# 6 Snow–Vegetation Interactions in Tundra Environments

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## 6.1 Overview

Snow affects the plant species and ecosystem processes of numerous biomes. Pomeroy and Brun (Chapter 2) discuss the important role of intercepted snow in boreal forest biomes and its effect on patterns of soil moisture, depth of freezing, soil temperatures, and soil heat flux (Pomeroy et al., 1994; Pomeroy and Gray, 1995), while Tranter and Jones (Chapter 3) have described the role of snow in nutrient fluxes and ecosystem chemical budgets. Begin and Boivin (Chapter 7) document the effect of wind and heavy snow accumulations on the morphology and growth of trees. In prairie and tundra regions, topography and wind play more important roles in the distribution and physical properties of the snow cover. The importance of snow to agriculture in northern grasslands has been long recognized, and a wide variety of snow-management techniques have been used to both increase and decrease snow in selected portions of agricultural landscapes (Staple and Lehane, 1952, 1955; Staple, Lehane, and Wenhart, 1960; Stepphun, 1981). Of all biomes, tundra regions are the most strongly affected by snow. This chapter synthesizes the extensive existing information on tundra snow–vegetation interactions. It points toward a unified hierarchical understanding of species-, community-, landscape-, and biome-level responses to various snow regimes. We use three different approaches to examine snow–vegetation interactions. The first describes the influence of snow on the distribution of plant communities along topographic gradients. The second considers the effect of snow, or lack of snow, on plant physiology and growth. The third examines an experimental approach to study the effects of altered snow regimes on a variety of ecosystem properties. This is an attempt to interpret the ecosystem impacts of apprehended climate change (see Groisman and Davies, Chapter 1).

## 6.2 Introduction

Snow has long been recognized as the single most important variable affecting the patterns of vegetation of alpine regions (Vestergren, 1902). Early descriptions of the influence of snow on alpine vegetation from the Swiss Alps mention "schneetälchen" (little snow valley) vegetation (Herr, 1836). These distinctive hollows were among the first vegetation units described in the vegetation literature of Europe, and many studies have since focused on descriptions of the vegetation in snowbeds and rocky windblown areas. Gjærevoll's (1956) classic monograph focused entirely on the snowbeds of Scandinavia, and Rønning (1965) described the vegetation of windblown areas of Svalbard. More recently, studies of plant ecophysiological response along snow gradients, experimental studies of plant response to altered snow regimes, and application of geographic information systems (GIS) have expanded our understanding of the extent and nature of snow-dominated arctic and alpine ecosystems.

## 6.3 Snow Gradients

Numerous studies have analyzed the more or less continuous changes in vegetation and soil properties that occur along snow gradients (Billings and Bliss, 1959; Billings, 1973; Flock, 1978; Hrapko and LaRoi, 1978; Bell and Bliss, 1979; Komárková, 1979; Burns, 1980; Alpert and Oechel, 1982; Burns and Tonkin, 1982; Miller, Mangan, and Kummerow, 1982; Ostler et al., 1982; Molenaar, 1987; Nams and Freedman, 1987a, 1987b). Billings (1973) developed the concept of a mesotopographic gradient to describe this variation; other similar approaches include the ecohydrological gradient of Molenaar (1987) and the synthetic alpine slope model of Burns and Tonkin (1982). The best-developed examples of snow gradients occur in windy temperate mountain ranges such as the east slope of the Colorado Front Range where deep snow drifts are interspersed with wind-scoured areas. A mesotopographic gradient for the Colorado Front Range is used throughout this chapter to discuss the effect of snow on site environmental factors and species response (Figure 6.1; Table 6.1).

### 6.3.1 Plant Species

Many arctic and alpine plants predictably occur in either windblown or snowbed habitats. In a study of plant species distribution on Niwot Ridge, Walker et al. (1993a,b) found that most species had an optimal range of snow depths where they were found most abundantly. For example, *Paronychia pulvinata*, a cushion plant, has its optimal distribution on stable, dry, windblown, rocky sites with less than 25 cm of mean maximum snow depth (Figure 6.2a). At the other end of the spectrum, the sedge *Carex pyrenaica* occurs only in deep snow areas with over 400 cm of mean maximum snow depth (Figure 6.2f). The species showing the clearest distributions

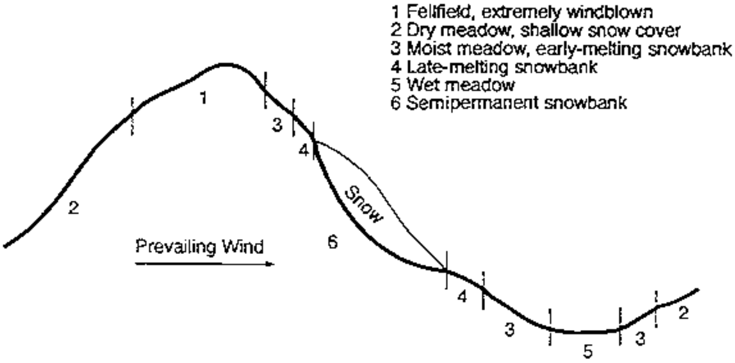


Figure 6.1. Mesotopographic gradient (Billings, 1973) adapted to the Niwot Ridge situation. Table 6.1 shows corresponding environmental information, associated vegetation, and soils. Summarized from Burns and Tonkin (1982), Komárková (1979), and May and Webber (1982).

with respect to the snow gradient are diagnostic taxa used to characterize the major plant associations of the Front Range (Komárková, 1979).

Wet areas beneath permanent snowpatches often contain rare plant species (e.g., the chionophytes *Saxifraga rivularis*, *Koenigia islandica*, *Phippsia algida* and *Haplomitrium hookeri* in the Front Range; *Stellaria umbellatus* in northern Alaska). *K. islandica* is rare in alpine areas of North America but occurs in the Colorado Front Range and again 700 km to the northwest in the Beartooth Mountains on the boundary between Wyoming and Montana. At the latter location, there are several scattered populations, all of which occur in wet mossy locations below long-lasting snowbanks (Johnson and Billings, 1962; Reynolds, 1984a, 1984b). Komárková (1979) notes that the restriction of many rare species to snowbed areas in the Colorado Front Range is typical of mountainous regions with strong winds (Jeník, 1959). Similar patterns are seen in the central European mountains of middle altitude, where snow redistribution into lee cirques has kept many of these areas free of forest vegetation during periods of treeline advance and allowed rare arctic–alpine plant species to survive warm postglacial periods (Jeník, 1959). Snow also appears to contribute to the high endemic ratio of forested areas subject to exceptionally high snowfall such as the Chubu District in central Japan (Uemura, 1989).

### 6.3.2 Plant Communities

Classification of snowbed communities has yielded much understanding of their environmental relationships. Braun-Blanquet (1949a, 1949b, 1950)

Table 6.1. *Site characteristics of the Niwot Ridge alpine snow gradient.*

| Site (code in Figures 6.3 and 6.4) | Microsite description | Snow-free days | Typical plant associations (Komárková, 1979) | Soils, US soil taxonomy (Burns, 1980) |
|---|---|---|---|---|
| Fellfield, extremely windblown (1) | Xeric, extremely wind-exposed ridges and west-facing slopes | >200 | *Sileno-Paronychietum, Potentillo-Carecetum rupestris, Trifolietum dasyphylli* | Dystric Cryochrept, Typic Cryumbrept |
| Dry meadow, windblown (2) | Subxeric to mesic turfs on gentle wind-exposed west-facing slopes | 150–200 | *Selaginello densae-Kobresietum myosuroidis* | Dystric Cryochrept, Typic Cryumbrept |
| Moist meadow, early-melting snowbank (3) | Earlier melitng snowpatches of the Front Range, subxeric to mesic snowpatches, leeward slopes and depressions | 100–150 | *Acomastylidetum rossii, Deschampsio caespitosae-Trifolietum parryi, Stellario laetae-Deschampsietum caespitosae* | Typic Cryumbrept, Pachic Cryumbrept, Dystric Cryochrept |
| Late-melting snowbank (4) | Later melting snowpatches of the Front Range, includes a wide variety of microhabitats from subxeric margins of late melting snow to subhygric, bryophyte-dominated, very late-melting snowpatches | 50–100 | *Toninio-Sibbaldietum, Caricetum pyrenaicae, Juncetum drummondii, Phleo commutati-Caricetum nigricantis, Poo arcticae-Caricetum hydenianae, Polytrichastro alpini-Anthelietum juratzkanae* | Dystric Cryochrept |
| Wet meadow (5) | Alpine fens, willow shrublands and springs; subhygric to hydric sites on mineral soils | >100 | *Caricetum scopulorum, Rhodiolo integrifoliae-Salicetum planifoliae, Clementsio-Calthetum leptosepalae* | Pergelic Cryaquept, Humic Pergelic Cryaquept, Histic Pergelic Cryaquept, Pergelic Cryohemist, Pergelic Cryaquoll, Histic Pergelic Cryaquoll |
| Semipermanent snowbank (6) | Snowbeds that occasionally melt, rocky unstable sites | 0–50 | *Oxyrio digynae-Poetum arcticae or no vegetation* | Lithic Cryochrept (headwall soil), Pergelic Cryoboralf over Pergelic Cryochrept (nivation hollow soil) |

*Note:* Summarized from Burns and Tonkins (1982) and Komárková (1979).

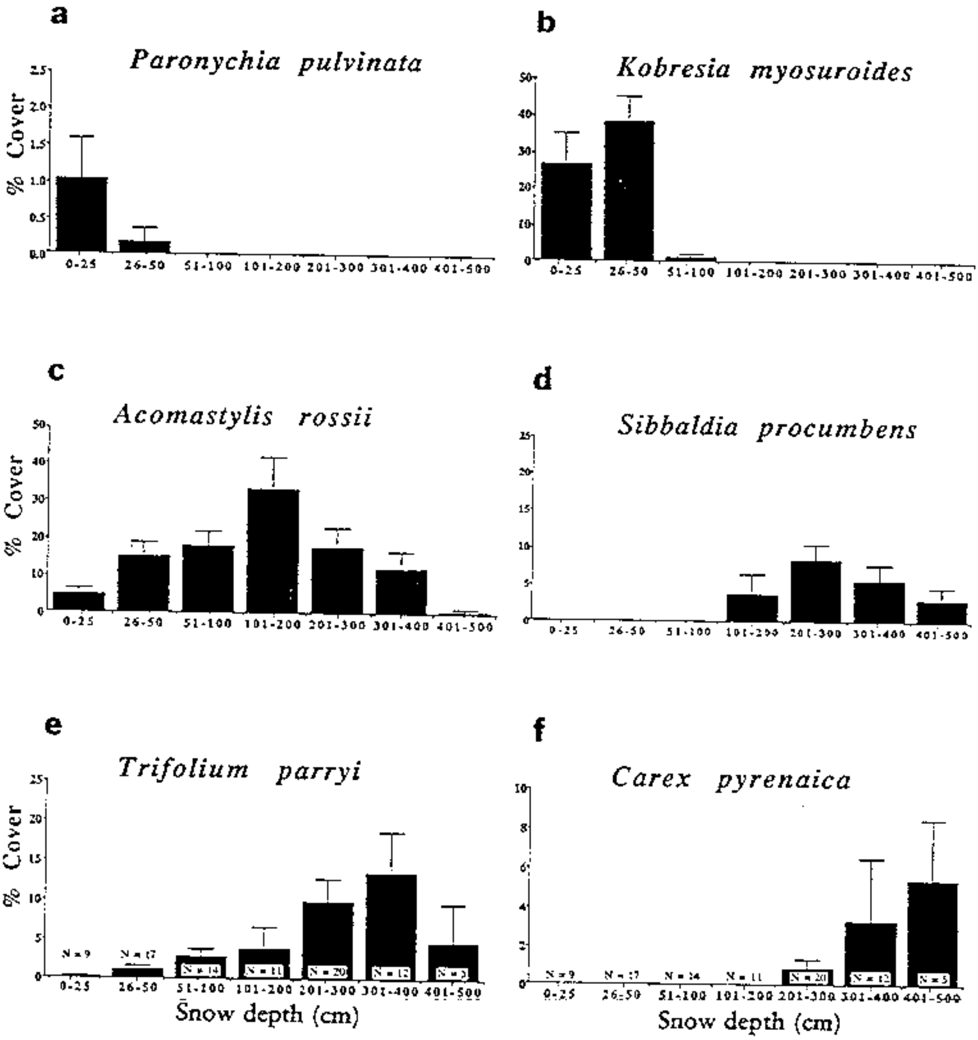


Figure 6.2. Distribution (plus or minus standard error) of six common species along the snow gradient. *Paronychia pulvinata* and *Kobresia myosuroides* are diagnostic taxa for the Alliance *Kobresio-Caricion rupestris*, which includes associations that are typical of broad, well-drained, stable windswept ridges in the Front Range. *S. procumbens*, *T. parryi*, and *C. pyrenaica* are diagnostic species for syntaxa within the snowpatch *Salicetae herbaceae*. *Acomastylis rossii* occurs across a broad range of snow-depth classes and is most abundant in areas with moderate snow cover. From Walker et al. (1993).

recognized a suite of nine alpine vegetation classes based on the characteristic alpine habitats in the Grison Mountains, European Alps. (The terminology used here for vegetation community names is that of the Braun-Blanquet approach [Westhoff and van der Maarel, 1978; Ellenberg, 1988]). Four of these classes are directly related to snow cover or the lack of it (*Salicetae herbaceae*, snowpatch swards; *Elyno-Seslerietea* and *Caricetea curvulae*, calcareous and acidic alpine swards; *Oxytropi-Elynion* and *Loiseleurio-Vaccinion*, calcareous and acidic windswept places; and *Vaccinio-Piceetea*, subalpine dwarf shrub heaths) and two others are related to meltwater from snowbanks (*Scheuchzerio-Caricetea*, fens; and *Montio-Cardaminetea*, spring communities). Tundra snowbed vegetation has been described worldwide including studies from the central European Alps (Lüdi, 1921; Braun-Blanquet, 1932, 1949a, 1949b, 1950; Dierssen, 1984); Appenines (Tomaselli, 1991; Ferrari and Rossi, 1995); Scandinavia (Vestergren, 1902; Fries, 1913; Nordhagen, 1928, 1936; Kalliola, 1939; Gjærevoll, 1950; Hedberg, Martensson, and Rudberg, 1952; Gjærevoll, 1954, 1956; Dahl, 1956; Gjærevoll and Bringer, 1965; Wielgolaski, 1997); Iceland (Hadac, 1971); Greenland (Böcher, 1954, 1959, 1963; Molenaar, 1976; Daniëls, 1982; Herk, Knaapen, and Daniëls, 1988); Svalbard (Elvebakk 1984a, 1984b, 1985, 1997); Canada (Lambert, 1968; Barrett, 1972; Bliss, Kerik, and Peterson, 1977; Hrapko and LaRoi, 1978; Bliss and Svoboda, 1984; Bliss, Svoboda, and Bliss, 1984; Nams and Freedman, 1987a; Nams and Freedman, 1987b; Bliss, 1997); the Presidential Range, New Hampshire (Bliss, 1963); the Colorado Rocky Mountains (Kiener, 1967; Komárková, 1979, 1980; Willard, 1979; Haase, 1987); Washington North Cascades (Kuramoto and Bliss, 1970; Douglas and Bliss, 1977; Evans and Fonda, 1990); Alaska (Gjærevoll, 1954; Cooper, 1986; Komárková and McKendrick, 1988; Walker, 1985, 1990; Walker, Walker, and Auerbach, 1994a; Walker and Walker, 1996); Chukotka, Russia (Razzhivin, 1994a); the central Himalayas (Miehe, 1997); Japan (Ohba, 1974); Australia (Williams, 1987; Williams and Ashton, 1987); and New Zealand (Mark, 1965, 1970, 1975; Mark and Bliss, 1970; Mark and Dickinson, 1997).

Gjærevoll's descriptions of the snowbed communities in Scandinavia remain the most thorough descriptions of snowbed plant communities (Gjærevoll, 1950, 1956). He described 65 snowbed plant communities based on a combination of lateness of snowmelt, soil pH, and site moisture. In the United States, Komárková (1979, 1980) used the Braun-Blanquet approach to classify the vegetation in the Indian Peaks, Front Range Colorado. She recognized a total of 52 alpine plant associations. Of these, 20 occurred in snowbeds, 7 in windblown areas, 6 in rock crevices, 12 in wet meadows, 8 in shrublands, and 4 in spring areas. Figure 6.1 shows the relationship of several of Komárková's associations to the conceptual mesotopographic gradient on Niwot

Ridge, Colorado. It includes a suite of six vegetated microenvironments: (1) extremely windblown fellfields found on ridge crests and knolls and dominated by cushion-plant communities (e.g., association *Sileno-Paronychietum*), (2) windblown dry sedge meadows found mostly on gentle windward slopes, (e.g., association *Selaginello densae-Kobresietum myosuroidis*), (3) moist meadows that are covered by shallow snowpatches with grass and forb communities (primarily association *Acomastylidetum rossii* and association *Stellario laetae-Deschampsietum caespitosae*), (4) late-melting snowpatches that include a wide variety of plant communities from association *Toninio-Sibbaldietum* in the relatively early melting, well-drained portions of snowbanks to well-drained late-lying snowbed areas dominated by sedges (association *Caricetum pyrenaicae*) to hydrophilous moss communities at the base of late-lying snowpatches (e.g., association *Polytrichastro alpini-Anthelietum juratzkanae*), (5) wet sedge meadows at the base of snowpatch runoff areas with fen communities, willow shrublands, and spring communities (e.g., association *Caricetum scopulorum*, association *Rhodiolo integrifoliae-Salicetum planifoliae*, and association *Clementsio rhodanthae-Calthetum leptosepalae*), and (6) semipermanent snowbeds that are for the most part unvegetated (e.g., *Oxyrio digynae-Poetum arcticae*) (Table 6.1).

Komárková (1979) commented on the large number of associations found in the snowpatch class (*Salicetae herbaceae*) compared with other alpine vegetation classes. She attributed this phenomenon to the steep environmental gradients within snowbed areas. Many studies have noted major floristic differences between early-melting and late-melting snowbed communities (Nordhagen, 1943; Gjærevoll, 1950, 1956; Molenaar, 1976; Komárková, 1979; Walker, 1985; Walker et al., 1993, 1994a; Razzhivin, 1994; Walker and Walker, 1996). Other descriptions have noted the differences between communities on acidic and nonacidic substrates (Gjærevoll, 1950, 1956; Elvebakk, 1984a, 1984b; Ellenberg, 1988; Razzhivin, 1994; Walker et al., 1994). Stability of the site and position with respect to summer meltwaters are other contributing factors. Komárková (1993) also noted that compared with alpine areas, snowbed vegetation types in the Arctic at all hierarchy levels are more numerous, less well defined, and less clearly distributed along the controlling environmental gradients. She attributes this to the more numerous surface disturbances in the Arctic associated with, for example, the thaw–lake cycle, extensive reworking by rivers, cryoturbation, and wind.

### 6.3.3 Snow Flush Areas, Ribbon Forests, and Krummholz

Of special note are the communities that occur along gradients at the extremes of tundra regions. For example, within the northern polar-desert regions, most landscapes are nearly totally barren because of a lack of soil moisture through

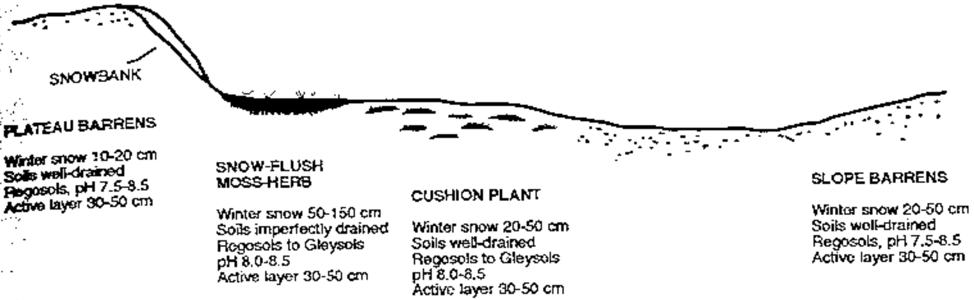


Figure 6.3. Generalized diagram to show the relationship of snow-flush, cushion-plant, and polar-barren plant communities within a polar-desert landscape. Modified from Bliss et al. (1984).

much of the growing season. Distinctive snow flush communities occur downslope of late-melting snowbeds and occupy about 3–5 percent of the polar desert areas (Figure 6.2f). Bliss et al. (1984) sampled twelve of these communities on three islands in the Canadian Archipelago, and reported species richness (9–14 spp.), and standing crop (120–740 g $m^{-2}$), compared to the polar barrens of the surrounding terrain (5–7 spp., and 5–60 g $m^{-2}$). A mesotopographic gradient for a polar-desert landscape (Figure 6.3) shows the landscape relationship of the snow-flush communities with respect to polar-barren and cushion-plant communities.

Billings (1969) has described a different wind–snow–vegetation gradient at the forest boundary that he terms the "Ribbon Forest–Snow Glade-Alternating Series" (Figure 6.4). This phenomenon occurs near alpine timberline in the Rocky Mountains from Canada to New Mexico on high, relatively level, windswept plateaus. In this series, snow blows laterally for considerable distances from the alpine tundra (either natural or fire caused) down into spruce-fir subalpine forest where it piles up within the forest. Parallel "ribbon forests" act as snow fences accumulating long-lasting snowdrifts that result in the grass- and sedge-dominated "snow glades" between the "forest ribbons" (Figure 6.4). These ribbon forests have been studied by Buckner (1977) and Earle (1993), and a similar wave pattern occurs in *Abies balsamea* forests in the Adirondack Mountains of northern New York State (Sprugel, 1976). The snowdrifts in the forests do not melt until late in the growing season. The result is the death of the older trees in parallel patterns where the snow is deepest and the soil most saturated with meltwater. The dead trees, over the years, are replaced by elongated parallel wet meadows ("snow glades").

Wind, topography, and snow also control patterns of krummholz (wind-shaped tree islands) at the forest-tundra ecotone on Niwot Ridge (Wardle, 1968; Marr, 1977;

Figure 6.4. Ribbon forest on Buffalo Pass, Colorado. Deep snowdrifts form in the open areas between strings of trees. Photo by David Buckner.

Benedict, 1984; Holtmeier and Broll, 1992; Pauker and Seastedt, 1996). These features form in shallow depressions on windswept ridges where site conditions are relatively favorable for seedling establishment (Figure 6.5). As the seedling grows it begins to form a snowdrift downwind, which changes the winter microclimate on the leeward side of the island. At maturity, the tree island totally controls the microsite. The island slowly dies off on the windward side because of physiological drought stress and frost damage, whereas the leeward side of the island is able to advance in the protection of the drift through the process of layering (Marr, 1977). Benedict (1984) estimated the leeward movement of krummholz to be about 2 cm year$^{-1}$ over the past 500 years. In places the islands actually migrate downwind, leaving trails of scattered woody root fragments up to 15 m long (Marr, 1977). Vegetation on the windward side of the islands is generally typical fellfields or dry meadows. Inside the tree island, the dense evergreen foliage prevents much growth except for a few meager individual plants such as *Polemonium delicatum* and *Ribes montigenum*. Downwind, the vegetation is much more luxuriant and is typical of many subalpine meadows (e.g., *Vaccinium scoparium*, *Vaccinium myrtilus*, *Deschampsia*

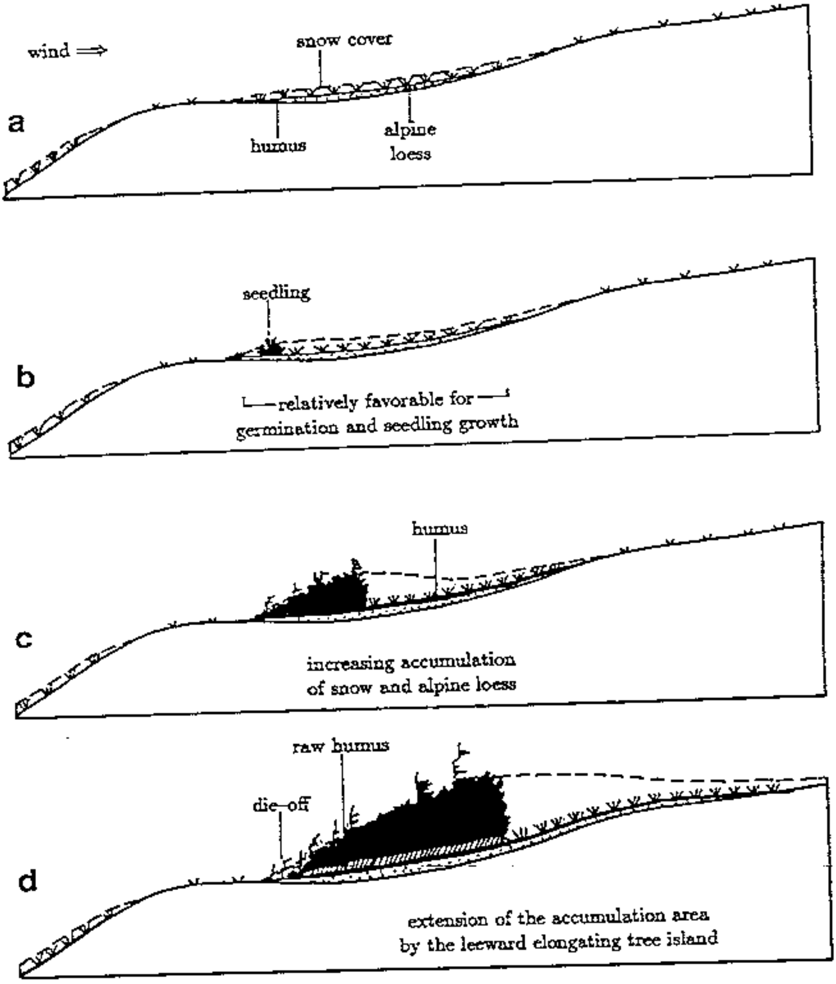


Figure 6.5. Development and migration of tree islands on Niwot Ridge. (a) Open alpine fellfield with slight depression and accumulation of fine-grained loess and humus. (b) Seedling establishment in area relatively favorable for germination and seedling growth and formation of incipient drift downwind of the seedling. (c) Tree island shaped by wind with modified habitat within and downwind of the island. (d) Tree island controls microsite, dieback occurs on windward side, and extension occurs on the leeward side through layering of the island. From Holtmeier and Broll (1992).

*caespitosa*). Species such as *Kobresia myosuroides* that are intolerant of deep snow are not present in the drift area (Bell and Bliss, 1979). There are also distinct trends of soil organic matter, nutrients (N, P, K), C/N ratios, cation exchange capacity, and pH associated with the island (Holtmeier and Broll, 1992; Pauker and Seastedt, 1996).

Within the tree island, soil formation is strongly influenced by the accumulation of evergreen leaf litter with thick organic horizons, relatively high soil moisture, and incipient podzolization (Holtmeier and Broll, 1992).

### 6.3.4 Soils

Soil development in arctic and alpine areas is slow and affected by snow cover and related conditions of drainage supply of meltwater, occurrence of permafrost, cryoturbation, and various forms of solifluction and mass wasting. The rootable soil is generally shallow, and rhizosphere biological activity is limited by the soil's instability, low temperatures, and wetness (Dierschke, 1977). Soils in many snowbed areas tend to be acidic and nutrient-poor because of leaching caused by large amounts of meltwater (Burns, 1980; Tomaselli, 1991; Stanton, Rejmánek, and Galen, 1994). However, snowbeds also trap windblown mineral and organic material, and the lower portions of snowbeds often accumulate this aeolian material. Regions with large annual inputs of loess, such as Prudhoe Bay, Alaska, have nonacidic snowbeds and support relatively rich plant communities (Walker, 1985, 1990). Soil fertility is also strongly correlated with the percentage of organic matter, and in very-late-lying snowbeds fertility declines sharply with later snowmelt dates (Stanton et al., 1994).

Snowbeds normally lie on hills with strong gradients of soil nutrients and water availability. Burns (1980) described a series of soils associated with the mesotopographic gradient on Niwot Ridge (see Figure 6.3). The chemical composition of snowbed soils is influenced by the local geology, the chemistry of the snowpack (Tranter and Jones, Chapter 3), nival biological activity (Hoham and Duval, Chapter 4), the breakdown of organic materials beneath the snowpack (Jones, 1991), and subsequent biological interactions with vegetation. Snowdrifts collect plant debris and mineral fines blown from the exposed places; part of this is carried off by meltwater, and some is held by the vegetation and adds to the fertility of the soil. Miller (1982) described a nitrogen and phosphorus gradient along an arctic–alpine hill-slope unit at Eagle Creek, Alaska. The upper portions of the snowbed were nitrogen-poor and composed of dwarf evergreen ericaceous shrub species (e.g., *Cassiope*, *Ledum*, *Vaccinium*, *Empetrum*). Nitrogen uptake was highest in lower snowbed areas receiving nitrogen and phosphorus from upslope and aeolian sources. Here, graminoid, forb, and shrub species with greater nitrogen demands were dominant (e.g., *Salix*, *Anemone*, *Artemisia*, *Pedicularis*) (Miller, 1982). The most nutrient-rich sites occurred near the bottom of slopes, whereas the sites poorest in nutrients were the heath communities near the top of the gradient.

The exchange of nutrients between communities was examined along a hillslope gradient associated with a river bluff in northern Alaska (Giblin et al., 1991;

Nadelhoffer et al., 1991). The flow of nutrients was measured through the soils and plants over permafrost from a hilltop *Dryas* heath community, across a late-lying snowbed community of dwarf shrubs, lupine (*Lupinus*), and horsetails (*Equisetum*) to wet sedge tundra and riverside willows beyond the base of the slope. The hilltop heath site was nearly snow free in winter because of wind. A large amount of dissolved inorganic nitrogen and phosphorus was found in the 2- to 3-m-deep snowbank over the hillslope shrub-lupine and footslope *Equisetum* communities and contributed up to 10 percent of the nitrogen and phosphorus requirements of the hillslope and footslope ecosystems. The snowbank is an important mechanism of lateral nutrient transport down the topographic gradient, supplementing the downslope flow of water and soil solution through the thawed layer above the permafrost, which acts as an impermeable "basement." The redistribution of snow by wind is partially responsible for a heterogeneous pattern of nitrogen deposition in alpine and arctic environments. In an alpine system at Niwot Ridge, Bowman (1992) measured the amount of $NO_3^-$ and $NH_4^+$ in snow and calculated the snow input as a percentage of the total atmospheric input in 1990–1991. Snowmelt nitrogen ranged from 5 to 20 percent of atmospheric input in dry meadows to 43 to 152 percent in the snowbed communities.

There are also important temporal nutrient patterns. Williams et al. (1995) developed a conceptual model of the mass balance of nitrogen pools and fluxes for the Emerald Lake watershed in the southern Sierras, which has a relatively pristine winter snowpack. They found that up to 90 percent of the annual wet deposition of nitrogen was stored in the seasonal snowpack and that about 80 percent of this was released in an ion-rich pulse with the first 20 percent of spring meltwater. This spring ionic pulse has been noted in numerous snow-dominated ecosystems (Tranter and Jones, Chapter 3). Mullen and Schmidt (1993) noted that the spring flush of nutrients occurs during times of low soil temperatures, and plants require special adaptations to take advantage of these early season conditions. For example, *Ranunculus adoneus*, the snow buttercup, is one of the few plants that flowers during the snowmelt. This plant accumulates phosphorus after seed set while the soil temperatures are relatively high and stores phosphorus over the winter to remobilize the following spring when the soil temperatures are close to 0°C. Phosphorus uptake appears to coincide with the development of vesicular-arbuscular-mycorrhizal (VAM) fungi in the roots of *R. adoneus*, indicating that these fungi are important to the phosphorus nutrition of the plants (Mullen and Schmidt, 1993). In contrast to phosphorus uptake, nitrogen uptake occurs very early in the growing season before new roots and active VAM fungal structures are formed. At this time $NH_4^+$ is the main form of inorganic nitrogen. *R. adoneus* takes advantage of the early season flush by using a preexisting root system that is heavily infected with a "dark septate" fungi. These fungi are able to grow both saprophytically and symbiotically and thus may be an important sink for the early season flush of nitrogen.

### 6.3.5 Subnivean Animals

Subnivean activity by small mammals (Aitchison, Chapter 5) affects the distribution, biomass, and nutrients of associated vegetation communities. The presence of these animals causes considerable disturbance to the vegetation and soils. For example, gophers (*Thomomys talpoides*) are abundant in moderately deep early-melting alpine snowbeds of Colorado (Stoecker, 1976; Thorn, 1978; Willard, 1979; Burns, 1980; Thorn, 1982). Approximately 90 percent of the gopher activity on the Niwot Ridge Saddle is restricted to areas with moderately deep winter snow cover (Burns, 1980). Presumably, these are areas with sufficient unfrozen winter soils to permit winter digging activities and sufficient vegetation cover as food for the gophers. Thorn (1982) found that gopher activity was strongly associated with snowbed vegetation types on Niwot Ridge. The most heavily impacted plant associations have up to 80 percent of their surfaces disturbed by gopher activity. Soils in these areas have a very thick A horizon (>40 cm) formed by homogenized A and upper B horizons (Pachic Cryumbrepts). Gophers maintain plant species diversity by creating gaps in the plant canopy, redistributing nutrients and soil, and suppressing species that otherwise would dominate (Halfpenny and Southwick, 1982; Tilman, 1983; Andersen, 1987; Huntly and Inouye, 1987; Inouye et al., 1987). Gophers strongly affect the nutrients and soil organic carbon content of alpine soils. Chronic frequent disturbance by gophers appears to homogenize the soil particle-size distribution, bulk density, and available nutrients of the upper soil horizons (Litaor, Mancinelli, and Halfpenny, 1996). Gopher-affected areas have lower carbon content and total concentrations of carbon, nitrogen, and exchangeable calcium and potassium but higher available nitrate and nitrogen fluxes (Cortinas and Seastedt, 1996; Litaor et al., 1996).

In the Arctic, subnivean animal activities are partially responsible for heterogeneous spatial and temporal patterns of nutrients within arctic landscapes. At Barrow, Alaska, population pulses of brown lemmings (*Lemmus sibiricus*) are associated with major pulses of nutrients that are released at snowmelt from stocks of urine, feces, and litter that accumulate beneath the snow during peaks in the lemming population cycle (Pitelka, 1964; Schultz, 1964, 1969; Batzli et al., 1980). The lemmings can drastically reduce the standing crops of live and dead aboveground biomass, consuming up to 50 percent of the annual aboveground production and 20 percent of the total net production. Approximately 70 percent of this is returned to the soil as highly soluble feces and urine. Other animals that conceivably could play important roles that affect nutrient regimes and vegetation patterns in arctic snowbeds include voles (*Microtus* spp.) (Batzli and Henttonen, 1990), collared lemmings (*Dicrostonyx rubricatus*), arctic ground squirrels (*Spermophilus parryi*), and willow ptarmigan (*Lagopus lagopus*) (Walker, 1990) (also see Aitchison, Chapter 5).

### 6.3.6 Other Factors Affecting Plant Composition of Snowbeds

Many snowbed plant species are found in relatively narrow ranges of habitats, particularly in alpine areas (Komárková, 1979; Walker et al., 1993). A good example is the snow buttercup *R. adoneus*, which occurs almost exclusively in late-melting snowbed areas and is nearly absent from adjacent turf and grassy meadow habitats, although habitats outside snowbeds appear to be favorable for *R. adoneus* growth (Scherf, Galen, and Stanton, 1994). One factor that restricts the movement of *Ranunculus* from snowbeds is that its seeds are rarely dispersed more than a few centimeters beyond the maternal plants. Secondary seed movement by water, gravity, and animals also appears to be limited. Transplanted *R. adoneus* seedling survival is statistically the same in meadow and snowbed sites, but causes of mortality are quite different. Seedling desiccation during the summer is much higher in the snowbed areas, whereas predation by small mammals occurs primarily in the meadow sites. This implies that genotypes appropriate for regeneration in the snowbed are probably poorly suited for colonization of adjacent plant communities. The sites most suitable for *R. adoneus* growth are those that offer opportunities for rapid infection by mycorrhizal fungi in the absence of neighboring vegetation. Scherf et al. (1994) conclude that such combinations of environmental factors are probably rare and ephemeral.

Ecotypic variation has been suspected in plants that occur across large portions of the snow gradients, such as *Dryas octopetala* and *Acomastylis rossii*, both of which show considerable morphological variation from fellfields to deep snow habitats (Billings and Bliss, 1959; May, Webber, and May, 1982; McGraw and Antonovics, 1983; McGraw, 1985a, 1985b, 1987). Billings and Bliss (1959) found that plants of *A. rossii* transplanted from a snowbed to a greenhouse maintained field morphological characteristics for at least 2 years, indicating possible ecoclinal or ecotypic status. Plants of *A. rossii* above the snowbank and toward the ridge were much smaller than the large, tall plants in the wet meadow. A similar pattern has been found in field reciprocal transplant experiments of *A. rossii* on Niwot Ridge (May, 1976; May and Webber, 1982; May et al., 1982), although reciprocal transplant studies with *R. adoneus* demonstrate that most phenotypic variation for this species across the snowmelt gradient is due to environmental, rather than genetic, variation.

Other factors that affect the composition of snowbed plant communities that have received some scientific study include different reproductive strategies (Marchand and Roach, 1980; Heide, 1992), pathogenic fungi (Sturges, 1989), wintertime herbivory by small mammals (Fox, 1981), seed germinability (Bock, 1976), and characteristics of the seed bank (Chambers, 1991, 1993; Chambers, MacMahon, and Brown, 1990).

### 6.3.7 Landscape and Regional Vegetation Patterns

The concept of snow gradients can be extended to three-dimensional landscapes with maps and GIS. In the Colorado Rocky Mountains, Walker et al. (1993a, 1993b) used a hierarchy of GIS databases to quantify the spatial correspondence between topography, snow, plant species, plant associations, and regional patterns of vegetation greenness. At the plant community level, 78 percent of Niwot Ridge is covered by vegetation that is typical of either windblown areas (class *Elyno-Seslerietea*) or snowpatches (class *Salicetea herbaceae*), an indication of the important role that wind and snow have in defining vegetation patterns at this site (Bell and Bliss, 1979; Komárková and Webber 1978). Correlations between snow depths and vegetation communities using a GIS analysis revealed that most plant associations, like plant species (see Section 6.3.1), are found in distinct portions of the snow gradient (Walker et al., 1993). These patterns reoccur in other portions of the Colorado Front Range. For example, Bell (1974) found that fellfields in Rocky Mountain National Park were totally snow free for 38 percent of February and March, whereas *Kobresia* meadows were snow free about 22 percent of the time, and snowbed communities were continuously covered during this period. Similar analyses have been done in the Alaskan Arctic foothills (Evans et al., 1989) and the Mosquito Range, Colorado (Stanton et al., 1994).

At regional scales, Walker et al. (1993) used SPOT satellite imagery and a digital terrain model to examine the patterns of the normalized difference vegetation index (NDVI) along elevation gradients on various slope aspects in the Front Range (Walker et al., 1993a, 1993b). They found that NDVI on east-, north-, and south-facing slopes decreased with elevation in response to the temperature gradient but that NDVI was low at all elevations on west-facing slopes because of the overriding influence of strong westerly winter winds that scour the west-facing slopes and constrain plant production at all elevations, particularly on the eastern slope of the Front Range. Measurements of NDVI at the 88 Niwot Ridge Saddle grid points and comparison with snow depth and soil moisture measurements at the same points confirmed an underlying relationship between soil moisture and vegetation greenness as inferred by NDVI (Walker et al., 1993). Duguay and Walker (1996) have shown that there can be high local variation in the NDVI–elevation relationship because of local climatic and topographic effects.

Table 6.2. *Comparison of wind, snow, and soil properties in moist nonacidic tundra and moist acidic tundra at the MNT-MAT boundary in northern Alaska.*

| Ecosystem property | MNT | MAT |
|---|---|---|
| Wind | + | – |
| Snow depth | – | + |
| Depth hoar | – | + |
| Wind slab | + | – |
| Vegetation canopy height | – | + |
| Summer heat flux into the soil | + | – |
| Permafrost temperature | – | + |
| Active layer depth | + | – |
| Upward freezing from the base of the active layer in early winter | + | – |
| Downward freezing from the soil surface in early winter | + | – |
| Time for freeze-up in fall | + | – |
| Cryoturbation | + | – |
| Movement of subsurface calcareous soils to the surface | + | – |

*Note:* Summarized from Walker et al. (1998).

In the Arctic, snow and its effect on soil thermal properties are thought to be at least partially responsible for the boundary between northern moist nonacidic tundra (MNT) and southern moist acidic tundra (MAT) ecosystems (Walker et al., 1998). The boundary stretches across all of northern Alaska near the northern edge of the Arctic foothills of the Brooks Range. The boundary is clearly visible on false color-infrared satellite images. The spectral boundary is caused by differences in greenness primarily because of greater shrub abundance (*Betula*, *Salix*, *Ledum*, and others) in MAT. Similar boundaries separate acidic Low Arctic from nonacidic High Arctic ecosystems in other parts of the Arctic (Alexandrova, 1980), but the boundary is enhanced in northern Alaska because of the strong climatic boundary at the northern front of the east-west-west trending Brooks Range. Differences in winter climate, primarily wind regimes, are thought to be one of the causes of the boundary (Table 6.2). Stronger more persistent winds on the northern coastal plain create thinner, more dense snowpack and colder soil surface termperature, which in turn promote more active cryoturbation (Sturm and Johnson, 1992; Benson et al., 1996; Zhang, Osterkamp, and Stamnes, 1996a, 1996b, 1997; Bockheim et al., 1998; Nelson et al., 1997a, 1997b; Sturm et al., 1997). The continual frost stirring of the soils tends to bring the nonacidic alluvial and aeolian subsurface deposits to the surface, which promotes the growth of nonacidic plant communities. Many of the shrub species dominant in acidic tundra are absent in nonacidic tundra; the shorter plant canopies also promote development of a thinner, less dense snowpack (Table 6.2).

Other integrated studies of snow–vegetation interactions involving mapping of snow and vegetation patterns have been done in the Apennines, Italy (Ferrari and Rossi, 1995) and Obergurgl, Austria (Hampel, 1963). An interdisciplinary ecographic approach used vegetation maps to analyze snow regimes and microclimatic conditions at the upper treeline (approximately 2,225 m) in the Ötz Valley near Obergurgl. Reforestation of the upper treeline is of great concern in the highly populated regions of the Alps. Much of the forest has been replaced by grazing lands, resulting in enhanced avalanche activity. Severe avalanche activity in 1951 and 1954 gave rise to studies that included site and vegetation description, ecophysiological studies of key species, microbiology, and investigation of engineered structures for avalanche prevention. The studies concluded that detailed maps of plant communities provided fundamental insights to habitat, particularly soil temperature, which controls root respiration, development of mycorrhizal mycelium, and other processes important for the establishment of trees at treeline.

Pomeroy, Marsh, and Gray (1997) applied a distributed snow model to analyze the interactions between vegetation patterns and snow hydrology in a 68-km$^2$ catchment near Inuvik, Northwest Territories, Canada. The model uses a Landsat-derived vegetation classification and a digital elevation model to segregate the basin into snow sources and sinks. The model relocates snow from the sources to sinks and calculates in-transit sublimation loss. The resulting annual snow accumulation in specific vegetation-landscape types was compared with the results of intensive field surveys of snow depth and density. On an annual basis, 28 percent of annual snowfall sublimated from tundra surfaces and 18 percent was transported to sink areas. Annual blowing snow transport to sink areas amounted to an additional 16 percent of annual snowfall to shrub tundra and an additional 182 percent to drifts. For the total budget, 86.5 percent of the total snowfall accumulated on the ground, 19.5 percent was lost to sublimation, and 5.8 percent was transported into the catchment.

Knowledge of snow–vegetation relationships has practical relevance for interpreting winter snowpack conditions during the summer months. During winter, the snow cover is often uniformly white on aerial photographs and other remotely sensed imagery, giving few clues about the depth of the snow. During summer one can estimate rather closely what the relative winter snowpack, or lack of it, is by inspection of the topography along with the floristic structure and height of the plant communities (Pomeroy and Gray, 1995). Gjærevoll (1952) used vegetation information to help identify snowbed areas in the engineering of mountain roads in Norway. In northern Alaska, such information is profitably used in routing wintertime seismic operations (Felix and Raynolds, 1989a, 1989b; Emers, Jorgenson, and Raynolds, 1995).

Numerous remote-sensing techniques have been developed to aid in estimating snow water equivalent (Hall and Martinec, 1985), including satellite-mounted microwave sensors (Bales and Harrington, 1995), airborne $\gamma$-ray sensors (Carrol et al., 1995), and approaches using time series of Landsat images, digital terrain models, and distributed energy balance models. In some instances, remote sensing of the vegetation cover during the summer can give a better clue about average wintertime snowpack conditions than remote sensing of the snow surface itself, and could be used to provide independent verification of drift and windblown areas.

## 6.4 Plant Physiological Responses

At the plant level, the presence of a winter snow cover offers plants protection against frost damage, dehydration, and physical damage from wind and windblown particles (Wardle, 1968; Tranquillini, 1979; Chapter 7). It limits intensive and deep freezing of the soil and suppresses soil instability caused by frost action and weathering (Pomeroy and Brun, Chapter 2). However, the protection that snow provides against winter climate extremes is bought at the price of a belated, short growing season. Conversely, snow-free places are exposed to severe winds, and plants in these places are subject to high rates of evapotranspiration (LeDrew, 1975; Bell and Bliss, 1979; Isard, 1986; Isard and Belding, 1989).

It is useful to consider the factors that influence the aboveground plant environment (foliosphere) separately from those that influence the rooting environment (rhizosphere) (Figure 6.6). The most important site factors influencing the foliosphere are light, temperature, and humidity, whereas the most important factors in the rhizosphere are temperature, soil stability, and availability of moisture, nutrients, and oxygen. All these site factors are strongly influenced by snow, through its effect on either the microclimate or the local hydrology (Gjessing and Øvstedal, 1975; Molenaar, 1987).

The microclimate within the foliosphere of tundra vegetation is quite different from the climate measured at nearby climate stations. There are larger fluctuations in air temperature and air saturation deficit, and wind velocity is much decreased (Geiger,

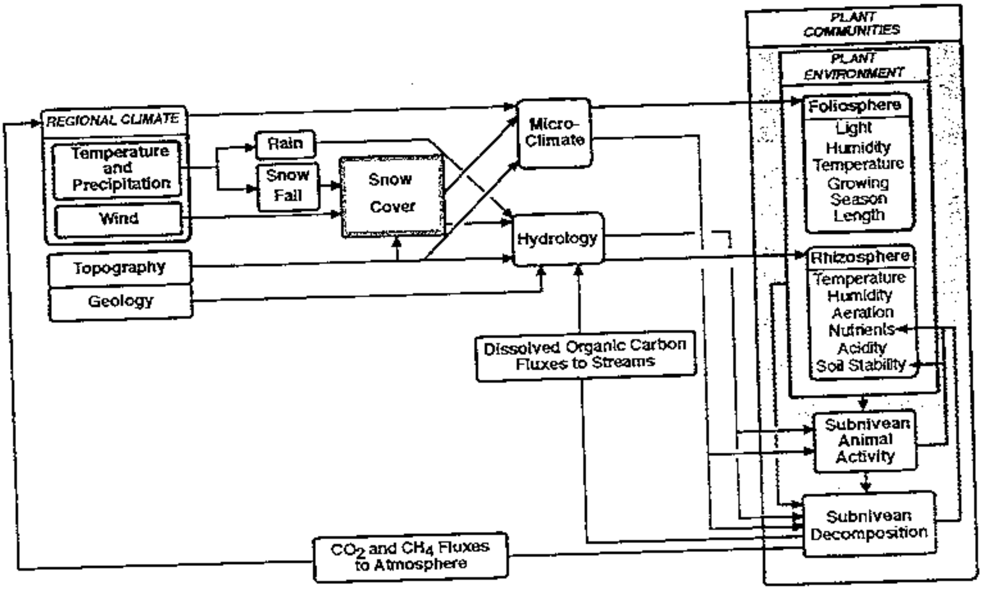


Figure 6.6. Conceptual diagram of snow–vegetation interactions. Regional climate, geology, and topography control snow distribution, which affects microclimates and hydrological regimes. The subnivean microclimate mainly influences the aboveground plant environment (foliosphere), whereas the hydrological regime mainly influences the belowground environment (rhizosphere). Subnivean animal activity is influenced by the subnivean microclimate and hydrology as well as availability of food; in turn it affects the stability and nutrient regime of the microsite. Subnivean decomposition is affected by animal activity, subnivean temperatures, and water availability; in turn it affects plant nutrient status as well as fluxes of trace gases to the atmosphere and dissolved organic matter to streams.

1965; Monteith, 1973). The intensity of irradiation and of heat loss, and thus the extremes of the microclimate, is especially great in high altitude sites but is also related to latitude, aspect, and slope of the site as well as the soil moisture conditions (Cline, 1995). The contrast between the microclimate of the foliosphere and that of the rhizosphere is particularly great in snow margin areas and can produce stressful conditions for many plants. The high surface temperatures promote photosynthesis at the same time the roots of the plant are near freezing, which limits uptake of nutrients and water.

### 6.4.1 Characteristics of Arctic and Alpine Snow Cover

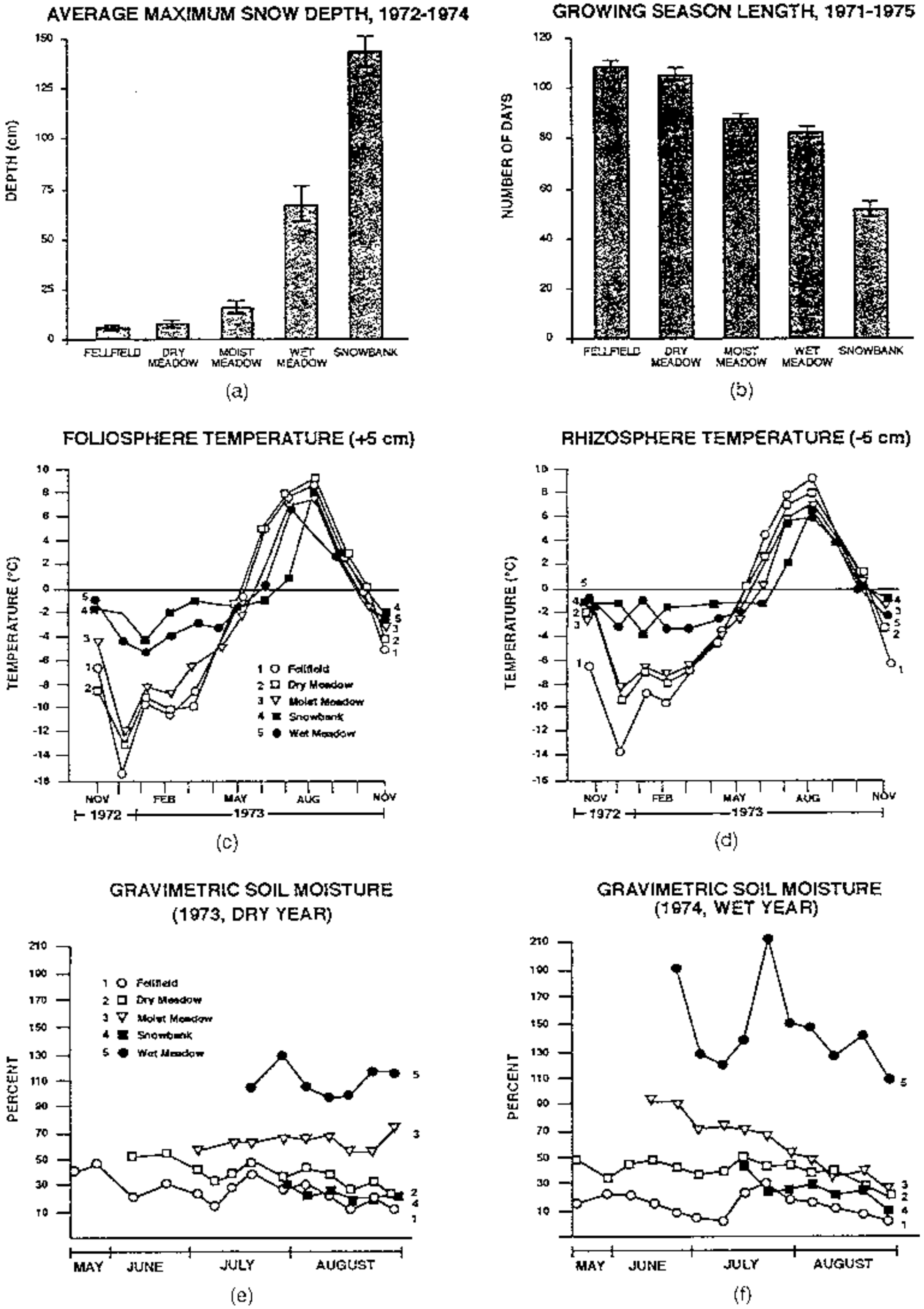
The properties of the snowpack itself are important to the subnivean environment through control of heat flux into and from the soil surface (Pomeroy and

Brun, Chapter 2). Tundra snow cover is quite different from that in forested and more temperate regions (Sturm, Holmgren, and Liston, 1995; Chapter 2). Arctic tundra snow cover occurs north of the boreal treeline. It generally consists of wind-hardened, thin (10–75 cm), cold snowpack with a few centimeters of loose granular depth hoar at the base of the snowpack, overlain by multiple wind slabs. Also, there are often hard surface drift forms and an absence of ice lenses and other winter melt features.

In alpine areas, the snow cover is generally warmer and more heterogeneous because of variable topographic and climatic influences related to latitude, altitude, and continentality (Barry, 1992; Sturm and Holmgren, 1995). Generally, alpine snowpacks are deeper (75–250 cm), with alternating layers of wind-packed and soft snow and often with basal depth hoar (Sturm and Holmgren, 1995). An important contrast between arctic and alpine snowpacks is that deeper snowdrifts in the alpine may remain unfrozen at the base all winter, whereas most arctic snowpacks remain below freezing, thus limiting most biological activity. The snow cover is also affected locally by variation in the height of the tundra plant canopy (Pomeroy and Gray, 1995; Tabler and Schmidt, 1986).

The amount of snow (snow-water equivalent) 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; Geiger, 1965; Miller, 1982; Walker et al., 1993; Stanton et al., 1994). Very deep snowpatches 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, humus poor, and unstable soils, results in areas completely void 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 previously discussed snow gradient on Niwot Ridge, Colorado (Figure 6.1), is used here to illustrate the effect of snow cover on growing season length and other site factors (Figure 6.7). Species composition, biomass, phenology, and site factors have been monitored in five vegetation types representing the portion of the snow gradient from exposed ridge tops to shallow snowbeds (May, 1976; Komárková and Webber, 1978; Komárková, 1979, 1980; Burns and Tonkin, 1982; May and Webber, 1982; Walker et al., 1994b; Walker, Ingersoll, and Webber, 1995). Snow depths were monitored year round in 1972–1974. The mean maximum depths ranged from less than 10 cm in the fellfield community (association *Sileno–Paronychietum*) to 120 cm in the shallow snowbeds (association *Toninio–Sibbaldietum*) (Figure 6.7a). The corresponding


AVERAGE MAXIMUM SNOW DEPTH, 1972-1974
DEPTH (cm)
0
25
50
75
100
125
150
FELLFIELD
DRY MEADOW
MOIST MEADOW
WET MEADOW
SNOWBANK
(a)
GROWING SEASON LENGTH, 1971-1975
NUMBER OF DAYS
0
20
40
60
80
100
120
FELLFIELD
DRY MEADOW
MOIST MEADOW
WET MEADOW
SNOWBANK
(b)
FOLIOSPHERE TEMPERATURE (+5 cm)
TEMPERATURE (°C)
1 ○ Fellfield
2 □ Dry Meadow
3 ▽ Moist Meadow
4 ■ Snowbank
5 ● Wet Meadow
NOV
FEB
MAY
AUG
NOV
1972
1973
(c)
RHIZOSPHERE TEMPERATURE (-5 cm)
TEMPERATURE (°C)
NOV
FEB
MAY
AUG
NOV
1972
1973
(d)
GRAVIMETRIC SOIL MOISTURE
(1973, DRY YEAR)
PERCENT
1 ○ Fellfield
2 □ Dry Meadow
3 ▽ Moist Meadow
4 ■ Snowbank
5 ● Wet Meadow
MAY
JUNE
JULY
AUGUST
(e)
GRAVIMETRIC SOIL MOISTURE
(1974, WET YEAR)
PERCENT
MAY
JUNE
JULY
AUGUST
(f)

growing season length varied from 109 days in the fellfield community to 52 days in the snowbed (Figure 6.7b). The length of the growing season and the effects on vegetation have also been monitored at other sites (Billings and Bliss, 1959; Holway and Ward, 1965; Bliss, 1966; Svoboda, 1977; Miller, 1982; Williams, 1987; Stanton et al., 1994).

### 6.4.2 Phenology

In the already short growing season of arctic and alpine regions, delayed snowmelt strongly affects patterns of greenup, flowering, seed set, and total primary production. It is not uncommon to see the flowering of snow-margin species, such as the snow buttercup *R. adoneus*, occurring along the melting edge of snowpatches and moving as a wave across the tundra through the growing season. Delayed greenup 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, shoot growth and even flowering may commence from overwintering buds near the soil surface under snow before melt. Good examples of such early season growth under snow are *Polygonum davisiae* (Beyers, 1983), *Erythronium grandiflorum* (Caldwell, 1969; Salisbury, 1985), *Caltha leptosepala* (Rochow, 1969), *Oxyria digyna* (Mooney and Billings, 1961), *R. adoneus* (Caldwell, 1968; Salisbury, 1985; Galen and Stanton, 1991, 1993, 1995; Mullen and Schmidt, 1993; Galen, Dawson, and Stanton, 1993; Scherf et al., 1994; Mullen, 1995; Mullen, Schmidt, and Jaeger, 1998), *Saxifraga oppositifolia* (Moser, 1967), and *A. 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 the species mentioned above and many others can leaf out and flower quickly because their leaf primordia and flower buds preformed during the previous growing season (Sørenson, 1941; Billings and Mooney, 1968; Mark, 1970; Billings, 1974). They are also metabolically active with relatively high dark respiration rates at low temperatures under the snow.

Figure 6.7. Variation in site factors for five plant communities along an alpine snow gradient, Niwot Ridge, Colorado, 1972–73. (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 5 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).

The effects of interannual climate variation on phenology of the alpine avens *A. rossii* and bistort *Bistorta bistortoides* have been studied over a 9-year period in the Colorado alpine (Walker et al., 1995). *B. bistortoides* showed a strong response to variation in the timing of snowmelt. During the heavy snowfall year of 1983, a major El Niño Southern Oscillation year in the southern Rocky Mountains, leaf lengths in *B. bistortoides* increased approximately 10 percent and the average number of leaves nearly doubled despite a much shorter growing season. Walker et al. (1995) concluded that the greater leaf lengths and number of leaves are related to soil moisture during the period of maximum growth, and this is controlled by the amount and timing of snowmelt. The positive role of deeper winter snowpack on plant growth is also supported in a subalpine study by Inouye and McGuire (1991), who showed a positive correlation between the number of flowers and cumulative snowfall at the Rocky Mountain Biological Laboratory, Crested Butte, Colorado, for the period 1973–1989. They found that, during years of lower snow accumulation, *Delphinium nelsonii* plants experienced lower temperatures between the period of snowmelt and flowering, which resulted in delayed and reduced floral production.

### 6.4.3 Production

Usually there is a gradient of plant production from the latest melting areas to the early-melting margins (Sorenson, 1941; Billings and Bliss, 1959; Holway and Ward, 1965; Bliss, 1966; Canaday and Fonda, 1974; May, 1976; Douglas and Bliss, 1977; Webber, 1978; Murray and Miller, 1982; Wijk, 1986a, 1986b; Nams and Freedman, 1987a, 1987b; Walker et al., 1994b). Billings and Bliss (1959) studied the effects of an alpine snowbank on soil moisture, plant growth, and productivity across a large snowbank at an elevation of approximately 3,350 m in the Medicine Bow Mountains of Wyoming at 41°20′N. Mean daily primary productivity and total production were much greater along the part of the transect below the snowbank (moist meadow) than along the transect above the snowbank (dry meadow). For the late-melting portions of the snowbank, daily primary production was 6.0 g $m^{-2}$ $day^{-1}$ and total production was 128 g $m^{-2}$, compared with 2.5 g $m^{-2}$ $day^{-1}$ and 36.2 g $m^{-2}$ on the upper transect. Billings and Bliss concluded that soil moisture appears to be the most critical factor affecting vegetation differences both above and below the snowbank.

Measurements of biomass along a snow gradient on Niwot Ridge, Colorado were made for 7 consecutive years (1982–1989) in the five Niwot Ridge plant communities discussed previously (Figure 6.1) (May, 1976; Walker et al., 1994b). The least biomass was in the snowbed, $113 \pm 15$ g $m^{-2}$, compared with $164 \pm 12$ g $m^{-2}$ in the fellfield, $197 \pm 18$ g $m^{-2}$ in the dry meadow, $218 \pm 23$ g $m^{-2}$ in the moist meadow, and

214 ± 21 g $m^{-2}$ in the wet meadow. Interannual climate variation accounted for 15–40 percent of the variation in phytomass in the five communities along the gradient. The biomass of fellfields and dry meadows was most sensitive to the previous year's precipitation, and the moist and wet meadow communities were most sensitive to the current growing season soil moisture. The only communities sensitive to growing season length were the snowbed communities. Surprisingly, none of the communities was sensitive to variation in the annual accumulated sum of daily mean temperatures above 0°C (thawing degree days). Soil moisture was overwhelmingly important to biomass production, and this was most strongly linked to the amount of spring precipitation, which mostly falls as snow. The amounts of winter and summer precipitation were less important.

### 6.4.4 Growth Strategies of Snowbed Plants

Several authors have commented on the growth strategies of plants in response to poor nutrient conditions found in snowbeds (Svoboda, 1977; Miller et al., 1982; Maesson et al., 1983; Nams and Freedman, 1987a; Williams, 1987; Williams and Ashton, 1987). In the High Arctic, evergreen *Cassiope tetragona* heaths are common in snowbeds. Above-ground to below-ground biomass ratios are high compared with other arctic plant communities. For example, biomass ratios of the *Cassiope* snowbeds on Ellesmere Island are nearly 1:1 compared with 1:3.8 to 1:6.7 in wet sedge-moss meadows (Miller et al., 1982; Nams and Freedman, 1987b). Evergreen species are long lived and slow growing and tend to have small below-ground biomass because of a storage of nutrients and photosynthates in leaves and stems, whereas deciduous shrubs and graminoids use large below-ground biomass as storage sites. Abundant attached dead tissue, common in snowbed plants such as *Cassiope* and *Dryas integrifolia*, also contributes to high aboveground : below-ground biomass ratios. Over 90 percent of the aboveground standing biomass in these heaths is composed of nonphotosynthetic tissues and 74 percent is dead tissue attached to live plants. These stress-tolerant species allocate a small proportion of total biomass to current-year production, and a large proportion of the total biomass is attached dead tissue. The accumulation of attached dead leaves also enhances snow accumulation in winter and creates a relatively favorable thermal regime in both summer and winter. The attached litter also may serve as a reservoir of nutrients (Nams and Freedman, 1987b).

Photosynthate is stored underground in the roots, rhizomes, or stem bases of these herbaceous perennials as carbohydrates in the form of sugars and starches (Mooney and Billings, 1960; Fonda and Bliss, 1966; Rochow, 1969; Shaver and Billings, 1976; Wallace and Harrison, 1978). Some of these plants, notably dwarf evergreen shrubs and evergreen rosette herbs, also store a considerable amount of lipids in their leaves (Billings and Mark, 1961; Hadley and Bliss, 1964). For example, the alpine *Celmisia viscosa* in New Zealand stores lipids and oils in such quantity in their silvery evergreen leaves that they are easily flammable. This species occurs primarily under the shallower parts of semipermanent snowbanks in the lee of solifluction terraces on the crests of the Old Man Range of Central Otago in the stormy westerlies of the Southern Hemisphere at 45°S (Billings and Mark, 1961).

### 6.4.5 Wind

Wind is a primary factor in the dominance of cushion-plant, evergreen dwarf-shrub, and tussock-graminoid growth forms in fellfields and exposed tundra turfs (Norman, 1894; Vestergren, 1902; Gelting, 1934; Dahl, 1956; Gjærevoll, 1956; Bliss, 1956, 1962, 1969; Billings and Bliss, 1959; Hadley and Bliss, 1964). The tightly packed stems and leaves of these growth forms minimize winter abrasion from wind-transported particles and reduce drought stress during the summer. In contrast, many snowbed and "snow cranny" plants that are protected by snow during winter have erect growth forms and soft leaves and are not drought resistant (Mooney and Billings, 1968).

Perhaps the most thorough winter study of plant physiology during severe winter conditions was that of Katherine Bell, who monitored *Kobresia myosuroides* growth 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 *Kobresia* tussocks. *Kobresia* does not occur in extreme windblown fellfields or in areas of even shallow snow accumulation. Bell was interested in the reasons for this limited distribution. She 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 1 April, well before snowmelt, to 20 October, after the beginning of drift development in snowbeds. Wintergreen *Kobresia* leaves can even elongate during warm periods (warmer than −4°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 obviates 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. Also, low soil water potentials create drought stress. In its preferred habitat, *Kobresia* takes advantage of shallow snow cover (approximately 15 cm) that melts in early spring, permitting 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.

### 6.4.6 Radiation

Two aspects of the shortwave radiation environment are particularly important to plant growth: (1) the penetration of visible light through snow, which affects many plant processes including seed germination, emergence from underground organs, and photosynthesis; and (2) reflection of harmful ultraviolet B (UV-B) radiation from the surface of the snow (Pomeroy and Brun, Chapter 2).

Several investigators have noted the ability of plants to germinate or emerge from organs beneath snow. Kimball, Bennett, and Salisbury (1973) found an inverse relationship between snow depth and the chlorophyll content of spring beauty *Claytonia lanceolata* and baby blue eyes *Nemophila breviflora*, suggesting that plants may be able to photosynthesize beneath deep snowpacks. Curl, Hardy, and Ellermeier (1972) speculate that low levels of red and far-red light beneath shallow snow may be sufficient for germination of algal blooms in snowpack (see Hoham and Duval, Chapter 4). Any physiological activity that occurs beneath the snow could be very important, particularly for plants that grow in very-late-melting snowbanks and ephemerals, such as the snow buttercup *R. adoneus*, which complete their growth and senesce within a few weeks after emergence from the snow.

In early summer, sunlight may penetrate the snowpack and warm the dark ground beneath, causing thawing to begin from below. A kind of greenhouse may develop under the snow, with relatively high temperatures and sufficient light for photosynthesis to achieve a positive balance. In these conditions, the growing season also may start somewhat earlier than might be expected, resulting in the well-known phenomenon of early formation of green shoots, buds, and even flowers beneath shallow snowpacks (Sørenson, 1941; Holway and Ward, 1965; Remmert, 1965; Salisbury, 1985). Richardson and Salisbury (1977) found that camas *Camassia quamash* exposed to the light penetrating 173 cm for 2 months began turning green and had begun to unroll, but camas plants kept in darkness were white and noticeably etiolated. Several subalpine and alpine herbaceous species either remain green all winter or turn green before meltout, including *A. rossii*, *R. adoneus*, and *E. grandiflorum* (Salisbury, 1985). Kimball et al. (1973) documented the synthesis of chlorophyll under snow. These observations are from a relatively warm subalpine environment at 2,300 m in the Bear River Mountains, Utah, and may not apply to the colder conditions in alpine and arctic regions. For example, Tieszen (1974, 1978), working in a much colder wet arctic tundra at 71°N latitude near Barrow, Alaska, before snowmelt in early and mid-June, measured net photosynthesis and carboxylation activity under snow cover in three species of tundra graminoids: *Eriophorum angustifolium*, *Carex aquatilis*, and *Dupontia fisheri*. Subnivean temperatures at the site remained near −7°C until meltwater percolated through the snow just before snow melting began. Only after the snow melted did plant temperatures rise above 0°C. Before the snow melted, the extinction of light through the snow resulted in $<33$ W m$^{-2}$ reaching the plants even at solar noon on clear days. This, in combination with the low temperatures, did not allow much net photosynthesis in the plants. Additionally, during this subnivean period, the plant leaves were not photosynthetically competent and, therefore, were poorly capable of using the light that did penetrate to the plant surface. One reason for the lack of plant competency is the lack of a full complement of carboxylase activity in the leaves. Tieszen concluded that most plants in the wet coastal tundra do not photosynthesize appreciably until after snowmelt. However, temperatures beneath deeper alpine and arctic snowbeds are considerably warmer than in the open tundra, and conditions similar to those described by Salisbury may be present locally. Also, other light or dark reactions in plants under snow, including those related to growth hormones such as indoleacetic acid, photoperiodic effects, and the damage caused by UV-B irradiation, may still be operative on the chlorotic emerging shoots (Richardson and Salisbury, 1977).

At high altitudes, plant shoots emerging from under melting snowbanks are exposed to very high reflected UV-B radiation from surrounding areas of snow plus high downward UV-B flux from the sky and the sun. The effective UV dose could be doubled under these conditions (Caldwell, 1981). Another concern for high-altitude plants is the cumulative effects of long-term increases in UV-B due to alteration of the ozone layer in the atmosphere. Caldwell et al. (1980, 1982) measured solar UV-B radiation in tundra and alpine ecosystems from Atkasook, Alaska (71°N), through the Cordillera of the Rocky Mountains, to the Peruvian Andes at 14°S. Although maximum daily total shortwave irradiance along this great latitudinal gradient varies by a factor of only 1.6, maximum integrated effective UV-B irradiance varies by a full order of magnitude because of elevation. If reflectance of these wavelengths is increased near snowbanks, the dose received by plants growing near the snow can be very great, especially in high middle-latitude and tropical mountains.

Caldwell (1968) found that extract absorbance values for *R. adoneus* both at 3,000 Å (UV-B) and 3,600 Å (UV-A) increased rapidly after being released from snow, whereas epidermal UV transmission decreased from approximately 13 percent under the snow to after the loss of the snow cover. This was accompanied by a sudden reddening of the stem tissue due to anthocyanin formation that effectively screened out UV-B irradiance. After a few days in the open sunlight, the stems turned green. The same phenomenon has been noted in the stems and leaves of *Polygonum davisiae* at the edge of snowbanks in the alpine zone of the Sierra Nevada, California, *B. bistortoides* on Niwot Ridge, and *A. rossii* in Colorado (Spomer, 1962). Caldwell (1968) found that *O. digyna* on Niwot Ridge, at an elevation of 3,700 m and 40°N latitude, screens out epidermally almost twice as much UV-B radiation as plants of the same species from Pitmegea River and Cape Thompson at 68°N in the Alaskan Arctic when grown together in growth chambers with normal visible irradiance plus UV-B. Within *Oxyria* there are, apparently, complex ecotypes in relation to light that involve at least UV-B inhibition of photosynthesis (30 percent) compared with that in arctic ecotypes (70 percent) (Caldwell et al., 1982).

### 6.4.7 Temperature

A surprising amount of biological activity occurs beneath deep snowpacks, and much of this can be attributed primarily to the relatively warm soil conditions (Salisbury, 1985; Pomeroy and Brun, Chapter 2). Winter soil temperature is intimately tied through various pathways to snow cover and hydrological conditions on the site and at sites upslope (see Figure 6.6). The effects of snow cover on rhizosphere and foliosphere temperatures are illustrated for five vegetation types along the alpine snow gradient on Niwot Ridge described earlier, where snow depth varied from less than 10 cm to about 150 cm and the growing season varied from 50 to 110 days (Figures 6.7a and b) (May et al., 1982). Mean monthly temperatures were monitored at 5 cm above the surface and 5 cm below the surface for 1 year (Figures 6.7c and d). During winter, the temperature contrast between the fellfields and snowbeds was the greatest. In December, the mean temperature of the fellfield foliosphere was −15.5°C, whereas the foliosphere of the snowbed community was a relatively warm −1°C. The mean monthly temperature of the snowbed foliosphere did not drop below −3.5° during the winter, but it also did not warm above the freezing point until mid-June, a full 6 weeks later than the fellfield, and remained cooler than the fellfield throughout the summer until September when senescence had begun in all the communities.

Foliosphere temperature of the dry and moist meadow communities was intermediate during both the winter and early summer (June–August) periods. Only during the late-summer-to-fall period (August–October) was the temperature comparable in all the communities. Temperatures in the rhizosphere were a few degrees warmer than the air temperature during the winter and few degrees cooler in the summer for all communities (Figure 6.7d). In winter, the greatest contrast between winter foliosphere and rhizosphere 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 soil moisture of the snowbed sites was relatively low because they are early-melting snowbeds on slopes (Figures 6.7e and f).

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 alpine areas, soil-surface temperatures are less variable during winter than during summer because of stronger wind velocities that produce windpumping and mixing within the snowpack. Differences between the soil-surface temperature and the air temperature at 120 cm are rarely greater than 1°C to 3°C. Frequent storms with strong winds slow diurnal heating at the soil surface and accelerate soil cooling in the afternoon. Their net effect is reduced heating in the foliosphere and a shortened period of relative warmth during the day. At average wind speeds, the highest temperature in early afternoon in the winter is several centimeters below the snow surface. Microdrifts 1–5 cm deep in the lee of plants have little effect on temperature profiles, because they allow maximum temperature gradients of only 1°C to 3°C between the soil surface and the snow surface. During midwinter, crusts of snow and ice sheets a few centimeters above the ground allow only a slight warming of surface soil and trapped air (Bell, 1974). Auerbach and Halfpenny (1991) examined midwinter soil-surface temperatures on north, south, and valley bottom sites for the period 1981–1988 at the Teton Science School, Grand Teton National Park, Wyoming. They found that, despite colder air temperatures on the north-facing slopes (mean of −13.8°C versus −8.9°C on south-facing slopes), soil temperatures were warmer on the northern slopes (−1.7°C versus −2.4°C on south-facing slopes) because of deeper winter snowpack and higher thermal indices of the snowpack, and the differences were most pronounced in years of deep snow. The same pattern was also noted in the Arctic near Toolik Lake, Alaska, where the prevailing southerly winds out of the Brooks Range deposit deep snowdrifts on north-facing slopes. Arctic subnivean soil temperatures are somewhat colder than those noted at the Niwot alpine site (Figure 6.8). Minimum temperatures beneath a 400-cm-deep drift at −2 cm in the soil remained at about −7°C through most of the

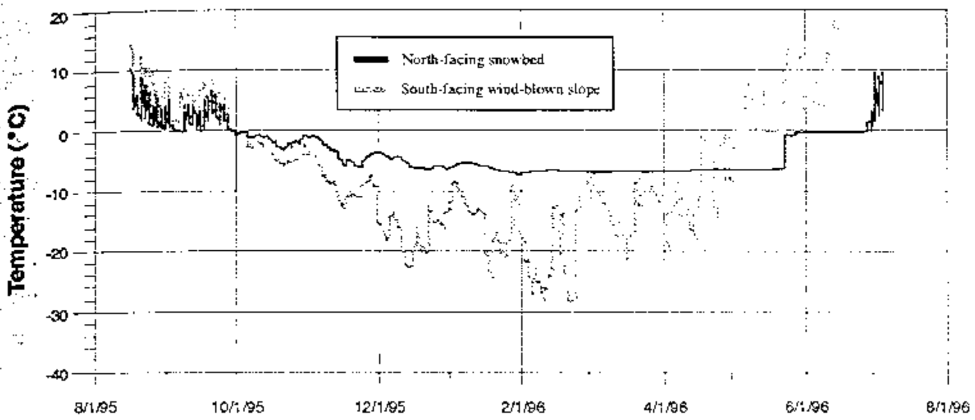


**Figure 6.8.** Soil temperature at 2-cm depth at two sites at Toolik Lake Alaska, August 1995–July 1996. (a) A windblown south-facing slope with minimal snow cover throughout the winter. Vegetation at this site is a dry *Dryas octopetela–Selaginella sibirica* community. (b) A deep north-facing snowdrift with over 500 cm of maximum snow accumulation. Vegetation at this site is a moist *Cassiope tetragona–Carex microchaeta* community.

winter, whereas soil temperatures dipped to about −30°C in a nearby windblown site.

In spring, wind speeds are much reduced, and the snow cover becomes the primary determinant of temperature profiles. Snow-free areas warm rapidly on sunny days. Bell (1974) found that fellfields and *Kobresia* meadows were 12°C to 15°C warmer than the air above on clear and overcast days. However, when snow falls in spring, the snow prevents any surface heating as long as it is present. Also, if the areas are inundated with water after the snow melts, the temperature around the plants remains 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 during May after the melt begins than during the time in April when only a small part of the tundra is snow free. In arctic Alaska, Liston (1986) found bare tundra patches averaging 15°C to 24°C just before the general snowmelt and an extreme temperature of 42°C.

Snowdrifts also affect the summer air temperatures of sites marginal to the drifts. 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. Billings and Bliss (1959) noted an average of 1.5°C cooling from the top to the bottom of a 100-m-long snowdrift 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 snowdrifts, and rhizosphere temperatures can be considerably colder than the foliosphere temperature in areas marginal to snowbeds (Holway and Ward, 1965). This can cause delayed phenology and reduced water and nutrient absorption at a time when photosynthetic activity is at a maximum. This can be important for phenological development. For example, Holway and Ward (1965) noted that alpine avens *A. rossii*, the most abundant alpine plant in the Colorado Front Range, consistently flowers only after the soil temperature at 3-cm depth exceeds 10°C, regardless of the aboveground temperatures.

Without a knowledge of the history of drift development during the winter and other influences of the site, it is not possible to predict soil temperatures on the basis of snow depth alone. Much variation in soil temperatures beneath snowpacks is related to the timing of drift development. A typical pattern for large late-lying alpine snowbeds is that the upper end of the snowbed forms early as snowdrifts into the snowbed depression (Dahl, 1956). These sites of early snow accumulation are sheltered from extreme temperatures throughout the winter, and soil temperatures are likely to remain relatively high (close to freezing) throughout the winter. As the drift builds, the lower ends of the snowbeds fill later after the soil temperatures have already been depressed. These sites may have deep snow cover and relatively cold soils.

Some decomposition occurs beneath deep snowpacks because of relatively warm winter soil temperatures (Bleak, 1970; O'Lear and Seastedt, 1994). Decomposition in soils, like many ecosystem processes, generally has a curvilinear response to snow depth (Webber et al., 1976; O'Lear and Seastedt, 1994). Decomposition is greatest in areas of intermediate snowpack and moderate soil moisture. A litterbag experiment on Niwot Ridge found that approximately 35 percent of green *Acomastylis* leaf litter and 70 percent of *Salix* leaf litter decomposed within 24 months in moderately wet snowbed areas, whereas 25 and 50 percent, respectively, decomposed in dry sites (Webber et al., 1976). O'Lear and Seastedt (1994) attribute the higher decomposition rates in the intermediate snow areas to relatively high microbial and invertebrate activities. Wintertime $CO_2$ and $N_2O$ fluxes are evidence of subnivean microbial activity (Kelley, Weaver, and Smith, 1968; Sommerfeld, Mosier, and Musselman, 1993; Brooks et al., 1994, 1995, 1996, 1997; Oechel, Vourliltis, and Hastings, 1997; Fahnstock et al., 1997). On Niwot Ridge, $CO_2$ production occurs with ground surface temperatures as low as −5°C and $N_2O$ production at a surface temperature of −1.5°C. The seasonal flux of $CO_2$ from snow-covered soils was related to both the severity of the freeze and the duration of snow cover. Whereas early-developing snowpacks resulted in warmer minimum soil temperature allowing production to continue for most of the winter, the highest $CO_2$ fluxes were recorded at sites that experienced a hard freeze before a consistent snowpack developed, suggesting that plant-cell freezing and lysis promotes

$CO_2$ flux. In contrast to $CO_2$, a hard freeze early in the winter did not result in greater $N_2O$ loss. $N_2O$ flux was related mainly to the length of time that soils were covered by a consistent snowpack. Brooks et al. (1997) concluded that subnivean microbial activity has the potential to mineralize from less than 1 percent to greater than 25 percent of the carbon fixed by aboveground net primary production, while the overwinter $N_2O$ fluxes range from less than half to an order of magnitude higher than the growing season fluxes (Brooks et al., 1997). Simulations by global terrestrial biogeochemical models consistently underestimate the concentration of atmospheric carbon dioxide at high latitudes during the non-growing season, but consideration of the subnivean soil respiration improves these simulations considerably (McGuire et al., 2000).

### 6.4.8 Soil Moisture and Drought Stress

The local groundwater regime is a function of the site's position with respect to snow and slope gradients (Molenaar, 1987). In little-irrigated sites situated above snowdrifts, the soil dries and warms rapidly. In contrast, other sites with an equally long persisting snow cover, but situated below the snowdrift, are irrigated and exposed to leaching and remain moist and cold for a longer period. In temperate alpine areas, water is released over a prolonged period of time because of cool nighttime temperatures and deep snowdrifts (Caine, 1992; Caine and Thurman, 1990). Abundant well-defined snowbed plant 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 (Figure 6.7, e and f). Soil moisture values are lowest in the fellfield and highest in the wet meadow at the lower margin of the Niwot Ridge snowdrift. The central part of the snowdrift has relatively low gravimetric soil moisture, comparable to that of the fellfield, because of rocky course-grained soils and a tendency to drain rapidly once the snow melts. The summer soil moisture in the fellfield and dry meadow generally declines throughout the summer but responds somewhat to rainfall events, whereas the moist meadow and wet meadow respond more to the supply of meltwater from the snowbed, remaining high in 1973 (Figure 6.7e), which had a relatively late meltout date, and declining during the low snow year of 1974 (Figure 6.7f). The lower margins of snowbanks melt early and are provided with a continuous supply of water as long as the snowbank persists.

A very different hydrological regime occurs in the Arctic, where the accumulated winter precipitation is released relatively quickly during the brief May–June snowmelt season because of continuous daylight and relatively warm nocturnal temperatures (Dingman et al., 1980; Kane et al., 1989, 1992; Everett, Kane, and Hinzman, 1996;

Hinzman et al., 1996). This water pools in low areas and persists on the soil surface throughout the summer because of the presence of permafrost. Snow is thus largely responsible for the wetland vegetation types and watertrack plant communities covering vast areas of the Low Arctic (Walker et al., 1989). Springs are relatively uncommon in the Arctic because of the lack of deep percolation of meltwater due to permafrost.

Soil moisture, in combination with timing of release from snow cover, governs plant water relations and primary production (Oberbauer and Billings, 1981; Beyers, 1983). Oberbauer and Billings (1981) did an intensive summer-long study of drought tolerance and water use in the Medicine Bow Mountains, Wyoming. They measured leaf water potentials and leaf stomatal conductances (predawn to sunset) in an array of species along a 420-m gradient from a windward slope across an alpine ridge at a 3,300-m elevation to a lee slope and wet meadow below a snowbank. The highest leaf water potentials and stomatal conductances occurred in the wet meadow and were lowest on the upper windward slope. Each of the 29 species measured at frequent intervals during the summer had its own individualistic distribution along the transect gradient. Rooting depth had considerable effect on leaf water potentials. For example, the deep-rooted *Trifolium parryi* always maintained steady midday leaf water potentials of approximately −2.00 MPa at each site, whereas its more shallowly rooted neighbors in stressed areas had very low potentials of near −3.5 to −4.0 MPa at midday.

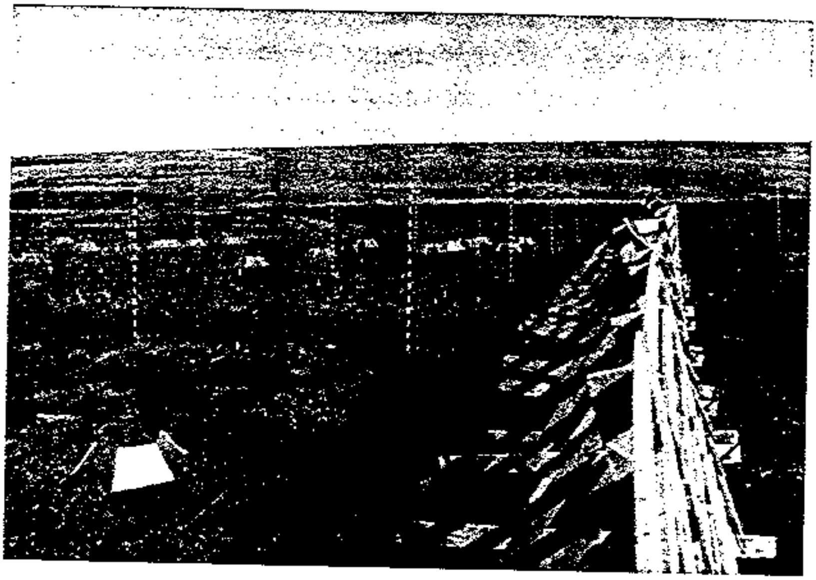
Beyers (1983) did research on leaf water potential and stomatal conductance in relation to photosynthesis of three species of alpine perennial plants, *Polygonum davisiae*, *Lupinus lepidus* var. *lobbii*, and *Eriogonum incanum*, across a mesotopographic snowbank gradient at 2,750 m on Meiss Ridge, northern Sierra Nevada, California. This site has heavy winter snowfall and many snowbanks that persist throughout the dry summers. All three species showed reductions in gross photosynthetic rates during the growing season that were correlated with a decrease in soil moisture at 10- to 15-cm soil depths. Photosynthetic rates of all three species were more independent of measures of plant water status at the moist lower snowbank site than at the site above the snowbank. Photosynthesis decreased most steeply per decrease in leaf water potential in *Polygonum* (a deeply rooted species) and least steeply in *Eriogonum* (a shallowly rooted species), with *Lupinus* intermediate to the others. *Polygonum* maintained higher water potentials throughout most of the season and, therefore, carried on photosynthesis at rates closer to the maximum for more of the growing season than did *Lupinus* or *Eriogonum* (Beyers, 1983).

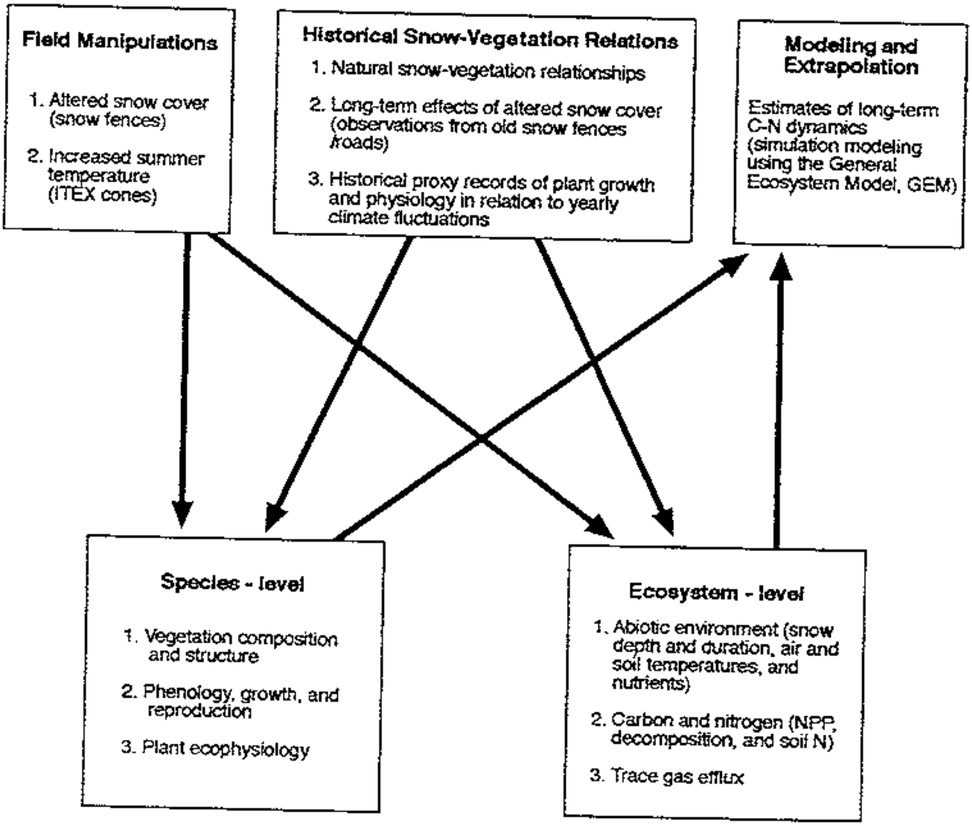
During the winter, snow protects plants from drought stress. Tranquillini (1964) noted that European alpine communities are seldom subjected to drought stress during the summer but that frozen soils and extreme winds often cause drought stress in evergreen species during winter. The effects of winter drought stress have been most thoroughly studied in evergreen trees, shrubs, and krummholz near treeline (Lindsey, 1971; Tranquillini, 1979). On sunny winter days such plants lose a great deal of water by cuticular transpiration in spite of closed stomates; the stress can become more severe as winter progresses as the water cannot be replaced because of frozen soils. The leaves lose so much water that osmotic values can rise to over 40 atmospheres (Tranquillini, 1979). Shrubs covered with snow, however, actually gain water by absorption so that the osmotic values drop during the winter.

Evergreen species vary widely in their winter drought resistance. For example, *Rhododendron ferrugineum*, a European snowbed evergreen shrub, has low drought resistance and loses water rapidly if denuded during midwinter and may be killed. On the other hand, *Loiseleuria procumbens*, a prostrate evergreen shrub found in exposed areas, is very drought resistant. This plant has shallow adventitious roots that allow it take up surface meltwater late in winter when the soils are frozen (Larcher, 1963). 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.

## 6.5 Experimental Studies

If the snowpack is changed either regionally via climate change or locally via alteration of the wind patterns caused by construction of roads or buildings, the vegetation will respond. The effects of past climate changes are perhaps most evident in long-lived rock lichen communities. Large areas of the Canadian Arctic that were snow covered during the Little Ice Age (350–100 years before present) are still noticeably barren of lichens (Andrews, Davis, and Wright, 1976; Locke and Locke, 1977). The relatively lichen-free areas are light-colored on satellite images and contrast strongly with the heavily lichen-covered rocks that were not snow-covered. Locke and Locke (1977) used satellite images of Baffin Island to estimate that perennial snow cover in the vicinity of the Barnes Ice Cap increased about 35 percent during the Little Ice Age. In a boulder transplant experiment in the Colorado alpine, Benedict (1990) noted that rock lichens were killed after 5 to 8 years of increased summer snow cover. The ecosystem response of more complex tundra plant communities to changes in snow regime is currently unpredictable and depends on changes that occur at several different levels of ecosystem organization. Tundra vegetation communities do not




Field Manipulations
1. Altered snow cover (snow fences)
2. Increased summer temperature (ITEX cones)
Historical Snow-Vegetation Relations
1. Natural snow-vegetation relationships
2. Long-term effects of altered snow cover (observations from old snow fences /roads)
3. Historical proxy records of plant growth and physiology in relation to yearly climate fluctuations
Modeling and Extrapolation
Estimates of long-term C-N dynamics (simulation modeling using the General Ecosystem Model, GEM)
Species - level
1. Vegetation composition and structure
2. Phenology, growth, and reproduction
3. Plant ecophysiology
Ecosystem - level
1. Abiotic environment (snow depth and duration, air and soil temperatures, and nutrients)
2. Carbon and nitrogen (NPP, decomposition, and soil N)
3. Trace gas efflux

equilibrate quickly because changes to the below-ground resources and the substrate require long periods to adjust. A series of transient plant communities unlike existing ones are likely to occur (Galen and Stanton, 1995).

The effects of anthropogenically altered snow regimes have been studied next to roads (Willard and Marr, 1970, 1971; Bell, 1974) in experiments with infrared heaters (Harte and Shaw, 1995; Harte et al., 1995), shading with white reflective cloth to delay snowmelt (Galen and Stanton, 1993), removal of the snow to accelerate snowmelt (Galen and Stanton, 1993; Oberbauer, Starrm, and Pop, 1998), and snow fences (Bell, 1974; Weaver, 1974; Knight and Kyte, 1975; Outcalt et al., 1975; Slaughter et al., 1975; Emerick, 1976; Webber et al., 1976; Weaver and Collins, 1977; Bell and Bliss, 1979; Emerick and Webber, 1982; Sturges, 1989; Walker et al., 1993b, 1999). The importance of establishing long-term experiments to examine the effects of altered snow regimes was demonstrated by an early experiment on Niwot Ridge. The experiment used 1.2-m-high snow fences to examine the effects of enhanced snowpack in a dry *Kobresia myosuroides* meadow (Emerick and Webber, 1982). Early-season phenology of the plant canopy was delayed but soon caught up with the other vegetation during the late summer, and there were no other significant changes observed in the vegetation canopy during the 3-year experiment. In the years following the study, most of *Kobresia* died, and there were numerous other changes to the community composition. Other studies have since shown that snow accumulation strongly controls the distribution of *K. myosuroides* (Bell, 1974; Bell and Bliss, 1979). The delayed mortality observed after the Niwot Ridge experiments may have been due to exhaustion of the carbohydrate reserves in *Kobresia*'s wintergreen leaves after the experiment ended. Because of the short term of the experiment, these changes were not documented.

A new snow-fence experiment was started on Niwot Ridge in 1993 and at Toolik Lake, Alaska, in 1994 with the goal of determining the transient and long-term ecosystem responses of arctic and alpine tundras to altered snow regimes (Figure 6.9)

**Figure 6.9.** The Toolik Lake, Alaska, snow alteration experiment. (a) The arctic experiment on a dry site near Toolik Lake, Alaska. Vertical snow poles monitor snow depths. Small plastic cones are used to increase air temperatures above targeted plant species. Wooden fence is designed to lay flat on the ground during the summer to prevent alteration of the summer wind regimes. (b) Major components of the snow-alteration experiment. Experiment contains temperature and snow alterations, studies of natural snow gradients and long-term observations along existing fences and other areas of altered snow regimes, and a modeling component to estimate changes in carbon and nitrogen dynamics. Numerous abiotic variables are being monitored along with a variety of ecophysiological, phenological, plant community, and soil variables.

(Walker et al., 1993b, 1999). The experiment uses tall (2.6 m), long (60 m) fences that can be removed during summer to prevent alteration of the summer wind regimes. Species composition, vegetation structure, soil-carbon stores, geochemical composition of surface waters, decomposition, invertebrate and vertebrate populations, and the spectral reflectance of the vegetation are being monitored along the snow gradient leeward of the snow fence. The experiment is examining the combined effects of altered snow regimes and increased air temperature. Small open-topped chambers are being used to raise the air temperature surrounding targeted plant species (Figure 6.9) (Marion et al., 1997; Henry and Molau, 1997). In the first season, the drift caused a 50 percent reduction in the length of the growing season and, in the deepest part of the drift, raised the soil temperatures at 15-cm depth 15°C during midwinter (Figure 6.10). The mean winter temperature in dry *Kobresia* meadows was raised about 5°C. Late-season soil moisture within the drift area was raised about 33 percent compared with *Kobresia* meadows outside the drift (Figure 6.10b). The difference in soil moisture is thought to be the primary factor causing an increase in leaf lengths in *A. rossii* (Figure 6.10c). The combination of warmer subnivean temperatures and greater soil moisture increased litter decomposition by about 13 percent in the drift area (Figure 6.10d). Fluxes of $N_2O$ and $CO_2$ increased as a result of the warmer winter soil temperatures (Figure 6.10e) (Brooks et al., 1995, 1996, 1997). Early September 1994 NDVI values in the deepest parts of the snowdrift area were about 30 percent greater than outside the fence, indicating delayed senescence in the drift area due primarily to greater soil moisture (Figure 6.10f). The opposite pattern is seen in early summer. Future monitoring at the experimental sites will document the long-term changes in plant community composition and ecosystem processes.

## 6.6 Conclusion

The initial motivation for this chapter was a perceived need for an integrated hierarchical approach to understanding snow–vegetation interactions. Although there is a long history of studies of the adaptations of organisms to cold and snow (e.g., Formozov, 1964; Halfpenny and Ozanne, 1989; Marchand, 1987; Merritt, 1984; Remmert, 1980), there has not been a synthesis regarding the role of snow in influencing alpine and arctic plant communities. This chapter reviews a variety of topics, many of which have not been previously emphasized in winter ecology texts.

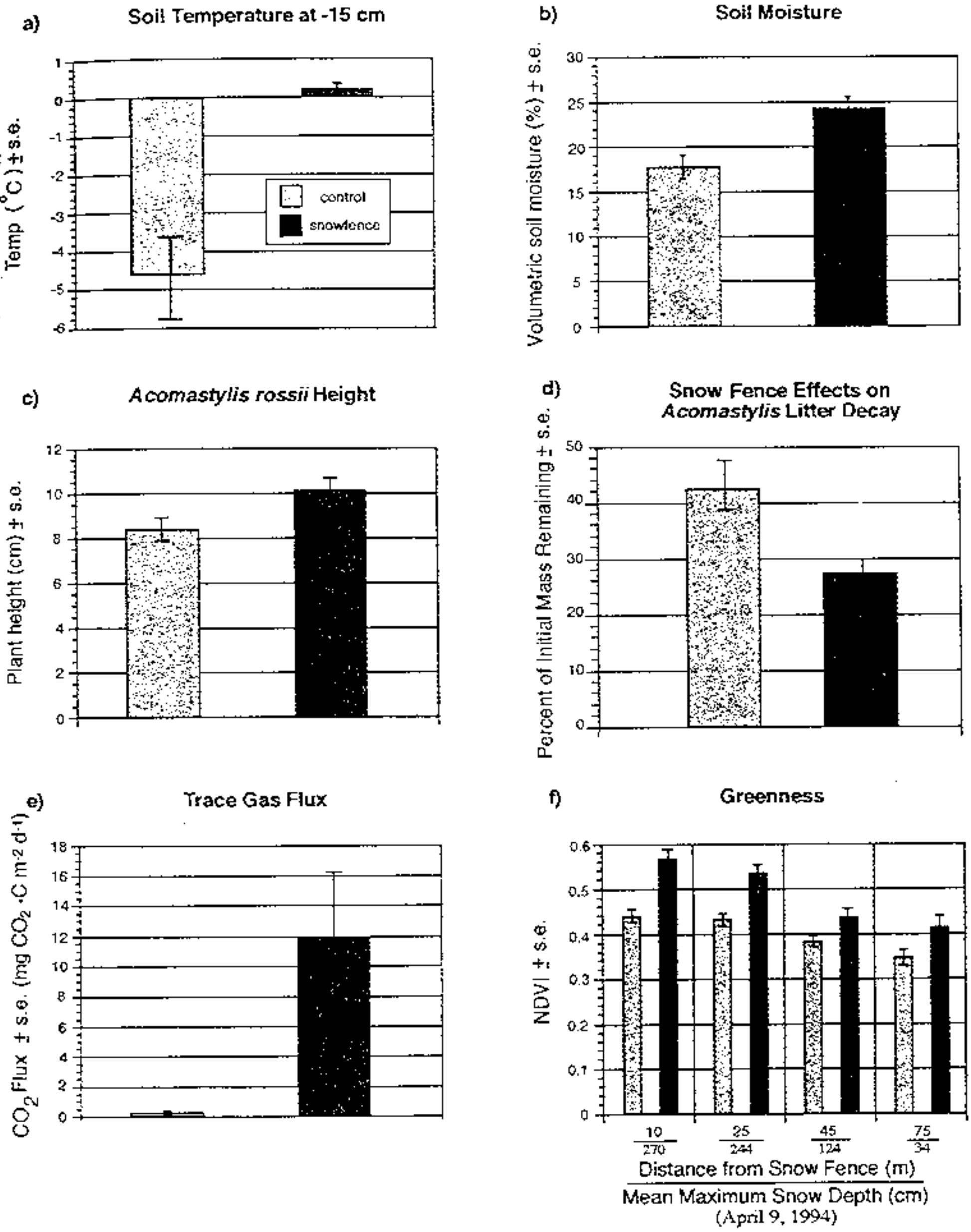


Figure 6.10. Ecosystem effects of the Niwot Ridge snow fence experiment. (a–e) Comparison of effects in a control *Kobresia myosuroides* meadow and in the same community under a 270-cm drift. (a) Soil temperature at −15-cm depth. Temperatures were monitored periodically throughout the winter with buried thermisters. (b) Volumetric soil moisture (August) determined by time-domain reflectometry. (c) Average height of *Acomastylis rossii*. (d) Decomposition of *Acomastylis rossii* leaves after 678 days in the field. (c) Annual $CO_2$ flux (Brooks et al., 1996). (f) NDVI of areas inside and outside the fence at four points along the snowdrift gradient. NDVI was monitored with a handheld spectrometer.

The need for snow–vegetation research in especially important in the face of possible rapid climate change in northern latitudes (Oechel, Callaghan, and Gilmanov et al., 1996; Maxwell, 1997; Groisman and Davies, Chapter 1). The effects of altered snow regimes are of particular concern in the Arctic and Subarctic where changes in winter snow regimes and associated vegetation changes could dramatically change soil surface temperatures and permafrost conditions (Tyrtikov, 1976; Nelson et al., 1993; Zhang et al., 1997), the flux of nutrients, energy, and greenhouse gases from the soil (Oechel and Billings, 1992; Shaver et al., 1992; Fahnestock, Jones, and Brooks et al., 1998; Kolchugina and Vinson, 1993; Oechel et al., 1997; McGuire et al., 2000), and the way in which these systems are utilized by animals and man (Eastland, Boyer, and Fancy, 1989; Pomeroy and Gray, 1995). Some of the key research needs are:

1. **Species-level studies.** More detailed winter autecological studies of key tundra plants are needed to provide a better understanding of how these organisms cope with subnivean conditions and exposed windy conditions during the winter. The biogeography of snowbed plant communities has also not been studied in much detail. Much is still unknown regarding the worldwide floristic characteristics of snowbed vegetation and the relationship to site factors. The role of subnivean herbivores, for example, gophers, in snowbed plant communities is also an understudied topic.
2. **Snow–ecosystem studies.** The feedbacks between snow, vegetation, and climate are complex and occur at multiple scales. A combination of models, observations along natural snow gradients, and experimental studies are needed to help predict aboveground and below-ground plant production and other ecosystem processes resulting from altered snow regimes. In windy environments, small changes in the amount of snow or wind could dramatically change snowdrift locations and sizes. Currently available snow distribution models (e.g., Pomeroy, Marsh, and Gray, 1997) need to be linked to ecosystem models to help develop predictions of change. Simulated changes to landscape paterns could be explored by linking ecosystem models to maps of modern vegetation through the use of geographic information systems, as has been done to examine the effects of altered precipitation in the Great Plains (Burke et al., 1990). At watershed scales, models linking topography, snow, vegetation patterns, and spectral reflectance through hydrological models appear to be quite promising (e.g., Ostendorf et al., 1996). Such models predict vegetation, spectral reflectance, biomass,

and nutrient patterns solely on the basis of runoff volumes derived from digital elevation models. The addition of heterogeneous snow cover to these models will undoubtedly increase their predictive power. Also examination of regional patterns of the normalized difference vegetation index (NDVI) in relation to snow cover could provide insights regarding climate-biomass that would be useful to predict changes caused by altered climate (Walker et al., 1993a). Experimental research using subnivean access chambers (Salisbury, 1985; Williams et al., 1996) and alteration of snow regimes through enhancement (Walker et al., 1999) or removal (Galen and Stanton, 1993) is needed in a wider variety of snowy ecosystems. Larger scale experiments are needed to examine the ecosystem effects of increased snowpack in whole watersheds or larger ecosystems (Steinhoff and Ives, 1976).

3. **Global snow-ecosystem patterns.** As Groisman and Davies (Chapter 1) point out, there is much that needs to be done linking ecosystems with snow climate and ecosystems in GCMs. Thus far, snow-vegetation interactions have not been successfully incorporated into global biogeochemical models (McGuire et al., 2000). There is a large need to examine global vegetation and NDVI patterns in relation to snow regimes and not merely as a function of precipitation and temperature. In the Arctic, snow cover patterns may be largely responsible for some of the zonal vegetation patterns observed on satellite imagery (Walker et al., 1998), and these boundaries could shift with a change in snow regimes.
4. **Paleo-snow-ecosystem studies.** Past northern ecosystems probably had very different snow regimes than the present. For example, relatively dry, less-snowy conditions in northeastern Siberia and Alaska during the late-Pleistocene resulted in colder permafrost, deeper summer thaw, and drier grassier, less-mossy environments with many grazers, such as the steppe bison, horse, saiga antelope, and mammoth (Guthrie, 1990). Knowledge of these patterns would be extremely useful for understanding past paleoecological relationships and for predicting the possible consequences of future snow regime scenarios. Unfortunately, the past effects of changes in snow regimes caused by climate change are not presently apparent from the paleorecord except for the recent past where there is a record in the tree rings of some species (Begin and Boivin, Chapter 7). Knowledge of past snow–ecosystem relationships, possibly through studies of diatoms

and pollen from plants, with known snow-regime preferences could help in predictions of future environments.

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