



Topographic controls on snow distribution, soil moisture, and species diversity of herbaceous alpine vegetation, Niwot Ridge, Colorado

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[1] The nature of the snowpack has the potential to strongly influence the patterns of alpine plant productivity and composition by governing soil moisture levels, growing season duration and the thermal regime of alpine soils. This study evaluates these relationships by modeling the interrelationships of snow depth, snow water equivalent (SWE), snow disappearance rate, soil moisture, attributes of the alpine plant community and selected terrain factors using decision-tree techniques at Niwot Ridge, Colorado Front Range. The modeling results showed a strong correlation ($r^2 > 0.9$, $P < 0.001$) between the snow disappearance rate and SWE and terrain factors that control the degree of shelter and exposure of a given local and elevation. The model was sufficiently robust to predict the spatial distribution of the snowpack for 12 years that exhibited average snow fall ($r^2 = 0.8$, $P < 0.001$), but yielded lower correlation ($r^2 = 0.2$, $P < 0.001$) in drought years. Soil moisture was significantly correlated ($r^2 = 0.7$, $P < 0.001$) with snow-fall amounts and terrain factors; however, meltwater and summer rain offset the potential soil moisture deficit in windward sites. Annual plant biomass did not correlate well with snow attributes and soil moisture because the cascading impact of topography on snowpack and soil moisture was not well captured by measurements of aboveground biomass. In contrast, the species richness index was significantly correlated with snow depth and soil moisture ($r^2 = 0.7$, $P < 0.001$), thereby demonstrating the importance of snow on some attributes of the alpine plant community.

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1. Introduction

[2] Factors controlling plant growth and primary production in the alpine tundra ecosystem include air temperature, wind exposure, short growing season, snow cover and antecedent soil moisture [Billings, 1988; Walker *et al.*, 1993]. Among these physical attributes, snow cover (snowpack distribution and duration) is considered the most critical because of its direct effect on soil temperature, soil moisture, and duration of the growing season, which in turn, control nutrient availability in the alpine environment [Burns and Tonkin, 1982; Williams *et al.*, 1998]. Snow cover also affects cycling of nitrogen (N) and carbon (C) by influencing microbial activity in subnivalian soils before plants become active [Brooks *et al.*, 1996]. The duration and distribution of the snowpack have an effect on the magnitude and timing of microbial biomass and soil inorganic N pools by controlling the freeze-thaw conditions of

the subnivalian soils [Brooks *et al.*, 1998]. In turn, the microbial biomass and N pools affect species richness and mediate species-specific responses to nutrient availability [Seastedt and Vaccaro, 2001]. Nonetheless, despite the major role of snow cover on the composition and productivity of the alpine tundra, there are only a handful of studies that have attempted to quantify the interactions among snow depth, melting rate, SWE and other snow attributes, soil moisture and the characteristics of herbaceous alpine plants.

[3] Many studies on the interactions between alpine plants and climate variables have been conducted in the Colorado Front Range. May and Webber [1982] showed qualitatively the causality between the spatial heterogeneity of the snow cover in Niwot Ridge, Colorado and the spatial variability of alpine plant communities. Walker *et al.* [1993] suggested that topography controls the snow depth, as well as the vegetation patterns on Niwot Ridge, based on a combination of field measurements and air photo interpretation. Walker *et al.* [1994] attempted to correlate aboveground phytomass with nine climate variables measured for a 9-year period on Niwot Ridge and they found that the climate variables accounted for only 15 to 40% of the variation in phytomass. These results highlighted the difficulty and the need to quantify basic field observations and descriptive models of alpine plant and soil development [e.g., Burns and Tonkin, 1982; Walker *et al.*, 1993].

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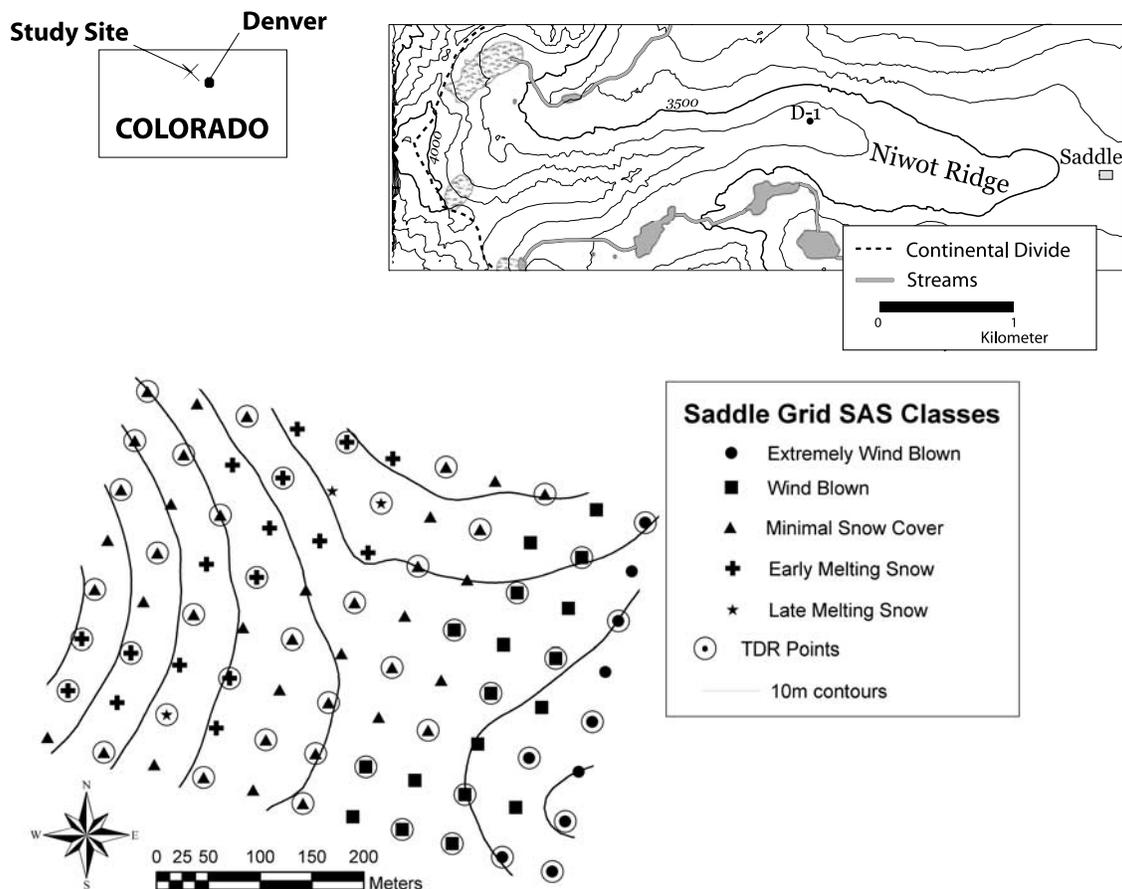


Figure 1. The study area in the saddle grid, Niwot Ridge, Colorado. The locations of the snow-free day categories according to the synthetic alpine slope (SAS) conceptual framework of *Burns and Tonkin* [1982]. The SAS consists of five categories: EWB, extremely wind blown; WB, wind blown; MSC, minimal snow cover; EMS, early melting snow bank; LMS, late melting snow bank and wet meadow.

[4] Recent trends in climate suggest some urgency for improving our understanding of interactions between snowpack and the alpine plant community. Snow accumulation has decreased over the past 50 years in many parts of the western U.S. [Mote, 2003]. Across Colorado and the Western U.S., drought conditions prevailed in the early 2000s. Declining ice thickness was observed in an alpine lake adjacent to Niwot Ridge [Caine, 2002], while maximum snow accumulation on the Niwot Ridge area in the early 2000s was below normal [Williams *et al.*, 2006]. A recent experiment that manipulated the snowpack on Niwot Ridge using a snow fence, showed that even modest changes in the timing, amount, and duration of snow cover could have large effects on soil temperature under the snowpack [Walker *et al.*, 1999]. Soil temperature influences the rates of C and N fluxes, potentially resulting in large changes in species composition [Williams *et al.*, 1998]. These flux modifications have been shown to influence biotic interactions and community diversity [Suding *et al.*, 2004]. The purpose of our research was to quantitatively evaluate the spatial relationships between terrain factors and selected snow cover attributes, soil moisture, aboveground biomass and species richness of herbaceous vegetation in an alpine

ecosystem. Data are presented in Data Sets S1–S3 (available as auxiliary material¹).

2. Methods

2.1. Field Site

[5] The study was conducted in the Niwot Ridge saddle (3500 m elevation), located in the Colorado Front Range of the Rocky Mountains about 5 km east of the Continental Divide (40° 03' N, 105° 35' W). The saddle site is a north-south oriented trough that becomes progressively steeper to the east and west. Within the saddle, a research grid 550 m long and 400 m wide was established in the late 1980s, marked by 88 stakes on 50-m centers [Walker *et al.*, 1993]. Niwot Ridge is a broad interfluvium, 10-km long, extending eastward from the Continental Divide, and is characterized by low rounded hills with shallow saddles in between (Figure 1). This site is a UNESCO Biosphere Reserve and a Long-Term Ecological Research (LTER) network site. The climate is characterized by long, cool winters and a short growing season (1–3 months). Since

¹Auxiliary materials are available at <ftp://ftp.agu.org/apend/jg/2007/jg000419>.

1951, mean annual temperature is -3.8°C and annual precipitation is 1,000 mm, recorded at meteorological station D1 located above the saddle site [Williams *et al.*, 1996]. About 80% of annual precipitation falls as snow [Caine, 1996] and is redistributed by westerly winds (255° to 275° , average velocity of $10\text{--}13\text{ m s}^{-1}$), causing snow depth at the site to vary by a factor of ten or more, depending on terrain factors.

[6] The dominant plant species of the Saddle grid include graminoids (monocots, grasses) and forbs (dicots, non-woody herbaceous plants). Woody species are restricted to occasional willow shrubs (*Salix* spp) that occupy much less than 1% of the study area on the Saddle grid [Walker *et al.*, 1994] and hence are not represented in this study. The more common plant species include the graminoid, *Kobresia myosuroides*, which dominates dry meadow areas, the forb, *Acomostylis rossi*, common across the moisture gradient, but particularly dominant in mesic areas, and the graminoid, *Deschampsia caespitosa*, which prefers mesic habitats. The herbaceous vegetation is perennial, low in stature, and easily covered by accumulating snow. Canopy heights and effectively snow-holding depths are taken from Liston and Elder [2006, Table 2], giving an effective surface roughness of 0.1 m for graminoid-dominated tundra to 0.2 m for wetland tundra. Detailed descriptions of the flora are found in Walker *et al.* [1994].

[7] The synthetic alpine slope (SAS) soil-geomorphic model of Burns and Tonkin [1982] and the vegetation nodal pattern of May and Webber [1982] described plant species distribution on Niwot Ridge. Sites that exhibit windblown (225 to 300 snow-free days/year) or extremely windblown conditions (>300 snow-free days/year) are characterized by a fellfield community. Sites that exhibit minimal snow cover (150 to 200 snow-free days/year) are characterized by dry meadow plant community, whereas sites that exhibit early melting snowpacks (100 to 150 snow-free days/year) are characterized by moist to wet meadow plant communities. Wet meadow, snowbed and shrub tundra plant communities are found at sites that exhibit a late-melting snowpack (50 to 100 snow-free days/year). These five types of alpine plant communities found in the study area reflect gradients in snowpack attributes and soil moisture regimes, and broadly represent the most common vegetation types on east-facing slopes of the Colorado Front Range [Walker *et al.*, 1993].

2.2. Snow Variables

[8] Since 1982, the depth of the snowpack has been measured monthly during the winter at 88 points within the saddle area at Niwot Ridge. Measurements during snowmelt were performed biweekly until all snow disappeared or until new snow began accumulating at the onset of the next winter. Measurements of snow depth were carried out to the nearest centimeter. The adequacy of the 88 grid points to capture the spatial variability of snow depth across the saddle site was tested using geostatistical modeling and fractal approach [Litaor *et al.*, 2002]. They found that the variograms of the annual mean snow depth on the saddle site exhibited a long-range spatial continuity with an estimated fractal dimension of 1.2 indicating smooth long range variations. Snow density was measured at about ten sites, following the protocols in Williams *et al.*

[1999]. We derived five variables that together provide a comprehensive description of snow dynamics. These five variables include maximum snow depth, maximum snow water equivalence (SWE) calculated as maximum snow depth at each grid location times average snow density, average yearly snow depth, average springtime snow depth (representing depth variation from April until snowmelt), and average springtime disappearance rate (Disa). The disappearance rate (cm day^{-1}) was estimated for each point, following a slightly modified procedure outlined by Anderton *et al.* [2004]:

$$Disa = \frac{D_{\max s}}{t_{\text{dis}} - t_{\max}} \quad (1)$$

where $D_{\max s}$ is maximum springtime snow depth (m), t_{\max} is the date of maximum recorded snow depth (Julian Day) and t_{dis} is the date of snow disappearance (Julian Day). It should be noted that Anderton *et al.* [2004] used the term “melt rate,” whereas we prefer “disappearance rate” because there is no energy flux term in the above equation.

2.3. Terrain Factors

[9] The basic terrain factors (elevation, slope and aspect) were derived from a 10-m digital elevation model (DEM), with 1-m vertical resolution. The 10-m digital elevation model (DEM) was generated from 1:12,000 scale stereoscopic images and ground control points collected in August 1990 [Williams *et al.*, 1999]. The influence of topography on wind sheltering, which influences the snow drift and, consequently, snow depth was quantified using an expression developed by Winstral *et al.* [2002] and Erickson *et al.* [2005] for an alpine terrain. The expression, denoted by the variable Shelter, describes the maximum up-wind slope (in degrees) relative to each location on the DEM:

$$Shelter = \max \left(\tan^{-1} \left(\frac{Elev(x_i) - Elev(x_0)}{|x_i - x_0|} \right) \right) \quad (2)$$

where x_0 is a vector of the horizontal coordinates of the cell of interest and $|x_i - x_0|$ is the separation distance. Increasingly negative Shelter values correspond to a lesser degree of shelter, higher wind speeds, and, therefore, an increased potential for snow erosion on windward slopes. Increasingly positive Shelter values correspond to a greater degree of shelter, lower wind speeds, and, therefore, an increased potential for snow deposition and accumulation. Because the prevailing wind direction at the saddle grid is 265° , the Shelter expression was determined along swaths of 5° increments within the upwind window (235° to 300°) and averaged to formulate the expression for mean maximum upwind slope:

$$Shelter_{d\max|x_i - x_0|} = \frac{1}{n_v} \sum_{A_1}^{A_2} Shelter \quad (3)$$

where $d\max$ is the maximum search distance defined for the upwind window, and n_v is the number of search vectors in the window defined by the azimuths A_1 and A_2 , with search distance separation between upwind cells (x_i) to each of the 88 grid locations (x_0). Search distances of

30-, 50-, 100-, 150-, 200-, 300-, 500-, 1000- and 2000 m were used to test the influence of near and far terrain cells derived from the DEM on the shelter ability in a given cell of interest to constrict the approaching wind flow. For a detailed description of this modeling approach, the reader is referred to *Winstral et al.* [2002].

[10] In addition to the Shelter variable, we evaluated two other wind-transport variables that describe the redistribution of snow by wind [*Anderton et al.*, 2004]. The first variable (AVE_{exp}) computes an average that is equally weighted for all wind directions. This variable assumes that any directional effects become obscured over the course of the entire snow season, but that there is an overall tendency toward removal of snow from local topographic maxima and deposition in local topographic minima. The second variable ($AVEW_{exp}$) is an average that is weighted according to the directional of the prevailing wind throughout the snow accumulation season. This variable assumes that the pattern of snow redistribution is governed by dominant wind direction throughout the course of the snow accumulation season. These two variables were calculated for the eight cardinal wind directions (N, NE, E, SE, S, SW, W, NW) and for upwind filter lengths of 30, 50, 100, 150, 200, 300, 500, 1000, and 2000 m. Both of these wind-transport variables (AVE_{exp} , $AVEW_{exp}$) are somewhat simpler to compute than the shelter variable, but they were never used simultaneously with the Shelter variable to predict snow variables, so we used them on a comparative basis to ascertain which variable better predicts the snow depth variables.

[11] We also computed the slope-aspect topoclimatic index (SA), which has previously been used in mapping plants associations in the saddle grid [*Frank and Isard*, 1986]. The SA is computed by multiplying the slope (degrees) by the difference in degrees between the aspect of the ground slope and due east. High values of SA indicate areas that are generally leeward snow accumulation sites, whereas low SA values indicate windblown, snowfree sites.

2.4. Solar Radiation

[12] An index of potential incoming solar radiation ($W m^{-2}$) was constructed over the saddle site using the TOPORAD algorithm [*Dozier*, 1980], which accounts for changes in shortwave irradiance caused by local solar zenith angle, terrain shading, and terrain reflectance. The TOPORAD algorithm has been extensively used in snow studies [e.g., *Elder et al.*, 1998; *Balk and Elder*, 2000; *Winstral et al.*, 2002]. Albedo inputs to the model were measured directly at the saddle site following protocols in *Williams et al.* [1999]. We then used the protocol that *Winstral et al.* [2002] and *Erickson et al.* [2005] employed with TOPORAD in the adjacent Green Lakes Valley and constructed an index of incoming solar radiation based on the summation of clear-ski conditions modeled on the 15th of each month during the winter season.

2.5. Soil Moisture

[13] Soil moisture was measured as the mean of three samples at each of 48 grid points (a subset of the 88 sampling points described above, see Figure 1) during each growing season starting at early June and extending through

late August. The grid points were distributed evenly among the 5 plant community types. These measurements were collected on a weekly to biweekly basis from 1994 to 2002, using the time domain reflectometry (TDR) method. The TDR probes were inserted into the top 15 cm of the soil, and soil moisture was measured as voltage waveforms using a Tektronix 1502B cable tester [*Taylor and Seastedt*, 1994].

2.6. Plant Biomass and Species Richness

[14] Aboveground plant biomass was determined during the peak biomass production (July) in 1992 to 1995 following the protocols detailed by *Walker et al.* [1994]. Dry sites were harvested first, and the collection period required 2–3 weeks, thereby accommodating later peak biomass in late-melting snow sites. Plant biomass was harvested from 10 sites, two each from fellfield, dry meadow, moist meadow, wet meadow and snowbed located within the 88 point saddle grid. At each site, five 50×20 cm quadrats separated by 2 m intervals were completely cleared of live and dead aboveground biomass during the peak of the growing season for each year. Samples were taken to the laboratory and sorted into graminoid, forb, and other live fractions. Dead material represented a separate fraction. These were then dried and weighed to the nearest 0.1 g. Species composition was determined using a $1 m^2$ point quadrat sampling method. These quadrats were located within 2 m of the 88 points used to collect snow depths. One plot was located in willow shrubs and was excluded from this analysis. The species composition data were collected in 1995 and 1997. From this data set, species richness (total number of species observed/ m^2 point quadrat) was tabulated for the point quadrat that corresponded with each transect. Based upon repeated measurements of species cover (LTER, unpublished results) and the persistence of the perennial alpine tundra plants in undisturbed areas, we assumed that there was no significant change in plant structure and composition between the two sampling periods. Additional methodological details and original data are available through the LTER data archive (<http://culter.colorado.edu/>).

2.7. Modeling: Binary Decision-Tree Analysis

[15] The binary decision-tree analysis examines the relationships between predictor variables and dependent variables in nonlinear or hierarchical manner through a sequence of binary decisions. The analysis delineates similar values of the dependent variables using stepwise reduction in model deviance [*Balk and Elder*, 2000]. Deviance is a measure of subset data heterogeneity used in the tree-growing algorithm, where a deviance of zero corresponds to a perfectly homogeneous subset [*Venables and Ripley*, 2002]. In the present study, the predictor variables are the terrain factors at each of the 88 grid points, and the dependent variables are the various snow attributes (i.e., maximum snow depth, SWE, average yearly snow depth, average springtime snow depth, and average springtime disappearance rate). In subsequent analysis, the dependent variables were soil moisture or plant attributes, while the predictor variables were the terrain attributes plus snow depth and melt variables. The fitting of a tree model was implemented by a binary recursive partitioning algorithm, which successively split

Table 1. Summary Statistics of Snow Depth (cm) on the Saddle Grid From 1982 to 2003

Year	N	\bar{X} ^a SD.	Range ^b
1982	1496	62 ± 78	328
1983	1848	84 ± 106	471
1984	1760	67 ± 120	683
1985	1144	18 ± 56	474
1986	791	31 ± 81	425
1989	616	20 ± 47	262
1990	616	48 ± 85	391
1992	351	33 ± 38	210
1993	1350	100 ± 120	605
1994	653	77 ± 93	410
1995	966	120 ± 130	542
1996	1495	88 ± 131	580
1997	1048	74 ± 104	560
1998	700	69 ± 100	515
1999	969	75 ± 96	470
2000	788	70 ± 91	400
2001	793	74 ± 91	440
2002	1055	29 ± 50	250
2003	792	87 ± 107	550

^aThe \bar{X} represents the average snow depth and its standard deviation for a given year across the entire saddle area using the 88 grid points.

^bThe range represents snow depth from zero snow accumulation to maximum snow depth for a given year using the 88 grid points across the saddle.

the data set into increasingly homogeneous subsets of the dependent variables. These subsets are termed nodes and their numbers increase during the fitting operation until they are homogenous or contain too few observations for further partitioning [Venables and Ripley, 2002].

[16] The binary decision-tree model was run using terrain factors (elevation, slope, aspect) and terrain-derived variables (SA topoclimate index, solar radiation, equally weighted wind exposure index, directionally weighted wind exposure index and the Shelter index). The wind exposure and shelter indices were computed using nine different search distances [30, 50, 100, 150, 200, 300, 500, 1000, and 2000 m].

[17] To test the spatial accuracy of the tree-based model for the saddle grid, we used various tests of cross-validation. Cross-validation was accomplished by sequentially removing each data point and then using the remaining observations to estimate the value of the removed datum. This procedure was repeated for all observations in the saddle grid. The true values were subtracted from the estimated

values to get the residuals. The residuals were used to compute the mean error (ME), root mean squared error (RMSE), mean absolute error (MAE), and a goodness-of-prediction R^2 estimate described by Schloeder *et al.* [2001]. We used the tree-based platform implemented in S-Plus software [Insightful, 2001] to download the tree-based model algorithms, including the pruning function from the public domain library section rpart, located at <http://www.mayo.edu/hsr/Sfunc.html>.

3. Results

3.1. Snow Attributes

[18] More than 19,000 individual measurements of snow depth were recorded at Niwot Ridge from 1982 to 2003. The average snow depth ranged from less than 30 cm in drought years (1985, 1986, 1989, and 2002) to more than 100 cm in wet years (1993 and 1995) (Table 1). Maximum snow depth for any given year ranged from 0 m for windward sites on the East Knoll, to more than 6 m in leeward zones below the West Knoll. The coefficient of variation for each of the 19 reported snow years ranged from 1.08 during the large snow year of 1995, to 3.11 during the low snow year of 1985.

[19] The mean and standard error of terrain factors for each of the five defined classes of the SAS conceptual framework are presented in Table 2. There were only small differences in elevation and slope angle between the five defined classes. On the other hand, the aspect noticeably separated the leeward areas from the windward slopes. The distribution of the modeled incoming solar radiation did not vary significantly across the study site (Table 2), ranging from 269 to 274 $W m^{-2}$.

[20] We selected the 1993 snow year for detailed characterization of the snow variables because each grid point was tested using five repeated measures of snow depth at each sampling date, thus it represents the most robust conditional cumulative distribution function for spatial analysis. The depth measurements were taken within a 10-m radius around each of the 88 grid points. For most sites, the magnitude of spatial variation at each grid point did not exceed 6%, except for the windblown and extremely windblown sites, which exhibited 20% and 30% variation, respectively. The distribution of selected snow variables across the saddle grid for 1993 showed a clear snow/topographic gradient where the lowest snow depths and SWE were observed in the extremely windblown sites, with

Table 2. Mean and Standard Error of Basic Terrain Variables, Along With Measured Snow Values in 1993, Presented as a Function of the Landscape Types in the SAS Model

Site ^a	N	Snow-Free Days per Year	Mean Depth, cm	Maximum Depth, cm	SWE, m	Elevation, m	Slope, deg	Aspect, deg	Radiation, $W m^{-2}$	Shelter, ^b deg
EWB	10	>300	7.2 ± 1.5	24 ± 3.4	0.1 ± 0.1	3542 ± 2.1	8 ± 0.9	291 ± 17	274 ± 1.6	-1.97 ± 0.12
WB	18	200 – 300	14.6 ± 2.4	50 ± 7	0.2 ± 0.03	3535 ± 1.3	5.3 ± 0.5	268 ± 22	277 ± 0.7	0.73 ± 0.11
MSC	38	150 – 200	102 ± 10	244 ± 17	1.1 ± 0.07	3544 ± 2.5	8.2 ± 0.6	91 ± 13	273 ± 0.9	8.76 ± 0.15
EMS	15	100 – 150	215 ± 15	391 ± 15	1.7 ± 0.07	3549 ± 4.8	11 ± 0.7	86 ± 8	269 ± 1.6	11.7 ± 0.12
LMS	7	50 – 100	298 ± 47	475 ± 40	2.1 ± 0.18	3532 ± 2.4	8.5 ± 0.8	51 ± 9	273 ± 1.0	10.7 ± 0.15

^aSite classification of Burns and Tonkin [1982]. EWB, extremely wind blown; WB, wind blown; MSC, minimal snow cover; EMS, early melting snow bank; LMS, late melting snow bank and wet meadow.

^bShelter is the variable that measures the degree of shelter/exposure for a given local taking into account the terrain upwind of this local at a distance of 150 m.

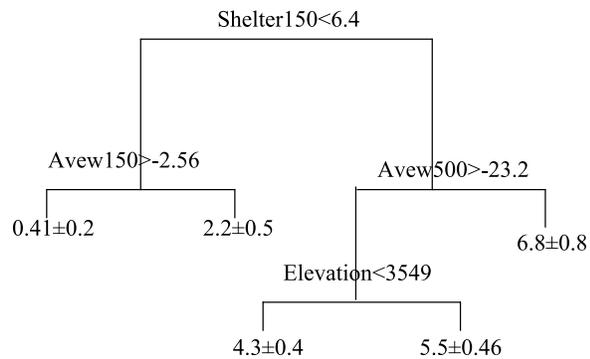


Figure 2. A binary tree model of snow disappearance rate measured during the 1993 snow survey using all terrain-related predictor variables. The values at each terminal node are the predicted value and the associated mean square error (MSE). The shelter and AVEW measure the degree of shelter/exposure for a given local taking into account the terrain upwind of this local at a distance of 150 and 500 m.

increasing values on the windblown sites and minimal snow cover sites (Table 2). The more leeward locations exhibited deep snow accumulation and large SWE values.

3.2. Modeling: Binary Decision-Tree Analysis

[21] The aggregation scheme of the snow accumulation at the saddle grid during the snow year of 1993 was modeled using each of the snow variables as dependent variables against the terrain factors and terrain-derived variables (Figure 2). The model results depicted in Figure 2 agreed reasonably well with the measured snow depth that was aggregated according to the SAS where the early wind blown (EWB) sites exhibited a minimal disappearance rate of 0.19 cm/d followed by wind blown (WB) (0.45 cm/d), minimal snow cover (MSC) (3.7 cm/d), early melting snow (EMS) (6.9 cm/d) and late melting snow (LMS) (7.9 cm/d) sites. We conducted a cost-complexity pruning exercise to reduce the tree endpoints without reducing goodness-of-fit. However, because the model tree is simple and bears physical interpretable splits, no pruning of the original tree was necessary.

[22] Modeling the other snow variables yielded similar splitting results. For example, wind-controlled terrain-derived predictor variables used in the modeling of the snow disappearance rate (Disa) were also selected for the SWE. The most significant variables in the modeling were the terrain attributes that quantify the degree of shelter or exposure for a given locale. These attributes take into account the bearing (e.g., 225, 270, and 315 degrees) and the extent of shelter/exposure characteristic provided by the terrain upwind at a distance of 150 and 500 m. Moreover, the simultaneous use of the shelter variable and directional exposure indices increased the predictive power of the model.

[23] The cross-validation results of the binary tree-based model suggest that snow variables in 1993 were reasonably described by the four terrain-related variables (Table 3). The r^2 values ranged from 0.75 to 0.91. The mean error was less than 4% for all snow variables. The results of the cross-validation analysis for 1993 suggest

Table 3. Cross-Validation Results of the Binary-Tree Model for All 88 Grid Locations in 1993

Variable	ME ^a	RMSE	MAE	r^2
Maximum snow depth, cm	3.8	57	42	0.88
SWE, m	-0.002	0.29	0.21	0.85
Average springtime snow depth, cm	1.4	60	44	0.85
Springtime disappearance rate, cm d ⁻¹	0.017	0.81	0.63	0.91
Average yearly snow depth, cm	2.67	47	33	0.75

^aME, mean error; RMSE, root mean squared error; MAE, mean absolute error.

that the binary tree-based model is sufficiently robust to predict snow accumulation and disappearance in other snow years at the Saddle site. The snow variables (maximum snow accumulation depth, SWE, and disappearance rate) from the other years were modeled using the four most statistically significant terrain-related variables from the 1993 snow survey as predictor variables. The years 1982 to 1984, 1994, 1996 to 2001 and 2003 exhibited high snow accumulation similar to the 1993 snow survey year and the model achieved high coefficients of determinants ($r^2 = 0.8$, $P < 0.001$). The years 1985, 1986, and 1989 to 1992 exhibited low snow accumulation with no significant correlation with the 1993 snow survey year. The year 1995 exhibited significantly higher snow accumulation than the model year (see Table 1); thereby reducing slightly the predictive power of the binary tree-based model ($r^2 = 0.67$). The results of modeling among years support the premise of a causal relationship between terrain-based variables and snow accumulation, thereby justifying the next step in the study, an evaluation of the relationship between terrain-related variables, snow variables and soil moisture.

3.3. Soil Moisture

[24] The distribution of the soil moisture measured from 1993 to 2002 across the saddle grid during the summer season (mainly late June, July and early August) indicated that the EWB sites were characterized by the lowest multiannual mean soil moisture values expressed as percent volumetric water (7.3 ± 0.9), followed by WB sites

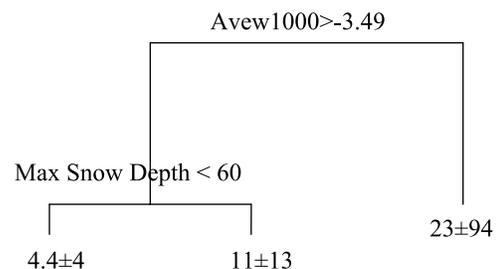


Figure 3. A binary tree model of soil moisture content across the saddle grid. The values at each terminal node are the predicted value and the associated mean square error (MSE). The AVEW represents the degree of shelter/exposure for a given local taking into account the terrain upwind of this local at a distance of 1000 m.

Table 4. Mean and Standard Error of Annual Biomass and Species Richness Across the Saddle Grid, 1993 to 1996

Site ^a	N	Forbs, g m ⁻²	Graminoid, g m ⁻²	Herbaceous, g m ⁻²	Species Richness
EWB	35	80 ± 9	60 ± 5	140 ± 8	27 ± 1.8
WB	69	100 ± 9	60 ± 5	160 ± 10	25 ± 1.3
MSC	125	120 ± 7	40 ± 3	160 ± 8	18 ± 1.2
EMS	45	90 ± 8	20 ± 4	110 ± 9	16 ± 1.2
LMS	18	50 ± 6	31 ± 3	81 ± 8	15 ± 4

^aEWB, extremely wind blown; WB, wind blown; MSC, minimal snow cover; EMS, early melting snow bank; LMS, late melting snow bank and wet meadow.

(14.9 ± 1.0), whereas the MSC and EMS sites had the highest moisture values (16.8 ± 0.7 and 17.1 ± 1.8, respectively). The soil moisture content was somewhat greater at the LMS sites (11.9 ± 1.5) than the EWB sites.

[25] The estimation of the soil moisture distribution across the saddle grid for 1993 was modeled using the snow variables, terrain factors and terrain-derived variables (Figure 3). The first predictor variable was the average wind shelter-exposure index using azimuths of 225, 270 and 315 degrees, with filter length of 1000 m that separated the saddle grid into dry sites and wetter sites, with the latter mainly on the leeward side of the slope. The binary-tree model was branched for maximum snow cover by separating out the windward sites into dry and moist areas. However, the binary decision tree model did not succeed in separation of the dry-to-moist locations from wet sites, which means that the model did not succeed to classify the soil moisture data into all the micro environmental categories of the SAS.

[26] The cross-validation analysis of the spatial distribution of soil moisture across the saddle grid showed moderate goodness of fit ($r^2 = 0.6$, $P < 0.001$) and a relatively large mean standard of error (MSE), compared with the exceptionally high degree of association ($r^2 = 0.8$) and low MSE computed for the snow variables. To test the general performance of the model to predict soil moisture content, we used the two most significant terrain-derived and snow variables depicted in Figure 3 to model between years variations. The model results for an 8-year period suggested the distribution of the soil moisture content in moderate to high snow years of 1994 and 1995 were moderately

correlated with the 1993 results ($r^2 = 0.51$, $P < 0.001$), whereas the distribution of the soil moisture content in low-snow years exhibited a low degree of association (r^2) with terrain-related and snow variables.

3.4. Biomass and Species Richness

[27] Annual herbaceous biomass at Niwot Ridge was maximum at about 160 g m⁻² at the WB and MSC landscape types (Table 4). Annual biomass decreased relative to these values at both the extremely windblown (EWB) and late melting snow (LMS) sites. The growth of alpine tundra plants appears to be constrained by too-little moisture on EWB sites and too short a growing season on LMS sites [Fisk *et al.*, 1998; Bowman and Fisk, 2001].

[28] Four years of biomass measurements were modeled using the 1993 snow year variables (maximum snow depth and average yearly snow depth), soil moisture and all the terrain-related variables (Figure 4). The overall coefficient of determination had limited predictive power ($r^2 = 0.4$, $P < 0.001$). All four terminal nodes were characterized by high MSE values, with predicted values that were quite different from the averaged measurements (Table 4).

[29] In contrast to biomass, the species richness index showed a clear trend, with the index value increasing from a low of 15 for the leeward sites (LMS) to a high of 27 for the most exposed sites (EWB) (Table 4). A binary-tree model for the species richness index was constructed using snow accumulation variables (average spring-time snow depth, maximum snow depth and soil moisture) (Figure 5). This model successfully predicted four out of the five categories of the SAS conceptual framework ($r^2 = 0.7$, $P < 0.001$), with

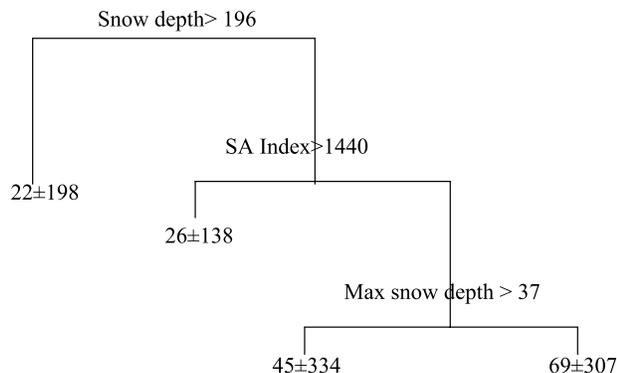


Figure 4. A binary tree model for biomass across the saddle grid. The values at each terminal node are the predicted value and the associated mean square error (MSE). The SA represents the slope-aspect topoclimatic index.

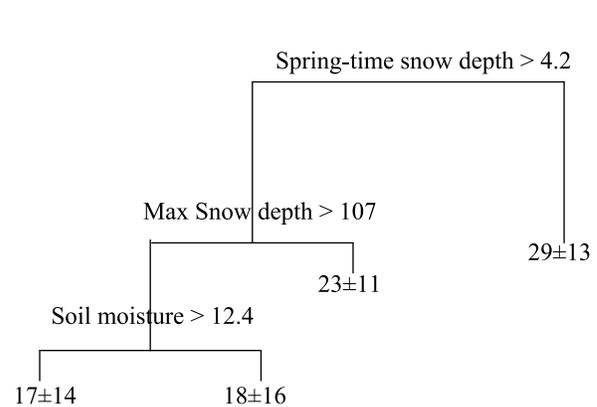


Figure 5. A binary tree model for species richness across the saddle grid. The values at each terminal node are the predicted value and the associated mean square error (MSE).

all terminal nodes exhibiting relatively low to moderate MSE values. The model successfully classified the EWB, WB and MSC sites, whereas the EMS and LMS were classified together.

4. Discussion

[30] The results of the binary decision-tree model using the selected terrain-derived variables explained between 85 to 91% of the observed variability for snow depth, SWE and snow disappearance rate. These modeling results yielded higher coefficient of determinants than other snow studies conducted in various locations across the Rockies. For example, *Balk and Elder* [2000] reported that their binary decision tree-based model explained 54 to 65% of the snow depth in the Loch Vale watershed located in the Rocky Mountain National Park, Colorado. In a comparison study of four spatial techniques at three sites in the Colorado Rocky Mountains, the tree-based models explained only between 18 to 30% of the observed variability in snow depth [*Erxleben et al.*, 2002]. Another study in the adjacent Green Lakes Valley to Niwot Ridge used a pruned model of 16 nodes to explain 50% of the observed variance in snow depth and as much as 60% with the overgrown tree [*Winstral et al.*, 2002].

[31] The study by *Winstral et al.* [2002] was the first to introduce terrain-derived variables (shelter at different search distances) to the standard terrain variables of elevation, aspect, slope and net radiation index. Without the terrain-derived variables, the model's r^2 was less than 0.40. *Anderton et al.* [2004] formulated additional terrain-derived variables in their construction of the tree-based model, which explained about 70 to 80% of the variance in snow depth measured in a small headwater catchment in the Spanish Pyrenees.

[32] The high coefficient of determinants of the current study in predicting snow attributes may be explained by the following reasons: (1) the relative homogeneity and smoothness of the saddle surface, compared with the large heterogeneity of rugged terrain watersheds, (2) the usage of all available wind-redistribution parameters [*Winstral et al.*, 2002; *Anderton et al.*, 2004], in addition to the standard terrain variables of elevation, slope, aspect and net radiation index, and (3) the present work focused on a small, regularly spaced grid with relatively low heterogeneity compared with larger scale studies cited above. The studies of whole catchment basins [*Winstral et al.*, 2002; *Anderton et al.*, 2004] consisted of irregularly spaced grids with large un-sampled areas; these factors increased the heterogeneity and, therefore, the spatial uncertainty.

[33] Incoming solar radiation was not a good predictor variable in the current study because potential incoming radiation ranged only from 269 to 274 $W m^{-2}$ (Table 2). In contrast, *Erickson et al.* [2005] used the same protocol for estimating potential incoming radiation for the adjacent Green Lakes Valley, with values ranging from 11 to 265 $W m^{-2}$ and a mean value of 160 $W m^{-2}$. Thus, the relatively flat topography with little elevation change and no horizon shading characteristic of the Saddle interfluvial when compared to the adjacent rugged glaciated terrain results in only small variations in potential incoming radiation.

[34] However, albedo most likely varied substantially over the Saddle domain during the snow season. Mean snow depths for the LMS and EMS plant communities were greater than 200 cm, with continuous snow cover. Little if any transmission of light through the snowpack occurs at these depths. Additionally, there was little if any bare ground in these areas. The effective albedo of these plant communities is that of the overlying snowpack, on the order of 0.8 to 0.9. In contrast, the EWB and WB plant communities had mean snow depths less than 15 cm, with discontinuous snow cover and exposed ground and vegetation. These snow depths are about the same as the surface roughness provided by herbaceous vegetation. The effective albedo of these plant communities was thus close to that of alpine tundra, on the order of 0.2. The lower albedo for the EWB and WB plant communities likely results in more absorption of incoming solar radiation and higher net shortwave radiation relative to the other three plant communities on the Saddle. The potentially higher net solar radiation for the EWB and WB plant communities may result in a positive feedback such that snow depths remain low throughout the snow accumulation season and result in earlier snowmelt.

[35] The results of the tree-based model support the conceptual SAS spatial soil-geomorphic model introduced by Burns and Tonkin in 1982 with respect to snow properties. The model successfully quantified the snow depth, SWE and snow disappearance rate in each of the five landscape types, however, the model exhibited only moderate success in classifying the spatial patterns in soil moisture. The years with moderate r^2 exhibited relatively low amounts of summer precipitation, between 180 to 240 mm. In contrast, the years with low r^2 had higher amounts of summer precipitation (290 to 415 mm). Snow distribution is thus an important predictor of soil moisture in years with low summer rain but not in years with higher amounts of summer rain. The drought year and low snowfall year of 2002 had the lowest r^2 of 0.10 for predicting soil moisture in the summer. Not surprisingly, winter snowfall is not an important component of summer moisture in low-snowfall years.

[36] The results of the tree-based model suggest that annual aboveground biomass exhibits a rather modest fit with snow depth, SWE, snow-disappearance rate and soil moisture. The reason appears to be too little moisture on EWB sites and too short a photoperiod or growing season on LMS sites. Hence, biomass appears to exhibit a curvilinear response to both these variables, with a maximum at MSC and EMS landscape types [*Fisk et al.*, 1998; *Bowman and Fisk*, 2001]. This nonlinear response is not characterized well by the regression tree model. In addition, inter-annual climate variability and species-specific differential responses to nutrients and water allocations [*Bowman and Fisk*, 2001] may contribute to the observed pattern. In particular, biotic responses in previous years affect current year's biomass, causing similar communities to be under different constraints within a particular year [*Walker et al.*, 1994]. This, in turn, may contribute to the lack of strong correlations between aboveground biomass and the topographic/snow variables presented here.

[37] Another possible reason for the modest fit between aboveground biomass and snow attributes is the fact that

only aboveground production is estimated here. *Fisk et al.* [1998] showed that the majority of the biomass production and N use for production were allocated for belowground component in the dry meadow (MSC) and wet meadow (EMS) sites. Plants attempt to allocate productivity either above- or belowground to minimize resource limitation [Chapin, 1991]. Thus, while we might expect the highest productivity in mesic areas, exactly how this productivity is allocated depends upon the relative limitation of light, nutrient, and water resources. In any event, the cascading impact of topography on snowpack and soil moisture is not well captured by annual aboveground biomass determinations.

[38] The correlation between snow attributes and species richness reflects the fact that snow depth dictates the length of the growing season, provides insolation from the abrasive action of the wind, minimizes the freezing conditions in the soils and reduces the water stress for plants. Other non-physical factors, such as pocket gopher activity in areas with more snow cover, may produce chemical and physical changes that favor some alpine plant species over others, thereby affecting the species richness index [Bowman et al., 1995; Litaor et al., 1996; Sherrod et al., 2005]. Other biotic factors that may influence species richness include competitive displacement of some species by others as demonstrated by Theodose and Bowman [1997], increased N mineralization due to prolonged deposition of atmospheric N [Steltzer and Bowman, 1998], and the process and type of mutualisms such as symbiotic N₂ fixation and abundance of mycorrhizae [Walker et al., 2001]. The fact that local species richness is highest in the most heterogeneous community (in terms of variables reported here) is noteworthy.

[39] These results provide insight on how snow properties, soil moisture, and species diversity may change in response to a warming climate. Plants from high-latitude and high-altitude sites are especially sensitive to climate warming [Aerts et al., 2005]. Because of the harsh climate conditions characteristic of cold environments, alpine organisms are on the edge of environmental tolerances [Williams et al., 1998]; consequently, these organisms and biogeochemical processes mediated by them may be sensitive to small environmental changes in climate and other parameters [Williams et al., 2002].

[40] There is an expectation that potential warming will increase the length of the growing season [Harte and Shaw, 1995], move greening and flowering dates forward [Dunne et al., 2003], and result in an increase in photosynthetic activity of terrestrial vegetation because of an increase in plant growth associated with a lengthening of the active growing season [Myneni et al., 1997]. However, snow manipulation experiments in a subarctic tundra plant community showed that earlier snowmelt was correlated with colder spring temperatures and a higher number of frosts [Wipf et al., 2006]. Similarly, at a subalpine forest site on Niwot Ridge, years with a reduced winter snowpack were accompanied by significantly lower rates of soil respiration due to colder soil temperatures, suggesting that a warmer climate may change soil carbon sequestration rates in forest ecosystems owing to changes in the depth of the insulating snow cover [Monson et al., 2006]. Our results suggest that

decreases in the duration and depth of the snow cover in herbaceous alpine tundra ecosystems may cause a shift from dry (MSC) and wet meadow (EMS) communities toward less productive alpine fellfields (WB and EWB sites). However, somewhat paradoxically, species richness may increase in response to the changing climate conditions.

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