

The Vegetation

Hierarchical Species-Environment Relationships

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Introduction

The vegetation of Niwot Ridge has a rich history of study, beginning with phytosociological studies directly on the Ridge and in the surrounding mountains and incorporating more experimental and dynamic approaches in later years. This chapter provides an overview of the spatial patterns of Niwot Ridge plants and plant communities relative to the primary controlling environmental gradients at scales from the individual to the landscape.

The spatial patterns of vegetation at all scales are dominated by physical forces, particularly the interaction of wind, snow, and topography (Fig. 6.1). The controls of biotic factors on the distribution and abundance of plant species on Niwot Ridge have received considerably less attention than have physical factors, but recent studies have revealed the importance of competition and certain mutualisms in structuring community composition.

Community research on Niwot Ridge has been organized around a hierarchy of spatial scales, from the plot to the region (Fig. 6.2). Plot-based studies have focused on physiological and ecological dynamics of specific species and communities, and more spatially extensive studies have provided a hierarchical framework for the plot studies. In this chapter, we first present an overview of the broader patterns in the vegetation, followed by descriptions of the communities, and then the specifics of physical and biotic controls on species and plant growth that drive the community patterns.

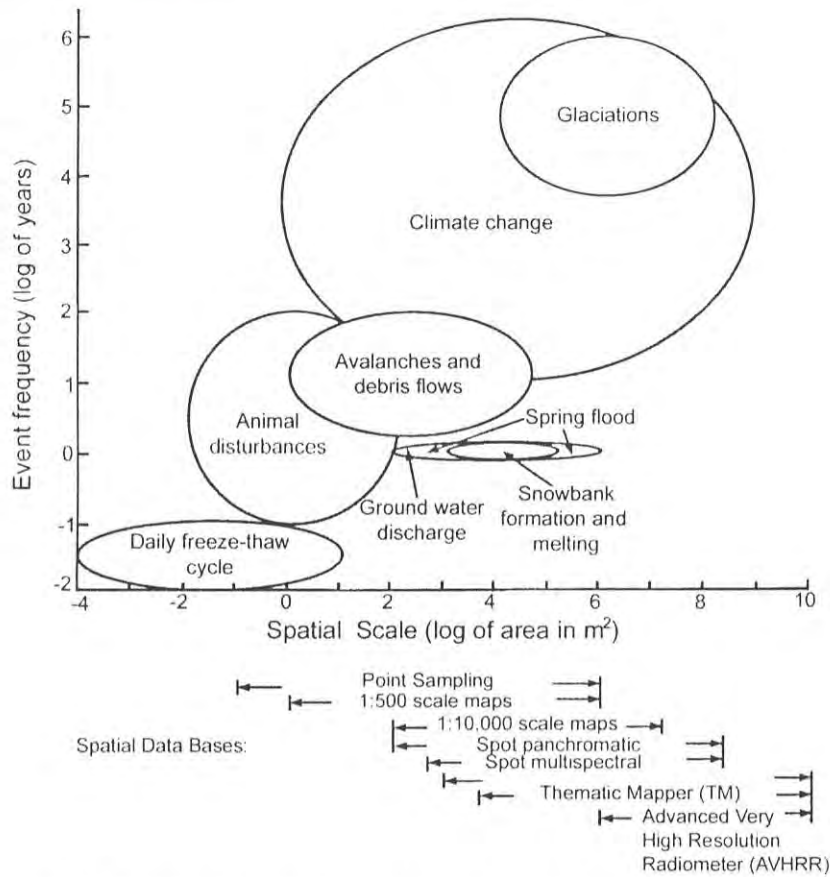


Figure 6.1. Spatial and temporal domains of natural disturbances and the available types of data for examining phenomena at each scale (modified from Walker et al. 1993).

Landscape and Regional Patterns

The landscape-scale patterns in the Niwot vegetation are driven by a complex elevation gradient, which is a combination of temperature and snow regime, with wind modifying and interacting with temperature and snow at all points along the gradient (chapter 2). Certainly the most critical boundary in the system is the upper tree limit, which defines the alpine system and which lies roughly between 3400 and 3600 m elevation on Niwot Ridge.

Billings (1988) provided a climatic-floristic-physiographic review of major North American alpine systems that helps to place Niwot Ridge into a larger perspective. Climatically, Niwot is intermediate between the dry Sierras, which have

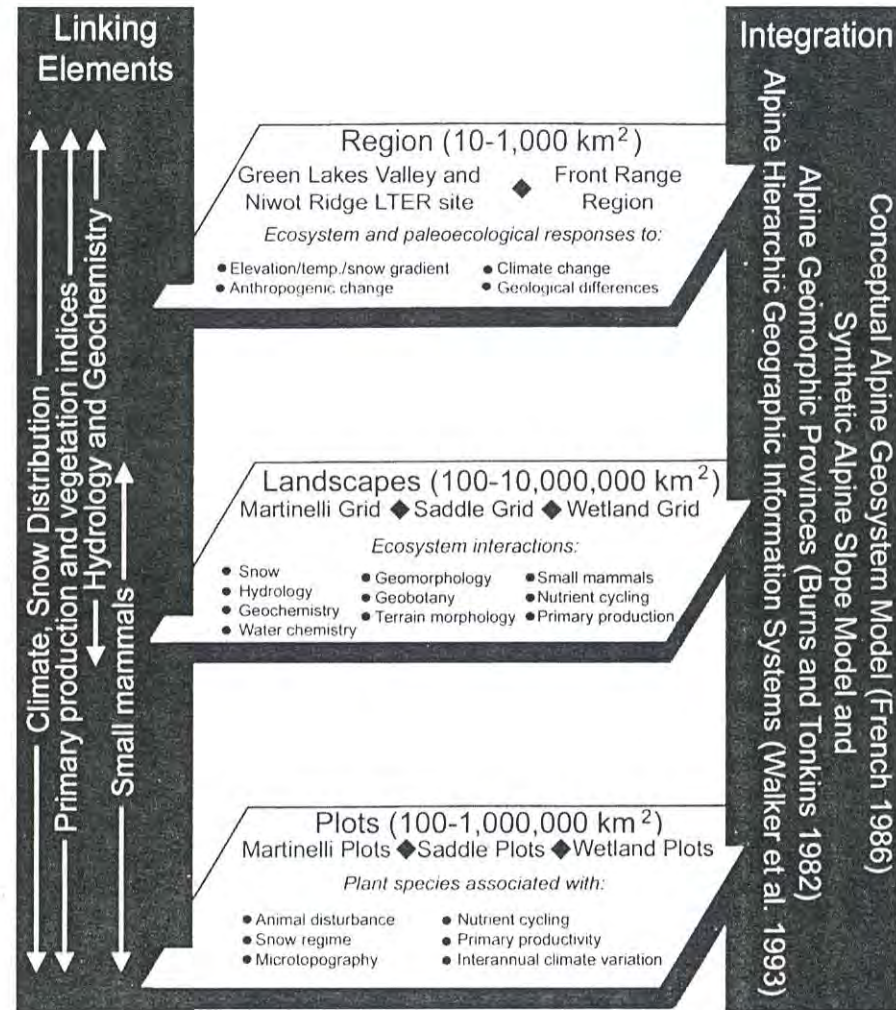


Figure 6.2. Conceptual framework for the Niwot hierarchic GIS, showing scales of research (plot, landscape, region), linking elements between scales, and types of integration (modified from Walker et al. 1993).

greater precipitation but almost none of it falling during the summer, and the wetter northern Appalachians (Mt. Washington), which have fairly even annual precipitation and no drought. Because of this intermediate position with respect to annual water balance, Niwot has the potential for some of the greatest ecological heterogeneity among North American alpine areas.

The origin of the flora is another key element in defining the vegetation. The flora has linkages to and elements of other North American and Asian alpine areas, to the

Arctic, to a lesser degree to the other major life zones that surround it, and also has a significant endemic element (Weber 1976; Komárková 1979). Weber and Willard (1967) listed 313 vascular taxa in the Colorado alpine, of which 67 were circumpolar and 130 were restricted to the alpine. Although the Rocky Mountain Cordillera provides the opportunity for northerly and southerly migration of species, there are few or no northern outliers of the Mexican highland flora present in the Colorado alpine, probably because of predominantly colder conditions than present during most of the last 20,000 years. Billings (1988) pointed out that although past climate and geographic connections are certainly important in explaining the importance of arctic species in the Colorado alpine and Appalachian alpine floras, the presence of adequate summer moisture is likely equally important in keeping them there, because those elements are largely missing in the drier Sierras. The discontinuity in the alpine zone in Wyoming may also play an important role in shaping the flora and therefore the vegetation of Niwot Ridge. The rich ericaceous flora of the Arctic and the Northern Rockies is largely missing in the Colorado alpine. Ericaceous species are particularly important in arctic snowbed vegetation, where they form dwarf-shrub heaths at the shallow end of the snow gradient. Therefore the snow-dominated communities of Niwot Ridge have little floristic affinities with either their Northern Rocky or arctic counterparts or with the snowbed vegetation of the alpine northern Appalachians, which maintains a strong ericaceous element and does have dwarf shrub vegetation (Bliss 1963).

The first landscape-scale view of Niwot Ridge was represented by the vegetation map of Komárková and Webber (1978), who mapped the alpine areas of the ridge at a scale of 1:10,000 using floristically defined units of the Braun-Blanquet system. The hierarchical nature of that system allowed them to map at different levels of floristic resolution depending on the spatial resolution of the units, so the polygons are coded as associations, alliances, orders, or classes depending on the situation. The map indicates a complex spatial mosaic across the entire ridge, but a trend toward drier communities dominated by *Kobresia myosuroides* at the eastern edge.

Walker et al. (1993) examined the landscape-scale patterns in more detail on remotely sensed images of normalized-difference vegetation index (NDVI). They looked at changes in NDVI with elevation on the east- and west-facing slopes on the two sides of the Continental Divide and found that while elevation explained significant variance in NDVI on the West Slope, on the East Slope the pattern only held true on east-facing slopes. The extremely high westerly winds apparently reduce the potential heterogeneity of these sites, acting as a stronger control on production and pattern than the complex elevation, temperature, and moisture gradient (80% of the winds are out of the west or northwest; see chapter 2). Walker et al. (1993) also mapped just the Saddle research area (Fig. 1.5) to the association level at a scale of 1:500, which also showed the east- and west-facing slope differentiation very clearly. The east-facing slope of the Saddle consists of a complex mosaic of communities differentiated by snow regime, moisture, and animal disturbance, whereas the west-facing slope is strongly dominated by a single community type.

Plant Communities and Their Controls

Classification of Niwot Vegetation

The first descriptions of the Niwot Ridge vegetation were by John Marr and his students as part of a general description of Eastern Slope ecosystems along a transect from the grasslands to the alpine (Marr, 1961). Marr's "D-1" site, at the western end of Niwot Ridge, served as the alpine representative along this major climate transect. Following Marr, work by Patrick Webber and students broadened the understanding of the vegetation patterns by developing formal classifications of the vegetation.

Two main systems of description have been applied to the Niwot vegetation, one based primarily on habitat, but with a floristic basis, the other on floristics and species (Table 6.1). May and Webber (1982) described six physiognomic-habitat-based units (noda) that were identified from their positions within a polar ordination diagram. Although this work was based on only 30 samples from the Saddle research site, the habitat-based approach was familiar to ecologists and physical scientists working on Niwot and thus became the standard for differentiating plant communities in other studies. Komárková (1979, 1980) used the Braun-Blanquet approach to classify the vegetation in the Indian Peaks region, of which Niwot Ridge is a part. Her detailed study was based on a total of 545 relevés (plots), of which 482 were used to produce the classification. Komárková recognized 52 plant associations (*sensu* Braun-Blanquet 1965, with class > order > alliance > association) in the Indian Peaks—20 of snowbeds, 7 of wind-blown sites, 6 of rock crevices, 12 of wet meadows, 8 of shrublands, and 4 of springs. Willard (1979) developed a classification for the alpine vegetation of Rocky Mountain National Park, approximately 20 miles to the north of Niwot. Table 6.1 shows the correspondence between the Komárková and May-Webber approaches.

The Niwot Ridge vegetation is most easily explained relative to a snow gradient, similar to the mesotopographic approach of Billings (1973, 1988) and recognized by Komárková (1979) and Burns and Tonkin (1982) (Fig. 6.3; Table 6.1). Here we present the major tundra habitats and their communities along a gradient of moisture and snow depth, excluding the vegetation associated with krumholz tree islands.

Fellfield, Extremely Windblown

Fellfield communities are one of the May-Webber noda, and they are well defined as a distinct physiognomic and habitat type. They occur on windblown slopes and ridge crests and are characterized by an open plant canopy and a high diversity of cushion plants. Crustose lichens reach their greatest diversity in these sites, and bryophytes are uncommon. About 10–50% of the ground is covered by cobbles or exposed gravel. Fellfields remain snow free throughout the year, although they may get a thin crust of snow in slight depressions. Important species, based on abundance, include *Carex rupestris*, *Paronychia pulvinata* (Fig. 6.4), *Minuartia obtusiloba*, *Trifolium dasyphyllum*, *Eritrichium aretioides*, and *Silene acaulis*. Komárková

Table 6.1. Summary of Front Range Vegetation Classification with Equivalent Noda (May and Webber 1982) and Typical Habitats

Syntaxonomic Unit and Author (Komárková 1979)	Habitat	Nodum (May and Webber 1982)
CLASS <i>Asplenietea rupestris</i> Meier et Br.-Bl. 1934	Rock crevices	
ORDER <i>Heuchero-Saxifragetalia</i> Komárková 1976	Rock crevices	
ALLIANCE <i>Heucherion bracteato-parvifoliae</i> Komárková 1976	Low-altitude, dry, south-facing rock crevices	
ASSOCIATION <i>Heucheretum bracteato-parvifoliae</i> Komárková 1976	Low-altitude, dry, south-facing rock crevices	
ALLIANCE <i>Saxifrago-Claytonia megarhizae</i> Komárková 1976	High-altitude, mesic, northwest-facing crevices	
ASSOCIATION <i>Besseyo alpinae-Caricetum nardinae</i> assoc. prov	Rocky, exposed ridges above 3800 m	
ASSOCIATION <i>Saxifragetum serpsifoliae</i> Kiener 1939 em. Komárková 1976	Northwest-oriented high peak faces in the subnival belt	
ASSOCIATION <i>Sagino saginoidis-Claytonietum megarhizae</i> Komárková 1976	Stable, snow-free, subseric ridges	
ASSOCIATION <i>Besseyo alpinae-Saxifragetum rivularis</i> Komárková 1976	Rock faces of sheltered and mesic ravines	
ASSOCIATION <i>Polystrichastro alpini-Poetium lettermanii</i> Komárková 1976	Wet rocks or scree at high altitude	
CLASS <i>Thlaspietea rotundifolia</i> Br.-Bl. 1948	Scree and gravel deposits	
ORDER <i>Aquilegio-Cirsietalia scopulorum</i> Komárková 1976	Scree and gravel deposits	
ALLIANCE <i>Aquilegio-Cirsion scopulorum</i> Komárková 1976	High-altitude scree and gravel	
ASSOCIATION <i>Oxyrio digynae-Ligularietum taraxacoidis</i> Komárková 1976	North-facing, fine-moving scree	
ASSOCIATION <i>Cirsietum scopulorum</i> Kiener 1939	South-facing, stable, medium-to-large scree	
ASSOCIATION <i>Minuartio biflorae-Caricetum arapahoensis</i> Komárková 1976	East-facing, stable, small-to-medium scree	
ALLIANCE <i>Cirsio-Phacelium sericeae</i> Komárková 1976	Warm, xeric, scree and gravel	
ASSOCIATION <i>Aquilegion coeruleae-Rubetum ulaei</i> Komárková 1976	Warm, xeric, scree near treeline	
ASSOCIATION <i>Aquilegion coeruleae-Ribesetum montigeni</i> Komárková 1976	Warm, xeric, stable scree near treeline	
ASSOCIATION <i>Phacelion sericeae-Polemonieta viscosi</i> Komárková 1976	Steep, south-facing, fine-moving scree	
CLASS <i>Elymo-Seslerietea</i> Br.-Bl. 1948	Well-drained, basophilous to weakly acidophilous alpine areas	
ORDER <i>Kobresio-Caricetalia rupestris</i> Komárková 1976	Climax habitats on well-drained gently sloping ridge tops of the Front Range	
ALLIANCE <i>Caricion tomeno-elysoidis</i> Komárková 1976	South-facing, warm, stable scree	
ASSOCIATION <i>Cerastio arvensi-Caricetum peneae</i> Komárková 1976	Steep, stable, fine scree	
ASSOCIATION <i>Caricetum elysoidei</i> Willard 1963	South- and east-facing, moderate, stable slopes	
ALLIANCE <i>Kobresio-Caricion caespitosae-Tritolietum parvi</i> Komárková 1976	Windy, stable, cool, well-drained broad interfluvies and ridges	
ASSOCIATION <i>Tritolietum caespitosae</i> Willard 1963	Subseric, snow-free >200 d	Fellfield
ASSOCIATION <i>Potentillo-Caricetum rupestris</i> Willard 1963	Xeric to subseric, south-facing slopes, snow-free >200 d	Fellfield
ASSOCIATION <i>Eriochloa-aretioidis-Dryadetum utopetalae</i> Kiener 1939 corr. Komárková 1976	Terrace sides on terraced ground	
ASSOCIATION <i>Sileno-Paronychieta</i> Willard 1963	Xeric, extremely wind-exposed fellfields, snow-free >200 d	Fellfield
ASSOCIATION <i>Sclaginelloidensisae-Kobresietum myosuroidis</i> Cox 1933 corr. Komárková	Subseric to mesic turfs on gentle slopes, snow-free 150-200 d	Dry meadow
CLASS <i>Salicetea herbaceae</i> Br.-Bl. 1948	Alpine snow patches	
ORDER <i>Trifolio-Deschampsietalia</i> Komárková 1976	Earlier-melting snow patches of the Front Range, snow-free 100-150 d	
ALLIANCE <i>Deschampsio-Trifolium parvi</i> Komárková 1976	Shallow meiotic depressions and broad leeward hill slopes	
ASSOCIATION <i>Acomastylidetum rossii</i> Willard 1963	Mesic, early-melting snow cover	Moist meadow
ASSOCIATION <i>Deschampsio caespitosae-Tritolietum parvi</i> Komárková 1976	Subseric to mesic, early-melting snow patches	Moist meadow
ASSOCIATION <i>Stellario laetae-Deschampsietum caespitosae</i> Willard 1963 corr. Komárková 1976	Mesic, early-melting snow patches	Moist meadow
ALLIANCE <i>Vaccinio-Danthionium intermediae</i> Komárková 1976	Subseric to mesic, early-melting snow patches at low elevations	
ASSOCIATION <i>Vaccinietum scoparii-caespitosi</i> Komárková 1976	Subseric to mesic, sloping snow patches at treeline	
ASSOCIATION <i>Solidagin spathulatae-Danthionium intermediae</i> Komárková 1976	Subseric to mesic, southeast- and northeast-facing prolonged snow patches	
ASSOCIATION <i>Artemisietum arcticae saxicolae</i> Willard 1963	Upper alpine belt on southeast-facing slopes	
ORDER <i>Sibbaldio-Caricetalia pyrenicae</i> Komárková 1976	Late-melting snow patches of the Front Range, snow-free <75 d	
ALLIANCE <i>Poo-Caricion haydenianae</i> Komárková 1976	Subseric to mesic, very prolonged snow patches, eroded	
ASSOCIATION <i>Sileno acaulis-Caricetum perobosae</i> Komárková 1976	Rocky snow patches	
ASSOCIATION <i>Oxyrio digynae-Poetium arcticae</i> Komárková 1976	Snow patch centers	
ASSOCIATION <i>Poo arcticae-Caricetum haydenianae</i> Komárková 1976	Southeast-facing, very late-melting snow patches	
ALLIANCE <i>Sibbaldio-Caricion pyrenicae</i> Komárková 1976	Late-melting snow patches of the low alpine	
ASSOCIATION <i>Tumino-Sibbaldietum</i> Willard 1963	Subseric to subhygic, margins of late-melting snow	Snowbed
ASSOCIATION <i>Caricetum pyrenicae</i> Willard 1963	Subseric to mesic, late-melting snow patches	Snowbed
ASSOCIATION <i>Juncetum drummondii</i> Willard 1963	Mesic, moderately late-melting snow patches	Snowbed
ASSOCIATION <i>Epilobio anagallidifoli-Antennarietum alpinae</i> Komárková 1976	Subhygic, late-melting snow cover, upper alpine	
ASSOCIATION <i>Epilobio anagallidifoli-Rorippetum alpinae</i> Komárková 1976	Lakeshores and streambanks with late-melting snow, accumulation of fine material	
ASSOCIATION <i>Phleo commutati-Caricetum nigricantis</i> Komárková 1976	Mesic to subhygic depressions below deep snow	Snowbed
ASSOCIATION <i>Sibbaldio procumbentis-Lewisietum pygmaeae</i> assoc. prov.	North-facing, stable sites, very prolonged snow cover	
ALLIANCE <i>Anthelio-Pohlion obtusifoliae</i> Komárková 1976	Bryophyte-dominated, very late melting snow patches	
ASSOCIATION <i>Solorino croceae-Polytrichetum piliferi</i> Komárková 1976	Late-melting snow patches in subnival belt	
ASSOCIATION <i>Polystrichastro alpini-Anthelietum juratzkanae</i> Komárková 1976	Hygic flat depressions on lakeshores	
ASSOCIATION <i>Polystrichastro alpini-Pohlion obtusifoliae</i> Komárková 1976	Mesic to subhygic springs and late-melting snow	Snowbed
ASSOCIATION <i>Bryo turbinati-Philonotidetum tomentellae</i> Komárková 1976	Very wet, late-lying snow	
CLASS <i>Scheuchzerio-Caricetea fuscae</i> Tx. 1937	Alpine bogs and marshes	
ORDER <i>Podulari-Caricetalia scopulorum</i> Komárková 1976	Marsh communities of the Front Range, snow-free period varies	
ALLIANCE <i>Bistorto-Caricion capillaris</i> Komárková 1976	Mesic to hygic, cold, prolonged snow cover	
SUBALLIANCE <i>Salicetion arctico-reticulatae</i> Komárková 1976	Moist depressions	
ASSOCIATION <i>Salicetum arcticae</i> Kiener 1939 em. Willard 1963	Early-melting snow patches with abundant moisture	
ASSOCIATION <i>Bistorto viviparae-Salicetum reticulatae</i> Komárková 1976	Mesic, snow-covered, stable sites	
SUBALLIANCE <i>Junco-Caricion capillaris</i> Komárková 1976	Wet rocks with fine soil accumulation	
ASSOCIATION <i>Carici capillaris-Bistortetum viviparae</i> Komárková 1976	Wet rocks, marsh margins, frost boils	
ASSOCIATION <i>Clemensio rhodanthae-Rhodiolaetum integrifoliae</i> Komárková 1976	Hydric to hygic sites with a continuous moisture supply	
ASSOCIATION <i>Bistorto viviparae-Caricetum microglochinis</i> Komárková 1976	Depressions with abundant moisture	
ASSOCIATION <i>Koenigietum islamicae</i> Willard 1963	Lakeshores and wet rocks	

(continued)

Syntaxonomic Unit and Author (Komárková 1979)	Habitat	Nodum (May and Webber 1982)
<p>ALLIANCE <i>Pediculari-Caricetum scopulorum</i> Komárková 1976</p> <p>ASSOCIATION <i>Drepanocladum esamulati-Caricetum riparietiae</i> Komárková 1976</p> <p>ASSOCIATION <i>Caricetum scopulorum</i> Kiener 1939 em. Willard 1963</p> <p>ASSOCIATION <i>Pediculari groenlandicae-Eleocharitetum</i> Komárková 1976</p> <p>ASSOCIATION <i>Clematis rhodanthae-Caricetum vernaculae</i> Komárková 1976</p> <p>ASSOCIATION <i>Philonotis tomentellae-Caricetum illinae</i> Komárková 1976</p> <p>ASSOCIATION <i>Pediculari groenlandicae-Caricetum squarilis</i> Komárková 1976</p>	<p>Wetter, warmer, shallower snow marsh communities of the Front Range</p> <p>Small depressions, lake shores, wet rocks</p> <p>Subhygric to subhydryc marshes on mineral soils</p> <p>Marshes in lower alpine belt</p> <p>Moist lakeshores, solifluction terraces</p> <p>Lakeshores, springs below snow patches</p> <p>Marshes near springs and lakes</p>	<p>Wet meadow</p>
<p>CLASS <i>Betula-Adenosvirgata</i> Br.-Bl. et. Tx. 1943</p> <p>ORDER <i>Salic-Trollietalia</i> Komárková 1976</p> <p>ALLIANCE <i>Salix-plumifoliosae</i> Komárková 1976</p> <p>ASSOCIATION <i>Bistorta viviparae-Salixetum villosae</i> Komárková 1976</p> <p>ASSOCIATION <i>Rhodola integrifoliae-Salixetum plumifoliae</i> Komárková 1976</p> <p>ASSOCIATION <i>Agropyro-Galiumagrostium canadensis</i> Komárková 1976</p> <p>ASSOCIATION <i>Carici scopulorum-Merenietum ciliatae</i> Komárková 1976</p> <p>ALLIANCE <i>Ligustico-Trollion laxi</i> Komárková 1976</p> <p>ASSOCIATION <i>Adoxa moschatellinae-Merenietum ciliatae</i> Komárková 1976</p> <p>ASSOCIATION <i>Ligustico filicini-Trollietum laxi</i> Komárková 1976</p> <p>ASSOCIATION <i>Ligustico filicini-Seneccietum triangulatis</i> Komárková 1976</p> <p>ASSOCIATION <i>Ligustico filicini-Athyrietum dilatifolii</i> Komárková 1976</p>	<p>Tall herb, grass, and shrub communities of the lower alpine and subalpine belt</p> <p>Tall herb and shrub communities of the Colorado subalpine</p> <p>Subverste to subhygric willow, shrublands, snow-free 100–150 J</p> <p>Subverste to mesic shrublands</p> <p>Mesic serees and streams near treeline</p> <p>Mesic meadows near treeline</p> <p>Streamlets and creeks</p> <p>Springs, streams, and other mesic locations near treeline</p> <p>At base of wet rocks, mesic sere</p> <p>Streambanks near treeline</p> <p>Streams and wet sere, lower alpine</p> <p>Southeast-facing, coarse, mesic sere</p>	<p>Shrub tundra</p> <p>Shrub tundra</p>
<p>CLASS <i>Montia-Cardaminetum</i> Br.-Bl. et. Tx. 1943</p> <p>ORDER <i>Primulo-Cardaminetalia</i> Komárková 1976</p> <p>ALLIANCE <i>Cardamo-Primulion purryi</i> Komárková 1976</p> <p>ASSOCIATION <i>Epilobion unguiculifolii-Cardaminetum cordifoliae</i> Komárková 1976</p> <p>ASSOCIATION <i>Philonotis tomentellae-Saxifragetum subrotundatae</i> Komárková 1976</p> <p>ASSOCIATION <i>Epilobion unguiculifolii-Primulion purryi</i> Komárková 1976</p> <p>ASSOCIATION <i>Clematis rhodanthae-Calthetum leptosepalae</i> Komárková 1976</p>	<p>Mountain to subalpine springs</p> <p>Spring communities of the Rocky Mountains, snow-free periods</p> <p>Spring communities of the Colorado alpine and subalpine</p> <p>West-facing, stable sites</p> <p>Springs in subalpine, lower alpine</p> <p>Subhydryc to hydryc springs, streams, and snow patches</p> <p>Springs and wet areas along streams, lower alpine</p>	<p>Snowbed</p>

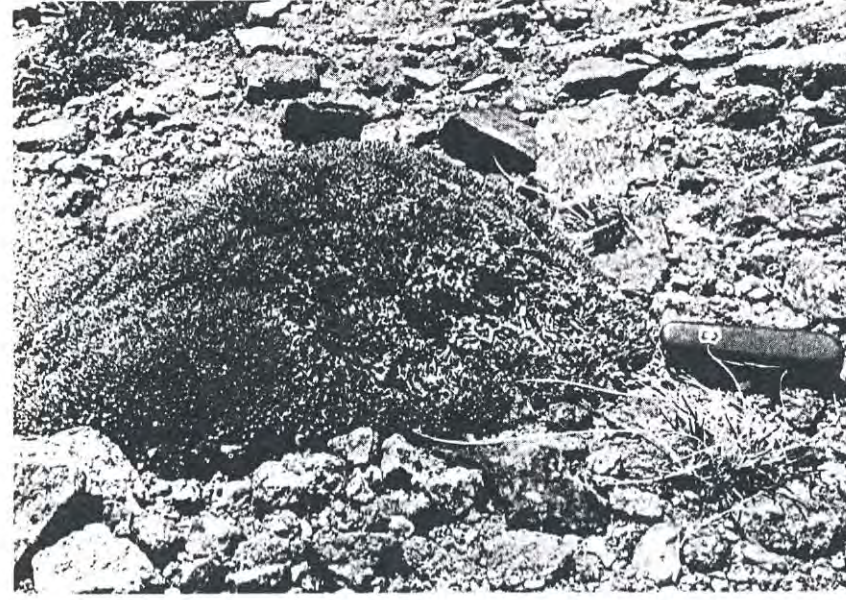


Figure 6.4. Cushion plant growth form, characteristic of fellfield communities, exemplified by *Paronychia pulvinata* (photo by William D. Bowman).

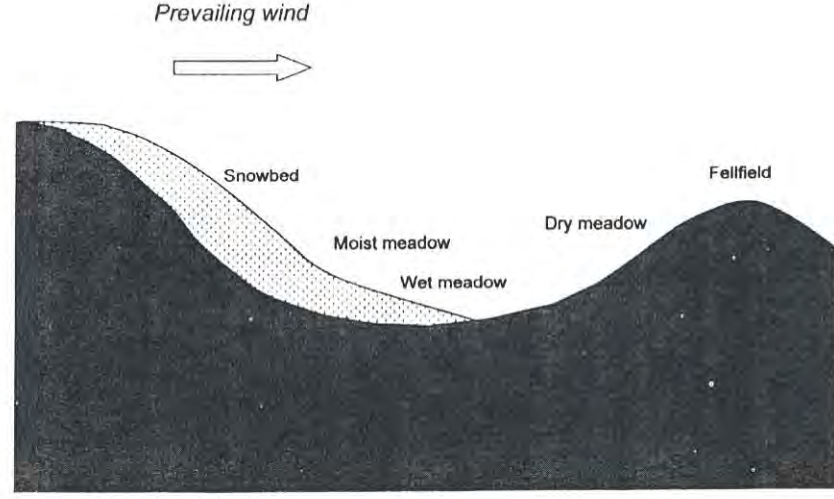


Figure 6.3. Idealized depiction of an alpine mesotopographic gradient, showing the position of major vegetational nodes in relation to snow distribution and topography (after Billings 1973).



Figure 6.5. Fellfield dominated by *Dryas octopetala*, a circumboreal community (photo by William D. Bowman).

placed these communities in the Alliance Kobresio-Caricion rupestris, which includes some associations in the slightly more mesic windblown dry meadows. The Alliance is the most extensive and well developed in the region. Typical fellfield associations include *Eritricho aretioidis*-*Dryadetum octopetalae* and *Sileno-Paronychietum*. *Sileno-Paronychietum* is the most common on Niwot, particularly in the Saddle area. *Dryas*-dominated types occur more frequently toward the eastern end of Niwot Ridge, and are some of the most microclimatically extreme types (Fig. 6.5). Čomárková (1979) noted a high degree of homogeneity within all of these stands, indicating very similar among-stand composition. Slightly more mesic fellfield sites, in minor depressions or transitional to dry meadows, are in the associations *Potentillo-Caricetum rupestris* and *Trifolietum dasyphylli*. These types have a higher canopy cover than the drier types, but still have a primarily open canopy.

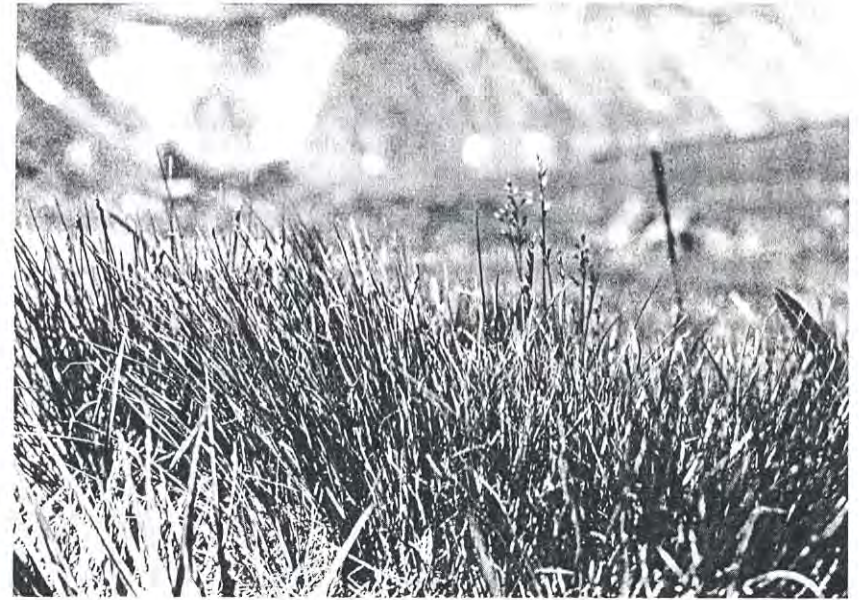


Figure 6.6. Dry meadow community dominated by *Kobresia myosuroides* (photo by William D. Bowman).

Dry Meadow, Windblown

Communities within the dry meadow *noda* described by May and Webber are dominated by the sedge *Kobresia myosuroides*, which forms extensive turfs (Fig. 6.6). Other important species include *Carex rupestris*, *Selaginella densa*, and *Thlaspi arvense*. These sites maintain a thin winter snow cover, which melts early, resulting in a growing season length of between 150 and 200 days. The dominance of the densely caespitose *K. myosuroides*, which is apparently unable to withstand the harsh winter conditions of the fellfield environment, allows for the development of thick soils and a complete plant cover (Bell and Bliss, 1979). Diversity is lower than in the fellfield stands, most likely due to the strong dominance of *K. myosuroides*. The Saddle dry meadow stands are placed in the association *Selaginello densae-Kobresietum myosuroidis*. Two other dry meadow types that do not occur in the Niwot Ridge Saddle include *Cerastio arvensi-Caricetum foenea* and *Caricetum elynoidis*, both of which occur primarily on south-facing slopes, often in association with pocket gophers (*Thomomys talpoides*). *Caricetum elynoidis* and *Cerastio-Caricetum* are in a separate alliance, *Caricion foeneo-elynoidis*, from the other dry types. All are united into the circumpolar arctic-alpine class *Kobresio-Caricetalia rupestris*. A key difference between the slightly more mesic *Caricion foeneo-elynoidis* and the drier *Kobresio-Caricion rupestris* is a greater predominance and diversity of erect forbs in the former and an abundance and importance of lichens as

characteristic taxa in the latter. *Caricetum elynoidis* is common on Niwot's southern slope and is often intermixed with small patches of *Cerastio-Caricetum*, which is much more common on the western side of the Continental Divide (Komárková 1979).

An "unsolved puzzle" in the Niwot Ridge vegetation is how *Kobresia myosuroides* can maintain such high dominance; about 30% of the live biomass of the dry meadows is this species (Walker et al. 1994). Viable seeds are rare in the Colorado population, and Humphries et al. (1996) reported that no one has yet found seedlings of this species at this latitude. However, Ebersole (unpublished data) observed seedlings on 20+-year-old disturbance plots on Niwot Ridge. *Kobresia myosuroides* has an arctic-alpine circumpolar distribution and is near the southern limit of its distribution in Colorado (it does extend into northern New Mexico, <http://plants.usda.gov/>). *Kobresia myosuroides* is globally important in dry arctic and alpine vegetation and is a key character taxa for this class of vegetation. Its persistence is apparently a function of life history traits that are "invisible" within the time frame of research. *Kobresia myosuroides* produces abundant viable seed in northern latitudes and often behaves as a colonizing species in those situations (Walker 1990). These lower latitude populations disperse their seeds before they are fully ripened, apparently using a degree-day sum as a dispersal cue. This results in inviable seeds in most years. *Kobresia myosuroides* is a tillering species, and a single individual may live upwards of 200 years, based on growth rates of individual tussocks (Bell and Bliss 1979). Humphries et al. (1996) demonstrated, using a life-history-based simulation model, that the species can persist in this environment as long as there is an occasional extremely cold year. Thus, *K. myosuroides* should continue to persist and dominate as long as there is adequate summer climatic variability to successfully reproduce on occasion. *Kobresia myosuroides* behaves more like a woody plant than an herbaceous one in this environment, both in its life history and growth characteristics.

Moist Meadow, Early-Melting Snowbank

The moist meadow noda is at the shallow end of the gradient of communities whose dynamics are controlled primarily by winter snow cover and melt patterns (Fig. 6.7). These sites get a modest snow cover and are usually released from snow relatively early in the growing season, for a total season length of 100–150 days. The combination of abundant moisture and reasonably long growing season makes these sites relatively rich and productive. They are predominated by a lush cover of forbs and grasses. Komárková (1979) placed all of the moist meadow associations in class *Salicetea herbaceae*, the circumpolar arctic-alpine snowbed class. The moist meadow noda recognized by May and Webber is dominated by the forb *Acomastylis rossii* and the grass *Deschampsia caespitosa*. Komárková's *Deschampsio-Trifolium parryi* alliance encompasses the noda. Komárková recognized three separate associations within the broader alliance: *Acomastylidetum rossii*, *Deschampsio casepitosae-Trifolietum parryi*, and *Stellario laetae-Deschampsietum caespitosae*. *Acomastylidetum* matches the concept of moist meadow that has been mainly used on Niwot. These stands are dominated by *A. rossii*, but the composition of individual stands is



Figure 6.7. Moist meadow in the Saddle research site, dominated by the tillering grass *Deschampsia caespitosa* and the clonal forb *Acomastylis rossii* (photo by William D. Bowman).

extremely variable. This association has one of the greatest total numbers of vascular species and one of the lowest average numbers of species (i.e., it has low alpha diversity and high beta diversity). *Deschampsio-Trifolietum* occurs in sites with slightly longer-lying snow and more mesic conditions, and *Stellario-Deschampsietum* is more mesic still. The latter type is far less variable than the first two.

A key difference between the *Deschampsia caespitosa*- and *Acomastylis rossii*-dominated associations is their linkages to other regions. *Acomastylis rossii* is a Beringian species limited to the Rocky Mountains, Alaska, and far northeast Siberia. Thus *A. rossii*-dominated alpine communities are unique to the Rocky Mountain Cordillera, occurring as far south as northern Arizona. *Deschampsia caespitosa*, on the other hand, has a circumpolar arctic-alpine distribution, occurring in many different ecological situations, although always associated with at least a moderate snow cover. Thus, distinguishing between these associations in field research would greatly aid in the strength of comparative studies with other alpine regions.

The alliance *Vaccinio-Danthonion intermediae* contains another group of three moist meadow associations that were not included within the May-Webber moist meadow concept. This alliance occurs primarily in the lower alpine belt, often in the tundra-forest ecotone, and thus could be classified as either tundra or subalpine meadow. However, explicit recognition of these types is essential, because they are quite distinct from the *Deschampsio-Trifolium*. *Vaccinio-Danthonion* stands are characterized by *Pedicularis parryi*, *Carex brevipes*, *Solidago spatulata*, *Dantho-*

nia intermedia, *Penstemon whippleanus*, and *Vaccinium scoparium* or *Vaccinium caespitosum*. Snow and moisture conditions are similar between the two alliances, but the former has a slightly longer growing season and presumably a higher degree-day sum due to its lower slope position.

Late-Melting Snowbank

Communities of late-melting snowbanks were identified by May and Webber (1982) as the snowbed noda, and Komárková (1979) recognized 14 distinct associations within this broad group, many of them infrequent. Because of the extreme conditions associated with late-melting snow, there is rapid turnover in species composition along a rather narrow environmental band. The late-melting snowbeds all fall within Order Sibbaldio-Caricetalia pyrenaicae. Komárková (1979) recognized the allegiance of this vegetation to the circumpolar snowbed class Salicetea herbaceae, and the nomenclatural species for the order, *Sibbaldia procumbens* and *Carex pyrenaica*, also have circumpolar arctic-alpine distributions. Thus, this vegetation is strongly related to other circumpolar arctic-alpine snowbed types.

Three alliances within the class represent a gradient of increasingly late-lying snow, with the most extreme communities having only a partial coverage of non-vascular plants and few or no vascular representatives. Disturbed, dry sites near the center of snowpatches are in Alliance Poo-Caricion haydenianae (Komárková 1979). Of the three associations within the alliance, only Poo arcticae-Caricetum haydenianae, named after the same species as the alliance, is frequent, occupying very late-melting snowpatches with southern exposures. These sites frequently have standing water during the melt period and have a high number of species tolerant to saturated soils. Stand composition is highly variable; important species include *Polytrichum piliferum* and *Toninia* spp. in addition to the nomenclatural species.

Alliance Sibbaldio-Caricion pyrenaicae, named after the same species as the order, is the most abundant snowbed group and encompasses the May-Webber snowbed type. Komárková recognized seven associations, corresponding with a soil moisture gradient. Toninio-Sibbaldietum, Caricetum pyrenaicae, Juncetum drummondii, Epilodia anagallidifolii-Antennarietum alpinae, Epilodia anagallidifolii-rorippetum alpinae, Phleo commutati-Caricetum nigricantis, and Sibbaldio procumbentis-Lewisietum pygmaea define an approximate moisture-snowmelt gradient within this large alliance. The drier end of the spectrum has affinities with the moist meadow types, particularly the Deschampsio-Trifolion, and the wet end intergrades with another snowbed alliance, Anthelio-Pohlion obtusifoliae.

Wet Meadow

May and Webber's wet meadow noda is represented by subhygric sites, which are downslope from snowbeds and thus receive inputs of surface water throughout most of the growing season (Fig. 6.8). Komárková (1979) placed these into the circumpolar arctic-alpine mire class Scheuchzerio-Caricetea fuscae. She also noted, however, that the Indian Peaks communities were lacking in many of the character taxa for the class and were related to it more by habitat than by floristics. They are also



Figure 6.8. Wet meadow, dominated by *Caltha leptosepala* and *Carex* species, on the north flank of Niwot Ridge, looking toward (left to right) Pawnee Peak, Mount Toll, and Paiute Peak (photo by William D. Bowman).

fairly distinct from arctic North American fens and bogs, which are dominated by *Carex aquatilis* and species of *Eriophorum*. There is a single order, Pediculari-Caricetalia scopulorum, within the class, 2 alliances, and 12 associations, all newly named by either Komárková (1976) or Willard (1963) from the Colorado Front Range.

The two alliances have distinct floristic composition and habitat. Communities of the Pediculari-Caricion scopulorum are found around small pools and have some affinities to spring communities. These habitats best typify the primary coverage of the wet meadow noda within the Niwot Ridge Saddle, but the Saddle communities are unusual because the pools are quite small and dry up during most growing seasons. Communities of the Bistorto-Caricion capillaris have relatively high cover and occur on small, gently-sloping seepage sites (Komárková 1979). This alliance grades into the moist meadow associations, primarily the Trifolio-Deschampsietalia, and thus also has representatives within the Saddle. There are many small pools in close physical approximation to snow flush sites in the Saddle, and thus these two distinct types are often found side-by-side and have been confused as a single distinct, but variable type.

The primary wet meadow associations in the Saddle are those dominated and characterized by *Carex scopulorum*, *Pedicularis groenlandica*, *Caltha leptosepala*, and *Rhodiola integrifolia*. These belong primarily to the associations Caricetum scopulorum and Clementsio rhodanthae-Rhodioletum integrifoliae, each of which belongs to different alliances (Table 6.1).

Because many of these types are found downslope of snowbanks, they share many characteristics controlled by these snowbanks. Cold air drainage, even off relatively small snowbanks, cools the area immediately downslope, resulting in cooler mean temperatures and shorter thaw seasons along snowbank margins (chapter 2). Billings and Bliss (1959) noted an average of 1.5°C cooling from the top to the bottom of a 100-m long snow drift in the Medicine Bow mountains. The combined effect of the cool air drainage and cold water from the drift can create an exceptionally cold environment at the base of very-late-lying snow drifts, and soil temperatures can be considerably colder than the shoot temperature in areas marginal to snowbeds (Holway and Ward 1965). This can cause delayed phenology and reduced water and nutrient uptake at a time when photosynthetic potential is at a maximum. This can be important for phenological development. For example, Holway and Ward (1965) noted that *Acomastylis rossii* consistently flowers only after the soil temperature at 3-cm depth exceeds 10°C, regardless of the aboveground temperatures. Thus its phenology is delayed in these sites relative to others (Walker et al. 1994). Conversely, these meadows senesce last in the autumn, which results in these sites being preferred by grazers such as elk (chapter 14).

The wet meadow associations reach their best expression in the lower alpine zone, and there are some rare associations, dominated by equally rare plants, that occur outside the Saddle. An example is the *Koenigietum islandicae*, known from only three locations in the Colorado Front Range, at the base of rock glaciers where there is a season-long moisture supply. *Koenigia islandica* is an extremely diminutive annual arctic-alpine species. Similar communities dominated by this plant have been found at the base of permanent snowfields on Alaska's North Slope and in the Chukotka region of eastern Siberia (Walker 1990; Razzhivin 1994).

Shrub Tundra

Shrub tundra dominated by erect *Salix planifolia* and *Salix villosa* is common in lower alpine areas along the margins of ponds and streams. They occur in similar situations in the alpine zone, such as the relatively protected innermost part of the Niwot Ridge Saddle. This area, which was used as the basis for the shrub tundra noda, has a mixed stand of these two species, with areas approximately 5–7 m across of fairly continuous shrub cover intermixed with open regions without shrubs. Maximum heights are about 45 cm, and the stands are associated with a region of inactive low-centered polygons.

The shrub tundra noda corresponds very well with the single alliance *Salicio planifolio-villosae*, which contains two associations, *Bistorto viviparae-Salicetum villosae* and *Rhodiolio integrifolia-Salicetum planifoliae*. *Salix villosa* reaches its optimum in the first, which occurs in slightly drier habitats, and *Salix planifolia* reaches its optimum in the second, which occurs in more mesic habitats. The shrub tundra communities grade into the *Clementsio rhodanthae-Rhodiolum integrifoliae* on the mesic end (i.e., the *Rhodiolio-Salicetum*) and into the *Kobresio-Caricetalia* and *Trifolia-Deschampsietea* on the dry end.

Komárková (1979) placed these shrub communities provisionally into the European Class *Betulo-Adenostyletea* but felt that a new North American class

should be named. These same willow taxa predominate alpine shrub vegetation throughout the Rocky Mountain chain and are found in similar situations in the Arctic (Viereck et al. 1992). Although the mix of *Salix* species increases in the overall landscape changes along this transect, the importance of *Salix planifolia* and *Salix glauca* (a close relative or synonym of *S. villosa*) remains constant in these situations. Komárková (1979) felt *Salix glauca* to be a distinct species and ecologically distinct from the alpine stands of *Salix villosa*.

Other Associations and Types Not Defined by the Saddle Noda

Rock Crevices and Scree Slopes

Habitats dominated by bare rock include rock crevices, boulder fields, and scree slopes. Communities of these sites are dominated by a great abundance of bare rock, with plants limited to narrow zones in crevices or in thin soil between or on rocks. These habitats do not occur within the Saddle and have received little attention from ecologists studying ecosystem processes because they have little soil and are not spatially extensive. These are important communities from a conservation perspective, however, containing some of the most rare species. Komárková (1979) placed all of these communities into the alpine class *Asplenietea rupestris*, described by Braun-Blanquet (1965), but felt that a North American class was required, because only one characteristic species for the class, *Cystopteris fragilis*, occurs in the Indian Peaks flora, and thus the primary association is by habitat. Komárková (1976) named a new order, the *Heuchero-Saxifragetalia*, which has the vascular taxa *Claytonia megarhiza*, *Saxifraga caespitosa*, *Draba fladnizensis*, *Draba lonchocarpa*, and *Saxifraga bronchialis* ssp. *austromontana* as characteristic taxa as well as the mosses *Tortula norvegica*, *Pohlia cruda*, and *Bryum algovicum* and the lichens *Physcia caesia*, *Peltigera malacea*, and *Orthotrichum indet.*

The order and class are further subdivided into two alliances and six associations, illustrating the diversity even in these rather depauperate sites. Many of these types have floristic connections to the nival and subnival zones of the Alps and to High Arctic and Polar Desert stands of the Arctic.

Springs

Komárková (1979) placed associations of springs and seeps into Class *Montio-Cardaminetea*, Order *Primulo-Cardaminetalia*, and Alliance *Cardamino-Primulion parryi*. There are four associations. Some of the key taxa for class, order, and alliance are *Caltha leptosepala*, *Primula parryi*, *Epilobium angallidifolium*, *Ranunculus escholtzii*, *Cardamine cordifolia*, and *Saxifraga odontoloma*. These types have some similarities to the wet meadow communities of small ponds (*Pediculari-Caricion scopulorum*) and to certain snowbed communities. The showy *P. parryi* is a striking visual clue to these communities, which do have some stands on the northern flank of the Saddle and in the lower alpine belt of Niwot Ridge.

Physical Factors Controlling Plant Communities

Physical controls of alpine vegetation on Niwot Ridge have been examined using ordination methods (Komárková, 1979, 1980; May and Webber 1982). A number of factors related to topography, wind, redistributed snow, and meltwater runoff are the main factors that correlate with species and vegetation patterns. Billings's (1973) classic alpine mesotopographic gradient portrays the typical vegetation associated with windward, ridge crest, leeward, and meltwater accumulation areas. An idealized adaptation to the Niwot Ridge situation shows the sequence of microsites, vegetation, and snow depth along the gradient (Fig. 6.3). The following discussion focuses on soil and hydrology as they relate to the plant environment along this gradient.

Growing Season Length: Effects on Phenology and Production

The amount of snow on a site is the single most important factor governing the length of the growing season and hence the total amount of warmth available for plant development and growth (Billings and Bliss 1959; Holway and Ward 1963, 1965; Walker et al. 1993; Stanton et al. 1994). At the plant level, the presence of a winter snow cover offers plants protection against frost damage, dehydration, and physical damage from wind and wind-blown particles (Wardle 1968; Tranquillini 1979). Early snow cover limits intensive and deep freezing of the soil, thereby lowering soil instability caused by frost action and weathering. However, the protection that snow provides against winter climate extremes also results in a belated, shortened growing season. Conversely, snow-free places are exposed to severe winds, and plants in these places are subject to high rates of evapotranspiration and high vapor pressure deficits (LeDrew 1975; Bell and Bliss 1979; Isard 1986; chapter 2). Very deep snow patches melt out in late summer or not at all in some years. In these extreme sites, the short growing season combined with other negative influences, such as wet, poorly developed, and unstable soils results in areas completely devoid of vegetation. In contrast, early-melting areas have the advantage of a relatively warm and protected winter environment combined with a long growing season, adequate soil moisture, and a relatively moderate summer microclimate (Billings and Bliss 1959; Stanton et al. 1994).

The Niwot mesotopographic gradient illustrates the effect of a variety of inter-correlated site factors. Species composition, biomass, phenology, and site factors have been monitored in five vegetation types representing the portion of the gradient from exposed ridge tops to shallow snowbeds (Fig. 6.3; May 1976, 1982; Walker et al. 1994, 1995). Snow depths were monitored year round in 1972–1974. The mean maximum depths ranged from less than 10 cm in the fellfield community (*Sileno-Paronychietum*) to 120 cm in the shallow snowbeds (*Toninio-Sibbaldietum*). The corresponding growing season length varied from 109 days in the fellfield community to 52 days in the snowbed.

In the already short alpine growing season, delayed snow melt strongly affects patterns of vegetative development, flowering, seed set, and total primary production. It is not uncommon to see the flowering of snow-margin species, such as

Ranunculus adoneus, occurring along the melting edge of snow patches and moving as a wave across the tundra through the growing season. Delayed vegetative development occurs in small depressions where the snow melts late, and conversely, delayed senescence may occur in the fall in snowbeds that are wetter than the surrounding dry tundra. In some alpine and arctic plants, nutrient uptake, shoot growth and flowering may commence under the snow before melt (chapters 9, 12). Good examples of such early season growth under snow at Niwot Ridge include *Bistorta bistortoides*, *Caltha leptosepala* (Rochow 1969), *Oxyria digyna* (Mooney and Billings 1961), *R. adoneus* (Caldwell 1968; Salisbury 1985; Galen and Stanton 1991; Galen et al. 1993; Galen and Stanton 1993; Mullen and Schmidt 1993; Scherf et al. 1994; Mullen et al. 1998), and *Acomastylis rossii* (Spomer and Salisbury 1968; Chambers 1991). Reradiation of heat from standing dead shoots from the previous season often melts slender holes in snow cover as deep as 20–30 cm. All of these species and many others can leaf out and flower so quickly because they have leaf primordia and flower buds preformed during prior growing seasons (Billings and Mooney 1968; Billings 1974; Mark 1970; Diggle 1997; Aydelotte and Diggle 1997).

Wind

Wind is a primary factor determining the dominance of cushion-plant and tussock-graminoid growth forms in fellfields and exposed tundra turfs. The tightly packed stems and leaves of these growth forms minimize winter abrasion from wind-transported particles and reduces drought stress during the summer. In contrast, many plants that are protected by snow during winter have erect growth forms, soft leaves, and are not drought resistant (Billings and Mooney 1968).

One of the most thorough winter studies of plant physiology in relation to severe winter wind conditions was that of Bell, who studied *Kobresia myosuroides* during winter in Rocky Mountain National Park, Colorado (Bell 1974; Bell and Bliss 1979). Although *K. myosuroides* is the dominant plant in large areas of the Colorado Front Range, it occurs only in a narrow range of snow accumulation regimes. It is a tussock-forming sedge that forms dense turfs in areas that are largely snow free during much of the winter, except for microdrifts that form leeward of the *Kobresia* tussocks. *Kobresia* does not occur in extreme wind-blown fellfields nor in areas of even shallow snow accumulation. Bell compared behavior of undisturbed *Kobresia* with that of transplants into habitats with more and less winter snow accumulation. She found that *Kobresia*'s success in snow-free meadows is related to rapid summer growth and to its use of an extended period for development, from about April 1, well before snowmelt over much of the tundra, to October 20, after the beginning of drift development in snowbeds. Wintergreen *Kobresia* leaves can even elongate during warm periods ($> -4^{\circ}\text{C}$) in midwinter, an apparently unique phenomenon in tundra plants. New leaves begin elongation in the autumn and complete growth the following summer. Most carbohydrates are stored aboveground in leaves, primarily as oligosaccharides, sugars that likely contribute to frost hardiness of the evergreen leaves. Storage of carbohydrates in the leaves obviate the need for translocation from the roots in frozen soils in winter. Transplanted *Kobresia* do not survive in fellfields because of mechanical damage by windblown snow and sand and low soil

water potentials. Early-spring melting of shallow snow cover (about 15 cm) in *Kobresia*'s preferred habitat permits leaf elongation in saturated soils. In sites of moderate to deep snow accumulation (>75 cm), autumn dieback is incomplete before drifts first form in September. A long snow-free period after early September is apparently necessary for proper onset of normal winter carbohydrate status in the leaf shoots. Winter freezing destroys the apparently unhardened leaf tissues and meristems, resulting in loss of carbohydrate reserves.

Temperature

The temperature environment within an alpine plant community is strongly influenced by microtopography and slope position (chapter 2). May and Webber (1982) monitored mean monthly temperatures in five nodes, at 5 cm above the surface and 10 cm below the surface for 1 year (Fig. 6.9). Only during the late-summer-to-fall period (Aug.–Oct.) was the temperature comparable in all of the communities. The temperature contrast between the fellfields and snowbeds was the greatest during winter. In December, aboveground mean temperature of the fellfield leaf environment was -15.5°C , whereas aboveground mean temperature of the snowbed community was a relatively warm -1°C . Mean aboveground monthly temperature of the snowbed did not drop below -3.5°C during the winter, but it also did not warm above the freezing point until mid-June, six full weeks later than the fellfield, and remained cooler than the fellfield throughout the summer until September, when senescence had begun in all the communities. Aboveground temperature of the dry and moist meadow communities was intermediate during both the winter and early summer (June–August) periods. Belowground temperatures were a few degrees warmer than the air temperature during the winter and few degrees cooler in the summer for all communities (Fig. 6.9). In winter, the greatest contrast between winter aboveground and belowground temperatures occurs in fellfields and the least contrast occurs in snowbeds. During the summer the situation is reversed, with the greatest contrast occurring in the snowbeds.

The winter climate within the plant canopy is strongly affected by the depth of snow cover. Bell (1974) found that in the Colorado alpine, plant canopy temperatures beneath >50 cm of snow are very stable. In windblown areas, temperatures are less variable during winter than summer due to the higher convective cooling of consistent winter winds. Differences between the soil surface temperature and the air temperature at 120 cm is rarely greater than $1-3^{\circ}\text{C}$. Frequent storms with strong winds slow diurnal heating at the soil surface and accelerate soil cooling in the afternoon.

In spring, wind speeds are much reduced, and the snow cover becomes the primary determinant of temperature profiles. Snowfree areas warm rapidly on sunny days. Bell (1974) found that fellfields and *Kobresia* meadows were $12-15^{\circ}\text{C}$ warmer than air above on clear and overcast days. If the areas are inundated with water after the snow melts, the temperature around the plants remain close to 0°C as long as the water remains. Bell (1974) found that this common situation paradoxically leads to cooler plant temperatures in fellfields and *Kobresia* meadows dur-

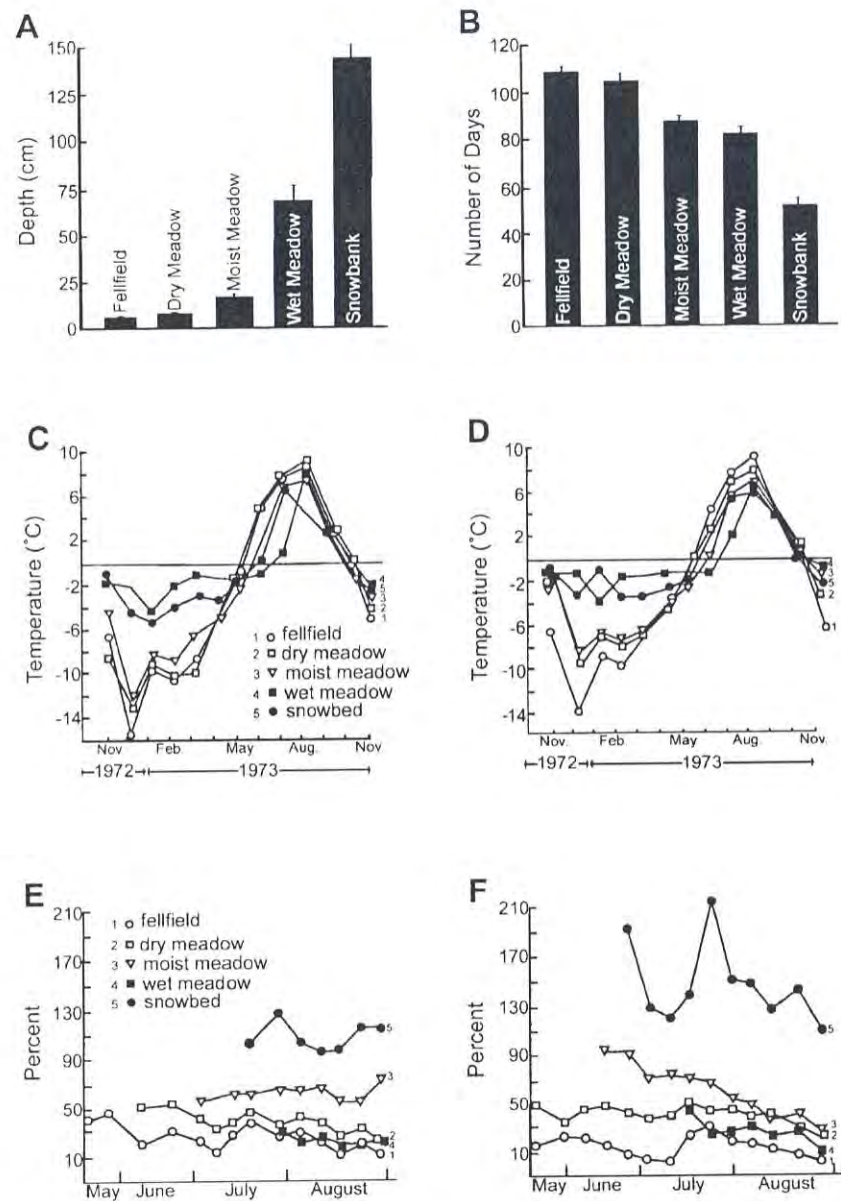


Figure 6.9. Variation in site factors for five plant communities along an alpine toposequence, Niwot Ridge, Colorado, 1972–1973. (a) Average snow depths. (b) Length of the growing season. (c) Foliosphere temperatures at 5 cm above the soil surface for the same five plant communities. (d) Rhizosphere temperatures at 10 cm below the soil surface. (e) Gravimetric soil moisture in 1973 (a dry year). (f) Gravimetric soil moisture in 1974 (a wet year) (adapted from May 1976).

ing May after the melt begins than during the time in April when only a small part of the tundra is snow free.

Soil Water

In temperate alpine areas, water is released from melting snow over a prolonged period of time due to cold night-time temperatures and deep snow drifts (Caine and Thurman 1990; Caine 1992; chapter 5). Abundant well-defined snow-bed vegetation communities, cold seeps, spring communities, and small wetlands are consequences of late-melting snow in alpine areas (Komárková, 1979). The relationship of snow depth to soil moisture conditions is illustrated by the five plant communities along the Niwot Ridge snow gradient (Fig. 6.3). Soil moisture values are lowest in the fellfield and highest in the wet meadow at the lower margin of the Niwot Ridge snow drift. The central part of the snowdrift has relatively low gravimetric soil moisture, comparable to that of the fellfield, due to rocky coarse-grained soils, and a tendency to drain rapidly once the snow melts. The summer soil moisture in the fellfield and dry meadow generally decline through the summer but respond somewhat to rainfall events, whereas soil moisture in the moist meadow and wet meadow are related more to the supply of meltwater from snow (Fig. 6.9). The lower margins of snowbanks melt early and are provided with a continuous supply of water as long as the snowbank persists.

Soil moisture, in combination with timing of release from snow cover, governs plant water relations and influences nutrient availability (Fisk et al. 1998; chapter 12). Long-term spatial patterns are an important control on community composition, and interannual variation is an important control on productivity. Oberbauer and Billings (1981) found a high correlation between the seasonal courses of plant water potentials and stomatal conductances along the mesotopographic gradient and the distribution of plant species and vegetation patterns along this same transect. Similar results were found for alpine tundra in the Sierra Nevada (Beyers 1983).

Winter drought stress may be particularly important in areas with little snow cover. Bell (1974) found that wintergreen plants in the Colorado *Kobresia* meadows and fellfields needed at least a small amount of protection provided by microdrifts. Wintergreen *Kobresia* leaf shoots elongated in winter only on warm days when the soil water was available and water potentials rose above -2.0 MPa.

Biotic Factors Controlling Plant Communities

The influence of interspecific interactions in climatically stressful environments has historically invited much debate, focused primarily on negative interactions such as competition (Grime 1977; Tilman 1987; Grace 1991). Ecologists have paid less attention to the importance of positive interactions in structuring plant communities. However, in environments where levels of physical stress are high, such as alpine tundra, facilitation may be a more important structuring force than competition is (Bertness and Callaway 1994).

Only a few studies have specifically examined interspecific competition in arctic or alpine tundra (Griggs 1956; McGraw and Chapin 1989; Wilson 1993; Theodose and Bowman 1997). All indicate that competition is an important structuring force in these communities. Theodose and Bowman (1997) experimentally demonstrated the role of interspecific competition in influencing the distribution of an alpine graminoid. Although the dry meadow dominant *Kobresia myosuroides* is absent from the moist meadow community due to physical factors, as discussed earlier (Bell and Bliss 1979), the moist meadow codominant *Deschampsia caespitosa* is apparently absent from the dry meadow due to competitive displacement by *Kobresia*. Several other studies have alluded to the possibility that interspecific competition may influence species composition on Niwot Ridge. Alpine graminoids from different communities differ in traits thought to influence competitive ability, potentially affecting distribution patterns across communities (Theodose 1995). Within the moist meadow, species differ greatly in several aspects of competitive ability, including growth rates and N uptake capacity, correlating with dominance relationships within that community (Theodose et al. 1996). In addition, mortality of transplanted species into communities differing from community of origin may have been due in part to interspecific competition (May 1976).

Herbivores have been studied extensively on Niwot Ridge, but little research has examined any direct effect of herbivory on alpine plant species composition (chapter 14). Belowground herbivory by gophers (*Thomomys talpoides*) has received much more attention than aboveground herbivory has (Halfpenny and Southwick 1982; Litaor et al. 1996; Cortinas and Seastedt 1996). Gopher activity is greatest in communities with high snowcover, especially snowbed communities (Stoecker 1976; Thorn 1978, 1982; Burns 1979; Willard 1979; Litaor et al. 1996). Direct feeding by gophers may reduce the abundance of preferred species, potentially reducing the degree of competitive exclusion (Halfpenny and Southwick 1982; Tilman 1983; Andersen 1987; Huntley and Inouye 1987; Inouye et al. 1987), although much of the gopher influence on species composition is indirect and dependent on changes in physical conditions of the soil. Gopher activity increases nutrient availability, particularly N, which favors some alpine plant species over others (Bowman et al. 1995; Cortinas and Seastedt 1996; Litaor et al. 1996). Plant community composition surrounding gopher mounds is different from that of undisturbed areas (Davies 1994).

Most Niwot Ridge herbivores seem to favor forb species over grasses (chapter 14). Thus herbivory may contribute to the abundance of graminoids on Niwot Ridge, exacerbating effects of increased atmospheric N deposition by increasing rates of N mineralization (Steltzer and Bowman 1998; Bowman and Steltzer 1998). Enclosure studies need to be conducted to establish these trends.

The influence of positive species interactions on the species composition of plant communities has received less attention than that of negative interactions (Thomas and Bowman 1998). This is particularly true for facilitation, an interaction that is important for plants in the seedling stage. Although sexual reproduction is considered less important than vegetative propagation in alpine tundra, seedling recruitment may be a colonization mechanism in disturbed sites (Chambers 1991). Seedling recruitment is considered an important colonizing mechanism in arctic tundra (Freedman et al. 1983; Gartner et al. 1983). In alpine tundra, mulch prevents small

seeds from being blown away by the wind (Chambers 1991), suggesting some plant cover may facilitate establishment. Facilitation may increase seedling survival in intact alpine communities as well. Alpine vegetation cover decreases the formation of needle ice, which contributes to seedling mortality (Bliss 1971; Roach and Marchand 1984). In alpine fellfields, cushion plants act as nurse plants, facilitating seedling establishment, although cushion plants may compete with the seedlings as well (Griggs 1956).

How plants are arranged in space and time within alpine communities is in part dependent on physical factors, but may also be directly or indirectly influenced by presence and type of mutualism. The influence of mutualisms such as symbiotic N_2 fixation and mycorrhizae on species composition in alpine tundra is just beginning to be understood. A few species having mutualistic relationships with N_2 -fixing bacteria occur on Niwot Ridge. These include three species of *Trifolium*, which constitute 12% of the projected cover on Niwot Ridge (May and Webber 1982; Bowman et al. 1996). The presence of N_2 -fixing plant species influences the species composition of the surrounding vegetation, increasing the abundance of some species but decreasing the abundance of others. Areas adjacent to patches of *Trifolium* have a species composition similar to that of N fertilization plots (Theodose and Bowman 1997; Thomas and Bowman 1998). The abundance of these N_2 -fixing species within a community may be related to soil P availability. In the dry meadow, the abundance of *Trifolium dasyphyllum* increased significantly following P fertilization but not following N fertilization. This response was in contrast to most other forb species whose abundance was N limited (Theodose and Bowman 1997).

Although mycorrhizal status of many alpine plants has been determined (Haselwandter and Read 1980; Read and Haselwandter 1981; Lesica and Antibus 1985; Gardes and Dahlberg 1996), the role of this mutualism at the plant community level has not been thoroughly examined. The alpine tundra has VA mycorrhizal species, non-mycorrhizal species, and is unique among herbaceous plant communities in its high number of herbaceous ectomycorrhizal species. Variation in the types of mycorrhizal infection may influence alpine plant distribution and abundance. In the dry meadow community, mycorrhizal species abundance increased following N additions, whereas non-mycorrhizal species abundance increased following P additions (Theodose and Bowman 1997). In the snowbed community, which has the shortest growing season, the early season *Ranunculus adoneus* depends on mycorrhizal infection for nutrient uptake. VA mycorrhizal fungi enable *Ranunculus* to obtain and later store P, whereas dark septate fungi may be a means of obtaining organic N without having to rely on soil N mineralization (Mullen and Schmidt 1993; Mullen et al. 1998). Thus, *Ranunculus* may be an important component of the snowbed community in part because of the symbiotic relationship with these fungi.

Summary and Conclusions

The vegetation of Niwot Ridge has a long history of study, with a particularly strong focus on spatial patterns and phytosociology. Most of the Niwot Ridge vegetation falls into a single class, the Elyno-Seslerietea, which encompasses the fellfield and

dry meadow noda, but includes additional associations not included in the original conceptions of those noda. The spatial patterns of Niwot Ridge vegetation is predominated by physical factors, but biotic interactions are particularly important in shaping microscale patterns and short-term dynamics.

The rich history of spatially focused study sets a precedent for work on temporal dynamics at a variety of scales. Because of the short growing seasons and long life spans of most alpine species, temporal studies are a particular challenge. A combination of modeling and carefully selected experimentation is necessary to understand dynamics and trends in the system and to make reasonable predictions about how it might change in response to a changing environment.

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