Grizzly bear digging in subalpine meadows: influences on nitrogen availability and the physiology of *Erythronium grandiflorum*

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Grizzly Bear Digging in Subalpine Meadows: Influences on Nitrogen Availability and the Physiology of *Erythronium grandiflorum*

by

Allison Robin Young

B.S., Towson State University- Towson, MD, 1995

Presented in partial fulfillment of the requirement for the degree of

Master of Science in Organismal Biology and Ecology

1998

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Date
In subalpine meadows of Glacier National Park, Montana, grizzly bears dig for the nutritious bulbs of glacier lilies. Previous work showed that mineral nitrogen was higher in digs than in undisturbed areas, bulbs of lilies growing in digs had higher nitrogen concentrations than those growing in undisturbed areas, and lilies in digs produced twice as many seeds. Therefore, lilies growing in digs should have higher photosynthetic rates. Photosynthetic rates were measured in summer 1997 for glacier lilies growing in digs and undisturbed areas using a LiCor 6200. Plants in digs had higher photosynthetic rates than plants in undisturbed areas (p<0.01). Soil temperature was higher in bear digs (p<0.05), but soil moisture was not different between digs and undisturbed meadow. Growth rate, seed number, seed weight, bulb biomass, and bulb %N and %C did not differ between locations.

In order to experimentally test glacier lily response to increased levels of N, NH$_4$NO$_3$ was added to digs and undisturbed areas at the rate of 4 g N/m$^2$. Fertilized plants had faster photosynthetic rates than controls (p<0.005). Plants in undisturbed meadow had a greater response to N-fertilization than plants in digs, probably due to greater N-limitation in undisturbed meadow. Cellulose was added at the rate of 400 g C/m$^2$ to test the hypothesis that C would cause microbes to take up N and reduce plant photosynthetic rates. C addition did not affect photosynthetic rates. N+C addition had no effect upon photosynthetic rates, as expected. Soil N was measured using ion exchange resin bags. Soil NO$_3^-$-N was higher in control digs, while NH$_4^+$-N was lower. NO$_3^-$-N was increased with N addition to undisturbed sites, and with N+C addition to digs and undisturbed sites. C treated plots had lower NO$_3^-$-N in digs. Growth rate, biomass, and tissue nutrients did not differ between treatments.

Grizzly bear digging is beneficial to glacier lilies due to increased soil N in digs, which increases photosynthetic rates of plants in digs.
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Chapter 1- Statement of Problem

When studying an ecosystem, ecologists often concentrate on effects of abiotic disturbances on plants. Biotic effects are equally important to consider, since they evolved within the constraints of the physical environment. Plant fitness can be increased or decreased by disturbances created by animals (Crawley, 1983), whether the animals are eating the plant, digging up its soil substrate, or eliminating wastes around it (McKendrick et al. 1980; Hobbs and Mooney, 1985; Bryant, 1987; Paige and Whitham, 1987; Huntly and Inouye, 1988; Pastor and Naiman, 1988; Whicker and Detling, 1988; Shachak et al. 1991; Contreras and Gutiérrez, 1991; Paige, 1992; Weltzin et al. 1997).

Foraging by vertebrate herbivores may increase turnover rates of nutrients, especially that of nitrogen (Jefferies et al, 1994). Models of nutrient cycling in the Serengeti Plains indicated that grazing stimulated plant N uptake, while in simulations of ungrazed systems, litter accumulation clogged the system by affecting soil temperature, moisture, and inorganic N input (McNaughton et al. 1988). The response of plants to defoliation is to increase N uptake, which in turn increases forage quality for herbivores (McNaughton et al. 1988). Bryant (1987) found that browsing of feltleaf willow by snowshoe hares increased shoot growth and affected succession by allowing alders to outcompete willows for light. Prairie dogs at Wind Cave National Park, South Dakota keep vegetation clipped at a low height, increasing nutrient availability and creating favorable habitat patches for grazing by bison and pronghorn antelope (Whicker and Detling, 1988). Huntly and Inouye (1988) showed that pocket gophers, by selecting early successional vegetation, increased soil nitrogen availability and slowed succession.

Digging by mammals has also been shown to have effects on soil nutrient availability. Indian crested porcupines in the Negev Desert, Israel, dig up patches of soil while foraging for geophyte storage organs, creating wetter sites that annual plants can
repopulate (Shachak et al. 1991). In Chile, burrows of the cururo allow increased germination of geophytes since conditions were suitable near burrows (Contreras and Gutiérrez, 1991). In particular, rodents reduce the abundance of large bulbs of *Leucocoryne ixioides*, while small bulbs increase in abundance, probably because of favorable germination conditions due to the effects of burrowing on soil structure and nitrogen availability. Burrowing animals can stimulate decomposition of organic matter by mixing it into the soil and increasing contact with decomposing organisms (Stevenson, 1986).

Herbivores can affect succession in plant communities. The eradication of prairie dogs in Texas has allowed shrubs and trees to invade grasslands, since prairie dogs kept woody plants from establishing by removing seeds, eating seedlings, and suppressing growth (Weltzin et al. 1997). Moose browse birch, aspen, and poplar preferentially, letting spruce trees grow tall and outcompete the preferred forage species (Pastor and Naiman, 1988). Badgers in a tall-grass prairie in Iowa dig for ground squirrels and create disturbed patches which have higher soil moisture than undisturbed prairie. Vegetation under the disturbance is killed, and a new assemblage of plants then colonize the patches, which slowly succeed to undisturbed prairie (Platt, 1975). Plants growing on gopher mounds in Northern California were larger and produced more seeds than plants growing on undisturbed grassland (Hobbs and Mooney, 1985). The gophers till the soil and produce bare patches, which is believed to be a factor allowing perennial grasses to persist in the serpentine grassland.

Some grazing animals contribute nutrients in the form of feces and urine to soil (Whicker and Detling, 1988). Caribou carcasses and wastes deposited near rodent burrows contribute nutrients to tundra soil and induce increased production of graminoids (McKendrick et al. 1980). Hence, herbivores have a variety of effects on plant fitness and
the dynamics of community structure, most of which are interdependent on other factors such as soil water and nutrient availability.

Some plants respond to the increase in nutrient availability due to grazing by overcompensation, which is seed and fruit production greater than the numbers the plant would produce in the absence of grazing (Chapin et al. 1986; Paige and Whitham, 1987; Paige, 1992). Certain species depend on biotic disturbances to achieve their greatest fitness. For example, scarlet gilia (*Ipomopsis aggregata*) was shown to exhibit overcompensation in response to grazing by mule deer and elk (Paige and Whitham, 1987; Paige, 1992). Plants can compensate for loss of tissue due to grazing by increasing photosynthetic rate in undamaged leaves, and by growing new leaves (Fitter and Hay, 1987).

An interesting and little understood plant-animal interaction occurs between grizzly bears (*Ursus arctos*) and glacier lilies (*Erythronium grandiflorum* Pursh (Liliaceae)) in subalpine meadows of the Rocky Mountains. In Glacier National Park, Montana, grizzly bears dig for the nutritious bulbs of glacier lilies that carpet large portions of the subalpine meadows at Logan Pass. Tardiff and Stanford (in press) hypothesized that the bears may be maintaining the patches of glacier lilies in the meadow by their feeding habits. The bears dig up areas from 1 to 100 m², turning over chunks of soil in the process. They then nip off glacier lily bulbs exposed in the turned-over soil. Bears have been observed redigging old digs, as if they were "farming" the glacier lilies.

Glacier lilies are herbaceous perennials that may require up to 8 years to reach sexual maturity (Kawano et al. 1982). Glacier lilies have a low carbon: nitrogen ratio, and they have been observed to be the first species colonizing new digs (Tardiff and Stanford, in press). In undisturbed areas adjacent to digs, plant species with high C:N dominated (unpublished data, Tardiff and Stanford). High nitrogen (N) plants provide
much needed protein building-blocks for herbivores, and plants with a low C:N ratio are
easier to digest because they contain fewer carbon-based compounds such as lignin and
 cellulose (Mattson, 1980). Glacier lilies growing in bear digs had more water-soluble
carbohydrates than lilies from undisturbed meadow (Tardiff and Stanford, in press).
Comparative data from ion exchange resin bags buried in soil in digs and in undisturbed
areas during the growing season indicated higher levels of plant available N (i.e., \( \text{NO}_3^- \)-N
and \( \text{NH}_4^+ \)-N) in digs than in undisturbed areas (Tardiff and Stanford, in press). Even in a
ten year old dig, the disturbed soil had more available \( \text{NO}_3^- \)-N and \( \text{NH}_4^+ \)-N.
Experimental digs at Logan Pass supported the hypothesis that the higher soil N was due
to bear digging rather than to preexisting conditions (Tardiff and Stanford, in press).
Bear digging directly affects the subalpine landscape by altering the availability of N to
plants, and therefore indirectly affects plant distributions (Tardiff and Stanford, in press).

Large herbivores can influence soil nutrient regimes, plant community
composition, and succession (Lindroth, 1989; Pastor and Naiman, 1992; Whicker and
Detling, 1988). Disturbance caused by bear digging likely has direct and indirect
influences on glacier lily ecology and physiology. Bear digging may provide bare sites on
which glacier lily seedlings can establish free from competition, and digging may also
enhance N availability in a way that is advantageous to glacier lilies. Tardiff and
Stanford (in press) have shown that bulbs of glacier lilies growing in digs have higher N
concentrations than those growing in undisturbed areas, and that glacier lilies in digs
produce more seeds than those in undisturbed areas. These results suggest that N may
limit glacier lily growth in undisturbed areas (McKendrick et al. 1980). When glacier
lilies grow back in dug areas without competitors, they are released from competition for
N, and seed set increases. Physiological effects of limiting N may be the cause of
reduced growth and fitness of glacier lilies in undisturbed sites.
Plants have photosynthetic rates proportional to the concentration of N in leaves, since most leaf N is used in photosynthetic enzymes and chlorophyll. Nitrogen is the element that most often limits terrestrial plant growth (Chapin, 1980), and growth is the process that is most affected by nutrient stress (Bryant et al. 1983). The importance of N to natural systems can be seen in responses to N fertilization, which usually produces high levels of response in species that require large amounts of N (Field and Mooney, 1983; Mattson, 1980). An increase in supply of a photosynthesis-limiting nutrient may cause the plant to allocate more of that resource to leaves, thereby increasing photosynthetic rates. Artificial N and P fertilization of tundra plants produced effects similar to those observed when herbivores contributed nutrients in the form of wastes or carcasses (McKendrick et al. 1980). Additions of N as \( \text{NH}_4^+ \text{NO}_3^- \) and urea to alpine and tundra plants led to increases in plant photosynthesis, leaf area, biomass, and tissue N concentration (Bowman, 1994; Bowman et al. 1993, Bowman and Conant, 1994; Bowman et al. 1995; Shaver and Chapin, 1980). Nitrogen and phosphorous are co-limiting to plants in alpine tundra (Bowman, 1994; Bowman et al. 1993; McKendrick et al. 1980; Shaver and Chapin, 1980). Alternatively, addition of a labile carbon (C) source should produce negative effects on tissue nutrient concentrations, growth, photosynthesis, and seed production since adding C in the form of cellulose causes a decrease in plant available nitrogen (Mengel and Schmeer, 1985). Schmidt et al. (1997) added labile C to subarctic alpine soil and found the microbial population temporarily immobilized available N and reduced plant biomass production.

Although there is no direct evidence, research results suggest that N may be a limiting nutrient to glacier lilies at Logan Pass (Tardiff and Stanford, in press). Since bear digging causes soil N to increase and plants in digs take up that nitrogen, photosynthetic rate should increase and, subsequently, either growth or storage. Here we investigate the hypothesis that grizzly bear digging is beneficial to glacier lilies because
of the increase in N availability in digs. Individual plant responses were measured in bear
digs and undisturbed meadow. Additionally, a fertilization experiment attempted to
simulate the increase in soil N that results from bear digging to show that the positive
effects of bear digging on glacier lilies are due mainly to the increase in soil N.
Chapter 2- Study Area and Methods

Study Site

Logan Pass is located at 48° 40' N, 113° 14' W along the Continental Divide in Glacier National Park, Montana (elev. ca. 2000 m). The rocks of Logan Pass are limestones and argyllites of the Cambrian Belt series, affected by uplift, erosion, deposition, and glaciation (Dyson, 1960). The soil developed on stream alluvium and glacial till (Choate and Habeck, 1967), and are moist but well-drained, medium to strongly acid alpine turf soils (Nimlos and McConnell, 1962, 1965). The soils are classified as loamy-skeletal, mixed, Typic Cryochrepts, or Lithic Cryochrepts where shallow (<20 inches) to bedrock. The surface soil is dark brown loam with 0-20% rocks 4-6 inches thick, and there is significant volcanic ash influence (Dutton and Marrett, 1997). The meadows at Logan Pass are covered by snow from October to July.

Temperatures at Flattop Mountain Snotel, which is located at the same elevation approximately 7 miles north of Logan Pass, ranged from -4° to 28°C, averaging 10° from July through September 1997 (Soil Conservation Service data).

Plant species in these moist but well drained meadows include Erythronium grandiflorum, Carex spp., Luzula hitchcockii, Sibbaldia procumbens, and Hypericum formosum (Choate and Habeck, 1967). Glacier lilies begin growing before snow has receded and flower a few weeks later. This produces a mosaic of life history stages across the meadows. Most bear digging activity occurs from mid-August into October,
after the lilies have produced seeds. Tardiff and Stanford have studied grizzly bear
digging at these meadows since 1993 (in press).

Methods

Twenty plots were established in a meadow at Logan Pass in July 1997. Ten plots
were in bear digs, approximately three years old, and ten were in adjacent undisturbed
sites. Old digs were used because they had glacier lilies growing in them, while fresh
digs have no plants growing in them. Soil temperature was measured approximately
weekly in each plot, between 1000 and 1330h four times in August and September. A
digital thermistor temperature probe was used to measure soil temperature at depths of
7.5 and 15 cm. Temperature at the soil surface was measured twice in September. Air
temperature was measured by the LiCor 6200 (see below). Soil samples were taken from
each plot at four weekly intervals during August and September for soil moisture
determination. A tulip bulb planter was used to extract soil samples to a depth of 10 cm.
Samples were then bagged and placed in a refrigerator until they could be weighed and
dried in the lab. Gravimetric water content was determined on subsamples dried at 40°C
for 48 hours. Soil nutrients were measured by installing four ion exchange resin bags 10
cm below the soil surface in each plot in July. Nylon bags containing 10g cation + anion
resin beads (J.T.Baker mixed-bed ion exchange resin) were incubated in situ for 51 days,
then were removed and analyzed for NO₃-N and NH₄-N at the Natural Resources
Research Institute at the University of Minnesota, Duluth. Soil N data were log₁₀

transformed for analysis since variance is significantly higher in digs than in undisturbed sites (Tardiff and Stanford, in press).

Within each plot, four glacier lilies were marked for study, making a total of 80 marked plants. In order to minimize variation in plant age, all plants measured had two leaves but no stem or flower. *Erythronium japonicum* plants take around 8-10 years to reach sexual maturity, and they continue to flower at least 2-5 years, so it is likely that *E. grandiflorum* plants without flowers are younger than flowering plants and therefore close together in age (Kawano et al. 1982). However, plants may take breaks between flowering years, so this method of aging is not perfect (Loewen, 1998).

Photosynthesis was measured for each plant on 5 dates over late July and early August, beginning approximately one week after snowmelt. A LiCor 6200 portable photosynthesis system (LiCor, Inc. Lincoln, Nebraska) was used to measure photosynthesis between 1100 and 1500 hours, MDT. Data collected under suboptimal conditions for photosynthesis were filtered so that sample sizes (n) for controls ranged between 15 and 25 (except on 2 August, when n= 4-5) and for treatments n ranged between 3 and 5. When photosynthetically active radiation (PAR) was less than 250 μmols m⁻² s⁻¹, measurements were removed from the data set because light was then limiting. This minimum PAR value was set using a light response curve of glacier lily photosynthetic rates. Values where vapor pressure deficit exceeded 14 kPa were removed since stomata of glacier lilies apparently closed when vapor pressure exceeded this value, as evidenced by greatly reduced photosynthetic rates.
Growth rates were calculated using leaf lengths measured at three dates over the growing season. Leaf length was used to estimate growth without destroying the leaf, since each leaf was also used in photosynthetic measurements throughout the season. However, leaf length is only a surrogate of growth rate; this measure misses leaf thickening, widening, and other attributes of total growth. Species with determinate leaf numbers usually respond to an increase in nutrient availability by increasing leaf size (Chapin, 1980). Four seed pods of mature unmarked plants were collected from each plot. Number of seeds per pod was counted and seeds were weighed. Plants were harvested on 19 August 1997 when senescence began, just over one month after snowmelt. Plants were separated into bulbs and shoots (all aboveground parts), oven dried at 60°C for 48 hours, and weighed to determine biomass. Bulbs were then ground in a Wiley mill and tissue nitrogen and carbon were measured using a Carlo-Erba Nitrogen Analyzer. Shoots were too far senesced at the time of collection, so there was not enough tissue for nutrient analysis.

To chart the allocation of biomass and nutrients to above and below ground tissues over the growing season, two plants were harvested from each of five undisturbed sites along the southern edge of the meadow at four weekly intervals. Plants in this area flowered and produced seed heads by the date of the last harvest. On 6 August, ten plants were collected from an additional nearby site to include the flowering stage, which had occurred between sampling dates at the original site. The two plants from each site and date were combined for measurements. Plants were separated into bulbs and shoots, oven dried at 60°C for 48 hours, weighed, ground in a Wiley mill and tissue %N and C were
measured. Differences in all plant and soil variables were analyzed using t-tests (SPSS 6.1).

Fertilization Experiment

In 1996 four different concentrations of N as NH₄NO₃ (0, 2, 4, 6 and 8 g N/m²) and P as KH₂PO₄ (0, 0.2, 0.4, 0.6, and 0.8 g P/m²) fertilizers were applied to 0.25 m² plots at Logan Pass to determine which concentrations of fertilizer would produce differences in tissue nutrient concentration. Glacier lilies and other plants in these plots were harvested separately, dried, and sent to the Natural Resources Research Institute at the University of Minnesota, Duluth for tissue nutrient analysis.

On 30 July 1997, each flagged plant in five dug plots and five undisturbed plots received one of 4 treatments with 1 liter water from nearby Reynolds Creek. Controls received water only. Nitrogen-amended plants received 4 g N/m² as NH₄NO₃ (Sigma Chemical Co. St. Louis, Missouri). Carbon-amended plants received 400 g C/m² as cellulose (Sigma Chemical Co.). Nitrogen+carbon-amended plants received both NH₄NO₃ and cellulose. Photosynthesis was measured on 25 and 29 July and on 2, 6, and 11 August. Leaf lengths were measured once prior to treatment and twice after treatment. Plants were harvested to measure biomass and tissue nutrient concentration in August, 1997, near the end of the growing season. Plant and soil responses to experimental treatments were analyzed with ANOVAs using date, location (in digs or undisturbed meadow), and treatment as independent variables and photosynthetic rate as the
dependent variable; mean separation was determined using least significant difference (SPSS 6.1).
Chapter 3- Results and Discussion

Soil temperature was higher in bear digs than in undisturbed areas at a depth of 7.5 cm for each date measured (p<0.05) and at a depth of 15 cm for the first three dates measured (p<0.01), likely as a result of greater solar energy absorption (Fig. 1). Surface soil temperature was higher in digs than in undisturbed areas, but significantly higher only for the second date measured (p<0.01).

Soil moisture was expected to be higher in undisturbed areas since a dig could conceivably dry out more quickly due to increased temperature. Soil moisture did not differ significantly between digs and undisturbed areas (Fig. 2). It is possible that drying of dug soil did occur, but was balanced by the lack of plants to take up water.

Resin bag data indicate higher NO₃⁻-N in bear digs than undisturbed meadow (p<0.01) (Table 1, Fig. 3). Soil NH₄⁺-N, on the other hand, was higher in undisturbed meadow (p=0.01) (Fig. 4). Soil NO₃⁻-N is more available in control sites in digs due to the removal of plants. Any available NH₄⁺-N in the digs is microbially converted to NO₃⁻-N, which pools since there is no C source for NO₃⁻-N immobilization.

Overall, glacier lily photosynthetic rates were higher in digs than in undisturbed areas (p<0.01) (Fig. 5). For individual dates, however, photosynthetic rates were significantly higher in digs only on 2 and 11 August (p<0.05, p<0.001, respectively). Average photosynthetic rates ranged between 9.4-17.8 μmol m⁻² s⁻¹ in digs, and 4.9-14.4 μmol m⁻² s⁻¹ in undisturbed meadow (Table 2).
Plants in undisturbed meadow exhibited more of a seasonal decline in photosynthetic rate than plants in digs, perhaps because N-limitation is more pronounced toward the end of the growing season (Fig. 5). Hamerlynck (1992) found maximum assimilation rates of 7-12 μmol m⁻² s⁻¹ for *E. grandiflorum* immediately after snowmelt, in a subalpine forest in Wyoming. Upon emergence, the Wyoming plants took only 4-6 days to reach maximal photosynthetic rates. In the open meadow at Logan Pass, glacier lily photosynthetic rates seemed to peak around 2 August, about two weeks after snowmelt.

Higher soil temperature in bear digs likely produced higher photosynthetic rates. Air temperature is positively correlated with photosynthetic rate, but it did not differ over bear digs and undisturbed meadow. However, soil temperature could have indirectly mediated photosynthesis by increasing the rate of N uptake by plants, although my results do not support this. Warmer soil temperatures could increase the length of the growing season and nutrient absorption for plants with underground storage organs (Chapin and Shaver, 1985). In bear digs, soil temperatures and soil nutrients probably interact to increase glacier lily photosynthetic rates. Warmer temperatures typically increase growth rates, but these data do not support this.

Leaf lengths were not significantly different between glacier lilies growing in bear digs and lilies growing in undisturbed areas (Fig. 6). By the time leaf lengths were measured, the plants had likely already formed most of that season’s leaf tissue. Growth of these early spring ephemerals begins before snowmelt is complete. The trend, however, was for plants in digs to have smaller leaf lengths than plants in undisturbed
meadow. If plants in digs had an earlier start on the growing season since soil was warmer in digs (see below), leaves in digs would have been more fully grown while plants in undisturbed meadow were still adding biomass.

Neither the average number of seeds per plant nor average weight of seeds per plant differed significantly between digs and undisturbed areas, although the trend was for seeds in digs to be slightly heavier, while plants in undisturbed meadow produced slightly higher numbers of seeds. Tardiff and Stanford (in press) showed that lilies in bear digs at Preston Park, another location in Glacier National Park, Montana, produced twice as many seeds as lilies in undisturbed areas. They found high between year variation in seed production, so the discrepancy between studies may reflect a difference in seed production between years, or a site difference, although sites were similar.

*Erythronium grandiflorum* was found to abort ovules in response to low nutrient conditions (Fritz-Sheridan, 1988). Viable and nonviable seeds were not distinguished in this study nor in the previous study (Tardiff and Stanford, in press).

Bulb and shoot biomass did not differ significantly between digs and undisturbed meadow (Figs. 7 and 8). The bulb: shoot biomass of plants in bear digs was 5.9, compared to 4.8 in undisturbed meadow, for nonreproductive control plants harvested in August, but this difference was not significant (Fig. 9). The slightly higher bulb: shoot biomass for plants in bear digs than for plants in undisturbed meadow could indicate greater allocation of nutrients to the bulb in conditions of higher nutrient availability, although tissue nutrient analysis results do not support this. Tissue %N and %C were not significantly different for bulbs from digs and undisturbed areas, although the trend was
as expected: bulbs in digs had more N and less C than bulbs in undisturbed meadow (Figs. 10 and 11). Likewise, the trend was for bulbs in digs to have lower C:N than bulbs from undisturbed meadow, although the difference was not significant (Fig. 12). Only two plants were dug up by bears over the study period.

Oven dry weights of bulbs and shoots collected over the season from undisturbed meadow revealed an increase in bulb biomass throughout the study period, and an increase in leaf biomass until the last date measured, when leaf biomass began to decrease in preparation for senescence (Fig. 13). Average bulb: shoot biomass was 1.4, ranging from 0.79 to 2.7 with a general increase over the growing season. Abrahamson (1979) found a bulb: shoot biomass of 10 for *Erythronium americanum*, and Muller (1979) found a bulb: shoot biomass of 0.91 for sexually reproductive individuals of *Erythronium albidum*, with higher ratios for asexually reproducing and nonreproductive individuals.

Allocation of tissue N to shoots and bulbs decreased significantly over the growing season, while allocation of C to bulbs and shoots remained fairly constant across dates (Figs. 14 and 15). Bulbs and shoots were composed of relatively the same percentages of C, but shoots had over twice as much N as bulbs. The C:N of bulbs increased from 22 to 58 from 21 July to 14 August, while the C:N of shoots fluctuated between 10 and 20.
Fertilization Experiment

In the 1996 fertilization experiment, NH4NO3 application at the rate of 4g N/m2^-2 significantly increased %NH4-N in glacier lilies (p<0.01) and meadow plants (p<0.01), while additions at the rates of 6 and 8g N/m2^-2 did not further increase glacier lily tissue %NH4-N. P additions did not produce significant responses.

In undisturbed meadow, soil NO3^-N was higher in N and N+C fertilized sites than in controls (p<0.05); NH4^+-N was higher in controls than in N and N+C fertilized plots (p<0.01) (Table 1; Figs. 9 and 10). In bear digs, soil NO3^-N was higher in controls than in cellulose treated plots, and higher in N+C treated plots than in controls (p<0.05). Soil NH4^+-N was higher in controls than in N and N+C fertilized sites (p<0.05).

Date, treatment, and location all had significant effects upon glacier lily photosynthetic rate, and there were no two- or three-way interactions among sources of variation, so sites were similar. Average photosynthetic rates of N-fertilized plants in bear digs ranged between 10.3-18.8 μmol m^-2 s^-1, and in undisturbed areas between 10.6-15.68 μmol m^-2 s^-1 (Table 2). Adding N to plants in digs had no significant effect on photosynthetic rates (Fig. 16a). Photosynthetic rates of N-fertilized glacier lilies were higher than controls in undisturbed meadow on the last two dates (p<0.01, p<0.001) (Fig. 16b). For individual dates there was no significant difference in photosynthetic rates of N-fertilized plants in and out of digs except for 29 July (before fertilization), during which photosynthetic rates were higher in digs due to natural variation, presumably (p<0.01).

Fertilizing glacier lilies with NH4NO3 produced physiological responses similar to those that occur due to bear digging. The response of glacier lilies to fertilization with NH4NO3
was much greater in undisturbed areas than in digs (Fig. 16a,b). This is probably due to greater N-limitation of plants in undisturbed areas.

The addition of a carbon source was expected to cause the microbial population to immobilize N and have the effect of reducing photosynthetic rates of glacier lilies. However, the cellulose was not mixed into the soil in order to avoid complicating disturbance effects, so probably only about a third of the C added actually entered the soil. Soil NO$_3^-$-N was reduced in cellulose treatments in digs (p<0.05). Photosynthetic rates of plants with cellulose additions ranged from 8.2-22.6 $\mu$mol m$^{-2}$ s$^{-1}$ in bear digs and from 8.5-15.9 $\mu$mol m$^{-2}$ s$^{-1}$ in undisturbed meadow (Table 2). On 25 July (prior to cellulose addition), cellulose-treated plants had higher photosynthetic rates than controls, due to natural variation presumably. Addition of cellulose did not affect plants in digs, but in undisturbed areas plants with cellulose treatments had higher photosynthetic rates than controls on 11 August (p<0.05) (Fig. 16c,d). This could have been due to a priming effect in which addition of C stimulates N mineralization, although soil N did not increase, and plant tissue N did not significantly increase with addition of cellulose, so it is unlikely that the plants experienced an increase in N availability after cellulose addition. In digs, cellulose addition had the effect of lowering surface soil temperature compared to surface soil temperature near controls (p<0.05), since the cellulose provided a reflective surface. The white residue on the soil could have reflected additional light to plants in cellulose amended plots, therefore increasing photosynthetic rates, although leaf temperatures did not differ between treatments. The cellulose formed a mat that could
have prevented evaporation from the soil below, which may have indirectly increased photosynthetic rates by raising soil temperature and increasing plant nutrient uptake rates.

The cellulose was not mixed into the soil, but some glucose and maltose probably moved into the soil upon attack by cellulase: Therefore, instead of producing a C:N of 100:1 as expected, the C:N was probably closer to 30-40:1. Plants in N+C treated plots had significantly higher photosynthetic rates on 29 July, attributed to natural variation. Addition of NH\textsubscript{4}NO\textsubscript{3} plus cellulose resulted in higher photosynthetic rates than controls in undisturbed areas on 11 August (p<0.05) (Fig. 16e,f). Plants in N+C treated plots had photosynthetic rates between 9.6-18.9 in digs and 8.0-16.3 in undisturbed meadow (Table 2). Soil NO\textsubscript{3}-N was higher for N+C treatments than controls in both digs and undisturbed meadow (p<0.05) (Figs. 3 and 4). This could be due to a priming effect in which C addition stimulates N mineralization. It is more likely that this priming phenomenon occurred with N+C addition than with C alone, since the breakdown of cellulose requires a source of N. In digs and undisturbed meadow, soil NH\textsubscript{4}-N was lowered with N+C addition (p<0.05). Tardiff and Stanford (in press) have found soil NH\textsubscript{4}-N to be highly variable in the meadows at Logan Pass.

Leaf lengths did not differ between treatments (Fig. 6). For clarity, only controls and N-amended plants are represented in Figure 6. Neither shoot nor bulb biomass of control and fertilized plants differed significantly (Figs. 3 and 4). There were no significant differences in bulb %N and %C between treatments (Figs. 5 and 6). Neither bulb:shoot nor C:N ratios differed significantly between treatments (Figs. 9 and 12).
Storage organs usually experience a greater increase in nutrient concentrations after fertilization than vegetative tissues (Chapin et al. 1990). Luxury uptake is considered important for perennials growing in low nutrient habitats (Chapin, 1980). Lipson et al. (1996) found a lack of increase in aboveground biomass when plants took up fertilizer N as luxury consumption because fertilized plants stored N in rhizomes. They suggested that alpine plants are limited by environmental factors that preclude the ability to use excess nutrients for growth, and instead store them. However, these results do not support allocation to storage within this growing season. If growth rates of perennials are affected by a one-time fertilization application, the results may not be visible until the following year. Water-soluble carbohydrate levels may be higher for bulbs from bear digs, as Tardiff and Stanford (in press) found, but this data was not collected. The results presented here suggest that N is limiting to glacier lilies at Logan Pass, and that digging by grizzly bears increases N uptake by glacier lilies as evidenced by higher photosynthetic rates; however, this was not supported by one season of growth and tissue %N measurements. One or both of these responses may be apparent in successive growing seasons, although the plants in this study were harvested in the first year for tissue nutrient analysis, so sampling in successive seasons was not possible.

If bears are found to be important regulators of the subalpine meadow ecosystem, conservation efforts may benefit from increased understanding of the relationships between these species. Grizzly bear digging may help maintain meadows carpeted with glacier lilies by increasing the rate and amount of nutrients cycling through the meadows.
These meadows, if left undisturbed, might succeed to woody shrub communities, which already occur in patches in these meadows (Tardiff and Stanford, in press).

It is important, also, to be able to predict the effects of changes in nutrient availability on plants because the impacts of these effects may increase drastically as human activity increases the release of nutrients into the environment. For example, N deposition is becoming increasingly important to ecosystem functioning (Aber et al. 1989; Sievering et al. 1992; Sullivan, 1993; Wright and Tietma, 1995; Kopacek et al. 1996). As anthropogenic additions of N to ecosystems increases, the effects of increased N deposition can be seen in ecological effects of acidification, N saturation of ecosystems, and changes in plant community structure and microbial activity (Aber et al. 1989; Wedin and Tilman, 1996). Long term additions of N are expected to break down the relationships between soil N cycling and plant and microbial uptake of N (McNulty et al. 1996; Wedin and Tilman, 1996). Therefore, experiments which examine the responses of plants and plant communities to nutrient additions are useful in predicting responses to future nutrient levels.

Higher photosynthetic rates were demonstrated for glacier lilies growing in grizzly bear digs. This is likely due to increased soil N, and may also be affected by increased soil temperature. Fertilizing plants in undisturbed meadow with N increased photosynthetic rates since these plants are N-limited; adding N to plants in digs had no effect on photosynthetic rate. Cellulose treatments depressed photosynthetic rates in digs but not in undisturbed meadow; N+C treatments may have caused a priming effect which raised soil N and photosynthetic rates of glacier lilies in undisturbed meadow. Increases
in photosynthetic rates were not supported by increases in biomass or tissue %N in one growing season.
Chapter 4 - Recommendations for Future Research

In retrospect, it would be ideal to make all measurements on the same day for a given plot: photosynthesis, soil temperature, moisture, and nutrients, biomass, and plant tissue nutrient concentrations. This would allow links to be made from increases in photosynthetic rate or biomass or tissue nutrient concentration to soil conditions, which might then be dependent upon broader environmental conditions.

Phenological studies would help this research greatly. There have been studies on other *Erythronium* species (Muller, 1978; Kawano et al. 1982), but less is known about *E. grandiflorum*. In addition to measuring %N and %C over the growing season, allocation of carbohydrates should be measured to complete the picture. Digging usually occurs in the fall, after shoots have senesced, so it is likely that most aboveground nutrients have been retranslocated to the bulb by this point, and this is the most energetically efficient time for bears to dig glacier lily bulbs. Phenology between plants in digs and undisturbed meadow may differ, since soil temperature in digs is higher, and there are few other plants in digs to compete with glacier lilies. Plants growing in bear digs could have a longer growing season due to warmer temperatures. It would be interesting, too, to age bulbs in bear digs. Tardiff (unpublished data) has found that larger bulbs grow deeper in the soil. If larger bulbs are also older, they may be left in bear digs after sod is ripped off. This would affect any plant response noted in bear digs, since older bulbs may have had more time to store nutrients.
Community response to bear digging is not yet well understood. A long term study of plant communities with reference to time since digging would probably show that plants with low C:N occur first, especially glacier lilies. These should then be replaced by sedges and other herbaceous plants with higher C:N, and finally woody shrubs are found in areas where bears have not dug for many years. The increase in soil N in digs may be due to the lack of plants to take up available N, since bears rip off around the top 10 cm of sod when they dig for bulbs. Competition between glacier lilies and other meadow plants should be measured to identify the importance of release from competition for nutrients or other resources to glacier lilies growing back in bear digs. Plants surrounding glacier lilies in undisturbed meadow could be covered to measure the effect of release from competition apart from effects of disturbance. Additionally, Tardiff (unpublished data) has found that artificial digs at Logan Pass experience an increase in soil N, so it is likely that glacier lilies transplanted into artificial digs would respond similarly to those measured for plants in bear digs.

This research covered only one growing season, and in fertilization studies of alpine and arctic plants, most measurements are made during the season following fertilization (Bowman, 1994; Bowman et al. 1995; Bowman and Conant, 1994; Bowman et al. 1993; Lipson et al. 1996; McKendrick et al. 1980; Shaver and Chapin, 1980). Following the responses of these perennials over several growing seasons would allow detection of differences in nutrient and water availability, temperature, and length of growing season between years. These environmental differences may be enough to make noticeable differences in plant responses between years. McKendrick et al. (1980) say
that four or more growing seasons may be needed to observe all the effects of fertilization of tundra soils. Arctic plants will allocate added nutrients to replace stores in underground structures or stems, so effects of fertilization on plant growth will not be seen until one or more seasons following application (Chapin and Shaver, 1985). In one season I have shown that glacier lilies in bear digs do in fact have higher photosynthetic rates than lilies in undisturbed meadow, and that fertilizing lilies with N produces physiological responses similar to those of bear digging, although links to increased growth rates and increased N storage were not made evident here.

The fertilizer should have been applied as early as possible, since growth occurs even before snow is completely gone. This might mean fertilizing the fall before measurements take place. The concentration of N used in this experiment was low compared to that of other alpine and arctic fertilization studies (Bowman, 1994; Bowman et al. 1995; Bowman and Conant, 1994; Bowman et al. 1993; Lipson et al. 1996; McKendrick et al. 1980; Shaver and Chapin, 1980). Sample sizes were intended to be larger, but logistically it was difficult to include so many samples, since photosynthetic rates of all 80 plants were measured in one day to avoid temperature and light effects. Plots were arranged so that digs, rather than plants, were replicated. Now that differences between digs and undisturbed meadow have been demonstrated, future studies could replicate plants to get more information about variation among plants. It might also be helpful to include digs in different meadows.

Tardiff and Stanford made experimental digs at Logan Pass (in press). While these digs have no plants growing in them yet, as they fill in with glacier lilies it will be
interesting to monitor the physiological responses of those plants to the increase in soil N and compare with plants in natural bear digs. Plants in experimental digs are expected to have higher photosynthetic rates, biomass, tissue N, and seed production than plants in surrounding undisturbed meadow.
Table 1. Soil NO$_3^-$-N, NH$_4^+$-N, and total inorganic N in bear digs and undisturbed meadow. Data are from ion exchange resin bags left *in situ* for 51 days. Values are means ±1 SE; n=2-17.

<table>
<thead>
<tr>
<th></th>
<th>NO$_3^-$-N</th>
<th>NH$_4^+$-N</th>
<th>Total N$_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Digs</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>353.5± 327.2</td>
<td>23.4± 7.3</td>
<td>30.7± 7.3</td>
</tr>
<tr>
<td>Nitrogen</td>
<td>596.7± 299.5</td>
<td>5.7± 2.2</td>
<td>9.0± 2.8</td>
</tr>
<tr>
<td>Carbon</td>
<td>32.9± 9.6</td>
<td>27.4± 4.9</td>
<td>30.7± 4.8</td>
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<tr>
<td>N+C</td>
<td>931.0± 397.1</td>
<td>6.9± 4.6</td>
<td>10.1± 5.1</td>
</tr>
<tr>
<td><strong>Undisturbed</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>23.6± 13.3</td>
<td>46.7± 16.6</td>
<td>54.3± 16.7</td>
</tr>
<tr>
<td>Nitrogen</td>
<td>814.8± 608.3</td>
<td>17.3± 7.5</td>
<td>21.0± 8.3</td>
</tr>
<tr>
<td>Carbon</td>
<td>13.2± 4.0</td>
<td>54.8± 17.0</td>
<td>58.5± 17.0</td>
</tr>
<tr>
<td>N+C</td>
<td>1988.9± 1473.9</td>
<td>3.5± 2.0</td>
<td>7.2± 2.7</td>
</tr>
</tbody>
</table>
Table 2. Photosynthetic rates of glacier lilies in digs and undisturbed meadow. Treatments were applied on 30 July. Values are means ±1 SE; n=4-25.

<table>
<thead>
<tr>
<th></th>
<th>25July</th>
<th>29July</th>
<th>2August</th>
<th>6August</th>
<th>11August</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Digs</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>14.5±3.8</td>
<td>13.1±4.2</td>
<td>17.8±2.6</td>
<td>11.8±3.2</td>
<td>9.4±4.0</td>
</tr>
<tr>
<td>Nitrogen</td>
<td>17.8±4.5</td>
<td>18.8±1.5</td>
<td>15.9±2.9</td>
<td>14.0±1.5</td>
<td>10.3±3.4</td>
</tr>
<tr>
<td>Carbon</td>
<td>22.6±10.1</td>
<td>17.1±2.3</td>
<td>15.0±2.5</td>
<td>14.2±2.2</td>
<td>8.2±3.6</td>
</tr>
<tr>
<td>N+C</td>
<td>17.2±5.6</td>
<td>18.9±2.1</td>
<td>17.9±3.0</td>
<td>13.5±2.4</td>
<td>9.6±4.1</td>
</tr>
<tr>
<td><strong>Undisturbed</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>14.2±3.1</td>
<td>12.1±4.4</td>
<td>14.4±3.8</td>
<td>9.5±3.3</td>
<td>4.9±2.8</td>
</tr>
<tr>
<td>Nitrogen</td>
<td>15.6±3.6</td>
<td>14.4±1.8</td>
<td>15.4±2.1</td>
<td>14.3±4.3</td>
<td>10.6±3.7</td>
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<tr>
<td>Carbon</td>
<td>15.9±2.6</td>
<td>14.5±3.6</td>
<td>14.8±2.6</td>
<td>11.7±3.2</td>
<td>8.5±4.1</td>
</tr>
<tr>
<td>N+C</td>
<td>14.6±1.4</td>
<td>16.3±2.7</td>
<td>14.3±2.4</td>
<td>11.7±1.2</td>
<td>8.0±1.5</td>
</tr>
</tbody>
</table>
Figure 1. Soil Temperature

Figure 2. Soil Moisture

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Figure 3.

Soil NO₃⁻-N

Soil NH₄⁺-N

Figure 4.

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Figure 5.

Photosynthetic Rates

μmol CO₂ m⁻² s⁻¹

25-Jul 29-Jul 2-Aug 6-Aug 11-Aug

* ***

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Figure 6.
Bulb Biomass

Figure 7.

Shoot Biomass

Figure 8.

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Figure 9.

Biomass Bulb: Shoot

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Bulb %Nitrogen

Figure 10.

Bulb %Carbon

Figure 11.
Figure 12.
Figure 13.

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Figure 14.

% Nitrogen

Figure 15.

% Carbon

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Figure 16.
Literature Cited


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