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Ecology of Alpine Snowbeds and the Impact of Global Change

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Abstract

The ecosystems of alpine snowbed habitats are reviewed with emphasis on ecosystem functioning and capability to adapt to current and predicted global change. Snowbeds form in topographic depressions that accumulate large amounts of snow during the winter months, and the final snowmelt does not occur until late in the growing season. Many species preferentially grow in snowbed habitats and some of these are even restricted to these habitats. In this review we identify several ecosystem services which snowbeds provide to the alpine landscape. For instance, snowbeds provide a steady water and nutrient supply to adjacent plant communities and offer newly emerged high-quality food for herbivores late in the growing season. We also propose that alpine snowbeds are much more productive than earlier thought, especially when the very short growing season and often high grazing pressure are taken fully into account. Furthermore, we propose that bryophytes and graminoids (grasses, sedges, and rushes) probably will be most negatively impacted by global change, and the snowbed plant communities will be invaded by species from adjacent plant communities, especially by shrubs and boreal species. As snowbed plants have special growth conditions, their sensitivity and ability to respond rapidly to changes in annual snowfall patterns make snowbed communities particularly vulnerable in a warmer climate, and thereby sensitive indicators of global change.

Introduction

Global climate change is projected to have large impacts in arctic and alpine areas. Future projections with increased temperature also include increases in precipitation, generally greatest in autumn and winter and smallest in summer (ACIA, 2005). In higher alpine terrain the increased precipitation will lead to a greater snow accumulation and even though winter precipitation increases, temperature increase will probably result in shorter duration of the snow cover (IPCC, 2001; ACIA, 2005). Between 1972 and 2000, the duration of the snow-free period in Northern Hemisphere land areas has increased by five to six days per decade, and earlier snow cover disappearance in spring has been observed by three to five days per decade (Dye, 2002). However, interannual variability of precipitation and snow conditions are high in alpine areas of the world, and projections for the future are more uncertain than for temperature (Watson and Haeberli, 2004 and references therein). Previous forecasts have so far been corroborated for arctic and alpine areas in the Northern Hemisphere as to winter warming, growing season prolongation, glacier retreat, and a balance shift in precipitation from snow to rain. Rain has already become more frequent in winter than before, as observed from the Latnjajaure Field Station in the northern Scandes (personal observation) and elsewhere. In the Arctic, observations from indigenous peoples indicate a similar shift in balance (ACIA, 2005).

Snowbed habitats develop in areas that accumulate high amounts of winter snow, and these habitats make up a pronounced component of the tundra biome, particularly in alpine areas due to the rugged topography and wind redistribution of snow (e.g., Gjærevoll, 1956; Billings and Bliss, 1959; Johnson and Billings, 1962). As there are species and communities restricted to snowbed habitats, these habitats make up a unique component of alpine biodiversity. In connection with forecasts of global warming, snowbed ecosystems are regarded as particularly vulnerable in the *Arctic Climate Impact Assessment* scientific report (ACIA, 2005). Few attempts have been made to study the impacts of simulated climate change on snowbed plant community structure and species' performance (Galen and Stanton, 1995; Sandvik and Heegaard, 2003; Sandvik et al., 2004). In a study from southern Norway, Sandvik et al. (2004) showed that snowbed communities, as opposed to other tundra plant communities, did not respond to any change in plant community structure or species richness after five years of temperature manipulation. In this review we provide an overview of the ecosystems of alpine snowbeds, emphasizing their adaptive capability to adapt to current and predicted global change.

Snowbed Plant Communities

Snowbeds in the subarctic have served as one of the main retreat ecosystems for High Arctic species to avoid competition from subarctic species when these areas were recolonized following deglaciation (Razzhivin, 1997). In the Northeastern Limestone Alps snowbeds are characterized by the predominance of endemic species (Dullinger et al., 2000). Alpine snowdrifts may be ''wind-limited'' in contrast to arctic snowdrifts, which instead are ''precipitation-limited'' (Sturm et al., 2001). Snowbed habitats are covered with substantial depths of snow for much of the year, lasting long into the landscape's thaw period of spring and summer. Consequently, the soil temperature of snowbed habitats is very stable during winter months (Shimono and Kudo, 2003; Björk unpublished) (Fig. 1).

There have been several attempts to divide snowbeds into different categories according to snow cover duration, snow depth, and/or phytosociology (Gjærevoll, 1956; Porsild, 1957; Johnson

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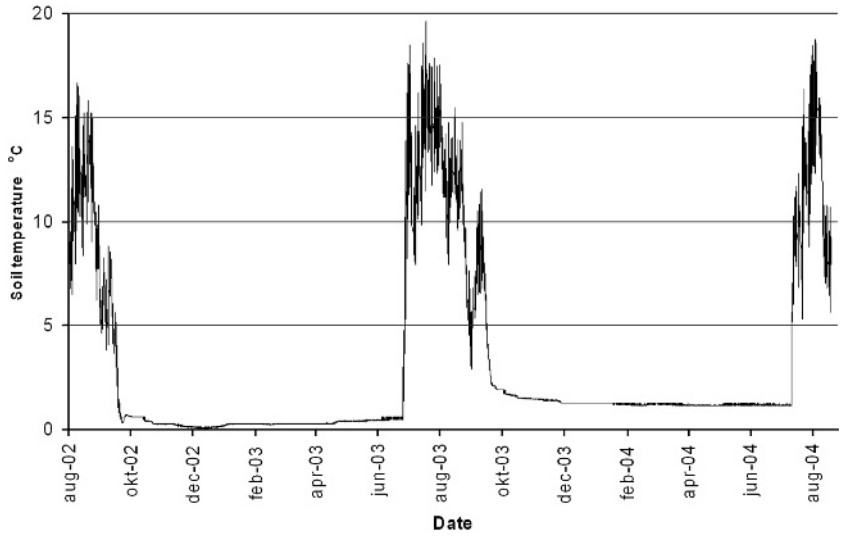


FIGURE 1. Soil temperature, 10 cm, August 2002 to August 2004 in a heath snowbed plant community at Latnjajaure Field Station, northern Sweden (Björk, unpublished).

and Billings, 1962; Ostler et al., 1982; Razzhivin, 1994; Kunitsky et al., 2000). However, the terminology used is often inconsistent, and these attempts have failed to develop any formal classification of snowbed categories (Table 1). In a path analysis, Walker et al. (1994) showed that the snowbed plant community was the only plant community in their study where phytomass was not significantly influenced by soil moisture or precipitation. Instead, phytomass in the snowbed community was strongly affected by date of snowmelt, with earlier dates resulting in higher quantities of standing biomass. However, other studies indicate that soil moisture may play an important role in snowbed communities. In fact, plants growing in snowbeds may be subjected to soil moisture stress once the supply of meltwater ceases (Ostler et al., 1982). Due to a low field capacity of snowbed soil and the high insolation according to the distributional pattern of snowbeds in the landscape, snowbeds exhibit substantial water loss, which can cause drying of the soil in the later part of the growing season (Isard, 1986). As snow-melting dates are expected to be earlier, snowpack duration shorter, and snowpack depths reduced, it is most likely that snowbed communities will increase in productivity.

Compared to other alpine plant communities, snowbed communities support low species richness—up to 18 (although usually 5 to 10) vascular plant species per m^2 (Gjærevoll, 1956; Onipchenko and Semenova, 1995; Björk, unpublished). In snowbed plant communities there are very few cushion plants, as opposed to communities on windy ridges (Billings and Bliss, 1959). Forbs constitute the dominate growth form, but are often lacking in very late melting snowbeds, which are almost completely dominated by bryophytes. The diversity of evergreen and deciduous shrubs gradually decreases with a shorter snow-free period, but a few dwarf shrubs, e.g. *Harrimanella stellariana* and *Salix herbacea*, are capable of growing in the snowbed environment. Graminoids have their largest diversity in moderate melting snowbeds and decrease in abundance toward both ends of a snow-free period gradient (Kudo and Ito, 1992). There are also a few lichens that reach their distribution optimum and are well developed in the snowbed habitats, for instance *Solorina croccea, Cetraria delisei*, and *Stereocaulon alpinum* (Gilbert et al., 1992).

Snowbed plant communities are regarded as having low productivity, with an aboveground live phytomass ranging from 21 to 129 g dry wt m^{-2} (Billings and Bliss, 1959; Scott and Billings, 1964; Ostler et al., 1982; Walker et al., 1994; Onipchenko et al., 1998) and nearly 10 times higher belowground phytomass in mid-July melt-out sites (moderate snowbeds) (Onipchenko et al., 1998). At the outermost part of the snowbed, the average net

TABLE 1

Terminology and categories used in different papers.

Author	Terminology	Melt-out date
Gjærevoll (1956)	Late snow-free alliance	End of June
	Very late snow-free alliance	Mid-July
	Extremely late snow-free alliance	End of July or not at all
Johnson and Billings (1962)	Snow patch	Before July
	Early snowbed	Mid-July
	Late snowbed	Late July to August
Ostler et al. (1982)	Light snowpack zone	13th of June
	Moderate snowpack zone	17th of June
	Heavy snowpack zone	25th of June
Razzhivin (1994)	Moderately snow-rich habitats	End of June to the first half of July
	Very snow-rich habitats	Mid-July or later
Kunitsky et al. (2000)	Kar type	
	Terrace type	
	Ravine type	
	Cliff type	

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TABLE 2

Groups of snow-bound species (chionophytes) indicating snow conditions. Modified from Table 2 in Razzhivin (1994).

Species group	Definition
Euchionophytes	Species that occur only in very snow-rich/late snow-free habitats.
Obligate chionophytes	Species that occur in all kind of snow-rich to moderately snow-rich habitats.
Weak chionophytes	Species that are typical of moderate snowbeds and are relatively rare both in very snow-rich habitats and transitional zones to mesic habitats.
Facultative chionophytes	Species that do not occur in moderate snowbeds, but are especially common and abundant in moderately snow-rich habitat.

productivity differs upslope (0.6 g m^{-2} and d^{-1}) and downslope (2.3 g m^{-2} and d^{-1}) of melting snowpack; the higher average net productivity downslope is likely related to the availability of a supplementary source of water from melting snow (Billings and Bliss, 1959). Similarly, upslope and downslope areas also differ in plant community composition (Johnson and Billings, 1962). In contrast to many other alpine plant communities, aboveground phytomass varies annually in snowbed communities; forbs, in particular, respond to interannual variation (Walker et al., 1994). Snowbed plants, such as *Sibbaldia procumbens* and *Gnaphalium supinum*, seem to produce a relatively large seed bank (Onipchenko et al., 1998).

The Environment and Species Adaptations

Snowbed plants (i.e. chionophytes), can be further divided into groups according to the snow conditions they prefer (Table 2) (Razzhivin, 1994). Typically, snowbed species are capable of surviving in a restricted growing period (Gjærevoll, 1956). Many species show an affinity to snowbed environments, and some of these (e.g. *Ranunculus adoneus, Primula parryi, Sibbaldia procumbens*, and *Oxyria digyna*) are restricted to snowbed habitats (Holway and Ward, 1963; Ostler et al., 1982; Stanton et al., 1994). Species that thrive in snowbed environments may be unable to tolerate environmental conditions that prevail in other habitats. For example, snowbed endemics may be intolerant of the extreme low temperatures and damaging wind abrasion that characterize snow-free habitats during the winter months (Johnson and Billings, 1962; Stanton et al., 1994), and many typical snowbed species avoid very acidic and basic habitats. Dwarf shrub and tussock communities, especially, are characterized by more acid conditions (Razzhivin, 1994). However, the environmental conditions of snowbed habitats may not actually be optimal for so-called "snowbed plants." These plants are capable of surviving in earlier snow-free habitats at higher altitudes and may nonetheless be restricted to snowbed habitats at lower altitudes because they afford reduced competition from co-occurring plants (Holway and Ward, 1963; Ostler et al., 1982; Razzhivin, 1994; Stanton et al., 1994; Heegaard, 2002; Heegaard and Vandvik, 2004).

Snowbed plants may require late-season soil moisture derived from melting snowpack (Billings and Bliss, 1959; Holway and Ward, 1963; Isard, 1986; Barbour et al., 1991) and must therefore also be able to complete a vegetative life cycle quickly. However, some plants are unable to complete a vegetative cycle in one year and must develop over multiple growing seasons (Billings and Bliss, 1959; Bell and Bliss, 1980). Snowbed plants also have the adaptive advantage of being physiologically active during snowmelt. These plants may emerge through the last remaining 5 cm of snow and start flowering within a few days of emergence (Mullen and Schmidt, 1993, Galen and Stanton, 1995). Also, some snowbed plants, such as the herb *Ranunculus adoneus* and the bryophyte *Kiaeria starkei*, have the ability to exploit the early flush of nitrogen prior to and during snowmelt (Woolgrove and Woodin, 1996a; Mullen et al., 1998).

Snowbed species are somewhat more tolerant to shade than other alpine species. However, their ability to flower decreases significantly in more shaded conditions as a result of accompanying carbon deficiency caused by the shading. Snowbed plants, like all alpine plants, are more sensitive to shading during the first part of the growing season than the second (Onipchenko et al., 2001). Moreover, snowbed plants seem to have a particularly high resistance to low-temperature photo-inhibition, thus making them able to maintain carbon gain on days following frost and high sunlight exposure (Germino and Smith, 2000). In the Scandes, snowbed species often tolerate frequent severe grazing by lemmings and the accompanying physical disturbance. The important plant groups, acrocarpic bryophytes and graminoids, may induce new growth from subterranean tissue to survive these disturbances (Moen et al., 1993; Virtanen et al., 1997).

A number of factors exclude many plants from snowbed habitats. Some species may have problems maintaining positive carbon balance (Bliss, 1971; Tieszen, 1975; Bell and Bliss, 1979), whereas others are excluded by sensitivity to infection by fungal pathogens, or prolonged soil water saturation (Sturges, 1989). The sparse vegetation cover and infertile soils that prevail in snowbeds can also result in conditions that reduce seedling emergence, growth, and survival (Callaghan, 1974; Chambers et al., 1990). Furthermore, long-lasting snow cover may affect saplings negatively by imposing mechanical stress (Barbour et al., 1991). A much shortened growing season in areas of snow accumulation may preclude temporal resource partitioning among species and increase the likelihood of competitive exclusion (Dawson, 1990). In a study by Kudo et al. (1999), boreal species were climatically restricted from alpine snowbeds due to problems maintaining growth and productivity in these environments. Even if boreal species respond positively to increasing growing season length, they are still more or less under large environmental stress at outpost alpine sites.

PHENOLOGY, SEED GERMINATION, AND SEEDLING ESTABLISHMENT

The timing of snow-melt and/or the beginning of autumn snow accumulation are clearly key factors in the timing of flowering and dormancy of alpine plants (Holway and Ward, 1963, 1965; Bliss, 1971). Plants released from the snow at later dates appear to require a slightly shorter time for flowering after emergence (Billings and Bliss, 1959; Holway and Ward, 1965), whereas some species also reach more advanced conditions of development at the time of release from snow (Holway and Ward, 1963). According to Kudo (1991), the phenology of alpine plants in snowbed habitats appears to be controlled primarily by growth-form. Shrub species abandon flowering and consequently seed production, whereas forbs or graminoids have flowers in any

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habitat. Other influential factors include the span of prefloration period and the period for the maturation of seeds (Kudo, 1991). In an irrigation experiment by Holway and Ward (1963), plant development was delayed substantially in plots receiving additional inputs of surface meltwater, resulting in increased soil moisture and decreased soil temperature, which reduced net photosynthesis (Bell and Bliss, 1980). Flowering was delayed about a week or more, and some plants were even showing inhibition of fruit and seed production and dispersal. In snowbed habitats, forbs and graminoids seem to be more adapted to sexual reproduction than shrubs, but even without seed production, most shrub species can reproduce vegetatively by layering and by producing adventitious roots (Kudo, 1991). For many of the snowbed species, the fluctuation in snow cover between years does not greatly influence flowering conditions, although some species that form the floral primordia in the preceding years are affected by the previous growing season's climatic conditions (Holway and Ward, 1965; Bliss, 1971; Bell and Bliss, 1980; Kudo, 1991).

Snowbed species, for instance *Oxyria digyna, Phippsia algida*, and *Saxifraga cernua*, seem to possess seed dormancy, and their seeds germinate at lower temperatures (i.e. below 5°C) than found in other species (Bell and Bliss, 1980). For *Potentilla matsumurae*, a species covering many alpine habitats in Japan, the snowbed ecotype did not germinate until the soil surface temperature had reached 13–15°C, even when snowmelt occurred unusually early (Shimono and Kudo, 2003). The most critical time for seedling establishment in the snowbed plant community is during seedling emergence, but as the snowpack increases, the seedling survival and the survival of juveniles and adults become more important (Welling, 2002). As the snowbed habitat is usually free from snow late in the season, fluctuations in air temperature may not be important for seed germination. The short growing season has no controlling effect on seedling survival, and late emerging seedlings are able to overwinter successfully in the snowbeds (Shimono and Kudo, 2003).

PLANT GROWTH ON RELEASE FROM SNOW COVER

Many alpine plants begin growth at air and soil temperatures near 0°C. The species comprising the snowbed vegetation are well adapted to this low temperature regime (Billings and Bliss, 1959), and the snowbed specialists have the potential to start subnivean growth (Hamerlynck and Smith, 1994). The light that reaches through the snowpack (Fig. 2), as the snowpack starts to melt, is enough to start subnivean photosynthesis at low levels (Starr and Oberbauer, 2003), and probably serves to activate the photosynthetic apparatus (Starr and Oberbauer, 2003 and references therein). This activation enables the plants to reach their maximum photosynthetic capacity rapidly once they emerge through the snow or melt has occurred (Starr and Oberbauer, 2003 and references therein). The ability for subnivean growth and a rapid growth response after snowmelt are also probably due to the presence of carbohydrates that are stored in the rhizomes and roots from the previous year. Carbohydrates may be translocated to shoot growth, facilitating early emergence through the snow and a rapid leaf expansion (Billings and Bliss, 1959; Mooney and Billings, 1960; Tieszen, 1975) to attain rapid photosynthetic development (Hamerlynck and Smith, 1994). Snowbed species that emerge through the snow, often in July, are subject to favorable environmental conditions as the soil and air have warmed up and are about to reach the yearly maximum temperature. At the same time, meltwater provides some protection against early drought (Mooney and Billings, 1960;

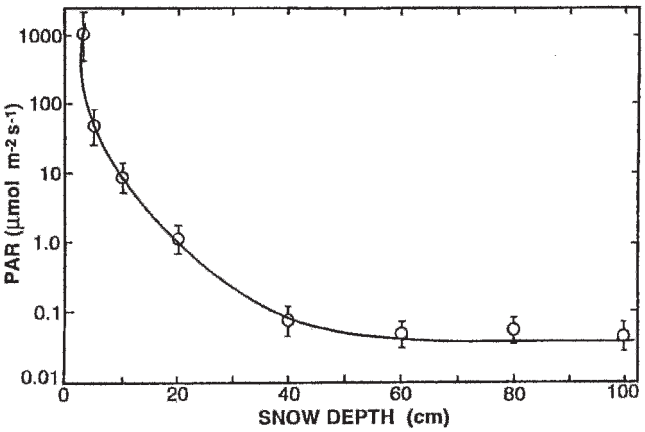


FIGURE 2. Photosynthetic photon flux density (PFD) beneath a given snow depth measured at three different sites on 12–14 June 1991. Each point represents the mean of three measurements at each of the three sites, along with indicated standard deviations. From Hamerlynck and Smith (1994). Reproduced with permission of *Arctic, Antarctic, and Alpine Research*.

Shimono and Kudo, 2003), and the daylight period is long (Onipchenko et al., 2001), accompanied by maximum CO_2 fixation (Tieszen, 1975). There is also a supply of nutrients from melting snow (Bowman, 1992; Woolgrove and Woodin, 1996b) and continued soil organic matter mineralization beneath the snowpack through the winter (Chapin et al., 1993; Brooks et al., 1996, 1997), which are released with the melting snowpack. Plants capable of subnivean growth have the advantages of an increased time for growth and earlier flowering time, which may reduce interspecific competition, and a quicker response to interannual or short-term changes in growing season length. On the other hand, in years with a prolonged snow cover, snowbed plants may have a higher respiratory cost to maintain the metabolic activity of the shoot primordia that may lead to reduced growth and even local extinction (Galen and Stanton, 1995).

Snowbed plants reach maximum daily productivity very soon after release from snow cover (within one to three weeks), which then tapers off erratically until the end of the growing season (Billings and Bliss, 1959). They also show a decreased growth rate with the duration of snow cover (Wijk, 1986a; Hamerlynck and Smith, 1994; Stanton et al., 1994). In years with longer growing seasons, woody snowbed plants (e.g. *Salix herbacea*) seem to use the excess energy to invest in new branch production (Wijk, 1986b).

Impact of Snow Cover on Plant Composition

The pattern of melting in the landscape usually remains consistent between years, but there may be considerable variation between the dates of snowmelt (Billings and Bliss, 1959; Johnson and Billings, 1962; Ostler et al., 1982; Wijk, 1986a; Stanton et al., 1994; Shimono and Kudo, 2003). The release from snow can vary by as much as five weeks between years with early snowmelt and years of late snowfall or low summer melt rate (Johnson and Billings, 1962). The date of snowmelt is the most important factor explaining differences in species distribution across the snowbed and also affecting soil depth (Ostler et al., 1982), soil organic matter content, and rock cover (Ostler et al., 1982; Stanton et al., 1994). Early melting sites have a thicker soil layer (Ostler et al., 1982) and greater content of organic matter (Ostler et al., 1982; Stanton et al., 1994), moisture, nitrogen, and phosphorus, but they

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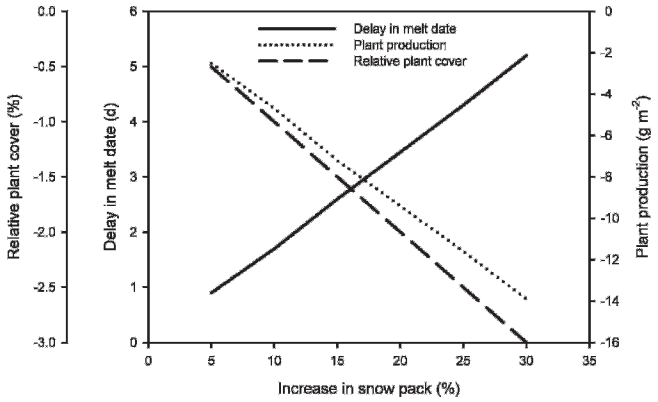


FIGURE 3. Predicted long-term impact of different relative increases in snowpack on plant growth in a subalpine snowdrift. Delay in melt date (d) (solid line), relative plant cover (%) (dashed line), and plant production (g m^{-2}) (dotted line). Plotted from Table 4 in Ostler et al. (1982).

also are subjected to increased acidity (Stanton et al., 1994). The seedling establishment for *Ranunculus adoneus*, which is most abundant in moderate snowbeds, is higher in the earlier melting sites, whereas a decreased snow cover has a large impact on the seedling establishment in the later sites (Galen and Stanton, 1999).

Woolgrove and Woodin (1996b) have shown a positive relationship between tissue nitrogen content and the duration of snowpack in the bryophyte *Kiaeria starkei*, a snowbed specialist. This demonstrates the fertilizing effect of the snowpack on the underlying plant community. Evergreen plants also show increased nitrogen content in the leaves coupled to the timing of snowmelt, as well as an increase in leaf thickness, whereas the sedge *Carex bigelowii* and the deciduous shrub *Salix herbacea* showed a decrease in leaf thickness (Kudo et al., 1999). This may reflect an adaptation of the leaves of evergreen plants to later melting sites by increasing their photosynthetic ability through increased nitrogen content and thickness, implying longer life spans of individual leaves (Kudo et al., 1999 and references therein), while the true snowbed plants may be even more energy efficient by not increasing their leaf thickness.

Plant species richness as well as productivity and cover decrease in sites that emerge very late from the snow. This is probably because only a subset of species can tolerate conditions deep within the snowbed or, alternatively, to become in control of interactions among plant species in late melting sites (Billings and Bliss, 1959; Stanton et al., 1994). Therefore, the effect of increasing snowpack, which also results in a prolonged snow cover (Fig. 3), is more pronounced in earlier melting snowbeds or parts of snowbeds (Ostler et al., 1982) than in later snowbeds, since very few plants are able to grow in these conditions.

The Soil and Nutrient Input

The controlling factor for microbial activity in the organic layer during winter in alpine areas is the development of a consistent snow cover, which effectively decouples the soil from the atmospheric temperature. The air and soil temperature during the days before snow cover development is important, as it sets the temperature conditions for the whole winter period (Björk, unpublished) (Fig. 4). Soil microbial activity is markedly reduced below temperatures of 0 to −5°C, when the soil starts to freeze and free water becomes limited (Brooks et al., 1997). Nitrogen mineralization, nitrification, and denitrification can, however, be maintained down to −4°C, and N_2O production (from denitrification) in frozen soils has potential to affect annual dynamics and budgets of N (although the soil pore water content prior to freezing is an important regulating factor for winter N_2O production) (Öquist et al., 2004). As the soil warms and the snowpack starts to melt, the microbial activity increases, and this is associated with increasing CO_2 and N_2O fluxes (Brooks et al., 1997). At this stage net N mineralization (Brooks et al., 1996) and readily decomposable organic matter (Schinner, 1983) become important controllers, as do other factors like substrate availability (Brooks et al., 1997, Bölter et al., 2003). Snowbed communities are rarely, if ever, subjected to temperatures as low as −5°C (Fig. 1), which implies that they may be favorable for microbial activity during the winter (Brooks et al., 2004; Bölter, 2004; Schimel et al., 2004). As the freeze/thaw cycles may be largely absent in these ecosystems (at least, once a consistent snow cover is present), winter microbial activity could experience substrate limitation, probably caused by insufficient labile carbon availability (Brooks et al., 1997, 2004), as opposed to summer microbial activities that are usually limited by nitrogen in tundra ecosystems (Schimel et al., 2004). Snowbed plant communities are rarely, if at all, nitrogen limited, due to a high ratio of net mineralization to plant biomass nitrogen (Makarov et al., 2003). In a snow fence experiment, Schimel et al. (2004) observed that after several years

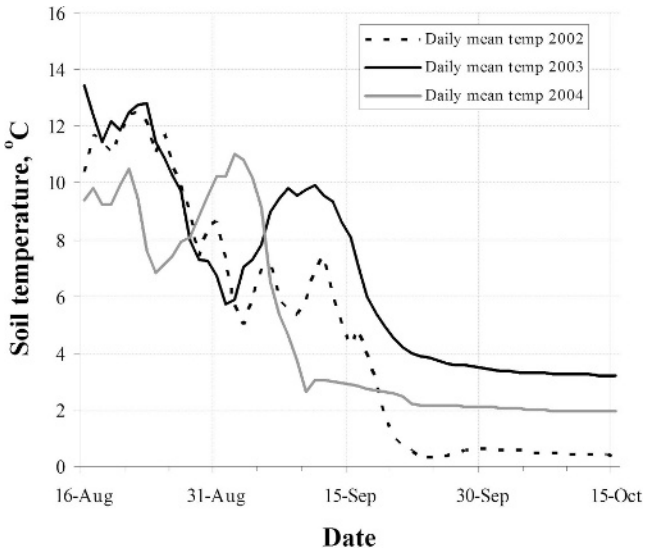


FIGURE 4. Daily mean soil temperature at 10 cm depth from mid-August to mid-October (2002–2004) in a heath snowbed plant community at Latnjajaure Field Station, northern Sweden, illustrating the importance of September soil temperature for winter soil conditions. Consistent snow cover from approximately the 20th of September in 2002 and 2003. In 2004 the snow cover development was different with earlier snowfall that melted after nearly a week, and the new snow cover was developed approximately the 1st of October, but it did not affect the winter soil temperature much (Björk, unpublished).

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of amplified snow cover, the resulting increase in microbial activity shifts the organic matter dynamics, leading to increased net mineralization throughout the growing season. After snowmelt, in snowbed plant communities, the microbial activity drops and reaches the lowest growing season activity within a month (mid-August). This drop in microbial activity begins later in snowbed plant communities than in earlier melting plant communities, but even the latter reach their lowest activities in mid-August (Schinner, 1983). This drop in microbial activity could be due to competition with vascular plants for the available nitrogen, but is not solely induced by plant competition as almost no new roots of *Ranunculus adoneus* were observed by Mullen et al. (1998) during early season nitrogen uptake, the time when the plant accumulated the most nitrogen, and the development of new roots did not reach the peak until mid-July.

Snow is an efficient scavenger of atmospheric pollutants (Woolgrove and Woodin, 1996b, 1996c and references therein). The inorganic nitrogen input from the melting snowpack in Niwot Ridge, Colorado, is 400–600 mg N m^{-2} yr^{-1} and can encompass up to 150% of the annual atmospheric nitrogen input in snowbed plant communities, largely due to the redistribution of snow (Bowman, 1992). The concentration of nitrogen within the snowpack varies considerably throughout the year, with a peak in spring, and there is also heterogeneity through the snow column, which results in an increased nitrogen concentration in subsurface layers. The heterogeneity is probably a result of subsequent refreezing at deeper layers of percolated nitrogen-rich snowmelt water. The heterogeneity diminishes in mid-June, indicating a potential input of nitrogen into the soil ecosystem. Horizontal flow of meltwater along ice lenses most likely reduces the nitrogen input to snowbed plant communities, but raises the input to down-slope plant communities (Bowman, 1992).

Snowmelt water polluted with NO_3^- and SO_4^{2-} is damaging, especially to the bryophyte vegetation, and causes reduced chlorophyll a:b ratios, decreased nitrate reductase inducibility, membrane damage, and increased susceptibility to damage resulting from exposure. The damaging effects become more pronounced if the bryophytes are subjected to drought after snowmelt, which is often the case in snowbeds, while subnivean plants are less damaged but face a reduced growing season to gain carbon reserves needed to repair the damage; the recovery rate after snowmelt is therefore slow (Woolgrove and Woodin, 1996c).

Studies of litter decomposition have shown that 48% (by dry weight) of the available litter in snowbeds is decomposed after one year in the Alps and that, in the snowbeds, litter decomposition is slower than adjacent meadows and cushion plant communities (Schinner, 1983). The *in situ* dinitrogen fixation activity, measured as acetylene reduction activity, shows a drop in activity within a month after snowmelt, but the lowest activity is not reached until September when no activity is evident. The annual nitrogen input from dinitrogen fixation in snowbed communities has been estimated to be approximately 2 mg N m^{-2}, and the activity is closely linked with soil moisture, especially during June and July, when the N-fixing organisms can benefit from the melting snowpack. Low soil pH (pH $<$ 5) also influences the fixation activity by limiting both the distribution and the fixing efficiency of the cyanobacteria (Wojciechowski and Heimbrook, 1984). Net N mineralization peaks before snowmelt and the early season N pulse is immobilized by soil microorganisms (Brooks et al., 1996, 1997) as well as by some plants (Mullen et al., 1998). The dominant inorganic form of nitrogen in the soil during this early season pulse is NH_4^+ (Mullen et al., 1998).

Animals Utilizing Snowbeds

Snowbeds constitute a key component in Norwegian lemming (*Lemmus lemmus*) population cycles, which are well known for large-scale interannual population fluctuations and are of great significance for the dynamics of alpine ecosystems, e.g. carnivore populations. The snowbeds promote lemming survival by ensuring good overwintering conditions, and during years of low density the lemmings preferentially graze in snowbeds while in peak years they graze all habitats (Nagy et al., 2003). Lemmings feed mainly on graminoids, especially *Carex bigelowii*, and mosses, e.g. Polytrichaceae, but avoid woody plants (Moen et al., 1993; Virtanen et al., 1997).

The annual movement cycle of large herbivores, e.g. reindeer (*Rangifer tarandus*) and mountain goat (*Oreamnos americanus*), in alpine environments is controlled by the snow cover and driven by enhanced access to high-quality food (Skogland, 1984; Fox, 1991). In winter, as snow cover increases in both density and compactness, the reindeer become restricted to the heath communities in the windswept ridges. Even though snowbeds comprise only 3–14% of the total vegetation cover (Skogland, 1984; Molau, 2004), they are the most consistently selected plant communities by reindeer during the snow-free season (Skogland, 1984; Edenius et al., 2003). When the snowmelt starts in spring, the reindeer follow the altitudinal melt-off gradient by selecting habitats with the highest level of green phytomass at the most favorable growth stage. By having the ability to offer a nutrient-rich diet during periods with poor food supply (Skogland, 1984; Fox, 1991), the accessibility of snowbeds can substantially affect the well-being of reindeer (Skogland, 1984). In late June to mid-August the peaks of the insect season and maximum temperature coincide, and late melting snowbeds function as relief habitats from insect harassment (Gaare et al., 1975; Skogland, 1984; Downes et al., 1986) and high temperatures (Downes et al., 1986; Ion and Kershaw, 1989; Andersen and Nilsen, 1998). The reindeer can thermoregulate either by benefiting from the cooler microclimate provided by the snowbeds or through ingesting the snow (Ion and Kershaw, 1989). A restraining factor for the reindeer summer ranges could therefore be the scarceness of accessible snowbeds (Edenius et al., 2003).

IMPACT OF SOIL DISTURBANCE AND GRAZING ON PLANT COMPOSITION

Other important factors in controlling the plant composition in alpine ecosystems are soil disturbances (and the type of disturbance), as well as their ecological effects, which may differ between early and late melting sites (Stanton et al., 1994). Two basic types of disturbance can be distinguished: (1) severe disturbance, caused by geomorphological events such as landslides and erosion, that remove soil surface horizons; and (2) less severe disturbance, such as those caused by small mammal activity, which leaves soil horizons in place (Thorn, 1982; Chambers et al., 1990).

Mammalian herbivory has profound effects on plant community composition, diversity, and biomass (Moen et al., 1993; Virtanen et al., 1997; Virtanen, 2000; Olofsson et al., 2002) and is essential for the survival of prostrate snowbed herbs, e.g. *Cassiope hypnoides, Gnaphalium supinum*, and *Sibbaldia procumbens* (Oksanen and Moen, 1994; Virtanen et al., 1997). Graminoids and bryophytes, the species preferred by the Norwegian lemming, are suppressed by grazing, and they increase in abundance when the grazing pressure decreases (Virtanen et al., 1997; Virtanen, 2000; Olofsson et al., 2002). In a study by Moen et al. (1993), graminoids

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decreased by nearly 33%, and mosses by 66%, while lemming feces increased, during the winter after a lemming population peak. The litter increased threefold, mainly due to lemmings biting the bases of graminoids and mosses. By leaving surface litter or plant parts in place, herbivory can contribute to trap higher numbers of seeds, thereby speeding up the recovery rate for plant communities subjected to this disturbance (Chambers et al., 1990). In the long term, a decreased grazing intensity is likely to lead to bryophytes being out-competed by graminoids (Virtanen, 2000). Another way to endure the intense grazing pressure to which snowbed plants can be subjected is to have subterranean rhizomes, which can evade any grazing damage and then start to regrow when the grazing intensity declines (Virtanen et al., 1997). In the Scandes, mammalian herbivory is also responsible for the reduction in biotic competition within snowbed plant communities (Olofsson et al., 2002).

Conclusions

Snowbeds are a crucial component of the alpine biome as these habitats provide important ecosystem services to the landscape (Molau, 2004), such as maintaining and increasing the productivity of adjacent earlier-thawing ecosystems, by providing a steady water and nutrient supply (Billings and Bliss, 1959; Bowman, 1992). Furthermore, as the forage quality and availability decrease over the summer in the landscape (Fox, 1991), snowbeds can support large herbivores by offering newly emerged high-quality food late in the growing season (Skogland, 1984; Fox, 1991). In addition, snowbeds promote lemming survival during years of low density and ensure good overwintering conditions (Nagy et al., 2003).

Snowbed plant communities are often regarded as of low productivity (Billings and Bliss, 1959; Scott and Billings, 1964; Ostler et al., 1982; Walker et al., 1994; Onipchenko et al., 1998; Olofsson et al., 2002), but this refers to annual total production. As they are more limited by the length of the growing season than resource availability (Seastedt and Vaccaro, 2001), they may be as highly productive as the surrounding plant communities during the short growing season in which they are active. It would be more accurate to compare primary production over shorter time units than accumulated standing biomass per year, especially in alpine plant communities where there is such a great difference in growing season length and grazing intensity. Other evidence for the higher productivity of the snowbeds is that they are capable of supporting a large part of the alpine mammalian herbivore population, which are down regulating the standing biomass, and still the snowbed plants are able to flourish and recover within a few years after intense grazing seasons (e.g. lemming years). In a study by Olofsson et al. (2002), the biomass increased almost to the extent of a tall herb meadow when herbivores were excluded from the snowbed vegetation. Snowbeds have a more sparse vegetation cover than the surrounding plant communities. This also reduces the competition among plants as they are evolved to endure, or at least cope with, the short growing season. This strategy is rewarded during the winter season with a favorable environment isolated from the extreme low temperatures and damaging wind abrasion that prevails above the snowpack.

Bryophytes represent an important growth form in the snowbed vegetation, yet they are especially threatened due to their ectohydric nature in combination with their unistratos leaves and lack of cuticle, which makes them extremely sensitive to high concentrations of pollutants in snow (Woolgrove and Woodin, 1996a, 1996b, 1996c). During the last century, the tissue nitrogen content of the snowbed bryophyte *Kiaeria starkei* has doubled in the central highlands of Scotland (Woolgrove and Woodin, 1996b). In the future, alpine snowbeds are predicted to receive an increased snowpack in the winter months, but will also melt out earlier due to temperature increases, which may lead to invasion of species from the surrounding plant communities. Boreal species (Kudo et al., 1999) and species with optima in intermediate snow habitats (Heegaard and Vandvik, 2004) will have the opportunity to establish in the snowbed plant communities. In fact, juvenile plants of *Salix phylicifolia*, normally not growing above the treeline, have appeared in nutrient-rich snowbeds in the mid-alpine zone in the northern Scandes during the last five years (Björk and Molau, personal observation). Snowbeds also accumulate wind-dispersed organic and inorganic debris, causing a natural indirect fertilization, and they function as plant diaspore traps (Larsson and Molau, 2001). Therefore, species turnover, establishment of new plant species, and a changed plant species composition (structure/richness) might be rapid in a warmer climate. As shown by transplantation experiments, snowbed plants are incapable of invading other plant communities (e.g., fellfields) while fellfield plants are able to grow in snowbed environments (Shimono and Kudo, 2003). This low invasion potential of snowbed species will lead to an alteration in plant composition (Galen and Stanton, 1995; Heegaard, 2002; Heegaard and Vandvik, 2004), and snowbed species will probably be the ones that suffer due to the effect of competition as their competitive ability is constrained (Heegaard and Vandvik, 2004).

In contrast to the majority of the alpine tundra vegetation, snowbed plants do not seem to be limited by nitrogen availability (Makarov et al., 2003) but rather constrained by the length of growing season and maybe phosphorus availability (Seastedt and Vaccaro, 2001). However, when snowbeds are invaded by non-snowbed plants and community changes are becoming substantial, ongoing changes in environmental factors (e.g., prolonged growing seasons and increasing deposition of plant-available nitrogen) may even accelerate the rate of community change. As a consequence, snowbeds will diminish and have a more scattered distribution in the tundra landscape. Snowbed-specific bryophytes and graminoids will probably decrease in abundance due to lengthened growing season and increased snow pollution by atmospheric N and other nutrients. Deciduous shrubs will increase in diversity and abundance, as they prefer earlier melting sites, and graminoids from other habitats may gain in the longer run because of high N availability. Since these life forms are important food sources for herbivores, such a change will inevitably have a substantial impact on higher trophic levels and the diversity of animal guilds. However, most studies so far have been conducted in areas receiving substantial inputs of airborne pollutant N with snowfall (e.g., Bowman, 1992; Woolgrove and Woodin, 1996a, 1996b, 1996c), and the results must be interpreted with this in mind.

Snowbed plants seem to be adapted to commence growth before and during snowmelt. The special growth conditions under which snowbed plants live and their sensitivity to annual snowfall patterns make snowbed communities particularly vulnerable in a changing climate and thereby sensitive indicators of global change.

Further Research

To date, research in snowbed ecosystems has been rather limited in comparison with other components of the alpine tundra landscape, particularly in recently developing research areas such

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as nutrient cycling and trace gas fluxes. Most studies addressing snow accumulation changes are dealing with snow addition by using snow fences, whereas very few attempts have been made to remove snow, which ought to be the most realistic simulation of a future arctic and alpine climate.

Few studies have addressed the ecology of bryophytes, an important snowbed plant group. As to community structure, we lack inclusive studies with a direct global change perspective, building on the BACI approach (Before-After-Control-Impact; Bernstein and Zalinski, 1983; Stewart-Oaten et al., 1986; Underwood, 1991, 1992), and employing factorial designs that are needed to isolate the causes of change (e.g. herbivory, nutrient limitation, and temperature).

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