Long-term Studies of Snow-Vegetation Interactions

A hierarchic geographic information system helps examine links between species distributions and regional patterns of greenness

D. A. Walker, James C. Halfpenny, Marilyn D. Walker, and Carol A. Wessman

Humans place a value on snowy alpine regions that far outweighs their small area compared with Earth's other major biomes. Mountains have long attracted people as places of spiritual and emotional refuge and physical challenge. They are scenic, contain pristine areas of high biodiversity, provide deep snowpack for skiers, and are a source of water for urban areas and agricultural regions. Scientists also recognize the importance of high mountains to regional hydrological, biogeochemical, and atmospheric processes. Alpine ecosystems are thought to be particularly sensitive to climate change and are known to have responded to such changes in the 12,000 years since deglaciation (Benedict 1970). Contributing factors for this sensitivity are the ecosystems' low productivity and tight nutrient cycling and their situation at an extreme for many plant processes (Bliss 1985).

Relationships among vegetation, wind, snow, and temperature regimes may help predict effects of climate change

General circulation models usually have lower confidence for predictions of precipitation than for temperature, and it is currently unclear whether global warming would lead to local increases or decreases in precipitation at high altitudes (e.g., Cess et al. 1991). There may also be a problem extrapolating from predictions at low elevations because the climates of alpine areas are often only weakly coupled to that of lowlands (Barry 1990, Greenland 1989).

Research at the Niwot Long-Term Ecological Research (LTER) site in the Indian Peaks of the Colorado Front Range focuses on the consequences of changed temperature and precipitation regimes. The distribution of snow patches and windblown areas, duration of the snow-free period, and position of meltwater drainages strongly affect the patterns of alpine plant communities. Furthermore, the hydrology of alpine watersheds responds quickly to changes in the quality of precipitation because of thin acidic soils, large volumes of snowfall, and low buffering capacity of the slow-weathering, predominantly granitic bedrock (Williams et al. 1991). One of the goals of the Niwot LTER project is thus to understand how current snowpack distributions affect patterns of vegetation from species to regional scales.

Hierarchic geographic information systems

We are using a hierarchic geographic information system to assist us in these studies. Geographic information systems (GIS) are computer hardware and software systems designed to store, manipulate, and display geographically referenced data (Star and Estes 1990). GIS databases are commonly used for multivariate analyses of spatial ecological information. Additionally, numerical models have been linked to regional and global spatial databases to develop extrapolations of ecosystem processes (e.g., Burke et al. 1991, Running et al. 1989). A hierarchic GIS (HGIS) is a nested set of GIS databases at several spatial scales. Long-term ecological studies often require data collected from a wide range of spatial domains so that, for example, changes observed in species distributions can be linked to changes in regional patterns of spectral reflectance as observed with Earth-orbiting satellites.

In this article, we demonstrate how a nested hierarchy of relatively fine-scale GIS databases can be used to help understand the links between species patterns at the level of plots, landscape patterns of plant communities, and regional patterns seen on satellite images. The methods described here focus on spanning the spatial domains—from that of individual plants

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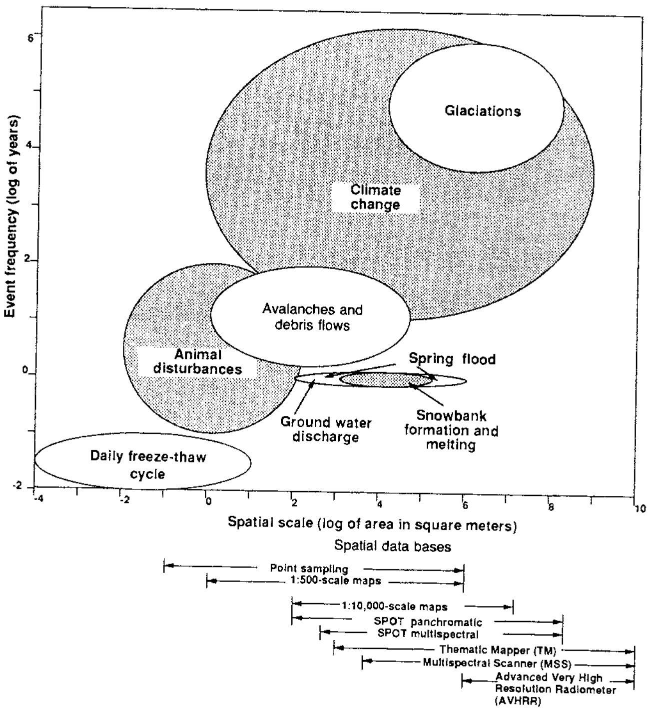


Figure 1. Spatial and temporal domains for natural disturbances at the Niwot LTER site. The shaded ellipses represent disturbance types that are major focuses of study at the site. The available data types for examining various scales of disturbance are shown at the bottom of the figure.

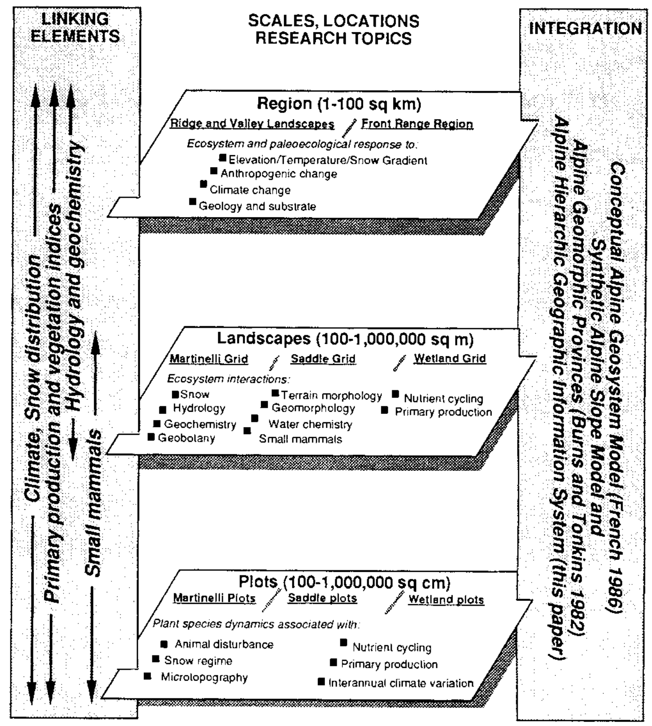


Figure 2. Conceptual framework for the Niwot hierarchical GIS.

(10^{-2} m^2) to that of SPOT[1] satellite images with pixel sizes of 10^2 m^2 and covering 60-kilometer-wide swaths (approximately 10^9 m^2 image size). We use a suite of standard mapping methods and vegetation legends to improve compatibility between tiers of the hierarchy and promote intersite comparisons.

Conceptual framework for the alpine HGIS. Our three primary goals for establishing the alpine HGIS are to provide accurate spatial frameworks for studies of ecosystem processes and geobotanical patterns at appropriate scales, develop baselines for long-term observations of natural and anthropogenic change, and provide geographically referenced data for models of ecosystem processes. The hierarchy of disturbances in the alpine ranges from soil heave caused by the formation of needle-ice crystals at spatial scales of 10^{-4}–10^1 m^2 (Washburn 1980) to the disturbance caused by glaciers, which currently cover areas as small as 10^4 m^2 but which covered areas as large as 10^8 m^2 in the Front Range during the Pleistocene (Outcalt and MacPhail 1965; Figure 1). The databases are prepared to address questions related to disturbances at plot, landscape, and regional scales.

A conceptual diagram of the HGIS (Figure 2) summarizes its tiers, the major topics of research at each scale, the themes that provide linkage between tiers, and models that provide conceptual integration. At plot-level scales (10^{-2}–10^2 m^2), we are interested in the plant species dynamics associated with snow distribution. Snowpack indirectly controls the distribution of many plant species by limiting the length of the growing season (Billings and Bliss 1959, May and Webber 1982). Wind-exposed sites (Figure 3) have extremely low winter soil temperatures and high moisture stress (Ehleringer and Miller 1975, Oberbauer and Billings 1981).

The distribution of pocket gophers (*Thomomys talpoides*) is also strongly controlled by snow patterns. Gophers are largely responsible for the fine-scale mosaic of many plant communities; they maintain species diversity by creating gaps in the plant canopy, redistributing nutrients and soil, and suppressing species that would otherwise dominate (Halfpenny and Southwick 1982, Osburn 1958, Thorn 1982, Willard 1979).

Our main long-term plot-level hypothesis is that plant species will react to changes in snowpack in a manner that is predictable from their present-day distribution along snow-depth gradients. In future years, we plan to test this hypothesis by artificially altering winter snow regimes with a series of large snow-fences at the Niwot LTER site. Before the experiment, we need to determine the patterns of species distribution with respect to natural snow distribution.

At the intermediate scale of landscapes (10^2 m^2–10^6 m^2), we are examining the patterns of vegetation communities, primary production, and small-mammal distribution associated with hill-slope toposequences, and snow gradients from wind-blown sites to deep snow patches (Figure 4). Rug-

[1]Systeme Probatoire l'Observation de la Terre-1 satellite: High-resolution visible with two modes of sensing—panchromatic black-and-white with 10-meter resolution over the range 0.51–0.73 5μm, and multispectral with 20-meter resolution in three channels (0.50–0.59, 0.61–0.68, and 0.79–0.89 5μm).

ged alpine topography and strong winds control snow distribution, resulting in highly heterogeneous, patchy landscapes (Billings 1973, 1988, Billings and Bliss 1959, Bliss 1985, Ellenberg 1988, Holway and Ward 1963, Komárková 1979, Marr 1967, May and Webber 1982, Swanson et al. 1988, Willard 1979). Abundant and complex boundaries (tension zones) are inherent in these patchy landscapes (Forman and Godron 1986), and if a climate change occurs, shifts in species composition would likely occur most quickly at boundaries and be observable at several scales (Nielson et al. 1989, Rosswall et al. 1988).

At the regional scale associated with the City of Boulder Watershed (10^3 km^3) or the Front Range (10^6–10^8 km^2), our primary focus is on the patterns of plant biomass associated with major elevation gradients (Figure 5). Also, we are interested to see if the fine-scale patterns associated with snow distribution at landscape scales have any influence on the regional trends in production. Estimates of production based on remotely sensed data provide an efficient means to examine regional patterns, yet there is relatively little research in the alpine regions, possibly due to the confounding influences of rugged topography and highly heterogeneous vegetation patterns. Our main regional hypothesis is that primary production is broadly controlled by gradients associated with changing elevation but also influenced by smaller-scale topographic interactions with wind and snow.

Topics linking all three tiers of the hierarchy include climate, snow distribution, primary production, and spectral reflectance. The influence of small mammals is a theme that links the lower two tiers; topics related to hydrology and geochemistry link the upper two tiers. Several conceptual models and the HGIS provide a framework for the Niwot LTER project.

Figure 3. Fellfield vegetation. At the plot level, we are investigating the distribution of plant species in relation to snow patterns. **a.** Association *Sileno-Paronychietum* is characteristic of windblown ridges. **b.** The herb layer is dominated by cushion and mat-forming plants, including *Paronychia pulvinata, Silene acaulis, Minuartia obtusiloba*, and *Trifolium nana*. Photos by D. A. Walker.

HGIS methods. In the Alaskan Arctic and the Colorado alpine, we are building HGIS databases that use a common suite of methods that permit comparative studies of vegetation patterns in arctic and alpine regions (Walker and Walker 1991). Most of the methods we use are described in the references cited in Table 1.

Geographically referencing ecological data. The LTER project is representative of many intensive ecological research programs that require topographic information and base maps at finer scales than is available from standard US Geological Survey (USGS) topographic maps. For example, the largest-scale topographic maps available for the Niwot site are at 1:24,000 scale, but the project also requires maps of the intensive research sites at 1:500 scale (Figure 6). To satisfy this requirement, an aerial-photograph mission provided black-and-white and false-color photographs at the necessary scale.

Before obtaining the aerial photographs, it was necessary to survey ground control points to maintain horizontal and vertical accuracy across the map and to register mapped information to satellite-derived data. In most remote regions, there are few accurately surveyed benchmarks to provide control for locating spatial data. Control points can be surveyed from existing benchmarks or with the use of the global positioning system

Figure 4. Snowbeds near treeline on Niwot Ridge in the Front Range of Colorado. The relationships among terrain morphology, redistribution of snow by wind, vegetation patterns, and animal activity are the primary subjects of study at the landscape scale (10^2–10^6 m^2). Photo by J. C. Halfpenny.

Figure 5. Treeline on Niwot Ridge. At the regional scale, HGIS focuses on phenomena associated with large-scale climate shifts, such as the position of the treeline and greenness of the tundra, which can be detected by means of remotely sensed data. Photo by J. C. Halfpenny.

(Michener et al. 1991, Wilkie 1990). Research grids were also surveyed for systematic field sampling and to establish a framework for georeferenced data collected at the site (Figure 7). These grids are established with reference to the universal transverse Mercator coordinate system with permanently marked grid points at 50-meter intervals.

Orthophoto topographic maps and digital terrain models (DTMs) were constructed from the black-and-white aerial photographs taken by a professional photogrammetric engineering company. DTMs are computer files containing horizontal and vertical (x, y, z) coordinates for arrays of geographic points. DTMs are particularly useful for modeling watershed characteristics and surface energy budgets based on slope and aspect information. Three-dimensional views of the landscapes can also be made (Figure 6).

Mapping techniques. The most detailed level of HGIS is that of the individual vegetation sample plots. At the Niwot site, these plots are located at each grid point of the Niwot Ridge Saddle grid. Permanently marked vegetation plots are established at each grid point of the Saddle grid. Vegetation is monitored using a point quadrat (Figure 7). The intent of these plots is to provide a baseline for measuring long-term changes to the vegetation and microtopography and to examine species response along topoedaphic or other environmental gradients. Current plans call for repeating the sampling at five-year intervals.

GIS products provide a visually comprehensible baseline portraying the species composition at the top and bottom of the plant canopy, height of the vegetation canopy, and microtopography of the soil surface. The data allow for detailed examination of the controls of microscale environmental variation because the data are spatially referenced, both with respect to the 350 x 500-meter Saddle grid and the 1 x 1-meter permanent plots. For this study, a direct gradient analysis (Whittaker 1978) was used to examine the cover of each species along the snow gradient. The cover value for a given species was compared with the mean May snow depth for 1982, 1983, and 1984 at each of the 88 grid points. Other studies are examining the relationship of species occurrence to microtopographic variation within the plots and temporal change related to gopher disturbance.

Landscape- and regional-scale mapping. Many GIS projects use an approach in which existing mapped information is digitized into the GIS database directly from the original sources. The maps may have different map scales, map-unit resolutions, dates of data collection, and classification systems. When these different sources are combined in a GIS, artifacts may arise due to boundary mismatches and scale incompatibility (Dangermond and Harnden 1990).

Integrated geobotanical mapping

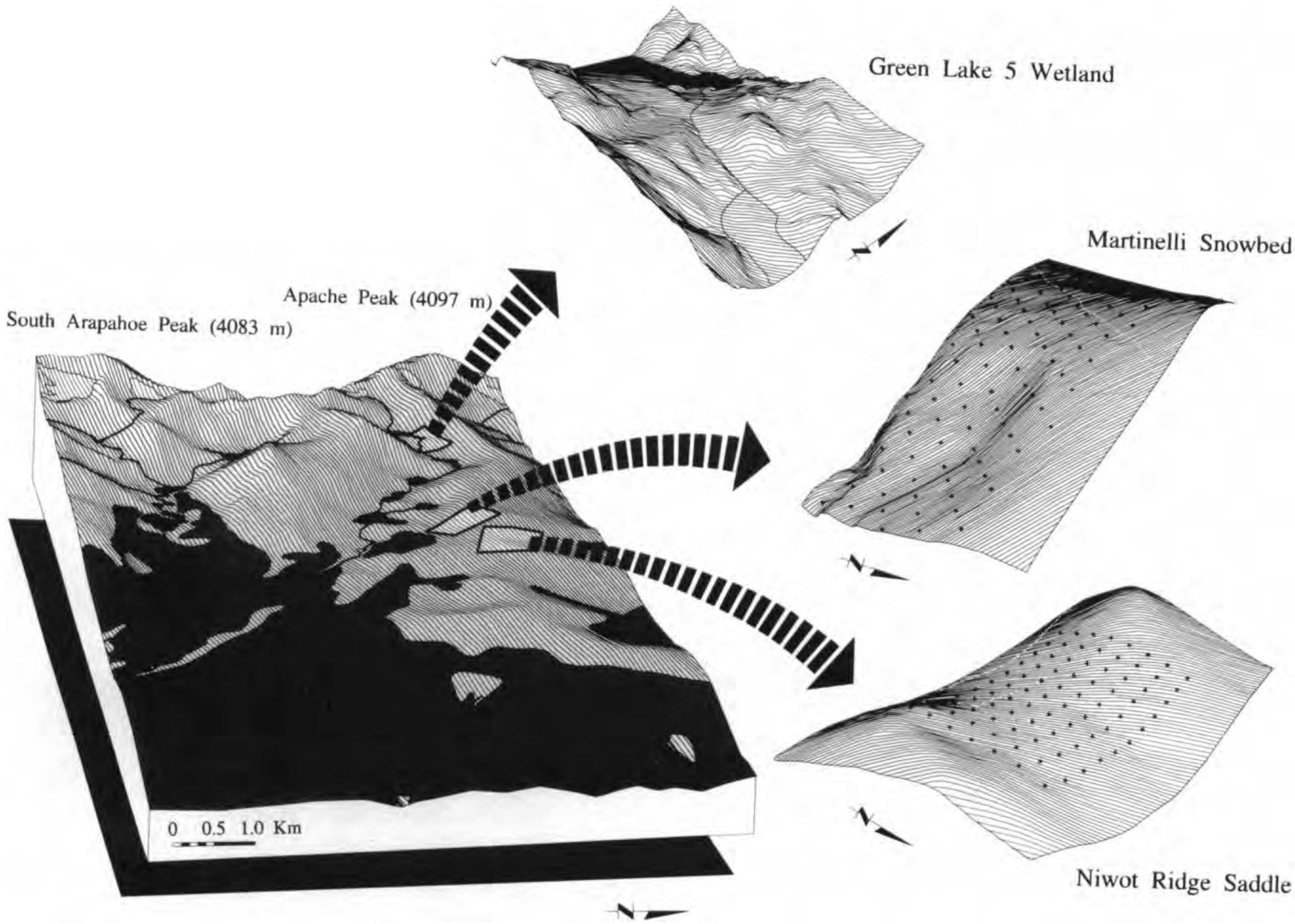


Figure 6. Hierarchy of digital terrain models for the Alpine HGIS. The DTM on the left covers the City of Boulder watershed at the headwaters of North Boulder Creek. The three smaller DTMs enclose the intensive research sites for the Niwot LTER project. Vertical exaggeration is 3.8x and for the DTM of the region and 1.5x for the three-site DTMs.

can minimize many of these problems. This method simultaneously maps vegetation and other terrain features that are interpreted on a common air-photo base (Everett et al. 1978, Walker et al. 1980). We use the term *geobotany* in its traditional European sense to refer to the study of plant communities and their relationship to geology, landforms, and soils (Braun-Blanquet 1932). Terrain geomorphic boundaries are used to guide the delineation on aerial photographs of most major vegetation boundaries similar to the landscape-guided vegetation mapping approach developed in Europe (Zonneveld 1988) and the integrated terrain unit mapping approach developed by the Environmental Systems Research Institute in redlands, CA (Dangermond and Harnden 1990).

In instances in which other maps already exist, the existing information is reinterpreted so that the boundaries match the geomorphic controls on the aerial photo. Additional boundaries are drawn to account for changes in geobotanical features that are not controlled by geomorphology. Each polygon is coded with a fractional code in which the numerator contains the vegetation information and the denominator contains the soil, landform, geomorphic, and geologic information (Walker et al. 1980, 1989). At scales finer than about 1:5000, most of the mapping is done in the field with supplemental photo-interpretation.

Standardized geobotanical legends are desirable for comparative studies. The Braun-Blanquet approach (Westhoff and van der Maarel 1978) is well suited for classifying and mapping alpine vegetation (e.g., Cooper 1986, Komárková 1979, Willard 1979). The US soil taxonomy (USSSS 1977) provides a similar framework for soils, but standardization is needed for other mapped attributes, including landforms and surface forms.

The geobotanical map is one layer in a GIS. Other layers include remotely sensed information, DTM, maps of political boundaries and infrastructure features (e.g., roads and buildings), maps of features that change over short time intervals (e.g., animal distribution), and features that are mapped using point samples, such as snow or soil characteristics. Maps of any element or combination of elements can then be prepared from the database.

In this study, we mapped the vegetation of the Saddle grid using 19 previously defined Braun-Blanquet vegetation associations (Komárková 1979; Table 2, Figure 8b). We also mapped the vegetation according to six vegetation noda that have been

Table 1. Methods used for hierarchic GIS databases.

Database considerations	Method	Reference	Purpose and advantages
General considerations			
Conceptual framework	Tier diagram	Walker and Walker (1991)	Specifies questions being addressed and linkages between tiers of the hierarchy and sources of integration
Georeferencing of spatial data			
Coordinate system	Universal transverse Mercator grid (UTM)	USGS	All spatial information is referenced to a common global coordinate system Coordinates are in meters All intensive research sites within a region have the same geographic reference system
Research grids	Grids with 50-meter grid point spacing labeled with UTM coordinates	Walker and Walker (1991)	Provides a grid for field sampling and accurate georeferencing of all data collected at the intensive research sites Finer or coarser grids are easily constructed with reference to UTM coordinate system
Basemaps and digital terrain models (DTMs) for fine-scale databases	Orthophoto topographic maps and DTMs prepared by photogrammetry companies using high-resolution aerial photographs	This article	Provides necessary resolution for fine-scale databases
Mapping techniques			
Geobotanical mapping	Integrated mapping approach	Everett et al. (1978), Walker et al. (1981), Dangermond and Harnden (1990), Zonneveld (1988)	Based on principle that the landforms are the primary control of vegetation patterns. Vegetation map unit boundaries are guided by geomorphic features. This is particularly useful for natural landscapes with low-growing vegetation and lends itself well to an integrated GIS approach Vegetation, soils, landforms, and surface forms (geobotanical elements with the same spatial domain and often having common boundaries) are mapped simultaneously Minimizes boundary mismatches in the GIS database All elements in the database are photointerpreted at the scale of the basemap instead of combining elements mapped at different scales with varying boundary resolution
Map legends	Braun-Blanquet vegetation classification	Westhoff and van der Maarel (1976), Barkman (1986)	Names of units are based purely on floristic composition It is a hierarchic approach whereby higher level units have regional or global significance Units are formally recognized by the International Botanical Congress Structural and functional characteristics of vegetation are useful for remote sensing and modeling studies
Maps of plant species	Permanently registered 1 × 1–meter point quadrats	Mueller-Dombois and Ellenberg (1974), Walker and Walker (1991)	Detailed information regarding microtopography, structure of vegetation canopy, and species composition is provided for 100 points in each 1 × 1–meter plot Permanently registered location allows resampling of same points for long-term studies

used for many vegetation studies on Niwot Ridge (May and Webber 1982; Figure 8a). We then quantitatively determined the spatial coincidence between paired data elements (vegetation associations, snow cover, and slope) by using a frequency analysis (Evans et al. 1989; Figure 8c,d,e).

Linking ground-level observations to remotely sensed information. The methods of interfacing remote sensing and geographic information systems are now well established (Marble and Peuquet 1983, Star and Estes 1990). A 60 x 60-kilometer SPOT image of the Front Range of Colorado was obtained on 4 September 1988 (Figure 9). We used this image to analyze for trends in the normalized difference vegetation index (NDVI)[2] along elevation gradients. NDVI is related to the amount of illuminated chlorophyll in the plant canopy with minimized contribution from background sources; it is often used as an index of green biomass or leaf area index (Goward et al. 1985). NDVIs have been shown to have near-linear relationships with canopy photosynthesis and conductance (Sellers 1985, 1987), and the index has been used for extrapolation of regional process estimates (e.g., Running et al. 1989, Schimel et al. 1991).

A preliminary analysis of an NDVI map of the Niwot LTER site suggested that the elevation gradient largely constrains the amount of green biomass in the alpine. This result seems intuitive because of the colder temperatures at high elevations and the prolonged snow cover. However,

[2]NDVI = (NIR - R)/(NIR + R), where NIR is the spectral reflectance in the near-infrared (0.725–1.1 mm), where light scattering from the canopy dominates, and R is the reflectance in the red chlorophyll-absorbing portion of the spectrum (0.58–0.68 5mm).

Table 2. Summary of nodum equivalents, area, and habitat of syntaxonomic units occuring on the vegetation map of Niwot Ridge Saddle grid. The syntaxonomic units are derived using the Braun-Blanquet classification approach (Komárková 1979). Nodum equivalents are from May and Webber (1982). Area summaries refer to Figure 8b. Habitat descriptions are based on Komárková (1979).

Syntaxonomic unit and author*	Area		Nodum[†]	Habitat
	m^2	Percent		
Class *Elyno-Seslerietea* Braun-Blanquet 1948				Well-drained, basophilous to weakly acidophilous alpine areas
Order *Kobresio–Caricetalia rupestris* Komárková 1976				Climax habitats on well-drained gently sloping ridge tops of the Front Range
Alliance *Kobresio–Caricion rupestris* Komárková 1976				Windy, stable, cool, well-drained broad interfluves and ridges
Association *Trifolietum dasyphylli* Willard 1963	7625	4.4	Fellfield	Subxeric, snow-free >200 d
Association *Potentillo–Caricetum rupestris* Willard 1963	2	0.0	Fellfield	Xeric to subxeric, south-facing slopes, snow-free >200 d
Association *Sileno-Paronychietum* Willard 1963	6100	3.5	Fellfield	Xeric, extremely wind-exposed fellfields, snow-free >200 d
Association *Selaginello densae–Kobresietum myosuroidis* Cox 1933 *corr.* Komárková 1976	36,926	21.1	Dry meadow	Subxeric to mesic turfs on gentle slopes, snow-free 150–200 d
Class *Salicetea herbaceae* Braun-Blanquet 1948				Alpine snow patches
Order *Trifolio-Deschampsietalia* Komárková 1976				Earlier-melting snow patches of the Front Range, snow-free 100–150 d
Alliance *Deschampsio–Trifolion parryi* Komárková 1976				Shallow mesic depressions and broad leeward hill slopes
Association *Acomastylidetum rossii* Willard 1963	45,659	26.1	Moist meadow	Mesic, early-melting snow cover
Association *Deschampsio caespitosae–Trifolietum parryi* Komárková 1976	13,570	7.8	Moist meadow	Subxeric to mesic, early-melting snow patches
Association *Stellario laetae–Deschampsietum caespitosae* Willard 1963	10,207	5.8	Moist meadow	Mesic, early-melting snow patches
Order *Sibbaldio–Caricetalia pyrenaicae* Komárková 1976				Later-melting snow patches of the Front Range, snow-free <75 d
Alliance *Sibbaldio–Caricion pyrenaicae* Komárková 1976				Late-melting snow patches of the low alpine
Association *Toninio-Sibbaldietum* Willard 1963	13,263	7.6	Snowbed	Subxeric to subhygric, margins of late-melting snow
Association *Caricetum pyrenaicae* Willard 1963	1684	1.0	Snowbed	Subxeric to mesic, late-melting snow patches
Association *Juncetum drummondii* Willard 1963	1567	0.9	Snowbed	Mesic, moderately late-melting snow patches
Association *Phleo commutati–Caricetum nigricantis* Komárková 1976	760	0.4	Snowbed	Mesic to subhygric depressions below deep snow
Alliance *Anthelio–Pohlion obtusifoliae* Komárková 1976				Bryophyte-dominated, very-late-melting snow patches
Association *Polytrichastro alpini–Pohlietum obtusifoliae* Komárková 1976	214	0.1	Snowbed	Mesic to subhygric springs and late-melting snow
Class *Scheuchzerio–Caricetea fuscae* Tüxen 1937				Alpine bogs and marshes
Order *Pediculari–Caricetalia scopulorum* Komárková 1976				Marsh communities of the Front Range, snow-free period varies
Alliance *Pediculari–Caricion scopolorum* Komárková 1976				Wetter, warmer, shallower snow marsh communities of the Front Range
Association *Caricetum scopulorum* Kiener 1939 *em.* Willard 1963	8890	5.1	Wet meadow	Subhygric to subhydric marshes on mineral soils
Class *Betulo-Adenostyletea* Braun-Blanquet *et* Tüxen 1943				Tall herb, grass, and shrub communities of the lower alpine and subalpine belt
Order *Salici-Trollietalia* Komárková 1976				Tall herb and shrub communities of the Colorado subalpine
Alliance *Salicion planifolio-villosae* Komárková 1976				Subxeric to subhygric willow shrublands, snow-free 100–150 d
Association *Bistorto viviparae–Salicetum planifoliae* Komárková 1976	1167	0.7	Shrub tundra	Subxeric to mesic shrublands
Association *Rhodiolo integrifoliae–Salicetum planifoliae* Komárková 1976	2960	1.7	Shrub tundra	Mesic to subhygric shrublands
Class *Montio-Cardaminetea* Braun-Blanquet *et* Tüxen 1943				Montane to subalpine springs
Order *Primulo-Cardaminetea* Komárková 1976				Spring communities of the Rocky Mountains, snow-free period varies
Alliance *Cardamino–Primulion parryi* Komárková 1976				Spring communities of the Colorado alpine and subalpine
Association *Epilobio anagallidifolii–Primuletum* Komárková 1976	577	0.3	Snowbed	Subhydric to hydric springs, streams, and snow patches
Other map units				
Abies lasiocarpa or *Picea engemannii* Krummholz	56	0.0		
Barren including lichen-covered rock	23,610	13.5		
Water	5	0.0		
Total	174,842	100.0		

*Komárková 1979.

[†]May and Webber 1982.

Table 3. Optimal snow depth classes for the 50 most common species on the Niwot Ridge Saddle grid. Species are placed in the snow class where their mean cover value is the highest. Cover is calculated as percent occurrence of 8448 random points (88 plots with 96 points each; 4 points in each sample are used as registration points for the point quadrat). Frequency is the percent of occurrences in the 88 1 × 1-meter plots.

Snow depth class (cm)	Species	Cover (percent)	Frequency (percent)
0–25	*Selaginella densa*	2.10	23
	Silene acaulis	0.77	18
	Xanthoparmelia taractica	0.66	18
	Oreoxis alpina	0.54	16
	Umbilicaria krascheninnikovii	0.38	7
	Sporastatia testudinea	0.19	3
	Arenaria fendleri	0.15	8
	Paronychia pulvinata	0.14	5
	Hymenoxis acaulis	0.13	8
	Phlox sibirica	0.13	7
	Luzula spicata	0.09	9
26–50	*Kobresia myosuroides*	10.25	26
	Carex rupestris	2.36	31
	Cladonia pyxidata	1.59	42
	Minuartia obtusiloba	1.18	41
	Trifolium dasyphyllum	0.85	24
	Lecanora rupestris	0.54	20
	Rhizocarpon geographicum	0.39	10
	Calamagrostis purpurascens	0.37	11
	Thamnolia subuliformis	0.25	14
	Cornicularia aculeata	0.24	15
	Campanula uniflora	0.15	8
	Cetraria islandica	0.13	8
51–100	*Artemisia scopulorum*	3.30	57
	Carex scopulorum	3.26	26
	Salix planifolia	1.09	1
	Erigeron simplex	0.84	24
	Gentianoides algida	0.56	18
	Salix arctica	0.50	16
	Lloydia serotina	0.41	20
	Bistorta vivipara	0.34	11
101–200	*Acomastylis rossii*	16.08	83
	Bistorta bistortoides	2.46	61
	Caltha leptosepala	1.31	16
201–300	*Deschampsia caespitosa*	5.55	40
	Sibbaldia procumbens	3.27	27
	Polytrichum piliferum	2.76	24
	Festuca baffinensis	0.98	35
	Lecidea atrobrunea	0.71	15
	Castilleja occidentalis	0.66	22
	Ranunculus adoneus	0.60	15
	Lecanora novo-mexicana	0.39	12
	Chionophila jamesii	0.33	11
	Lewisia pygmaea	0.20	12
301–400	*Trifolium parryi*	5.50	44
401–500	*Carex pyrenaica*	0.95	9
	Primula parryi	0.63	3
	Juncus drummondii	0.47	3
	Poa arctica	0.34	7
	Erigeron melanocephalus	0.24	7

closer inspection of the NDVI image indicated that some large high-elevation areas are greener than areas at lower elevation, suggesting that exposure to prevailing winds and site moisture may control production over large areas of the alpine.

To quantify the relationships between NDVI and elevation, we stratified the alpine area above the tree line in the Front Range using the forest boundary as depicted on 1:24,000-scale USGS topographic maps. NDVI was regressed against elevation, using the NDVI values in 50-meter elevation classes derived from a digital terrain model. To determine if there was a systematic effect of slope or aspect, we stratified the data according to slope-aspect classes (e.g., north, northeast, and east), and 5% slope classes. The data were also stratified according to areas east and west of the Continental Divide to assess the effects of different orographic precipitation regimes. Most of the snow on the west side of the Divide occurs with storm systems from the Pacific with westerly flow, whereas the East Slope receives the largest amount of precipitation during upslope conditions with strong southerly to easterly flow (Barry 1973).

Ground measurements of spectral reflectance were used to calibrate the SPOT NDVI values with mapped vegetation information in the Saddle grid GIS. We used a field-portable radiometer to obtain mean spectral reflectance values for the major vegetation types portrayed on the vegetation map. The measurements were taken during the same week that the SPOT image was taken. Spectral reflectance was measured at each of the 88 grid points in the Saddle grid. We also obtained a clip harvest of the vegetation to determine relationship between NDVI and biomass at each grid point.

Vegetation-snow relationships in the Colorado alpine

Plant species–snow relationships. Eighty-four plant species were recorded at the Saddle grid plots. We examined the distribution of the 50 most common species along the snow gradient (Table 3). These species represented 77% of the cover in the 88 plots. Most of the remaining 23% was rock (11.4%), soil (4.3%), and litter (2.5%).

Many of these species are found in narrow ranges of snow depth. For example, *Paronychia pulvinata* is a cushion plant that has its optimal distribution on stable, dry, windblown, rocky sites with less than 25 cm of maximal May snow cover; it is rare in areas with more than 50 cm of snow (Figure 3, Figure 10a). Other plants with a similar distribution include *Oreoxis alpina*, *Phlox sibirica*, and

Selaginella densa. *Kobresia myosuroides*, although one of the most abundant plants in the Saddle (10.2% cover), has a relatively narrow distribution with respect to snow depth. Its optimal cover occurs in dry, windy sedge meadows with shallow snow cover 26–50 cm deep (Figure 10b). A large group of dry meadow species have a similar distribution pattern, including *Campanula uniflora*, *Carex rupestris*, and *Trifolium dasyphyllum*.

Other species are limited to sites with deep snow cover. Included here are *Sibbaldia procumbens* (Figure 10d), *Carex pyrenaica*, *Chionophila jamesii*, *Erigeron melanocephalus*, *Juncus drummondii*, *Poa arctica*, and *Ranunculus adoneus*. Some species, such as *C. pyrenaica* (Figure 10f) and *E. melanocephalus*, occur only in the deepest snow areas, whereas others, such as *S. procumbens* and *Trifolium parryi* (Figure 10d,e), occur across a broader range of snow cover, but they have their optimal distribution in remotely deep snow beds.

A few species span a large portion of the snow-depth gradient. The most cosmopolitan species, *Acomastylis rossii*, occurs in all snow depth classes, with its optimal occurrence in 1–2 m of snow (Figure 10c). *A. rossii* is also the most abundant species on Niwot Ridge, covering approximately 16% of the Saddle grid. Other species with wide distributions along the snow gradient (and high frequency values in Table 3) include *Artemisia scopulorum*, *Bistorta bistortoides*, *Carex scopulorum*, *Cladonia pyxidata*, *Deschampsia caespitosa*, *Erigeron simplex*, *Festuca baffinensis*, *Minuartia obtusiloba*, *Polytrichum piliferum*, and *T. parryi*. Snow plays a less important role in the distribution of these species. Other factors, such as site moisture and disturbance by gophers, may be more important to these species; nonetheless, most of these widely distributed species have a range of snow depths where their growth is optimal.

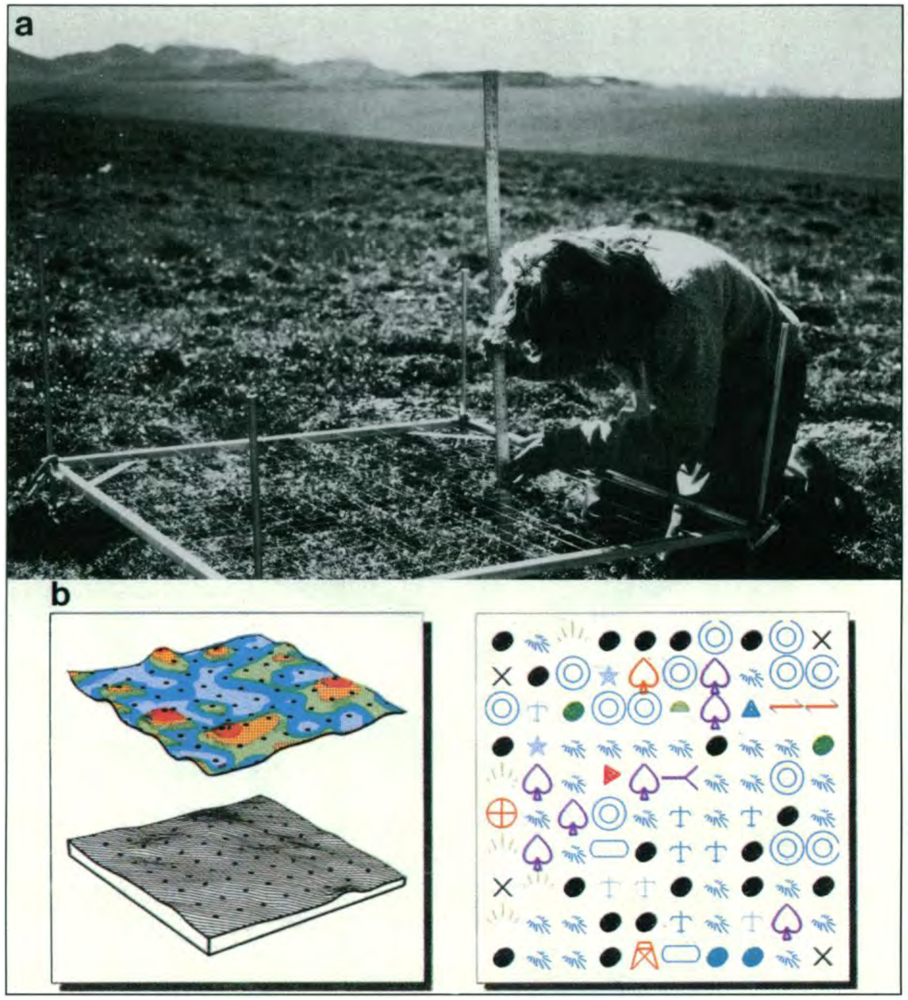


Figure 7a. Point quadrat. The metal frame has 100 gridpoints where plant species are recorded. The point quadrat can be repositioned exactly by the use of metal registration points that are nailed into the tundra. Each plot is sampled at 10-centimeter intervals. Two parallel grids of monofilament fishing line spaced 2 centimeters apart reduce the problem of parallax when sighting down on the vegetation. The quadrat frame has four small levels on each side of the frame. At each point, the observer records the species at the top and bottom of the vegetation canopy and the vertical distance of the plants from the plane of the frame. **b.** Example of microsite GIS database. The terrain model on the left portrays the microtopography at the base of the plant canopy (lower layer) and the height of the vegetation canopy (upper layer). The colors represent 5-centimeter height classes. The diagram on the right portrays the species composition at 10-centimeter grid point spacing at the base of the plant canopy. Separate diagrams (not shown) are made for the species at the top and bottom of the plant canopy for each grid point. The colors denote growth forms, and the shapes of the symbols denote species.

Landscape-level patterns of plant communities. The control of snow on the distribution of the dominant alpine species is also reflected at the community level. Many of the species with the clearest distributions with respect to the snow gradient are diagnostic species for the vegetation classification units, or syntaxa,[3] on the vegetation map of the Saddle grid (Figure 8). For example, among the species shown in Figure 10, *Paronychia pulvinata* and *Kobresia myosuroides* (Figure 10a,b) are diagnostic taxa[4] for alliance *Kobresio–Caricion rupestris* in class *Elyno-Seslerietea* (Komárková 1979; Table 2). This alliance includes associations that are typical of broad, well-drained, stable, windswept ridges of the Front Range. *P. pulvinata* has its optimal distribution in the fellfield association *Sileno-Paronychietum* (as described in the association tables of

[3]The hierarchical units of the Braun-Blanquet vegetation classification system (class, order, alliance, and association) are collectively referred to as *syntaxa* in much the same way that units of species classification (class, order, family, genus, and species) are collectively called *taxa*.

[4]In the Braun-Blanquet classification approach, diagnostic taxa are used for characterization of syntaxa; they have relatively narrow distributions within a given syntaxon even if they are not strictly restricted to that syntaxon.

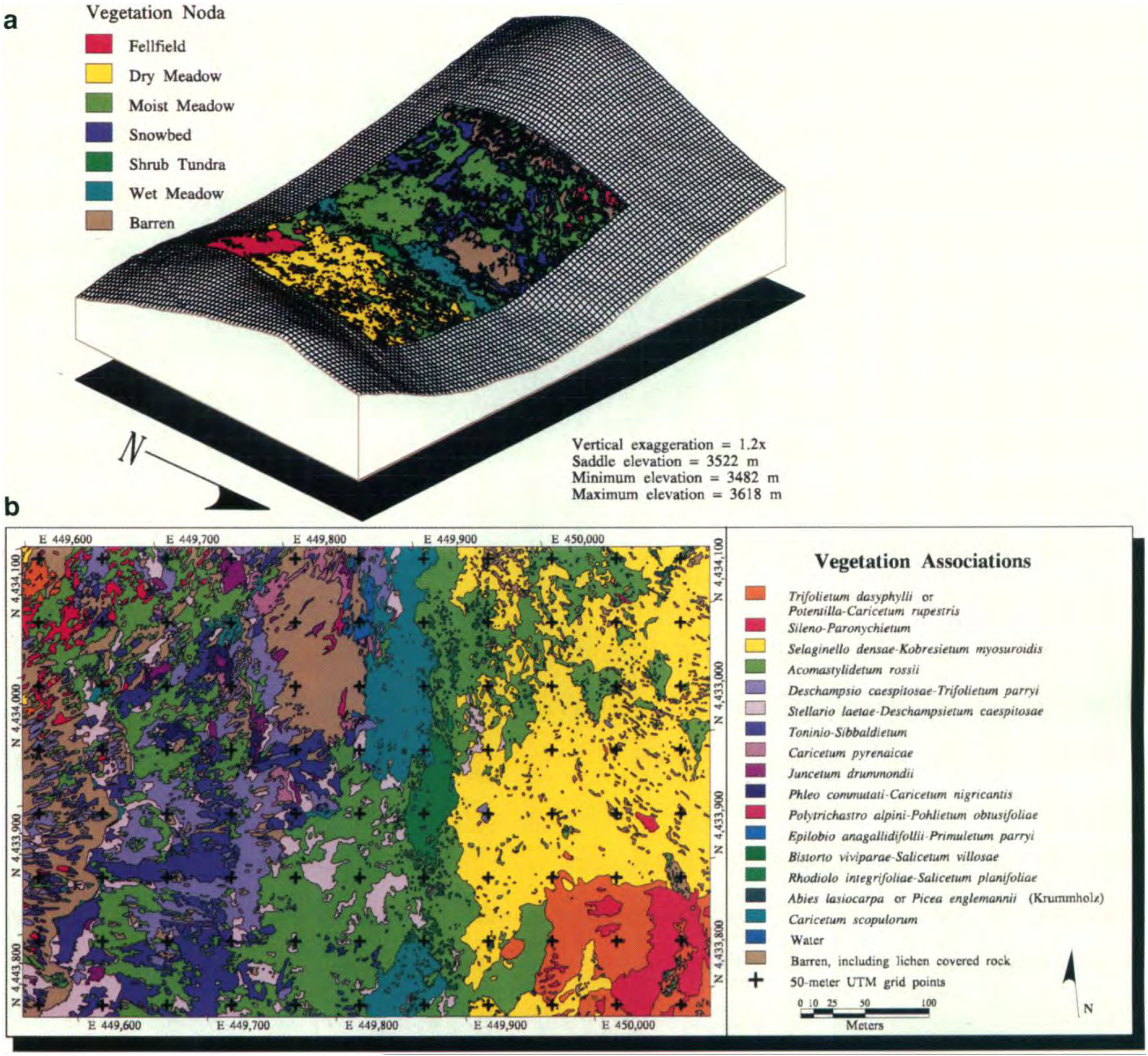
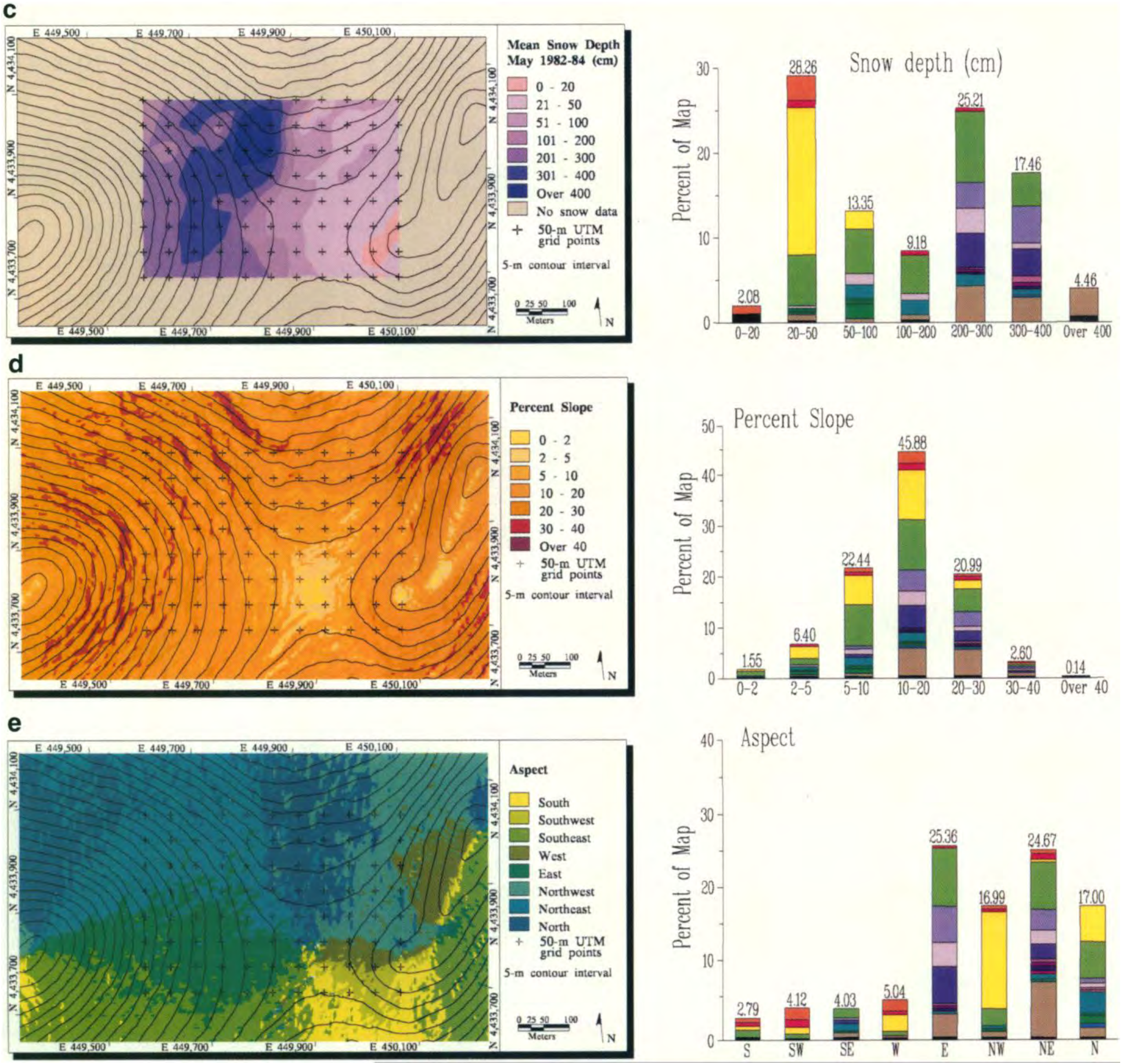


Figure 8. Vegetation, terrain, and snow depth on the Niwot Ridge Saddle grid. **a.** Vegetation noda (May and Webber 1982) draped over a 3-D view of the Saddle. **b.** Vegetation associations mapped according the classification of Komárková (1979). **c.** The snow map is interpolated from average May snow depths at the 88 grid points in 1982, 1983, and 1984. **d** and **e.** Slope and aspect maps derived from the digital terrain model. The bar graphs with each map portray the percentage of each map covered by the classes shown along the x-axes. Each bar is divided into sections representing the percentage of the class covered by the vegetation associations in **b.** The bottom cell of each bar represents the lumped total of vegetation types with area percentages too small to be shown as separate sections.

Komárková 1979). *K. myosuroides* has its maximal distribution in the dry meadow association *Selaginello densae–Kobresietum myosuroidis*. *Acomastylis rossii* (Figure 10c) is a widespread species that is not a diagnostic for any syntaxon, but it reaches is optimal distribution in the moist meadow association *Acomastylidetum rossii* (Komárková 1979).

S. procumbens, *T. parryi*, and *C. pyrenaica* (Figure 10d,e,f) are diagnostic species for syntaxa within the snow-patch class *Salicetea herbaceae*. *S. procumbens* is a diagnostic species for the class and reaches its optimal distribution in association *Toninio-Sibbaldietum*. *T. parryi* is a diagnostic species for the shallow-snow-patch order *Trifolio-Deschampsietalia*, and reaches its optimum distribution in association *Deschampsio–Trifolietum parryi*. *C. pyrenaica* is a diagnostic species for the deep-snow-patch order



Sibbaldio–Caricetalia pyrenaicae, and has its optimum distribution in the association *Caricetum pyrenaicae*. Numerous other diagnostic species for the syntaxa of the classes *Elyno-Seslerietea* and *Salicetea herbaceae* have distributions that are clearly related to winter snowpack and length of the growing season.

The spatial distributions of syntaxa of the classes *Elyno-Seslerietea* (wind-blown sites) and *Salicetea herbaceae* (snowbed sites) are strongly controlled by the distribution of snow. Syntaxa of these two classes cover 79% of the Saddle grid (Table 2) and 78% of the alpine area on Niwot Ridge (Komárková and Webber 1978), an indication of importance of wind and snow cover in this alpine landscape. The maps of the vegetation associations and snow depths (Figure 8b and c) show a strong correspondence. Areas with less than 50 cm of snow are dominated by alliance *Kobresio–Caricion rupestris*. Association *Sileno-Paronychietum* covers 60% of the areas with less than 20 cm of snow, and association *Selaginello densae–Kobresietum myosuroidis* covers 69% of the areas with 21–50 cm of snow. In snow-patch areas, associations of order *Trifolio-Deschampsietalia* predominate in areas with snow depths from 50 to 200 cm (58% cover), whereas associations of order *Sibbaldio–Caricetalia pyrenaicae* and barren gravel predominate in areas with more than 200 cm of snow (45% cover).

The topographic control of these patterns is apparent (Figure 8c,d). West-facing slopes are predominantly blown free of snow. The primary vegetation types on west-facing slopes

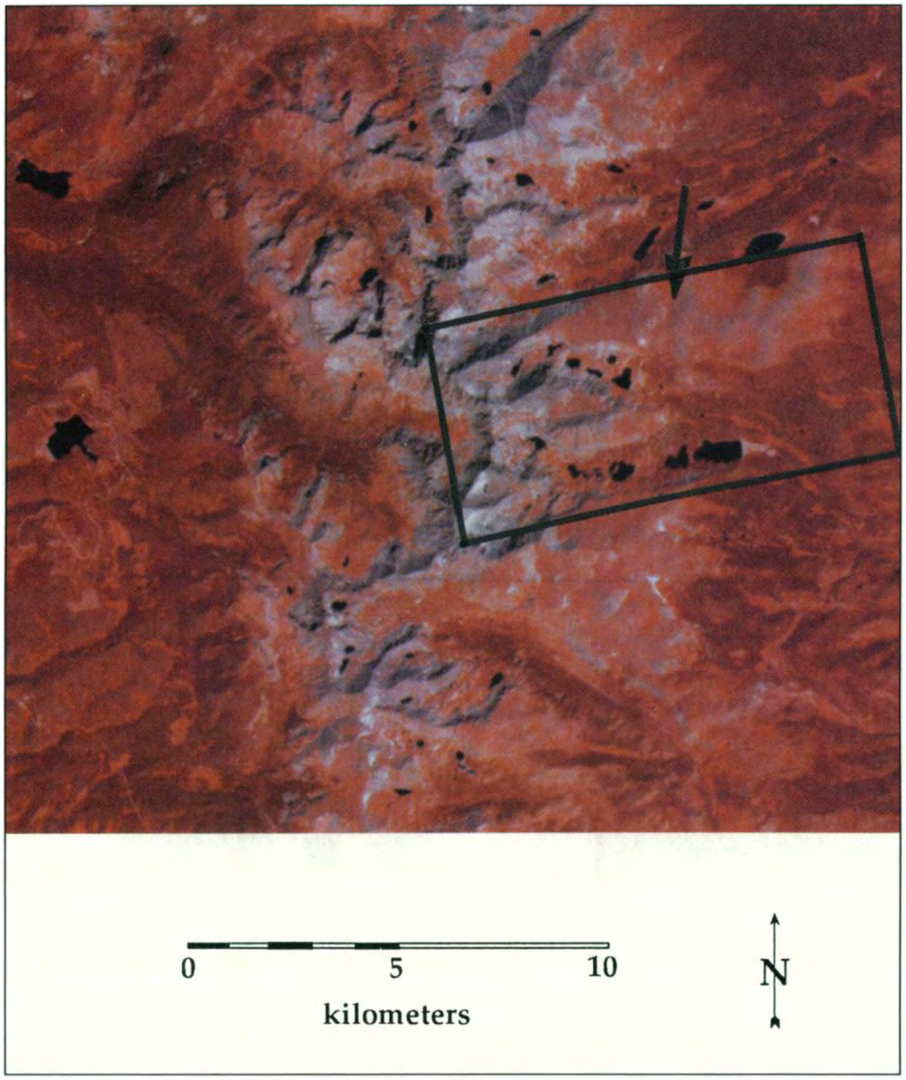


Figure 9. False-color SPOT satellite-derived image of the Front Range. The rectangle outlines the Niwot LTER site and the City of Boulder watershed. The arrow points to the Niwot Ridge Saddle area.

are either fellfield associations (*Trifolietum dasyphylli* and *Sileno-Paronychietum*) or dry sedge meadow associations (*Selaginello densae–Kobresietum myosuroidis*). These three associations occur on 85% of the west-facing aspects, 82% of the southwest-facing aspects, and 78% of the northwest-facing aspects. In contrast, east-facing slopes have a predominance of deep snow accumulation areas and associations of class *Salicetea herbaceae* (84% cover on east-facing slopes, 54% cover on southeast-facing slopes, and 58% cover on northeast-facing slopes).

Strong westerly winds are responsible for these patterns. At the D-1 weather station, 2 km west of the Saddle, 79% of the hourly mean wind directions were from the west and the mean wind velocity was 11 m sec^{-1} during the winter months (October-April) from January 1988 to December 1989. Maximal wind speeds exceeded 30 m sec^{-1} during all winter months. During the same period, winds were somewhat more variable at the Saddle due to topographic steering of winds around the west knoll of the Saddle, but still more than 81% of the winds were out of either the west or northwest.[5]

The derived slope and aspect maps (Figure 8c,d) indicate considerable topographic variation at scales finer than the 50-meter resolution of the Saddle grid used to make the snow map. This topographic variation undoubtedly affects snow distribution at a finer scale than is portrayed in Figure 8c. The correspondence between snow depth and vegetation would, therefore, likely be even stronger if the snow were mapped at the same resolution as the vegetation.

Regional patterns of NDVI. Comparison of NDVI values with snow-depth and soil-moisture values suggest an underlying relationship between soil moisture and vegetation greenness, as inferred by NDVI (Figure 11b). Within the Saddle grid, NDVI shows a trend of increasing value from barren to fellfield to dry meadow to snowbed to moist meadow to wet meadow to shrub. High NDVI values in the shrub and wet meadow areas are due to late-season greenness resulting from moisture supplied by the late-melting snow. The low NDVI values for fellfields (associations *Sileno-Paronychietum* and *Trifolietum dasyphylli*), dry meadows (association *Selaginello densae–Kobresietum myosuroidis*), and windswept, primarily west-facing, areas in general (i.e., alliance *Kobresio–Caricion rupestris*) are likely due to low production caused by droughty site conditions. In contrast, moist meadows typical of early-melting snow patches on east facing slopes (alliance *Deschampsio–Trifolion parryi*) have relatively high soil moisture and high NDVI values. Late-melting snow patches (alliance *Sibbaldio–Caricion pyrenaicae*) are covered by snow during much of the growing season and experience a prolonged melt that washes away finer particles to leave a rocky bed with low production and low NDVI.

Regional patterns of NDVI along elevation gradients are strongly influenced by the contrast between east- and west-facing slopes. Regressions of NDVI versus elevation show the expected general decrease in NDVI with increasing elevation, with considerable scatter about the mean due to landscape heterogeneity (Figure 12a–c). This trend applies to almost all slopes and aspects on both the east and west side of the Continental Divide. The only aspects showing no trend in NDVI with elevation are west-facing aspects on the east side of the divide, probably due to the influence of strong westerly winds that constrain production on these sites at all elevations (Figures 3, 12d). The lack

[5]Niwot LTER, unpublished data, 1988–1989.

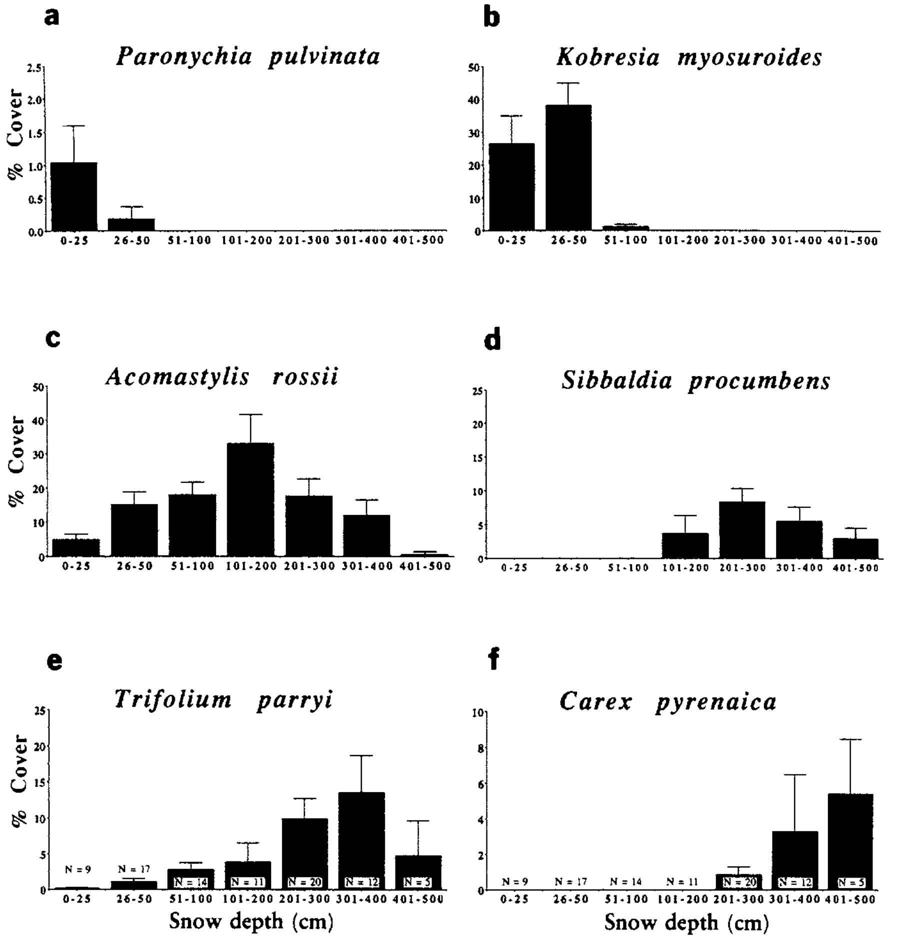


Figure 10. Distribution (plus or minus standard error) of six species along the snow gradient. Species cover values are from the 88 1 x 1-meter plots at the gridpoints of the Saddle grid. Snow measurements are the means of maximal snow depths measured at the gridpoints in May of 1982, 1983, and 1984. N = number of plots in each snow-depth class.

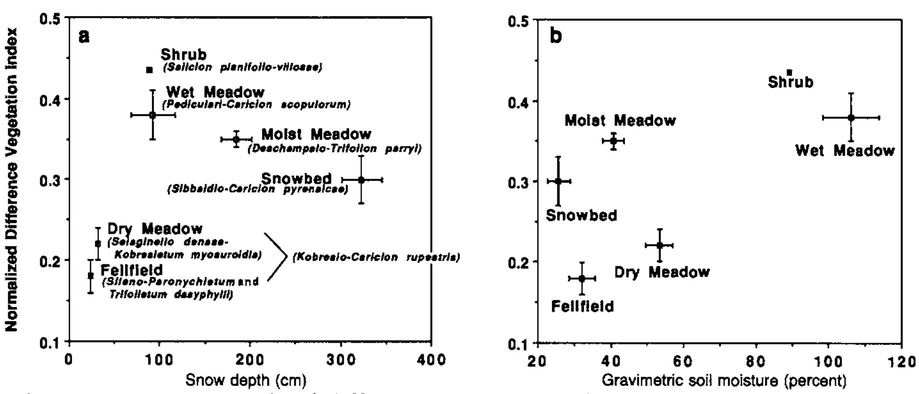


Figure 11. Mean normalized difference vegetation index for the vegetation noda on the Saddle grid (plus or minus standard errors). Noda are arranged along a snow gradient (**a**) and along a soil moisture gradient (**b**). The relatively high gravimetric soil moisture values for dry meadows compared to moist meadows is due to high organic content (low bulk density) of the *Kobresietum* soils.

of a similar relationship on west-facing aspects west of the Continental Divide suggests that a different wind regime exists on the West Slope. Although there are no climate stations on the west side of the Divide in the Indian Peaks, other investigators have observed that krummholz and stands of *Sileno-Paronychietum* are uncommon west of the Divide, suggesting generally calmer conditions (Komárková 1979). East-facing slopes on the east side of the Divide have the steepest regression, possibly due to the generally moister soil conditions at low elevations and the constraining influence of later-melting snowpack at higher elevations. The presumably calmer conditions on the west side of the Divide result in less contrast between east- and west-facing slopes, although the y-intercept and the slope of the regression curve are greater for the east-facing slopes on both sides of the Divide.

The contrast in the regression lines between the east and west sides of the Divide suggest that the NDVI-versus-elevation relationship could be used to compare the effects of different climates on regional patterns of greenness in the alpine. For example, in a humid summer climate such as the White Mountains of New Hampshire, we might find generally higher NDVI values at all elevations above the treeline, causing a shift of the regression line upward (assuming that the x-axis portrays elevation above the treeline, instead of above sea level). On the other hand, mountain ranges with dry summer climates, such as the Sierras, may have relatively low NDVI for all aspects at all elevations. A combination of warmer summer temperatures and higher precipitation may shift the line to the right. On mountain ranges with light winds, such as some areas of the Brooks Range, climates may show little contrast between windward and leeward aspects; whereas windy ranges such as the Big Horns should show a strong difference in the slopes of the regression lines on wind-influenced aspects. Similar logic could be used to predict the consequences of various climate change scenarios in the Front Range. Of course, substrate would also have a strong influence on site moisture regimes, and it would be interesting to use mountain ranges with a variety of bedrock types to examine the influence of bedrock on the NDVI-versus-elevation relationship.

Linking pattern to process. The hierarchic analysis of alpine vegetation patterns emphasizes that plant species, community, and green-biomass patterns are largely controlled by snow distribution, which varies greatly with

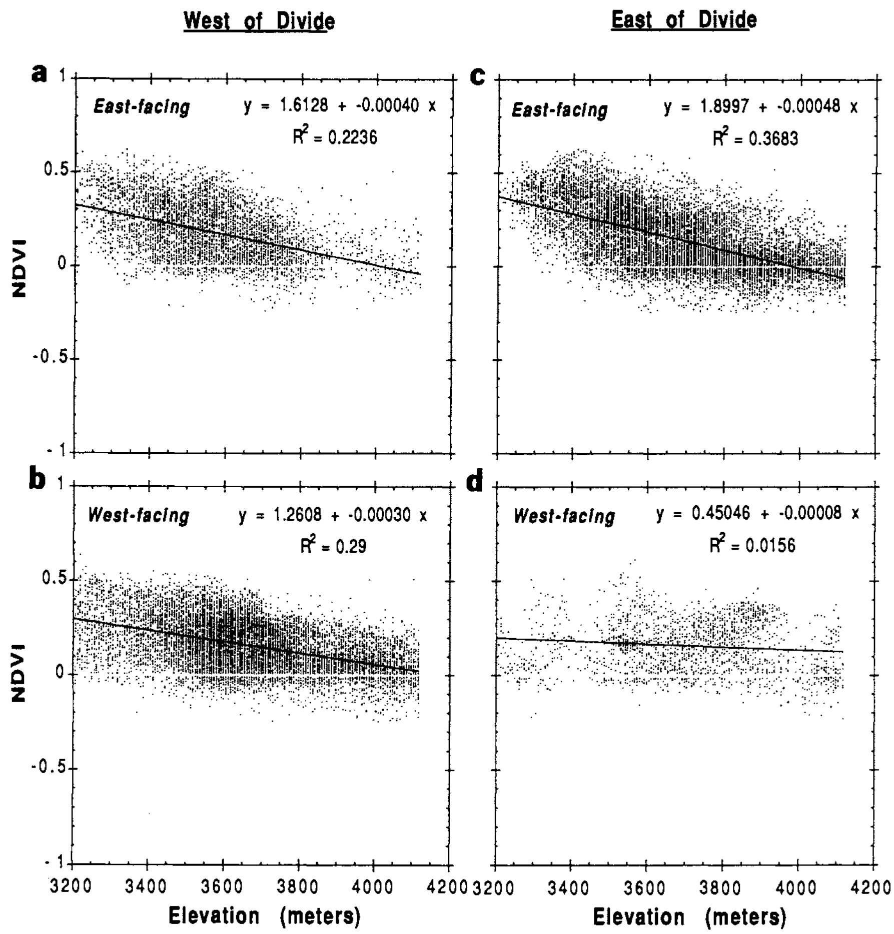


Figure 12. Normalized difference vegetation index versus elevation for two aspect classes on 6–15% slopes on the west and east sides of the Continental Divide; $p < 0.001$ for all regressions.

topography and wind patterns. The snow regime affects water availability, soil and leaf temperature, surface microclimate, and timing and duration of the growing season. Because snow meltwater is a major source of nutrients to nitrogen- and phosphorus-deficient alpine systems, landscape-level patterns of available soil nutrients are also likely to be closely linked to snow distribution patterns (Bowman 1992, Reddy and Caine 1990). Modification of snow and moisture regimes through variations in climate or direct anthropogenic impacts may significantly alter nutrient and vegetation patterns and, as a consequence, landscape-level processes.

Specific questions currently being addressed by research at Niwot Ridge include: Will changing snow regimes influence the spatial distribution of nutrients and directly affect ecosystem-level nutrient fluxes? How will alpine ecosystems adjust to altered snow regimes, and how will these adjustments manifest at different levels of ecosystem organization? The answers to these and other process-level questions are being addressed with an experiment in which we are altering snow regimes through the use of snow fences. A prediction of the effects of future altered precipitation regimes requires a hierarchical approach to examining alpine ecosystem response, comparative studies in mountain ranges with other climates, and experimental research on the effects of altered precipitation regimes.

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