The Ecology of Snow and Snow-covered Systems: Summary and Relevance to Wolf Creek, Yukon

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Abstract

There is an increasing perception that northern ecosystems should be studied in a more integrative manner, in which individual studies make use of principles and results from related environmental disciplines. A recent addition to the integrative fields of study, snow ecology, is the science of the relationships between organisms and their environment whether it be in snow cover or snow-covered regions. Wolf Creek Research Basin is unequivocally qualified as a subject for the study of snow ecology because of its long snow-covered period >7 months, cold climate, largely intact ecosystem and representation of several northern Canadian biomes. In this paper, we discuss the role of snow as a factor in global climate and as a habitat for organisms with relation to its physical and chemical properties. The interactions between snow and micro-organisms, vegetation, and animals is also presented with emphasis on the capacity of individuals and communities to adapt to the cold. Finally we consider the role of snow and soil in the nutrient cycling of snow-covered ecosystems and the net losses and/or gains of nutrients by these systems during spring runoff. In doing so we hope to demonstrate how environmental science can be conducted and improved using a framework of habitat, environment and rigorous application of physical, chemical and biological principles. The potential applications of snow ecology to Wolf Creek are identified and promoted as a demonstration of multi-disciplinary, integrative science.

The Role of Snow Cover in Ecology: Scalar Considerations

Although snow has long been the subject of scientific investigation, the vast majority of the studies have been limited to various disciplines in the physical and biological sciences. As a result, very few works permit a full appreciation of snow cover and/or snow-covered regions as functional ecosystems. An ecosystem, or ecological system, is a set of interacting, interdependent living and non-living components or sub-systems (Tivy and O'Hare, 1982); the system or sub-systems functioning over different scales - from the global biosphere to microbiological communities. Even at the global scale, climate, cryosphere and terrestrial ecology are intimately related and, although snow and ice may cover lesser areas of the Earth than non-snow areas at any one time, strong feedback mechanisms between snow, ice and the atmosphere can influence the whole biosphere. Thus snow and ice can be considered to play a role in the dynamics of all ecosystems (Groisman and Davies, 1999). An example of the large-scale effects of snow-cover climate interactions is the influence of snow cover in Eurasia on the global climate. An above-normal snow cover in Eurasia and/or the Tibetan plateau will delay or weaken the Indian monsoon giving lower-than-normal precipitation, and also effect the climate in the tropical Pacific and North America (Barnett *et al.*, 1989). Hence the climate of Wolf Creek is interconnected with the climate of other snow-covered regions, being influenced by those in Alaska and Asia and in turn influencing those to the south and east in North America.

At the biome-continental scale, the duration of snow cover is one of the key factors in determining biological productivity (Hammond, 1972). The increase in recent knowledge on relationships between climate, snow cover and biome ecology has been facilitated by techniques of remote sensing and the modelling of the Earth's atmosphere with Global Circulation Models (GCMs; Groisman and Davies, 1999). However, snow also plays a more direct role in the ecology of organisms at much smaller scales. In the following sections we discuss some of the basic physical and chemical properties of snow that allow it to be a habitat for different snow communities and the types of organisms that are found in, under and on snow during the winter.

Snow as a Habitat and Habitat Cover: Physical and Chemical Properties

Seasonal snow cover may be considered as an atmospheric sediment of short duration. In a snowy environment such as Wolf Creek, it is a sedimentary layer of fundamental importance to almost all forms of life in the basin. The snow cover is a dynamic system, subjected to physical metamorphism, phase changes and chemical transformations that make it a habitat for certain forms of life. Life can continue in and under snow due to the unique physical texture of the milieu. In the subnivean world, organisms and soil rely on the insulating capacity of snow cover for heat retention so that extreme thermal fluctuations in the atmosphere are dampened at the soil surface (Pomeroy and Brun, 1999). However, snow not only mediates heat but also light between the atmosphere and the ground and many micro-organisms and plants have adapted to light levels in snow that are optimal for photosynthesis particularly during the spring melt. The structure and heat exchange of snow with the atmosphere, above-snow vegetation and the soil are key elements in the timing of runoff in spring (Pomeroy and Brun,1999). This is the time when many ecosystems receive the majority of their water resource of the year. Snow cover, however, acts not only as a hydrological reservoir for whole ecosystems but also as a source of nutrients (e.g. N, S.) on which true nival and subnival organisms rely for growth and reproduction (Tranter and Jones, 1999). Snow acquires these nutrients by various processes during formation in the atmosphere (Barrie,1991), by atmosphere-snow exchange (Cadle, 1991) snow-soil transfer and by fallout from forest canopies (Jones, 1991). In snow-covered soils, nutrient cycling continues throughout the winter, and, in particular, gives rise to gaseous emissions (e.g. CO_2, N_2O) at the snow-soil interface (Sommerfeld *et al.*, 1993). Gaseous emissions under snow may represent a significant part of the annual flux of C fixed by photosynthesis (see below *Nutrient cycling in snow-covered soils*; Zimov *et al.*, 1993). In the melt period, water soluble inorganic species of nutrients such as NH_4 and NO_3 allow microbial communities to flourish; much of the nutrient content is transformed by microbiological activity into organic matter within the snow cover while the rest is discharged to the soil and streams (see below *Nutrient cycling in snow-covered soils*; Jones, 1991). The disappearance of the snow habitat at the end of winter drives a marked change in organism behaviour: spring comes to the North. Physical snow studies in Wolf Creek are summarized later in this volume by Pomeroy *et al.* (1999) where the accumulation of snow as a habitat in various vegetation/elevation zones is described. Our snow chemistry studies of the basin have found the snows to be dilute, ($Cl^- < 0.14$; $NO_3^- < 1.4$; $SO_4^{2-} < 0.87$; $Ca^+ < 0.48$ μg/ml) with concentrations of major geochemical anions and cations near to "remote-location" baseline levels. Wolf Creek is not yet subject to acid snow, however as shown in this volume by Gregor *et al.* (1999) there is an organic contaminant input.

True Snow Microbial Communities

The microbial community is made up largely of snow algae, bacteria, yeasts and snow fungi. True snow algal populations grow and reproduce wholly within the water retained by snow during snowmelt. The algae possess structural and reproductive adaptations that permit them to successfully complete these essential phases of their life cycle during the relatively short melt season. These include the algae from mountainous and continental snow cover (Hoham, 1980), the ice algae and cyanobacteria from dry valley lakes in Antarctica (Parker *et al.*, 1982) and the algae from permanent glaciers (Ling & Seppelt, 1993). Studies on other organisms such as snow fungi (Hoham *et al.*, 1993; Stein and Amundsen, 1967), ice fungi (Abyzov, 1993), and eubacteria have also been reported (Margesin & Schinner, 1994). Before the mid 1960s, research emphasized the systematics, taxonomy and distribution of snow and ice algae; however, since the 1960's the life histories, biochemistry, physiology and ecology have now been added as some of the principal subjects of study (Hoham and Duval, 1999).

Cell structures allow microbes to adapt to snow cover characteristics. Many of the snow algae are flagellates and they move to sites of nutrients and optimal light levels through meltwater in the pack. Physiological changes include enzymes that permit optimal growth at low temperatures (Hoham, 1980), resistance to freeze-thaw cycles (Morris *et al.*, 1979) and, in the case of snow covers in open areas, the production of pigments which protect the cell and impede the photoinhibition of photosynthesis by light of short wavelengths e.g. carotenoids in *Chloromonas nivalis* (Hoham and Mullet, 1978) and astaxanthin esters in *Chlymadomonas* (Bidigare *et al.*, 1993). Particular interest is now being shown in the capacity of snow micro-organisms to support nival food webs which allow communities in snow-covered regions to survive over winter (Hoham and Duval, 1999; Aitchison-Benell, 1999; Walker *et al.*, 1999). No studies of micro-organisms in snow nor of nival food webs have been reported for the Yukon Territory. The results of any future studies in Wolf Creek should prove of general interest because of the paucity of data for this region of the world.

Animals and Snow

Animals that are active throughout the winter live in, under and on snow. Some small animals such as invertebrate grazers like ciliates, rotifers and collembola, can feed on snow microbe populations (Aitchison, 1989, Hoham *et al.*, 1993) which live in and under snow. The microbial productivity thus serves as a base for a part of the energy transfer through the higher invertebrate levels e.g. mites and spiders and the vertebrates such as voles, shrews, birds, etc. (Aitchison-Benell, 1999) thus extending the food chain in the cold season.

Both invertebrates and vertebrates, have had to adapt physiologically to the cold temperatures in order to move, find and devour prey on, in and under snow. In many north-temperate and deep mountainous snow covers the subnivean temperatures are close to 0°C and the freezing of bodily fluids does not pose a major problem for invertebrates inhabiting this ecological niche as it does vertebrates which are active on the snow surface or in subarctic or arctic subnivean space. Aitchison-Benell (1999) discussed the way active nival and subnival invertebrates succeed in overcoming freezing by lowering the freezing point of the haemolymph by anti-freeze agents such as thermal-hysteris-proteins and low molecular weight cryoprotective alcohols (e.g. glycerol; Lee, 1991). For example, the winter-active spider *Bolyphantes index* can maintain normal activity down to -5°C. However, at -9.3°C it becomes comatized (chill coma) and below the supercooling point of -15.3°C will freeze solid (Hågvar, 1973). The springtail *Isotoma hiemalis* can remain active down to -6°C, experiences chill-coma at -8°C and has a supercooling point of -15°C. Isotoma hiemalis is also an example of an invertebrate which undergoes a morphological change of the locomotory appendages from summer to winter called cyclomorphosis which allows the organism to move to the snow surface; the change then reverses in the spring with the disappearance of snow cover (Zettel, 1984). Springtails and mites are the arthropods most tolerant of cold (Sømme, 1993).

Vertebrates may be active on, in or under the snow cover. The majority of subnivean vertebrates are small mammals such as the microtines and insectivores (Cranford, 1984; Pruitt, 1984). These usually weigh less than 250 g and serve as prey for larger mammals e.g. weasels, foxes, birds. To survive the cold, insectivores possess high metabolic rates and have to feed almost continuously. Shrews will favour habitats with litter, deep humus or snow cover where they construct nests to conserve heat (Aitchison-Benell, 1999). As in the case of the invertebrates, vertebrates will undergo physiological and morphological change in winter. The thyroid, pituitary, adrenals and parathyroid glands of soricine shrews become inactive, and changes in the salivary glands occur; brown adipose tissue is also converted to heat, all of which reduce metabolism and activity (Aitchison, 1987). Shrews also show morphological changes which include reductions in brain volume and weights of the kidneys, liver and spleen, and shortened body length (Merritt, 1986). The reduced size increases the hair density, giving greater insulation per unit surface area (Mezhzherin, 1964). However, even these methods fail to enable the animals to survive continuous cold and the northern limit of shrew distribution is the -30°C mean January isotherm in the Former Soviet Union (F.S.U.), the coldest areas being inhabited by the smallest *Sorex* species, e.g. *S. minutissimus* (mean weight of about 4 g) (Mezhzherin, 1964).

Shrews and other small mammals such as lemmings are an integral part of the winter food web being the prey for weasels, foxes, birds and larger mammals. Formazov (1946) published a comprehensive review on the importance of snow cover in the ecology of both small and large mammals which drew heavily both on the knowledge of indigenous hunters and his own observations of animals and snow cover relationships in different regions of the F.S.U. In his classic work 'Snow cover as an integral factor of the environment and its importance in the ecology of mammals and birds' the author extended the concept of climatic and edaphic factors in ecology to cover 'chionic' factors (Formazov, 1946). These represent snow cover characteristics such as distribution, longevity, depth, density, and hardness which are determinant in the success or failure of populations to survive in snow-covered regions. Species were classified as either chionophiles (well adapted to snow cover), chioneuphores (partially adapted to snow cover), or chionophobes (having great difficulty to function in snow covered environments). Following Formazov, studies on large mammals and birds have been numerous and have contributed greatly to our knowledge of snow ecology e.g. wolves (Huggard, 1993), muskoxen (Nellemenn, 1997), caribou (Ouellet *et al.*, 1993), goshawks (Tornberg, 1997). The scope of the research has been expanded to include physiological, biochemical, and other more fundamental biological attributes of species snow interactions e.g. ungulate feeding and excretory metabolism in snow-covered terrain (DelGiudice *et al.*, 1989; White *et al.*, 1997).). In the northern Yukon, several studies by the Canadian Wildlife Service have clearly demonstrated the linkage between snow cover conditions and caribou herd behaviour. As elsewhere, the caribou of Wolf

Creek are observed to use wind-blown snow-free ridges for winter travel and feeding and summer snowpatches for escape from insects and heat.

Vegetation and Snow

The whole basic vegetative mosaic of certain biomes (e.g. the boreal forest and tundra) depends on snow-vegetation interactions. Regional vegetation patterns in alpine, arctic and cool temperate landscapes are strongly dependent on the distribution and physical characteristics of the snowpack (Walker *et al.*, 1993). In the boreal forest, wind and snow accumulation are two of the most important factors in the dynamics of soil temperature, soil moisture, depth of freezing, and heat flux and the subsequent growth and distribution of plant communities. Tundra regions are extensively influenced by snow and wind. Snow has long been recognized as a strong factor in the make-up of mountain vegetative communities. Many plants in cold regions will survive under deep snow cover due to the high thermal insulation capacity of the snow (Pomeroy and Brun, 1999; Walker *et al.*, 1999). Others adapt to shallow or intermittent cold snow cover by retaining a large amount of dead tissue which can trap snow for insulation, by storing large amounts of high-energy reserves (sugars, starches, lipids) for frost hardiness (Bell and Bliss, 1979) and by developing growth forms resistant to desiccation (Bliss, 1966). Many plants show rapid spring growth and flowering even under snow from over-wintering buds (Galen and Stanton, 1995). International Tundra Experiment studies that are being initiated in Wolf Creek will help to elucidate the relationships between vegetation and snow that help to govern vegetation patterns in the basin.

In forest areas trees intercept snow and play a major role in soil moisture dynamics and forest hydrology (Pomeroy and Brun,1999). Sublimation of the intercepted snow will consume considerable amounts of energy from the forest environment and reduce the transfer of moisture from the atmosphere to the soil (Harding and Pomeroy, 1996). As forests become more open, the abrasive nature of wind-blown snow crystals is a key factor in tree survival. The damage and kill to trees above the snow surface due to wind-blown snow is a common sight in high-alpine and taiga regions. Pockets of mostly deformed trees (krummholz) survive only where the topography is favourable to obtain a foothold (Daly, 1984; Begin and Boivin, 1999). Due to the combined influence of wind-induced drought stress, freezing and snow drifting, these islands of trees gradually die off on the windward side and advance through the drift on the leeward side thus gradually moving in line with the wind (e.g. 0.02 m year^{-1}; Benedict, 1984). These krummholz are extremely important for the survival of plant communities in the immediate area as the protected downwind side will provide a microsite for a more luxuriant and diverse vegetation than the upwind area (Walker *et al.*, 1999). These types of snow-vegetation relationships are used in paleoecological studies e.g. the reconstruction of past snow regimes by the study of tree morphology (Begin and Boivin, 1999).

In addition to these severe physical stresses on vegetation, nutrient distribution is also a key factor in plant distribution and productivity. Soil nutrient content may vary widely due to atmospheric deposition, aeolian erosion, temperature regimes and snow depth. In some cases subnival animal activity will also influence nutrient availability. For example, lemmings can reduce the standing crops of vegetation (live and dead above-ground biomass) by 50% of the annual above-ground production and 20% of the total annual production and redistribute nutrients through the excretion of faeces and urine (Walker *et al.*, 1999).

Nutrient Cycling in Snow-covered Soils

Thus plants, animals, micro-organisms are all tightly bound in the transfer of nutrients throughout snow-covered systems from snow to soil to the atmosphere (Jones, 1991; Williams, 1996). An important source of nutrient loss from soil is by gas emissions to the atmosphere. Respiration and allied microbiological processes such as denitrification and nitrification continue to produce CO_2, CH_4, N_2, NO, N_2O and other gases throughout the winter. The extent to which seasonal snow cover will influence gaseous emissions from soil will vary with the duration and depth of snow during the cold, dry accumulation period, and with the discharge rates and chemical composition of meltwaters during the melt season (van Bochove *et al.*, 1996). Due to the porous nature of snow, gases released from the soil will give rise to either consistent gaseous concentration profiles in the snow cover (Sommerfeld *et al.*, 1993) or ephemeral localized gas-rich pockets of air within the snow cover (Zimov *et al.*, 1993). The distribution of gases in snow cover depends on soil temperature and texture, and the physical structure of the snow cover and its interaction with the atmosphere (Massmann *et al.*, 1995). Ice lenses are impermeable to gaseous diffusion and considerably reduce gaseous fluxes between soils and the atmosphere (Winston *et al.*, 1995).

Gaseous emissions under snow may represent a significant part of the annual Carbon cycle. Sommerfeld *et al.* (1993) estimated that CO_2 emissions from an Alpine soil under snow constituted approximately 25% of the total annual amount of C fixed by photosynthesis. Zimov *et al.* (1993) reported that emissions of CO_2 under snow cover in the open taiga of Siberia could theoretically represent the respiration of over 60% of the annual organic C production. In the case of N_2O. Brooks *et al.* (1996) estimated that the winter/spring N losses by denitrification (N_2, N_2O) represented 50% of the annual gaseous N loss and van Bochove *et al.* (1996) have shown that the rates of N_2O emissions from snow-covered agricultural soil represented 25% of the annual emissions. Emissions were very high during the spring snowmelt period.

The spring melt period is also a time of both gains and losses of nutrients for soil by hydrological input and output respectively. The soil will gain the nutrient loads of discharged meltwaters by infiltration and biological assimilation but can also lose nutrients by gaseous emissions and runoff (Williams *et al.*, 1993). Jones and Roberge (1992) found that the export of NO_3 in a boreal forest was greatest during the meltwater runoff period. This has also been found to be true for other ecosystems such as hardwood forests (Rascher *et al.*, 1987) and high-altitude alpine sites (Williams *et al.*, 1993). NH_4 discharged by meltwaters is generally fixed or assimilated by the soil and practically no loss of N occurs by direct transfer of this species through the soil by meltwater to surface waters (Williams *et al.*, 1996). As NO_3 is far more mobile than NH_4 in soils, the export of NO_3 by surface waters may originate both from the solute in the meltwaters (Williams *et al.*, 1993) and/or from the leaching of the species from soil after over-wintering mineralization of organic matter (Rascher *et al.*, 1987). However, it is extremely difficult to distinguish between the two sources of NO_3 in conventional studies. Williams *et al.* (1996) used $K^{15}NO_3$ as a tracer in a study to elucidate the relative importance of the two sources. Their results suggested that soil mineralization under the seasonal snow, rather than snowmelt release of NO_3, may be the main control on the concentrations of NO_3 in surface waters and the export of N in spring. However, the difference between regional snow covers, soils and spring precipitation, may cause the relative importance of the sources to change from year to year and export pathways may depend on many factors including the amount of snow, the rate of melt, soil texture, and soil microbiological activity. The result can either be a net loss or gain of nutrients. Jones and Bedard (1987) showed that variations in inter-annual hydrologic exports of N during snowmelt in a boreal forest can give rise to total spring exports which are either greater or less than the amounts of the nutrient discharged from the snow cover. The nutrient cycling between snow, terrestrial and aquatic systems is unknown for Wolf Creek but considered to be of the utmost importance for primary productivity in the respective systems. It is hoped that future studies will focus on this topic.

Concluding Remarks

This brief overview of the functioning of snow and snow-covered systems has covered some of the principal aspects of snow ecology. Life in snow and in the cold represents how adaptable life is to survive in harsh natural environments. Wolf Creek Basin provides an example to the world of a particularly well-understood snow ecosystem in a northern environment. In the case of Humanity, technology now facilitates our existence in cold regions but the impact of human activity on these fragile systems is considerable. Wolf Creek is particularly vulnerable as it lies partly within the urban boundary of the largest Canadian city north of the 60th parallel. Human impacts on Wolf Creek have changed dramatically in the last century as mining, subdivisions and motorized transport proliferate. We need knowledge on how cold ecosystems function so that technological and natural communities can co-exist while maintaining the diversity and quality of life in such severe and spectacular environments.

References

Abyzov, S.S., 1993. 'Micro-organisms in the Antarctic ice'. In: ***Antarctic Microbiology***, Editor, Friedmann, E. I., Wiley-Liss, New York. p. 265-295.

Aitchison, C.W., 1987. 'Review of winter trophic relations of soricine shrews', ***Mammal Rev.*, 17,** 1-24.

Aitchison, C.W., 1989. 'The ecology of winter-active collembolans and spiders', ***Aquilo Ser. Zoologica*, 24,** 83-89.

Aitchison-Benell, C.W., 1999. 'The effect of snow cover on small animals'. In: *Snow Ecology*, editors Jones, H.G., Pomeroy, J.W., Walker, D.A. and Hoham, R., Cambridge University Press, Cambridge, UK.

Barrie, L., 1991. 'Dry deposition to snowpacks'. In: Seasonal snowpacks: Processes for compositional change. Proceedings of the NATO Advanced Research Workshop on processes of chemical change in snowpacks, Maratea, Italy, July 1990. Editors, Davies, T.D., Tranter, M. and Jones, H.G., Springer-Verlag, Berlin, Series G, *Ecological Sciences*, **28,** 1-20.

Barnett, T.P., Dumenil, L., Schlese, U., Roeckner, E. and Latif, M., 1989. 'The effect of Eurasian snow cover on regional and global climate variations', *J. Atmos. Sci.*, **46,** 661-685.

Begin, Y. and Boivin, S., 1999. 'Tree-ring dating of past snow levels in Northern Québec', In: Snow Ecology, editors Jones, H.G., Pomeroy, J.W., Walker, D.A. and Hoham, R., Cambridge University Press, Cambridge, UK.

Bell, K.L. and Bliss, L.C., 1979. 'Autoecology of *Kobresia bellardii*: why winter snow accumulation limits local distribution'. *Ecological Monographs*, **49,** 377-402.

Benedict, J.B., 1984. 'Rates of tree-island migration, Colorado Rocky Mountains USA'. *Ecology*, **65,** 820-823.

Bidigare, R.R., Ondrusek, M.E., Kennicutt II, M.C., Iturriaga, R., Harvey, H.R., Hoham R.W. and Macko, S.A.,. 1993. 'Evidence for a photoprotective function for secondary carotenoids of snow algae', *J. Phycol.*, **29,** 427-434.

Bliss, L.C., 1966. 'Plant productivity in alpine microenvironments on Mount Washington, New Hampshire', *Ecological Monographs*, **36,** 136-155.

Brooks, P.D., Williams, M.W. and Schmidt, S.K., 1996. 'Microbial activity under alpine snowpacks, Niwot Ridge, Colorado', *Biogeochemistry*, **32,** 93-113.

Cranford, J.A., 1984. 'Population ecology and home range utilization of two subalpine meadow rodents (*Microtus longicaudus* and *Peromyscus maniculatus*)'. In: *Winter Ecology of Small Mammals*, Editor, Merritt, J.E., Carnegie Museum of Natural History, Pittsburg, Special Publication No. 10. ISBN 0-935868-10-0, p. 285-292.

Daly, C., 1984. 'Snow distribution patterns in the alpine krummholz zone', *Progress in Physical Geography*, **8**, 157-175.

DelGiudice, G.D., Mech, L.D. and Seal, U.S., 1989. 'Physiological assessment of deer populations by analysis of urine in snow'. *J. Wildl. Manage.*, **53**, 284-291.

Formazov, A.N., 1946. *Snow cover as an integral factor of the environment and its importance in the ecology of mammals and birds.* Moscow Soc. Naturalists, Materials for Fauna and Flora U.S.S.R. Zool. Section, New Ser. **5**, 1-152. English translation: Prychodko, W., and Pruitt, W. O., (1963). Occasional Paper 1, Boreal Inst. Univ. Alberta, Edmonton.

Galen, C. and Stanton, M.L., 1995. 'Responses of snowmelt species to changes in growing season length', *Ecology*, **75**, 1546-1557.

Groisman, P.Ya. and Davies, T., 1999. 'Snow cover and the Climate system'. In: *Snow Ecology*, editors Jones, H. G., Pomeroy, J. W., Walker, D. A. and Hoham, R., Cambridge University Press, Cambridge, UK.

Hågvar, S., 1973. 'Ecological studies on a winter-active spider *Bolyphantes index* (Thorell) (Araneida, Linyphiidae)'. *Norsk ent. Tiddskr.*, **20**, 309-314.

Hammond, A.L., 1972. 'Ecosystem analysis: Biome approach to ecosystem research', *Science*, **175**, 46-48.

Harding, R.J. and Pomeroy, J.W., 1996. 'The energy balance of the winter boreal landscape', *J. of Climate*, **9**, 2778-2787.

Hoham, R.W., 1980. 'Unicellular Chlorophytes - Snow algae'. In: *Phytoflagellates*, Editor Cox, E., Elsevier North Holland, Inc. p. 61-84.

Hoham, R.W. and Mullet J.E., 1978. '*Chloromonas nivalis* (Chod.) Hoh. & Mull. comb. nov., and additional comments on the snow alga *Scotiella*'. *Phycologia*, **17**, 106-107.

Hoham, R.W., Laursen, A.E., Clive, S.O. and Duval, B., 1993. 'Snow algae and other microbes in several alpine areas in New England'. In: *Proceedings of the Fiftieth Annual Eastern Snow Conference*, Québec City, Québec, Canada, June 8-10, p. 165-173.

Hoham, R.W. and Duval, B., 1999. 'Microbial ecology of snow and fresh-water ice with emphasis on snow algae'. In: *Snow Ecology*, Editors Jones, H.G., Pomeroy, J.W., Walker, D.A. and Hoham, R., Cambridge University Press, Cambridge, UK.

Huggard, D.J., 1993. 'The effect of snow depth on predation and scavenging by Gray Wolves'. *J. Wildlife Manage.*, **57**, 382-388.

Jones, H.G., 1991. 'Snow chemistry and biological activity: a particular perspective of nutrient cycling'. In: *Seasonal snowpacks: Processes for compositional change.* Proceedings of the NATO Advanced Research Workshop on processes of chemical change in snowpacks, Maratea, Italy, July 1990. Eds., Davies, T.D., Tranter, M, and Jones, H.G. Springer-Verlag, Berlin. Series G, *Ecological Sciences* **28**, 21-66.

Jones, H.G. and Bedard, Y., 1987. 'The dynamics and mass balances of NO_3 and SO_4 in meltwater and surface runoff during springmelt in a boreal forest'. In: *Forest Hydrology and Watershed Management.* IAHS Publication **167**, 19-31.

Jones, H.G. and Roberge, J., 1992. 'Nitrogen dynamics and sub-ice meltwater patters in a small boreal lake during snowmelt', In: *Proceedings of the 49th annual meeting of the Eastern Snow Conference.* Editors, Ferrick, M. and Pangburn, T., p. 169-180.

Lee, R.E., Jr., 1991. 'Principles of insect low temperature tolerance'. In: Lee, R.E., Jr., & D.L. Denlinger (eds.), *Insects at Low Temperature.* Chapman & Hall, New York and London, p. 17-46.

Ling, H.U. and Seppelt, R.D., 1993. 'Snow algae of the Windmill Islands, continental Antarctica. 2. *Chloromonas rubroleosa* sp. nov. (Volvocales, Chlorophyta), an alga of red snow'. *Eur. J. Phycol.* **28**, 77-84.

Margesin, R. and Schinner, F., 1994. 'Properties of cold-adapted microorganisms and their potential role in biotechnology'. *J. Biotech.* **33**, 1-14.

Massman, W., Sommerfeld, R., Zeller, K., Hehn, T., Hudnell, L. and Rochelle, S., 1995. 'CO_2 flux through a Wyoming seasonal snowpack: diffusional and pressure pumping effects'. In: *Biogeochemistry of seasonally snow-covered catchments,* Editors, Tonnessen, K.A., Williams, M.W. and Tranter, M., IAHS Publication **228**, 71-80.

Merritt, J.F., 1986. 'Winter survival adaptations of the short-tailed shrew (*Blarina brevicauda*) in an Appalachian montane forest'. *J. Mamm.*, **67**, 450-464.

Mezhzherin, V.A., 1964. 'Dehnel's Phenomenon and its possible explanation'. *Acta theriologica,* **8**, 95-114.

Morris, G.J., Coulson, G. and Clarke, A., 1979. 'The cryopreservation of *Chlamydomonas.*' *Cryobiology,* **16**, 401-410.

Nellemenn, C., 1997. 'Grazing strategies of muskoxen (*Ovibus moschatus*) during winter in Angujaartorfiup Nunaa in western Greenland', *Can. J. Zoology,* **75**, 1129-1134.

Ouellet, J.P., Heard, D.C. and Boutin, S., 1993. 'Range impacts following the introduction of Caribou on Southampton Island, Northwest Territories, Canada', *Arctic and Alpine Research,* **25**, 136-141.

Parker, B.C., Simmons, G.M., Jr., Seaburg, K.G., Cathey, D.D. and Allnut, F.C.T., 1982. 'Comparative ecology of planktonic communities in seven Antarctic oasis lakes', *J. Plankton Res.* **4**, 271-286.

Pomeroy, J.W. and Brun, E., 1999. Physical properties of snow. In: *Snow Ecology*, Editors Jones, H.G., Pomeroy, J.W., Walker, D.A. and Hoham, R., Cambridge University Press, Cambridge, UK.

Pruitt, W.O. Jr., 1984. 'Snow and small mammals' In: *Winter Ecology of Small Mammals*, Editor, Merritt, J.E., Carnegie Museum of Natural History, Pittsburg, Special Publication No. 10, ISBN 0-935868-10-0, p. 1-8.

Rascher, C.M., Driscoll, C.T. and Peters, N.E., 1987. 'Concentration and flow of solutes from snow and forest floor during snowmelt in the West-Central Adirondack region of New York', *Biogeochemistry*, **3**, 209-224.

Sommerfeld, R.A., Mosier, A.R. and Musselman, R.C., 1993. 'CO_2, CH_4 and N_2O flux through a Wyoming snowpack and implications for global budgets', *Nature*, **361**, 140-142.

Sømme, L., 1993. 'Living in the cold', *Biologist*, **40**, 14-17.

Stein, J. and Amundsen, C.C., 1967. 'Studies on snow algae and snow fungi from the Front Range of Colorado', *Can. J. Bot.*, **45**, 2033-2045.

Tivy, J. and O'Hare, G., 1982. Human impact on the Ecosystem. Oliver and Boyd, Edinburgh, 243 pp.

Tornberg, R., 1997. 'Prey selection of the goshawk *Accipter gentilis* during the breeding season: The role of prey profitability and vulnerability', *Ornis Fennica*, **74**, 15-28.

Tranter, M. and Jones, H.G., 1999. 'The chemistry of snow: processes and nutrient cycling'. In: *Snow Ecology*, Editors Jones, H.G., Pomeroy, J.W., Walker, D.A. and Hoham, R., Cambridge University Press, Cambridge, UK.

van Bochove, E., Jones, H.G., Pelletier, F. and Prévost, D., 1996. 'Emissions of N_2O from agricultural soils under snow cover: a significant part of N budgets', *Hydrological Processes*, **10**, 1545-1550.

Walker, D.A., Billings, W.D. and De Molenaar, J.D., 1999. 'Snow-vegetation interactions in tundra environments'. In: *Snow Ecology*, Editors Jones, H.G., Pomeroy, J.W., Walker, D.A. and Hoham, R., Cambridge University Press, Cambridge, UK.

Walker, D.A., Halfpenny, J.C., Walker, M.D. and Wessman, C., 1993. 'Long-term studies of snow-vegetation interactions', *BioScience*, **43**, 287-301.

White, P.J., Garrolf, R.A. and Heisey, D.M., 1997. 'An evaluation of snow-urine ratios as indices of ungulate nutritional status', *Can. J. Zoology*, **75**, 1687-1694.

Williams, M.W., Brown, A. and Melack, J.M., 1993. 'Geochemical and hydrological controls on the composition of surface waters in a high-elevation basin, Sierra Nevada', *Limnol. Oceanogr.* **38,** 775-797.

Williams, M.W., Brooks, P.D., Mosier, A. and Tonnessen, K.A., 1996. 'Mineral transformations in and under seasonal snow in a high-elevation cathment in the Rocky Mountains, United States', *Water Resour. Res.,* **32,** 3161-3171.

Winston, G.C., Stephens, B.B., Sunquist, E.T., Hardy, J.P. and Davis, R.E., 1995. 'Seasonal variability in CO_2 transport through snow in a boreal forest'. In: *Biogeochemistry of seasonally snow-covered catchments,* Editors, Tonnessen, K.A., Williams, M.W. and Tranter, M. IAHS Publication **228,** 61-70.

Zettel, J., 1984. 'The significance of temperature and barometric pressure changes for the snow surface activity of *Isotoma hiemalis* (Collembola)', *Experientia,* **40,** 1369-1372.

Zimov, S.A., Zimova, G.M., Daviodov, S.P., Davidova, A.I., Voropaev, Y.V., Voropaeva, Z.V., Prosiannikov, S.F., Prosianikova, O.V., Semiletova, I.V., and Semiletov, I.P., 1993. 'Winter biotic activity and production of CO_2 in Siberian soils: a factor in the Greenhouse Effect', *J. Geophys. Res.*, **98,** 5017-5023.