Predicting vegetation types at treeline using topography and biophysical disturbance variables

Brown, Daniel G.

Department of Geography, Michigan State University, East Lansing, MI 48824-1115, USA; E-Mail BROWN@LARIX.GEO.MSU.EDU

Abstract. The relationships between four vegetation types and variables representing topography and biophysical disturbance gradients were modeled for a study area in east-central Glacier National Park, Montana. Four treeline transition vegetation types including closed-canopy forest, open-canopy forest, meadow, and unvegetated surfaces (e.g. rock, snow, and ice) were identified and mapped through classification of satellite data and subsequent field verification. Topographic characteristics were represented using a digital elevation model and three variables derived from topoclimatic potential models (solar radiation potential, snow accumulation potential, and soil saturation potential). A combination of generalized additive and generalized linear modeling (GAM and GLM, respectively) techniques was used to construct logistic regression models representing the distributions of the four vegetation types. The variables explained significant amounts of variation in the vegetation types, but high levels of variation remained unexplained. A comparison of 'expected' and 'observed' vegetation patterns suggested that some unexplained variation may have occurred at the basin scale. A suite of tools and techniques is presented that facilitates predicting landscape-scale vegetation patterns and testing hypotheses about the spatial controls on those patterns.

Keywords: Geographic information systems; Remote sensing; Glacier National Park; Gradient modeling; Logistic regression; Topographic influences.

Abbreviations: DEM = Digital Elevation Model; GAM = generalized additive modeling; GIS = Geographic information systems; GLM = generalized linear modeling; GNP = Glacier National Park; MSI = Matrix Symmetry Index; SPI = Snow Potential Index.


Introduction

Much of the environmental variability controlling vegetation patterns at treeline might be attributable to topographical factors and their influence on climate (Daubenmire 1954; Peet 1988). However, active geomorphic and disturbance regimes can cause vegetation patterns to deviate from those predicted by climate alone (Billings 1969; Baker et al. in press). This study uses logistic models to examine the control of vegetation types at treeline by topographic and disturbance variables.

The logistic models are designed to address three sets of primary questions. First, what is the relative importance of topographic versus disturbance factors for explaining vegetation patterns within the alpine treeline ecotone, what direction and linearity do their effects have, and what is the overall level of statistical explanation? Second, how important are topographic and disturbance variables for predicting vegetation types when elevation is excluded from the modeling equations? And third, is there conspicuous spatial pattern in the differences between the observed and expected distributions of alpine treeline vegetation types, and do any such differences correspond to specific basin characteristics.

This study starts with the hypothesis that structural vegetation types are correlated with topographic gradients and biophysical disturbances. Predictive models of four vegetation associations, defined by canopy composition and structure and representing components of the treeline transition, are constructed using acquired and derived data organized within a GIS environment. Derived measures of elevation (Daubenmire 1954), direct summer season insolation potential (Bonan 1989), topographic soil moisture potential (Peet 1988), and snow accumulation potential (Daly 1984) serve as the topoclimatic descriptor variables. Boundaries of recent fires, snow avalanches, talus debris, and severe slopes are also related to the observed pattern of the alpine treeline ecotone. The observed pattern of the ecotone assumes that vegetation dynamics and their controlling influences are in equilibrium in the study area (Butler et al. in press), an assumption under dispute elsewhere (Ives & Hansen-Bristow 1983; Shankman 1984). Although predictive modeling of vegetation is not new (Austin et al. 1990; Davis & Goetz 1990; Lowell 1991; Periera & Itami 1991), the approach has not previously been applied to treeline vegetation. In addition, this study extends the predictive modeling approach by
incorporating residual analysis to identify and assess unexplained spatial patterns in the predicted vegetation.

Study area

The study area is in the east-central portion of Glacier National Park (Fig. 1), and has an area of approximately 28,000 hectares. Glacier National Park (GNP) lies in the Montana portion of the Rocky Mountains along the U.S./Canada border, straddling the Continental Divide. The Divide acts as a natural barrier between two different climatic regimes: Pacific-mari-
time climatic influences to the west and drier continental climate controls to the east. The study area was restricted to sites east of the Continental Divide.

The contemporary landscape of GNP is a rugged remnant of the Pleistocene glaciations; moraines, cirques, and glacial lakes are abundant. Elevations in the study area range from 1120 to 3006 m. The rugged topography contributes to an environment that has an active natural disturbance regime. Snow avalanches, common winter occurrences in the Park (Butler & Walsh 1990), leave swaths of herbaceous and shrubby vegetation which are often surrounded by dense forest stands (Malanson & Butler 1986). Rock and debris avalanches are not infrequent (Butler et al. 1986) and talus accumulations have developed at the bases of many of the slopes (Carrara 1990). Approximately 85% of the study area is underlain by limestone or argillite, though siltstones and mudstones also occur (Ross 1959).

Grazing and timber harvest have not been permitted in the study area since the establishment of the Park in 1910. No evidence exists to suggest that such practices have ever affected the upper treeline (Ayres 1898). An outbreak of Mountain pine beetle (Dendroctonus ponderosae) occurred within the Park between 1972 and 1984 (McGregor et al. 1985). However, a U.S. Forest Service field and aerial survey of Mountain pine beetle, Western balsam bark beetle (Dryocoetes confuses) and Spruce beetle (Dendroctonus rufipennis), indicated that the infestations of these insects were almost entirely within closed canopy subalpine forest and had minimal effect at treeline.

Climate is strongly influenced by topography in GNP (Finklin 1986). Average mean July temperature in the study area ranges from 11.7 °C to 15.8 °C, depending on elevation. Precipitation tends to be greater at higher elevations and closer to the Continental Divide. The highest rainfall amounts and deepest snow packs occur in leeward cirques, like that containing Grinnell Glacier (Fig. 1). Soils grade from Cryoboralfs and Cryborolls under the subalpine forests and meadows, respectively, to Cryochrepts and other Inceptisols at higher elevations (Anon. 1980; Butler & Malanson 1989; Nimlos & McConnell 1965). Detailed soil surveys have not been conducted for GNP.

Two treelines are evident along the eastern front of the Continental Divide (Walsh et al. 1990). The lower treeline (ca. 1200 m) grades from subalpine forest or aspen (Populus tremuloides) woodland to short-grass prairie below. The upper treeline (ca. 2100 m) is the subject of this study. Picea engelmannii and Abies lasiocarpa dominate the forests at and immediately below the upper treeline in the study area. Abies usually dominates at higher elevations and Picea at lower elevations (Pfister et al. 1977). The shade intolerant Pinus contorta var. latifolia, Populus tremuloides, and Larix occidentalis are common post-disturbance tree species. Pinus albicaulis, P. flexilis, and Larix lyallii are less common tree species restricted at treeline to environmentally severe sites.

Fig. 1. The study area in east-central Glacier National Park, Montana.
Methods

Data sources

The source data set for the terrain variables was a combination of four 7.5-minute USGS digital elevation models (DEMs) (Anon. 1987). The procedure of photogrammetric interpretation from stereographic pairs of aerial photographs by which the DEMs were produced is known to cause a number of data quality problems. Elevations are overestimated where tall, dense vegetation is present (Davis & Dozier 1990), and scanning the aerial photographs and construction of elevation profiles can lead to banding or striping errors in the data errors which systematically affect whole rows or groups of rows of data at regular intervals (Brown & Bara 1994). These errors are magnified in the estimation of slope angle and slope curvature. For this reason, the DEMs were filtered with a 3 × 5 low-pass (averaging) filter oriented in the north-south direction to correspond to the direction of the known biases (Brown & Bara 1994).

A Landsat Thematic Mapper (TM) image (August 6, 1986) was preprocessed using standardized procedures to remove geometric, spectral, and radiometric distortions (Jensen 1986). Additionally, a technique presented by Civco (1989) was used to minimize variations in spectral radiance values resulting from topographically induced solar illumination angles.

The two primary data sets (DEM and Landsat TM data) were collected using a raster (grid) data structure with a spatial resolution of 30 m. All other data sets were converted to the same data structure. The spatial resolution of the DEMs (elevations are sampled at 30 m intervals), together with the filtering to reduce systematic errors, probably resulted in an underestimation of slope angle and slope curvature values (Chang & Tsai 1991). The level of detail in the vegetation classification was also affected by the spatial detail, in part because species-level information is very difficult to resolve from spectral reflectance data obtained at a 30 m × 30 m resolution. Results were interpreted with an understanding of these limitations.

Vegetation components of treeline

Vegetation types were mapped from satellite-spectral and field-survey data using a three-stage approach. First, 50 spectral clusters in the pre-processed Landsat spectral values were identified using the ISODATA (Iterative Self-Organizing Data Analysis Technique) procedure (Anon. 1991). The visible, near-infrared, and middle-infrared bands of the electromagnetic spectrum (TM channels 3, 4, and 5), and a band ratio between channels 4 and 5 to further reduce topographic effects, were used for cluster identification. All pixels were classified into one of the 50 clusters using the maximum-likelihood classification routine (Jensen 1986).

The map of 50 classes was used to stratify the field sampling, which was designed to provide canopy composition information through transect-based sampling. 30 meter transects were used to record information on the percentage canopy composition for each forested cluster. Two transects were used to sample each spectral cluster that represented forested land. Transects were located near the center of spatially contiguous and spectrally homogeneous pixel groups that were at least 2.25 ha (3 pixels by 3 pixels) in size. In non-forested clusters, percentage ground cover was estimated by mapping categories; barren ground, shrubs, krummholz, and trees. Estimates of canopy closure for all field sites were made from 1:58 000 scale color infrared aerial photography, acquired on August 21, 1984. Finally, information about the canopy compositions, canopy closures, spectral signatures, and spatial autocorrelation (measured with the join-count statistic in relation to other classes) of the 50 classes, defined by the ISODATA clustering approach, was used to iteratively join similar spectral classes and to assign them to one of the four treeline classes or to an ‘other’ class (Brown 1992).

The class descriptions for the four treeline classes...
were based on samples acquired at 77 sites with which composition and density were measured directly for the 30 forested sites and visually estimated at the 47 non-forested sites. The closed-canopy forest class represented coniferous trees with a canopy cover of at least 80%. However, successional forests dominated by *Populus tremuloides* were included in this class, provided that *A. lasiocarpa* and/or *P. engelmannii* seedlings were common in the understory. These successional forest sites were distinguished from open-canopy forests through information on the boundaries of recent fires. Open-canopy forests were defined as those forests that were mature (i.e. the canopy was dominated by mature *A. lasiocarpa* and/or *P. engelmannii*) but had canopy densities of less than 80%. Although not dominant, *Pinus albicaulis* commonly was found on open-canopy forest sites. Meadows included a range of cover densities (20 to 80%) of grasses, forbs, and other herbaceous species, and a range of communities from sparse to dense tundra to dense subalpine meadows with scattered trees. The unvegetated component contained less than 20% vegetation cover at most sites. Spectral classes representing communities that did not belong to one of the four treeline components were not included in the analysis. These included dense brush, rock ledge, and forest/meadow transition, and are referred to as 'other'.

Field classification of 83 sites to one of the four treeline component classes or to the ‘other’ category was carried out for map accuracy assessment. Ten of the sites were in closed-canopy forest, 28 in open-canopy forest, 19 in meadow, 12 in unvegetated, and 15 in other vegetation types. An error matrix, or contingency table comparison of field-based and classification-derived vegetation type designations, indicated that the overall classification accuracy (i.e. percentage of sites correctly classified) of the four treeline components was about 84%, with a \( \kappa \) statistic of 0.80 (see below). Any classed map resulting from reclassification which has fewer classes than the original map will have a higher accuracy than the original map (Lanter & Veregin 1992). The accuracies of binomial maps of closed-canopy forest, open-canopy forest, meadow, and unvegetated locations were 98, 93, 94, and 96%, respectively. The models of the closed-canopy forest and unvegetated components were more likely to be accurate because the vegetation maps on which they were based were more accurate. Although no sensitivity analysis was performed to thoroughly test the effects of map errors on the models, the varying degrees of accuracy in the treeline components were considered in the interpretation of results.

![Fig. 3. Relative summer season insolation potential, calculated as component scores on Principal Component 1 from the analysis of eight daily insolation images throughout the summer season. Lighter tones, which indicate higher levels of summer season potential insolation, tend to occur on south-facing slopes. Heavily shaded sites are darker.](image)

**Topography-related variables**

Elevation and DEM-derived measures of slope angle, slope aspect, and slope curvature, were used to represent the climatic elements potentially important for plant distribution (Fig. 2). Calculation of DEM derivatives is a possible source of error that can propagate through the analysis and add uncertainty in the estimation of topographic gradients. Davis & Dozier (1990) demonstrated that relative map accuracy was lower for slope angle and solar exposure than for the elevation, especially in areas of steep slope or exposure gradients, like ridges and ravines. For this reason the removal of areas with highest and lowest elevations (i.e. valley bottoms and ridge tops) from the data set will likely improve the accuracy of the analysis (see Spatial sampling below).

The relative potential direct beam solar radiation (Fig. 3) was calculated by combining daily estimates of solar radiation potential at ten-day intervals throughout the summer season. The daily estimates were calculated using a program called SOLARPOT (Brown 1992). Direct solar radiation was estimated for hourly intervals throughout each of the sample days using the equation
reported by Dubayah et al. (1990). Each of the hourly estimates was summed to represent the daily potential direct insolation.

Shadowing by adjacent terrain was included in the calculation of hourly insolation by defining the position of intervening topography relative to direct rays from the sun at specific time steps. If a cell was determined to be in shadow, direct insolation was set to zero for that time step. The shadowing correction was incomplete near the edges of the study area where adjacent terrain data were not available. This edge effect may have introduced a slight bias in the analysis, but its effect was highly localized at each time step and not obvious on the summer season composite image.

Daily direct insolation estimates were treated as relative values, and combined through principal components analysis to represent a seasonally aggregated relative measure. The first principal component (Fig. 3) represented ca. 97% of the variation in the eight daily insolation samples and was used as the measure of relative summer season insolation.

The index presented by Beven & Kirkby (1979) was used to represent the topographic effects on soil moisture redistribution (Fig. 4). In a simplified form, the index is the natural logarithm of the ratio between the upslope area draining through a given location and the surface slope in °. The index was developed to model the effects of subsurface throughflow on water accumulation and soil moisture in catchments that do not experience predominantly overland flow (Beven 1978). Although soil water holding capacity has an impact on the spatial variability of soil moisture potential, no data were available to characterize such variability. The index provided a surrogate for soil moisture potential, assuming that the topographic redistribution of moisture was a more important component of soil moisture availability than was the distribution of precipitation amounts or the influence of soil characteristics. The applicability of the index for steep forested slopes is evidenced by the strong influence of topography and lateral flows on soil moisture distribution (Beven 1978). An adaptation of the index was calculated following Wolock et al. (1989). Other applications of the index for modeling surface soil water content have been presented by Burt & Butcher (1986), O’Loughlin (1986) and Moore et al. (1988).

The snow potential index (SPI) was developed to represent the potential for snow accumulation at specific sites, based on the prevailing winter wind direction,
slope curvature, and elevation (Fig. 5). The index is similar to the slope-aspect index proposed by Frank (1988) and the aspect scalar used by Burke et al. (1989). Prevailing winter winds are from the southwest (an azimuth of 225° from north) at most locations in the study area (Finklin 1986). Convex slopes tend to be more exposed and windblown than concave slopes, that tend to capture blowing snow. Wind speed varies as a direct function of elevation, as does the total amount of precipitation and the proportion that arrives as snow (Barry 1981). High snow accumulations can shorten the growing season at a site by reducing the potential number of snow-free days. The following equations, based on the slope aspect of a given location, were used to calculate the snow potential index (SPI):

for slopes where: 45° ≤ aspect < 225°
SPI = \((225 - A_s) \times C \times (E - E_{min})/E_{range}\) (1)

for slopes where: 0° ≤ aspect < 45°
SPI = \((180 - (45 - A_s)) \times C \times (E - E_{min})/E_{range}\) (2)

for slopes where: 225° ≤ aspect < 360°
SPI = \((135 - (360 - A_s)) \times C \times (E - E_{min})/E_{range}\) (3)

where: SPI = Snow Potential Index
C = unitless curvature
E = elevation in m
A_s = slope aspect in ° clockwise from north

Higher values of the index were obtained on slopes that were leeward (i.e. closer to northeast exposure), concave, and at higher elevations. Curvature was averaged from measures derived for transects oriented in the four cardinal directions (see Brown 1991). Curvature values less than one indicated convexity, greater than one concavity, and a value of one constant slope. The values used for \(E_{min}\) and \(E_{range}\) were derived from the DEM for the entire study area and were 1120 m and 1886 m, respectively.

The SPI was compared with the locations of glaciers digitized from the 7.5-minute topographic quadrangles and late-lying snow packs identified on the August 6, 1986 Thematic Mapper image to verify the effectiveness of the index. An ANOVA test on a systematic sample of sites, to reduce spatial autocorrelation, indicated that glaciers or snow covered sites had significantly higher index values than did other sites (α = 0.0001), but that the fit of the relationship was weak (\(R^2 = 0.09\)) given the relatively small number of glaciers and snow-covered sites in the image (29 out of 816 cells tested).

Table 1. Relationships between rotated factors and topographical variables (i.e. factor loadings).

<table>
<thead>
<tr>
<th>Factor</th>
<th>Factor 1</th>
<th>Factor 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elevation</td>
<td>-0.041</td>
<td>0.688</td>
</tr>
<tr>
<td>Solar potential</td>
<td>0.758</td>
<td>0.204</td>
</tr>
<tr>
<td>Soil moisture potential</td>
<td>-0.005</td>
<td>-0.580</td>
</tr>
<tr>
<td>Wind/snow potential</td>
<td>-0.739</td>
<td>0.352</td>
</tr>
</tbody>
</table>

**Factor analysis**

The four topographic variables were significantly correlated with each other. Absolute Pearson’s \(r\) values ranged from 0.15 to 0.59. To reduce the redundancy in the variables and the risks associated with multicollinearity in regression, factor analysis was used to extract orthogonal variables from the four derived topographic variables. Four principal factors calculated from the variables had eigenvalues of 1.57, 1.26, 0.86, and 0.30 for Factor 1 through Factor 4, respectively. Only the first two factors, which had eigenvalues greater than one, were used in subsequent analyses (Mulaik 1972; Preisendorfer et al. 1981).

The two rotated factors were constructed using a Varimax orthogonal factor rotation (Anon. 1985) in order to improve their interpretability. The factor loadings (Table 1) indicated the strength of relationship between each topographic variable and each factor. Factor 1 was strongly related to direct beam solar radiation (a positive relationship) and wind/snow potential (a negative relationship). High values of Factor 1, therefore, indicated a high degree of exposure to wind and direct beam radiation, while lower values indicated more sheltered and cooler sites and, therefore, a greater likelihood of snow lingering into the growing season. Both solar potential and wind/snow potential loaded highly on Factor 1 because of the similarities in the directionality of the wind patterns (from the southwest) and the incoming solar radiation (from the south).

Factor 2 represented elevation (positively) and topographic soil moisture potential (negatively). Wind/snow potential also was positively related to Factor 2, but had a lower loading (0.35). Higher values of Factor 2 corresponded to higher elevations, higher snow potentials, and lower soil moisture potentials.

The two derived rotation factors were similar in function to the elevation (Factor 2) and relative topographic moisture (Factor 1) gradients commonly used to explain vegetation patterns. However, by quantifying the soil moisture, snow accumulation, and solar radiation potential patterns and their relationships with the resultant factors, the description of the biophysical processes affecting vegetation patterns are improved. Further-
more, the approach allows for the automation and repeated calculation of these topoclimatic gradients, and the extension of analyses to sites not been visited in the field.

**Disturbance-related variables**

Two variables were derived to represent past disturbances likely to have influenced contemporary vegetation patterns. A fire history map representing all burns within the study area larger than approximately 120 ha and younger than approximately 80 yr old was obtained from Glacier National Park Headquarters (Van Horn pers. comm.). This map was augmented with information regarding ‘recently burned’ areas as reported by Ayres (1898), digitized and converted to a raster format compatible with ERDAS software. Snow avalanche paths for the study area had been previously mapped and digitized (Butler & Walsh 1990). Slopes steeper than 34° were mapped from the digital elevation model to represent sites too steep for soil development and plant community establishment. Talus slopes, mapped by Carrara (1990), identified areas where geomorphic processes are likely to have impeded forest establishment and growth (Moriwasa 1966). The areal extent of each of these features was incompatible in a single map that represented geomorphic processes capable of affecting plant communities at alpine treeline.

**Spatial sampling**

A systematic sampling scheme was used to reduce the level of spatial autocorrelation in the data (Haining 1980). High spatial autocorrelation can bias statistical tests of correlation between variables and lead to the incorrect rejection of a null hypothesis. By increasing the distance between samples, spatial autocorrelation and sample size are reduced. Sample size decreases quadratically as a function of sample distance. A sampling interval of 20 pixels (600 m in the north-south and east-west directions) was employed to balance the need to reduce data bias as a function of location and to generate a sufficiently large sample ($n = 816$).

Moran’s coefficient (MC) was used to represent the degree of spatial autocorrelation (Cliff & Ord 1981; Odland 1988). The MC was calculated using the IDRISI (version 3.2) GIS software (Eastman 1990). MC has a possible range from $+1$ to $-1$ where high positive and negative values indicate a high degree of positive and negative spatial autocorrelation, respectively, and zero indicates no spatial autocorrelation (a random distribution). At the 20 pixel lag, closed-canopy forest, open-canopy forest, meadow, and unvegetated surfaces had MC values of 0.26, 0.18, 0.12, and 0.21, respectively. MC values for the independent variables, Factors 1 and 2, were 0.51 and 0.78, respectively (all of these values of MC were significant at the 0.05 confidence level).

The data set was subdivided further to meet the stated objectives of the research. First, the analysis was limited to sites east of the Continental Divide to remove variations in vegetation patterns that may result from regional climatic differences. Second, to focus on the relationships between vegetation and the topoclimatic factors at treeline, an elevation zone was identified that encompassed the range of treeline conditions. Sites at elevations too low for treeline to occur (below 1600 m) were removed, as were sites that were non-vegetated (above 2350 m). This elevation range was selected by using on-screen cursor control in ERDAS to display the elevations and vegetation types at selected sites throughout the study area. The data set resulting from this stratification contained 523 samples.

A validation data set was constructed for assessing the accuracy of the predictive models. The validation data set was sampled from the full raster data set, at a sampling interval of 20 pixels (600 m), but offset from the originally sampled data set by 10 pixels (300 m). The sample size of this validation data set was nearly identical to the sample size of the original data set.

**Statistical analysis**

Generalized additive and linear models (GAM and GLM, respectively) were used to construct logistic regression models representing the distributions of the four associations. The Generalized Additive Interactive Modeling software (GAIM) was used for generalized additive modeling (Hastie & Tibshirani 1990), whereas the Statistical Analysis Software (SAS version 6.06) was used for generalized linear modeling (Anon. 1985). Separate models were constructed for each of the four treeline vegetation types using topographical factors and biophysical disturbance variables.

Logistic regression models were constructed in two stages. The first stage involved constructing generalized additive models (GAMs) for each of the treeline components. The GAM procedure models the response of a binary variable to a predictor variable(s) through a smoothing operation (Hastie & Tibshirani 1990; Yee & Mitchell 1991). The smoothed GAM functions were visually examined to fit an appropriate polynomial approximation that was estimated through generalized linear modeling (McCullagh & Nelder 1989). Linear and second-order polynomial approximations were judged sufficient to estimate the GAM responses in all cases. Three functions required quadratic approximations (Fig. 6), while all others were not significantly different from linear (see Hastie & Tibshirani 1990 for a
discussion of the test for linearity). In each of the non-linear cases, the forms of the responses were similar to the Gaussian form expected in the case of biological gradients. The logit link function was used to convert linear predictor values, which were estimated through GLM, to vegetation type probability values.

Residual analysis

The fit and accuracy of the derived models were characterized using $R^2$ and the $\kappa$ statistic (Cohen 1960; Bishop et al. 1975), respectively. $\kappa$ indicates the level of model accuracy (i.e. proportion of correctly classified pixels compared with the original classification map) with respect to the accuracy expected with a random assignment of pixels to classes and was used to assess the accuracy of individual models and the overall accuracy of the four models combined. A program by Congalton (1991) was used to compare $\kappa$ values calculated from different contingency tables (e.g. comparing accuracies of different models), through the use of a test statistic which is based on the standard normal deviate.

MC values were calculated to assess the amount of spatial autocorrelation in the model residuals at the sampling interval used in model development (i.e. 20 pixels). Spatially autocorrelated residuals in the derived vegetation patterns may indicate a missing, spatially autocorrelated predictor variable or a spatial process absent from the model (Cliff & Ord 1981).

The probability of occurrence of each component was calculated for each of the derived treeline models and for each sample within the validation data set. The presence/absence of a component was characterized for each cell, depending upon a probability threshold. The resultant pattern for each individual component was compared to the observed pattern using the $\kappa$ statistic, calculated from the two-by-two contingency table.

A map of the ‘expected’ pattern of the four vegetation types was constructed from the logistic regression models. The four best logistic regression models (one for each treeline component) were used to classify each grid cell in the study area as one of the four components. For each treeline component, the model with the highest significant $\kappa$ value was used. Overall ‘expected’ and ‘observed’ vegetation patterns were compared visually and through contingency table analysis to assess the fit of the four models taken together. The contingency table was constructed using a random sample of 300 cells from each map.

Residual analysis stratified by drainage basins was used to explore the possibility of basin-scale controls on vegetation patterns at treeline. Four-by-four contingency tables were constructed for each drainage basin and the $\kappa$ statistic was calculated. A matrix symmetry index (MSI) was developed to determine whether the drainage basins were more or less forested than ‘expected’ based on the models:

$$\text{MSI} = \log \left( \frac{\sum_{i=1}^{6} U_i}{\sum_{i=1}^{6} O_i} \right)$$

where: $\text{MSI} =$ matrix symmetry index; $U_i =$ cells in the $4 \times 4$ contingency table which represented under-predicted pixels (i.e. pixels which actually - from satellite observation and interpretation - had more tree cover than the models predicted); $O_i =$ cells in the $4 \times 4$ contingency table which represented over-predicted pixels.
Table 2. Significant variables and estimated coefficients for each treeline component model. In Model 1 the only predictor variable was elevation; Model 2 contained only the two topographic factors (F1, F2); Model 3 included the two topographic factors and disturbance variables (Geo = Geomorph). *

<table>
<thead>
<tr>
<th>Model 1</th>
<th>Closed forest</th>
<th>Open forest</th>
<th>Meadow</th>
<th>Unvegetated</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elev</td>
<td>+14.99</td>
<td>-48.82</td>
<td>-52.93</td>
<td>-14.40</td>
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<tr>
<td>Elev2</td>
<td>-0.009 Elev</td>
<td>+0.054 Elev</td>
<td>+0.051 Elev</td>
<td>+0.007 Elev</td>
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<table>
<thead>
<tr>
<th>Model 2</th>
<th>Closed forest</th>
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<th>Meadow</th>
<th>Unvegetated</th>
</tr>
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<tbody>
<tr>
<td>F1</td>
<td>-11.77</td>
<td>+10.03 F1</td>
<td>-1.59 F1</td>
<td>-2.02 F2</td>
</tr>
<tr>
<td>F12</td>
<td>+15.12 F1</td>
<td>+4.96 F2</td>
<td>+3.4 F1</td>
<td>-0.35 F1</td>
</tr>
<tr>
<td>F2</td>
<td>-1.85 F2</td>
<td>-1.31 F22</td>
<td>+4.96 F2</td>
<td>+1.18 F2</td>
</tr>
<tr>
<td>Geo</td>
<td>-1.78 Geo</td>
<td>+0.78 F22</td>
<td>+1.07 Geo</td>
<td>+0.76 Fire</td>
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<table>
<thead>
<tr>
<th>Model 3</th>
<th>Closed forest</th>
<th>Open forest</th>
<th>Meadow</th>
<th>Unvegetated</th>
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<tbody>
<tr>
<td>F1</td>
<td>-11.91</td>
<td>+9.63 F1</td>
<td>-10.38</td>
<td>-5.33</td>
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<tr>
<td>F12</td>
<td>+15.12 F1</td>
<td>+5.05 F2</td>
<td>+1.48 F1</td>
<td>-0.33 F1</td>
</tr>
<tr>
<td>F2</td>
<td>-1.85 F2</td>
<td>-1.08 F22</td>
<td>+5.49 F2</td>
<td>+1.59 F2</td>
</tr>
<tr>
<td>Geo</td>
<td>-1.78 Geo</td>
<td>+0.78 F22</td>
<td>+1.07 Geo</td>
<td>+0.76 Fire</td>
</tr>
</tbody>
</table>

* The sign represents the direction of the effect (+ or -). The first listed number for each model is the estimated intercept; all other numbers are model coefficients.

The amount of tree cover in each class increased sequentially from unvegetated through meadow and open-canopy forest to closed-canopy forest. A MSI value of zero indicated an equal number of over-predicted and under-predicted pixels. Positive values of the MSI represented vegetation patterns that had more tree cover than expected, whereas negative values indicated less tree cover than expected. The index was used to compare drainage basins and their relative degrees of forest cover compared with the model expectations. The map of residuals was classified to indicate whether pixels were correctly, over-predicted, or under-predicted.

(i.e. pixels which actually - from satellite observation and interpretation - had less tree cover than the models predicted).

Fig. 7. Response surfaces showing the relationships between the vegetation types and the two topoclimatic factors. The contour lines represent lines of equal probability of vegetation type occurrence. A. Closed-canopy forest; B. Open-canopy forest; C. Meadow; D. Unvegetated.
Table 3. Measures of fit ($R^2$), accuracy ($\kappa$), and residual spatial autocorrelation (MC) for each logistic regression model shown in Table 2.

<table>
<thead>
<tr>
<th></th>
<th>Closed forest</th>
<th>Open forest</th>
<th>Meadow</th>
<th>Unvegetated</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model 1</td>
<td>$R^2$</td>
<td>0.28</td>
<td>0.08</td>
<td>0.05</td>
</tr>
<tr>
<td></td>
<td>$\kappa$</td>
<td>0.35 *</td>
<td>0.17</td>
<td>0.13</td>
</tr>
<tr>
<td></td>
<td>MC</td>
<td>0.08 *</td>
<td>0.16 *</td>
<td>0.12 *</td>
</tr>
<tr>
<td>Model 2</td>
<td>$R^2$</td>
<td>0.29</td>
<td>0.09</td>
<td>0.06</td>
</tr>
<tr>
<td></td>
<td>$\kappa$</td>
<td>0.36 *</td>
<td>0.15 *</td>
<td>0.10 *</td>
</tr>
<tr>
<td></td>
<td>MC</td>
<td>0.09 *</td>
<td>0.16 *</td>
<td>0.11 *</td>
</tr>
<tr>
<td>Model 3</td>
<td>$R^2$</td>
<td>0.35</td>
<td>0.10</td>
<td>0.07</td>
</tr>
<tr>
<td></td>
<td>$\kappa$</td>
<td>0.46 *</td>
<td>0.20 *</td>
<td>0.07 *</td>
</tr>
<tr>
<td></td>
<td>MC</td>
<td>0.10 *</td>
<td>0.16 *</td>
<td>0.11 *</td>
</tr>
</tbody>
</table>

* = Value is significant at $\alpha = 0.05$.

Results and Discussion

Topography, disturbance, and vegetation relationships

Three GLM models were produced to estimate the response of each of the four treeline components to the independent variables (Table 2). The first model, representing the response of each component to elevation, was constructed as a null model for comparison to the other derived models. The second model was constructed using the topographic factors as the only predictor variables, whereas the third model included the biophysical disturbance variables and topographic factors. The gradient diagrams (Fig. 7) represent a graphical depiction of the estimated relationships between each of the treeline components and the two topographical factor gradients (the second model).

Overall, the models were weakly significant. The topographic and disturbance variables did not explain the majority of variation in the vegetation patterns. Missing variables, use of surrogates for topoclimatic data, and the aggregated level of analysis limited the levels of model explanation. Nonetheless, the statistical significance of the models warrants their interpretation.

The lower levels of fit and accuracy for the models of open-canopy forest and meadow (Table 3) suggested that these classes might be better explained by different gradients. For example, soil depth and texture may have contributed to the explanation of open-canopy forest and meadow classes. Also, meadow and open-canopy forest can have larger variation on both the upper and lower elevation edge, whereas closed-canopy forest and non-vegetated are fixed on one side of the ecotone. Additionally, the lower accuracies of the binomial maps of open-canopy forests and meadows probably contributed to their lower fits and accuracies.

In three out of four cases, the $\kappa$ values generated by models that incorporated both topoclimatic and disturbances factors were higher than those generated by models that used elevation as the only descriptor variable (Table 3). However, only in the case of the unvegetated component was the improvement in model performance by inclusion of disturbance significant at the 0.05 confidence level. Also, for all of the treeline components, Factor 2, which was strongly correlated with elevation, remained the most significant variable in models containing topoclimatic factors. This indicated that elevation was the strongest overall control on component patterns.

Closed-canopy forests were more likely to occur at lower elevations and at medium to high levels of exposure to wind and solar radiation (Table 2 and Fig. 7a). Sheltered sites probably experienced persistent snow accumulations that reduced the growing season length.

The significance of fire in the closed-canopy forest model (Table 2) was an artifact of the vegetation classification methods. Fire boundaries were used as an aid in classifying closed-canopy forests. Burned sites were classified as closed-canopy forest if they showed dense cover of seral species and regeneration of *Abies lasiocarpa* and/or *Picea engelmannii*. Therefore, no conclusions about the influence of fire can be drawn from the closed-canopy and open-canopy forest models.

Factor 2 and the elevation variable were significantly related to open-canopy forest (Table 2 and Fig. 7b). However, the occurrence of the mapped geomorphic conditions significantly reduced the likelihood of closed-canopy and open-canopy forest occurrence. Shallow soil depths may have better explained the distribution of the open-canopy forest class.

Alpine meadow was the most difficult vegetation type to model because of its broad range of vegetation densities. This vegetation type included a mixture of tundra, meadow, and krummholz. The meadow class occurred at higher elevations than the forested components and was more likely to occur on exposed sites (Table 2 and Fig. 7c). The influence of exposure is probably related to its influence on microclimate, especially temperature as controlled by solar radiation. Growing season length, as affected by snow-pack accumulation, may also play a role in the occurrence of meadows. Sheltered sites are more likely to be cooler and experience snow cover for longer periods of time. Fire had a positive influence on the meadow communities. This vegetation type may, in some cases, be established and maintained by fire occurrence. Peet (1988) indicated that soil texture also can be important for explaining meadow distributions. Where soils are deep and fine-
Table 4. Significant variables and estimated coefficients for each treeline component model at each elevation zone. All significant variables are listed; where no model is listed none of the variables explained significant levels of variation. Variables are as in Table 2.

<table>
<thead>
<tr>
<th>Elevation Zone (in m)</th>
<th>1600-1750</th>
<th>1900-2050</th>
<th>2200-2350</th>
</tr>
</thead>
<tbody>
<tr>
<td>Closed forest</td>
<td>+0.29</td>
<td>-0.86</td>
<td>-2.179</td>
</tr>
<tr>
<td></td>
<td>-2.69 Geo</td>
<td>-1.41 Geo</td>
<td>-42.75 Geo</td>
</tr>
<tr>
<td>Open forest</td>
<td>-0.54</td>
<td>-44.13 Fr</td>
<td>-46.3 Geo</td>
</tr>
<tr>
<td></td>
<td>-4.38 Fr</td>
<td>-2.19 Geo</td>
<td>+1.41 F1</td>
</tr>
<tr>
<td></td>
<td>-46.08 Geo</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Meadow</td>
<td>-</td>
<td>-</td>
<td>-4.019</td>
</tr>
<tr>
<td></td>
<td>+0.98 F1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Unvegetated</td>
<td>-</td>
<td>+0.525</td>
<td>-0.545</td>
</tr>
<tr>
<td></td>
<td>-0.78 F1</td>
<td>+1.61 Geo</td>
<td>+1.67 Geo</td>
</tr>
</tbody>
</table>

* The sign represents the direction of the effect (+ or –). The first listed number for each model is the estimated intercept; all other numbers are model coefficients.

Table 5. Measures of fit ($R^2$), accuracy $(\kappa)$, and residual spatial autocorrelation (MC) for each logistic regression model, by elevation zone, shown in Table 4.

<table>
<thead>
<tr>
<th>Elevation Zone (in m)</th>
<th>1600-1750</th>
<th>1900-2050</th>
<th>2200-2350</th>
</tr>
</thead>
<tbody>
<tr>
<td>Closed forest</td>
<td>0.10</td>
<td>0.05</td>
<td>0.16</td>
</tr>
<tr>
<td>$\kappa$</td>
<td>0.24 *</td>
<td>0.11 *</td>
<td>0.11 *</td>
</tr>
<tr>
<td>MC</td>
<td>0.28 *</td>
<td>0.71 *</td>
<td>0.39 *</td>
</tr>
<tr>
<td>Open Forest</td>
<td>0.25</td>
<td>0.11</td>
<td>0.12</td>
</tr>
<tr>
<td>$\kappa$</td>
<td>0.25 *</td>
<td>0.12 *</td>
<td>0.07</td>
</tr>
<tr>
<td>MC</td>
<td>-0.05</td>
<td>0.28 *</td>
<td>0.08</td>
</tr>
<tr>
<td>Meadow</td>
<td>-</td>
<td>0.11</td>
<td>-</td>
</tr>
<tr>
<td>$\kappa$</td>
<td>-</td>
<td>0.20</td>
<td>-</td>
</tr>
<tr>
<td>MC</td>
<td>-</td>
<td>0.09</td>
<td>-</td>
</tr>
<tr>
<td>Unvegetated</td>
<td>-</td>
<td>0.16</td>
<td>0.15</td>
</tr>
<tr>
<td>$\kappa$</td>
<td>-</td>
<td>0.44 *</td>
<td>0.39 *</td>
</tr>
<tr>
<td>MC</td>
<td>-</td>
<td>0.15 *</td>
<td>0.39 *</td>
</tr>
</tbody>
</table>

* Value is significant at $\alpha = 0.05$.

textured, a dense sod can form inhibiting tree regeneration.

The unvegetated sites had their highest probability of occurrence at high elevations and in sheltered locations (Table 2 and Fig. 7d) where deep snow-packs occurred. Glaciers and semi-permanent snow packs were located on the most sheltered sites, where temperatures were lower and snow accumulation was greater. Where snow avalanche paths, talus slopes, and steep slopes exist, sites are more likely to be unvegetated.

Models by elevation zone

Separate models were constructed by elevation zone to examine the relative influences of the topographic and disturbance variables on vegetation pattern. Table 4 lists the models constructed by elevation zone and by treeline component. Table 5 lists the $R^2$, $\kappa$ and MC values for the same models.

Geomorphic disturbances were significantly related to vegetation patterns, but explained only a small portion of the variation in the occurrence of the vegetation types. The pattern of closed-canopy forest in elevation zones 1 through 3 was significantly related to geomorphic disturbances. Geomorphic disturbances also were significantly (although weakly) related to the pattern of open-canopy forests in elevation zone 4, and the unvegetated component was positively related to geomorphic disturbance in zones 3 and 4. The forest

classes were removed or never became established and, in some cases, were replaced by the unvegetated class at lower elevation sites where the geomorphic processes were active. In many cases, snow avalanche paths were revegetated by dense brush.

At the highest elevations of its range, the open-canopy forest tended to occur on more exposed, and therefore warmer, sites. Similarly, meadows occurred on more exposed sites within zone 3. More sheltered sites within zones 3 and 4 were given over to unvegetated surfaces.

Overall residual patterns

The Moran coefficient (MC) values indicated that, for the majority of the models, significant residuals in the spatial autocorrelation remained in most of the models (Tables 3 and 5). The processes of regeneration at treeline might explain some inherent spatial autocorrelation in vegetation patterns. For example, sites nearer to forested sites may be more likely to be colonized than sites further away from forested sites. Alternatively, the residual spatial autocorrelation may be attributable to other spatially autocorrelated predictor variables (e.g. soil type).

The expected treeline component pattern (Fig. 8b), classified on the basis of logistic model probabilities, was compared with the actual occurrence of the four treeline components from the satellite-based classification (Fig. 8a). Fig. 9 shows areas of over or under-prediction based on that comparison. Only areas occurring within the 1600-2350 m elevation range, east of the
Agreement
Under-prediction
Over-prediction
Basin outline

Continental Divide, and belonging to one of the four treeline components are shown in Figs. 8a, 8b, and 9.

Of the 300 cells used to assess the differences between the ‘expected’ and ‘observed’ vegetation patterns, 55.5 % were classified identically on both maps (Table 6). All pixels classified as ‘other’ in the vegetation map were excluded from the contingency table. The \( \kappa \) statistic for the contingency table was 0.38 \( \pm 0.08 \), indicating a significant similarity between the expected and actual classification patterns at the 0.05 confidence level. The matrix symmetry index (MSI) (Table 6) was 0.08, indicating that the residuals of vegetation patterns were nearly balanced (i.e. no great degree of under or over-prediction).

A map (as in Fig. 8b) and a contingency table (as in Table 6) were constructed for the four elevation-only models (Model 1 in Tables 2 and 3) for comparison. The resultant matrix had a \( \kappa \) statistic of 0.259 \( \pm 0.080 \), indicating a significant level of similarity between the expected and actual patterns. The test statistic (z-score) for the difference between the best-model classification and the elevation-only classification (2.023) indicated that the best-model classification was slightly, but significantly, better than the elevation-only classification at the 0.05 confidence level.

Residuals by drainage basin

As expected on the basis of component model accuracies, the majority of misclassifications occurred in the middle elevations (Fig. 9), between the closed-canopy forest and unvegetated components. The misclassifications (i.e. over or under-predictions) appeared to be spatially autocorrelated at the basin scale. For example, the majority of misclassifications in the Siyeh Creek...
basin (see Fig. 1) was due to under-prediction, whereas the majority of misclassifications in Cataract Creek basin (see Fig. 1) was due to over-prediction (Fig. 9). Such basin-scale differences also were identified in the MSI values for those basins (Table 7; 0.93 and –0.73, respectively).

The $\kappa$ accuracies of the models differed quite substantially between the drainage basins (Table 7). All but one of the basins had a $\kappa$ statistic that was significantly higher or lower than the overall $\kappa$ value (0.38). In some cases, higher $\kappa$ values resulted because of higher percentages of closed-canopy forest or unvegetated components for basins whose models had better fits. The patterns of model residuals (Fig. 9) in the six basins were assessed to suggest additional explanatory variables or processes for model incorporation at the basin scale.

In the Apikuni, Baring, and Cataract Creek basins (see Fig. 1), the MSI value of the residual patterns suggested a depression of the treeline ecotone relative to model expectations. Open forests were dominant where dense, closed-canopy forests were expected, and meadows were dominant where open-canopy forests were expected. Although, detailed data on wind patterns within the study area were not available, anecdotal evidence and field observations suggested that local wind patterns and intensities may partially account for model discrepancies in at least two of the basins. Strong winds were noted in the Baring and Apikuni Creek basins during the summers of 1990 and 1991. Indeed, the forest boundary was abrupt in both basins and flagged *Picea* and *Abies* (i.e. trees with branches on only the lee sides of the trunks) were present near the basin outlets. The winds may have been caused by strong temperature gradients between the largely southeast-facing basins and the large lakes at their outlets - Lake Sherburne and St. Mary Lake. Therefore, strong, desiccating winds may have contributed to the depression of vegetation patterns in Apikuni and Baring Creeks relative to the models. Additional field work should target these basins to further explore the reasons for the lowered treeline.

The discrepancies between vegetation patterns and model predictions in the Cataract and Siyeh Creek basins may have been related to general basin configuration. The Siyeh Creek basin, which exhibited more forested area than expected, was the only basin that was oriented towards due south. Conversely, the Cataract Creek basin was the only basin which opened towards due north, and it had a depressed treeline relative to the models. The energy budgets within each of these basins may have been altered by their orientations in such a way that local direct insolation estimates were insufficient for characterizing local thermal properties. In addition to a site’s location relative to solar angles, the overall orientation of the basins probably affected the energy balance at sites within the basins. Characterization of indirect insolation, resulting from re-radiation from surrounding terrain, may be necessary to adequately represent the effects of orientation in such basins (Dozier et al. 1981; Dubayah et al. 1990).

Overall, vegetation tended to be under-predicted in the Reynolds Creek basin (MSI = 0.73). Sites with more tree cover than expected were concentrated in the broad, gentle uplands just south of Logan Pass. It is likely that the form of the topography in this area (i.e. a high elevation, broad and gently sloping, hanging valley) explains the deviations. The gentle nature of the terrain permits the establishment of denser forest cover than expected. The topographic variables used in the models appear to be insufficient for characterizing the topographic situation of these sites. An additional landform variable representing different classes of landforms (e.g. ridges, hanging valleys, and valley bottoms) might help explain some of the vegetation patterns in areas like this.

---

**Table 6.** Contingency table comparing pixel classifications using the logistic regression models and the satellite spectral data (i.e. expected and observed, respectively).

<table>
<thead>
<tr>
<th>Spectral classification</th>
<th>Logistic regression model classification</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Closed</td>
</tr>
<tr>
<td></td>
<td>forest</td>
</tr>
<tr>
<td>Closed forest</td>
<td>21</td>
</tr>
<tr>
<td>Open forest</td>
<td>19</td>
</tr>
<tr>
<td>Meadow</td>
<td>4</td>
</tr>
<tr>
<td>Unvegetated</td>
<td>1</td>
</tr>
</tbody>
</table>

**Table 7.** Level of agreement ($\kappa$) and nature of deviations (symmetry), by drainage basin, between classifications from the logistic regression models and the satellite spectral data.*

<table>
<thead>
<tr>
<th>Basin</th>
<th>$\kappa$ Matrix</th>
<th>Symmetry</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apikuni Creek</td>
<td>0.24 (+)</td>
<td>-0.60</td>
</tr>
<tr>
<td>Baring Creek</td>
<td>0.20 (+)</td>
<td>-0.62</td>
</tr>
<tr>
<td>Boulder Creek</td>
<td>0.44 (+)</td>
<td>-0.03</td>
</tr>
<tr>
<td>Canyon Creek</td>
<td>0.41 (+)</td>
<td>-1.05</td>
</tr>
<tr>
<td>Cataract Creek</td>
<td>0.26 (-)</td>
<td>-0.73</td>
</tr>
<tr>
<td>Reynolds Creek</td>
<td>0.32 (-)</td>
<td>0.73</td>
</tr>
<tr>
<td>Rose Creek</td>
<td>0.42 (+)</td>
<td>0.79</td>
</tr>
<tr>
<td>Siyeh Creek</td>
<td>0.28 (-)</td>
<td>0.93</td>
</tr>
<tr>
<td>Swiftcurrent Creek</td>
<td>0.36 (-)</td>
<td>-0.06</td>
</tr>
<tr>
<td>Twin Lakes</td>
<td>0.11 (-)</td>
<td>1.01</td>
</tr>
<tr>
<td>Wilbur Creek</td>
<td>0.45 (+)</td>
<td>-0.03</td>
</tr>
</tbody>
</table>

* A sign following $\kappa$ indicates that the basin had a significantly better (+) or significantly worse (-) fit compared to the entire study area. No sign means no significant difference.

---
Conclusions

Remote sensing, geographic information systems (GIS), and statistical and spatial analyses were used to examine the relationships between selected components of the alpine treeline ecotone and topographic and disturbance descriptor variables. Satellite image processing was used to characterize the spatial pattern of the observed position of the alpine treeline ecotone; spatial coverages within a GIS were processed and integrated to derive variables that represented sets of biophysical processes and disturbances; generalized linear and additive models were developed to map the expected position of the ecotone; spatial autocorrelation was used to assess the possible ordering of values as a function of location; and regression residuals were mapped to explore model performance as a function of scale.

Landsat Thematic Mapper digital data were transformed to yield a set of spectral channels that reduced spectral biasing as a consequence of topography and represented a sensitivity to leaf pigmentation, chlorophyll content, and leaf moisture in mapping the ecotone. The mapped patterns were modeled through a set of derived site variables and indices that represented biophysical processes and site characteristics. The shapes of the response functions derived by generalized additive modeling and used in the logistic regression modeling were consistent with ecological processes that control composition of vegetation communities (i.e. linear and near-gaussian relationships). Elevation was the most significant variable related to vegetation patterns for the four treeline components modeled. The derived topoclimatic models of solar radiation, snow accumulation, and topographic soil moisture potential also were significant predictors of the observed vegetation patterns. Geomorphic processes and disturbance agents were important in the steep, glaciated topography of the Park where they apparently served to influence the pattern of the vegetation at the local scale. Information regarding the frequency, magnitude, and nature of disturbance processes (Overpeck et al. 1990; Baker et al. 1991) needs to be represented in spatial models of vegetation dynamics.

Because topography and climate are significantly related to vegetation patterns within the ecotone, digital elevation models proved critical in characterizing landscape conditions related to energy and moisture inputs. The integrative nature of the GIS facilitated derivation of variables, spatial alignment of data sets, reformatting of data to meet modeling requirements, and spatial examination of model residuals. Data representing biophysical disturbances were converted from analog to digital data within the encoding processing and organized as spatial data layers for subsequent modeling. Interfaces between GIS and modeling software were important to the objectives of this research.

The results of the predictive modeling suggested the importance of alternate variables (e.g. soil depth and texture) for defining the spatial pattern of the alpine treeline ecotone, and the significance of integrating variables that represented different spatial scales. Mapping regression residuals identified the importance of disturbance at the basin scale and the possible importance of differences in basin-wide energy budgets resulting from general orientation. Residual maps can also be used to identify sites where additional field studies might be target because of significant deviations between the observed and the expected vegetation patterns. Finally, maps of regression residuals might be used to suggest sites that are more or less sensitive to climate changes exerted on the ecotone by identifying the magnitude and direction of differences in the observed versus expected patterns of vegetation.

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