

THE NIWOT RIDGE 1994-95 LTER ANNUAL REPORT

(also see the NWT-LTER homepage: <http://culter.colorado.edu:1030/>)

Below are questions and hypotheses taken from the 1992 NWT LTER Proposal. All 1992 material is in quotes. This report emphasizes work in progress and new hypotheses under study during the 1995 field season.

Overall goal: "To understand the influence of snowpack and summer precipitation on ecosystem processes and landscape patterns and to use this understanding to predict responses to climatic change."

1995 Update: This overall goal remains largely unchanged. Climatic data continue to support the rationale for these analyses.

Is the total net energy input to the alpine/sub-alpine decreasing on Niwot Ridge, and, if so, what are the biological responses?

Specifically, the lapse rate between the subalpine and alpine climate stations is decreasing (-0.039 degrees Celsius/km/yr, $P < 0.01$ level) since 1953, and the short-wave solar radiation has decreased at both climate stations (approximately 3 watts/m²/yr) since 1972 (Losleben, unpubl.). The lapse rate decrease reflects changes in atmospheric water vapor, cloud cover, and air mass stability. These factors all contribute to feedback processes involving precipitation, temperature, and snowpack.

In addition to the physical aspects of increased snowpack, emphasis has been given to examination of enhanced nitrogen deposition on biotic processes, on quantifying the nitrogen cycle, and on the mechanisms controlling nitrogen fluxes. Another areas of emphasis has been on the morphological and physiological adaptations of plants to abiotic and biotic interactions.

LTER General Objectives:

1. "Process studies will improve our understanding of relationships between rainfall, dryfall, and snowpack patterns, biological processes, and the landscape."
2. "Modeling will link studies of processes and patterns with remotely sensed data to predict the effects of changed precipitation regimes."
3. "Integrated long-term research will continue to document interrelations between precipitation patterns and ecosystem properties at a variety of scales."

1995 Evaluation of these objectives: We have made excellent progress towards the completion (and expansion) of objective 1. We have made some contributions for objective 3; a proposed synthesis volume on the Niwot Ridge should move us well along towards this objective. We have made preliminary progress for objective 2, as evidenced by the modeling efforts of Cline (1995) and Bryant (in prep). Several new modeling efforts have developed based on collaborative efforts with the CPR LTER and a project involving ITEX and the Toolik Lake LTER site.

Key Questions (four were identified in the proposal):

(1) "How do changes in snowpack, summer precipitation, and wetfall and dryfall nutrient inputs affect soil-water regimes, runoff, and stream geochemistry?"

Primary investigators: Caine (surface geomorphology and hydrology), Sievering (atmospheric inputs), Williams (biogeochemistry).

1995 status report: LTER studies have demonstrated the relationship between snow cover and geomorphic processes, including direct transport and erosion (Caine 1995). Surface water export and surface water chemical studies are essential to the evaluation of the nitrogen saturation hypothesis (Williams et al, submitted). A major effort, spearheaded by Williams, was the construction and instrumentation of the subnivean access chamber. This facility is currently monitoring the volume and chemistry of moisture during the spring snowmelt, as this moisture is converted from snow into runoff within the snowpack, soil surface runoff, and soil percolates. A complete, annual record of surface energy balance is being concurrently obtained with these data (Cline 1995).

In 1993-94, excellent data were obtained on the air concentrations of nitric acid, ammonium, and nitrate at the Saddle site. The atmospheric deposition of N at Niwot Ridge is represented fully by the sum of HNO₃, NH₄, NO₃, and ammonia (NH₃). On the assumption that the net flux of NH₃ is nearly zero, the annual atmospheric deposition of N has been estimated, based on observed air concentrations, as 7-8 kg N/ha/yr (Sievering et al. in review). About 3-5 kg N/ha/yr of this wet plus dry deposited N is made available to tundra plants. About 90% of this deposited N is due to anthropogenic activities.

Present and future research is and will be devoted to continued assessment of atmospheric inputs and outputs. Since the annual biomass harvests do not yet show a growth trend (i.e., we may, tentatively, assume the internal cycle to be in near balance) the identification of output fluxes needs further attention. We had assumed the net flux of NH₃ to be zero at the tundra. This may not be so if air concentrations of NH₃ are below the compensation point of the tundra, i.e., the concentration of NH₃ in the substomatal cavities of tundra plants. Preliminary data at the Saddle site indicate this may be so during the growing season. Thus, a new hypothesis is in order: the NH₃ emission flux from the tundra is negative.

We have begun NH₃ air conc. measurements at the Saddle site during 1995. This is a difficult task and was, therefore, not previously attempted. It is expected that sufficient data on NH₃ will be available by the end of 1996 or, at the latest, by the end of the 1997 growing season to approximate the magnitude of NH₃ emission and deposition fluxes on short time bases as well as obtain a first estimate of the magnitude of its annual flux at the Niwot tundra.

(2) "How do snowpack and summer precipitation affect tundra processes of nutrient cycling, production, and decomposition?"

Primary investigators: Bowman (ecophysiology), Diggle (morphology), Monson (ecophysiology), Schmidt (microbial ecology), Seastedt (soil ecology), M. Walker (plant community ecology), S. Walker (landscape ecology), Wessman

(remote sensing).

Although the physical environment exerts strong control over most ecosystem processes, there is also strong biotic control over the response of the system to environmental change. The biotic control is determined by the degree of physiological and morphological plasticity of organisms, which, in turn is related to the predictability and timing of resource supply changes within the communities. These physiological and morphological characteristics are being evaluated and/or tested through a number of experiments. In addition, the patterns of essential resource availability and the landscape controls over the 'most-limiting resource' are also being evaluated with a series of manipulations.

Over the past three years we have monitored baseline N-cycling and trace gas fluxes in the three dominant plant communities on Niwot Ridge. The findings of these investigations are currently in press or are being prepared for publication. We have also studied processes more specifically related to the present proposal. This work includes studying the effects of different nitrogen species on N₂O and CH₄ fluxes during the summer, and preliminary studies of microbial activity and trace gas fluxes beneath winter and spring snow packs. We have also studied the effects of added N on both plants and soil microbial communities, including studies of the relative abilities of plants and microorganisms to assimilate added N. More details of these studies are given in the following paragraphs.

As part of on-going investigation of N gas fluxes on Niwot Ridge, we have quantified summertime fluxes of N₂O and CH₄ from soils fertilized with N. A dramatic increase of N₂O emissions that we observed the year following fertilization with 25 g N/m²/y in the form of urea (Neff et al. 1994). We have extended these investigations to determine the fluxes of N₂O, NO, N₂, and CH₄ in response to different levels of fertilization and during the snow covered months (Brooks et al. in press).

We have also carried out preliminary studies of the abilities of soil microorganisms to assimilate and/or transform N under the snow pack. The highest fluxes observed in these measurements were higher than any fluxes from unfertilized plots that we have recorded during the past two summers on Niwot Ridge. These fluxes occurred when soil temperatures had reached values close to 0 degrees Celsius and soil nitrate levels were very high. No fluxes were observed when soil temperatures were below -3 degrees Celsius, i.e., for most of January, February, and March. These findings indicate that conditions are very good for N₂O losses just prior to and during snowmelt. ¹⁵N measurements were used to determine whether or not the source of this N was from atmospheric deposition in snowpack (Brooks et al. in press).

Our results from fertilized plots during the growing season and fall also reveal interesting patterns of microbial uptake of excess N. Soil microbial biomass did not take up excess N during the growing season but was able to assimilate excess N in the fall when the vegetation was inactive (Fisk and Schmidt, 1995a,b; Jaeger et al., 1995). This uptake of excess N also occurs under the snow pack when vegetative uptake of N is also minimal (Brooks et al., 1995).

Data collected from both Niwot Ridge (Fisk and Schmidt, 1995) and elsewhere

point to a 3-8 fold imbalance in the potentially available N from microbial mineralization and plant uptake. Dry alpine meadows dominated by the sedge *Kobresia myosuroides* demonstrate net mineralization rates of 1 g N/m², whereas uptake ranged from 3.4-5.3 g N/m². Our recent research efforts have focused on measurements of organic N uptake by the alpine sedge, *Kobresia myosuroides*, a process that might account for the gap between N mineralization and plant N uptake.

We have adopted a two-fold approach to investigating this issue with *Kobresia myosuroides*. In controlled-environment growth chamber studies initiated in the autumn of 1993, we collected 26 *Kobresia* tussocks from Niwot Ridge and repotted the plants to soil-less potting mix (vermiculite:perlite:adsorbent) and split into two groups, differing only in the source of nitrogen. One group received NH₄NO₃, the other glycine, all other nutrients as 1/4-strength Hoaglands Solution. Plants were cultured in this way for 3-4 months.

Plants were capable of considerable amino acid uptake. Just prior to measurement, the entire root system was gently rinsed and placed in a cylindrical root cuvette containing a stirred aqueous nutrient solution. Samples were withdrawn from the incubation solution at periodic intervals. NO₃⁻ and NH₄⁺ concentrations that remained in the aqueous solution were measured with a Dionex 4500I Ion Chromatograph System. Amino acid concentrations were measured with a Milton-Roy SM 4000 HPLC System. Plants that had been fertilized with glycine, exhibited glycine uptake rates that exceeded NO₃⁻ uptake rates for plants that had been fertilized with NO₃⁻. Roots of *K. myosuroides* were not capable of NH₄⁺ uptake.

Microscopic observations revealed a complete lack of mycorrhizae in these plants. Extensive measurements of the incubation medium have revealed no evidence of mineralization or nitrification during the measurements of amino acid uptake. Thus, the plants appear to be taking up intact glycine. This is currently being verified with dual-labeled glycine (14C and 15N) -- a check to see if both labels are assimilated during the incubations. When the roots of *K. myosuroides* were bubbled with N₂ gas, instead of air, or treated with 10 mM CCCP (a protonophore), amino acid uptake ceased.

The results presented above only have ecological meaning to the extent that amino acids are a principal component of the available N in situ. Measurements of NO₃⁻, NH₄⁺, and amino acids were made in soil pore-water using a new type of microlysimeter (Rhizosphere Research Products, Wageningen, Netherlands). Sixteen microlysimeters were buried in short transects in *Kobresia* meadows at Niwot Ridge, Colorado. Results demonstrated that NH₄⁺ concentrations averaged 240 mM on the first sample date in early May, decreasing to non-detectable levels for the remainder of the growing season. Concentrations of NO₃⁻ rose to 450 mM during mid-May, decreasing to values of 10-100 mM by June and remaining at these levels throughout the remainder of the season. Amino acid concentrations were 20-100 mM throughout the growing season up to the final date in mid-October. Amino acids initially present at the highest concentrations were glycine (10-100 mM), glutamate (0-70 mM), and late in the season, cysteine (0-10 mM). There is little work on natural soils, with which to compare this data. In past studies, levels of free amino acids ranged from 10-20 mM in agricultural soils and 8-80 mM in arctic tundra soils.

Based on these observations we have posed some new hypotheses to be tested during the next several years:

- (1) What are the spatial and seasonal patterns of soil organic N in meadows of the alpine ecosystem?
- (2) Does the ability to take up amino acids provide *Kobresia myosuroides* with a means of capitalizing on freeze-thaw events and drying-rewetting events by capturing organic N released through microbial death?
- (3) How widespread is the capacity for organic N uptake among alpine, herbaceous plants?
- (4) Does mycorrhizal *Kobresia* attain the capacity for NH_4^+ uptake -- a capacity not present in nonmycorrhizal *Kobresia* -- and what is the role of mycorrhizae in amino-acid uptake?
- (5) Does the mycorrhizal relationship between *Kobresia* and its fungal associates provide advantages in terms of early-season inorganic and organic N uptake when soils are cold?
- (6) What is the biochemical nature of the amino acid transporter responsible for organic N uptake by *Kobresia* roots?

Walker et al. (1994) demonstrated that alpine plants show delayed growth responses to precipitation. Diggle suggested in the 1992 proposal that this lag in vegetation response was due to preformation (the initiation of structures one or more seasons before they mature and function). Diggle developed an extensive dynamic model of development and phenology in *Polygonum viviparum* that is consistent with this hypothesis. Leaves and inflorescences are initiated four years in advance of function. In order for plants to produce additional biomass, they must initiate, develop and mature the component structures. Because of the lengthy period from initiation to maturation, changes in the developmental processes that produce additional biomass will not be manifest for a year or more following the initial stimulus.

Thus, developmental process of alpine plants pose a significant constraint on within season variation in biomass production. Studies of other dry meadow species are on going, however, cursory examination suggests that preformation is a general phenomenon among species of this community.

We have also examined development in the alpine willow, *Salix glauca*, and find that this species preforms all organs nearly a full year before maturation and function. These results are consistent with observations of Bowman et al. (1994), on delayed responses of *S. glauca* to nitrogen fertilization. Walker et al. (1993) showed that there was not a pronounced lag in biomass production in the wet meadow. This observation generated a new hypothesis (not posed in the 92 proposal) that species of the wet meadow have the capacity to neoform structures (initiate and mature in the same season). In collaboration with a graduate student, Allison Aydellote, a developmental morphological analysis of the wet meadow species, *Caltha leptosepala*, was initiated in 1994. We predicted that *C. leptosepala* would show a combination of preformation and neoformation consistent with community level response.

Contrary to expectation, we found that *C. leptosepala* has little, if any, neoformation. Most or all of the leaves and flowers are preformed. Our current hypothesis is that the duration of leaf expansion and maturation affect within season plasticity. *Caltha leptosepala*, differs from *P. viviparum* in the pattern of leaf expansion. In *P. viviparum*, as in many other species of the moist and dry meadow communities, emergence, expansion, and maturation of leaves occurs over a matter of weeks at the beginning of the growing season. After this time, no additional photosynthetic surface or biomass is added during that season. In *C. leptosepala*, in contrast, leaf emergence, expansion, and maturation are more protracted. Successive leaves emerge from below ground, mature, and function, for a significant portion of the growing season. Because leaf characters such as size and thickness are determined during development and cannot be altered following maturation, phenotypic response to within season variation can only occur during the time that expansion and maturation are occurring.

By virtue of the longer period of time in which leaf expansion occurs in *C. leptosepala*, it may be more plastic. The importance of the duration leaf expansion and maturation for phenotypic responsiveness will be investigated further.

A related avenue of research that has been supported by the LTER grant concerns genetic variation within populations on Niwot Ridge. Diggle initially planned to test levels of phenotypic plasticity in *P. viviparum* using molecular markers. Because *P. viviparum* reproduces asexually (exclusively) by dispersed propagules, Diggle wanted to identify individual ramets of the same genet, and measure phenotypic plasticity as morphological variation among genetically identical members of a genet. What we found is unexpectedly high levels of genetic variation in this species. Among 150 individuals, 50 each from the dry and wet meadows and the scree of the west knoll, we found 23 distinct multilocus genotypes.

This is as much genetic diversity as the highest levels occurring in other clonal organisms that have some mode of sexual reproduction. The answer to the original question about phenotypic plasticity is yes. There is morphological variation within genets. Plants do have the capacity to respond to differences in their environment over the long run; it is only short term responses that are precluded by preformation. But, the high levels of genetic variation are both interesting and surprising. If this little herbaceous perennial with no apparent sexual reproduction and no obvious means of dispersal is maintaining levels of diversity such as we measured, what are the sexual species are up to?

(3) "How do snowpack, summer precipitation, and nutrient availability affect patterns of community production and populations of plants and animals in a hierarchy of spatial scales?"

"Our primary regional hypothesis is that primary productivity in alpine environments is broadly controlled by gradients associated with changing elevation, but strongly influenced by smaller scale topographic interactions with wind, snow and radiation."

"Natural shifts in snowpatch boundaries due to climate change should result in movement of plant community gradients and areas of animal usage that are evident at the site level."

"Species will react individualistically to changes in snowpack and will shift in a manner that is predictable from their present-day distribution patterns."

Principal Investigators: S. Walker, M. Walker, C. Wessman.

Results supporting the above hypotheses was presented in Walker et al. (1993), with additional results presented by Walker et al. 1994 and in press). New areas of research on these questions involve a collaboration with the International Tundra Experiment (ITEX), a program sponsored by NSF-DPP. Major questions address how changes in winter snowpack and summer temperature regimes affect phenology and growth of key tundra species, plant community composition, and key ecosystem parameters such as soil moisture and respiration rates? Will alpine and arctic ecosystems have similar responses to these changes?

The 1992 proposal focused on snow as an key climatic control on alpine ecosystems. However, analysis of long-term biomass, growth, and phenology data indicate that the combination of summer temperature and winter snow conditions together define growth conditions (Walker et al. 1994, 1995). We are using the methods of the International Tundra Experiment (ITEX), in combination with the LTER snowfence, to look at the effects of increased summer temperature under a gradient of changed snow conditions. A companion project using the same experimental design has been established at the arctic LTER site at Toolik Lake, Alaska, allowing for arctic-alpine comparisons.

Analysis of the first two years of temperature manipulation and the first year of snow manipulation indicate that many species will respond positively to changes in temperature (an expected) result. The surprise is that certain species also indicated a positive growth response to severely increased snowpack. Natural populations of these same species had shown increased growth to high snowpack/delayed snowmelt (Walker et al. 1995), and the experimental result seems to confirm this response. However, this response is predicted to be transient, as these species do not perform well in natural snow communities. The physiological and life history characteristics that result in these different response types are under investigation.

New Collaborative Research: J. Welker, Principal Investigator

As of June, 1993 a dry tundra site, 1 km east of the Saddle dominated by *Dryas octopetala* is the location of an additional ITEX research site. For the past two years, study plots have been exposed to increases in summer temperature using hexagonal, open-topped fiberglass chambers and a portion of the tundra has also been receiving supplemental summer water. The temperature and water manipulation study is configured as a 2 x 2 factorial design replicated four times. Air temperatures in the chambers are on average 2.5 degrees Celsius warmer than those outside and soil temperatures at 5 cm below the surface are 1 degree Celsius warmer.

Our findings to date suggest that in general, temperature responses are only observed under wetter conditions indicating that summer rainfall is a principal controlling factor in dry tundra as opposed to temperature. Organismic studies have found that the C/N ratio of *Dryas* leaves is significantly increased under warmer or wetter conditions which we anticipate will over the long term slow decomposition and curtail nutrient availability. Pilot studies of soil

respiration indicate that CO₂ efflux is significantly higher under wetter conditions, but warmer temperature initially had no effect. We plan to intensify these ecosystem studies examining diel patterns of carbon loss and the extent to which soil solution chemistry is altered by warmer summer temperatures and increases in summer rainfall. These studies in Dryas dominated systems are central to the ITEX network because they provide the truest comparative tundra systems ranging from high alpine to high arctic. Studies similar to those in the Dryas system on Niwot Ridge are being undertaken in Alaska, Canada, and in Scandinavia.

Drs. Bowman and Welker will be quantifying the extent to which tundra plants rely on snow melt water as opposed to summer rainfall using measures of $\delta^{18}O$ and δD in snow, snow melt water, rainfall and plant water. We anticipate that the extent that alpine plants use snow melt water will be dependent on phenology, rooting patterns and plant lifeform. Early emerging and early flowering plants with deep roots will likely use snow melt water as a principal source of water while shallow rooted, late flowering species will be those most likely to use primarily summer rainfall as a source of water. While these divergences in summer water sources may modify water use and alter plant transpiration, carbon assimilation and the net exchange of CO₂ between alpine tundra and the atmosphere.

A second facet of our study will explore the extent to which long-lived woody alpine plants have used snow melt water during the summer growth period and couple this to integrative measures of gas exchange using the abundance of carbon-13/carbon-12 ($\delta^{13}C$). This will be accomplished by harvesting annual growth increments, extracting cellulose, and conducting co-isotopic analysis (δD and $\delta^{13}C$). We anticipate that in years in which snowmelt water was the principal source of plant water that carbon discrimination is greatest indicating high levels of CO₂ exchange in summers following wet winters.

"Altered snowpack regimes will result in changes in gopher activity and consequent changes in patterns of plant species and communities."

Primary investigator: T. Seastedt, with historical data sets collected by J. Halfpenny, M. I. Litaora, and M. Walker.

Status report: Litaora et al. (submitted) have summarized the effects of gopher mounding activities on the soil chemistry and soil solution chemistry of alpine tundra. Cortinas and Seastedt (submitted) demonstrated that soil organic matter is not reduced by gopher disturbances under nominal conditions; only when vegetation fails to recolonize mounds are significant reductions in carbon observed. This hypothesis is currently being more rigorously tested and expanded to include nitrogen responses. The relationship between gopher densities and landscape patterns of snowpack is also under study.

This study has changed the current emphasis of the research from climate effects on populations to the effects of populations of keystone species on ecosystem characteristics such as soil chemistry. We anticipate the return to a more traditional population focus when we hire a tenure-track vertebrate ecologist in EPO Biology.

A second, new project has emerged that has a similar thrust to the gopher

research. Pauker and Seastedt (in review) began a study of krummholz effects on soil characteristics. Tree islands, which move across the tundra, convert the tundra, Mollisol-like soil to a forest, Alfisol-like soil. The extent to which this disturbance parallels gopher disturbances is a current focus. Both studies, however, emphasize the importance of biological intrusions into the landscape-level controls exhibited by snowpack gradients. We hypothesize that these keystone species, as disturbances to soil processes, have the ability to severely modify landscape patterns of soil carbon storage and soil fertility.

(4)"What have been the effects of past changes in snow regime on alpine ecosystems and are these appropriate analogs of predicted future changes?"

Primary investigator: Scott Elias, with dendrochronology work provided by Connie Woodhouse.

1995 Status Report: Our main emphasis has been on late Holocene fossil records from Front Range sites (there are no usable sites on Niwot Ridge; we have studied cores and peat profiles from the adjacent alpine/subalpine valleys and other bogs in the Indian Peaks region).

Our principal study sites are located in the ecotone between the upper montane and subalpine forest zones. The Longs Peak Inn Bog site yielded a pollen record spanning the last 4700 yr and insect assemblages ranging in age from recent to 3500 yr BP. The pollen spectra indicate that an essentially modern lodgepole pine forest surrounded the bog throughout the last 4700 yr. The insect fossil record suggests climatic cooling at about 1800 yr BP and between 250 and 300 yr BP. The forest vegetation may be more complacent or resistant to short-term environmental change than the insect fauna. Work from additional sites will test this hypothesis.

Another site, a fluvial deposit on the Roaring River at Cascade Camp, Rocky Mountain National Park, yielded fossil insect and pollen data suggesting the development of more park-like vegetation, with a decrease in tree cover and increasing grasses, between about 92 and 166 yr BP (A.D. 1784-1858). This may have been a result of climatic change, windfalls, more frequent fire episodes, and/or an increase in bark beetle attacks.

The Longs Peak Inn bog site insect data suggest that dramatic climatic cooling took place in the Front Range region during the last 2000 years, especially the interval from 1700-1850 A.D. Even with no increase in snowfall during that interval, the cooling alone may have fostered greater snow cover through the year, and retention of the alpine snowpack through much of the summer season. We need to resolve the discrepancy between pollen and insect interpretations, and this summer we intend to sample another high-altitude (above treeline) site at Guanella Pass for insect and plant remains. The new data will hopefully bring us closer to answering our research questions.

In addition, Woodhouse (1993) demonstrated the historical relationships between treeline NPP and ENSO events for the Colorado Front Range. These results indicate that, in contrast to the belief that tree growth is temperature as opposed to moisture sensitive at treeline, growth is stimulated by high precipitation events.

Literature Cited:

NOTE: All citations except those listed below are in the NWT LTER publication list, accessible through the WWW or Gopher system.

Walker, M.D. 1995. Patterns of arctic plant community diversity. pages 1-18 in F.S. Chapin III and C. Korner (eds.). Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences. Ecological Studies 113. Springer Verlag NY.

Walker, M.D., F.J.A. Daniëls and E. van der Maarel (eds.) 1995. Circumpolar arctic vegetation. Special Features in Vegetation Science #7, Opulus Press, Uppsala. 176 pp.