Plant quiz 4

12 examples plants from the teaching collection for you to identify with the following information:

1) Latin name (Genus, species), 2) Family name,

- **Latin names are underlined (or italicized).**
- **Capitalize the genus name, no caps on the species name.**
- **Items like ssp., var. cf. are not italicized.**
- **Family names are not italicized.**

Flash Cards

For remaining species, Edie will do these.

Next discussion papers: Monday after spring break

Discussion Group 1: one or the other

1. Walker, D. A., J. C. Halfpenny, M. D. Walker, and C. Wessman. 1993. Long-term studies of snow-vegetation interactions. Bioscience 43:287–301.

2. Aitchison, C. W. 2001. The effect of snow cover on small mammals. P. 229-265 in Jones H.G. et al. Snow Ecology. Cambridge: Cambridge University Press.

Discussion Group 2: Both

1. Ehrich, D., J.-A. Henden, R. A. Ims, L. O. Doronina, S. T. Killengren, N. Lecomte, I. G. Pokrovsky, G. Skogstad, A. A. Sokolov, V. A. Sokolov, and N. G. Yoccoz. 2011. The importance of willow thickets for ptarmigan and hares in shrub tundra: the more the better? Oecologia 168:141–151.

2. Tape, K. D., R. Lord, H.-P. Marshall, and R. W. Ruess. 2010. Snow-Mediated Ptarmigan Browsing and Shrub Expansion in Arctic Alaska. dx.doi.org 17:186–193.

Next discussion papers: Monday after spring break

Discussion Group 1:
Frehill, Victoria A.
Friedrich, Kayla D.
Garrett, Emily
Gilbert, Breanne M.
Grimes, Amanda L.
Hendricks, Amy S.
Hogan, David A.
Jones, Samantha N.
Klingensmith, Sara M. (group leader)

Discussion Group 2:
Liebermann, Robert J.
Luce, Jamie R.
McClendon, Stephanie A.
Nakanishi, Eri
Pavic, Karolina
Skinner, Kailey E.
Strehlow, Leigh E.
Suzuki, Aina
Swanberg, Sheila R.
Yancey, Laramie L. (group leader)

Research Papers

Send me title and expanded outline by end of March 19.

Field trip, Mar 9 & 10

1. Saturday & Sunday, Mar 9 and 10. Meet in the parking lot west side of Arctic Health Building at 9 am both days.

2. Saturday: North Campus Lands, Smith Lake.
    a. Snow pit descriptions: Forest and lake.
    b. Winter vegetation.
    c. Animal winter activity and tracks.
3. Sunday: Murphy Dome.
    a. Snow pits in the alpine.
    b. Observations of wind pack, sastrugi, animal tracks, etc.
    c. Fun day in the alpine if the weather permits.

4. Need snow shoes or skis for both days. On Saturday walking may be possible because we will be near the walking trails on the NCL.

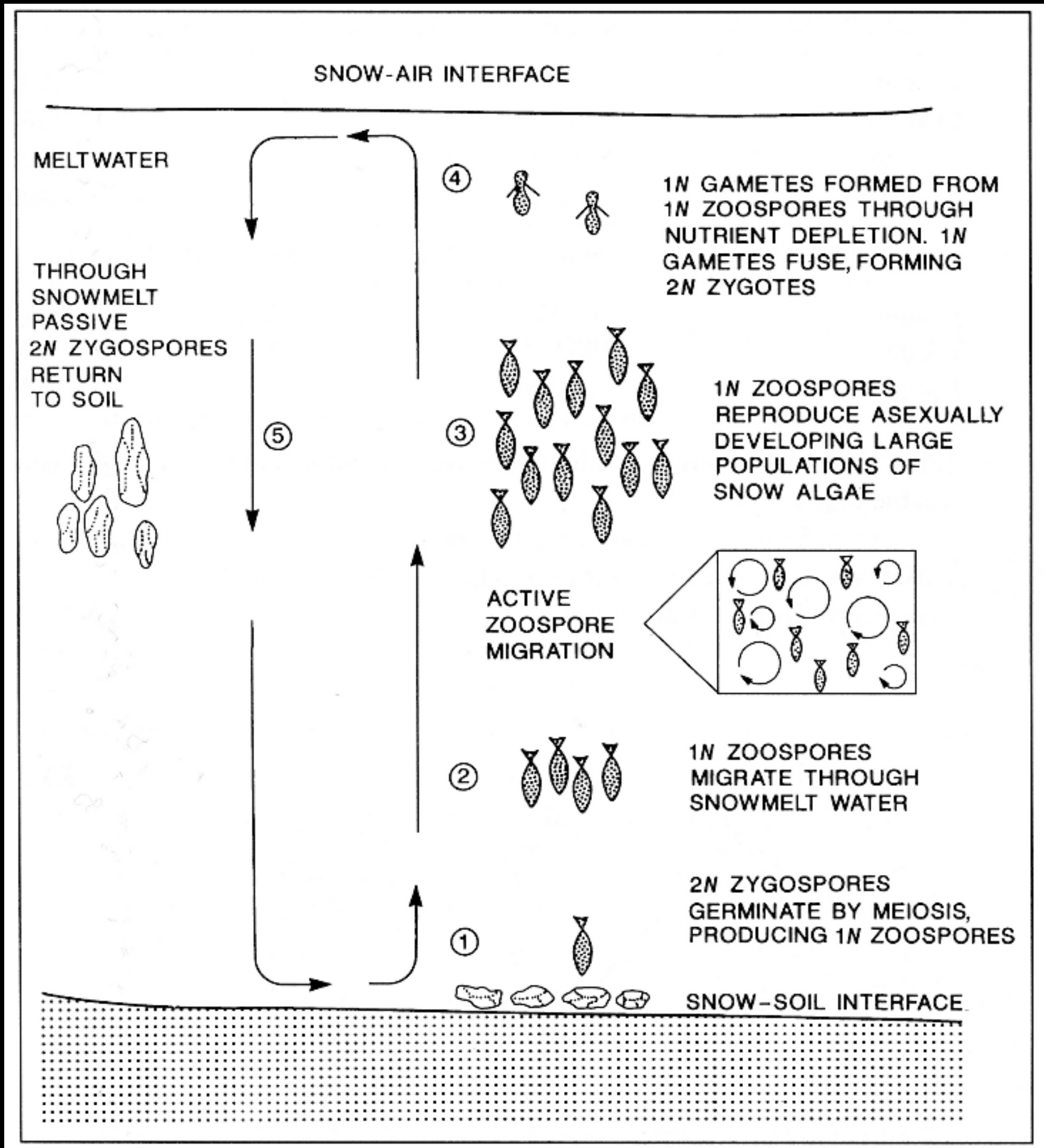
5. Bring a sack lunch both days. We will set up Coleman stoves for hot drinks at Smith Lake. Sunday will likely be a half day trip.

Field trip equipment list (now posted on the web in course schedule for Mar 9, 10)

Take home points from Lecture 8

1. Understand the life cycle associated with snow algae (slides 9-15).
2. Understand the components of the snow food chains, the role of snow algae, fungi, collembolla and other invertebrates, capable of surviving on and in the snow pack (slides 16-18).
3. Understand the processes of low-temperature-gradient (equilibrium) and high-temperature-gradient (kenetic) snow metamorphosis (slides 33-39).
4. Be able to recognize the physical properties of tundra, tiaga, prairie, alpine, and maritime snow (slides 40-43).
5. Be able to describe the major processes contributing to changes in snow chemistry in the atmosphere, in dry snow on the ground, and during the snow melt period (slides 44-48).

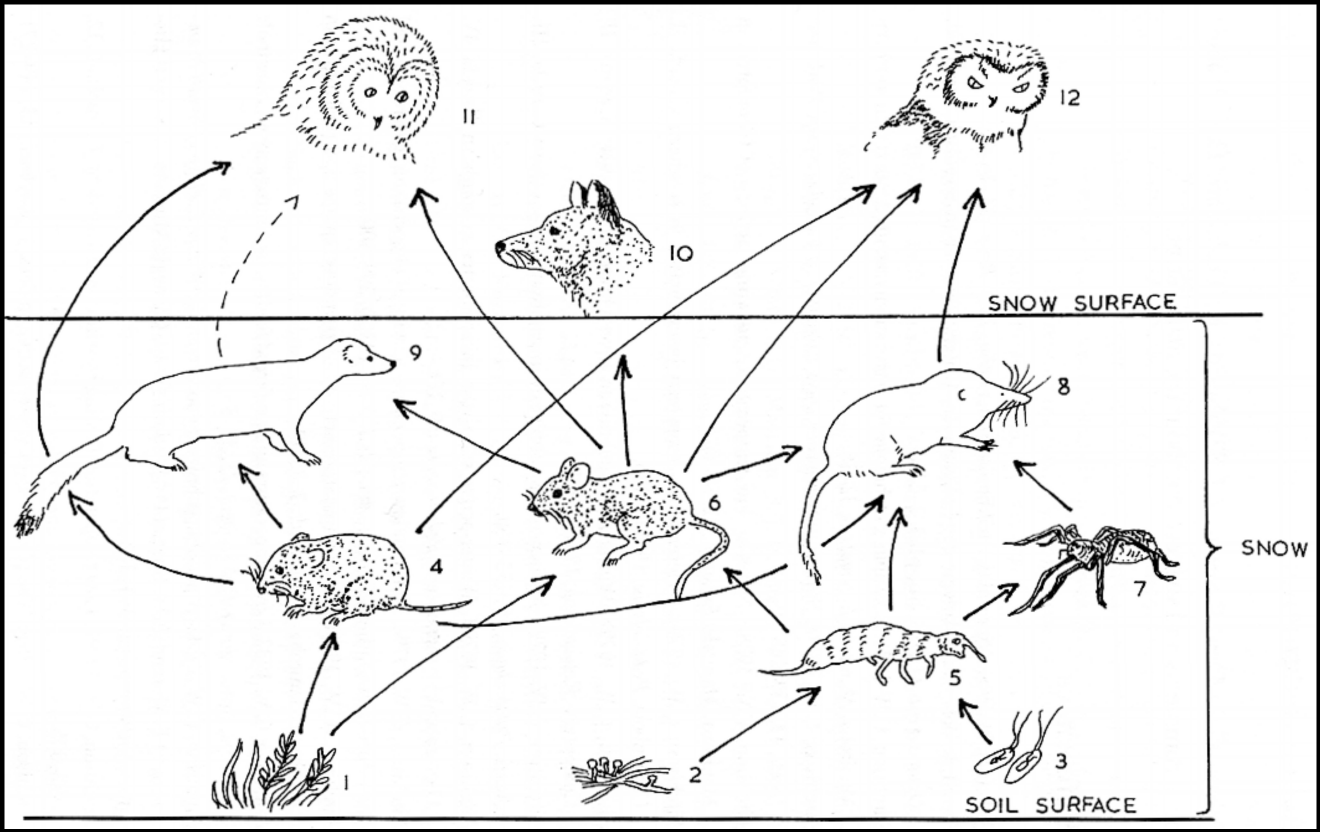
Life cycle of algal flagellate, *Chloromonas*



1. 2N Zygospores germinate by meiosis on soil surface producing bi-flagellated 1N zoospores.
2. 1N Zoospores “swim” upward to snow surface within liquid water surrounding snow crystals of isothermal snow.
3. Zoospores reproduce asexually developing large populations of snow algae.
4. Zoospores create visible blooms of snow algae on the snow surface. With nutrient depletion, 1N gametes from 1N zoospores fuse to form 2N resting zygotes.
5. Zygotes return to soil passively through meltwater percolation and settling of the snow.

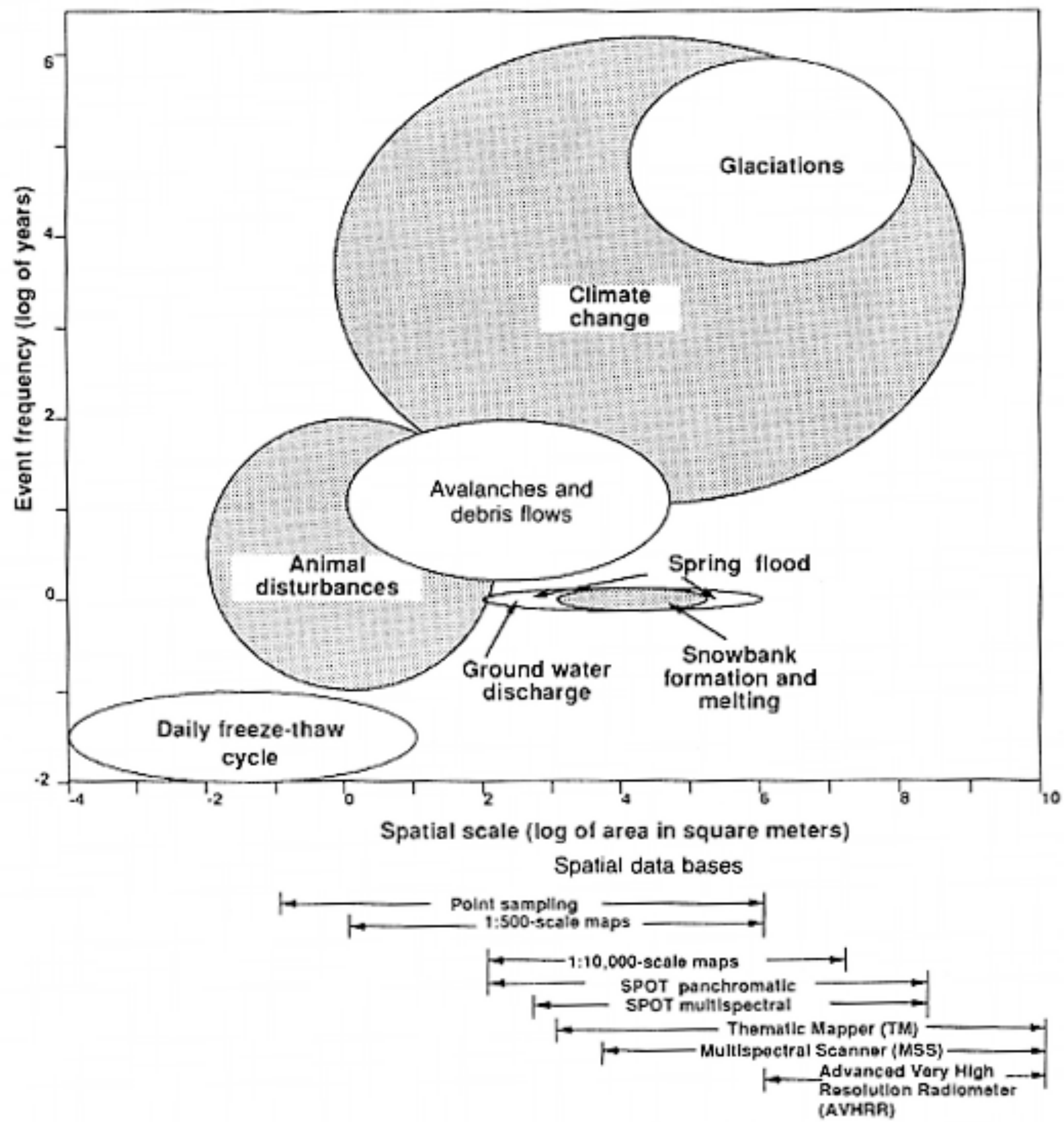
Hoham, R. W. and B. Duval. 2001. Microbial ecology of snow and freshwater ice with emphasis on snow algae. Pages 168-228 in H. G. Jones, J. W. Pomerory, D. A. Walker, and R. W. Hoham, editors. Snow Ecology. Cambridge University Press, Cambridge.

Snow as a habitat: Snow ecosystem food chains



Aitchison, C. A. 2001. The effect of snow cover on small animals. Pages 229-265 in H. G. Jones, R. W. Hoham, J. W. Pomeroy, and D. A. Walker, editors. Snow Ecology. Cambridge University Press, Cambridge.

1. **Subnivian plants.**
2. **Fungi**
3. **Snow algae**
4. **Red backed vole (*Clethrionomys gapperi*)**
5. **Collembola (*Isotoma* sp.)**
6. **Deer mouse (*Peromyscus maniculatus*)**
7. **Wolf spider (*Pardosa* sp.)**
8. **Masked shrew (*Sorex cinereus*)**
9. **Shorttail weasel (*Mustela erminea*)**
10. **Red fox (*Vulpes fulva*)**
11. **Great gray owl (*Strix nebulosa*)**
12. **Boreal owl (*Aegolium funereus*)**



Snow-Vegetation Interactions:

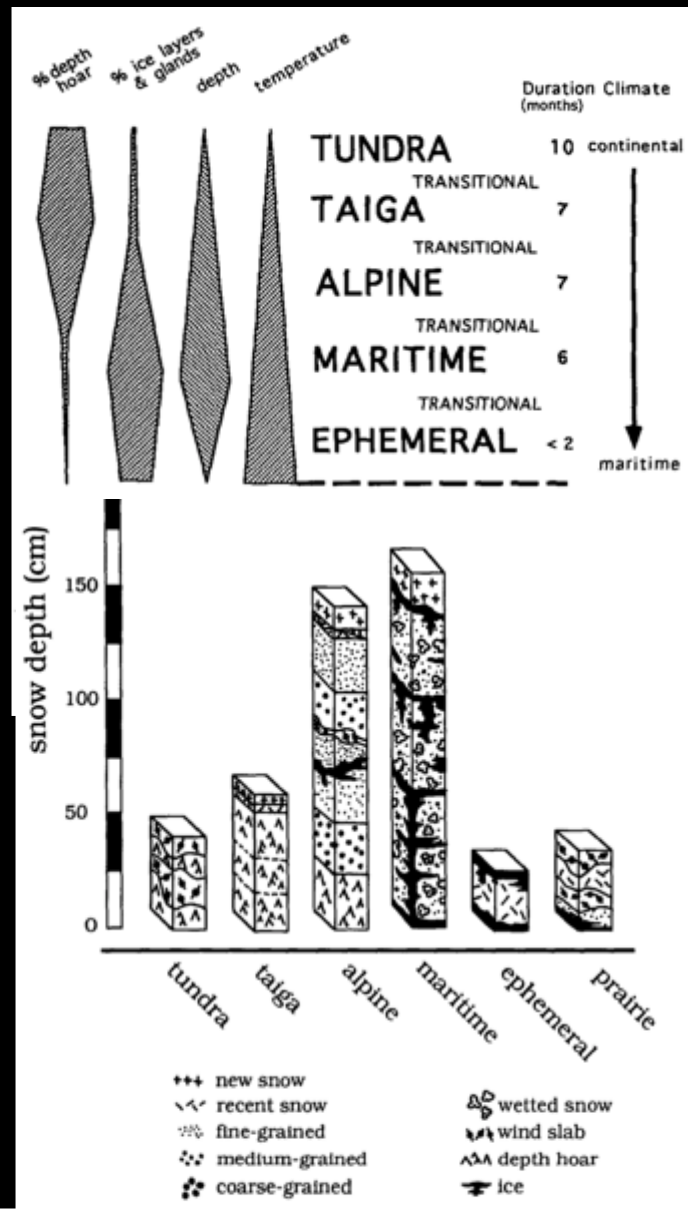
Spatial scale of snow-related effects on vegetation

Snow has effects on vegetation at nearly all spatial and temporal scales of study, and is best approached with with a hierarchic conceptual framework .

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

Alpine snow beds are different than arctic snow beds

- **Different types of snow (Tundra vs. Alpine snow of Sturm et al. (1995)**
- **Alpine: Generally deeper snow, warmer, much deeper drifts, many remain unfrozen at base all winter. Stronger contrast and more variation in micro-environments and in snowbed plant communities and fellfield communities.**
- **Arctic: Soils remain frozen most of winter.**



Long-term Studies of Snow-Vegetation Interactions

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

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

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

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

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

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

Hierarchic geographic information systems

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

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

D. A. (Skip) Walker and Marilyn D. Walker are codirectors of the Joint Facility for Regional Ecosystem Analysis, Institute of Arctic and Alpine Research, and assistant professors attendant rank in the Department of Environmental, Population, and Organismic Biology, University of Colorado, Boulder, CO 80309. James C. Halfpenny is formerly of the Institute of Arctic and Alpine Research and now lives in Gardiner, MT. Carol A. Wessman is a fellow at the Center for the Study of Earth from Space, Cooperative Institute for Research in Environmental Sciences, and an assistant professor in the Department of Environmental, Population, and Organismic Biology, University of Colorado, Boulder, CO 80309.

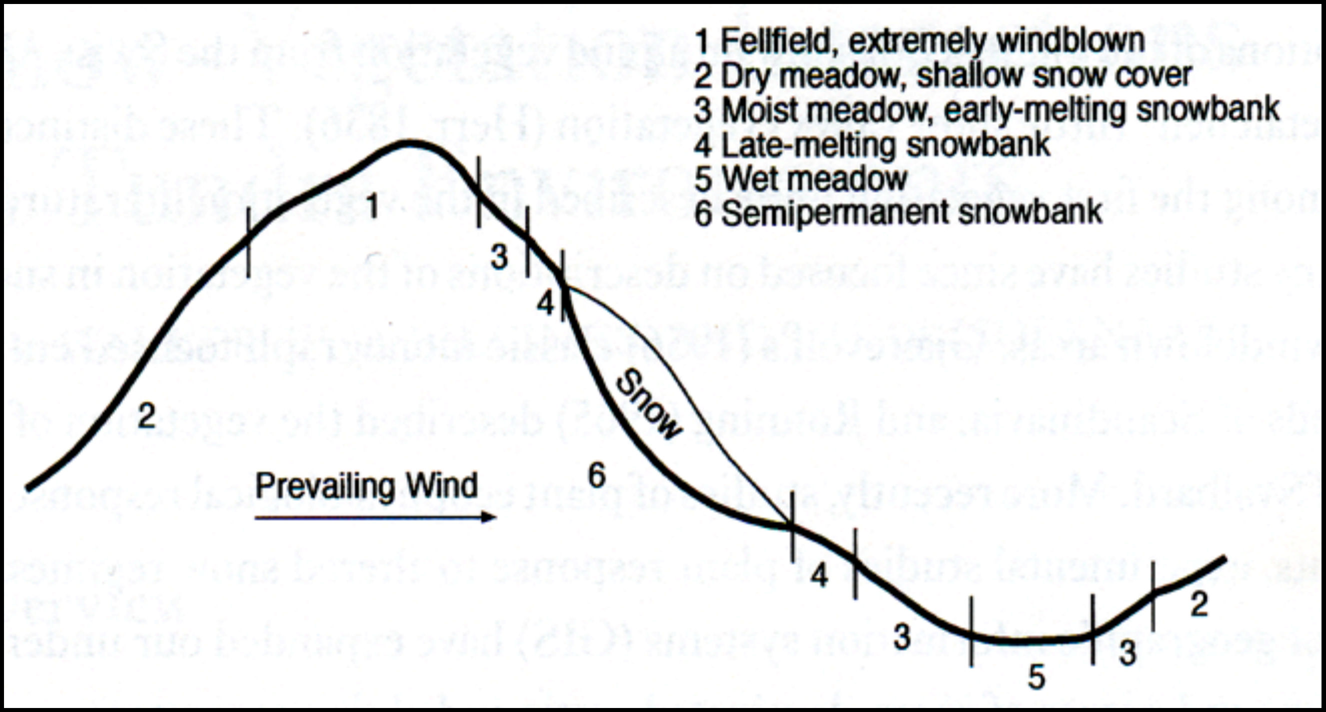
Comparison of snow studies at Niwot Ridge and Toolik Lake LTER sites

Both LTER sites utilized a multi-scale GIS approach to looking at snow-vegetation interactions.

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

Characteristics of snowbed environments along mesotopographic gradients

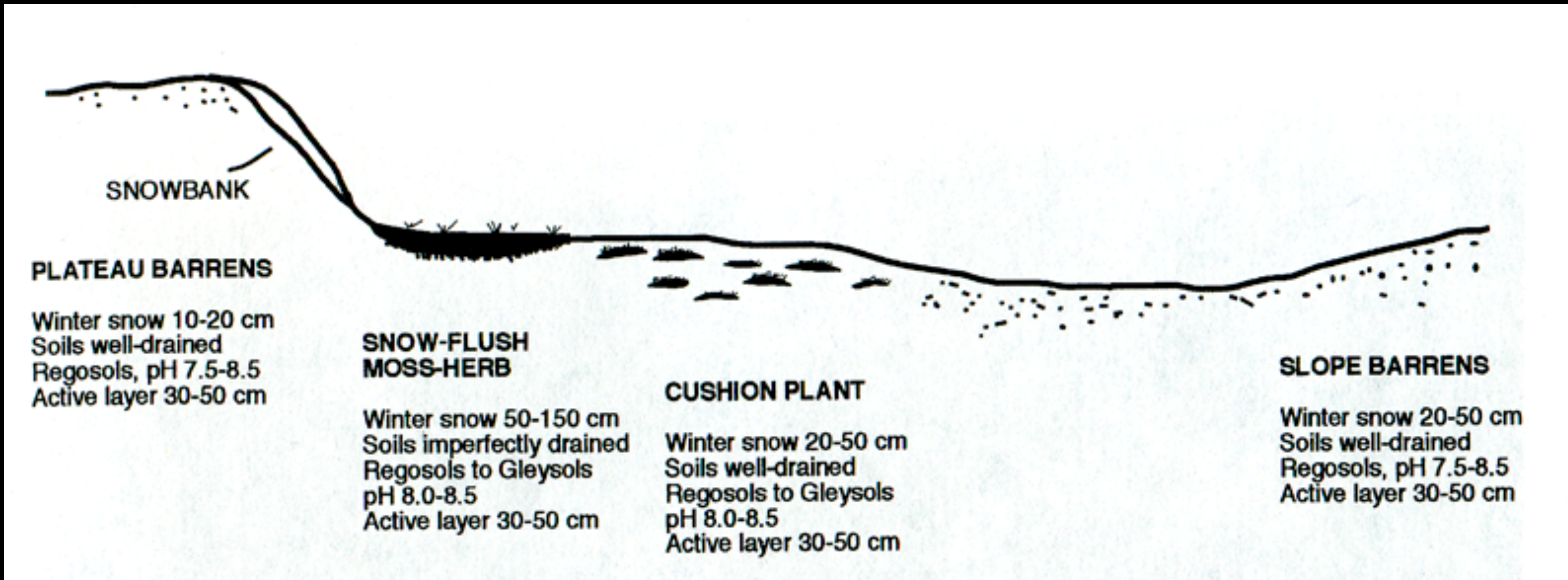
- **Described world-wide from many mountain ranges.**
- **Most comprehensive studies:**
  - **Gjaerevoll (1950, 1954, 1956) in Sweden and Alaska**
  - **Ellenberg's (1988) summary of Braun-Blanquet's work in the Central European Alps.**
- **Mesotopographic framework of Billings (1973) (right) was used on Niwot and in Alaska.**



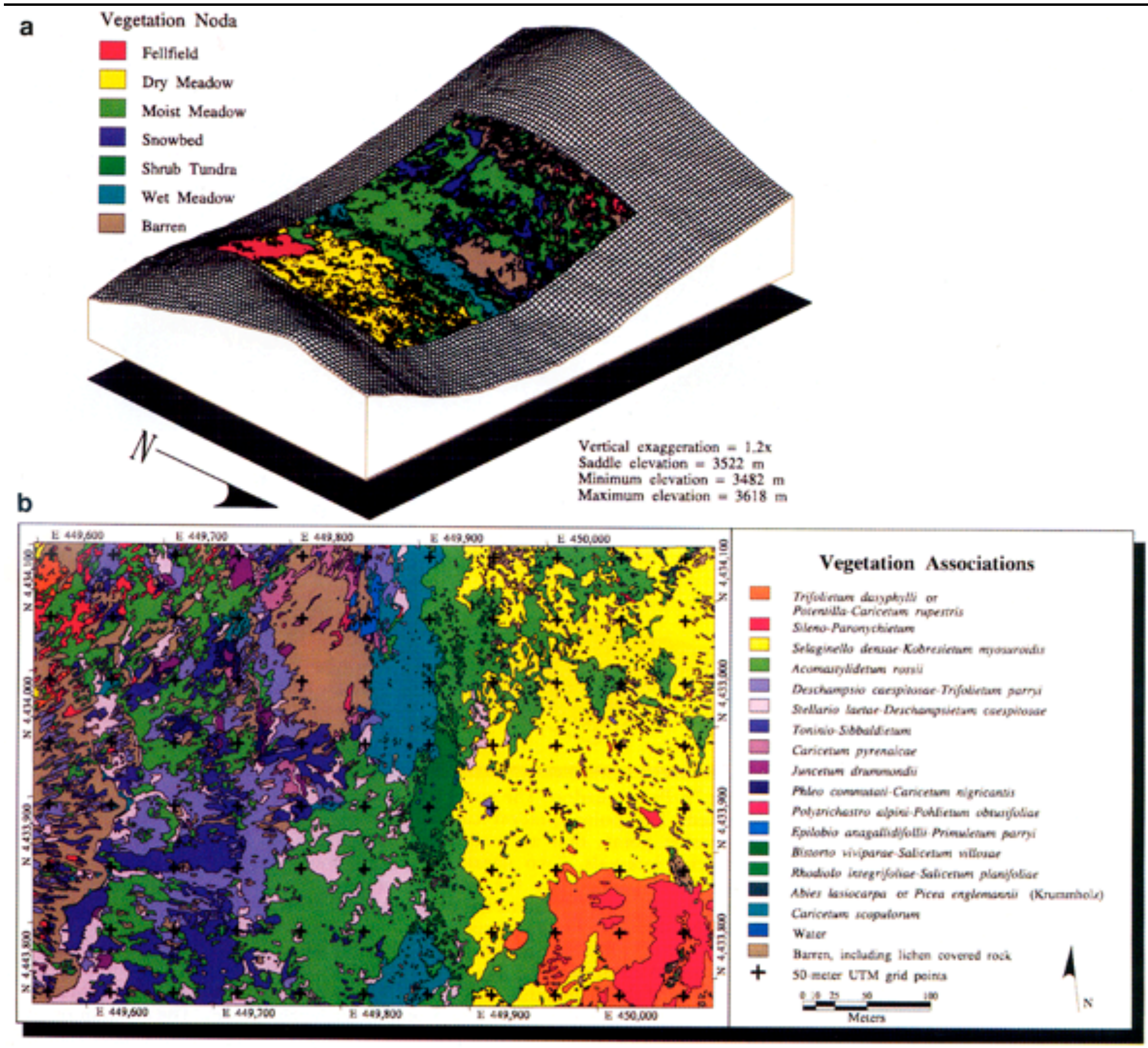
- **Walker, D. A., W. D. Billings, and J. G. de Molenaar. 2001. Snow-vegetation interactions in tundra environments. Pages 266-324 in H. G. Jones, R. W. Hoham, J. W. Pomeroy, and D. A. Walker, editors. Snow Ecology. Cambridge University Press, Cambridge.**

Cryptobiotic crusts in snow flush sites in High Arctic

Typical Toposequence in Canadian Extreme High Arctic



Bliss, L. C. and J. Svoboda. 1984. Plant communities and plant production in the western Queen Elizabeth Islands. Holarctic Ecology 7:325-344.



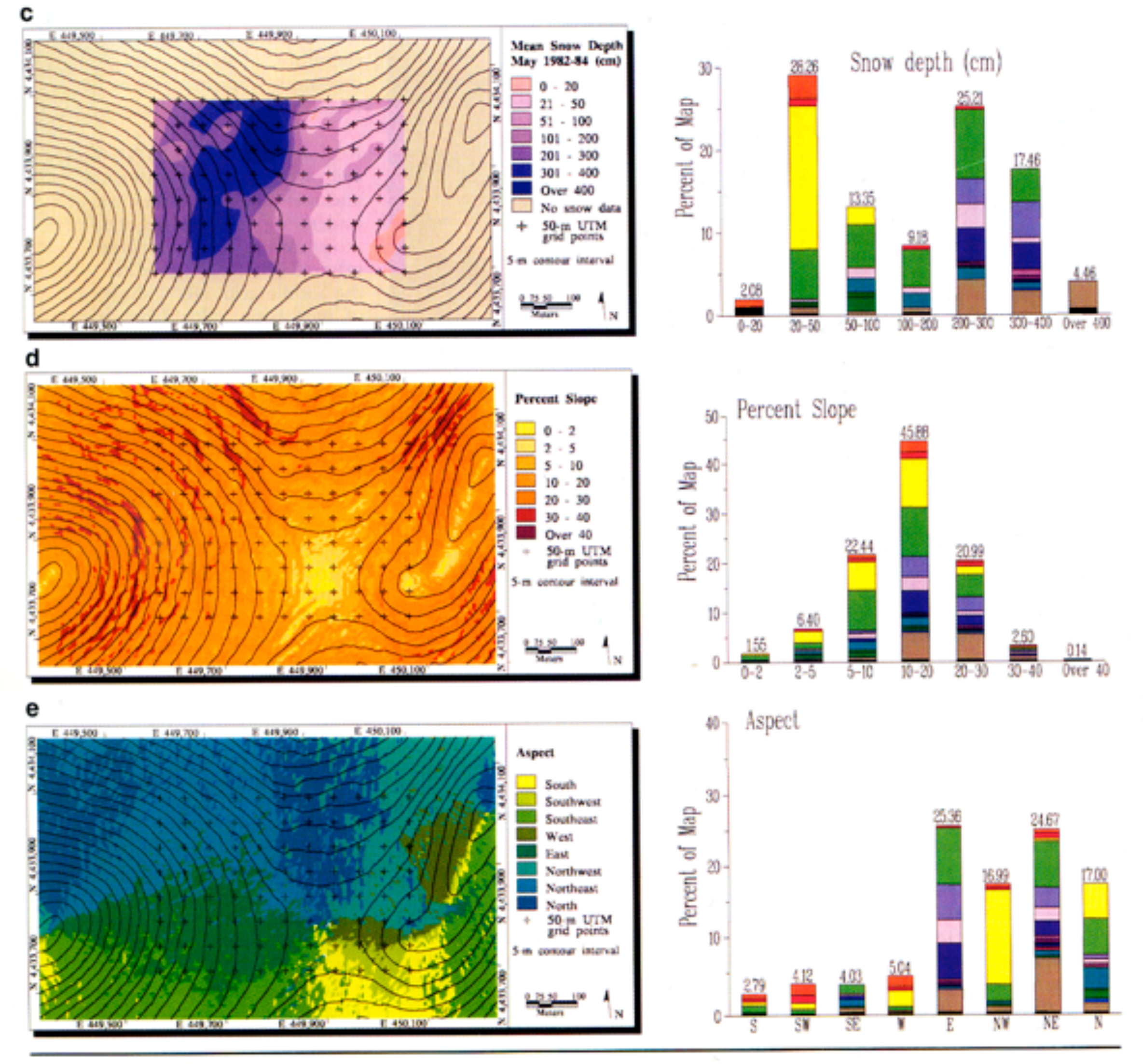
Vegetation was mapped during the summer

Mapped according to plant associations of Komárková (1980) and May and Webber (1982) vegetation noda.

Grid points (+) are marked in the field at 50-m spacing.

Komárková, V. 1980. Classification and ordination in the Indian Peaks area, Colorado Rocky Mountains. Vegetatio 42:149-163.

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



GIS database of Niwot Saddle Grid

- Distribution of vegetation types within snow depth, slope and aspect classes.

Walker, M. D., D. A. Walker, J. M. Welker, A. M. Arft, T. Bardsley, P. D. Brooks, J. T. Fahnestock, M. H. Jones, M. Losleben, A. N. Parsons, T. R. Seastedt, and P. L. Turner. 1999. Long-term experimental manipulation of winter snow regime and summer temperature in arctic and alpine tundra. Hydrological Processes 13:2315-2330.

Plant species responses to variations in snow cover, Niwot Ridge, CO

- **Komárková recognized these as characteristic taxa for plant communities along the snow gradient.**

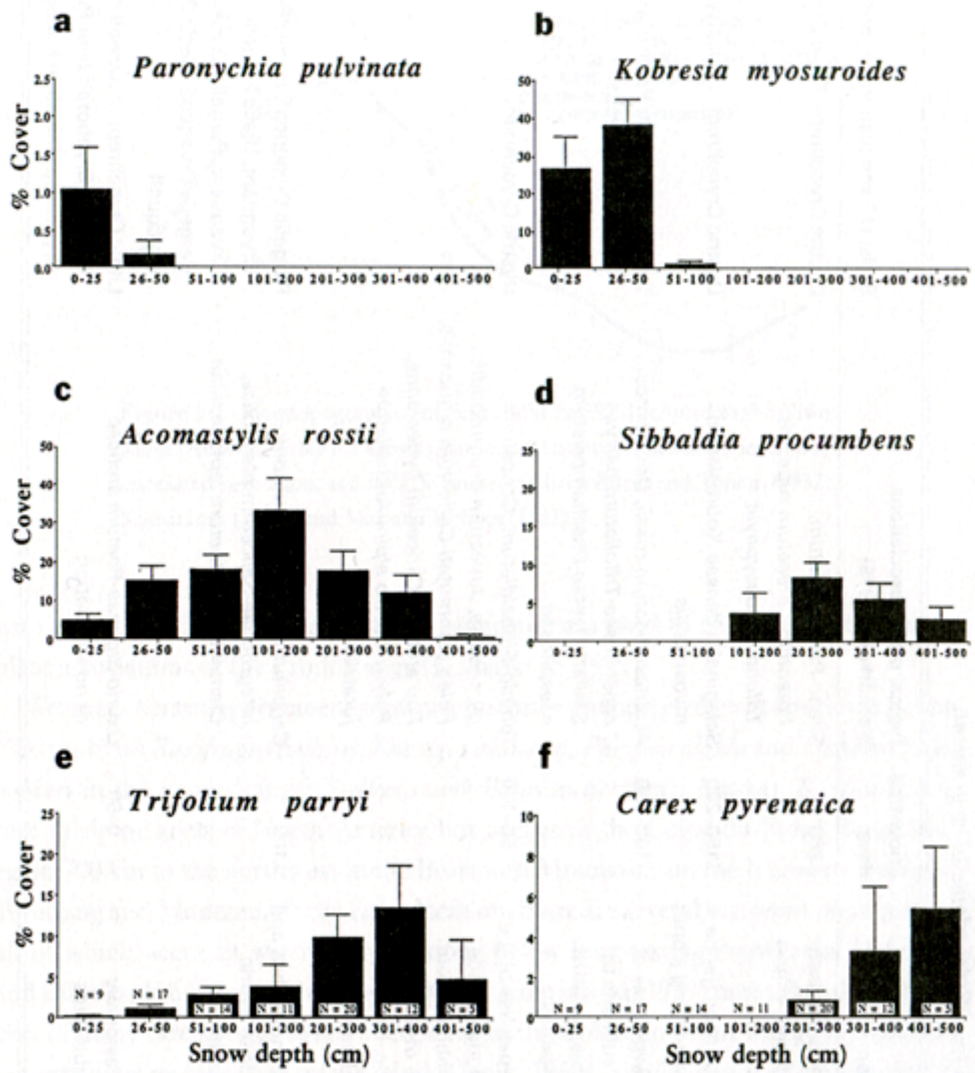


Figure 6.2. Distribution (plus or minus standard error) of six common species along the snow gradient. *Paronychia pulvinata* and *Kobresia myosuroides* are diagnostic taxa for the Alliance *Kobresio-Caricion rupestris*, which includes associations that are typical of broad, well-drained, stable windswept 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).

- **Walker, D. A., W. D. Billings, and J. G. de Molenaar. 2001. Snow-vegetation interactions in tundra environments. Pages 266-324 in H. G. Jones, R. W. Hoham, J. W. Pomeroy, and D. A. Walker, editors. Snow Ecology. Cambridge University Press, Cambridge.**

Six charateristic plant species along Niwot snow gradient

FELLFIELD

Paronychia pulvinata

Photo D. A. Walker

DRY MEADOW

Kobresia myosuroides

Photo: D.A. Walker

MOIST MEADOW 1

Acomastylis rossii

Photo: ?

MOIST MEADOW 2

Sibbaldia procumbens

Photo D. A. Walker

MOIST MEADOW 3

Trifolium parryii

Photo: D.A. Walker

DEEP SNOWBED

Carex pyrenaica

Photo: D.A. Walker and f Flora de Aragon,
http://flora-aragon.blogspot.com/

Other plant species showing differenential responses to variations in snow cover, Niwot Ridge, CO

- **Komárková also recognized most of these as differential taxa for plant communities along the snow gradient.**

- Walker, D. A., W. D. Billings, and J. G. de Molenaar. 2001. Snow-vegetation interactions in tundra environments. Pages 266-324 in H. G. Jones, R. W. Hoham, J. W. Pomeroy, and D. A. Walker, editors. Snow Ecology. Cambridge University Press, Cambridge.

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

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

Chionophytes: Adapted to high snow environments

Chionophila jamesii,
Niwot Ridge, CO
Photo: D.A. Walker

But what makes a chionophyte a chionophyte?

Growth strategies of snowbed plants

Some adaptations to poor nutrient conditions & short growing season:

- **Evergreen leaves** (e.g. *Empetrum*, *Cassiope*)
- **Long-lived, slow-growing** species. (However, note that many deep Arctic snowbeds are dominated by deciduous shrubs (e.g. *Salix rotundifolia, S. herbacea*), and at Niwot there are no evergreen shrubs in snowbeds.
- **High above-ground to below-ground biomass ratios** compared to other Arctic plant communities. (e.g. biomass ratio in *Cassiope* community on Ellesmere Island is 1:1 compared to 1:3.8-1:6.7 in wet sedge-moss meadows).
- However, many moderate snow-bed plants especially in the alpine have well-developed roots, rhizomes, and stem bases for storage of photosynthate.
- **Abundant attached dead contributes to high aboveground:belowground ratios.** Over 90% of aboveground standing biomass is non-photosynthetic tissues. Attached dead may improve thermal regime of plants.
- Animals complicate the nutrient picture (more on this later).

Cassiope tetragona
Photos: D.A. Walker

Growth strategies in snow bed plants

- **Foliosphere** (aboveground plant parts)
  - Function most influenced by light, air temperature, humidity, wind.
- **Rhizosphere** (belowground)
  - Most influenced by soil temperature, soil stability, and water, nutrient and oxygen availability.

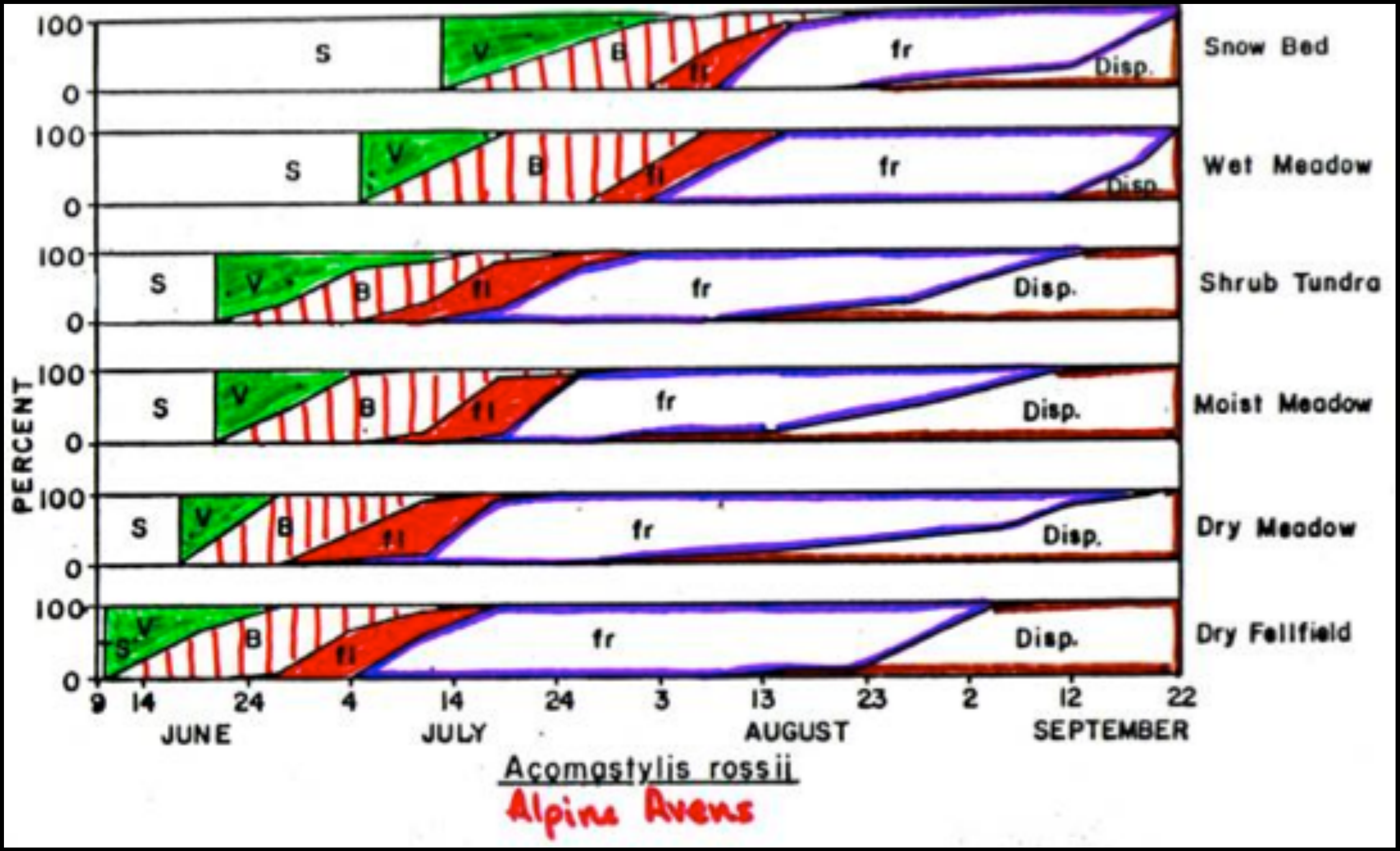
- **Contrast between foliosphere and rhizosphere microclimates can be extreme**
  - especially in high alpine snow bed sites with intense solar radiation and high temperatures in the foliosphere vs. very cold rhizosphere environment caused by snow meltwaters.
- Microenvironments within snowbeds are spatially very complex.
  - Soil temperature, length of growing season, and exposure to winds are highly dependent on snow depth and timing of snow melt.
  - Soil moisture conditions highly dependent on topographic situation.

- Very hard to study this environment.

Short growing season: Phenology

- The study of the time of appearance of characteristic periodic events in the life cycles of organisms and how these events are influenced by factors, such as temperature, latitude, altitude, and snow. Example shows timing of phenology events for *Acomastylis rossii* after snow melt in each of the major plant noda on Niwot Ridge.

Acomastylis rossii
Photo: D.A. Walker



Growth strategies for fellfield plants

Much more information on tundra plants growing in extreme cold and windy environments:

Adaptations to windy cold-winter conditions:

- **Cushion forms and tightly packed small leaves minimize effects of abrasion by wind-blown snow and mineral material (Billings and Mooney 1968).**

High UV radiation (high UV):

- **Anthocyanin (red) pigments (Caldwell 1968) decrease epidermal UV penetration. Common red tissues in many alpine plants.**

Billings, W. D. and H. A. Mooney. 1968. The ecology of arctic and alpine plants. Biological Review 43:481-529.

Billings, W. D. 1974. Arctic and alpine vegetation: plant adaptations to cold summer climates. Pages 403-443 in R. G. Barry and J. D. Ives, editors. *Arctic and Alpine Environments.* Methuen, London.

Fellfield community, Niwot Ridge with aerodynamic cushion plant growth forms. Photo: D.A. Walker

Paronychia pulvinata
Photo D. A. Walker

Production

- Measurements of production in Niwot communities (Table, May, 1976; M.D. Walker 1994) and showed the least production in the deepest snowbed (less than the fellfield).
- However, heavy snowfall years (for example following El Niño years in the Colorado alpine) often correspond to years of high productivity in moderate and low snow areas (M.D. Walker et al. 1995).
- Greater leaf lengths and number of leaves related to higher soil moisture from snow melt during period of maximum growth.
- McGuire (1991) showed positive correlation between number of flowers and cumulative snowfall. Cold winter soil temperature in low-snow years appear to negatively affect production.
- In the alpine, soil moisture was overwhelmingly important to biomass production, and is most strongly linked to spring soil moisture.

Plant community	Production ($g\ m^{-2}\ day^{-1}$)
Fellfield	164 ± 12
Dry meadow	197 ± 18
Moist meadow	218 ± 23
Wet meadow	214 ± 21
Snowbed	**113 ± 15**

Conclusion: Very difficult to make generalities about the nature of chionophytes

- Highly variable nature of snowbed environments creates high diversity of adaptations to survive in these environments.

- Best approaches are detailed autecological studies of the physiology of the plants such as those of Katherine Bell’s (1979) heroic efforts to study *Kobresia myosuroides* year round in the alpine of Rocky Mountain National Park.

(Bell, K. L. and L. C. Bliss. 1979. Autecology of Kobresia bellardii: Why winter snow accumulation limits local distribution. Ecological Monographs 49:377-402.)

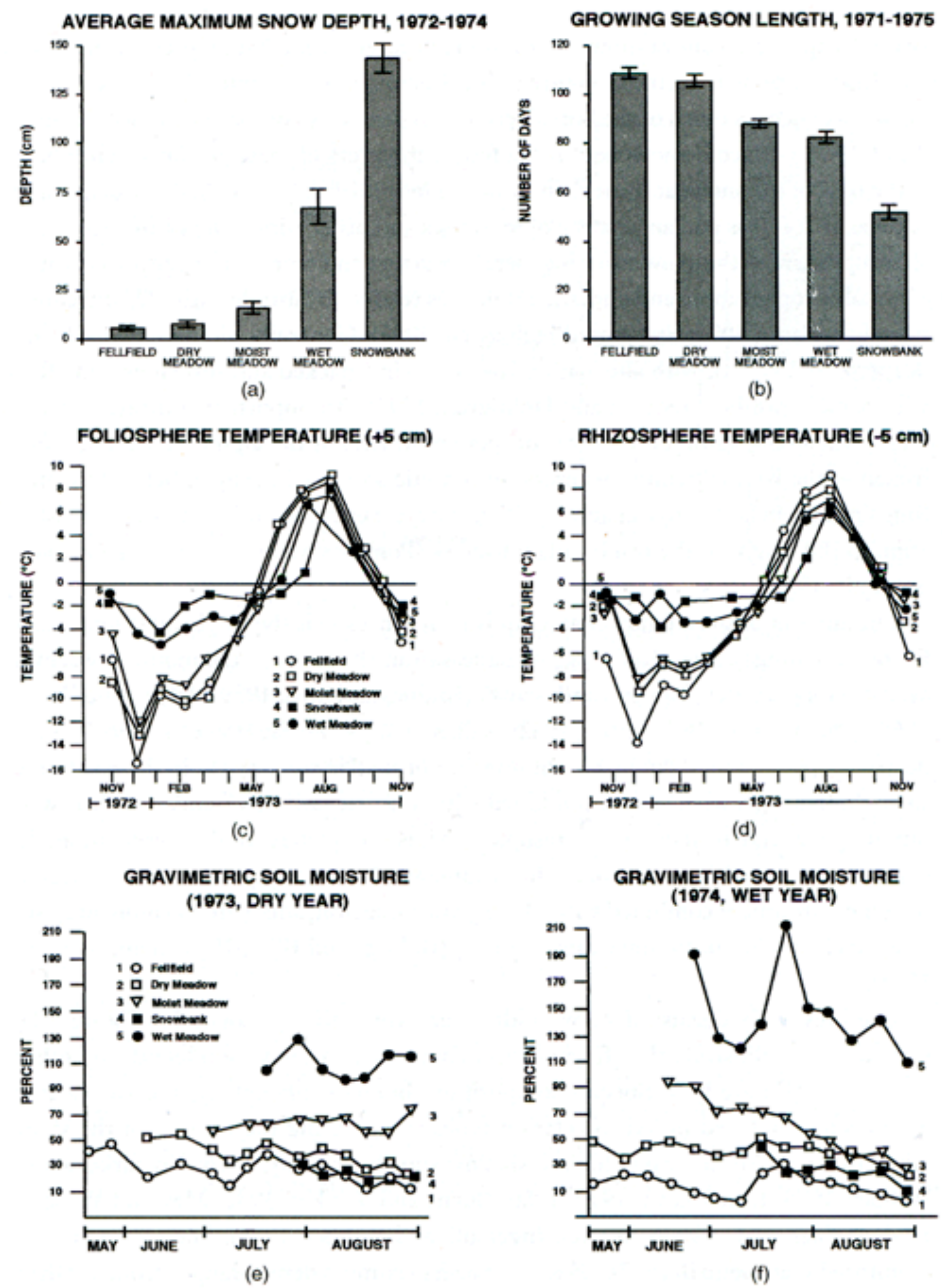
Subnivian temperature

Much biological activity occurs beneath the snow because of relatively warm conditions, especially in the lower alpine of temperate regions.

But other factors are also important:

- Shortened growing season
- Delayed warming in spring.
- Large year-to-year effects on soil moisture (depending on position in snow bed)

- Walker, D. A., W. D. Billings, and J. G. de Molenaar. 2001. Snow-vegetation interactions in tundra environments. Pages 266-324 in H. G. Jones, R. W. Hoham, J. W. Pomeroy, and D. A. Walker, editors. Snow Ecology. Cambridge University Press, Cambridge.



Subnivian Temperatures much colder in the Arctic

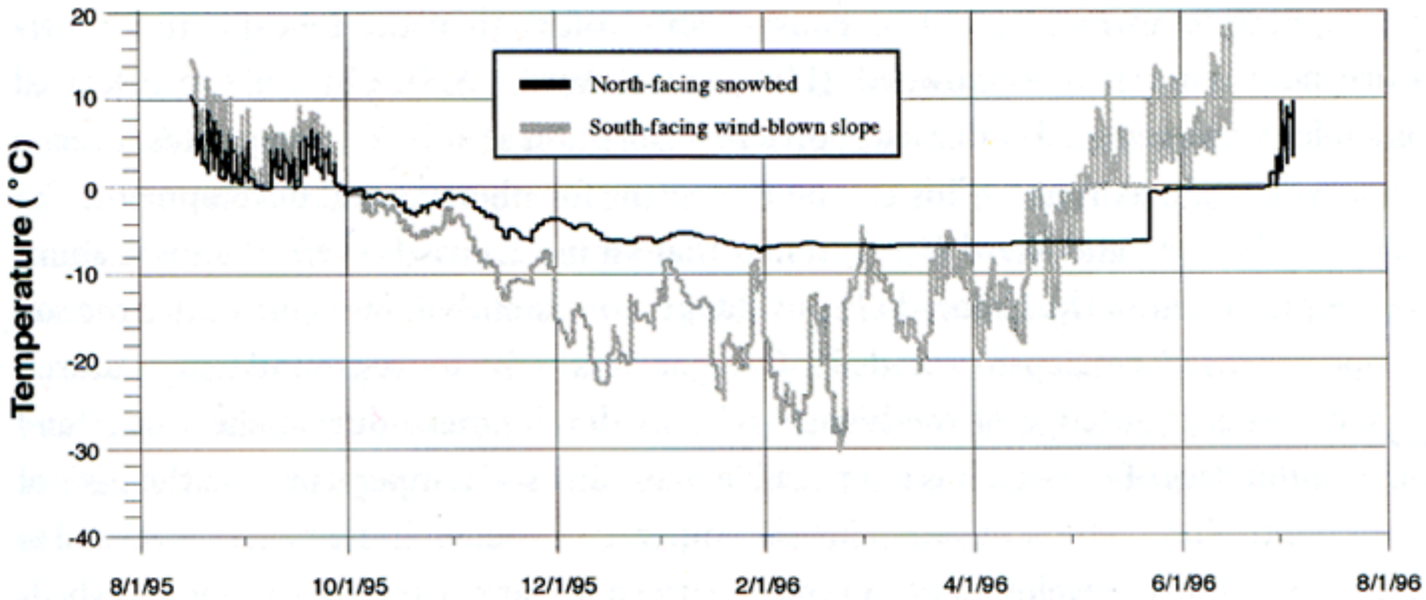


Figure 6.8. Soil temperature at 2-cm depth at two sites at Toolik Lake Alaska, August 1995–July 1996. (a) A windblown south-facing slope with minimal snow cover throughout the winter. Vegetation at this site is a dry *Dryas octopetela–Selaginella sibirica* community. (b) A deep north-facing snowdrift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

Note: warmer soil temperatures on north-facing slope because of deeper snow.
Auerbach and Halfpenny (1991) found the same in the Tetons despite colder mean air temperatures.

Walker, D. A., W. D. Billings, and J. G. de Molenaar. 2001. Snow-vegetation interactions in tundra environments. Pages 266-324 in H. G. Jones, R. W. Hoham, J. W. Pomeroy, and D. A. Walker, editors. Snow Ecology. Cambridge University Press, Cambridge.

Landscape-scale response to snow: heterogeneous alpine and arctic snow environments

Marked effect of topography and snow distribution on on soil conditions and plant communities.

Photo: Niwot Ridge treeline area, D.A. Walker

Photos: D.A. Walker

Windblown sites:
(Fellfields)

- **Association: *Sileno – Paronychietum* Willard 1963**
- **Dry wind-exposed fellfields , >200 snow-free days.**

Dry meadows, shallow snow

- **Association: *Selaginello densae – Kobresietem myosuroidis* Cox 1933**
- **Subxeric to mesic turfs on gentle slopes, 150-200 snow-free days.**

Photos: D.A. Walker

Moist meadows, early melting snow beds

Photos: D.A. Walker

Subxeric to mesic turfs on gentle slopes, often with strong gopher disturbance, 100-150 snow-free days.

- **Upper left: Association*: Stellario laetae – caespitosae* Willard 1963 (mesic)**
- **Lower left: Association: *Acomastyletum rossii* Willard 1963 (mesic)**
- **Right: Association*: Deschampsio caespitosae – Trifolietum parryi* Komárková 1976 (subxeris to mesic)**

Late-melting snowbeds

- At least 5 associations including Association *Caricetum pyrenaicae* in deep well drained snowbeds, snow free <75 days.

Photos: D.A. Walker

Carex pyrenaica
Photo: D.A. Walker

Site characteristics along alpine snow gradient at Niwot Ridge, CO

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).

Interactions between snow, soil temperatures, gophers, vegetation and ecosystem function on Niwot Ridge

- **In winter gophers excavate tunnels in the snow and in the soil beneath the snow.**
- **They only are able to dig in unfrozen soils, so their distribution is limited to snow beds where the subnivian soil temperatures are near freezing.**
- **They stuff their snow tunnels with soil from their soil diggings and these long tubes then form the snake-like deposits (gopher castings) seen in spring on the soil surface after snow melts.**

Photos: D.A. Walker

Photo: Niwot LTER. http://culter.colorado.edu/Field_trip/gophtunl.html

Distribution of gophers by vegetation type along the snow gradient

Plant community	Gophers per ha
Fellfield (Sileno-Paronychietum & Trifolietum dasyphyllum)	3.6 ± 5.7
Dry meadow (Selaginello-Kobresietum myosuroidis)	7.1 ± 13.5
Moist meadow (Acomastylidetum rossii & Stellario-Deschampsietum caespitosae)	18.2 ± 25.1
Snowbank communities (Toninio-Sibbaldietum & Caricetum pyrenaicae	67.0 ± 72.9

Thorn, C. E. 1982. Gopher disturbance: its variability by Braun-Blanquet vegetation units in the Niwot Ridge alpine tundra zone, Colorado Front Range, U.S.A. Arctic and Alpine Research 14:45-51.

Evolution of gopher mounds during the summer

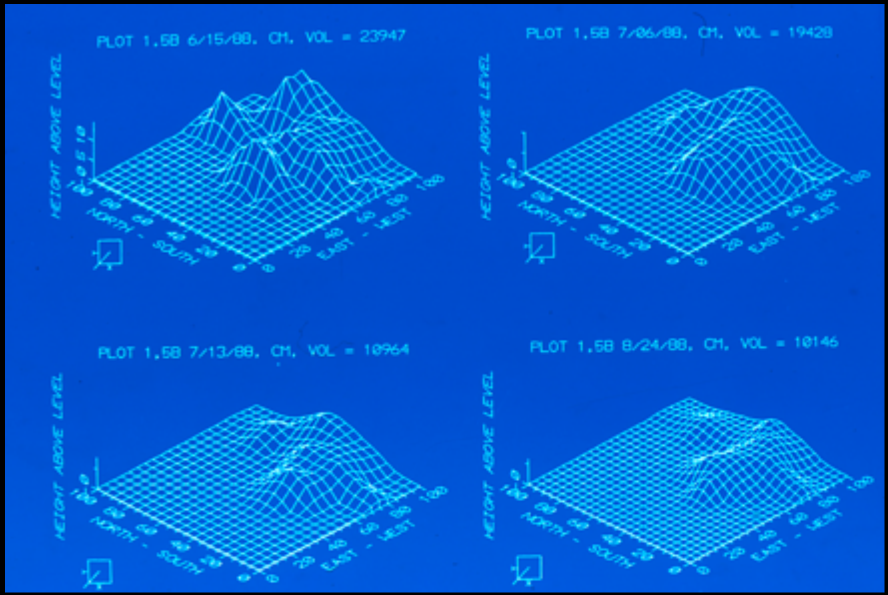
- **Strong winds winnow fine-grained silts and clays out of the mounds, leaving the courser particles.**

Thorn, C. E. 1982. Gopher disturbance: its variability by Braun-Blanquet vegetation units in the Niwot Ridge alpine tundra zone, Colorado Front Range, U.S.A. Arctic and Alpine Research 14:45-51

Photos: D.A. Walker

Evolution of gopher mounds during the summer

- Jim Halfpenny studied gopher mounds for many years in the Martinelli snowbed on Niwot Ridge.
- Made detailed maps of mounds in relationship to vegetation and tracked through time.
- Susan Sharrod followed with a Ph.D. dissertation that looked at nutrient and plant community details (Sharrod and Seastedt 1989; Sharrod et al. 2005)



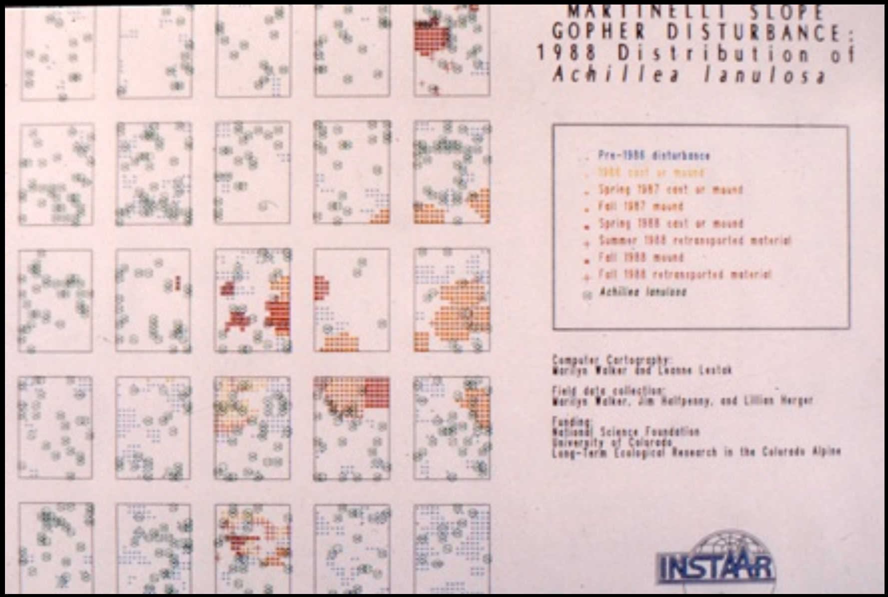


Photo: D.A. Walker. Maps courtesy of Jim Halfpenny

Soil biogeochemistry monitored at Martinelli Snowbed grid points using suction lysimeters

Photo: D.A. Walker.

Litaor, M. I., R. Mancinelli, and J. C. Halfpenny. 1996. The influence of pocket gophers on the status of nutrients in alpine soils. Geoderma 70:37-48.

Three key gopher publications

GEODERMA

Geoderma 70 (1996) 37–48

The influence of pocket gophers on the status of nutrients in Alpine soils

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Biogeochemistry **55:** 195–218, 2001.

Effects of the northern pocket gopher (*Thomomys talpoides*) on alpine soil characteristics, Niwot Ridge, CO

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Key words: alpine tundra, disturbance, erosion, northern pocket gopher, soil nutrients

Abstract. Effects of the northern pocket gopher (*Thomomys talpoides*) on surface soil characteristics were examined at the alpine site of Niwot Ridge, CO. We measured erosion of soil from gopher mounds and compared the characteristics of gopher mound (disturbed) and undisturbed soils in two major plant community types. Our measurements of erosion indicate long-term susceptibility of gopher-disturbed soils to redistribution by water and/or wind in this ecosystem. Ecosystem heterogeneity introduced by the gopher is reflected in significantly lower SOM in gopher mounds than in surrounding undisturbed soils, a characteristic which appears to be causally associated with other effects of gopher disturbance including changes in soil texture and significantly lower clays, total C, total N, total P, and labile P. In contrast to plant-available P, NO_3^- was higher and steadily increased for the short term in both gopher mound soils and those beneath the mounds. These pools of NO_3^- then decreased to pre-disturbance levels by the following spring. Collectively our results indicate that, through the physical manipulation of soil and subsequent effects on soil resources, the northern pocket

Arctic, Antarctic, and Alpine Research, Vol. 37, No. 4, 2005, pp. 585–590

Northern Pocket Gopher (*Thomomys talpoides*) Control of Alpine Plant Community Structure

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Abstract

We evaluated the importance of the northern pocket gopher (*Thomomys talpoides*) in controlling plant species composition and richness in two alpine tundra plant communities. We hypothesized that forb diversity and relative abundance is modified by gopher mounding activities in moist meadows of Niwot Ridge, Colorado, U.S.A., where both the pocket gopher and forbs are most concentrated. We tested this hypothesis with simulated gopher mounds. Forbs recovered faster following burial than graminoids or cushion plants, demonstrating a resilience that we propose confers a competitive advantage over other growth forms and favors forb dominance in moist meadows. Gopher effects on species richness varied according to spatial scale of measurement and community type. For one decade we monitored the responses of a sedge-dominated community to gopher activity in 1.5 m^2 plots that included both gopher mounds and intermound spaces and found that species richness was significantly positively correlated with recent disturbance. Species richness on the simulated gopher mounds (0.2 m^2) immediately declined significantly after burial but recovered within a year. When evaluated in conjunction with studies of gopher diet preferences and effects on ecosystem biogeochemistry, our findings suggest that the northern pocket gopher is instrumental in constructing a locally diverse alpine plant community.

Major conclusions:

- Gopher are a keystone species in these ecosystems and are particularly important geomorphic agents, altering the physiochemical environment of the alpine tundra (Thorn 1982, Sharrod et al. 2005, Litaor et al. 1996).
- Mixing activities of gophers lower the concentration of SOM, C, N, total P, exchangeable Ca, and K in mounds compared to surface horizons (Litaor et al. 1996), but NO_3^- and plant available P increased in the short term (Sharrod et al. 2005).
- Concentration of nitrate and ammonium in soil and interstitial water indicate that gophers greatly increased N cycling in well aerated soils (Litaor et al. 1996).
- Forbs recovered fastest from the disturbance, bestowing a competitive advantage to many flowers contributing strongly to species richness of the forb-rich communities found in most moist alpine meadows (Sharrod et al. 2005).

Treeline phenomena

- Krummholz
- Flagged trees
- Tree islands
- Ribbon forests

Niwot Ridge Treeline, Photo D.A. Walker

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

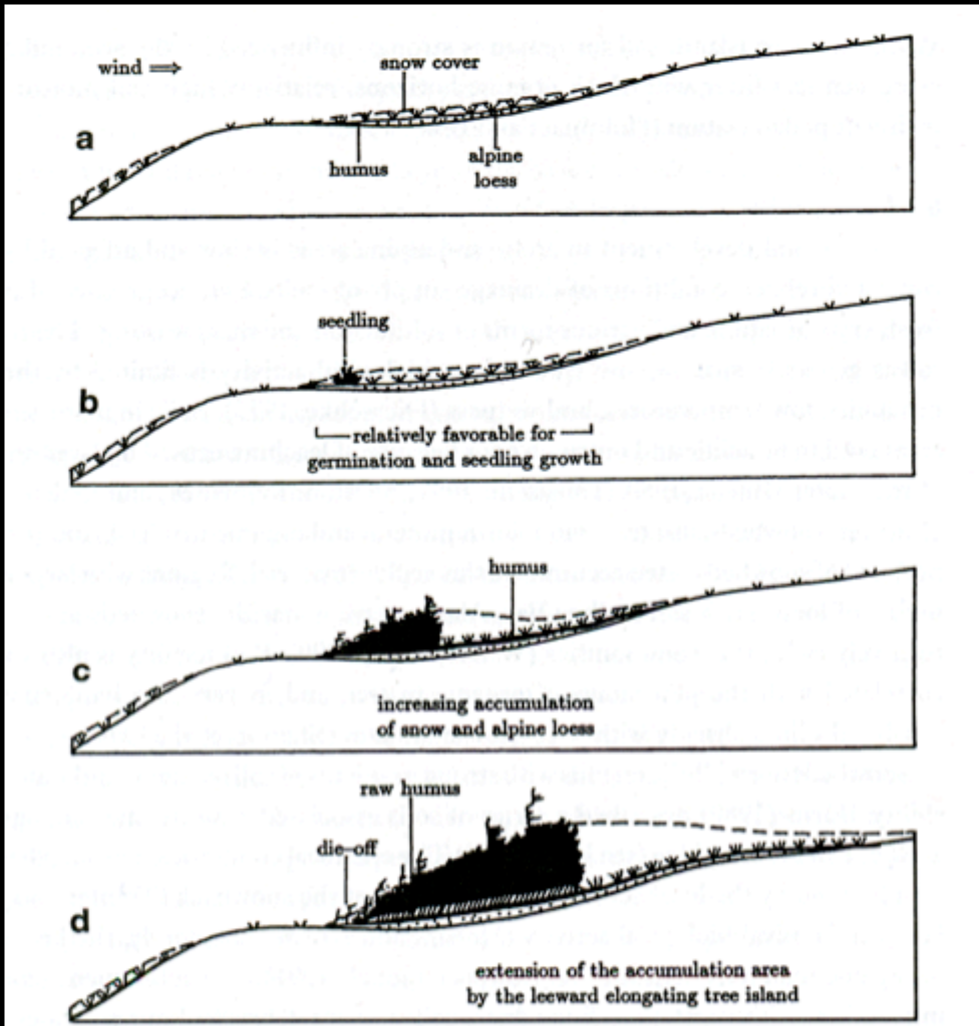
Ribbon forests on Buffalo Pass, CO. Photos courtesy of Dave Buckner

Ribbon forests

Parallel tree ribbons with snow glades between the ribbons occur in areas of deep winter snow and strong winds. Contributing causes include:

- **natural topographic high points such as solifluction lobes for seedling establishment,**
- **shortened growing season,**
- **more pocket gophers,**
- **late seed germination or germination failure,**
- **breakage and bending of the few trees that do become established,**
- **higher frequency of parasitic snow molds (Buckner 1979).**

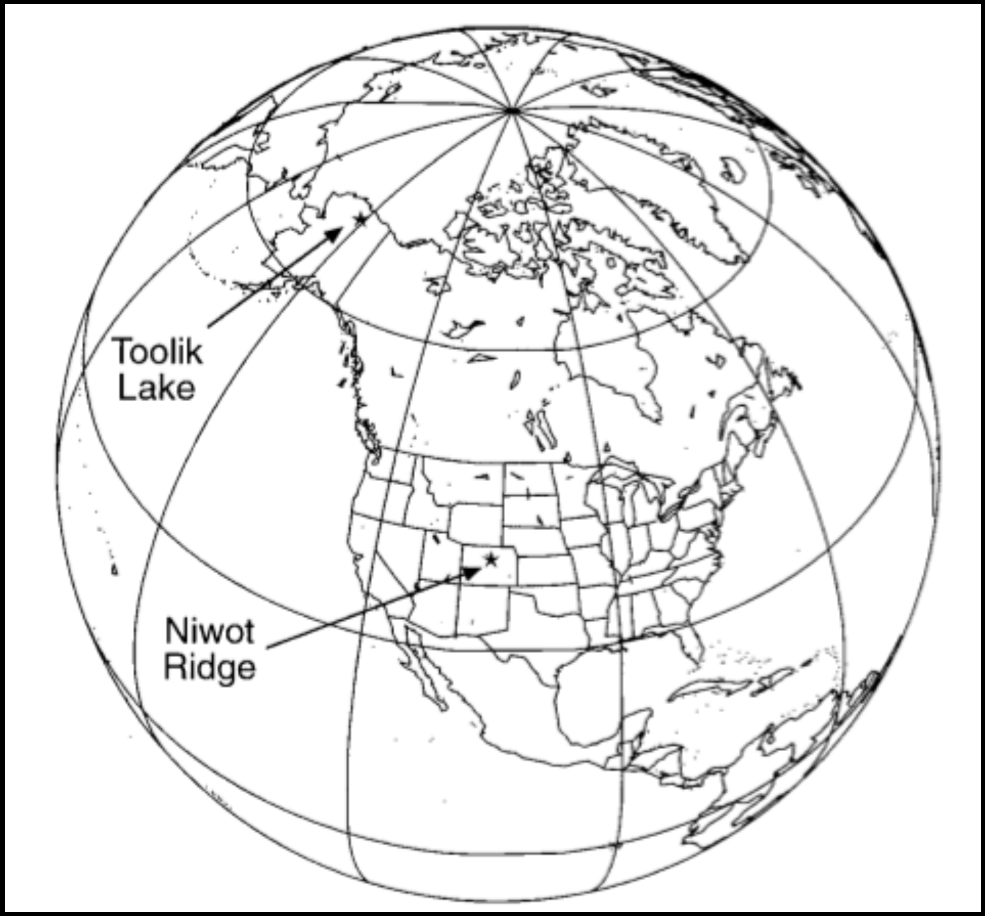
Migration of tree islands



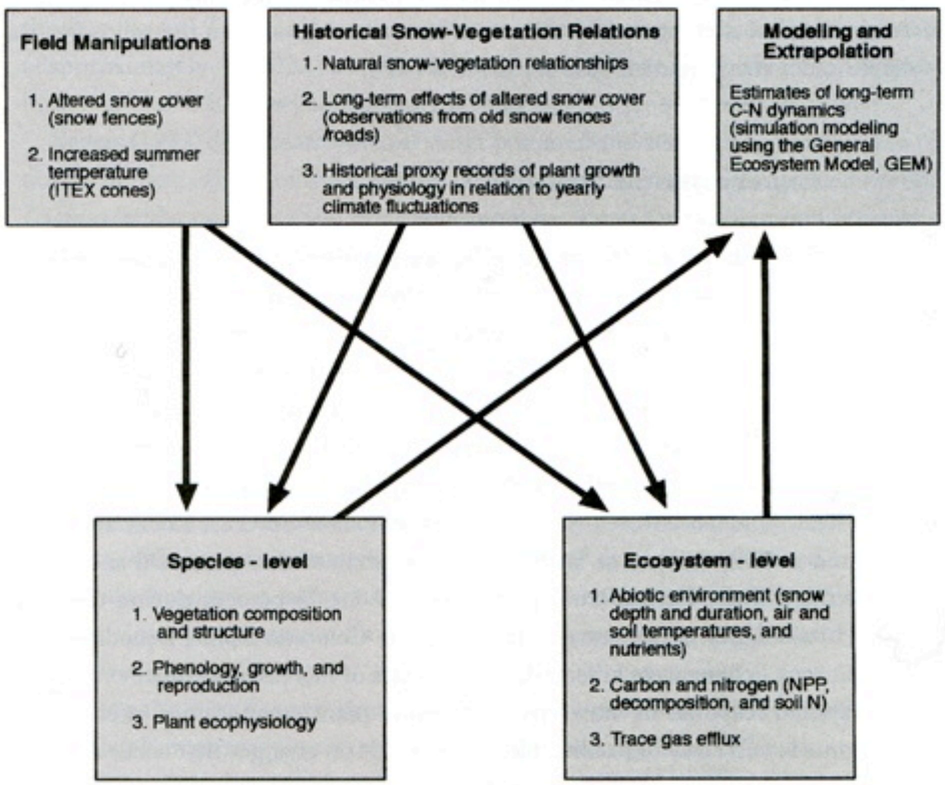
a. Open alpine fellfield with slight depression where fine grained loess and humus accumulate.
b. Seedlings establish in areas favorable for germination and growth, forming an incipient snow drift downwind of the seedling.
c. Tree island shaped by the wind with modified habitat within and downwind of the island.
d. Tree island controls the microsite, dieback on the windward side, and extension occurs on the leeward side through layering of the island.

Holtmeier, F.-K. and G. Broll. 1992. The influence of tree islands and microtopography on pedoecological conditions in the forest-alpine tundra ecotone on Niwot Ridge, Colorado Front Range, U.S.A. Arctic and Alpine Research 24:216-228.

Snow manipulation experiments



- Arctic site at Toolik Lake, AK
- Alpine site at Niwot Ridge, CO



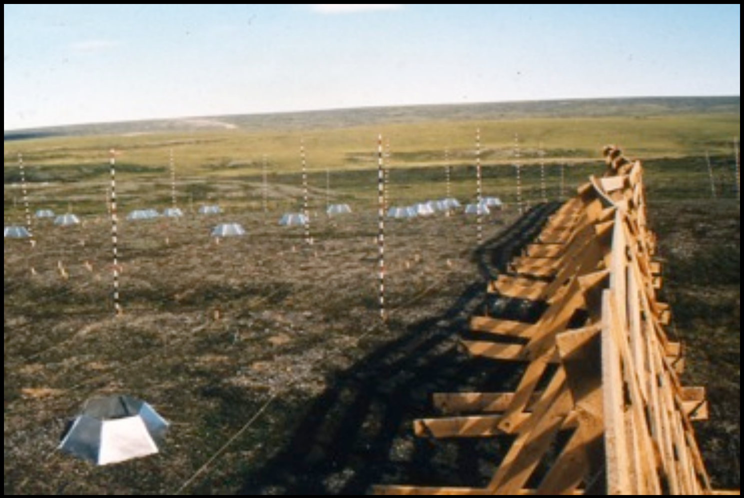
Experimental alteration of snow cover and temperature

- 2-m high snow fences at Toolik Lake and Niwot Ridge.
- International Tundra Experiment (ITEX) open-topped chambers (OTCs, greenhouses) to increase temperature.

Walker, M. D., D. A. Walker, J. M. Welker, A. M. Arft, T. Bardsley, P. D. Brooks, J. T. Fahnestock, M. H. Jones, M. Losleben, A. N. Parsons, T. R. Seastedt, and P. L. Turner. 1999. Long-term experimental manipulation of winter snow regime and summer temperature in arctic and alpine tundra. Hydrological Processes 13:2315-2330.

Niwot and Toolik snow fences

Toolik Dry Site Fence



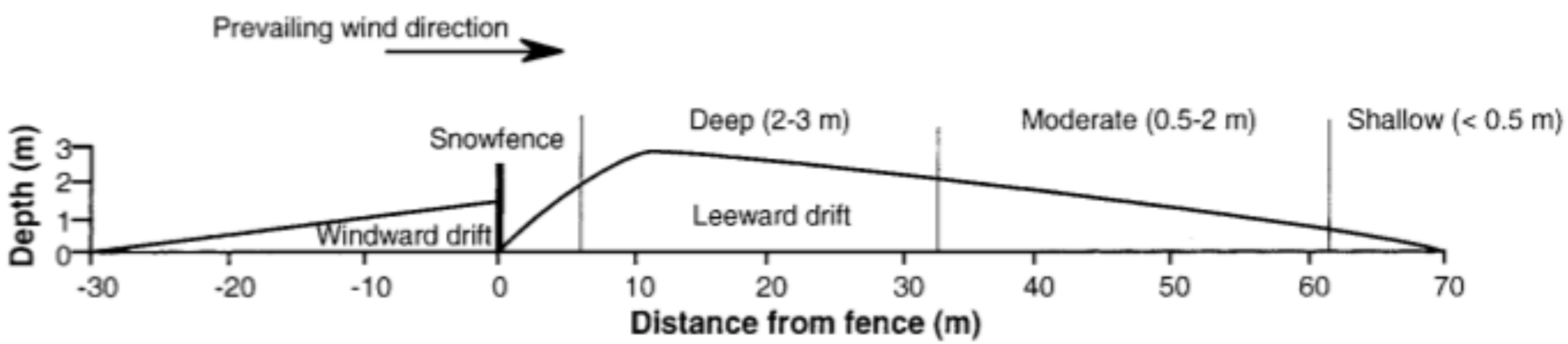
Toolik Moist Site Fence

Both Toolik Fences in Winter

Niwot Fence and Drift in Spring

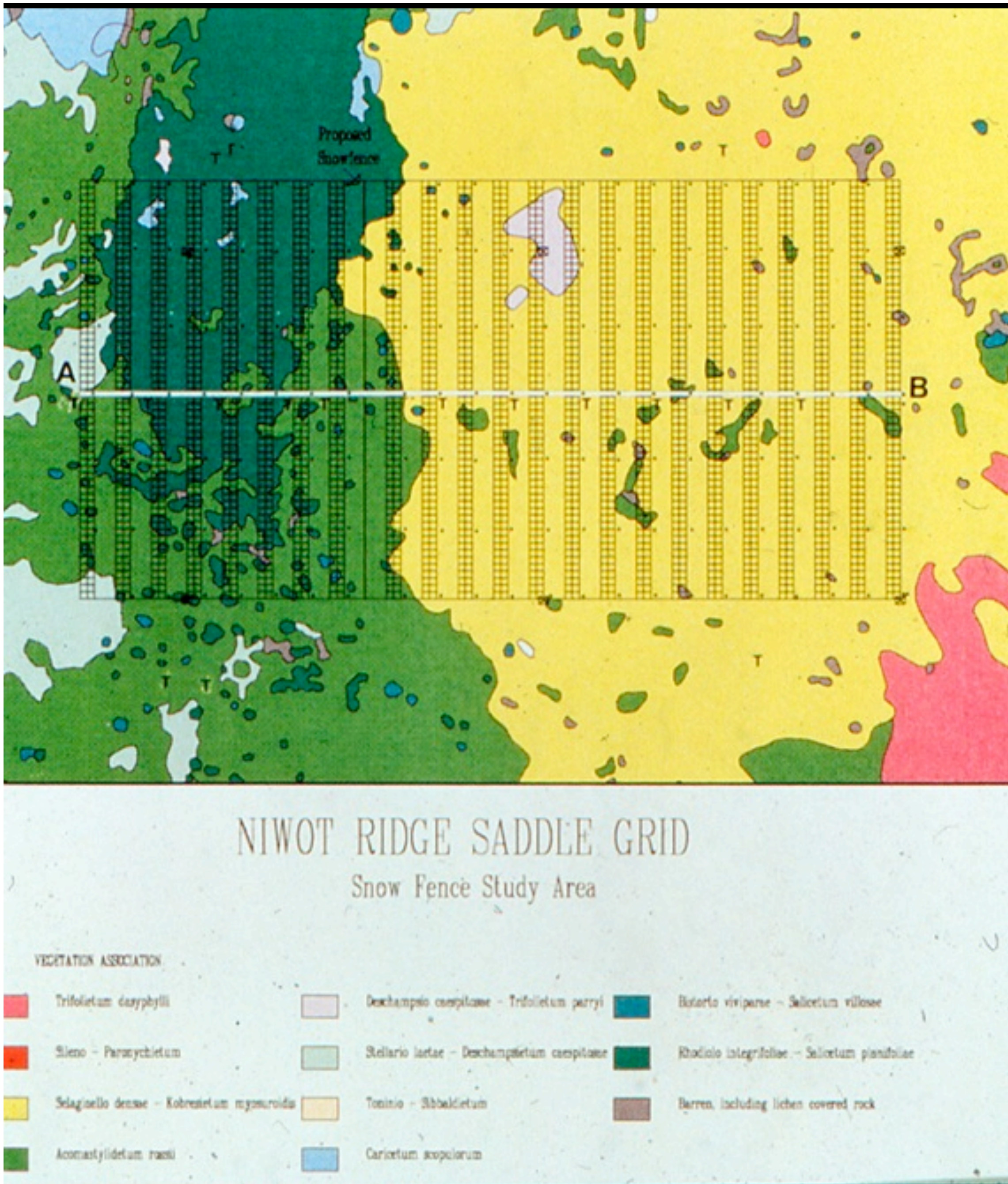
Photos: D.A. Walker

Snow drift depth zones

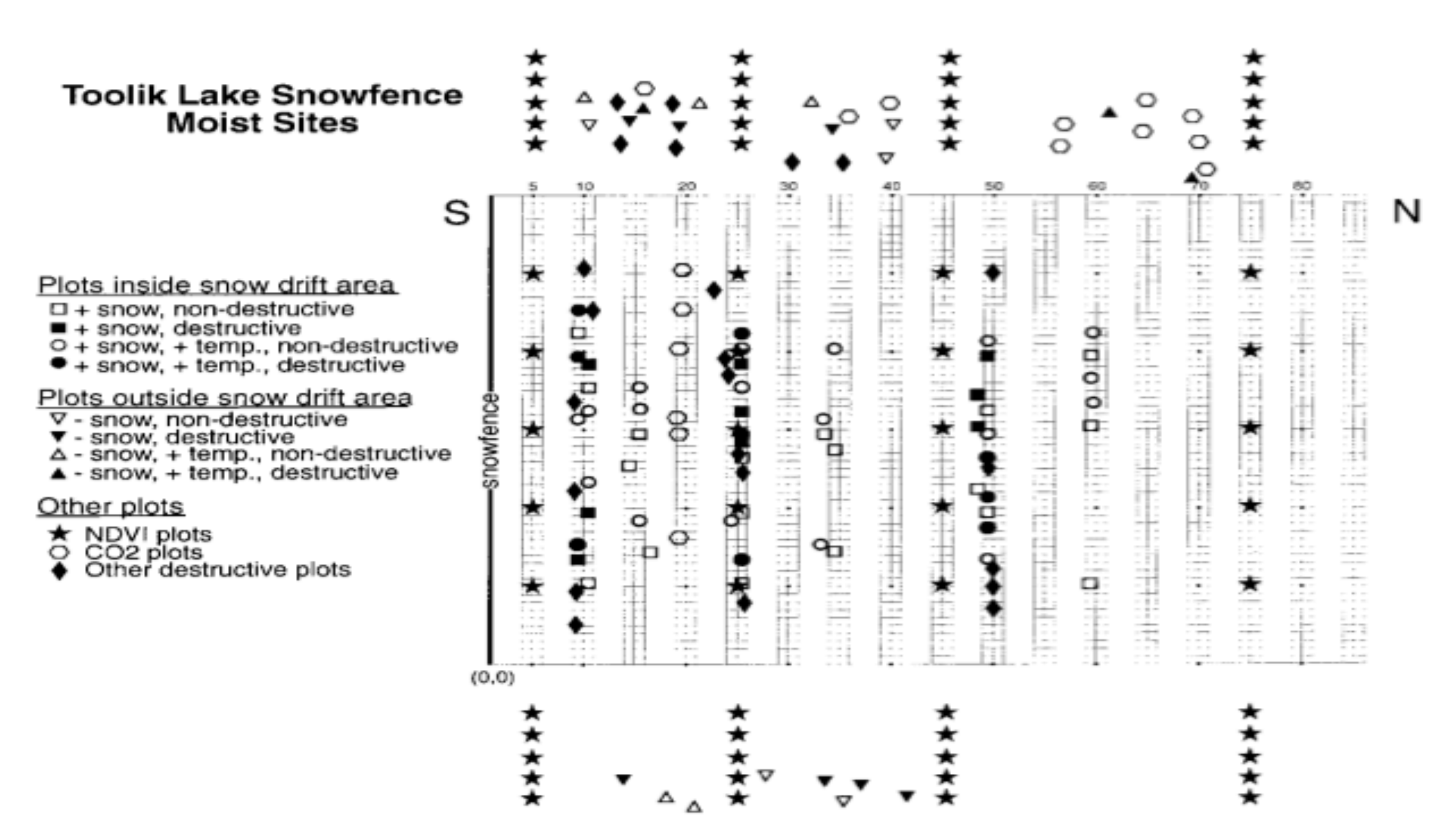


Walker, M. D., D. A. Walker, J. M. Welker, A. M. Arft, T. Bardsley, P. D. Brooks, J. T. Fahnestock, M. H. Jones, M. Losleben, A. N. Parsons, T. R. Seastedt, and P. L. Turner. 1999. Long-term experimental manipulation of winter snow regime and summer temperature in arctic and alpine tundra. Hydrological Processes 13:2315-2330.

Vegetation Map of snow-fence area



Experimental layout



Walker, M. D., D. A. Walker, J. M. Welker, A. M. Arft, T. Bardsley, P. D. Brooks, J. T. Fahnestock, M. H. Jones, M. Losleben, A. N. Parsons, T. R. Seastedt, and P. L. Turner. 1999. Long-term experimental manipulation of winter snow regime and summer temperature in arctic and alpine tundra. Hydrological Processes 13:2315-2330.

Fence effect on subnivian soil temperatures

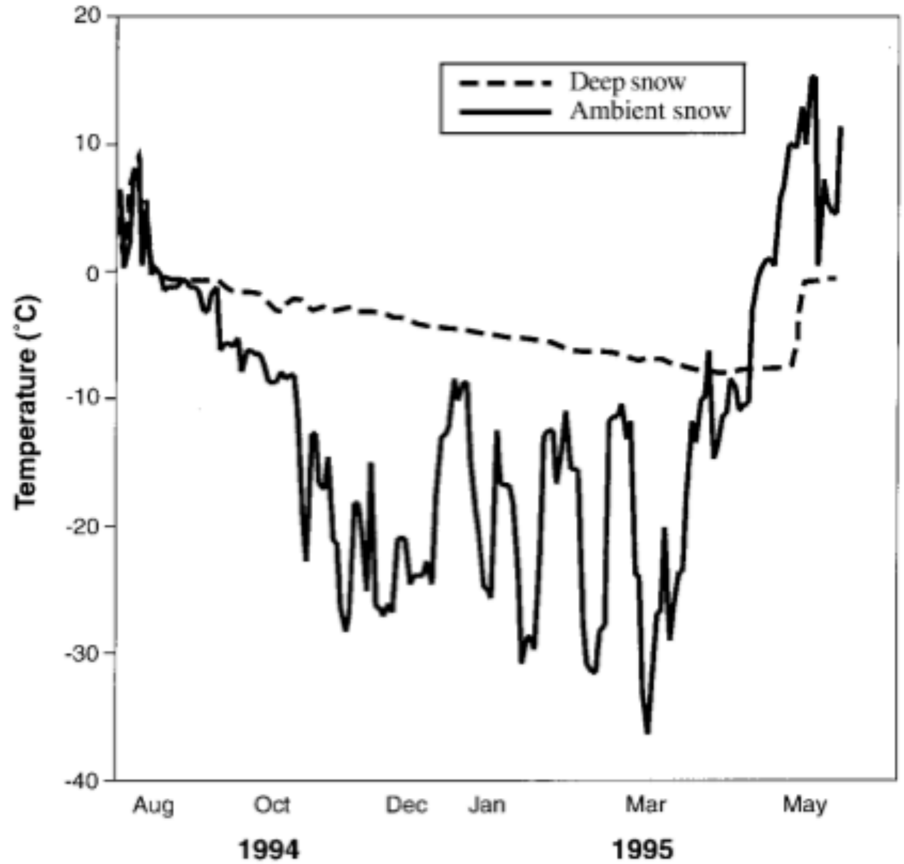
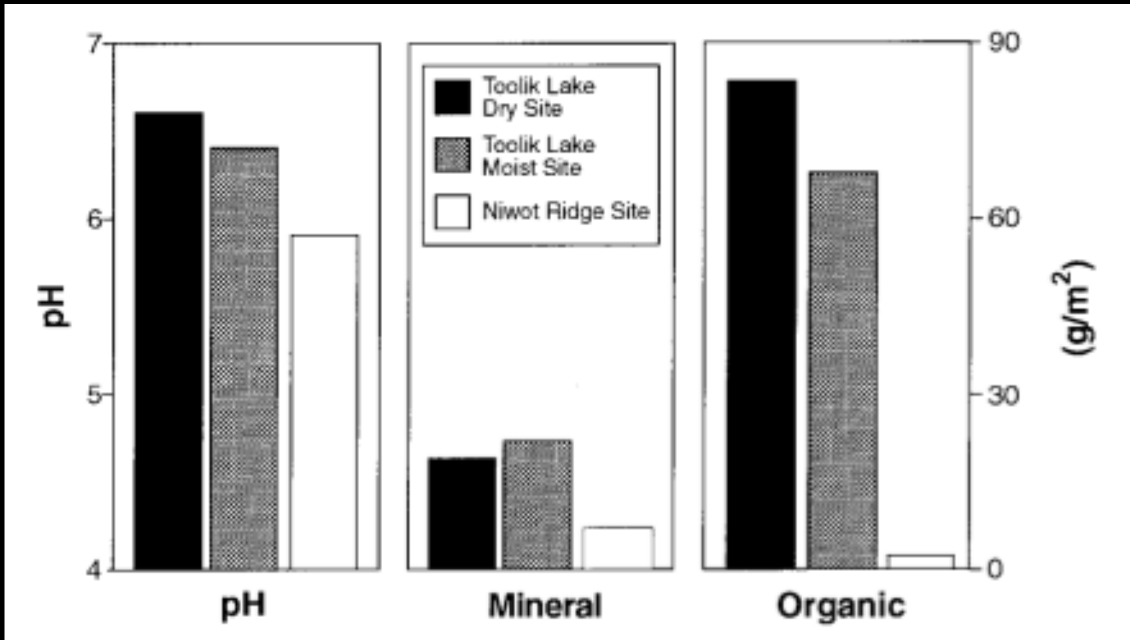
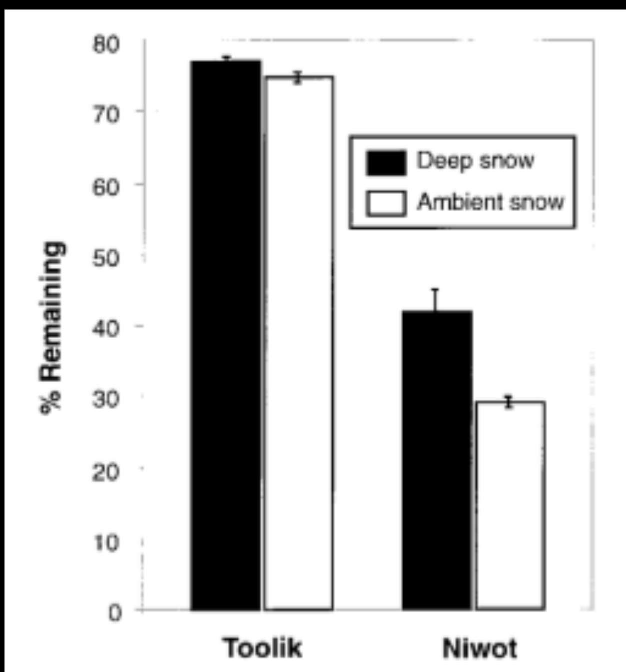


Figure 6. Soil surface temperatures beneath the Toolik Late dry-site fence and control plots, winter 1994–1995. Temperatures were recorded every 48 minutes using Hobo temperature logging devices (Onset Computer Corporation, Pocasset, MA). A very similar pattern was found at Niwot Ridge

Walker, M. D., D. A. Walker, J. M. Welker, A. M. Arft, T. Bardsley, P. D. Brooks, J. T. Fahnestock, M. H. Jones, M. Losleben, A. N. Parsons, T. R. Seastedt, and P. L. Turner. 1999. Long-term experimental manipulation of winter snow regime and summer temperature in arctic and alpine tundra. Hydrological Processes 13:2315-2330.



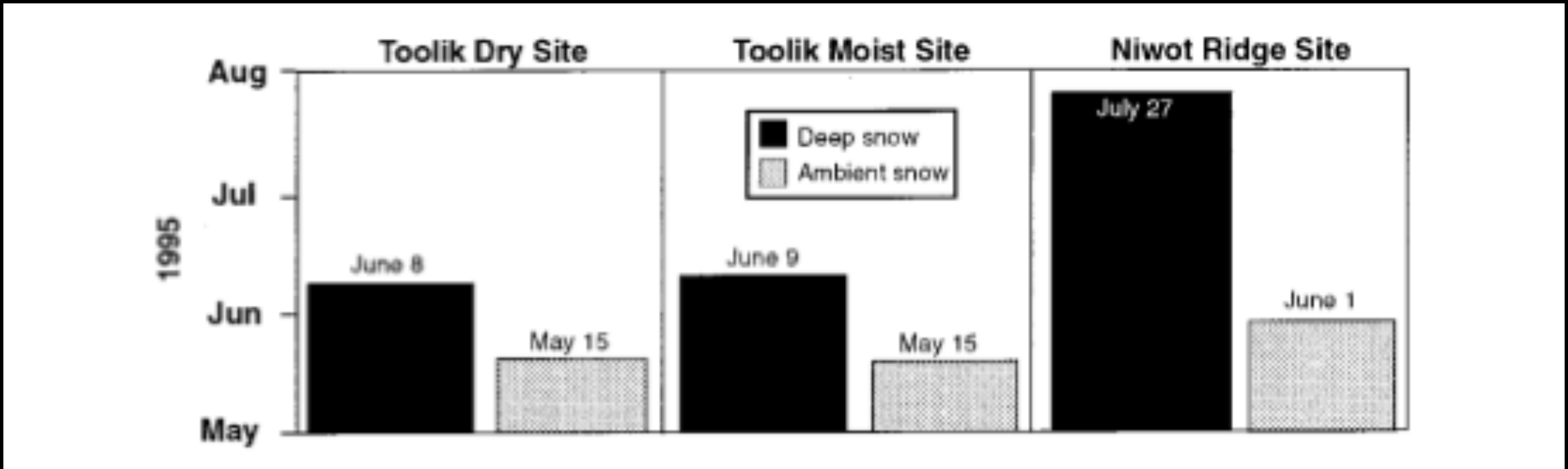
Comparison of effects of Niwot and Toolik fences on snow pH, mineral and organic-matter deposition and decomposition



- More imput of loess and organic debris in snow pack at Toolik
- Higher snow pH at Toolik
- Fence had greater effect on decomposition rates at Niwot because of warmer soils.

Walker, M. D., D. A. Walker, J. M. Welker, A. M. Arft, T. Bardsley, P. D. Brooks, J. T. Fahnestock, M. H. Jones, M. Losleben, A. N. Parsons, T. R. Seastedt, and P. L. Turner. 1999. Long-term experimental manipulation of winter snow regime and summer temperature in arctic and alpine tundra. Hydrological Processes 13:2315-2330.

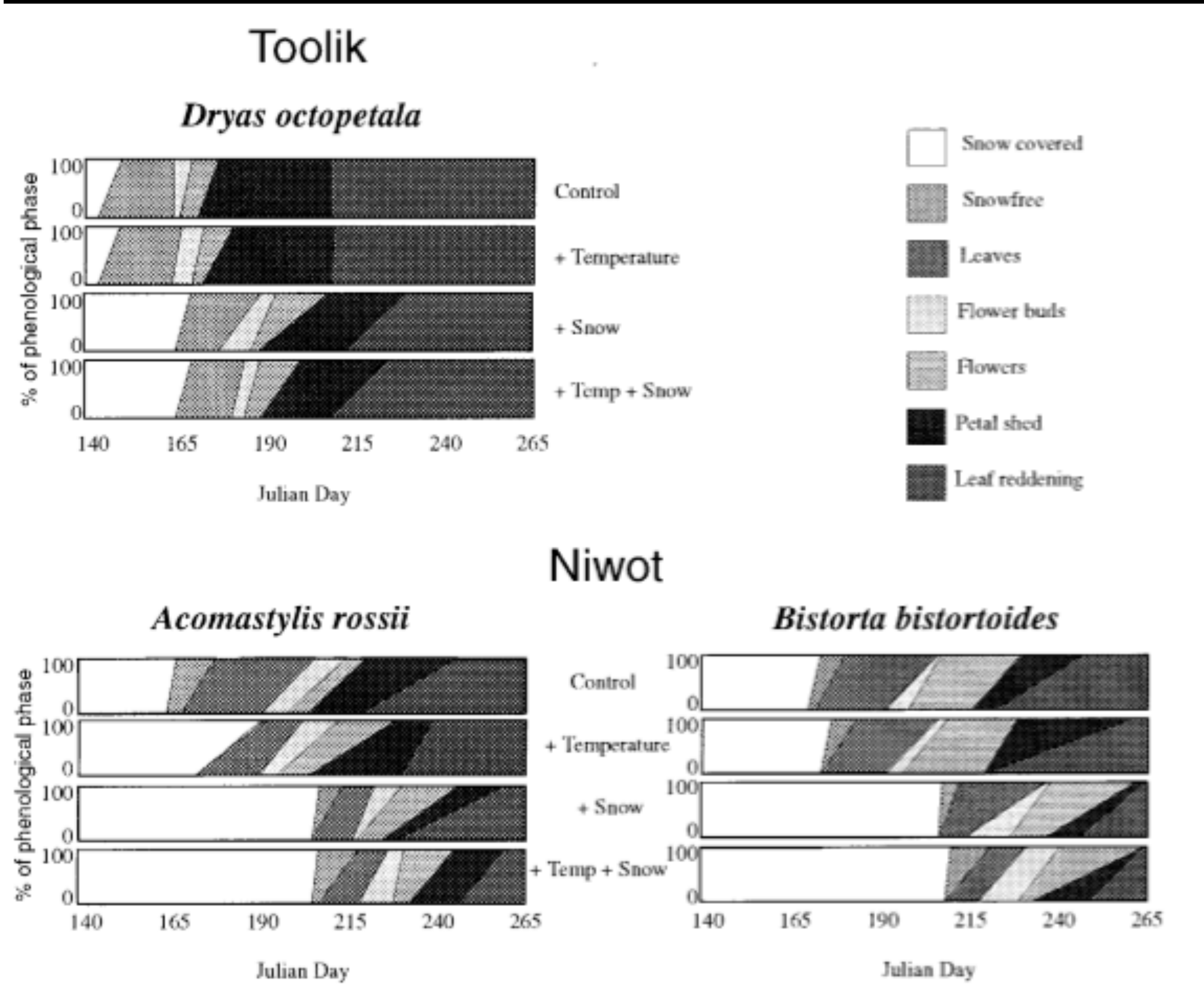
Meltout dates at Toolik and Niwot



- **Much later meltout dates in alpine, for both experimental and ambient plots.**

Walker, M. D., D. A. Walker, J. M. Welker, A. M. Arft, T. Bardsley, P. D. Brooks, J. T. Fahnestock, M. H. Jones, M. Losleben, A. N. Parsons, T. R. Seastedt, and P. L. Turner. 1999. Long-term experimental manipulation of winter snow regime and summer temperature in arctic and alpine tundra. Hydrological Processes 13:2315-2330.

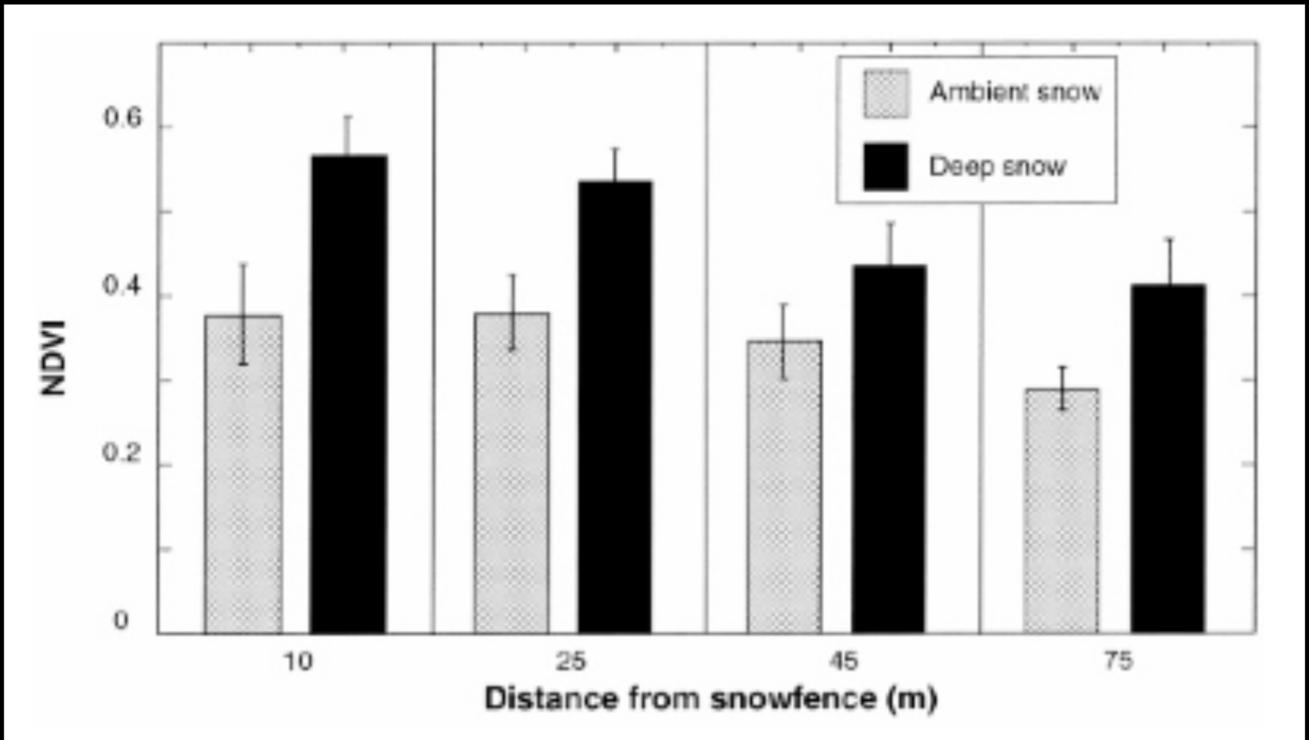
Experimental effects of increased temperature and snow on plant phenology



- Phenological events recorded weekly.
- Earlier start and end to growing season at Toolik.
- Compressed phenology on snow treatment plots.
- Increased snow had much greater effect on phenology than temperature.
- Greater effects of both temperature and snow in the alpine.

Walker, M. D., D. A. Walker, J. M. Welker, A. M. Arft, T. Bardsley, P. D. Brooks, J. T. Fahnestock, M. H. Jones, M. Losleben, A. N. Parsons, T. R. Seastedt, and P. L. Turner. 1999. Long-term experimental manipulation of winter snow regime and summer temperature in arctic and alpine tundra. Hydrological Processes 13:2315-2330.

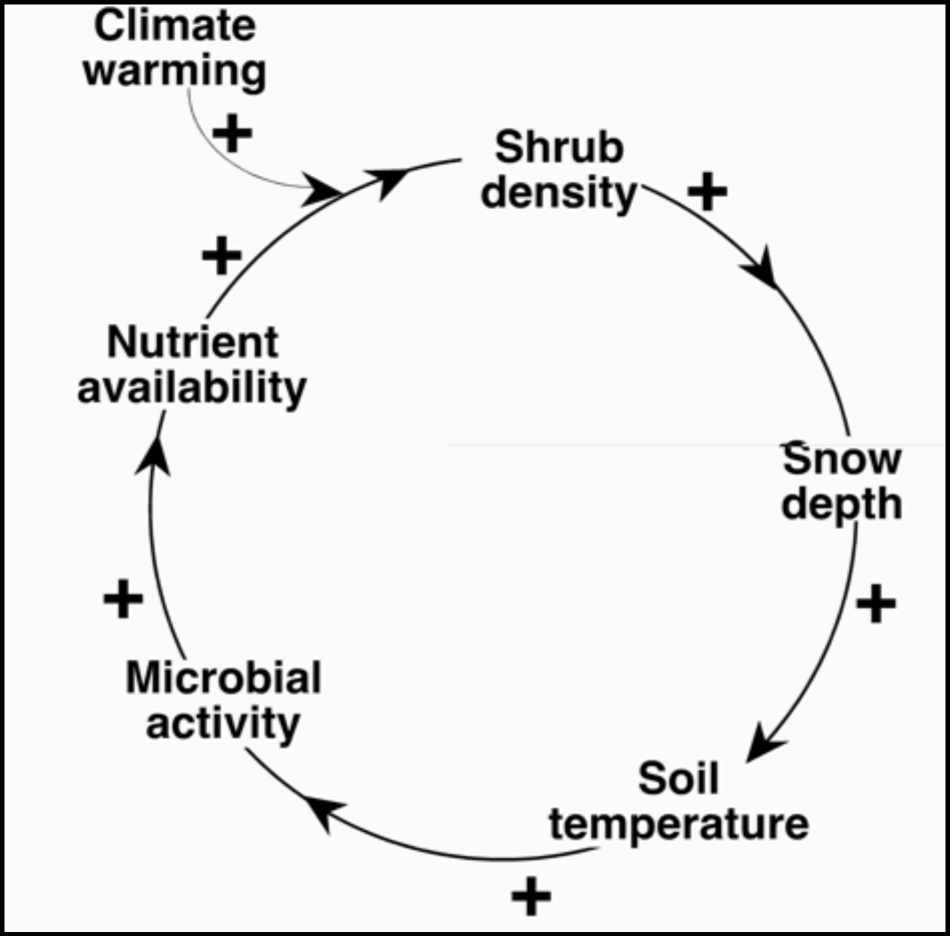
Experimental effects of increased snow on vegetation NDVI at Niwot Ridge



- End of season NDVI (early Sept.) at four distances from the snow fence.
- Ambient areas are just outside fence area at same distances.
- Natureal gradient reflects drier conditions downwind from the fence area
- Fence has significant effect at all distances.

Walker, M. D., D. A. Walker, J. M. Welker, A. M. Arft, T. Bardsley, P. D. Brooks, J. T. Fahnestock, M. H. Jones, M. Losleben, A. N. Parsons, T. R. Seastedt, and P. L. Turner. 1999. Long-term experimental manipulation of winter snow regime and summer temperature in arctic and alpine tundra. Hydrological Processes 13:2315-2330.

Snow-shrub hypothesis



Sturm, M., McFadden, J.P., Liston, G.E., Chapin III, F.S., Racine, C.H., Holmgren, J. 2001. Snow-shrub interactions in arctic tundra: a hypothesis with climatic implications. Journal of Climate. 14:336-344.

Experimental effects of increased snow on nitrogen mineralization and phenology

Arctic, Antarctic, and Alpine Research, Vol. 40, No. 1, 2008, pp. 27–38

Effects of Simulated Climate Change on Plant Phenology and Nitrogen Mineralization in Alaskan Arctic Tundra

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Abstract

This study was part of the International Tundra Experiment (ITEX) and examined the effects of increased winter snow depth and decreased growing season length on the phenology of four arctic plant species (*Betula nana*, *Salix pulchra*, *Eriophorum vaginatum*, and *Vaccinium vitis-idaea*) and seasonal nitrogen availability in arctic snowbed communities. Increased snow depth had a large effect on the temporal pattern of first date snow-free in spring, bud break, and flowering, but did not affect the rate of plant development. By contrast, snow depth had a large qualitative effect on N mineralization in deep snow zones, causing a shift in the timing and amount of N mineralized compared to ambient snow zones. Nitrogen mineralization in deep snow zones occurred mainly overwinter, whereas N mineralization in ambient snow zones occurred mainly in spring. Concentrations of soil dissolved organic nitrogen (DON) were approximately 5 times greater than concentrations of inorganic nitrogen (DIN) and did not vary significantly over the season. Projected increases in the depth and duration of snow cover in arctic plant communities will likely have minor effects on the rate of plant phenological development, but potentially large effects on patterns of N cycling.

DOI: 10.1657/1523-0430(06-099)[BORNER]2.0.CO;2

- **Borner, A.P., Kielland, K., Walker, M.D. 2008. Effects of simulated climate change on plant phenology and nitrogen mineralization in Alaskan arctic tundra. Arctic, Antarctic and Alpine Research. 40:27-38.**

- **Focus of Literature Discussion group 2 on Thursday.**

Take home points

1. Snow affects ecosystems at a variety of scales and has different effects in temperate alpine areas compared to the Arctic (slides 10-14).
2. Landscape-level effects of snow can be seen in the pattern of plant species, plant communities, plant phenology, plant production, rhizosphere and foliosphere temperatures, and soil moisture along mesotopographic gradients, and these vary in alpine compared to arctic areas (slides 15-34).
3. Compared to windy sites, site factors within snow drift environments are quite complex and species responses and plant communities reflect this complexity (slides 15-29).
4. Subnivian animals complicate the effects of snow cover. For example, gopher distribution is controlled by snow in the Colorado alpine and has a major effect of biogeochemistry and plant communities of alpine environments (slides 35-40).
5. Treeline tree growth is altered by snow and wind (e.g., krummholz, migrating tree islands, ribbon forests) (slides 41-43).
6. Snow fence studies in Arctic and alpine areas are examining the possible effects of altered snow regimes due to climate change (slides 44-54).