probably not twice as wet as a ranking of 2. The topographic indices are also constructed from judgements of site moisture status where again a moisture ranking of 4 is probably not twice as wet as a ranking of 2. The relative, rather than absolute gradients make it difficult to define distributions of community parameters such as species richness and beta-diversity.

This study seeks to test if plant species tolerances can be defined using simple models of energy and moisture processes developed by hydrologists, physical geographers, and physiologists (e.g. Beven and Kirkby 1979, Running 1984). Traditional climate and moisture gradients are more precisely defined by temperature, solar radiation, potential evapotranspiration, precipitation, and drainage. The energy available for plant growth and reproduction is approximated using photosynthesis to scale the importance of temperature and solar radiation (Jarvis and Leverenz 1983). Precipitation, potential evapotranspiration and drainage processes define the relative amount of water available to the plants for biochemical processes and structural support (Scheidegger 1991). The available moisture is the result of climatological processes input to the hillslope processes.

One advantage of physically based models is that the link between the structure of the terrain and the gradients of abiotic resources is explicit. For example, the complexity of the terrain should determine the length of the moisture gradient because the terrain controls the drainage of water. The longest gradient should occur where there is the greatest variety of hillslope shapes and lengths to control drainage (Carson and Kirkby 1972, Beven and Kirkby 1979). The gradient length will define the spatial heterogeneity of moisture on the terrain. One consequence is that the greatest spatial heterogeneity should lead to the greatest species diversity because there is a greater range of resources to be divided up between species. Also, if the structure includes mountains, then regional gradients in temperature, solar radiation, precipitation, and evapotranspiration will correlate to elevation change (Hewitt 1972).

This paper presents the energy and moisture models adapted from the literature to characterize the resources on the structured landscape. Field data of subalpine plant species abundances from the Kananaskis and Spray valleys of the south-eastern Canadian Rockies are used to define tolerances on the modelled resources and the terrain. A vegetation cover map was made to show the power of using these species tolerances to predict spatial patterns of species composition. The modelled resources and species tolerances were used to show the effect of spatial heterogeneity on diversity. The energy and moisture gradients are also compared to traditional indirect and direct ordination approaches to understanding species composition. An ecosite typing shows how the tolerances on the energy and moisture gradients can be applied.

The Models

The physical models are designed to characterize resources as they are controlled by the terrain and climate. The equations are simple so they have easily measured input terms and intuitively understandable behaviour. The energy and water resources are independent of species specific interactions with the environment, so that definitions of species tolerances do not depend on a priori knowledge of species distributions. The resulting variables are continuous and measurable.

The landscape

Every landscape is a set of hillslopes with varying lengths, steepness, and shapes (Carson and Kirkby 1972). A hillslope is a three-dimensional construct of slope profiles that all end in the same stream course. A slope profile is the two-dimensional line that a drop of water would follow from a ridge to a stream course (Carson and Kirkby 1972). A profile usually consists of an upslope convexity from erosion, a concave base, and the main slope in between that reflects weather-limiting erosion processes. When contours are not parallel, converging profiles create wet areas, and diverging profiles create dry areas (Hack and Goodlett 1960, Carson and Kirkby 1972). Hillslope shapes are influenced by the geomorphic processes that created them. For example, erosional landforms tend to be concave, whereas depositional landforms tend to be convex. Steeper angles cause water to flow faster, resulting in less percolation through the substrate and drier sites (Gerrard 1981).

The way the terrain of a landscape is assembled creates the regional spatial pattern of abiotic conditions. Mountainous terrain has steep hillslopes and a steep network of streams (Hewitt 1972). This assemblage pattern results in climatological processes changing within the watershed, creating a regional temperature gradient from warmer at lower elevations to colder at higher elevations (McGregor 1984). The cooler temperatures result in more condensation and therefore more total precipitation at higher elevations. Cooler temperatures also reduce evapotranspiration rates. At higher elevations there is also less atmosphere above the site, so less solar radiation is absorbed by the atmosphere. Therefore a greater proportion of solar radiation reaches the ground at higher elevations (Nikolov and Zeller 1992). Southern aspects and gentler slope angles, especially in mountainous terrain, also have higher solar radiation input and duration. The variation of resources on the terrain can be defined with models of energy and moisture processes.

Energy available for growth and reproduction

Temperature and solar radiation place fundamental limits on plant physiology (Jarvis and Leverenz 1983, Larcher 1995). A photosynthesis model scales the relative impact of temperature and solar radiation into an energy term that is appropriate to plant physiology. Running (1984) has developed a model that accurately predicts gross photosynthetic rates for conifers. This model can be modified to characterize an energy resource with only temperature and solar radiation. The result is the amount of energy available (e_a) to plants, as controlled by the terrain. The equation for energy available in g$\cdot$ cm^{-2} leaf area$\cdot$ s^{-1} is:

$$e_a(x,y) = \frac{\Delta CO_2 \cdot g_m \cdot k_{max}}{(g_m + k_{max})} \qquad (1)$$

where x,y is a site location, ΔCO_2 is the carbon dioxide gradient across the leaf surface (g$\cdot$ cm^{-3}), which is taken as a constant (Running 1984), g_m is the mesophyll conductance (cm$\cdot$ s^{-1}), and k_{max} is the leaf conductivity of water (cm$\cdot$ s^{-1}). The mesophyll conductance depends on ambient temperature (which decreases with elevation) and solar radiation input (which varies with elevation, aspect and slope angle). The predawn water potential and relative humidity of the original model are eliminated to separate the effects of water from the effects of temperature in leaf conductivity (k_{max}). The leaf conductivity (k_{max}) is then affected only by the temperature change with elevation.

The behaviour of Eq. 1 in this study showed that the energy available decreases regionally with elevation. This is the result of decreasing temperatures with elevation outweighing the effect of increasing solar radiation with elevation. Also, solar radiation change with aspect has less effect on the amount of energy available when compared to elevational change.

Moisture available

The water available to plants is determined by climatological scale processes of precipitation and potential evapotranspiration (Thornthwaite 1948) and hillslope scale processes of catchment areas and slope angles (Beven and Kirkby 1979). Thornthwaite's model includes elevation, monthly temperatures, and latitude affect on sunlight duration to determine climatological effects of water availability. The climate water flux model is:

$$c(x,y) = p - pet \qquad \textbf{(2)}$$

where input of water to the site c, (m. y^{-1}) is measured by precipitation (p) and the loss of water is measured by potential evapotranspiration (pet). In this study, precipitation and potential evapotranspiration vary only with elevation, since latitude does not change significantly within the study area. More complex potential evapotranspiration models that incorporate solar radiation, humidity, wind, or plant parameters usually give higher estimates, but follow the same trends between different locations as Thornthewaite's (1948) model (McKenney and Rosenberg 1993). The behaviour of Eq. 2 shows an increase in climate water flux as elevation increases, since inputs increase and losses decrease.

The local hillslope processes distribute the water input from the climate water flux (Eq. 2). The model of hillslope wetness is:

$$w(x,y) = \ln\frac{A}{\tan\beta} \tag{3}$$

where β is the slope angle in the site and A, the area drained ($m^2 \cdot m^{-1}$), is the size of the area that collects the water that flows through one meter of contour length (Beven and Kirkby 1979). This model of hillslope processes has been shown to be effective, despite its simplicity and the assumption of uniform ground water loss (Beven et al. 1984, Wolock et al. 1989).

The behaviour of Eq. 3 shows that wetness is lowest on ridges because there is so little area drained, despite the flat angles. Further down a hill slope the area drained increases, but so does the slope angle, so the wetness increases slightly. At the bottom of a hill there is a large area drained, and flat slopes, so the wetness is highest. I did not use more detailed models that include soil texture and variation in the water flux within the drainage area (e.g. O'Loughlin 1986) because I lacked precise data.

To get a complete picture of the water available to the plants, the local hillslope processes (Eq. 3) had to be adjusted to take into account the impact of larger scale climatological processes (Eq. 2). The simplest scaling relationship is to multiply the site wetness (w) by the site climate water flux (c) so:

$$m_a(x,y) = w \cdot c \tag{4}$$

where the moisture available (m_a) has the units $m^2 \cdot y^{-1}$. The moisture available is a physically based index which is correlated to the actual moisture available to the plants. It is simple to calculate and uses measurements that do not require qualitative judgements.

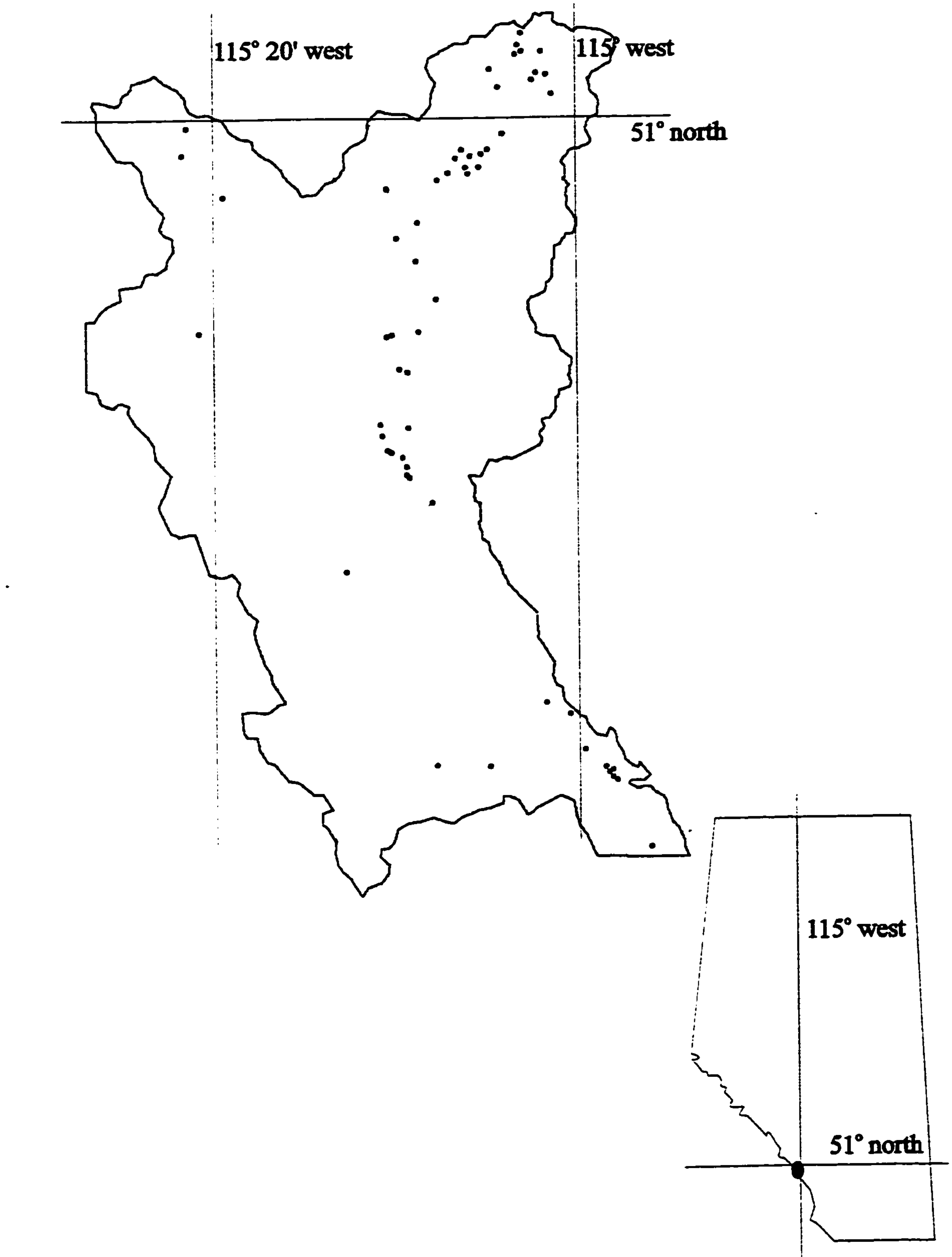
The behaviour of Eq. 4 reflects the interplay of the two processes. Steep, short, high elevation slopes have more moisture available than long, low elevation slopes because of the variable climate input. The bottoms of long hillslopes have more moisture available than the steep, short sites at the same elevation.

Study Area

Fifty-eight study sites were located in the Kananaskis River and Spray Reservoir watersheds, located in the front ranges of the Southern Canadian Rockies (Fig. 1). The watersheds occupy 1184 km^2 of high relief mountains, with the outflow from the valley at 1350 m a.s.l., and the mountain peaks between 2400 and 3000 m a.s.l..

The structure of the front ranges is defined by a series of thrust faults that resulted in parallel ridges of older (Palaeozoic) limestone over younger (Cretaceous) sandstone

FIG. 1. Location of the study area in Alberta and location of the stands in the study area.


115° 20' west
115° west
51° north
115° west
51° north

and shale. Erosional processes on these bedrock layers formed valleys in the softer sandstone and shale, leaving the more resistant limestone as ridges (McMechan 1988).

Extensive Pleistocene glaciation and continuing glacial, freeze-thaw, mass transport, and alluvial processes created the landforms of the Kananaskis. Landforms characteristic of glacial processes include: cirques, angular ridges, U-shaped valleys, morainic ridges and till sheets. Freeze-thaw forces erode the bedrock, resulting in cliff faces above colluvial deposits (Milus Tress Barron Ltd. 1976). The majority of the watershed area consists of active valley slopes with high rates of erosion. The slopes are mantled with colluvium from a wide variety of parent materials that overlays rock weathered in place or till deposits (Bayrock and Reimchen 1977). Actively eroding gullies possess steep, irregular longitudinal profiles and generally V-shaped valleys with steep side slopes. The surficial geology of the lower Kananaskis River valley bottom consists of coarse alluvium deposits due to large debris loads and underfit stream size (Milus Tress Barron Ltd. 1976, Bayrock and Reimchen 1977). Alluvial and debris fans frequently interrupt the braiding and terraces of the main river.

Climate in the Kananaskis river watershed is a transition between the Continental climate and the Cordilleran climate. The average precipitation regime has a winter maximum (22.3 mm) and a summer maximum (102.6 mm), with minima in late winter and again in autumn (Janz and Storr 1977). The annual temperature profile follows a typical pattern for this latitude, with the lowest average temperatures in January (-6 °C), and the highest in July (14 °C) (Kananaskis Field Stations, 1410 m a.s.l.).

The climate also changes spatially with elevation (Storr and Ferguson 1972). The average annual precipitation increases linearly from 474.5 mm at 1400 m to 1110.5 mm at 2400 m, based on an eight-year study of a sub-basin in the watershed. Data from the same study showed that average of the July maximum daily temperature decreases from 21.9 °C at 1400 m to 14.2 °C at 2400 m respectively (Janz and Storr 1977).

Large sized fires that are high in intensity and re-occur within the lifetime of post-fire generation trees dominate the disturbance regime in the subalpine forest (Johnson and Larsen 1991). The frontal fire intensities are so high that all vegetation is burned independent of forest type or elevation, therefore, the same disturbance rate occurs throughout the study area.

Human disturbances have had little impact on most of the study area (Johnson and Fryer 1987). Logging occurred in limited parts of the Kananaskis valley from 1886 - 1947. This disturbance effectively ended when the leases were burned by a large fire in 1936. The logging did not significantly impact species composition. Development in the study area is restricted to recreational facilities, hydroelectric dams and reservoirs.

The subalpine forest is primarily coniferous and ranges in elevation from 1350 to around 2350 m. Lodgepole pine *(Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.), white spruce *(Picea glauca* (Moench)Voss), white spruce/Engleman spruce hybrids (*Picea engelmanni* x *Picea glauca)* and trembling aspen (*Populus tremuloides* Michx.) are the predominant trees in the lower subalpine. Engelman spruce *(Picea engelmanni* Parry ex. Engelm.), and subalpine fir *(Abies lasiocarpa* (Hook.)Nutt.) with some subalpine larch *(Larix lyallii* Parl.) at tree- line, are the predominant trees in the upper subalpine. The most common understorey shrubs are buffaloberry (*Shepherdia canadensis* (L.) Nutt.), and willow (*Salix* sp.). Common herbaceous plants are asters and erigerons (Compositae), strawberry (*Fragaria virginianum* Duchesne), twinflower (*Linnaea borealis* L.), feather moss (*Pleurozium schreberi* (Brid.) Mitt.), heart-leaved arnica (*Arnica cordifolia* Hook.), *Peltigera apthosa* (L.) Wild. and *Cladonia* species. Steep gully walls were too small to be included in this study, but are often occupied by dwarf adult trees of *Populus balsamifera* (L.), *Pinus contorta* or *Pinus flexilis* (James).

Methods

The methods are organized as follows: first is the model calculations for the sites in the study area, next is the field sampling of plant abundances and environmental descriptors at the same sites, and finally the analyses. The analyses section describes the methodology of an ecosite system, diversity calculations, mapping, indirect ordination, and direct ordination (using the environmental descriptors).

Model Calculations

The location (x,y) of each site was measured with a global positioning system that was differentially corrected for an accuracy within five meters. The stands were identified by their location on a 30 m resolution (or 30 x 30 m pixel size) Thematic Mapper satellite image. The image was taken on August 8, 1984, with a sun elevation of 49.3° and azimuth 138.1°. The image was geocorrected to the Universal Trans-Mercator grid, and a 25 m digital elevation model (DEM) was registered to it (PCI Inc. 1996).

Energy available (e_a)

The energy available (Eq. 1) was calculated using data for an average July day because July has the highest maximum daily temperatures in the course of a year. The energy available for a site was the average of the values for the pixels sampled along the vegetation transect (see "Field Sampling").

The carbon dioxide gradient from the atmosphere to the carboxylation site of the leaf (ΔCO_2) is negligible, so was set at the constant 6 x 10^{-6} g$\cdot$ cm^{-3} following Running (1984) . The mesophyll conductance (g_m) was calculated according to Running's (1984) model:

$$g_m = \frac{I - I_o}{I - I_{0.5}} \cdot (0.0182 + 0.0105 \cdot T_J + 0.000194 \cdot (T_J)^2) \qquad \textbf{(5)}$$

Where I is the incoming radiation from Nikolov and Zeller's (1992) model (described below), I_o is the constant light compensation point where net photosynthesis is zero, measured as 0.001 W$\cdot$ cm^{-2} in Running (1984), and $I_{0.5}$ is the irradiance at which g_m is half of its maximum value, measured as 0.0225 W$\cdot$ cm^{-2} in Running (1984). The remaining values within the equation are empirically fitted regression coefficients for a variety of conifers (Running 1984). In this study, the input air temperature (T_J) for Eq. 5 is the mean July maximum temperature as calculated in Eq. 7. The relationships were not varied for deciduous species because that would require a priori knowledge of the deciduous species distributions.

The incoming shortwave radiation for an average July minute was calculated using the DEM and Nikolov and Zeller 's (1992) algorithm for estimating solar radiation received by mountain slopes. The calibration used hourly solar radiation data from the Kananaskis Field Stations. Nikolov and Zeller 's (1992) model uses elevation, aspect and slope angle, which vary considerably within the study area, as well as latitude and date. The horizon was set at 15 degrees to compensate for the mountain shadows on the predominantly N-S valley. The solar incidence angle and solar altitude angle were calculated for each daylight hour of an average July day, then averaged across the hours. The incoming solar radiation was then calculated for an average July day. The daily solar radiation was divided by 600 to convert to minutes, because the average solar input length for a July day is 10 hours (based on a 15 degree horizon).

The leaf conductivity, in cm. s^{-1}, as a result of the maximum July temperatures (T_J) from Eq. 7, was:

$$k_{\mu\alpha\xi} = k_{\sigma\alpha\tau} + (k_{\sigma\alpha\tau} \cdot i \cdot (T_{\vartheta} - 10)) \qquad \textbf{(6)}$$

where k_{sat} is the measured leaf conductivity when conifers are not water stressed (0.15 cm. s^{-1}) and i is the change in leaf conductivity due to air temperature (Running 1984). When the air temperature is above 10 °C, leaf conductivity has been measured to increase modestly (i = 0.003 cm . s^{-1}. °C^{-1}). k_{max} is the maximum leaf conductivity possible at a given elevation because of the saturated starting condition and the highest input temperatures possible for a year.

The mean July maximum temperature in degrees Celcius (T_J) input into Eqs. 5

and 6 changes with elevation in meters (E) such that:

$$T_J = 32.7 - 0.00771 \cdot E \quad (7)$$

where E is the elevation from the DEM. This linear regression relationship was determined over eight-years for a sub-basin of the Kananaskis watershed. The study used seven weather stations ranging from 1370 m to 2285 m (Janz and Storr 1977).

Moisture available (m_a)

The moisture available (Eq. 4) was calculated on an annual basis because the known relationship between precipitation and elevation in the study area was for an average year, and other climate data were not available across the elevation range in the study area.

Precipitation (mm$\cdot$ y^{-1}) values for Eq. 2 were calculated from:

$$p = -415.9 + 0.636 \cdot E \quad (8)$$

Where E is average elevation (m) of the site from the DEM. This relationship was empirically determined for a sub-basin of the Kananaskis (Storr and Ferguson 1972). The eight-year study used eleven precipitation gauges at elevations ranging from 1780 m to 2285 m.

The potential evapotranspiration (cm$\cdot$ month^{-1}) for Eq. 2, were calculated as:

$$pet_m = c \cdot (T_m)^a \quad (9)$$

Where pet_m is for a month (m). Coefficients c and a vary with latitudinal affects on sunlight duration and mean monthly temperatures, and were obtained from Thornthwaite (1948). T_m is the mean monthly temperature at the site's elevation, in degrees Celcius. T_m was calculated using the long term monthly mean temperatures of the Kananaskis Field Stations, the adiabatic lapse rate (loss of 6 degrees per thousand meters elevation gain) and the average elevation of the site from the DEM. Note that Janz and Storr's (1977) local empirical relationships were not used because they were only available for July and January, and the regression slopes for these two months differ.

The monthly potential evapotranspiration estimates were summed to give the annual value (pet), and multiplied by 10 to convert to millimeters. Once the annual potential evapotranspiration (Eq. 8) was subtracted from the annual precipitation (Eq. 7), it was converted to meters by dividing by 1000.

The area drained values for the wetness model (Eq. 3), were based on an accumulation algorithm where the water from each pixel (30 m x 30 m on the DEM), flows into the lowest elevation pixel of its eight neighbouring pixels (Jenson and Domingue 1988, PCI Inc. 1996). The first step was to use this accumulation algorithm to determine the upslope area of each pixel by calculating how many pixels drained into each pixel. This was done by tracing the flow of water upslope from the pixel in question, until the point where the pixels in the path are no longer the lowest in a neighbourhood and water ceases to flow into them. The second step was to calculate the median of the accumulation within a site. This step was necessary to smooth out some of the high variance in accumulation that is a consequence of all of the flow from a pixel going into a single neighbouring pixel so one pixel may have 5 pixels draining into it but its neighbour may have only one pixel draining into it (Tarboton 1997). In the third step, the value one was added to the median, so that each site had at least its own climate water flux as input. In other words, the minimum upslope area was one pixel. The last step was to convert from pixels to meters, by multiplying the number of pixels by the area of a pixel (900 m^2), and then dividing the product by 30 m, the length of a pixel edge. The result was the area drained per meter contour length for a site; assuming that water flows out of a pixel edge.

The $\tan \beta$ values for Eq. 3 were the mean of the $\tan \beta$ for each pixel in a site. The angle of the slope (β) was calculated as the angle of the plane formed by the vector connecting the left and right neighbour pixels, and the vector connecting the upper and lower neighbours of the pixel in question. Finally, to calculate the annual absolute moisture (Eq. 4), the climate flux (Eq. 2) was multiplied by the wetness value (Eq. 3).

Field Sampling

Selection criteria for the 58 forest stands was: 1) as wide a range of species and habitats as possible, 2) only stands greater than three hectares, 3) visual homogeneity in height, diameter, and species, 4) lack of standing water, 5) absence of human disturbance (i.e. no cut stumps and a minimum of 30 m from trails or roads).

In each stand, vegetation was sampled along a transect with fifteen points which were fifteen or thirty meters apart. This transect encompassed up to 9 pixels on the TM image. Canopy trees, saplings and shrubs were sampled with the point centered quarter method (Cottam et al. 1953). Canopy trees (≥7 cm diameter at base) were sampled for frequency, density and db. A tree is defined as a species that could grow to the height of the canopy in the study area. Saplings (trees <7 cm diameter at base and ≥ 1 m tall) and shrubs (non-trees ≥1 m tall) were measured for their density. At each point, herbs, (non tree species <1 m tall), were sampled for their presence in two 25 x 25 cm quadrats. Seedlings, (tree species <1 m tall) were also sampled for frequency in two 1 x 1 m quadrats. Importance values were calculated as: the average of relative frequency, relative density and relative basal area for canopy trees; relative densities of understorey sapling trees and shrubs; and absolute frequencies for herbs and tree seedling (Greig-Smith 1983). Voucher specimens are stored in the herbarium at the Kananaskis Field Stations.

Descriptive environmental measures were collected at each stand. Elevation was measured with a global positioning system that was differentially corrected for an accuracy within five meters. Soil pits were dug at points one and eight along the transect, and a constant volume (3 x 3 x 15 cm) of mineral soil was taken immediately below the duff. The samples were mixed and air dried. The depth of organic matter was measured and averaged. Soil texture was classed as "rocky" when the volume of the coarse material (>2 mm) was > 50%, as "less rocky" when the volume was 20-50%, and "not rocky" when the volume was < 20% (modified from Kalra and Maynard 1991). Plains Innovative Laboratory Services, Saskatoon, Saskatchewan analysed the fine fraction for texture using the feel method, classes were: sand, sandy loam, loam, clay loam, and organic by. This company also analysed the soil chemistry from 32 randomly selected stands. A 1:2 soil:water suspension was used to measure pH, which was later converted to hydrogen ion concentration. Available NO_3-N was extracted with 0.001 M $CaCl_2$, cation exchange capacity was determined with 1N $BaCl_2$ at a pH of 8, and extractable P and K were determined with a modified Kelowna extractant. Extractable K, SO_4-S, Ca, Mg, and Na were determined with inductively coupled plasma emission spectrometry.

On topographic maps (1:50,000) the slope angle was measured as the vertical fall between the contour lines on either side of the stand, divided by the horizontal length of the fall line that goes through the stand. Aspect was the perpendicular to the direction of the fall line. The aspects were divided into 45 degree classes and put into the ordination analyses as nominal variables. Position on slope 1, the minimum, occurred where slope angle <0.2 and there were no contour lines above the stand (ie. ridge). Position on slope 3 occurred where slope angle > 0.4 (i.e. steep side slope). Position on slope 5, the maximum, occurred where slope angle <0.2 and there were contour lines above the stand (i.e. bottom of the hillslope). Surficial geology was determined from Bayrock and Reimchen's map (1977).

Analyses

Overlapping tolerance curves on traditional ordination axes are often used to group species into ecosite types. The modelled resources offer measurable gradients to improve the definition of the tolerances, and therefore improve ecosite systems. An ecosite typing was completed for the Kananaskis in order to compare it with a traditional ecosite system that is based on ordinations. The comparison was assessed on the usefulness for field work. The indicator species used by Archibald et al. (1996) were used to define vegetation classes in the Kananaskis. The tolerances of the indicator species on the energy available and moisture available gradients were overlain on each other, and the arbitrary areas of overlap were included in the polygons shown in the Discussion. Ecosite f - thimble berry (lodgepole pine canopy) was excluded because it occurs in the extreme southern part of the province. Ecosite g - dwarf birch/tufted hair grass (dwarf birch canopy) and ecosite h - horsetail (Engelman/white spruce canopy) were excluded from the comparison because they occupy saturated soils, which were not sampled in this study.

Diversity is also a consequence of overlapping species tolerance curves. Tree richness in a stand was measured as the number of species present in the canopy trees sampled along the transect. The greater the number of tolerance curves that overlap, the greater the species richness. The beta-diversity was first determined by ranking the stands along each gradient. Next, was the absolute value of the number of species in a stand that were different from the species that occurred in the previous stand on the gradient. The beta-diversity increases when there are partially overlapping tolerance curves, or when species have narrow tolerance curves.

The mapping of vegetation spatial patterns by remote sensing usually uses characteristics such as spectral signature and attributes such as elevation which are divorced from species tolerance curves (Avery and Berlin 1992, Franklin et al. 1994). Consequently, the resulting maps are not very helpful when trying to understand spatial patterns of landscapes. The energy and moisture models employ the physical terrain captured in the DEM and the established tolerance curves on the gradients to predict the spatial pattern of the vegetation. In order to show how this physical approach can be used to predict vegetation spatial patterns, the DEM and Eqs. 1 to 9 were used to define the energy and moisture resources for every pixel in the study area. Since the mapping was done on a per pixel basis, energy and moisture values for a site were no longer useable. As a result the differences from the calculation of the resources described above was that the site median and averaging were not done, and the area drained (*A*) was calculated as the median of a 3x3 pixel neighbourhood.

The spatial pattern of the vegetation was predicted using vegetation classes. Definition of vegetation classes used the sampled abundances so that the accuracy of the map was maximized. If a canopy tree species had an importance value of >16% then that species was included in the class name, e.g. the name lodgepole pine was applied to stands that had only lodgepole pine with a >16% importance value. The resulting tree classes were: lodgepole pine (63 pixels), trembling aspen (35 pixels), lodgepole pine & Engelman/white spruce (100 pixels), and subalpine fir & Engelman/white spruce (75 pixels). Pixels characterizing the bare rock & alpine class, the lake class, and the stream class were identified by Thematic Mapper spectral signatures and air photos. Two thirds of the pixels that were sampled in the field were assigned to the classes and used to train a maximum-likelihood classifier (PCI Inc. 1996). This classifier used the distributions of the classes on the energy and moisture resource gradients to assign the rest of the pixels in the study area to the classes. The remaining one third of pixels with known classes were compared to the assigned classes to test the accuracy of the map.

The traditional indirect ordination of correspondence analysis (CA) was run on the species importance values and used to define the major gradients of changing tolerances (ter Braak 1992). Correspondence analysis is considered the best general purpose ordination method because it assumes a unimodal frequency distribution and is relatively robust against curvilinear distortion (Fasham 1977, Gauch et al. 1977). To reduce distortions caused by species which are absent in a large number of sites (see Swan 1970), species present in <60% of the stands were deleted from the analysis. When ordinations were run with species present in <10% to <60% of the stands, the patterns of species and stand distribution along the ordination axes were consistent. However when species presence was above or below these thresholds, the pattern changed markedly.

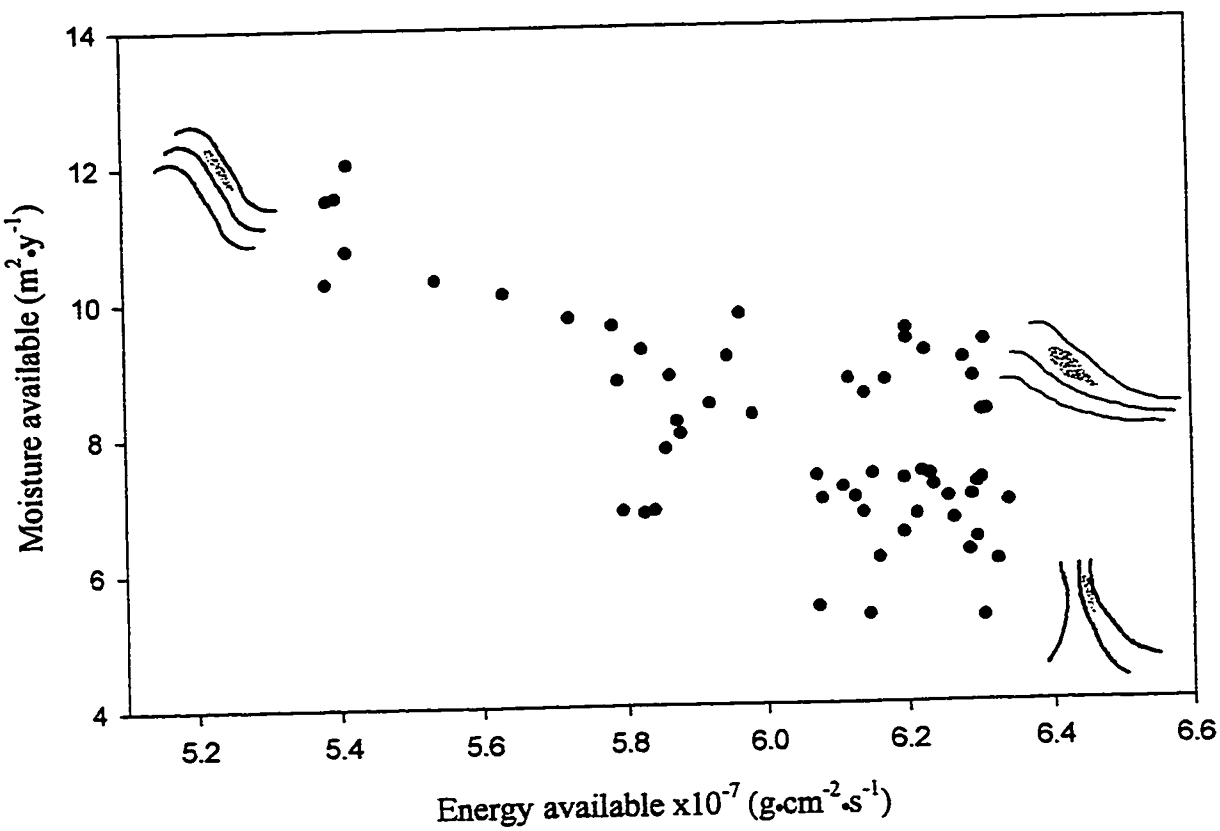
In order to compare the traditional approach with the modelled resources, a direct ordination was done using the same species data with the addition of the descriptive environmental data. Canonical correspondence analysis (CCA) was used as the direct technique complimentary to CA (Gauch 1982). Stepwise CCA in CANOCO, using Monte Carlo simulations, were used to eliminate extra environmental variables.

Results

Modelled resources

The physical processes in Eqs. 1 and 4 gave the relative position of each site on the moisture and energy gradients (Fig. 2). Sites in the upper left corner of the graph had high moisture and low energy available, in contrast, sites in the lower right had low to medium moisture values and high energy available. The pattern of sites showed a trend

FIG. 2. Stands distributed on the modelled resource gradients (dots). Slope profiles (curved lines) creating hillslopes and consequent drained areas (grey shapes) are schematics of the terrain.


14
12
10
8
6
4
5.2
5.4
5.6
5.8
6.0
6.2
6.4
6.6
Moisture available ($m^2 \cdot y^{-1}$)
Energy available $x10^{-7}$ ($g \cdot cm^{-2} \cdot s^{-1}$)

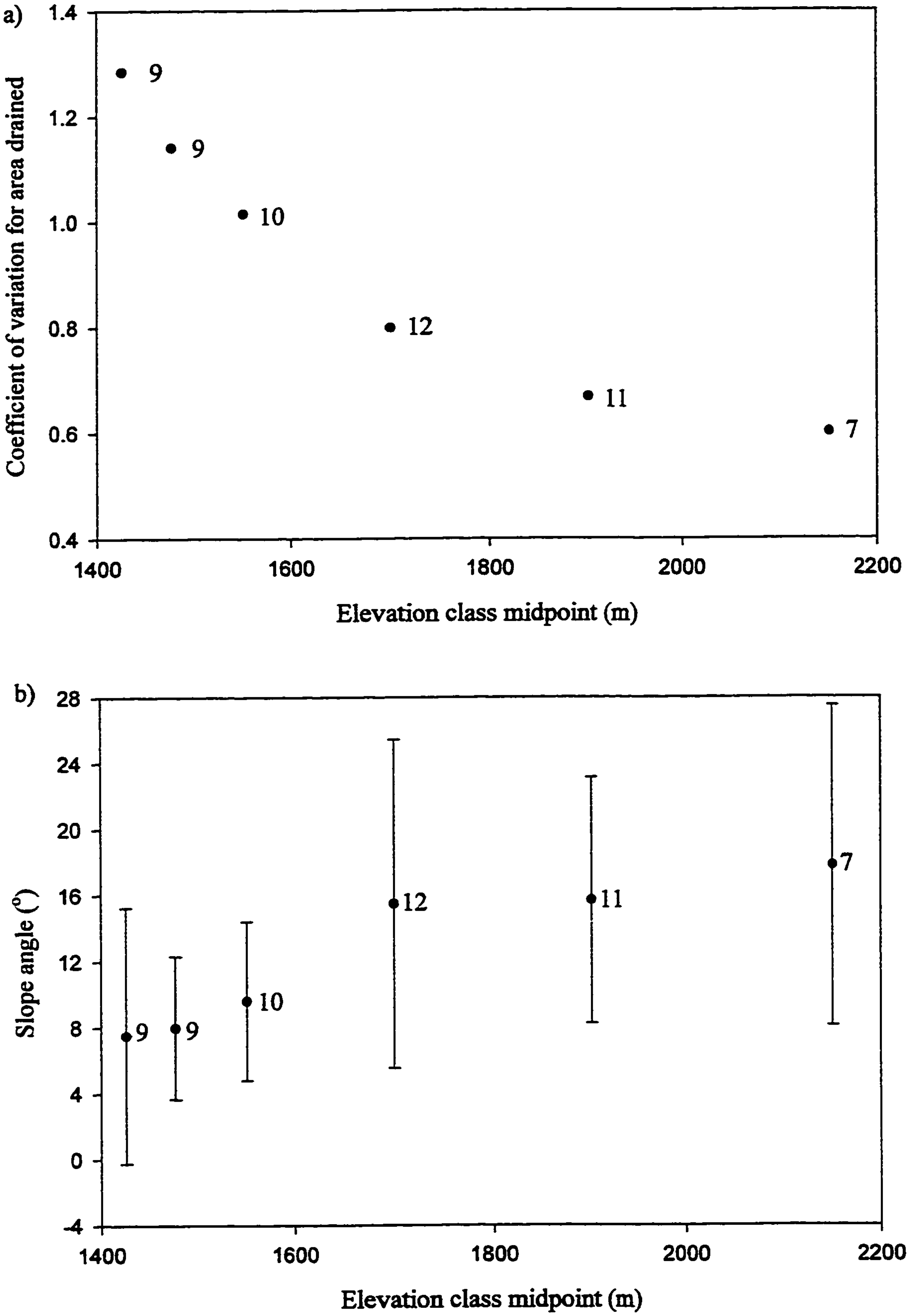
of decreasing moisture with increasing energy. Notice that the range in moisture available values also increased with increasing energy.

Fig. 2 also describes the structure of the terrain as it affects plants. For example, at the wetter end of Fig. 2 (upper left), hillslopes had higher rainfall and lower evapotranspiration. The variation in moisture was lower because there was limited variety of hillslope lengths and shapes, which created little variance in drained area (Fig. 3a). The variance lengths was low because the slopes were near the peaks or cliffs (Fig. 3b). The variance in shapes was low because high erosion rates created a surficial geology of mainly colluvium with very little till (Bayrock and Reimchen 1977).

At the drier end of Fig. 2 (bottom right) hillslopes were at lower elevations with lower rainfall and higher evapotranspiration. The variation in moisture was higher because there was a range in hillslope shape and a variety of surficial geology types that created a wider range of area drained sizes (Fig. 3a). The hillslopes were far from the peaks, so longer hillslopes were possible, whereas cliffs and ridges created shorter hillslopes as well. Larger drained areas occurred at the bottom of long gentle hillslopes, but there were smaller drained areas near the top of gentle hillslopes or on short, steep hillslopes. The surficial geology was primarily till, colluvium, alluvial fans, and alluvial benches (Milus Tress Barron Ltd. 1976, Bayrock and Reimchen 1977). Surfaces eroded by water tend to be concave, while alluvial deposits tend to be convex. The difference in hillslope shapes resulted in differences in the area drained, even when the hillslopes had a similar length (Carson and Kirkby 1972). The distance from the peaks and the wide

FIG. 3a. The coefficient of variation for the area drained in each elevation class (classes based on similar sample sizes). Numbers associated with each point are the sample sizes.

FIG. 3b. The mean $\pm$ 1 standard deviation for the slope angles in each elevation class. Numbers associated with each class are the sample sizes.

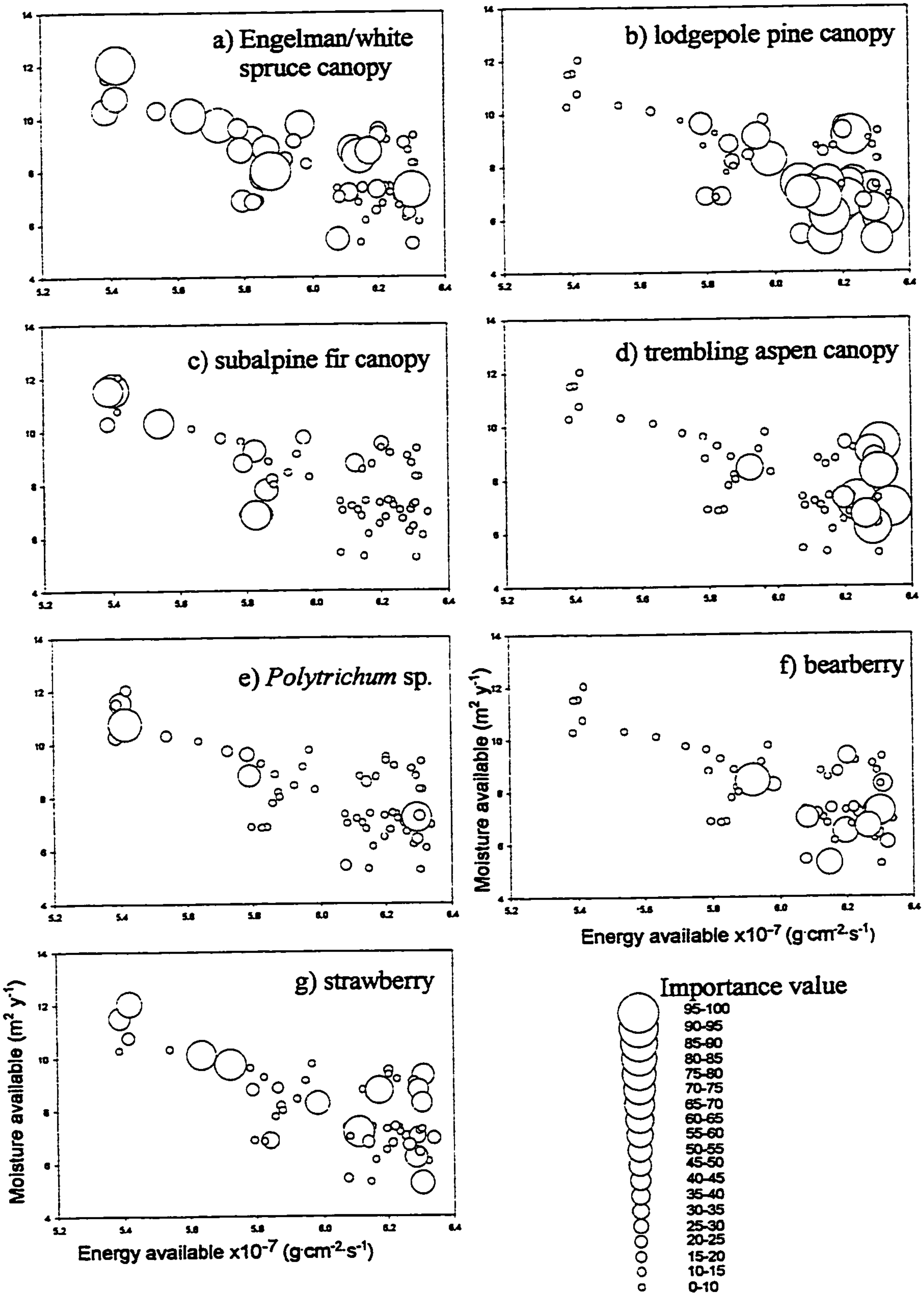

a)
Coefficient of variation for area drained
1.4
1.2
1.0
0.8
0.6
0.4
9
9
10
12
11
7
1400
1600
1800
2000
2200
Elevation class midpoint (m)
b)
Slope angle (°)
28
24
20
16
12
8
4
0
-4
9
9
10
12
11
7
1400
1600
1800
2000
2200
Elevation class midpoint (m)

U-shaped main valley resulted in the mean slope angle increasing with elevation (Fig. 3b).

Species tolerances

Plant abundances responded to the change in modelled energy and water resources across the terrain. Engelman/white spruce was found in high abundance in the upper two-thirds of Fig. 4a, defining a tolerance to wet and moist conditions, with little effect of energy on abundance. Topographically, Engelman/white spruce was found in high abundance on sites that were higher in elevation, or at lower elevation sites located at the bottom of long and gradual hillslopes. Lodgepole pine was found in high abundance in the lower right corner, and in moderate abundance in the middle of Fig. 4b. This pattern showed that lodgepole pine had a tolerance for lower moisture at higher energy levels, and survived in moist conditions at intermediate energy availability. Topographically, lodgepole pine was found in high abundance at lower elevations on the steep hills, and only in moderate abundance at intermediate elevations. Subalpine fir was found in high abundance in the left side of Fig. 4c. This pattern defined a tolerance for low and intermediate energy levels with little effect of moisture on abundance. Topographically, subalpine fir was found in high abundance at higher and intermediate elevations, along the length of hillslopes. Trembling aspen was found in high abundance in the right edge of Fig. 4d. This pattern defined a tolerance for high energy levels with little effect of moisture on abundance. Topographically, trembling aspen was found in

FIG. 4. Species abundances distributed along modelled resource gradients for seven common species.



a) Engelman/white spruce canopy
b) lodgepole pine canopy
c) subalpine fir canopy
d) trembling aspen canopy
e) *Polytrichum* sp.
f) bearberry
g) strawberry
Moisture available (m² y⁻¹)
Energy available x10⁻⁷ (g·cm⁻²·s⁻¹)
Importance value
95-100
90-95
85-90
80-85
75-80
70-75
65-70
60-65
55-60
50-55
45-50
40-45
35-40
30-35
25-30
20-25
15-20
10-15
0-10

high abundance at lowest elevations along the length of hillslopes. *Polytrichum* spp. was found in high abundance in the upper left of Fig. 4e. This pattern defined a tolerance for high moisture and low energy. Topographically, *Polytrichum* spp. was found in high abundance on higher elevation hillslopes. Bearberry occupied the lower right corner of Fig. 4f. This pattern defined a tolerance for dryness and high energy available. Topographically, bearberry was found at lower elevations on shorter and steep hillslopes, or near the top of longer hillslopes. Strawberry had high abundances across both resource gradients (Fig. 4g), so was found on all parts of the topography.

Ecosite typing

The use of physical processes should improve the applicability of ecosite systems to field work because traditional ecosite systems are based on judgement and categorical variables. See the Discussion for a complete comparison between the Archibald et al. (1996) subalpine ecosite system and the Kananaskis ecosite system. One discrepancy between the two ecosite systems was for ecosite e - false azalea/grouseberry (lodgepole pine & Engelman/white spruce canopy) (species scientific names in Appendix A). In the Kananaskis, there was no overlap in the distribution of *Alnus crispa* and the other indicator species identified by Archibald et al. (1996), so the polygon was drawn excluding *Alnus crispa*. The distribution of *Alnus crispa* in the Kananaskis fell clearly in ecosite b - bearberry/hairy wild rye (lodgepole pine canopy). Ecosites i and j were created for ecosites not described by Archibald et al. (1996) and not encircled on the plot. Ecosite i - buffaloberry/billberry (lodgepole pine & Engelman/white spruce canopy) was similar to ecosite e, except there was no false azalea or grouse-berry. Ecosite j - prickly rose/solidago (no twinflower) (trembling aspen canopy), included the trembling aspen stands of the Kananaskis in the ecosite system.

Diversity

The overlapping tolerance curves on the resource gradients define the patterns of diversity on the terrain. Tree richness appears to tripled in range from lower to higher energies (Fig. 5a). Beta-diversity also increased as energy available increased (Fig. 5b). Plotting diversity along the energy gradient produces a valid distribution because the gradients are independent of categories and judgement variables.

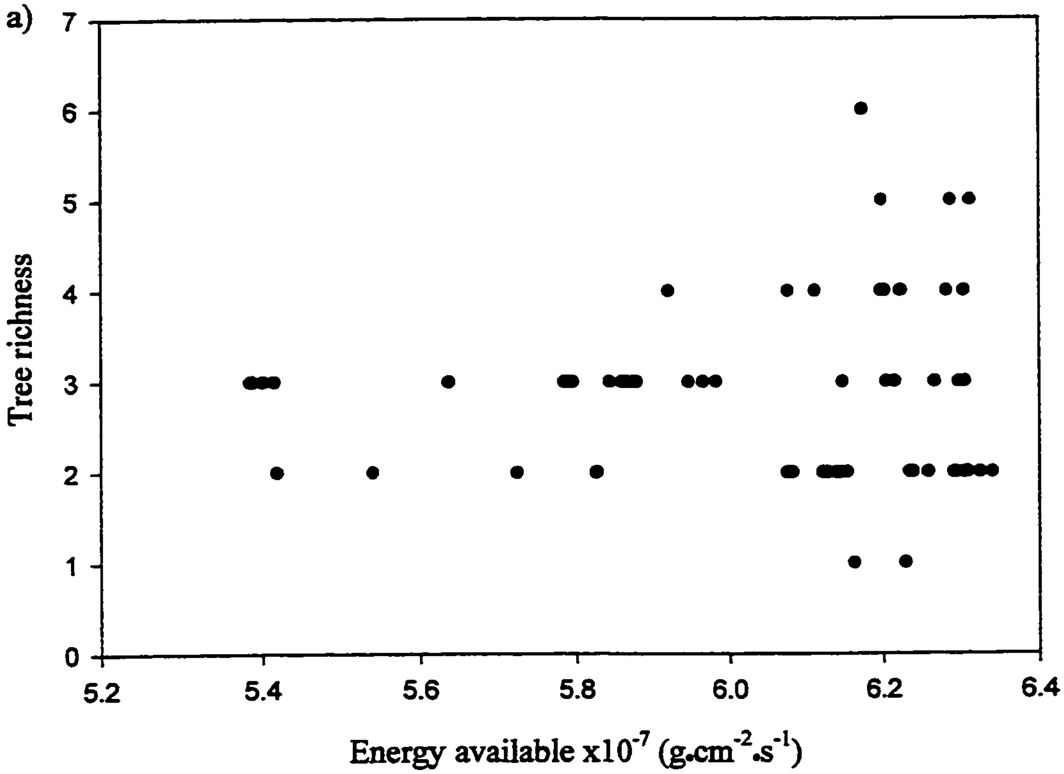
Predicting spatial patterns

The spatial pattern of vegetation can be mapped on the landscape using the tolerance curves and the digital elevation model. The result is a mechanistic understanding of vegetation spatial patterns (Fig. 6). Equations 1 and 4 can also improve the standardization and accuracy of predictions because the relationship between the terrain and the species does not rely on the judgement of the researcher. Throughout the study area, classes were accurately classified 66%, on average. Forests were accurate 50% of the time for trembling aspen, 81% of the time for lodgepole pine, 35.1% of the time for lodgepole pine & Engelman/white spruce, and 88% of the time for subalpine fir & Engelman/white spruce.

FIG. 5a. Tree richness along the energy available gradient.

FIG. 5b. Tree beta-diversity along the energy available gradient.

a)


Tree richness
0
1
2
3
4
5
6
7
5.2
5.4
5.6
5.8
6.0
6.2
6.4
Energy available x10^{-7} (g.cm^{-2}.s^{-1})

b)

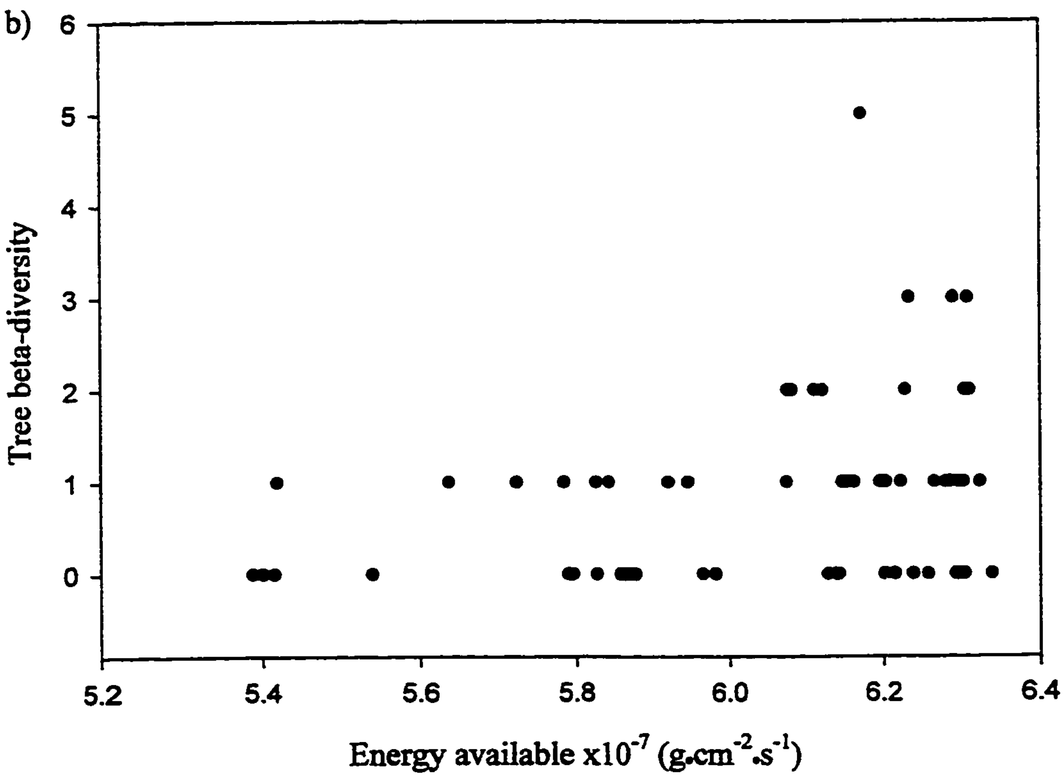
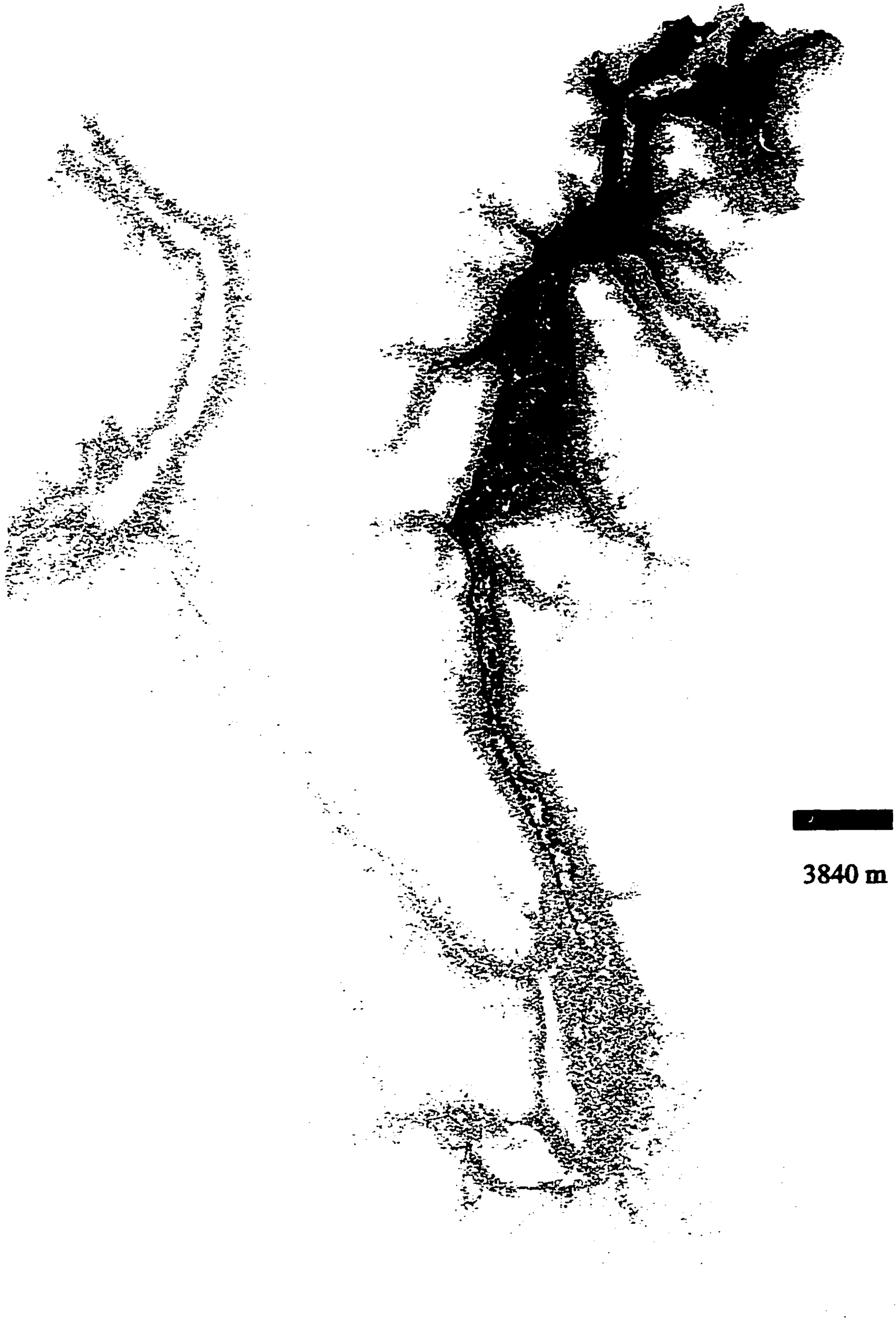
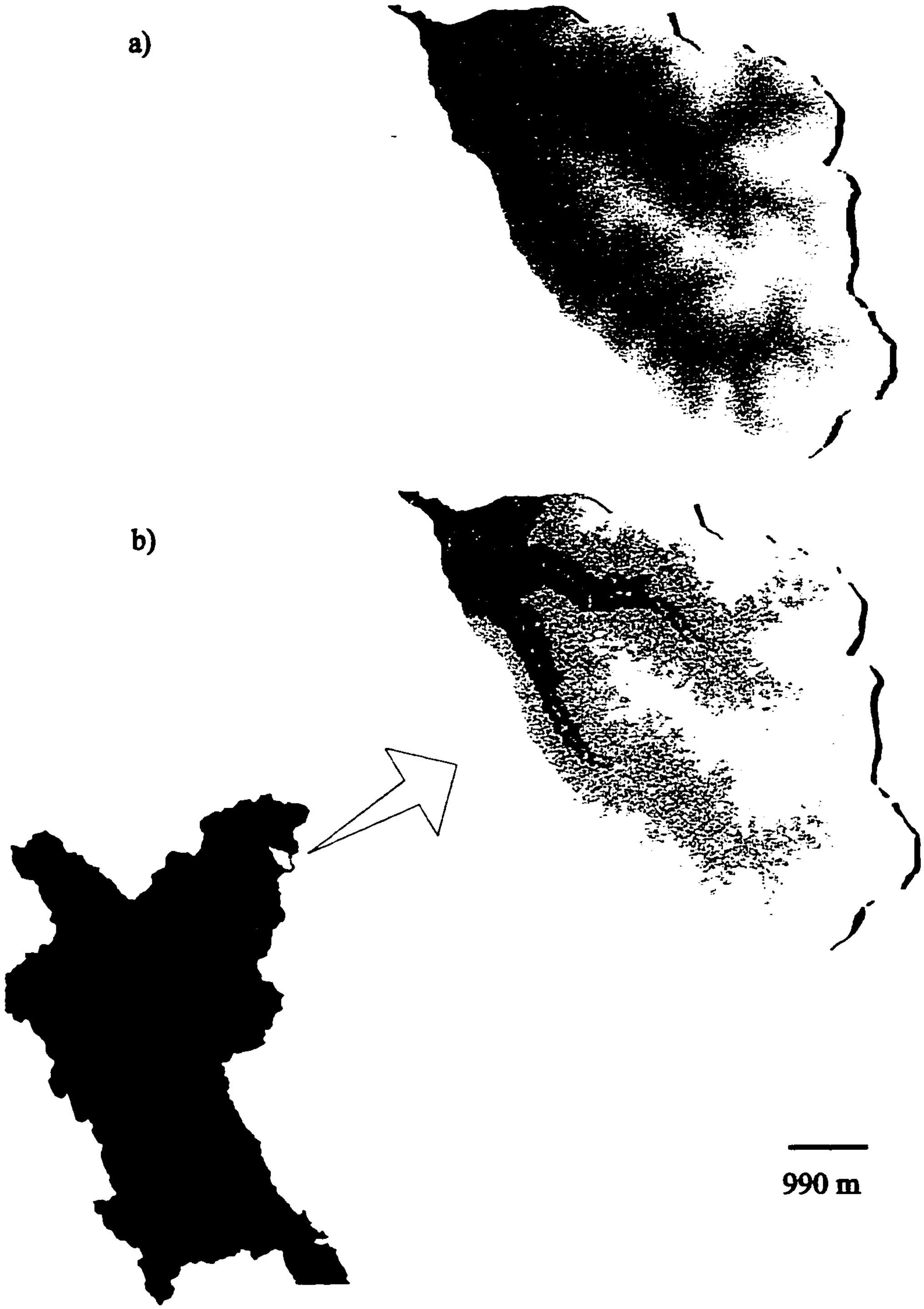

Tree beta-diversity
0
1
2
3
4
5
6
5.2
5.4
5.6
5.8
6.0
6.2
6.4
Energy available x10^{-7} (g.cm^{-2}.s^{-1})

FIG. 6. The vegetation distribution of the Kananaskis and Spray Reservoir watersheds. Trembling aspen class is black, lodgepole pine class is dark grey, lodgepole pine & Engelman/white spruce class is medium grey, subalpine fir & Engelman/white spruce class is light grey. Trees are absent at the highest elevations, in streams, and in lakes (white). The null class is also white for clarity (0.38% of study area).


3840 m

I will use the Porcupine Creek watershed as an example to explain why the spatial pattern of vegetation classes on the terrain occurs (Fig. 7). At the outflow of Porcupine Creek is an alluvial fan that is at a low elevation, is convex in shape, and has gradual slope angles. These conditions created high energy available sites with a range of moisture values. The result was trembling aspen stands intermixed with lodgepole pine stands on the driest sites. Running perpendicular to the Porcupine Creek watershed is a large alluvial bench along the main Kananaskis river valley. This bench is the result of vast quantities of water flowing out of the study area after Pleistocene glaciation. The low elevation bench has steep and convex hillslopes that created dry and high energy conditions. The result was that lodgepole pine stands dominated the alluvial bench. In the Porcupine Creek valleys, the valley bottoms and lower slopes are steep erosional hillslopes at relatively low elevations. This terrain created high energy and dry sites. The result was lodgepole pine stands occurred along the valleys. Feeding Porcupine Creek are steep, erosional hillslopes at intermediate elevations. This terrain created intermediate energy levels and mesic moisture conditions. The result was lodgepole pine & Engelman/white spruce stands occurred along the intermediate hillslopes. Furthest away from Porcupine Creeks are steep and erosional hillslopes at very high elevations. This terrain created low energy and high moisture conditions. The result was subalpine fir & Engelman/white spruce stands occurred along the hillslopes below tree-line.

FIG. 7. a) the terrain as the DEM and b) the resulting canopy species distribution (supervised classification), in the Porcupine Creek watershed. For a), the lighter the shade, the higher the elevation. For b), trembling aspen class is black, lodgepole pine class is dark grey, lodgepole pine & Engelman/white spruce class is medium grey, subalpine fir & Engelman/white spruce class is light grey. Trees do not grow at the driest, lowest energy sites, and in the streams (white). Inset is the location of the Porcupine Creek watershed in the study area.


a)
b)
990 m

Comparison to ordinations

Indirect ordinations have been used extensively to define species tolerances and community composition gradients (Gauch 1982). It is therefore important to understand how energy and moisture processes relate to ordination axes. The first correspondence analysis (CA) axis explained 29.1% of the species variance and the second CA axis explained 20.8% of the species variance (Fig. 8). The species changed on the first axis from asters at the negative end to *Peltigera apthosa* at the positive end. On the second axis species changed from strawberry at the negative end to lodgepole pine at the positive end.

The energy available gradient (Eq. 1) is well correlated to the first CA axis (r^2=0.45, n=58, P<0.001) (Fig. 9a). The moisture available gradient (Eq. 4) is moderately correlated to the second CA axis (r^2=0.27, n=58, P<0.001) (Fig. 9b), and only slightly correlated to the first CA axis (r^2=0.11, n=58, P<0.001).

Direct ordinations are often used to define species tolerances on the terrain descriptors. The first axis of the canonical correspondence analysis (CCA) explained 19.6% of the species variance and the second axis explained 9.8% of the species variance (Fig. 10). The first CCA axis correlated negatively with elevation and slope angle, and correlated positively with hydrogen ion concentration. Aspect changed from west to south-east as the first CCA axis increased. Species changed along the first axis from Engelman/white spruce and *Peltigera apthosa* at the negative end, to lodgepole pine and grasses at the positive end. The second CCA axis correlated positively with slope angle and soil rockiness, and correlated negatively with elevation, and NO_3-N.

FIG. 8. Correspondence analysis scatter plot with 58 stands and 13 species.

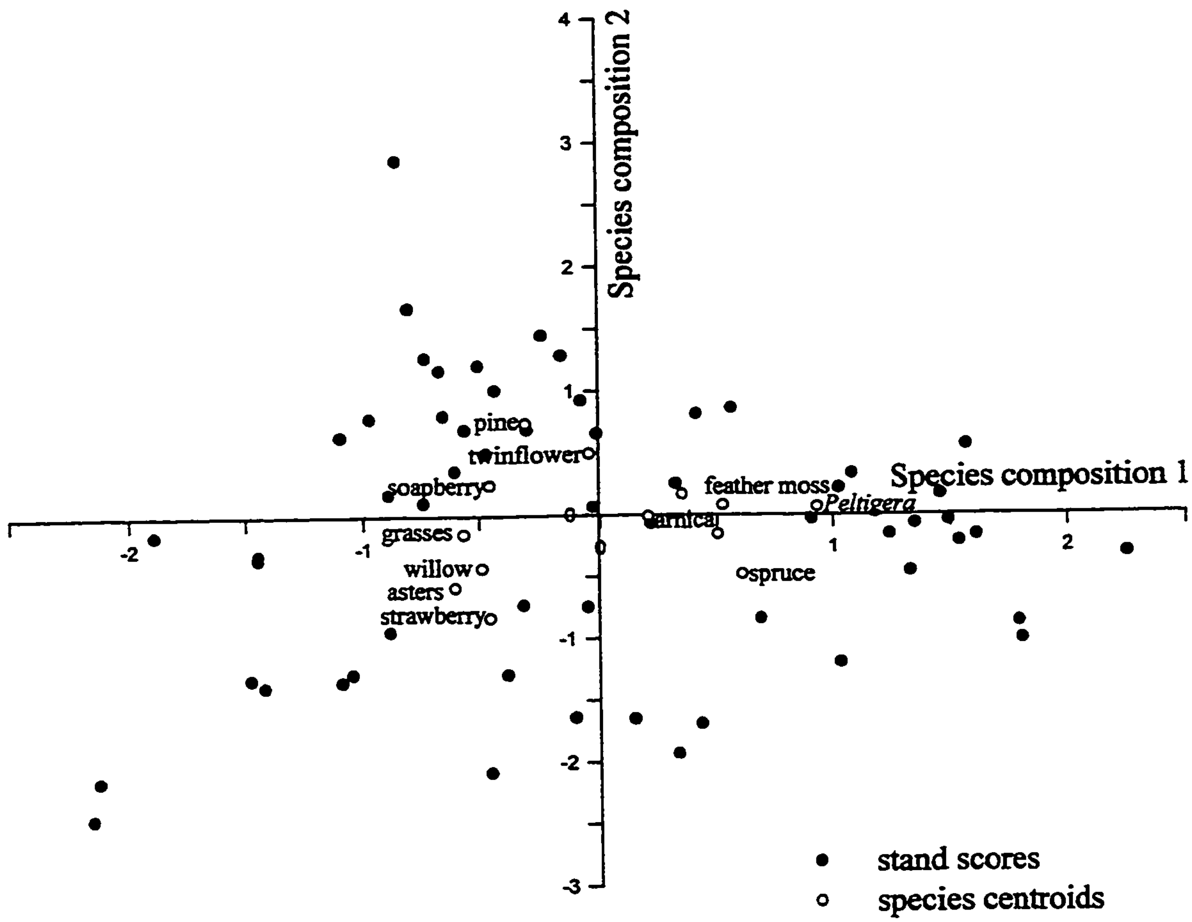
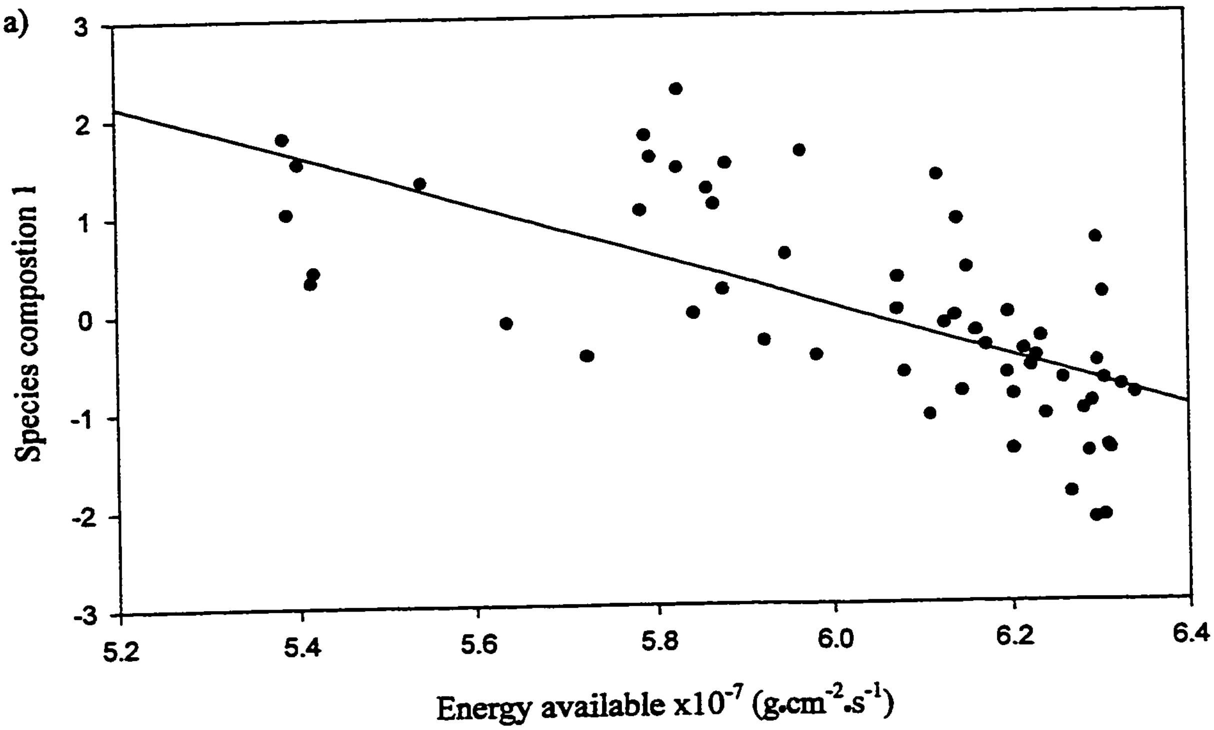

Species composition 2
Species composition 1
pine
twinflower
soapberry
grasses
willow
asters
strawberry
feather moss
Peltigera
arnica
spruce
stand scores
species centroids
4
3
2
1
0
-1
-2
-3
-2
-1
0
1
2

FIG. 9a. The species composition from the correspondence analysis axis 1 showing changes in species composition as energy available increases. The line is a linear regression (r^2=0.45).

FIG. 9b. The species composition from the correspondence analysis axis 2 showing changes in species composition as moisture available increases. The line is a linear regression (r^2=0.27).

a)


Species compostion 1
3
2
1
0
-1
-2
-3
5.2
5.4
5.6
5.8
6.0
6.2
6.4
Energy available x10^{-7} (g.cm^{-2}.s^{-1})

b)

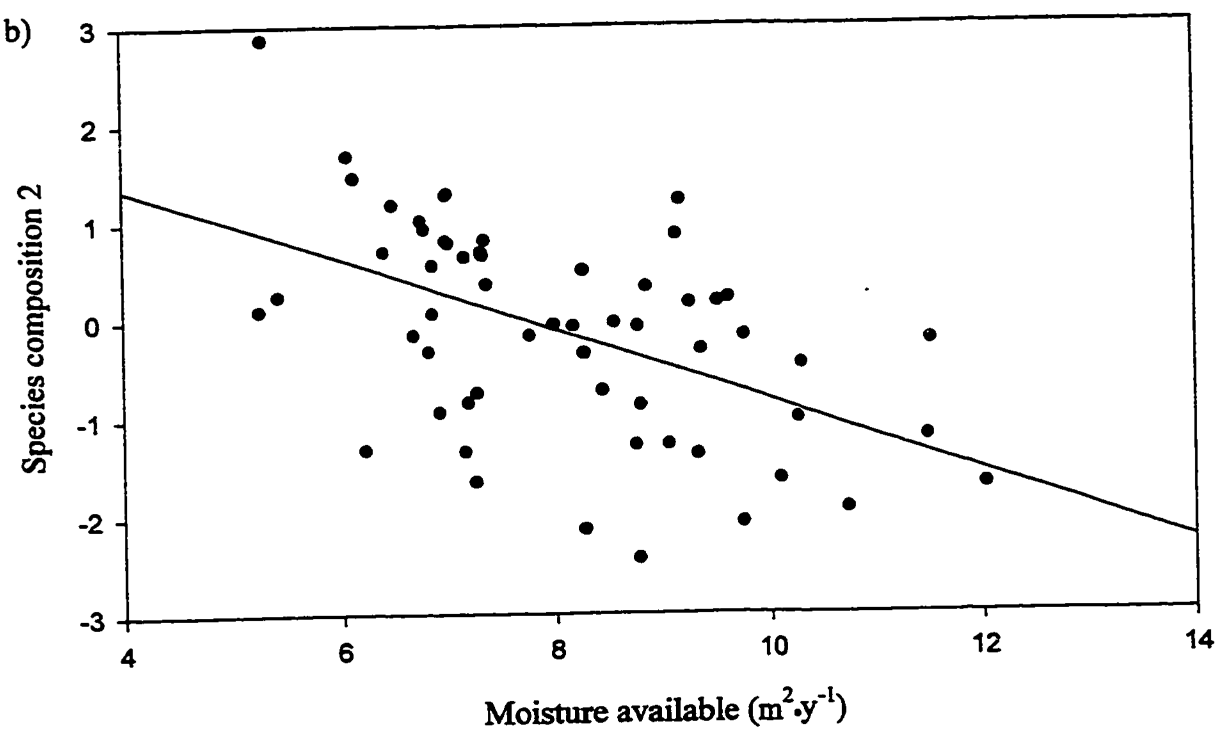
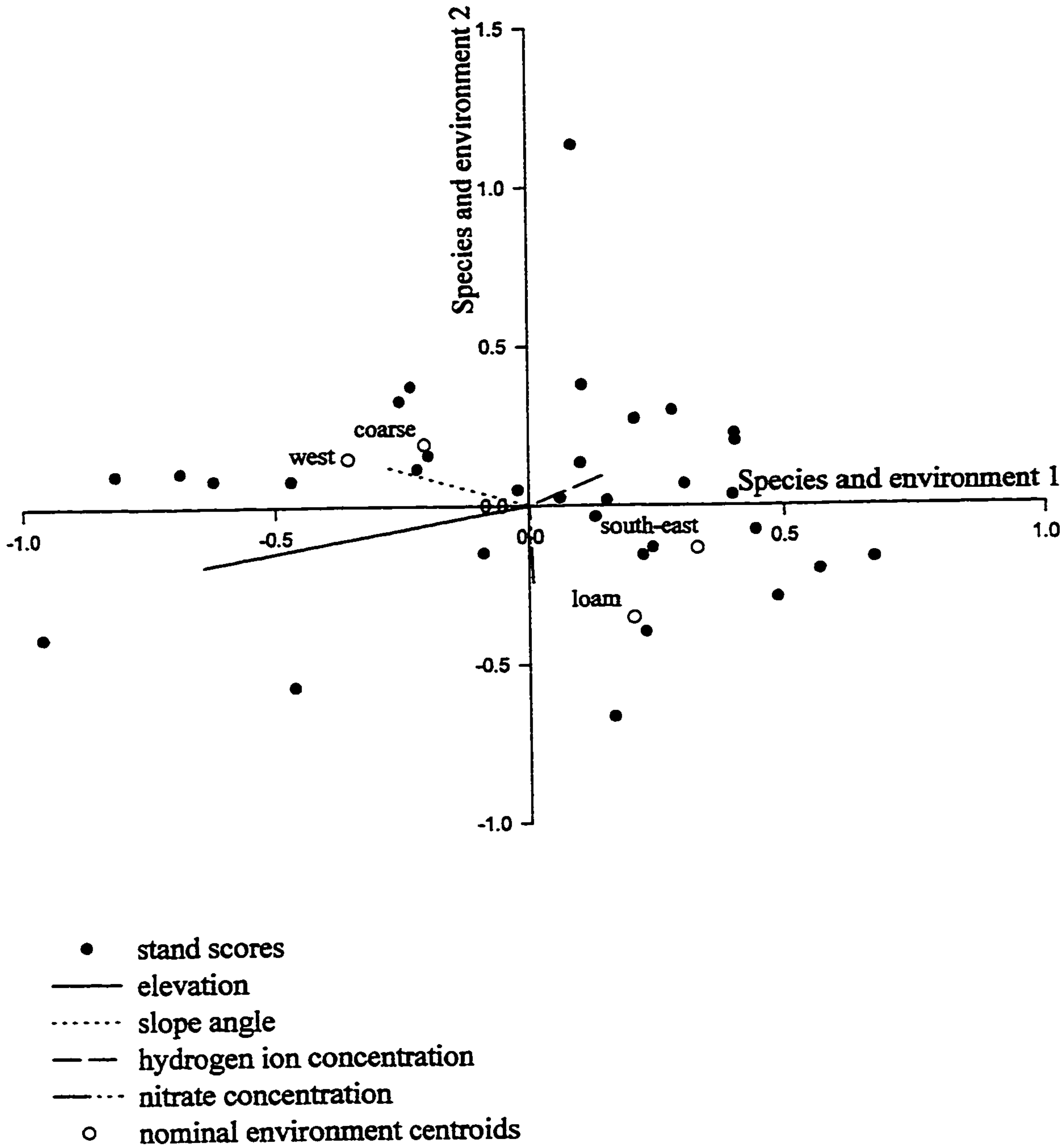

Species composition 2
3
2
1
0
-1
-2
-3
4
6
8
10
12
14
Moisture available (m^2.y^{-1})

FIG. 10. Canonical correspondence analysis of 32 stands, 13 species (not shown) and 8 environmental descriptors that explained >2% of the variance.


Species and environment 2
Species and environment 1
1.5
1.0
0.5
0.0
-0.5
-1.0
0.5
1.0
coarse
west
south-east
loam
stand scores
elevation
slope angle
hydrogen ion concentration
nitrate concentration
nominal environment centroids

Species changed along the second axis from strawberry and asters at the negative end to lodgepole pine and *Peltigera apthosa* at the positive end. The stand scores generally matched the CA results (r_s=-0.872 for axis 1, 0.629 for axis 2, n=32, P<0.01).

Discussion

A species tolerance is the segment of a resource gradient that allows reproduction and survival, i.e. it is one dimension of a niche (Hutchinson 1957). Tolerance curves underlie much of ecological theory from ordinations (Bray and Curtis 1957), ecosite systems (Lacate 1969), and diversity (Huston 1994) to spatial patterns on a landscape (Watt 1947). The definition of a species tolerance hinges on the definition of the resource gradient. Here, I try to define gradients using physical processes only. These processes are causally linked to plant tolerances and consequent spatial patterns. This physical approach is distinct from traditional ordinations, from studies employing physiological measurements (e.g. Wuenscher and Kozlowski 1971, Zobel et al. 1976) and from ecosystem models (e.g. Lauenroth et al. 1993, Neilson 1995). Rather than using physical processes to understand plant distributions, these approaches emphasize the interaction of plants with the environment and, as a result, tell us little about the characteristics of the resources.

Energy and moisture gradients have greater explanatory power than elevation and topographic indices because they are the resources that plants use. Elevation correlates with precipitation, evapotranspiration, solar radiation, and temperature, while topographic indices represent drainage patterns and solar radiation. However, by combining these variables into processes of water movement, net water input, and photosynthetic energy, we have defined the physical resources that plants use.

Tolerances based on gradients of the resources plants use and that are defined by the structure of the terrain, should clarify our understanding of species abundance patterns. For example, Peet (1978) could not separate trembling aspen from lodgepole pine on the traditional gradients of elevation and moisture within the latitudes of the U.S. Rocky Mountains (Table 1). On the terrain at the south-latitudes lodgepole pine was absent and trembling aspen was abundant from flat, ravine bottoms to very steep hillslopes. At mid-latitudes lodgepole pine was abundant on north-facing, steep slopes and trembling aspen was abundant from flat ravine bottoms to steep slopes. At north-latitudes, lodgepole pine was abundant from gentle bottom slopes to steep slopes and trembling aspen was abundant on flat alluvial bottom lands and exposed rocky ridges.

In the far north latitudes of the Kananaskis we see a similar pattern of trembling aspen and lodgepole pine on the terrain as in Peet's (1978) north-latitude site (Table 1). We can understand the species distributions using the energy available gradient to define tolerances. Trembling aspen has high abundances on the highest energy sites (Fig. 4d), while lodgepole pine has high abundance on the driest high energy sites and sites that are slightly lower in energy than the trembling aspen sites (Fig. 4b). In the Kananaskis and at Peet's (1978) north site, trembling aspen occupies the flat parts of the terrain These sites have the highest energy available because of the aspect (Nikolov and Zeller 1992). In contrast, lodgepole pine is high in abundance on steep slopes and higher in elevation, that have lower energy available locally (Nikolov and Zeller 1992). By defining

TABLE 1. Lodgepole pine and trembling aspen distributions on elevation and moisture gradients in the Rocky Mountains. South, mid and north latitude results are from Peet (1978), and far north latitude results are from this study.

	Lodgepole pine		Trembling aspen	
Latitude	elevation	moisture	elevation	moisture
south	n/a	n/a	most	all
mid	middle	middle	most	most
north	middle	most	middle	extremes
far north	lower	lower	lowest	higher

energy tolerances, a resource plants use, the pattern of lodgepole pine and trembling aspen can be clearly seperated.

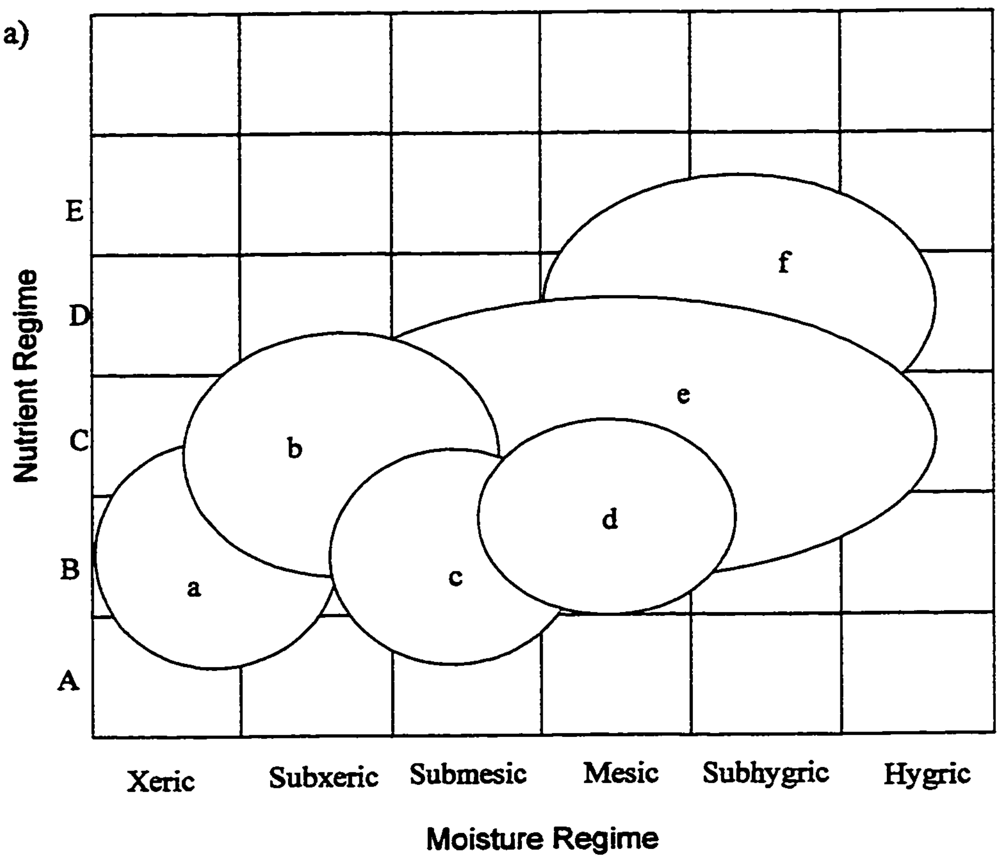
Using this new perspective of energy available, we can also understand the species pattern along the latitudinal gradient in the U.S. Rocky Mountains. Trembling aspen decreases in abundance and distribution as solar radiation levels and temperatures decrease with latitude (Stevens 1989). Lodgepole pine increases in abundance and distribution as solar radiation levels and temperature decrease with latitude (Stevens 1989). The occurrence of lodgepole pine only on north-facing slopes at mid-latitudes is consistent with the energy hypothesis because these sites will have the lowest local solar radiation and temperatures.

Species tolerances defined by the energy available and moisture available gradients can also clarify vegetation ecosite systems based on traditional ordinations. Archibald et al. (1996) for example, have produced an ecosite typing for south-western Alberta that is based on traditional ordination and cluster analysis. This ecosite system is intended to "organizes ecological information into a format that facilitates understanding and provides a structure for ecologically based management." Archibald et al. (1996) use gradients of moisture and nutrients that do not include elevation. Apparently, they excluded elevation despite that "characteristic species vary ... elevationally" because the "ecological relationships are not completely understood." The result is the overlap of many species tolerance curves, and therefore a system with substantial overlap between ecosite types (Fig. 11a). One example of the misleading overlap is the ecosite (c) subalpine larch/heather (subalpine larch, subalpine fir & Engelman/white spruce canopy)

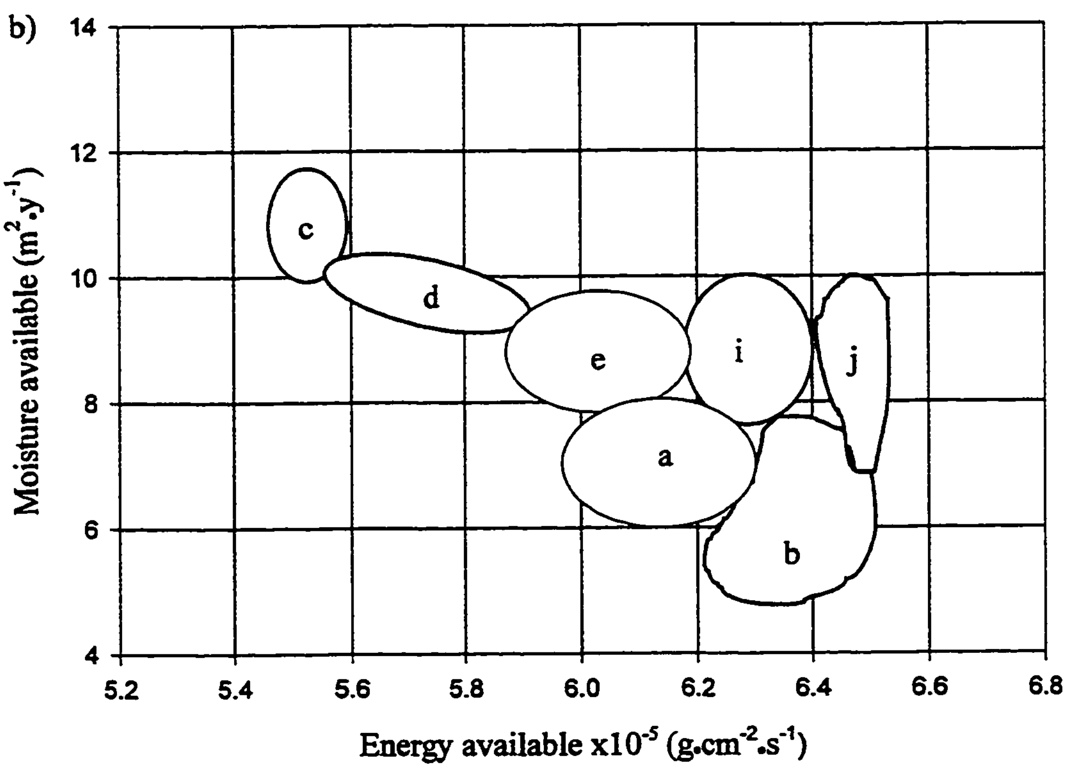
FIG. 11a. Southwestern Alberta subalpine ecosites on moisture/nutrient gradients (from Archibald et al. 1996). Ecosites: a - lichen (lodgepole pine canopy), b - bearberry/hairy wild rye (lodgepole pine canopy), c - subalpine larch/heather (subalpine larch, subalpine fir & Engelman/white spruce canopy), d - spruce/heather (subalpine fir & Engelman/white spruce canopy), e - false azalea/grouse-berry (lodgepole pine & Engelman/white spruce canopy).

FIG. 11b. Kananaskis subalpine ecosites on energy available and moisture available gradients. Ecosites defined by Archibald et al. (1996). The only exceptions are that e has no *Alnus crispa* and there are the additional sites i - buffalo berry/low bilberry (lodgepole pine & Engelman/white spruce canopy) and j - rose/solidago (trembling aspen canopy).

a)


E
D
C
B
A
Nutrient Regime
f
e
b
d
c
a
Xeric
Subxeric
Submesic
Mesic
Subhygric
Hygric
Moisture Regime

b)


14
12
10
8
6
4
Moisture available (m2.y-1)
c
d
e
i
j
a
b
5.2
5.4
5.6
5.8
6.0
6.2
6.4
6.6
6.8
Energy available x10-5 (g.cm-2.s-1)

and (b) bearberry (lodgepole pine canopy) occupying much of the same gradient space, but bearberry and subalpine larch are not found together in the forest.

One problem in all traditional ecosite systems is the large amount of environmental data to be collected at each site (Lacate 1969). This is a result of not having a clear mechanistic relationship between the physical environment and the plants to specify the appropriate variables. As a consequence, the environmental data are often indirectly related to plant resources, and many are redundant. For example, soil texture, slope angle and soil drainage are often included in defining the moisture regime, but drainage is based on texture and slope angle. Another problem with ecosite systems is the judgement-based variables (e.g. topographic position, soil drainage classes), that will result in different typings by different users. Since both climate water flux and energy are neglected, and there is inherent subjectivity in distinguishing ecosites, it is difficult to ascertain how much overlap in Archibald's system is due to subjective and redundant variables (Fig. 11a). For example, ecosites (b) bearberry (lodgepole pine canopy) and (e) false azalea/grouse-berry (lodgepole pine & Engelman/white spruce canopy) overlap considerably in the gradient space. This is despite the fact that, in the forest, bearberry is generally found on drier conditions than false azalea.

The Kananaskis ecosite typing reported here is based on tolerance curves defined by resources changing on the terrain. The mechanistic link of the plants to energy and moisture processes specifies the appropriate variables to measure. The energy available and annual moisture available gradients require the measurement of elevation, aspect, slope angle, upslope area, and latitude for input to the models (Eqs. 1 to 9). There is less overlap in the Kananaskis ecosites because the species tolerance curves are more accurate (Fig. 11b). For example, the ecosite (c) subalpine larch/heather (subalpine larch, subalpine fir & Engelman/white spruce canopy) is wetter than ecosite (b) bearberry (lodgepole pine canopy) because of the inclusion of climate water flux in the moisture gradient. This pattern more accurately reflects what occurs in the field. The ecosites (b) bearberry (lodgepole pine canopy) and (e) false azalea/grouse-berry (lodgepole pine & Engelman/white spruce canopy) have little overlap on the moisture gradient because of the measured variables, including the climate water flux. Again, this more accurately reflects field conditions. It is difficult to determine if measuring the hillslope processes would be enough to separate the ecosites along a moisture gradient.

Spatial heterogeneity is one of the strong correlates to diversity (Huston 1994). Spatial heterogeneity for plants is usually defined by empirical measurements of local nutrients (e.g. Wittig and Neite 1985). Instead, I will develop a concept of spatial heterogeneity based on the spatially explicit hillslope and climate processes that define the moisture available. First, terrain complexity must be understood using hillslope processes. The terrain complexity is determined for a population of hillslopes that have a common climate. A common climate is important because climate affects hillslope processes (Derbyshire 1976). Hillslope wetness is defined by the area drained and the slope angle (Eq. 3). Hillslopes are the fundamental units for geomorphic processes because they are the paths of water movement to a stream course (Carson and Kirkby 1972). The area drained by a point on a hillslope generally increases as the distance to the ridgeline increases, in other words, as the pathway collecting water lengthens. The area drained by a point also increases as the hillslope becomes more concave because the pathways converge, so there are more pathways leading into a point. Likewise, the area drained decreases as the hillslope becomes more convex because the pathways diverge, and there are fewer pathways leading to a point. Using convex hillslopes as an example, the relationship between area drained per unit contour length (A) and hillslope shape and length, is:

$$A = \frac{\rho}{x - \rho} \tag{10}$$

where x is the distance to the divide, and ρ is the radius of curvature of the contours (negative on convex hillslopes) (Carson and Kirkby 1972). The area drained indicates how much area collects water that will flow into a site.

The slope angle (β) increases when the vertical distance from the divide (y) increases faster than the horizontal distance (x). The result is that the vector of water flow approaches the vector of gravity, so the water flows faster and the site will be drier (Carson and Kirkby 1972).

$$\tan\beta = \frac{y}{x} \tag{11}$$

The wetness is the amount of water draining into a point, divided by the rate water will be flowing through that point. For example, when two sites have the same area drained, the steeper one will be drier. A large variation in wetness is the result of complex terrain, where terrain complexity is the amount of variation in hillslope length, shape and slope angle. Increasing terrain complexity will also result in a longer moisture gradient, because the variation of moisture available depends on the variation of wetness (Eq. 4). The spatial heterogeneity of moisture within a population of hillslopes corresponds to the length of the moisture gradient for the population (Fig. 2). Remember that the gradient length is the range in moisture where the change from 2 to 3 $m^2.y^{-1}$ is equal to the change from 3 to 4 $m^2.y^{-1}$, i.e. a ratio variable. This is in contrast to traditional categorical indices where the length of the gradient was determined by the researcher's categories.

The concept of spatial heterogeneity is not restricted to populations of hillslopes within climate zones. Spatial heterogeneity of water within the region must take into account the spatially changing climate. The moisture available gradient includes the hillslope processes and the climate processes in its estimation of water (Eq. 4). When we look at the entire study area, the climate water flux increased the moisture available length from 5 $m^2.y^{-1}$ at lower elevations, to 7 $m^2.y^{-1}$ when higher elevations are included (Fig. 2).

We can use this concept of spatial heterogeneity and species tolerances on the same gradient to test the effect of changing spatial heterogeneity on diversity. The tree richness increased in quantity and in variation with increased length of the moisture available gradient in the Kananaskis (Fig. 5a). Diversity is plotted on the energy gradient so that the effect of the spatial heterogeneity of moisture on diversity can be compared between populations which are defined by a common energy level. The longer moisture gradient at higher energy available increased tree diversity because species with different tolerances can exist in high abundances on different places on the gradient. Where their tolerance curves overlap there will be higher richness. This pattern is shown in Fig. 4a, b and d where Engelman/white spruce, lodgepole pine, and trembling aspen are found in high abundances on different parts of the moisture gradient. But there are many sites where the tolerance curves overlap and all three species coexist, creating high diversity sites. In contrast, when the moisture gradient is shorter at lower energies, Engelman/white spruce and subalpine fir have very similar tolerance curves (Fig. 4b and c). There is little overlap of tolerance curves between tree species other than Engelman/white spruce and subalpine fir, so there is low diversity. With traditional descriptors, the only available explanation of this pattern was that richness increased with increasing productivity (e.g. Whittaker and Neiring 1965). The distribution of moisture on the terrain does include drier sites at low energies, but these sites are not occupied by subalpine forests.

Using species tolerances defined on the physical gradients of energy and moisture resulted in a fairly accurate map of the vegetation spatial patterns. Because there is a mechanistic link between the pattern and the physical processes, the map can be used to understand how the pattern arose. This kind of procedure could also be used to test other theories of how spatial patterns arise. Remember that traditional remote sensing and GIS maps have no inherent link between pattern and process. My study showed that the proportion of the landscape covered by a species is a consequence of the terrain structure because of the dependence of the resources on the physical environment. For example, there is a large proportion of the Kananaskis covered by lodgepole pine trees (Fig. 6). This is not because lodgepole pine has wide tolerances (Fig. 4b). Rather, the wide distribution of lodgepole pine is partly a consequence of extensive Pleistocene glaciation erosion resulting in a large proportion of the Kananaskis being at low elevations, and therefore medium to high energy levels. The wide distribution is also a consequence of the thrust faulting construction of the mountains and large Pleistocene alluvial deposits. The construction of the mountains created high erosion rates and steep slopes, and the alluvial deposits tend to be convex and steep, all of which create dry sites.

Trembling aspen has a restricted spatial distribution (Fig. 6) because it is limited to the highest energies available in the watershed (Fig. 4d). The presence of trembling aspen in the watershed is probably due to the extensive glaciation of the main valley that created a wide, U-shaped valley with a river that occupies little of the valley floor. The glacial erosion created the low elevation, gentle hillslopes with little shading due to aspect that are very high energy sites. Engelman/white spruce is widespread in the Kananaskis, likely due to its wide tolerance with respect to energy, and for all but the driest sites (Fig. 4a). In effect, it can live in high abundances on all but the steepest terrain at the lowest elevations. Subalpine fir occupies a lower proportion of the Kananaskis, likely due to its tolerance for low energy and moist sites (Fig. 4c). There is a limited distribution of high elevation hillslopes because of the original thrust faulting pattern and high erosion rates.

Conclusions

I have redefined species tolerances by using gradients of resources plants use. The gradients are more appropriate than elevation and topographic indices to define subalpine species tolerances. The physically based tolerances were used to clarify the ambiguous relationship between trembling aspen and lodgepole pine, and to improve an ecosite system of the subalpine. The gradients defined spatial heterogeneity and the tolerances showed how heterogeneity affects species diversity. The linking of species tolerances to the terrain was used to understand and predict species spatial patterns.

The energy available and moisture available models are purposefully simple, but more complexity could be added. For example, southerly aspects are warmer, and will therefore have higher potential evapotranspiration (Thornthwaite 1948, Bristow and Campbell 1984). Soils with higher porosity will have lower hillslope wetness, all else being equal (O'Loughlin 1986). Soil nutrients can be predicted with Beven and Kirkby's (1979) wetness model when parent material and soil development are consistent (Moore et al. 1993). Finally, the below canopy solar radiation could be estimated with a model of canopy density (Jarvis and Leverenz 1983).

Literature Cited

Allen, R.B. and R.K. Peet 1990. Gradient analysis of forests of the Sangre de Cristo Range, Colorado. Canadian Journal of Botany 68:193-201.

Archibald, J.H., G.D. Klappstein, and I.G.W. Corns 1996. Field Guide to Ecosites of Southwestern Alberta. Special report 8, CFS NW Region, University of British Columbia Press, Vancouver.

Avery, T.E. and G.L. Berlin 1992. Fundamentals of remote sensing and airphoto interpretation, 5th edition. MacMillan.

Bayrock, L.A. and T.H.F. Reimchen 1977. Surficial geology: Alberta foothills and Rocky Mountains, maps 4 and 5. Alberta Research Council, Edmonton.

Beven, K.J. and M.J. Kirkby 1979. A physically based, variable contributing area model of basin hydrology. Hydrological Science Bulletin 24:43-69.

Beven, K.J., M.J. Kirkby, N. Schofield, and A.F. Tagg 1984. Testing a physically-based flood forecasting model (TOPMODEL) for three U.K. catchments. Journal of Hydrology 69:119-143.

Bray, J.R. and J.T. Curtis 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27:325-49.

Bristow, K.L. and G.S. Campbell 1984. On the relationship between incoming solar radiation and daily maximum and minimum temperature. Agricultural and Forest Meteorology 31:159-166.

Carson, M.A. and M.J. Kirby 1972. Hillslope Form and Process. Cambridge University Press, New York.

Cottam, G., J.T. Curtis, and B.W. Hale 1953. Some sampling characteristics of a population of randomly dispersed individuals. Ecology 34(4):741-757.

Derbyshire, E.D. (editor) 1976. Geomorphology and climate. Wiley, New York.

Fasham, M.J.R. 1977. A comparison of nonmetric multidimensional scaling, principal components and reciprocal averaging for the ordination of simulated coenoclines, and coenoplanes. Ecology 58(3):551-561.

Franklin, S.E., D.R. Connery, J.A. Williams 1994. Classification of alpine vegetation using landsat thematic mapper, spot HRV and DEM data. Canadian Journal of Remote Sensing 20(1):49-56.

Gauch, H.G. Jr., 1982. Multivariate analysis in community ecology. Cambridge University Press, New York.

Gauch, H.G. Jr., R.H. Whittaker, and T.R. Wentworth 1977. A comparative study of reciprocal averaging and other ordinations. J. Ecol.65:157-174.

Gerrard, A.J. 1981. Soils and Landforms: An integration of geomorphology and pedology. George Allen & Unwin, Boston.

Greig-Smith, P. 1983. Quantitative Plant Ecology 3rd edition University of California Press, Los Angeles.

Hack, J.T. and J.C. Goodlett 1960. Geomorphology and forest ecology of a mountain region in the central Appalachians. Geological Survey Professional Paper 347.

Hewitt, K. 1972. The mountain environment and geomorphic processes. *in* Mountain Geomorphology: Geomorphological processes in the Canadian Cordillera, O. Slaymaker and H.J. McPherson editors. Tantalus Research Ltd., Vancouver.

Hutchinson, G.E. 1957. Concluding remarks. Population studies: animal ecology and demography. Cold Spring Harbor Symposia on Quantitative Biology 22:415-27.

Huston, M.A. 1994. Biological Diversity: The coexistence of species on changing landscapes. Cambridge University Press, New York.

Janz, B. And D.Storr 1977. The Climate of the Contiguous Mountain Parks. Project No. 30, Applications and Consulting Division, Environment Canada, Edmonton.

Jarvis, P.G. and J.W. Leverenz 1983. Productivity of temperate, deciduous and evergreen forests, in, Encyclopedia of Plant Physiology. Volume 12D Physiological Plant Ecology Chapter 8, O.L. Lange, P.S. Nobel, C.B. Osmond and H. Zeigler, editors. Springer-Verlag, New York.

Jenson, S.K. and J.O. Domingue 1988. Extracting topographic structure from digital elevation data for geographic information system analysis. Photogrammetric Engineering and Remote Sensing 54(11):1593-1600.

Johnson, E.A. and C.P.S. Larsen 1991. Climatically induced change in fire frequency in the southern Canadian Rockies. Ecology 72(1):194-201.

Johnson, E.A. and G.I. Fryer 1987. Historical vegetation change in the Kananaskis Valley, Canadian Rockies. Canadian Journal of Botany 65:853-858.

Kalra, Y.P. and D.G. Maynard 1991. Methods manual for forest soil and plant analysis. Information Report NOR-X-319, Forestry Canada, Edmonton.

La Roi, G.H. and R.J. Hnatiuk 1980. The *Pinus contorta* forests of Banff and Jasper National Parks: a study in comparative synecology and syntaxonomy. Ecological Monographs 50(1):1-29.

Lacate, D.S. 1969. Guidelines for biophysical land classification. Department of Fisheries and Forestry, Canadian Forestry Service Publication No. 1264.

Larcher, W. 1995. Physiological Plant Ecology 3rd edition. Springer-Verlag, New York.

Lauenroth, W.K., D.L. Urban, D.P. Coffin, W.J. Parton, H.H. Shugart, T.B. Kirchner, and T.M. Smith 1993. Modeling vegetation structure-ecosystem process interactions across sites and ecosystems. Ecolgical Modelling 67:49-80.

McGregor, C.A. 1984. Ecological Land Classification and Evaluation: Kananaskis Country. Volume 1 - Natural resource summary. Energy and Natural Resources Report No. T/11 - No. 10, Edmonton.

McKenney, M.S. and N.J. Rosenberg 1993. Sensitivity of some potential evapotranspiration estimation methods to climate change. Agricultural and Forest Meterology 64:81-110.

McMechan, M.E. 1988. Geology of Peter Lougheed Provincial Park, Rocky Mountain Front Ranges, Alberta. Map (scale 1:50,000). Open file 2057 Geological Survey, Ottawa.

Milus Tress Barron Ltd. 1976. Geology, Soils, Surficial Deposits and Landform Inventory and Mapping: Kananaskis Provincial Park. Alberta Parks, G 760C, Edmonton.

Moore, I.D., P.E. Gessler, G.A. Nielsen, and G.A. Peterson 1993. Soil attribute prediction using terrain analysis. Soil Science of America Journal 57:443-452.

Neilson, R.P. 1995. A model for predicting continental-scale vegetation distribution and water balance. Ecological Applications 5(2):362-385.

Nikolov, N.T. and K.F. Zeller 1992. A solar radiation algorithm for ecosystem dynamic models. Ecological Modelling 61:149-168.

O'Loughlin, E.M. 1986. Prediction of surface saturation zones in natural catchements by topographical analysis. Water Resources Research 22(5):794-804.

PCI Inc. 1996. Version 6.1 EASI/PACE software. Richmond Hill.

Peet, R.K. 1978. Latitudinal variation in souther Rocky Mountain forests. Journal of Biogeography 5:275-289.

Peet, R.K. 1981. Forest vegetation of the Colorado Front Range. Vegetatio 45:3-75.

Running, S.W. 1984. Documentation and preliminary validation of H2OTRANS and DAYTRANS, two models for predicting transpiration and water stress in western coniferous forests. USDA Forest Service Research Paper RM-252.

Scheidegger, A.E. 1991. Theoretical Geomorphology, 3rd edition. Springer-Verlag, New York.

Stephenson, N.L. 1990. Climatic control of vegetation distribution: the role of the water balance. American Naturalist 135(5):649-670.

Stevens, G.C. 1989. The latitudinal gradient in geographical range: how many species can coexist in the tropics. American Naturalist 133(2):240-256.

Storr, D. and H.L. Ferguson 1972. The distribution of precipitation in some mountainous Canadian watersheds *in* Proceedings, Geilo Symposium - Distribution of Precipitation in Mountainous Areas. World Meterological Organization. Geneva, WMO/OMM No. 326, Volume 1: 243-263.

Swan, J.M.A. 1970. An examination of some ordination problems by use of simulated vegetational data. Ecology 51(1):89-102.

Tarboton, D.G. 1997. A new method for the determination of flow directions and upslope areas in grid digital elevation models. Water Resources Research 33(2):309-319.

ter Braak, C.J.F. 1992. CANOCO - a FORTRAN program for canonical community ordination. Microcomputer Power, Ithaca.

Thornthwaite, C.W 1948. An approach toward a rational classification of climate. Geographical Review 38:55-94.

Watt, A.S. 1947. Pattern and process in the plant community. Journal of Ecology 35:1-22

Wentworth, T.R. 1981. Vegetation on limestone and granite in the Mule Mountains, Arizona. Ecology 62(2):469-482.

Whittaker, R.H. 1973. Direct gradient analysis: techniques. *in* Handbook of Vegetation Science, Volume 5: Ordination and Classification of Communities, R.H. Whittaker editor Dr. W. Junk, The Hague.

Whittaker, R.H., S.W. Buoi, W.A. Neiring, and Y.H. Havens 1968. A soil and vegetation pattern in the Santa Catalina Mountains, Arizona. Soil Science 105(6):440-450.

Whittaker, R.H., W.A. Neiring 1965. Vegetation of the Santa Catalina Mountains, Arizona II. A gradient analysis of the south slope. Ecology 46:429-452.

Wittig, R. and H. Neite 1985. Acid indicators around the trunk base of Fagus sylvatica in limestone and loess beechwoods: distribution pattern and phytosociological problems. Vegetatio 64:113-119.

Wolock, D.M., G.M. Hornberger, K.J. Beven, and W.G. Campbell 1989. The relationship of catchment topography and soil hydraulic characteristics to lake alkalinity in the northeastern United States. Water Resources Research 25:829-837.

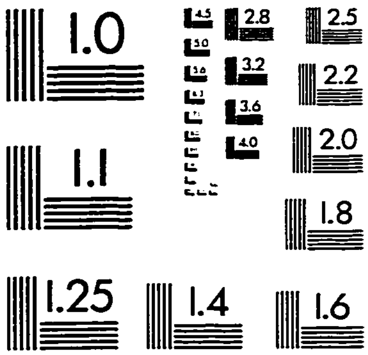
Wuenscher, J.E. and T.T. Kozlowski 1971. Relationship of gas-exchange resistance to tree-seedling ecology. Ecology 52(6):1016-1023.

Zobel, D.B., A. McKee, and G.M. Hawk 1976. Relationships of environment to composition, structure, and diversity of forest communities of the central western Cascades of Oregon. Ecological Monographs 46:135-156.

Appendix A

Common names (Archibald et al. 1996)	Species
dwarf birch	*Betula pumila* L.
false azalea	*Menziesia ferruginea* J.E. Smith
grouse-berry	*Vaccinium scoparium* Leiberg
hairy wild rye	*Elymus innovatus* Beal.
heather	*Phyllodoce* spp.
horsetail	*Equisetum pratense* Ehrh., *E. arvense* L. and *E. scirpoides* Michx.
lichen	*Cladina* spp. and *Cladonia gracilis* (L.) Wild.
prickly rose	*Rosa acicularis* Lindl.
solidago	*Solidago* spp.
spruce	*Picea engelmanni* Parry x Engelm.
subalpine larch	*Larix lyallii* Parl.
thimbleberry	*Rubus parviflorus* Nutt.
tufted hair grass	*Deschampsia cespitosa* (L.) Beauv.
buffalo berry	*Sheperdia canadensis* (L.) Nutt.
low billberry	*Vaccinium myrtyllus* L.

IMAGE EVALUATION TEST TARGET (QA-3)



150mm

6″

APPLIED IMAGE . Inc

1653 East Main Street
Rochester, NY 14609 USA
Phone: 716/482-0300
Fax: 716/288-5989