THE EFFECTS OF COLLARED PIKA GRAZING ON ALPINE TUNDRA VEGETATION IN SOUTHWESTERN YUKON, CANADA

by

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General Abstract

In alpine tundra vegetation, rates of plant production were as low in 15-17 day short-term *in situ* pika removal exclosures as they were in control, unexclosed plots. After nearly two seasons of herbivore exclusion, sites with a history of grazing had much higher production than sites with no history of grazing, demonstrating an important influence of past grazing pressures. I also found that the pattern of pika grazing influence changed between two disjunct field sites separated by 40km: pikas had a detectable impact up to 7 m from talus in one site, but only up to 2 m in the other. When the effect of grazing on leaf demography for three species was examined, grazing history, rather than current season grazing, was found to affect growth traits. In a common garden experiment, grazing history affected plant response to simulated pika herbivory in a sedge but not in a composite. In all three experiments, grazing history was found to have a profound and very important impact on plant growth.

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General introduction

The effects of vertebrate herbivores on plants are remarkably diverse (Crawley, 1983, 1997). For instance, plant production has shown a continuum from negative to positive effects of grazing (Maschinski and Whitham, 1989; Whitham *et al.*, 1991; Paige, 1992); plants have been shown to alter their secondary compound production and allocation (Bryant, Chapin and Klein, 1983; Coley, Bryant and Chapin, 1985); plant architecture and the timing of tissue production may be altered (Briske, 1986; Mulder and Harmsen, 1995); a plant's photosynthetic rate and other physiological processes may be increased or decreased (McNaughton, 1979); and, herbivores may directly contribute nutrients for plant use via urine and fecal inputs (Ruess and McNaughton, 1987; Hobbs, 1996). Ecological research has focused on observing, understanding and predicting these patterns under a diverse array of conditions and in a diverse array of plants.

Much of the research has concentrated on the curious and unexpected finding of overcompensation, either as increased fitness or as increased vegetative production in grazed plants compared to ungrazed plants (McNaughton, 1979; Paige and Whitham, 1987; Paige, 1999). While evidence for the existence of overcompensation in natural systems has been increasing (Hik and Jefferies, 1990; Paige, 1992; Alward and Joern, 1993; Lennartsson, Tuomi and Nilsson, 1997), the rarity and idiosyncratic nature of its occurrence makes it difficult to predict. There have been a number of theoretical attempts to explain patterns of overcompensation (Oksanen, 1983; van der Meijden, 1990; Vail, 1992; de Mazancourt, Loreau and Abbadie, 1998; but see Georgiadis *et al.*, 1989; Westoby, 1989), but these have generally not accounted for the diverse and remarkable strategies plants use to compensate for the loss of tissue from herbivory (Belsky *et al.*, 1993; Bergelson, Juenger and Crawley, 1996).

It has been proposed that because overcompensation exists, herbivores benefit plants—that some plants have improved fitness or growth as a result of herbivory (Owen and Wiegert, 1976, 1981; Verkaar, 1986; Vail, 1992). This theory is contentious and other hypotheses have been proposed which account for the increased production without requiring that herbivory "benefits" plants. Plants have other adaptations which allow them to respond quickly to damage. Examples include removal of apical dominance (Aarssen, 1995; Irwin and Aarssen, 1996), the existence and release of dormant buds (Tuomi, Nilsson and Åström, 1994), adaptations to improve competitive ability (Aarssen and Irwin, 1991; Järemo, Nilsson and Tuomi, 1996), and a generalized adaptive response to reducing the effects lost tissue (Belsky *et al.*, 1993). Regardless of the proposed mechanism for compensation, the persistence of many herbivore populations relies on the ability of plants to tolerate grazing and maintain highly palatable tissue (Rosenthal and Kotanen, 1994). The ability to regrow after damage is particularly interesting if herbivores do not graze at levels at which plant production is maximized ("herbivore optimization"; Dyer, 1975; McNaughton, 1979; Dyer *et al.* 1982), since evidence suggests that herbivores do not necessarily graze at these "optimum" levels (McNaughton, 1979). The intensity of grazing in a system, the details of regrowth capacity and the factors that influence plant response are important to understanding the interrelationships between plants and herbivores and the persistence of heavily grazed plant communities.

Underlying many plant response studies is an attempt to understand the relationships between the effects of herbivory occurring in isolation from other factors and the more complex influences which may alter the impact of herbivory. Multiple levels of grazing intensity, timing of herbivory, local climate and climatic history, and grazing history have all been shown to alter the response of plants to herbivory (Dyer, 1975; Maschinski and Whitham, 1989; Painter, Detling and Steingraeber, 1989; Hik and Jefferies, 1990; Milchunas *et al.*, 1995; Oleksyn *et al.*, 1998; Suzuki, 1998). Few clear patterns have emerged. A common limitation of many of these studies lies in the removal of the naturally occurring herbivore itself from the study, instead, favouring controlled experimentation whereby individual features of the herbivore are reproduced by hand (e.g., clipping, nutrient additions). Of the aforementioned influences, only multiple levels of grazing intensity has good theoretical predictions as to how plants would respond (Dyer, 1975; Noy-Meir, 1975; Noy-Meir, Gutman, Kaplan, 1989; Dyer, Turner and Seastedt, 1993), but few natural systems contain readily manipulated grazing gradients to allow for direct experimentation under natural conditions. As a result, in spite of numerous theoretical models that have proposed biphasic patterns of plant response to grazing (e.g., Dyer *et al.*, 1982; de Mazancourt, Loreau and Abbadie, 1998), relatively few examples have been found in natural systems (Belsky, 1986; Belsky *et al.*, 1993). Brown and Allen (1989) suggested that not all studies find these patterns because of problems of scale. They propose that the biphasic patterns occur often, but many studies only observe sections of the biphasic pattern. Further, few strong generalizations have been found that allow good predictions as to how plants will respond to herbivory in terms of biomass production, species shifts, leaf turnover rates, aboveground-belowground allocation and other growth parameters under the complex conditions that often occur in natural systems. As for the influence of grazing history, current climate and climatic history, and timing of herbivory, our understanding is so limited, that there is very little predictability. In particular, grazing history has been largely ignored in most studies in native systems, in spite of the well documented occurrence of ecotypic adaptations among plants to conditions under which they survive (Clausen, Keck and Hiesey, 1948; Painter, Detling and Steingraeber, 1993).

The persistence of palatable vegetation is one of the fundamental concerns for small non-migrating herbivores—particularly those which repeatedly forage the same areas and whose populations are not cyclic. Traditionally, with the view that herbivores cause negative responses in vegetation (Crawley, 1993), vegetation has generally been thought to persist because it is only infrequently grazed and highly unpalatable (Hairston, Smith and Slobodkin, 1960; White, 1993). In many systems, however, grazing reoccurs regularly and frequently, and recent studies have demonstrated substantial compensatory mechanisms (Frank and McNaughton, 1993; McNaughton, Banyikwa and McNaughton, 1997). The most commonly cited examples of highly and repeated grazed ecosystems are grasslands where it is hypothesized that there are coevolutionary processes that allow for such positive responses to grazing (Owen and Wiegert, 1976; Stebbins, 1981; Coughenour, 1985). Systems where these coevolutionary processes are less likely to have occurred generally have not shown comparably high levels of grazing on wide scales and thus herbivores have not shown dramatic long-term influences on vegetation (Jefferies, Klein and Shaver, 1994). But, in some non-grassland ecosystems—such as tundra—heavy grazing may occur (Batzli, White and Bunnell, 1981), particularly on smaller than ecosystem scales (Cargill and Jefferies, 1984). Sites which do show high levels of chronic grazing seem to show lower levels of production, particularly of highly palatable vegetation, than sites with infrequent grazing (Vinton and Hartnett, 1992; Turner, Seastedt and Dyer, 1993). The question remains, what are the mechanisms of persistence of highly palatable plants in areas that are repeatedly and highly grazed?

The impacts of herbivores in arctic and alpine tundra systems are interesting because they are often characterized by low nutrient soils, low temperatures and low production, but may carry high biomass of herbivores (Batzli, White and Bunnell, 1981). Particularly interesting is the effect of small mammals whose influence in arctic and alpine ecosystems may be locally substantial (Jefferies, Klein and Shaver, 1994). For instance, the collared pika (*Ochotona collaris*), a small food caching mammal, has a dramatic effect on the vegetation immediately surrounding alpine boulderfields in northwestern North America. While virtually no ecological work has been performed on this species, pika herbivory likely causes shifts in the vegetation in the areas immediately adjacent to home ranges and due to the spatially localized intensity, could change the genetic or species compositions of local plant assemblages. While some studies have attempted to address the level of community change or the nature of plant tolerance in these arctic and alpine systems (except see Batzli, 1975; Oksanen and Oksanen, 1992; Moen and Oksanen, 1998), the more fundamental question of how these plant communities persist indefinitely under consistent and heavy grazing is still poorly understood.

In this study, I have attempted to address three general questions concerning the effects of collared pika foraging on alpine tundra vegetation and the plant morphological responses induced by the herbivory. First (Chapter 2), what is the effect of collared pikas on aboveground live biomass, net aboveground primary productivity and species richness? Pikas feed outward from boulderfields and create easily observable multiple grazing intensities over very small distances. Their populations also have appeared to show long-term (>100 years) persistence and thus plants adjacent to talus likely have long grazing histories. Using mesh exclosures near pika activity, I can address the effects multiple grazing intensities and of grazing history at the community scale. In addition, pika grazing usually intensifies throughout the summer in preparation for winter haypile construction, so plant growth may be expected to be strongly affected. Specifically, is plant tolerance to herbivory an important strategy of coping with pika herbivory and how is this tolerance affected by grazing history and multiple grazing intensities? Does the nature and timing of pika herbivory allow exact- or overcompensation to occur and what spatial and temporal scales are important? Finally, in this chapter, by measuring plant community response, I can examine the nature of persistence in these communities.

Second (Chapter 3), how are leaf births, leaf deaths, flower production and leaf length altered in three diverse plant species by *in situ* naturally occurring pika grazing under current season grazing and under long-term (>100 years) chronic grazing? By examining the leaf level patterns of plant regrowth with and without long-term grazing pressure and orthogonally contrasting that with presence of current season grazing, I can examine morphological plant responses and determine the relative importance of longer and shorter term processes. Due to the long-term persistence of pika populations and their chronic pattern of grazing, pikas are ideal to address questions of short and long-term herbivory.

Finally (Chapter 4), using transplanted individuals of two alpine plant species from three climatically and physiognomically distinct sites that contain pikas, how do the past history of grazing and the site of origin affect the ability for plants to further tolerate two levels of simulated pika grazing? Transplant experiments are particularly useful for examining ecotypic differentiation as the effect of local environment can be removed. In this chapter, I use a common garden to contrast the relative importance of site history or grazing history in the response of plants to simulated pika herbivory.

The first question addresses coarse scale effects on community processes, while the leaf demography experiment attempts to understand the finer scale, within-plant effects and directly contrasts the relative influences of current season grazing with grazing history. In the final chapter, I use a common garden to address how the within-plant effects change across a diversity of sites and different grazing histories, while experimentally controlling and standardizing the intensity of grazing. In the immediately following sections, I briefly describe the general characteristics of the sites and the focal animal and plant species with which I addressed the above questions.

Study sites

Field work was carried out at three locations (Fig. 1-1)—the Front Range Mountains (central; FR: 60°57'N, 138°32'W; Fig. 1-2a), the Icefields of the St. Elias Mountains (most westerly; IF: 60°36'N 139°25'W; Fig. 1-2b) and the Ruby Range Mountains (most easterly; RR:

Figure 1-1. Map of southwestern Yukon territory showing alpine study sites. A) Ruby Range site, B) Front Range site, and C) Icefields site.

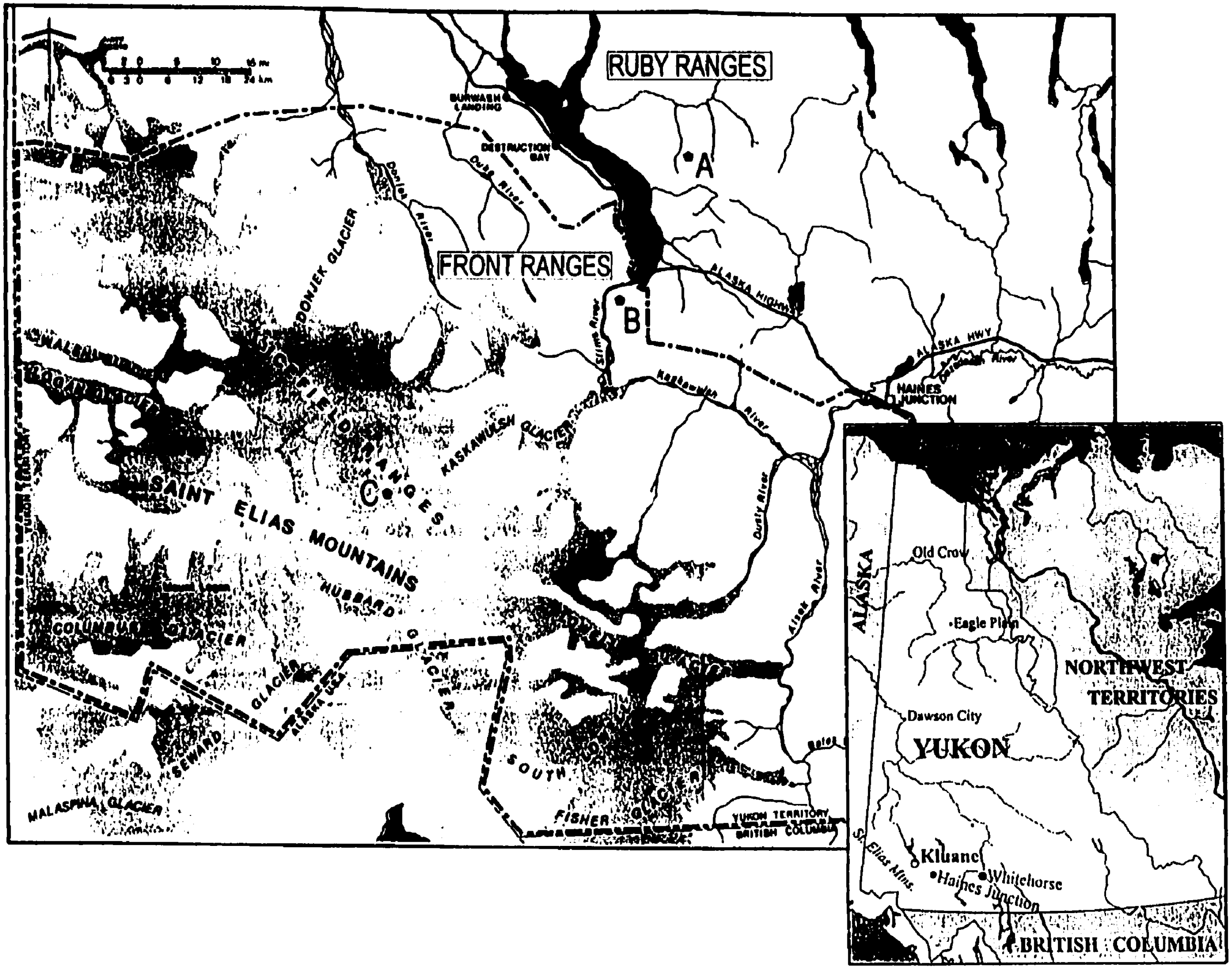
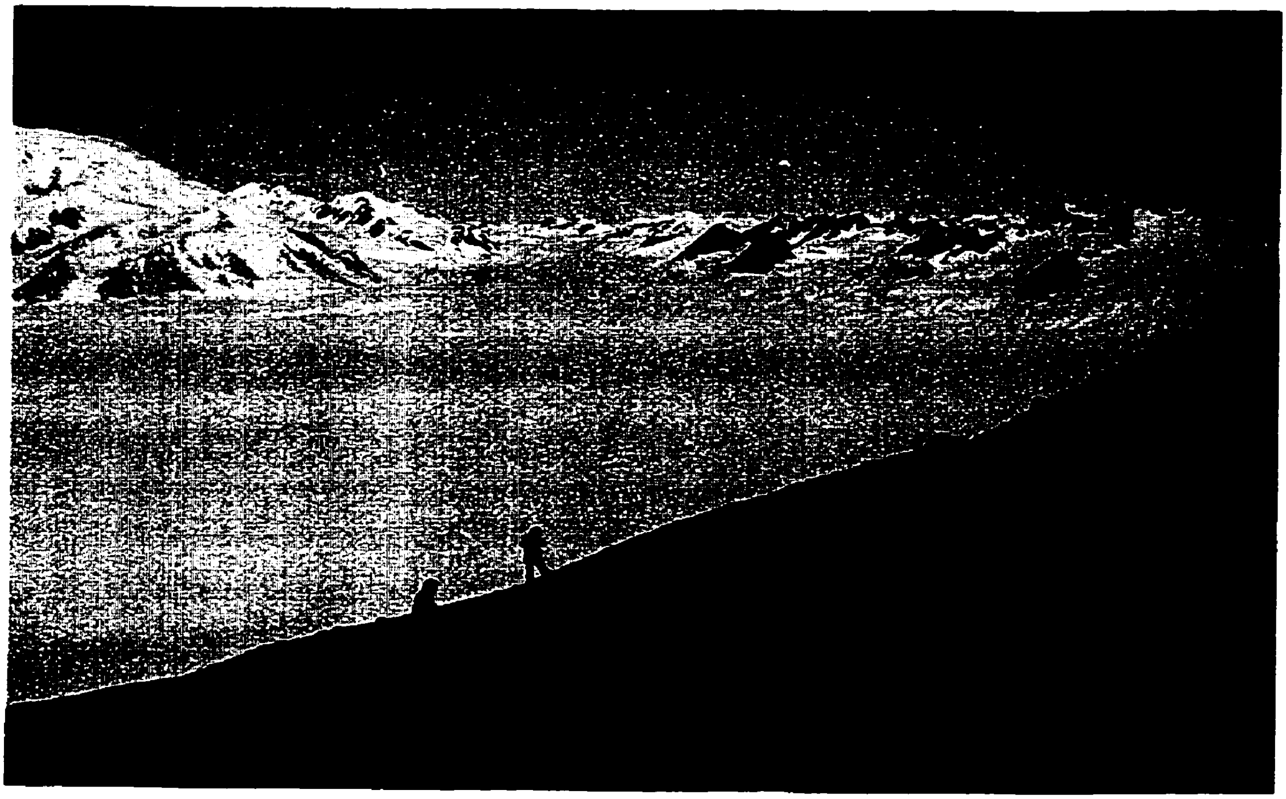
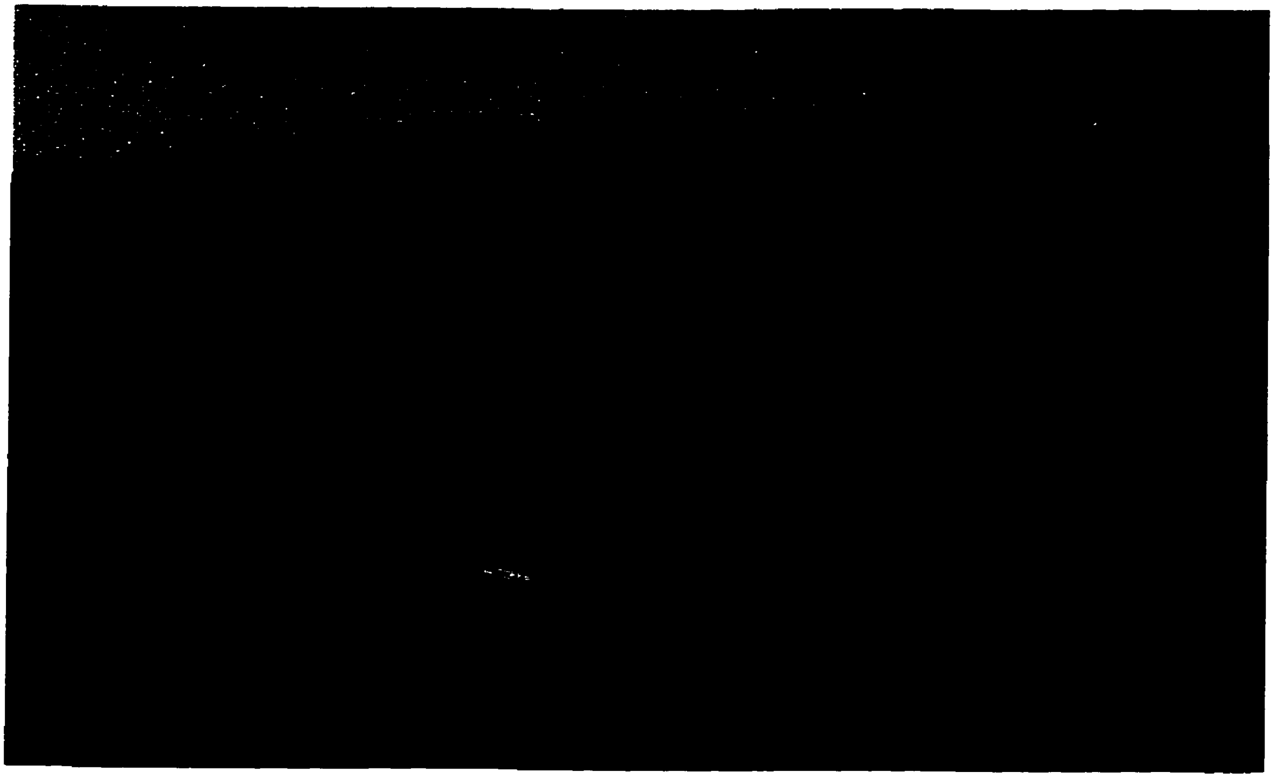

N
RUBY RANGES
BURWASH LANDING
DESTRUCTION BAY
Duke River
Donjek River
A
FRONT RANGES
B
DONJEK GLACIER
Slims River
ALASKA HIGHWAY
ALASKA HWY
Dezadeash River
HAINES JUNCTION
Kaskawulsh River
KASKAWULSH GLACIER
ICEFIELD RANGES
C
SAINT ELIAS MOUNTAINS
HUBBARD GLACIER
COLUMBUS GLACIER
SEWARD GLACIER
MALASPINA GLACIER
Dusty River
Alsek River
SOUTH
FISHER GLACIER
YUKON TERRITORY
BRITISH COLUMBIA
ALASKA
Old Crow
Eagle Plain
NORTHWEST TERRITORIES
Dawson City
YUKON
St. Elias Mtns.
Kluane
Whitehorse
Haines Junction
BRITISH COLUMBIA

Figure 1-2. Photographs of the (a) Front Ranges site, (b) Icefields site, and (c) the Ruby Ranges site.

a)



b)



c)

61°13'N, 138°16'W; Fig. 1-2c)—in southwestern Yukon Territory, Canada. The sites are situated at approximately 50 km intervals along a 100km transect (D. Hik, in review). The Ruby Range Mountain site formed part of a southern arm of the Beringian intermittently ice-free land mass during the last glaciation (Hughes *et al.*, 1968). This range consists of geologically old, rolling mountains which create a contiguous community of alpine vegetation. As a result, meadows in the Ruby Range site are more continuous and are not distinctly separate from surrounding areas of similar quality due to limited talus. The Front Range mountains, located at the eastern edge of the St. Elias Mountains in Kluane National Park, are geologically younger mountains (<10 mya.) and are characterized by discontinuous meadows interspersed among rocky slopes, likely due in part to recent glaciation during the Wisconsin. Our site is relatively isolated from other similar sites due to ca. 800m high rock slides descending on all sides. Indeed, preliminary genetic analysis of the pikas in the Front Ranges indicate that they are very isolated, showing a very reduced number of haplotypes (T. Bubela *et al.*, unpub. data). The Icefields site is characterized by large extant glaciers with emergent nunataks upon some of which are located alpine meadow vegetation and collared pikas. These isolated islands of vegetation are usually small (<2000m^2) and are usually separated from one another by at least 2-5 km of glacial ice or barren rock. There is very little apparent threat of predation in these meadows, however, ermine scat and one pika mortality has been observed on nunataks occupied by pikas (Hik, 2000). We used two nunatak meadows for the source of Icefields transplants into the common garden. We selected these three locations because of their similarity in altitude (RR: 1700m-1900m, FR: 1800m-2000m, and IF: 2100m-2300m), the presence of extant collared pika populations, and generally comparable plant species composition.

All sites are characterized by alpine tundra vegetation. The sites differ, however, in several abiotic factors, notably glacial history and present climate, so we could contrast small scale plant-herbivore interactions under different physical conditions. Daily summer surface temperatures on meadows at all sites may fluctuate from below 0°C to over 40°C (D. Hik, unpub. data). The Ruby Range site contained >100 plant species and was dominated by *Salix polaris* (Wahlenb), and *Carex consimilis* (Holm), while the Front Ranges site contained >50 species and was dominated by *Dryas octapetala* (L.), *Salix polaris*, and several graminoid species including *Carex consimilis*. Species composition varied substantially between nunataks in the Icefields and often dominant species between sites would be different. Total species numbers on the nunataks are not certain, though one of our sites had >20 species. All but one locally uncommon species (*Vaccinium vitis-idaea* L.) in all three sites were deciduous perennials. Plant species names follow Cody (1996) and a species list for the three sites is presented in Appendix 1.

The Front Ranges and Icefields sites are relatively disjunct from other meadows and extant pikas may form sink populations within larger metapopulations. In spite of this, the pika numbers have been relatively stable over the past 6 years (D. Hik, pers. obs.), with more than 12 individuals in a given season in the Front Range site and 2-3 pikas in each of two inhabited Icefields nunataks. Movements to the Front Range site and between the Icefields nunataks are thought to exist (D. Hik and E. McIntire, pers. obs.). At the Ruby Range site, the pika population of over 70 individuals in a given year has shown small fluctuations but has shown no incidence of regular cyclicity, a pattern that has been observed in the Rocky Mountains for *Ochotona princeps* (Southwick *et al.*, 1986). Preliminary mitochonrial DNA analysis (T. Bubela *et al.*, unpub. data) indicates that pikas here are likely part of a larger population that extends beyond the boundaries of our study and readily exchanges individuals. All sites have a very short growing season in these areas (<90 days) and generally low nutrient soils (D. Hik *et al.*, unpub. data).

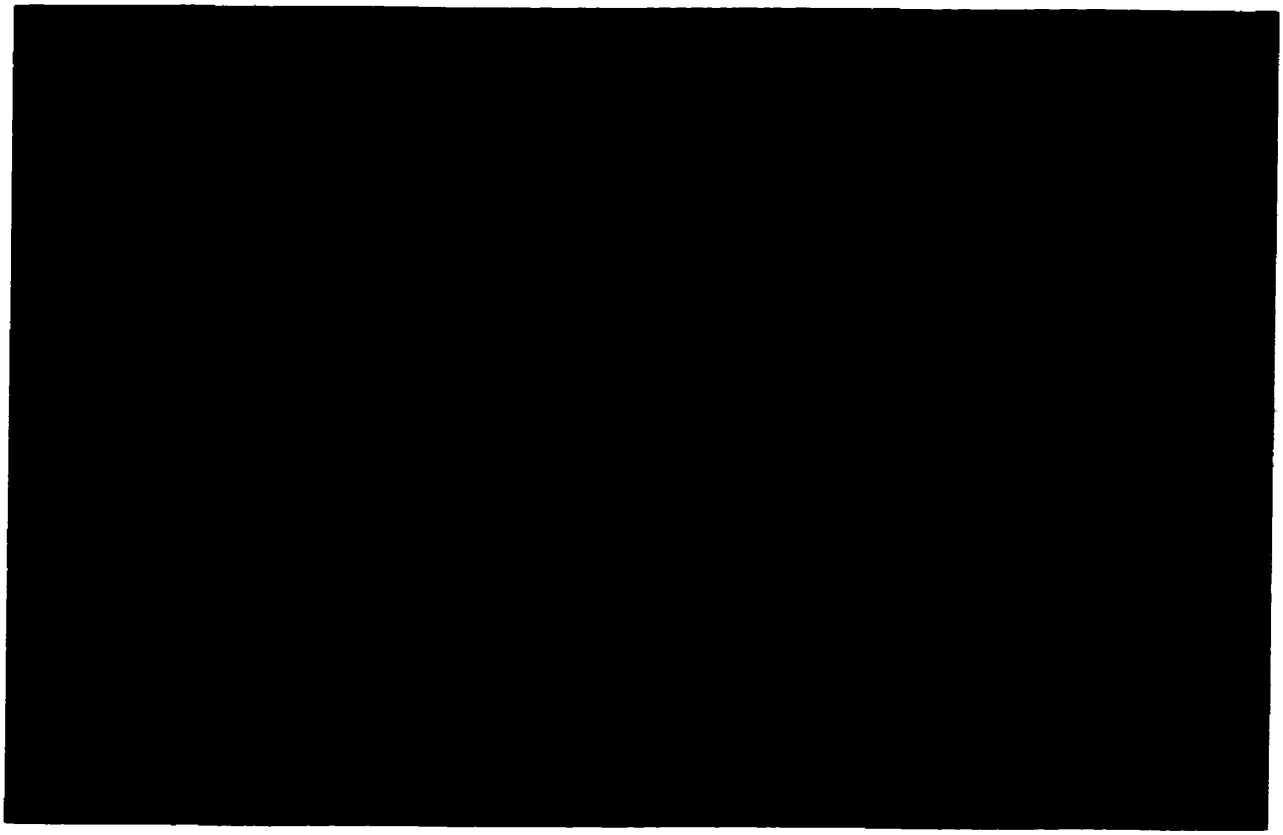
Study species

Ochotona collaris

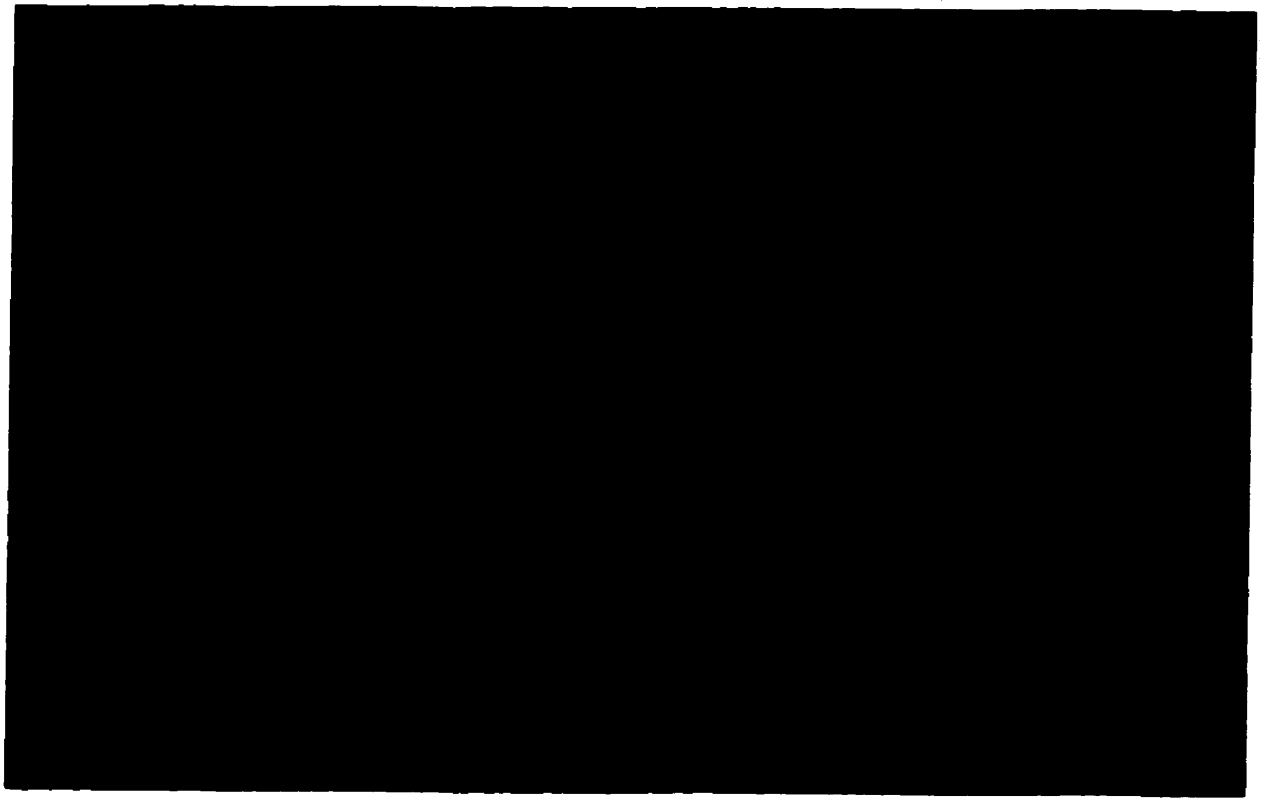
Collared pikas (*Ochotona collaris*) are small lagomorphs of alpine regions, endemic to south and central Yukon and central Alaska (Fig. 1-3a; MacDonald and Jones, 1987). Largely because of high predation risk (Huntly, 1987), they are strictly confined to and feed adjacent to boulderfields or talus slopes, thus functioning as central place foragers (Andersson, 1978). Virtually all knowledge of pikas in North America is derived from studies on the American pika (*O. princeps*) which occurs throughout the Rocky mountains and other mountain ranges in the western parts of the United States and Canada. It has been proposed that *O. collaris* became a distinct species during the Wisconsin glaciation due to isolation from *O. princeps* (Guthrie, 1973). Throughout this thesis, references to previous work on pikas are made, but since few previous investigations have been performed on collared pikas, most citations are to work on the American pika. We do not assume or expect that the behaviour and effects of these two species of pikas are identical, but they appear to be similar in many respects.

Adult pikas are philopatric, have very low adult dispersal and show relatively stable, non-cyclic interannual population levels (*O. princeps*; Southwick *et al.*, 1986; *O. collaris*; Hik unpub. data). Pikas do not hibernate, instead, they collect and store food in haypiles during the short summer (8-12 weeks) to support their needs for the whole year. Other important ecological features distinguishing the effect of pikas from other small mammals include virtually no alteration of the physical structure of the area surrounding a haypile (e.g., due to burrowing animals; see Huntly, 1991), and gradual intensification of harvesting late in the growing season collecting vegetation for haypiles (MacDonald and Jones, 1987). Pikas use latrines within the rock piles for defecation and urination resulting in a very low rate of direct nutrient returns to the areas that are most heavily grazed (Aho *et al.*, 1998), eliminating a commonly observed beneficial return of nutrients following herbivore grazing (Cargill and Jefferies, 1984;

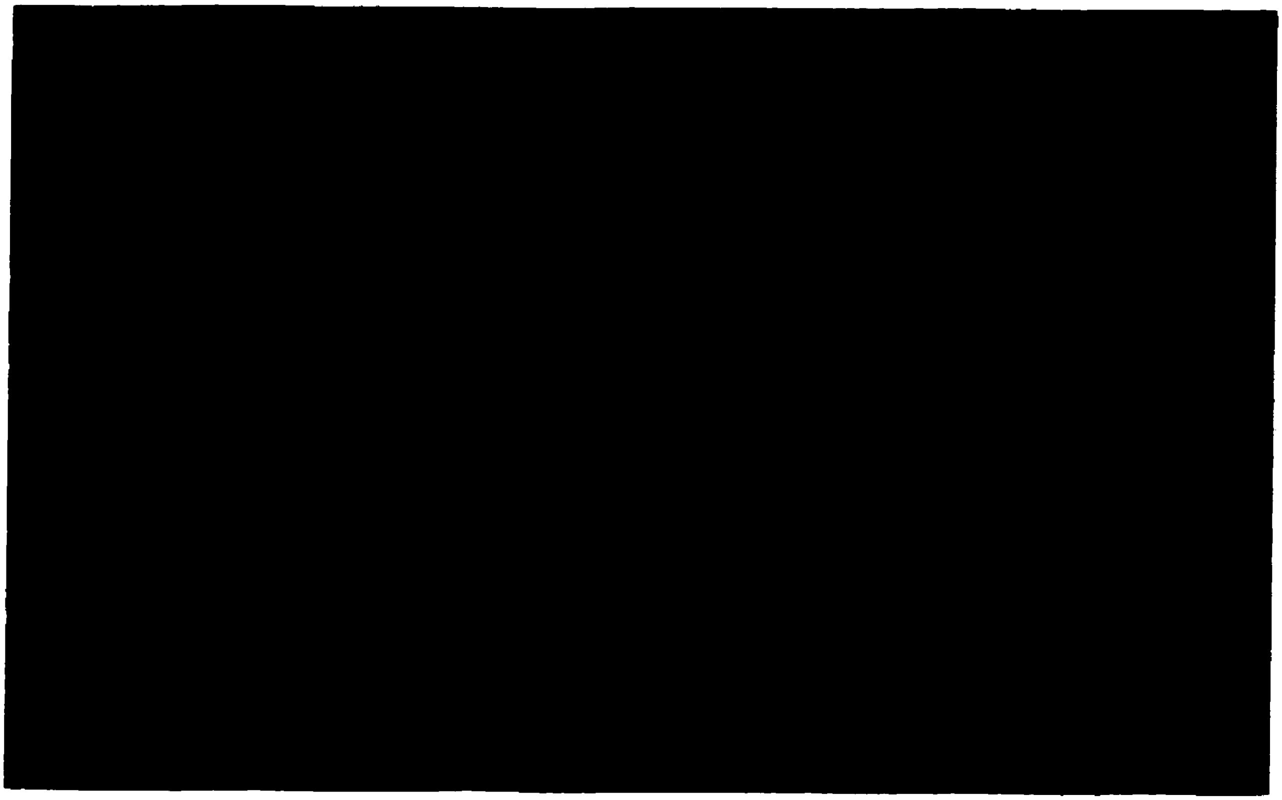
Figure 1-3. Photographs of (a) *Ochotona collaris*, (b) *Erigeron humilis*, (c) *Kobresia myosuroides*, and (d) *Oxytropis nigrescens*.



a)



b)



c)

d)

McNaughton, 1985; Ruess and McNaughton, 1987). Pikas are generalist herbivores, consuming most vascular species, though evidence suggests some selectivity in plant choice (MacDonald and Jones, 1987; Dearing, 1996; E. McIntire pers. obs.; D. Hik *et al.*, unpub. data). The combination of non-cyclic and only small fluctuations in population size creates repeated grazing between years, and focused feeding and haying during a short period and in a small area within years, resulting in very intensive and extremely localized grazing patterns at distances <3m from talus edge (Smith and Ivins, 1983; Dearing, 1996). This grazing pattern causes the vegetation surrounding talus patches to be heavily grazed, sometimes creating visual "halos" around talus piles. Vegetation progressively further from the margin of the talus is less grazed. Since pikas consistently graze the same patches year after year—unlike many populations of arctic and alpine herbivores (Jefferies, Klein and Shaver, 1994)—they likely select for grazing tolerant plant genotypes (McNaughton, 1983; Herms and Mattson, 1992). As most vegetation in these areas have either very few defense chemicals and are edible (although they may be relatively low in nutritional value; Batzli, White and Bunnell, 1981) or the overwinter decay of vegetation in pika haypiles causes a reduction of secondary compounds to insignificant levels (Dearing, 1997a), the primary plant defense against the negative effects of pika grazing is likely to be some type of tolerance mechanism or escape.

Plant species

For the leaf demography and the common garden experiments, we selected three plant species which were present in all three sites and were readily consumed by collared pikas. *Erigeron humilis* Graham (Asteraceae), a circumpolar arctic and alpine composite, has a very different growth form with a basal rosette of leaves, an erect single stalked flower and a taproot (Fig. 1-3b). *Kobresia myosuroides* (Vill.) Fiori & Paol. (Cyperaceae) is a common densely tufted, dry area sedge (Fig. 1-3c). As with most other graminoids, this species has a basal meristem, allowing immediate leaf growth by means of extant leaf elongation after herbivore harvesting. It is a circumpolar species distributed in North America from Labrador to Alaska and south in the mountains to Utah and Colorado. Being densely tufted, a commonly observed graminoid response to grazing of initiation of axillary meristems as a mechanism for prostrate growth (Bazely and Jefferies, 1989) may not occur. *Oxytropis nigrescens* (Pall.) Fisch. (Fabaceae), a high altitude legume, has a densely tufted caespitose growth, at times almost a cushion plant in form, with large, nutritious seeds (Fig. 1-3d). It is amphi-Beringian in distribution, extending eastwards to the Mackenzie Mountains in the Northwest Territories. Legumes have been often cited as being highly prized food for herbivores because of their nitrogen fixing abilities (see Ritchie and Tilman, 1995). Both dicotyledons must have growth strategies that favour new leaf initiation in response to grazed tissue rather than grazed leaf elongation because they lack active intercalary meristems. This latter method of regrowth is thought to require more plant resources to respond successfully to grazing (Mulder and Harmsen, 1995), and so depending on the timing of harvest, herbivory may have more adverse affects on these plants. In the common garden, post-transplant survival of *Oxytropis* was too low to allow examination of this species. Plant names and species descriptions used follow Cody (1996).

Chapter 2: Within- and between-season impacts of the collared pika along a steep grazing gradient: detecting the influence of grazing history in slow growing alpine perennials

Abstract

We used an *in situ* natural grazing gradient of collared pikas on alpine tundra vegetation to examine the within-season, between-season and longer term dynamics of three levels of grazing on aboveground live biomass, plant productivity and species richness. We showed that depending on the observation date and plant life form, aboveground live biomass in experimental control plots monotonically increased, monotonically decreased, or showed a biphasic growth pattern along a decreasing collared pika grazing gradient. Using temporary exclosures to measure herbivory offtake, we found pika grazing to be focused late in the season, corroborating previous behavioural observations.

Using experimental mesh exclosures, plants subject to past pika grazing produced surprisingly different effects at different time scales. Aboveground productivity in highly grazed areas adjacent to talus was not significantly different in 15-17 day temporary exclosures compared to control plots indicating no detectable plant response to short-term within-season release from grazing. Final season aboveground live biomass in the first year following pika exclusion showed no significant effect of distance from talus (62, 78 and 68 $g \cdot m^{-2}$, adjacent, intermediate and far, respectively) suggesting that even following release from the majority of grazing within a season, plant production response is not detectable. Net annual above-ground production after the second consecutive year of herbivore exclusion, however, was greatly increased in highly and lightly grazed areas compared to the previous year and not in the ungrazed sites far from talus (116, 130 and 82 $g \cdot m^{-2}$, respectively). Importantly, the net annual

above-ground production was highest in areas with past influence of pika grazing, suggesting much higher aboveground production in plants that had a grazing history compared to those without a grazing history but only after 2 years of release from herbivory. This type of between year measurement of growth is particularly relevant in long lived perennials in regions of low productivity. In addition, the periodic and haphazard pika haypile vacancies would give individual vegetation patches infrequent 1 to 2 year releases from pika grazing, allowing the continued persistence of highly palatable, highly grazing vegetation even in low productivity locations. In a separate analysis, we compared the effect of pikas at two geographically disjunct sites and we provide evidence showing that the impact of pikas differs among sites of varying biological and physical properties.

Current understanding of the effects of multiple grazing levels on aboveground live biomass and productivity is limited by the lack of analysis of within-season, between-season and long-term dynamics and there is little experimental support for theoretical predictions. In this study, we demonstrated the importance of species composition, site effects, time scale, grazing intensity and grazing history on the response of plants to a small mammalian herbivore. We emphasize that these factors interact to produce observed patterns in natural systems.

Introduction

Evaluations of the impact of mammalian herbivores on vegetation have tended to address a single level of grazing intensity by a natural herbivore (e.g., fenced or not; Cargill and Jefferies, 1984; Paige and Whitham, 1987; Bergelson and Crawley, 1992a; Frank and McNaughton, 1993; Hulme, 1996) or multiple levels by simulated, modeled or unnatural herbivory (Hik and Jefferies, 1990; Brown and Stuth, 1993; Turner, Seastedt and Dyer, 1993; Ouellet, Boutin and Heard, 1994; Bergelson , Juenger, and Crawley, 1996; Nilsson, Tuomi and Åström, 1996) with only few studies addressing multiple levels in a natural setting, in spite of evidence demonstrating complex plant responses to varying grazing intensities (Dyer, 1975; Noy-Meir, 1975; Noy-Meir, Gutman, and Kaplan, 1989; Hik, Sadul and Jefferies, 1991; Dyer, Turner and Seastedt, 1993). This is unfortunate because examining *in situ* natural grazers has the clear advantage compared to simulation studies in that long-term grazing pressures may pre-exist and may produce selective pressures on plants within the habitat (Huntly, 1991; Holland *et al.*, 1992; Carpenter and Kitchell, 1993; Dyer, Turner and Seastedt, 1993; Hobbs, 1996) and may cause changes in soil nutrient processes (Ruess and Seagle, 1994; McNaughton, Banyikwa, and McNaughton, 1997), leading to "grazed" communities with unique vegetation composition and vegetation response (McNaughton, 1983).

One reason for the lack of explicit experiments at naturally occurring multiple grazing intensities is the rarity of easily discerned and easily manipulated small scale grazing intensity gradients, especially in terrestrial systems (Huntly, 1991). These gradients occur, however, around herbivores that forage outward from refuges which offer them protection from predation (e.g., prairie dog towns; Holland *et al.*, 1992) or caches for food (e.g., pikas; Huntly, 1987). In addition, because of this refuging behaviour and the subsequent heavy reliance on adjacent vegetation, these herbivores may exert extreme levels of localized grazing. In spite of the clear importance of examining multiple levels along a grazing gradients in understanding the multiple roles of herbivores, very few studies have attempted to address these issues in naturally occurring herbivore systems. The collared pika (Ochotonidae, *Ochotona collaris*) is a generalist refuging herbivore that creates extreme grazing gradients over very short distances and thus provides a system in which to examine multiple herbivore effects within a single habitat.

The range of compensation of aboveground primary production in response to grazing has been considered to be a continuum from positive to negative responses (Robertson, 1933; Cook, Stoddart and Kissinger, 1958; Ellison, 1960; Vickery, 1972; Dyer, 1975; McNaughton, 1976; McNaughton, 1979; McNaughton, 1983; Paige and Whitham, 1987; Hik and Jefferies, 1990; Whitham, *et al.*, 1991; Alward and Joern, 1993; Dyer, Turner and Seastedt, 1993; Frank and McNaughton, 1993; Turner, Seastedt and Dyer, 1993; Nilsson, Tuomi and Åström, 1996) and likely depends on other factors including time of recovery (Oesterheld and McNaughton, 1991) and relative availability of nutrients (Georgiadis *et al.*, 1989; Chapin and McNaughton, 1989). Given that the proposed conditions under which overcompensation may occur are quite particular and infrequent (Belsky, 1986; Verkar, 1986; Crawley, 1987; Maschinski and Whitham, 1989; Belsky *et al.*, 1993; Järemo, Nilsson and Tuomi, 1996)—e.g., low competition, nutrient availability, high predictability of the grazer and environment—more interesting questions arise concerning the persistence of repeatedly and highly grazed swards that appear not to exhibit exact- or overcompensation (McNaughton, Banyikwa and McNaughton, 1997).

Some studies indicate that in systems in which herbivore damage reduces net production, animals will not regraze the same sites because of the reduced aboveground live biomass availability or other more defensive plant responses (Drent and Prins, 1987). For instance, large herbivores, such as caribou, may not return to an area of previous grazing for decades (Oksanen, 1983; Jefferies, Klein and Shaver, 1994; Manseau, Huot and Crete, 1996). Herbivore survival may be affected if unable to migrate to places with more food (caribou, Klein, 1987) or may be limited by food during the dry season (wildebeest, Sinclair, Dublin and Borner, 1985; Sinclair, 1995). Grazing pressure by greylag geese in northern Netherlands have been shown to seasonally deplete resources to the point where exploitation is no longer profitable (Drent and Prins, 1987). The periodicity of populations of small herbivore (e.g., *Lemmus lemmus*) may be partially caused by defensive plant response (Seldal, Andersen and Högstedt, 1994). In some locations, however, vegetation has evolved tolerance mechanisms that enable them to persist under repeated heavy grazing conditions (Rosenthal and Kotanen, 1994; Nilsson, Tuomi and Åström, 1996; Strauss and Agrawal, 1999). Examining tolerance mechanisms would be most interesting in locations of persistent, heavy grazing, because plants would be placed under extreme conditions, and the herbivores themselves rely on plant tolerance to survive. Collared pikas (*Ochotona collaris*) are particularly suited to examining these questions about tolerance, persistence and compensation. They are territorial and rarely disperse from their talus (*O. princeps*, Peacock, 1997) and vacated haypiles are usually rapidly reinhabited. As a result, adjacent to talus meadows can be highly and repeatedly grazed (*O. princeps*, Huntly, 1987). Thus, pikas might be expected to cause a continued decline of vegetation, preventing exact- or overcompensation, and grazing tolerance mechanisms among plants would be expected to be important.

The persistence of a productive plant community may not necessarily imply an unchanging species composition. Rather, the dynamic responses to grazing among plant species will vary due to herbivore selectivity, different abilities to tolerate grazing and diverse environmental conditions (Belsky *et al.*, 1993). For example, in some salt marshes, vegetation selectivity of a generalist herbivore has been shown to drive the observed vegetation patterns (Bakker, de Leeuw and van Wieren, 1984; Noy-Meir, Gutman and Kaplan, 1989). The predictions of which plant groups will prosper under heavy, intermediate or low grazing are weak and variable. In prairie dog towns, graminoids disappear in heavily grazed, older areas, while forbs and shrubs appear to increase in abundance (Coppock *et al.*, 1983). Conversely, in Colorado, Huntly (1987) examined the American pika (*Ochotona princeps*) and found that graminoids were more abundant in highly grazed areas, while forbs were least abundant, a pattern thought to be due to selective feeding by the pikas. This range of plant response is known among different herbivores and different habitats, but few studies have examined the consistency of effects caused by a single grazer between sites of different physical and biological conditions. The effects of multiple grazing levels within sites and among diverse sites would be expected to cause shifts in species abundances, but are largely unpredictable.

As with the spatial scale of herbivory, within-season dynamics of an herbivore can be very complex and important in understanding grazing impacts. For instance, Whitham *et al.* (1991) suggest that the timing of herbivory is perhaps the most important external factor affecting the ability for plants to recover from damage. Several studies have shown that plants can compensate from early season grazing more readily than late season grazing (Archer and Tieszen, 1980; Maschinski and Whitham, 1989; Hik and Jefferies, 1990; Hik, Sadul and Jefferies, 1991; Crawley, 1997; Lennartsson, Nilsson, and Tuomi, 1998). Herbivore grazing may be affected not only by spatial distribution of plants, but also by the temporal distribution of quality forage availability (i.e., progressive nutrient decline with leaf age; Mattson, 1980; Coppock *et al.*, 1983) and the life-history of the herbivore. Predictions for spatial patterns of grazing, therefore, may be modified by temporal considerations. For example, Archer and Tieszen (1980) showed that different seasonal leaf production exists among species, which may be responsible for easily digestible young leaves of one set of species (e.g., *Salix*) to occur early in the season, while easily digestible leaves of another group of species (e.g., *Carex*) continue to be formed into the middle of the summer. Differential among-species patterns of nutrient decline within leaf tissue through the summer were also found in prairie dog towns (Coppock, *et al.*, 1983). Thus, predictions for vegetation selectivity along the grazing gradient may differ, depending on the date within the growing season. Similarly, vegetation responses to grazing will depend of the timing and intensity of defoliation.

We report the results from an *in situ* mesh exclosure experiment examining the impacts of the collared pika on aboveground live plant biomass and net aboveground productivity, as well as species richness at three distances along a strong grazing gradient outward from talus slopes. Our objectives were (i) to quantify herbivore offtake of net aboveground primary productivity throughout the season to understand the nature, timing and intensity of pika herbivory, (ii) to examine the effect of distance from talus on the aboveground live biomass, net aboveground primary productivity and species richness of graminoids, dwarf shrubs, and forbs, and how this effect varies within and between growing seasons, and (iii) to compare the effect of pikas between two spatially distinct sites to examine the consistency and predictability of pika grazing pressure.

Methods

Study sites and species

Field work was carried out at two locations, the Ruby Range Mountains (RR: 61°13'N, 138°16'W) and the Front Range Mountains (FR: 60°57'N, 138°32'W), in southwestern Yukon Territory, Canada. The Ruby Range Mountains are located approximately 50 km northeast of the Front Range Mountains, and formed part of a southern arm of the Beringian intermittently ice-free land mass during the last glaciation (Hughes *et al.*, 1968). This range consists of old, rolling mountains which create a contiguous community of alpine vegetation. As a result, meadows in the Ruby Range site are more continuous and are not distinctly separate from surrounding areas of similar habitat due to limited boulder fields, or talus. The Front Range mountains, located at the eastern edge of the St. Elias Mountains in Kluane National Park, are geologically younger mountains and are characterized by relatively more discontinuous meadows interspersed among rocky slopes, in part due to recent glaciation during the Wisconsin. The Front Range site is relatively isolated from other similar sites due to ca. 800m high rock slides descending on all sides.

Both sites are characterized by alpine meadow vegetation. We selected these two sites because of their similarity in altitude (RR: 1700m-1900m and FR: 1800-2000m), the presence of extant collared pika populations, and comparable plant species composition. The sites differ, however, in several abiotic factors, notably glacial history and present climate, so we could contrast small scale plant-herbivore interactions under different physical conditions. Summer surface temperatures on meadows at both sites may fluctuate daily from below 0°C to over 40°C (Hik, Hughes and McIntire, in review). The Ruby Range site contained >100 plant species and was dominated by *Salix polaris* (Wahlenb), and *Carex consimilis* (Holm), while the Front Ranges site contained >50 species and was dominated by *Dryas octapetala* (L.), *Salix polaris*, and several graminoid species including *Carex consimilis*. All but one locally uncommon species (*Vaccinium vitis-idaea* L.) in both sites are deciduous perennials. Plant species names follow Cody (1996).

The collared pika, a small lagomorph endemic to the mountain regions of south and central Yukon and central Alaska, is strictly confined to talus slopes and consequently feeds near the edges of talus piles (MacDonald and Jones, 1987). During winter pikas do not hibernate, but rather they collect and store enough food during the short summer (8-12 weeks) to support their needs for the rest of the year (Dearing, 1997c). As a result, pikas are central place foragers because they must return to a haypile after foraging bouts. As a direct consequence, and because of high predation risk far from talus, the costs and risks of foraging are thought to increase with distance from talus (Andersson, 1978). This feeding in a short period and in a small area can be very intensive and extremely localized (<3 m from talus edge; Dearing, 1996a) causing the vegetation surrounding talus patches to be heavily grazed, creating distinct grazing "halos". Pikas are also known to have very low adult dispersal rates (*O. princeps*, Smith and Ivins, 1983; Peacock, 1997), so the same bands of vegetation are repeatedly grazed in most years. While the total pika population size is generally similar from year to year, (D. Hik, unpub. data), some patches of vegetation are periodically ungrazed as pika mortality events may create temporarily vacant haypiles on territories that may or may not be immediately recolonized. Most vacated haypiles are recolonized within 0-2 years (D. Hik, unpub. data). In addition, pikas are generalist herbivores, consuming many species, though some evidence suggests selectivity in plant choice

(MacDonald and Jones, 1987; Dearing, 1996). These two factors contribute to visually apparent herbivore impacts on plants in the population.

The Front Range site is relatively disjunct from other meadow sites but even here pikas are probably part of a larger metapopulation. Preliminary genetic analysis of these pikas show that they are very isolated in terms of the number of haplotypes (T. Bubela *et al.*, unpub. data). In spite of this, the pika numbers have been relatively stable over the past 6 years (D. Hik, unpub. data), with more than 12 individuals in a given season. Dispersal to this site from other areas, however, is thought to exist (D. Hik and E. McIntire, pers. obs.). At the Ruby Range site, the pika population of 65-100 individuals in a given year also appears relatively stable and non-cyclic (D. Hik, in review), a pattern that has been observed elsewhere for *O. princeps* in the Rocky mountains (Southwick *et al.*, 1986). In contrast to the Front Ranges, observed pikas show much greater genetic variability and are part of a much larger population that extends beyond the boundaries of our study and readily exchanges individuals (T. Bubela *et al.*, unpub. data). Both sites have a very short growing season in these areas (60-90 days) and generally low nutrient soils characteristic of alpine soils in general (Bridges, 1978; Mattson, 1980).

2-year exclosures

To experimentally prevent grazing by pikas, we installed 79 wire exclosures (2.5 cm mesh) in early to mid summer, 1997, each covering approximately 0.5 m^2 (about 0.8 m X 0.6 m) of alpine vegetation. The Front Range exclosures were installed on 28 June 1997, whereas the Ruby Range exclosures were installed between 20 July and 25 July 1997. Exclosures were randomly placed in one of three distance classes from a talus edge immediately adjacent to an active pika haypile: as close as possible to the talus (herein referred to as "adjacent" exclosures, <2 m from talus; RR: n=15, FR: n=11), far away from the talus ("far", >8 m from talus; RR: n=15, FR: n=11) and at intermediate distances from the talus ("intermediate", between 3 and 7 m from talus; RR: n=10, FR: n=8). We attempted where possible to arrange exclosures in close trios (RR: 10 sets of 3, FR: 8 sets of 3) whereby a single set of three exclosures (adjacent, intermediate and far) would be placed in a linear array outward from talus (for placement of exclosures at RR, see Fig. 2-1). We also randomly placed several other exclosures (RR: n = 10 and FR: n = 6) in either adjacent or far locations to increase replication at the extremes. We treated exclosures in each distance class as independent replicates because pikas are territorial and are known to actively defend home ranges from other pikas so there is generally little overlap of feeding areas. Thus, we assumed exclosures were independent of each other. While exclosures were installed in trios, plant species variation outwards from talus was sufficiently great that we did treat the trios of exclosures at individual haypiles as an experimental block in the design. Although there may be several ecological factors responsible for observed variation outward from talus effects (e.g., soil depth, presence of bryophytes), most of these distance from talus differences were attributed to pika herbivory, *a priori*, based on the absence of a visual gradient at nearby sites without pikas. Consequently, we chose to replicate the experiment at two different sites (FR and RR) rather than attempt to quantify small differences within each of the study sites.

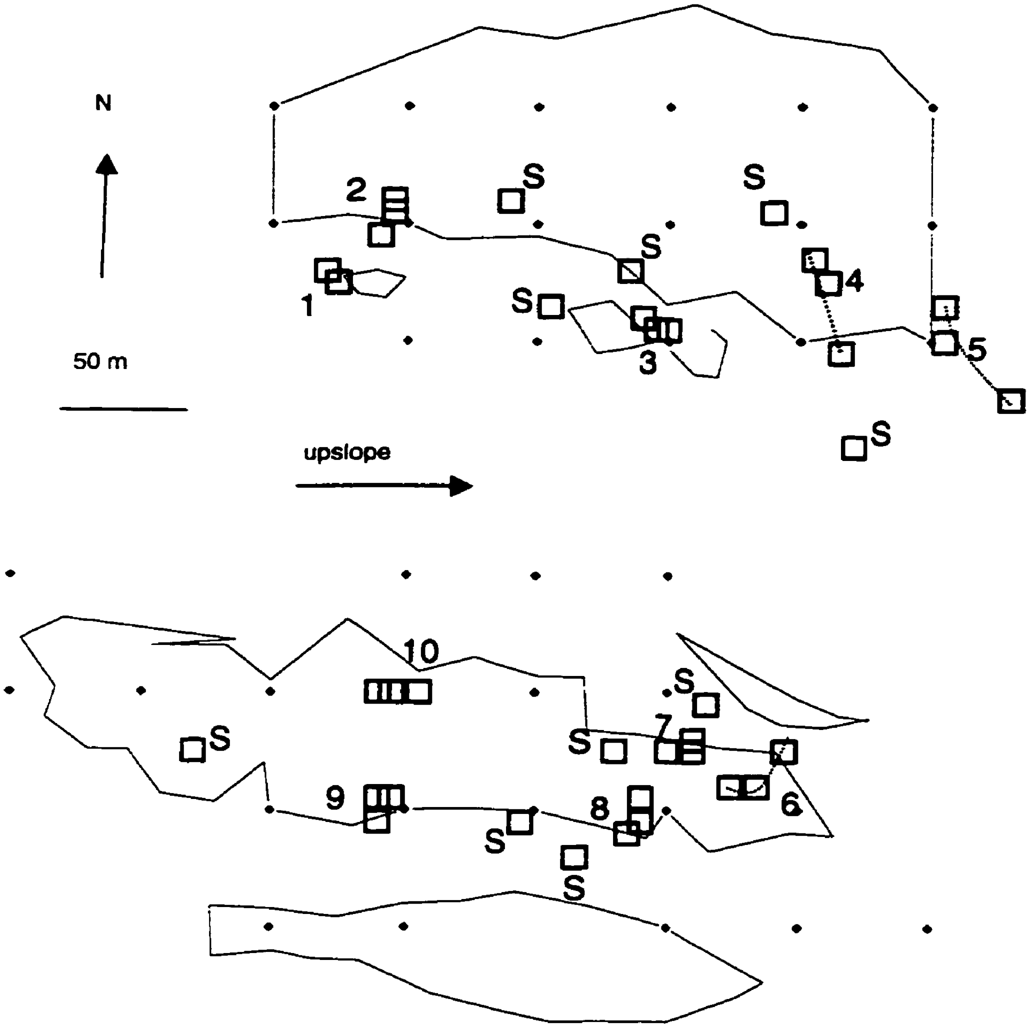
We did not use a standard length (e.g., 5 m) for each distance class because the “edge” of a talus is often not discrete, making an absolute measure of distance from talus edge impossible. Instead, intermediate exclosures were installed in a band located at least 3 m and no more than 7 m from a more or less recognizable talus edge, determined by how diffuse the edge was.

On 14 August 1997 and on 23 June, 10 July, 27 July, and 14 August 1998, we sampled all sites in the Ruby Ranges. On 2 July and 29 July 1998 we sampled all sites in the Front Ranges. On 28 June 1997 (FR) and on 26 July 1997 (RR) we sampled initial baseline aboveground live biomass values upon erection of the exclosures in the control plots only. These initial values were not paired inside/outside samples, so were not used in analyses on pika herbivory. Each sampling period took one to three days to complete, so exclosures were sampled in the same order each period to allow consistent growth increments between exclosures. Multiple within-season sampling during 1998 enabled us to calculate aboveground production increments (net productivity) and to examine the timing of grazing and the variability in effect of pikas throughout the season.

At each sample period, two 10 X 10 cm plots were clipped both inside and immediately outside of each exclosure (paired inside/outside samples). We determined this to be the maximum possible plot size from which we could obtain multiple samples over several years and still work within exclosures that were of ecologically meaningful spatial scales given the patchy nature of the talus/meadow edge. In all data analyses, to account for the variability between the two sampled plots within each exclosure or control, the effect of plot was nested within other main effects to test for pseudoreplication (Underwood, 1997). If this effect was not significant at the p=0.25 level, we pooled samples (Underwood, 1997). During clipping, we recorded all species present. All clipped samples were dried at 60°C to constant mass. During sorting, only green vegetation (aboveground live biomass) was separated, and all samples were sorted into life form groups (graminoid, dwarf shrub, and forb) and weighed to determine abundances by dry biomass. Species lists were written at time of collection and reconfirmed for each sample during sorting. Virtually no specimens were unknown species. We conservatively identified vegetative graminoids (particularly *Carex*) and our graminoid species richness values were likely underestimates.

From 6 August to 18 August 1998, we installed 6 temperature data loggers on the soil surface (HOBO XT Temperature Logger, Onset Computer Corp., Pocasset, MA, USA), inside and outside of three adjacent to talus exclosures to determine the effect of exclosures on soil surface temperatures, a factor which may influence soil microbial processes and nutrient availability (Flanagan and Veum, 1974; Chapin, 1983; Vitousek *et al.*, 1994). We selected three

Figure 2-1. Sketch map of arrangement of exclosures at Ruby Range site. Thin lines delineate the extent of talus fields with 50 m grid stakeposts shown for scale and proximity. Numbers indicate exclosures arranged in trios and single exclosures also labeled (S). Where exclosures do not appear obviously as part of a trio, dotted lines are used to clarify the relationship.


N
50 m
upslope
1
2
3
4
5
6
7
8
9
10
S

sites which had visually striking effects on aboveground live biomass, so these temperature measurements are likely overestimates of the average effect.

Temporary exclosures

A consequence of the slow response of perennial plants to removal of herbivores is that any differences observed between the aboveground live biomass inside exclosures and that from the control plots immediately outside exclosures will be the result of two separate responses. First, we may be detecting the immediate aboveground removal of vegetation, or within-season production removal. The second response results in the longer term effects of photosynthetic tissue loss on plant storage and resource allocation and the subsequent ability of the plants to maintain rates of production, in spite of losses due to herbivory. As a result, the effect of the 2-year exclosures will not be a good indicator of how much the pikas are removing ("offtake") in a given sampling period. To calculate this amount, we installed 9 temporary exclosures in adjacent to talus locations (equivalent to 2-year exclosures above) in the Ruby Ranges in July, 1997, and a total of 15 at the beginning of the summer in 1998 to examine short intervals (15-17 day) of primary productivity throughout the season. By temporarily installing exclosures in grazed locations, clipping a sample at the time of installation ("before") and 15-17 days later ("after"), the potential production rate of grazed plants can be measured. When not exclosed, productivity estimations of grazed plants will be an underestimate of the actual productivity because of the herbivore offtake. Moving these temporary exclosures <1 m to a new grazed sward every 15-17 days throughout the summer, we measured the full season production of "grazed" plants. The difference between productivity of these plants and productivity of unexclosed plots provided an estimate of herbivore "offtake", while the difference between these plants and exclosed plants indicated the effect of herbivores on aboveground primary productivity.

Locations for exclosures were selected to minimize the effect of other vertebrate herbivores, thus we attributed the effects of exclosures to removal of grazing by pikas. Other mammalian herbivores in the study areas include voles (*Clethrionomys rutilus*, *Microtus gregalis*, *M. miurus*), the arctic ground squirrel (*Spermophilus parryii*), hoary marmot (*Marmota caligata*), Dall sheep (*Ovis dalli*), moose (*Alces alces*), and caribou (*Rangifer tarandus*). All the larger mammals—except sheep in the Front Range site—are so sparse in the areas of study that their effects are likely not apparent. Although sheep were active in the Front Range site, there was no preconceived reason to expect that their foraging habits would differ depending on distance from talus. Thus, any distance pattern observed would be due to pikas. Arctic ground squirrels generally use meadows away from talus, preferring to forage in well developed meadows nearer their burrows and marmots roam over very large territories distributing their grazing over much larger distances than pikas (D. Hik *et al.*, unpub. data; a pattern also found for American pika, hoary marmot and Columbian ground squirrel in the Rockies; Barash, 1973). It was not totally possible to remove the effects of all these vertebrate herbivores, though the dominant grazer in all the sites chosen was the collared pika (D. Hik and E. McIntire, pers. obs.).

Data analysis

Sample biomass measurements were standardized to $g{\cdot}m^{-2}$ values and tested for normality and homogeneity of variances before statistical analysis. Some samples did not conform to the assumptions of normality, however, sample sizes were sufficiently large in all cases so violations were likely not strongly influential (see Box, 1953; Underwood, 1997). We measured the "effect of exclosures" by calculating the difference between the aboveground live biomass inside an exclosure and the aboveground live biomass in the control plot immediately outside the exclosure. When this difference is significantly non-zero, we assumed that the effect is due to pika grazing or haying. Most data analyses are performed on these differences rather than on absolute biomass values. This method allows for more formal examination of the effect of pika grazing. In all analyses, we used the mixed model procedure because it is the most generalized technique for analysing repeated measures data. We treated all effects as being fixed.

The difference in productivity between the temporary exclosures (actual productivity) and the grazed controls (apparent productivity) indicates the herbivore "offtake". Comparing these two measures of productivity throughout the season allows us to determine the timing and intensity of herbivore grazing. We tested for temporal variation in offtake levels during the summer using a one-way Repeated Measures Analysis of Variance (RM-ANOVA; PROC MIXED, SAS INSTITUTE INC., 1998) on the differences as the response variable.

To measure the effects of distance-from-talus and time on the aboveground live biomass , we analyzed the data using a two-way RM-ANOVA (DISTANCE and DATE) on total, graminoid, dwarf-shrub and forb aboveground live biomass differences. We included *Dryas octapetala*, a very common and high aboveground biomass sub-shrub species (Cody, 1996), within dwarf shrubs. Similar tests were performed on species richness differences (total, graminoid, dwarf-shrub, and forb). We examined aboveground live biomass and species richness by life form to test for grazer selectivity and differential regrowth after pika defoliation.

To examine the effects of pikas on vegetation productivity throughout the growing season we calculated rates of production on a 15-17 day cycle for the grazed controls, the temporary exclosures and the 2-year exclosures by subtracting aboveground live biomass at the earlier date from the later date. 2-year exclosures allow us to calculate community productivity on the same 15-17 day intervals, during the second summer after vertebrate herbivore exclusion. Control plots allow for estimation of apparent vegetation productivity of grazed plants (actual productivity – productivity removed by herbivores), while the temporary exclosures enable us to estimate the actual productivity of grazed plants. Since the temporary exclosures were only installed near to talus, we only used 2-year exclosures and control sites in the "<2 m" distance class in all analyses of productivity. To examine the effect of pikas on vegetation productivity throughout the summer, we used a two-way RM-ANOVA on 15-17 day productivity levels as a function of level of grazing and date (GRAZING and DATE).

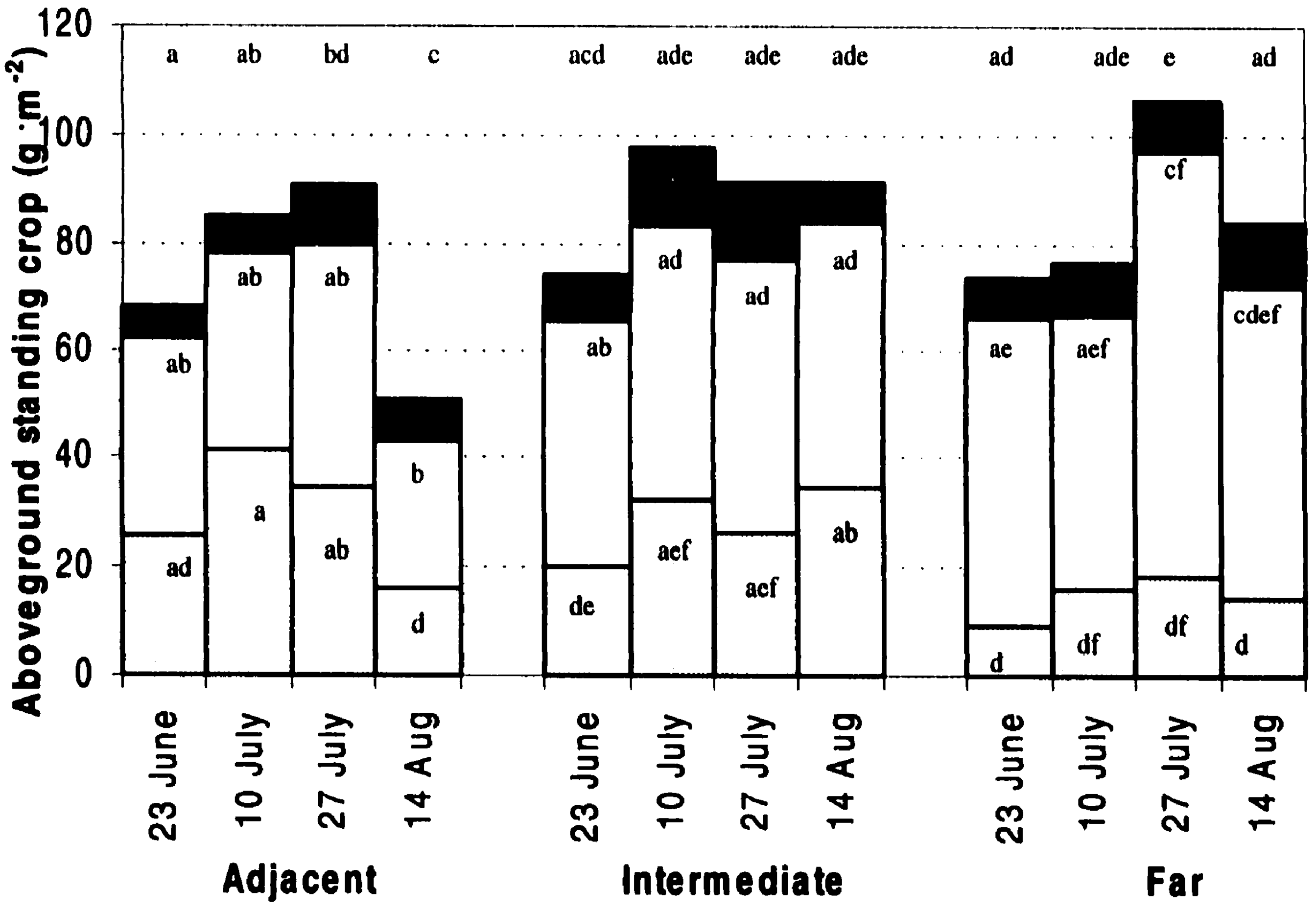
Finally, we contrasted the effect of pikas at the Ruby Range site with pikas at the Front Range site by examining aboveground live biomass and species richness inside and outside of exclosures. We tested whether the location alone affected these measures, or whether location altered the distance-from-talus or temporal effects seen in the Ruby Range site by way of three-way RM-ANOVAs (SITE, DISTANCE, and DATE) on live aboveground live biomass measures (total, graminoid, dwarf-shrub and forb) and species richness measures (total, graminoid, dwarf-shrub, forb). In 1998, the sampling dates of the Front Range and the Ruby Range were not identical. To analyse the main effect of DATE, we attempted to account for this discrepancy between early sampling dates by running two RM-ANOVAs. In the first, we used 23 June (RR) and 2 July (FR) as the "early" date, and in the second, we used 10 July (RR) and 2 July (FR) as the "early" date. In both analyses, we used 27 July (RR) and 29 July (FR) as the "later" date.

Results

Baseline patterns: aboveground live biomass, species richness and herbivory offtake

Total aboveground vegetation in control plots in 1998 indicated differences in abundance of forbs, dwarf shrubs and graminoids under natural levels of grazing (DISTANCE X DATE: $F_{6,40}$=5.6, P=0.0003; Fig. 2-2). At all distances-from-talus, forbs represented a small fraction of the total aboveground biomass, with graminoids and dwarf shrubs contributing the largest fractions. Graminoids and dwarf shrubs, however, do not show identical patterns along the gradient away from talus. In adjacent plots, graminoids represent a proportionally larger fraction

Figure 2-2. Aboveground live biomass in control plots in the Ruby Range by distance from talus, date and life form (graminoid [⊡], dwarf shrub [□] and forb [■]), in 1998. Bars which share lower case letters above indicate non-significant differences ($P<0.01$) between all measures of aboveground live biomass throughout the season. Shared lower case letters within the bars indicate non-significant differences (Tukey adjusted LSD, $P<0.05$) between all measures at all dates within each life form. The effect of DISTANCE X TIME on aboveground live biomass was highly significant ($F_{6,40}=5.6$, $P=0.0003$).


Aboveground standing crop (g m-2)
120
100
80
60
40
20
0
a
ab
bd
c
acd
ade
ade
ade
ad
ade
e
ad
ab
ab
ab
b
ab
ad
ad
ad
ae
aef
cf
cdef
ad
a
ab
d
de
aef
aef
ab
d
df
df
d
23 June
10 July
27 July
14 Aug
23 June
10 July
27 July
14 Aug
23 June
10 July
27 July
14 Aug
Adjacent
Intermediate
Far

of total aboveground biomass than at intermediate distance or far from talus. The relative contribution of dwarf shrubs to total aboveground biomass was greatest furthest from talus.

In plots furthest from talus, total peak aboveground live biomass occurred at the end of July. At intermediate distances, aboveground live biomass in control plots were not distinguishable between 10 July and 14 August. Adjacent plots obtained near peak aboveground live biomass levels by 10 July and 27 July, but lost almost 50% of the July values by mid August.

Species richness in the control plots showed very little within-season variability. Distance from talus showed a highly significant effect on total ($P<0.005$), graminoid ($P<0.005$), dwarf shrub ($P<0.005$), and forb ($P<0.01$) species richness (Fig. 2-3). Total species richness is highest at intermediate distances. This pattern is driven by significantly higher forb and graminoid species richness in adjacent plots and significantly higher dwarf shrub species richness in intermediate and far plots. Thus, shrubs have lower richness in highly grazed sites and graminoids have lowest richness in sites with little herbivory. Forbs (species richness range: 1.8 to 2.8) and graminoids (species richness range : 2.0 to 2.8) make up the majority of the species at all distances and dates, though dwarf shrubs (species richness range : 1.2 to 1.9) have higher species richness furthest from talus.

Herbivore offtake approximates the aboveground production removed by pikas by calculating the difference between apparent productivity and actual productivity of grazed plants (Fig. 2-4). No measurable offtake on any species group is observed before 27 July (Early or Mid) in these adjacent exclosures. Between 27 July and 14 August (Late), however, there is a highly significant offtake, a pattern driven primarily by graminoids. Forbs have a significant negative offtake between 10 July and 27 July (Mid) while detectable offtake of dwarf shrubs is near zero, with an increase in the final growth period ($P=0.07$), but this does not significantly vary over the season.

Figure 2-3. Effect of distance from talus on species richness in control plots in the Ruby Range, by life form (total [▲], graminoid [○], dwarf shrub [□] and forb [△]), in 1998 (mean±S.E.). Level of significance of distance from talus on total species richness and on life form groups are indicated in figure legend (* $0.01<P<0.05$; ** $0.005<P<0.01$; *** $P<0.005$). Points within each life form that share lower case letters are non-significantly different (Tukey adjusted LSD, $P<0.05$).

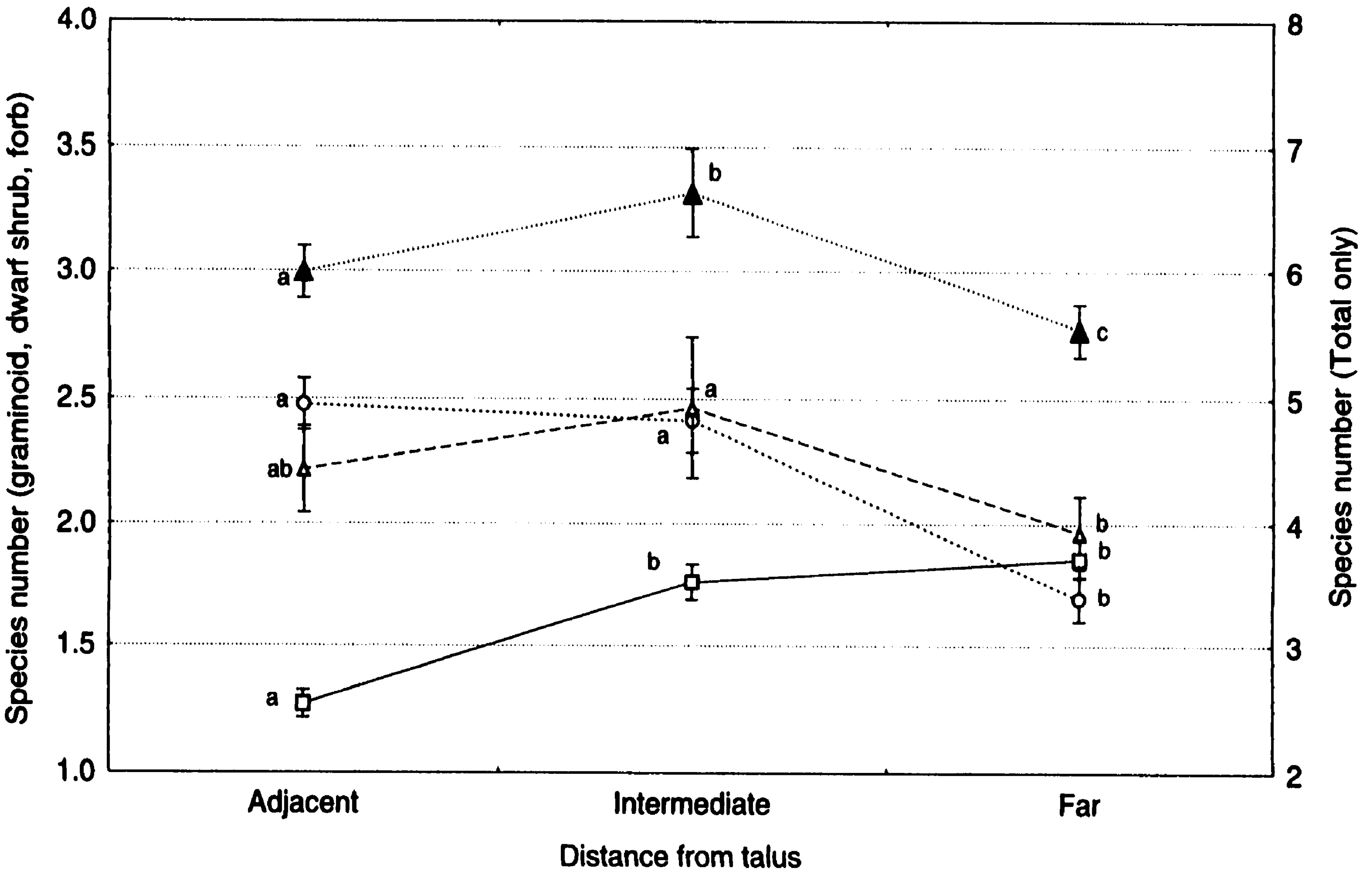
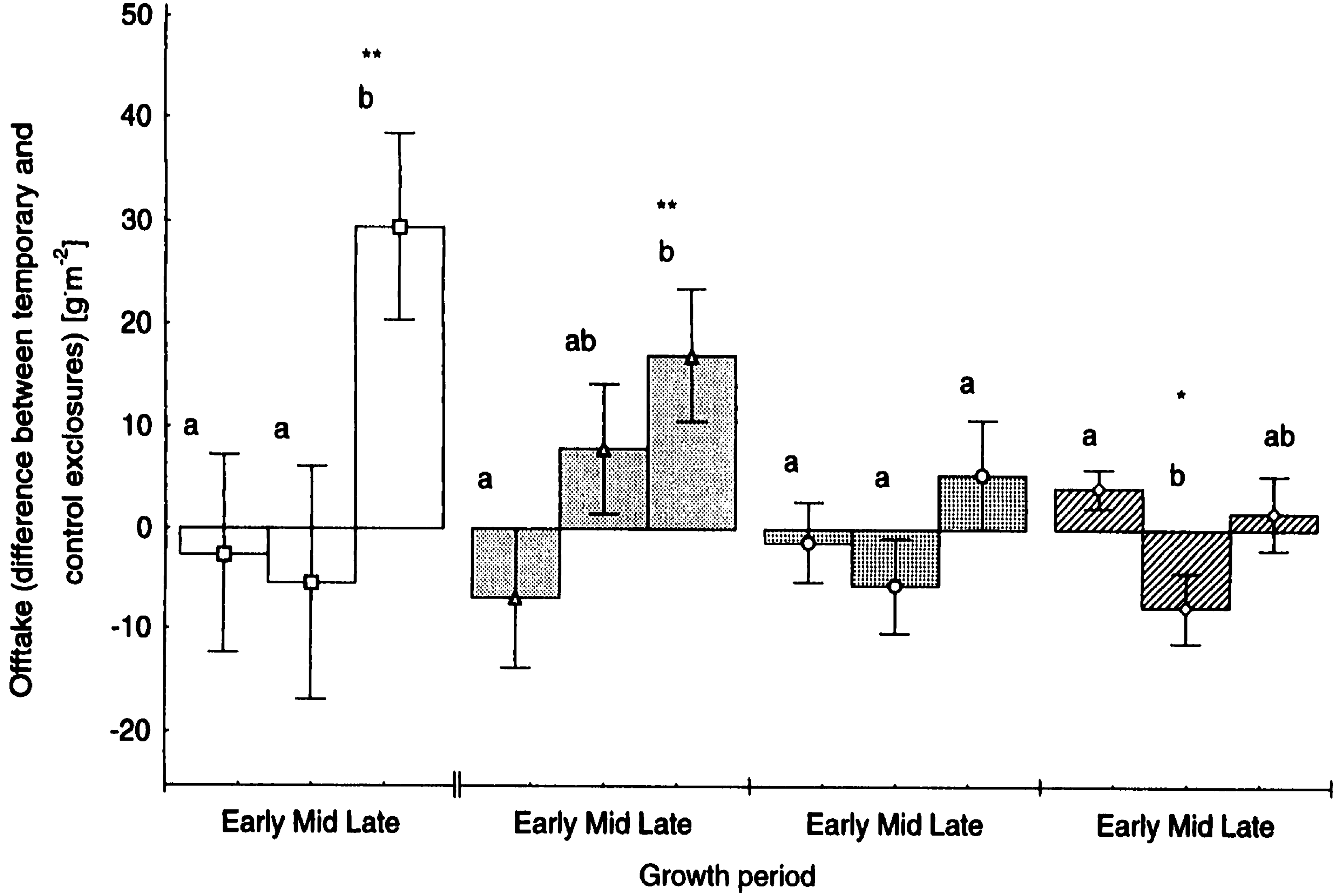

Species number (graminoid, dwarf shrub, forb)
4.0
3.5
3.0
2.5
2.0
1.5
1.0
Species number (Total only)
8
7
6
5
4
3
2
a
ab
a
a
b
a
a
b
c
b
b
b
Adjacent
Intermediate
Far
Distance from talus

Figure 2-4. Offtake levels (see text) by date and life form (total [□], graminoid [▦], dwarf shrub [▢] and forb [▨]), in 1998 (mean±S.E.). Offtake is defined as the actual aboveground productivity (in temporary exclosures) minus the apparent aboveground productivity (in unexclosed plots), in 15-17 day intervals. Growth period intervals are Early (23 June – 10 July), Mid (10 July – 27 July) and Late (27 July – 14 August). Bars that are significantly different than zero are indicated with asterisks (LSM, * $0.01<P<0.05$; ** $0.005<P<0.01$; *** $P<0.005$). Points within each life form that share lower case letters are non-significantly different (Tukey adjusted LSD, $P<0.05$).


Offtake (difference between temporary and control exclosures) [g·m-2]
50
40
30
20
10
0
-10
-20
a
a
**
b
a
ab
**
b
a
a
a
a
*
b
ab
Early Mid Late
Early Mid Late
Early Mid Late
Early Mid Late
Growth period

Effect of pika exclusion on aboveground live biomass and species richness

During the summer of 1998, aboveground live biomass inside exclosures increased significantly more compared to aboveground live biomass in control plots outside of exclosures, demonstrating the overall "effect of pikas" (Fig. 2-5a and Table 2-1). In particular, the effect of pikas on aboveground live biomass was significantly stronger in adjacent and intermediate plots, and this distance-from-talus effect changed significantly throughout the summer (DIST X DATE effect). Far exclosures (>8m) showed no significant effect of pikas, while adjacent and intermediate exclosures (<2 m and 3-7 m) were significant (Fig. 2-5a). From 24 June to 27 July, the effect of adjacent and intermediate exclosures did not differ significantly, while on 14 August, the effect of adjacent exclosures was more than 60 $g \cdot m^{-2}$ (115 $g \cdot m^{-2}$ vs. 50 $g \cdot m^{-2}$, exclosed vs. control) and this effect was significantly greater than intermediate exclosures (difference=39 $g \cdot m^{-2}$, Least Significant Differences [LSD] at $P<0.05$). Overall, the effect of pikas increased spatially towards talus, and was greatest in adjacent exclosures on the final sampling date (14 August).

When the effect of exclosures on aboveground live biomass is broken down among three life forms, graminoids, dwarf-shrubs, and forbs, specific patterns of grazing emerge. Dwarf shrubs and forbs showed a significant DIST effect (Fig. 2-5b, 2-4d and Table 2-1), but only among graminoids and dwarf-shrubs did this effect vary significantly over time (Fig. 2-5b, 2-5c and Table 2-1). Among graminoids, intermediate exclosures showed a very large peak on 27 July (+30 $g \cdot m^{-2}$), while adjacent exclosures showed the greatest effect on 14 August (+29 $g \cdot m^{-2}$), though not significantly higher than the intermediate exclosures (Fig. 2-5b). Among dwarf-shrubs, the effect of pikas was greatest in adjacent exclosures on both 27 July and 14 August (Fig. 2-5c). Forbs showed no significant interaction effect of DIST X DATE.

Figure 2-5. Effect of two year exclosures on aboveground live biomass (inside minus control plots), by distance from talus (adjacent [■], intermediate [○], far [△]), date and life form, in 1998 (mean±S.E.). ANOVA results for DATE X DISTANCE effect are shown on each graph. Within each graph, all points that are significantly different than zero are indicated with asterisks (LSM, * $0.01<P<0.05$; ** $0.005<P<0.01$; *** $P<0.005$). Points within each graph that share lower case letters are non-significantly different (Tukey adjusted LSD, $P<0.05$). (a) All species, (b) graminoids, c) dwarf shrubs, and d) forbs.

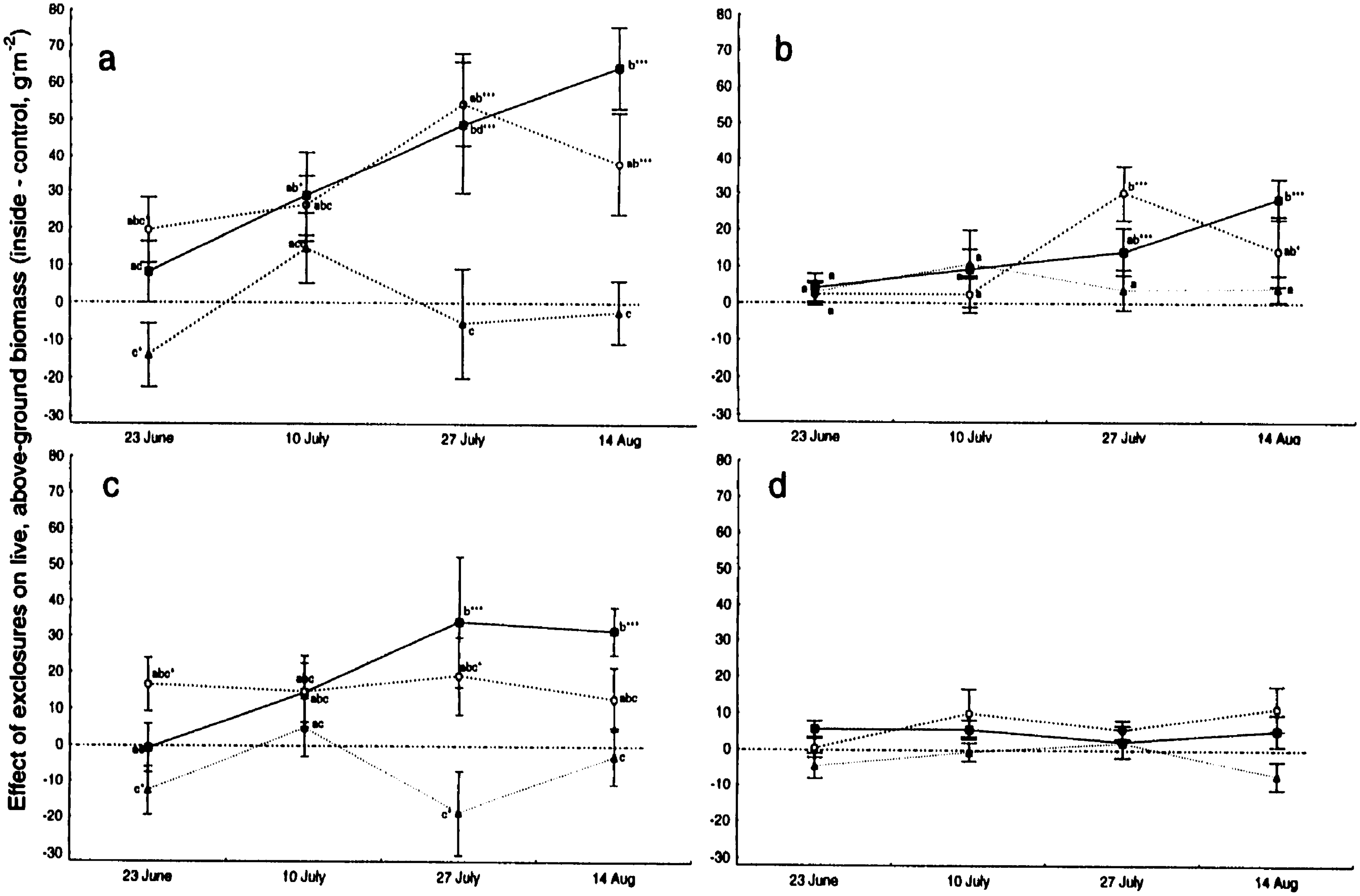
Effect of exclosures on live, above-ground biomass (inside - control, g·m^{-2})
a
b
c
d
80
70
60
50
40
30
20
10
0
-10
-20
-30
23 June
10 July
27 July
14 Aug
abc'
ac
c'
ab'
abc
ac
ab'''
bd'''
c
b'''
ab'''
a
b'''
ab'''
ab'
abc'
abc
b'''
abc'
c'
b'''
abc
c

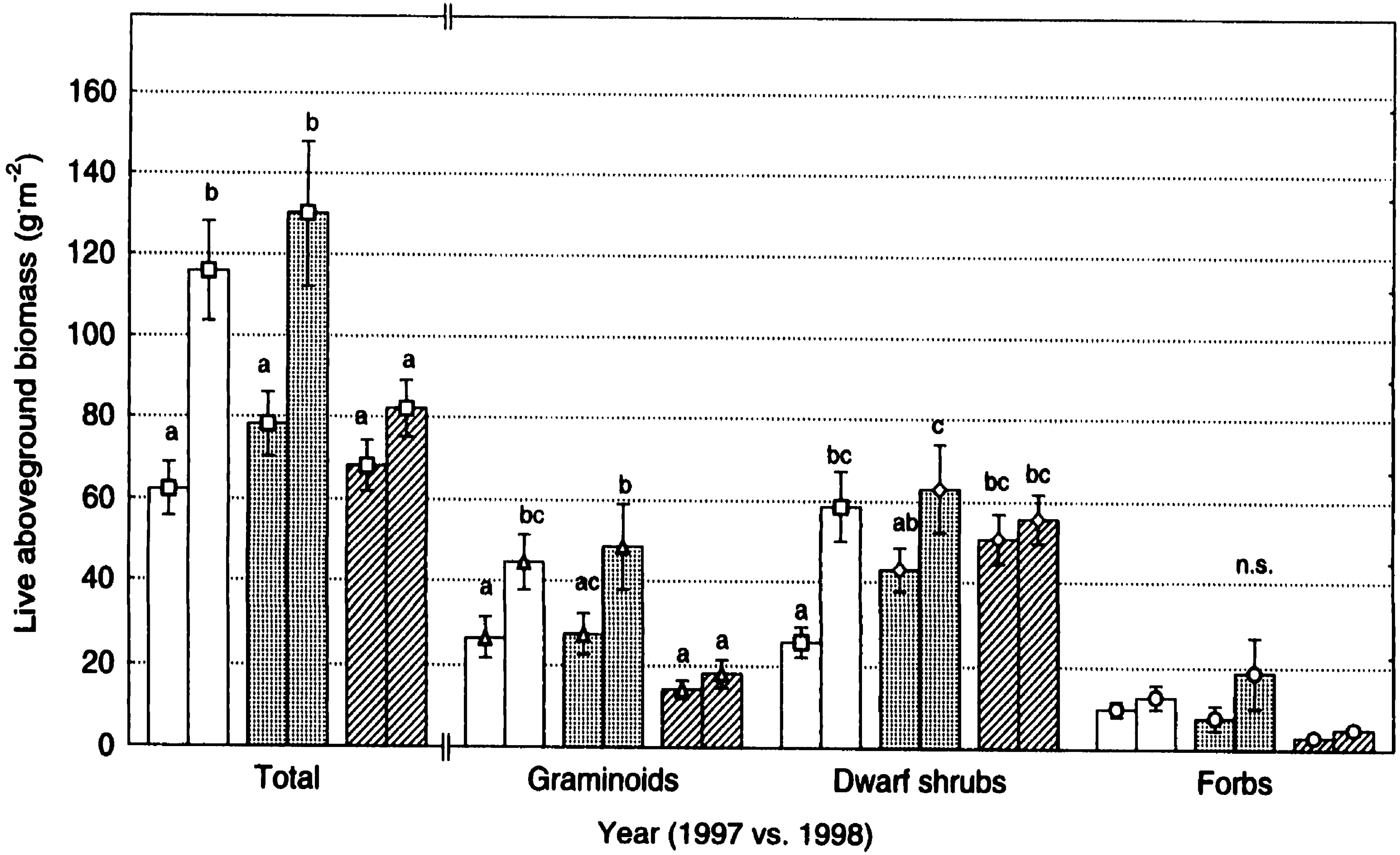
Table 2-1. Summary of F-values from RM-ANOVAs for aboveground live biomass and species richness in the Ruby Range exclosures. Main effects are distance from talus (DIST), sample period throughout the summer (DATE) and PLOT (see methods). *: $0.05<P<0.01$, **: $0.01<P<0.005$, ***: $P<0.005$

		Aboveground live biomass				Species richness			
Source	Num/Den DF	Total	Graminoid	Forb	Dwarf shrub	Total	Graminoid	Forb	Dwarf shrub
DIST	2/40	21.13^{***}	2.21	6.43^{**}	26.35^{***}	7.06^{**}	1.28	6.23^{**}	1.54
DATE	3/40	8.05^{***}	7.22^{***}	0.75	3.11^{*}	4.06^{**}	0.29	3.99^{**}	0.68
DISTXDATE	6/40	3.19^{**}	4.01^{**}	1.23	2.81^{*}	1.32	1.11	1.15	1.55
PLOT(DISTXDATE)	148/40	2.82^{***}	1.68^{*}	1.11	4.23^{***}	1.94^{**}	1.31	1.96^{**}	2.27^{**}

Final season (14 August) aboveground live biomass inside exclosures in 1997 shows that in the first year of exclosure (about three and a half weeks of exclosure presence), values at all distances were similar levels (Fig. 2-6). By the second year of herbivore exclusion (two seasons removal of pika grazing), final season aboveground live biomass in both intermediate and adjacent exclosures had significantly increased aboveground live biomass compared to far exclosures (YEAR X DIST $F_{2,80}$=6.7, P=0.002). The same analysis on samples collected during peak aboveground live biomass—27 July, 1997 and 1998—showed a similar pattern whereby adjacent and intermediate exclosures show very high biomass (141 $g \cdot m^{-2}$ and 146 $g \cdot m^{-2}$, respectively in 1998) and the far exclosures show no significant increase (101 $g \cdot m^{-2}$ in 1998). The observed increases between 1997 and 1998 final season aboveground live biomass is driven by increases in graminoids and dwarf shrubs (YEAR X DISTANCE, graminoid $F_{2,80}$=2.55, P=0.08; dwarf shrub $F_{2,80}$=6.19, P=0.003 Fig. 2-6). At the end of the 1998 growing season, the comparatively elevated total aboveground live biomass within adjacent and intermediate exclosures as compared to far exclosures is driven primarily by graminoids and less by forbs (Fig. 2-6). Shrubs do not differ in final season aboveground live biomass along the grazing gradient in 1998.

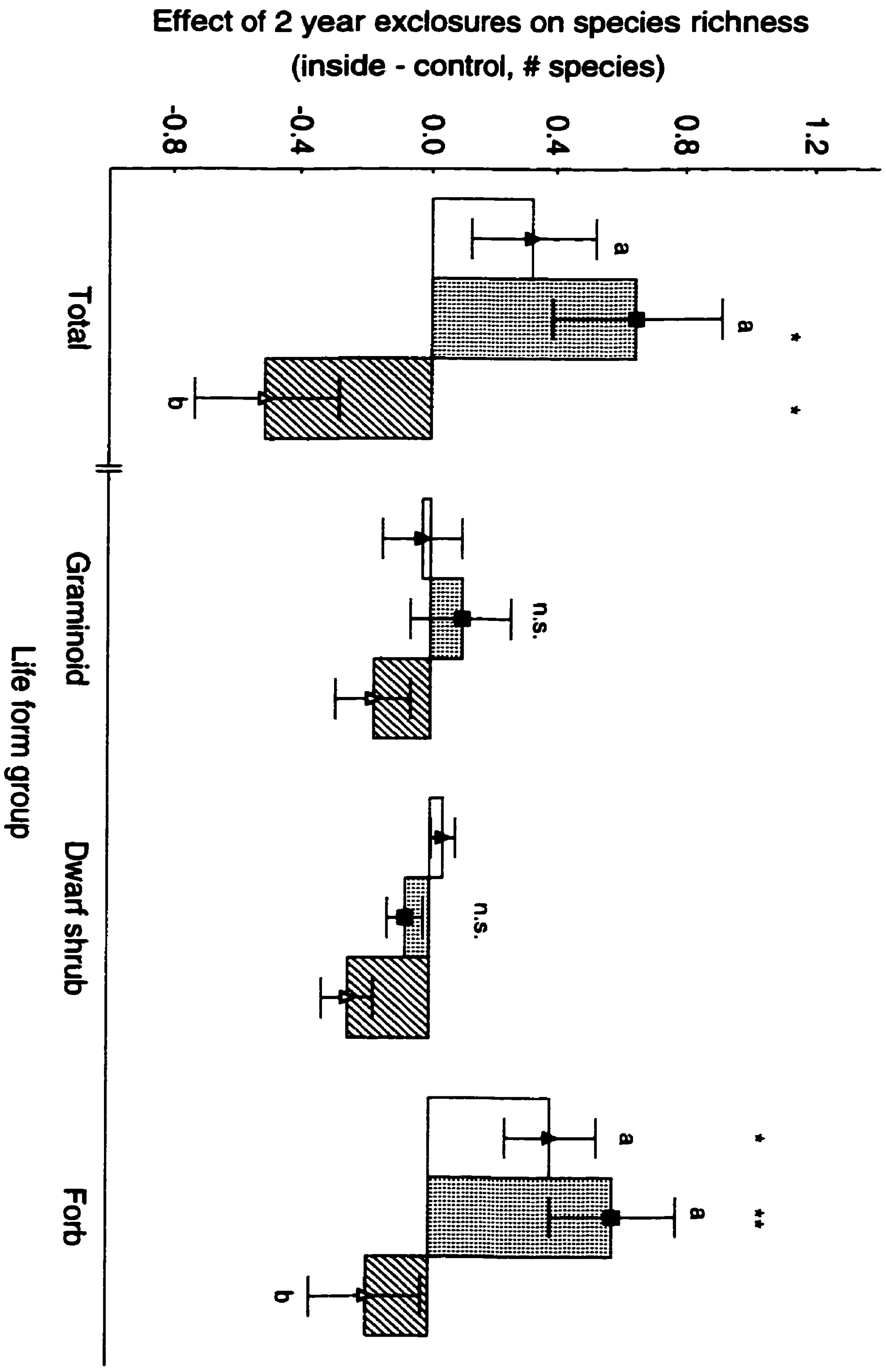
The effect of exclosures on species richness changed with DISTANCE and DATE, though there is no significant interaction effect for any group of species (Table 2-1). For total species richness, adjacent exclosures showed no significant effect, while intermediate exclosures showed a significant positive effect and far exclosures showed a significant negative effect (Fig. 2-7). Graminoids show no effect of exclosures at any distance from talus or date. Shrub species richness is reduced slightly in the far exclosures but is unaffected by any other exclosures. Forbs show the largest effect of exclosures with significant positive responses in adjacent and intermediate exclosures, indicating that removal of pikas causes an increase in forb species richness. The significant main effect of DATE for total and forb species richness reflects a

Figure 2-6. Comparison of final season aboveground live biomass inside exclosures after 1 year and 2 years (14 August, 1997 vs. 14 August, 1998), by distance from talus (adjacent [□], intermediate [⊡], and far [▨]), in the Ruby Range (mean±S.E.). ANOVA results for DATE X DISTANCE effect are shown above each life form. Each pair of bars shows 1997 (left) and 1998 (right) values. Points within each life form group that share lower case letters are highly non-significantly different (Tukey adjusted LSD, $P<0.005$).



Live aboveground biomass (g·m^{-2})
0
20
40
60
80
100
120
140
160
a
b
a
b
a
a
a
bc
ac
b
a
a
a
bc
ab
c
bc
bc
n.s.
Total
Graminoids
Dwarf shrubs
Forbs
Year (1997 vs. 1998)

Figure 2-7. Effect of 2-year exclosures on species richness, by life form group and distance from talus (adjacent [□], intermediate [⊡], and far [▨]) in 1998 in the Ruby Range (mean±S.E.). Data shown are pooled across all dates because the effect of DATE was not significant. All bars that are significantly different than zero are indicated with asterisks (LSM, * $0.01<P<0.05$; ** $0.005<P<0.01$; *** $P<0.005$). Within each life form group, points that share lower case letters are non-significantly different (Tukey adjusted LSD, $P<0.05$). n.s. indicates that the effect of distance from talus was not significant for that life form group


Effect of 2 year exclosures on species richness
(inside - control, # species)
-0.8
-0.4
0.0
0.4
0.8
1.2
a
a
b
*
*
n.s.
n.s.
a
a
b
*
**
Total
Graminoid
Dwarf shrub
Forb
Life form group

monotonically increasing exclosure effect with time (23 June to 14 August: Total=-0.30 to 0.63; Forb=-0.10 to 0.56; Table 2-1).

Effect of exclosures on soil surface temperatures

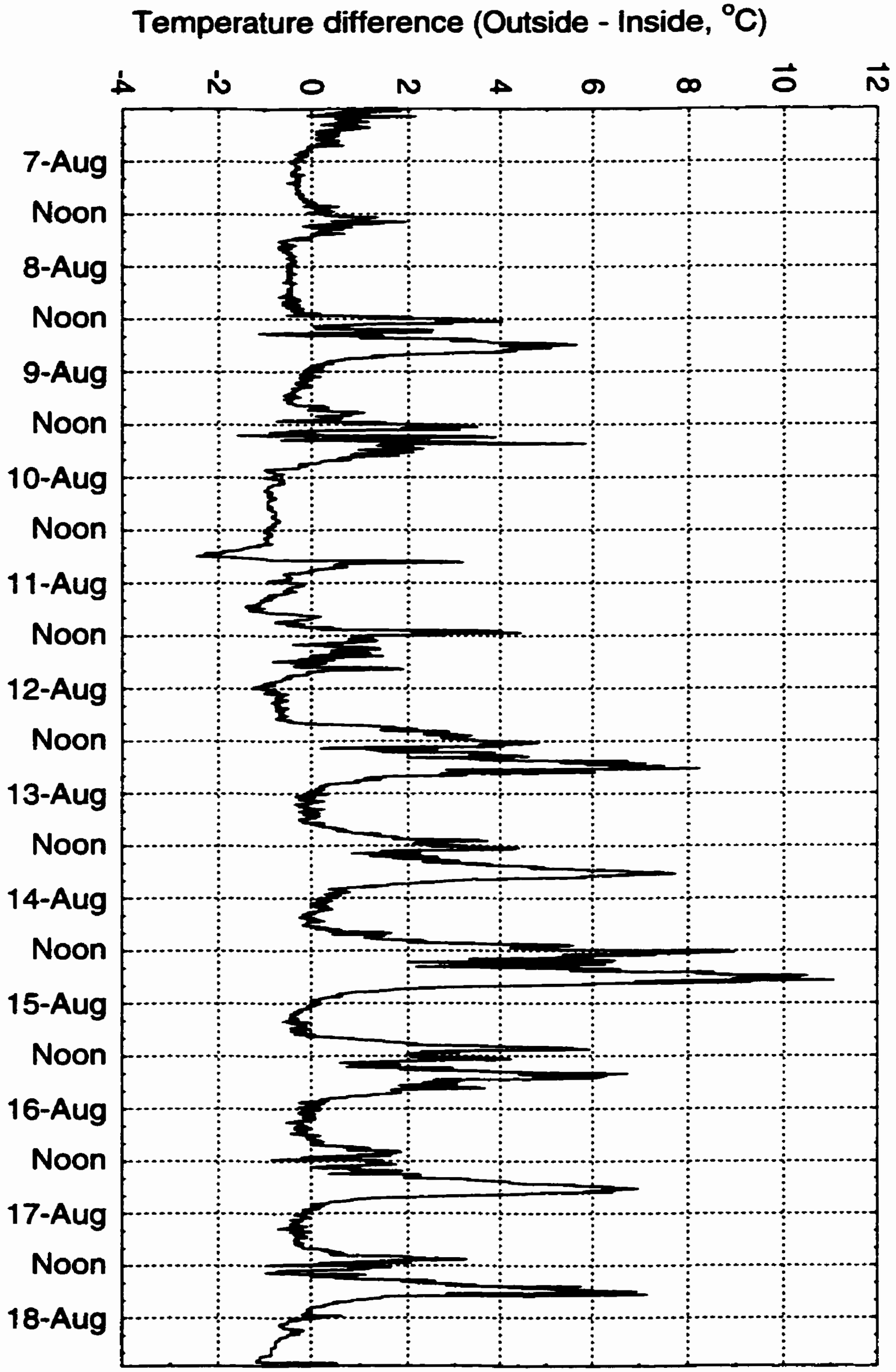
From 6 August to 18 August 1998, the soil surface temperatures of three selected exclosure sites were approximately 4-8°C higher in adjacent control plots than adjacent exclosure plots during the warm parts (afternoon) of many of the days (Fig. 2-8).

Effects of pikas on aboveground short-term aboveground productivity

Generally, 2-year removal of pikas caused an increase in aboveground primary productivity in our sites, but primarily early in the growing season (Table 2-2; Fig. 2-9a). Ungrazed plant productivity (2-year exclosures) was significantly higher early in the summer until the 27 July – 14 August growth increment when there are enormous significant losses (negative productivity). The substantial levels of earlier season productivity are not matched in the grazed plants, though actual productivity of grazed plants (temporary exclosures) does not show the same magnitude of early August decline. Apparent productivity of grazed plants (controls) does show a similar significant decline in the last growth increment. Detectable positive aboveground productivity ceases after 27 July inside the 2-year exclosures and after 10 July in either the temporary exclosures or control plots. We included "negative" productivity because most of the herbivory occurs during these later season periods and lower levels of negative productivity indicate that the photosynthetic capacity within the plants continued later.

Aboveground primary productivity among graminoids occurs early in all plots and levels off at near zero in the 2-year exclosures and the temporary exclosures (Table 2-2; Fig. 2-9b). Since aboveground productivity as we have measured it confounds senescence and productivity (thus allowing negative productivity), late season zero values likely indicate a balance between

Figure 2-8. Indirect effect of pikas on soil surface temperatures (control temperatures minus inside exclosure temperatures), in three adjacent to talus exclosures in 1998 in the Ruby Ranges. Positive values indicate warmer soil surface temperatures in the unexclosed control plots.

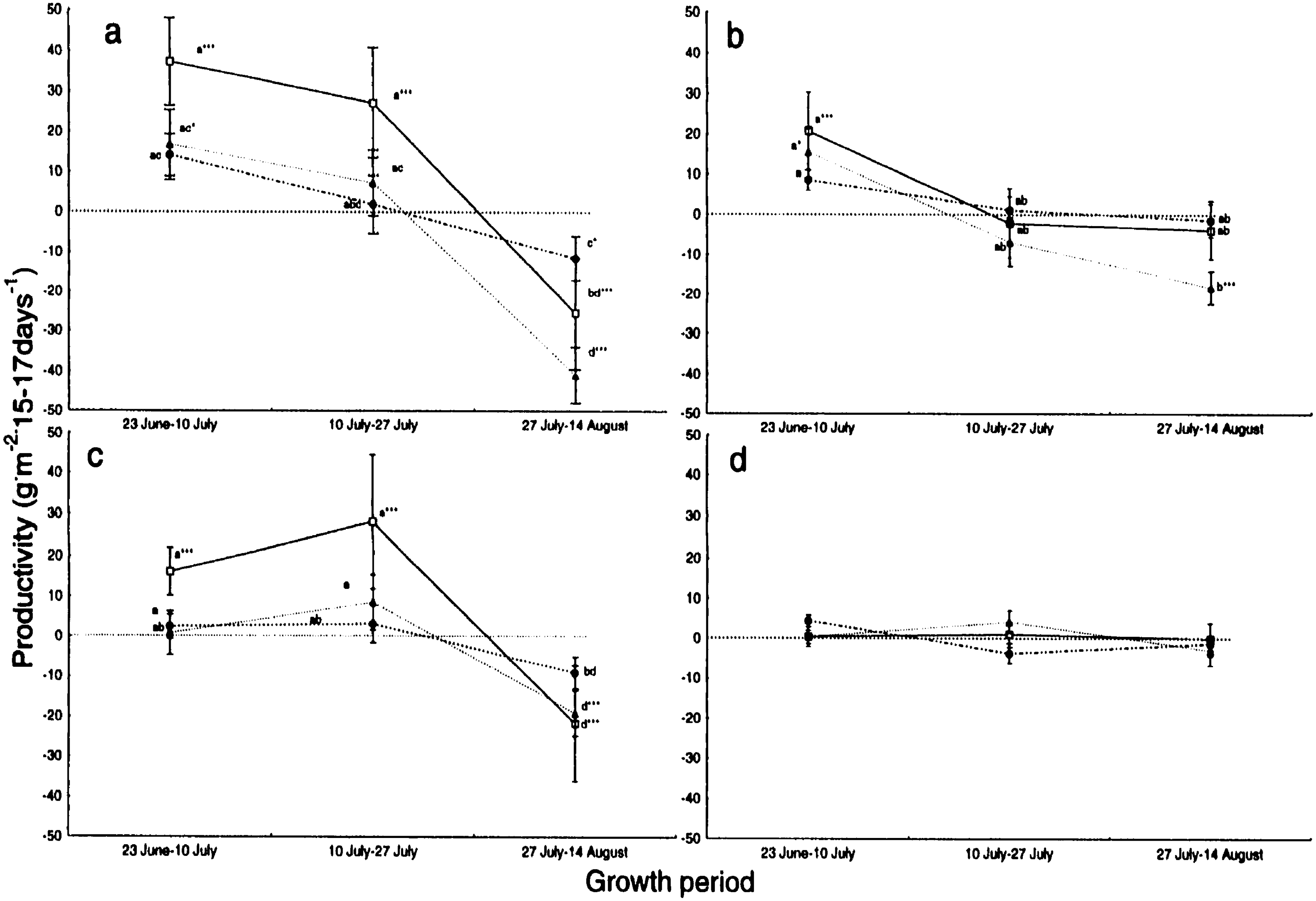


Indirect effect of pikas on soil surface temperature

Table 2-2. Summary of RM-ANOVAs for productivity in the temporary, 2-year and control plots adjacent to talus. Main effects are the time of herbivore exclusion (GRAZING), sample period throughout the summer (DATE) and PLOT. *: 0.05<P<0.01, **: 0.01<P<0.005, ***: P<0.005.

Source	Total	Graminoid	Forb	Dwarf shrub
GRAZING	12.15***	7.64***	0.15	4.69**
DATE	52.77***	12.68***	1.29	41.68***
GRAZING X DATE	3.58*	1.37	1.45	2.61*
PLOT (GRAZING X DATE)	2.83***	1.73*	1.08	7.14***

Figure 2-9. Aboveground rates of production (primary productivity) in 1998 in two year exclosures (□), temporary exclosures (15-17 days, ●) and unexclosed controls (△) , by distance from talus, date and life form (mean±S.E.). ANOVA results for DATE X DISTANCE effect are shown on each graph. Within each graph, all points that are significantly different than zero are indicated with asterisks (LSM, * $0.01<P<0.05$; ** $0.005<P<0.01$; *** $P<0.005$). Points within each graph that share lower case letters are non-significantly different (Tukey adjusted LSD, $P<0.05$). When lower case letters are not shown, the ANOVA was non-significant and thus pair-wise contrast are not meaningful. (a) All species, (b) graminoids, c) dwarf shrubs, and d) forbs.


a
b
c
d
Productivity (g·m⁻²·15-17days⁻¹)
50
40
30
20
10
0
-10
-20
-30
-40
-50
23 June-10 July
10 July-27 July
27 July-14 August
Growth period
a***
ac*
ac
abd
bd***
c*
d***
a*
a
ab
b***
bd
d***

senescence and new growth. The grazed controls have significantly lower productivity than either exclosure plots, a difference most apparent late in the season. Among dwarf shrubs, exclosure treatment is a significant factor affecting productivity, a pattern driven by the 2-year exclosures (Table 2-2; Fig. 2-9c). The final period of growth showed significant negative productivity in both treatments and control, suggesting that the balance between senescence and productivity in dwarf shrubs is negative. The temporary exclosures and the control plots are not significantly different at all dates. Forb productivity is generally very low for all treatments, and there is no detectable effect of GRAZING, DATE or GRAZING X DATE interaction (Table 2-2; Fig. 2-9d).

Comparison of effect of pikas at Front Ranges and Ruby Ranges

Important and significant species differences in control, grazed plots exist between Front Ranges and Ruby Ranges. There are significantly fewer graminoids in the Front Ranges ($F_{1,70}$=116.23, $P<0.0001$), significantly fewer forbs ($F_{1,70}$=15.09, $P=0.0002$) and significantly more shrubs ($F_{1,70}$=103.68, $P<0.0001$) (Fig. 2-10). In addition, the differences for dwarf shrubs and forbs are affected by the distance from talus (dwarf shrubs $F_{2,70}$=7.59, $P=0.001$; forbs $F_{2,70}$=3.73, $P=0.03$; Fig. 2-10). Shrubs are least abundant adjacent to talus and forbs are most abundant adjacent to talus. Graminoid abundances are not statistically affected by distance from talus, though the decreasing trend outward from talus is similar to that of forbs.

Three-way RM-ANOVA on DISTANCE, DATE (only 2 sampling dates) and SITE revealed that DATE was not a detectably significant main effect using either 23 June or 10 July from the Ruby Ranges as a comparison (Table 2-3). As a result, we re-analyzed the data using a simplified two-way ANOVA on DISTANCE and SITE with all samples taken on 27 July (RR) and 29 July (FR), as these samples occurred during the period of peak aboveground live biomass and showed a greater magnitude of exclosure effects. As with the analysis of the Ruby Range

Figure 2-10. Aboveground live biomass in control plots in the Ruby Range and Front Ranges by distance from talus and life form (graminoid [⊡], dwarf shrub [□] and forb [■]), on 27 July (RR) or 29 July (FR), 1998. Bars which share lower case letters above indicate non-significant differences ($P<0.01$) between measures of total aboveground live biomass. Shared lower case letters within the bars indicate non-significant differences (Tukey adjusted LSD, $P<0.05$) between measures within each life form.

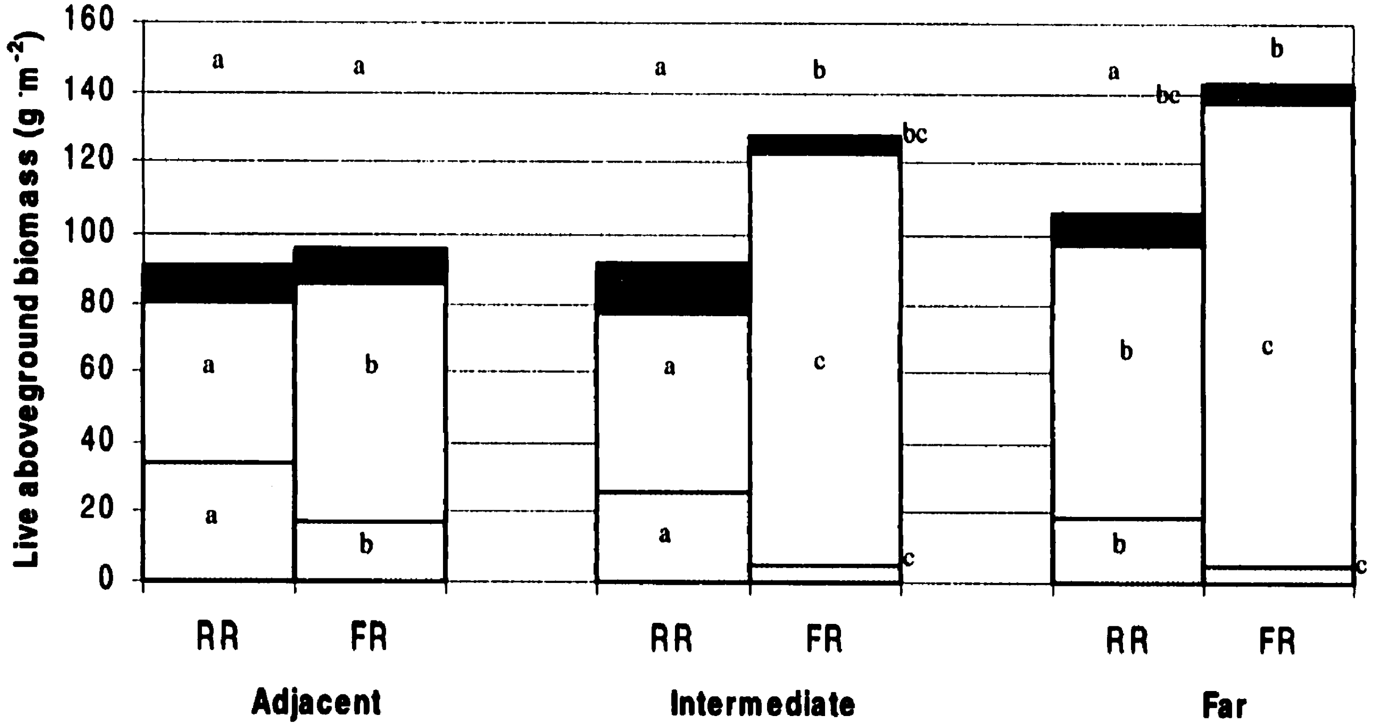

Live aboveground biomass (g m^{-2})
160
140
120
100
80
60
40
20
0
a
a
a
b
a
b
bc
bc
a
b
a
c
b
c
a
b
a
b
c
c
RR
FR
RR
FR
RR
FR
Adjacent
Intermediate
Far

Table 2-3. Summary of F-values from 3-way RM-ANOVAs for effect of exclosures on aboveground live biomass and species number between FR and RR. Main effects are as in Table 2-1, with the effect of SITE added. *: 0.05<P<0.01, **: 0.01<P<0.005, ***: P<0.005.

		Aboveground live biomass				Species number			
Source	Num DF	Total	Graminoid	Forb	Dwarf shrub	Total	Graminoid	Forb	Dwarf shrub
DIST	2	14.6***	0.60	2.64	16.6***	1.84	0.29	1.16	1.94
SITE	1	0.00	10.66**	2.99	0.84	3.08	0.88	0.43	0.00
DATE	2	2.10	1.99	2.81	0.25	0.66	0.10	1.21	0.74
SITE X DIST	2	2.57	4.19*	0.22	0.76	6.06**	1.19	4.77**	3.43*
SITE X DATE	1	4.65*	8.96**	0.30	1.38	0.00	0.22	0.00	3.74
DIST X DATE	4	$2.28^{0.06}$	1.65	0.40	5.17**	1.29	1.51	0.80	0.66
SITE X DIST X DATE	2	0.42	3.09*	2.11	0.03	0.02	1.06	0.69	3.47*
PLOT (DIST X DATE)	64	3.09***	2.33***	2.39***	3.58***	2.42***	1.98**	2.36***	2.27***

Table 2-4. Summary of F-values from 2-way ANOVAs for effect of exclosures on aboveground live biomass and species number between FR and RR. *: 0.05<P<0.01, **: 0.01<P<0.005, ***: P<0.005.

		Aboveground live biomass				Species number			
Source	Num DF	Total	Graminoid	Forb	Dwarf shrub	Total	Graminoid	Forb	Dwarf shrub
DIST	2	21.50***	4.09*	0.89	19.2***	0.14	0.23	0.07	4.3*
SITE	1	3.80*	12.27***	1.78	0.13	2.15	0.12	0.29	3.81*
SITE X DIST	2	2.56$^{0.08}$	5.44**	0.50	0.38	3.09*	1.60	1.12	9.74***
PLOT (DIST X DATE)	64	4.14***	2.06***	1.83**	4.02***	1.86**	1.15	1.77**	2.93***

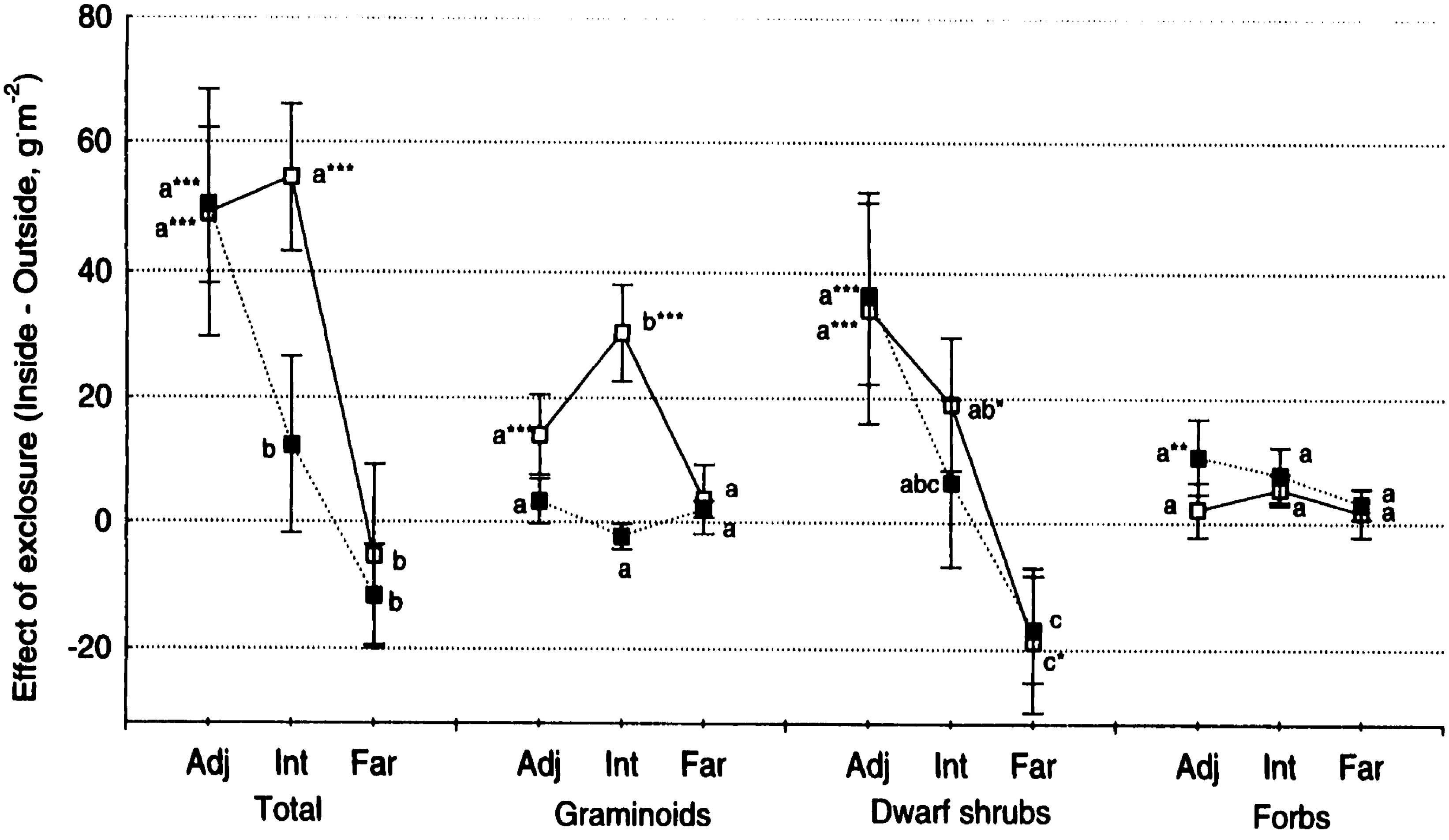
exclosures beyond 3 m from talus is not detectable (Fig. 2-11). This discrepancy between the Ruby Range and the Front Range does not exist for adjacent or far exclosures. Analyzed separately by life-form group, graminoids appear to drive this pattern, while dwarf shrubs and forbs show no differences between sites. In the Ruby Ranges, aboveground live biomass of graminoids in exclosures increases by over 30 $g \cdot m^{-2}$ compared to controls at the intermediate distance from talus. At the Front Ranges, the effect of exclosures on graminoids does not differ significantly from zero. Thus, in pair-wise comparisons, no distance effect of exclosures is detectable at the Front-Ranges on 29 July for graminoids.

The effect of pika exclusion on plant species richness affected the two sites differently (Fig. 2-12 and Table 2-4). Total species richness was significantly more affected far-from-talus in the Front Ranges than at the Ruby Ranges, however, no differences were detected in adjacent or intermediate exclosures. Analyzed by growth form, only dwarf shrubs showed a significant difference between sites, though the effect was not strong.

Discussion

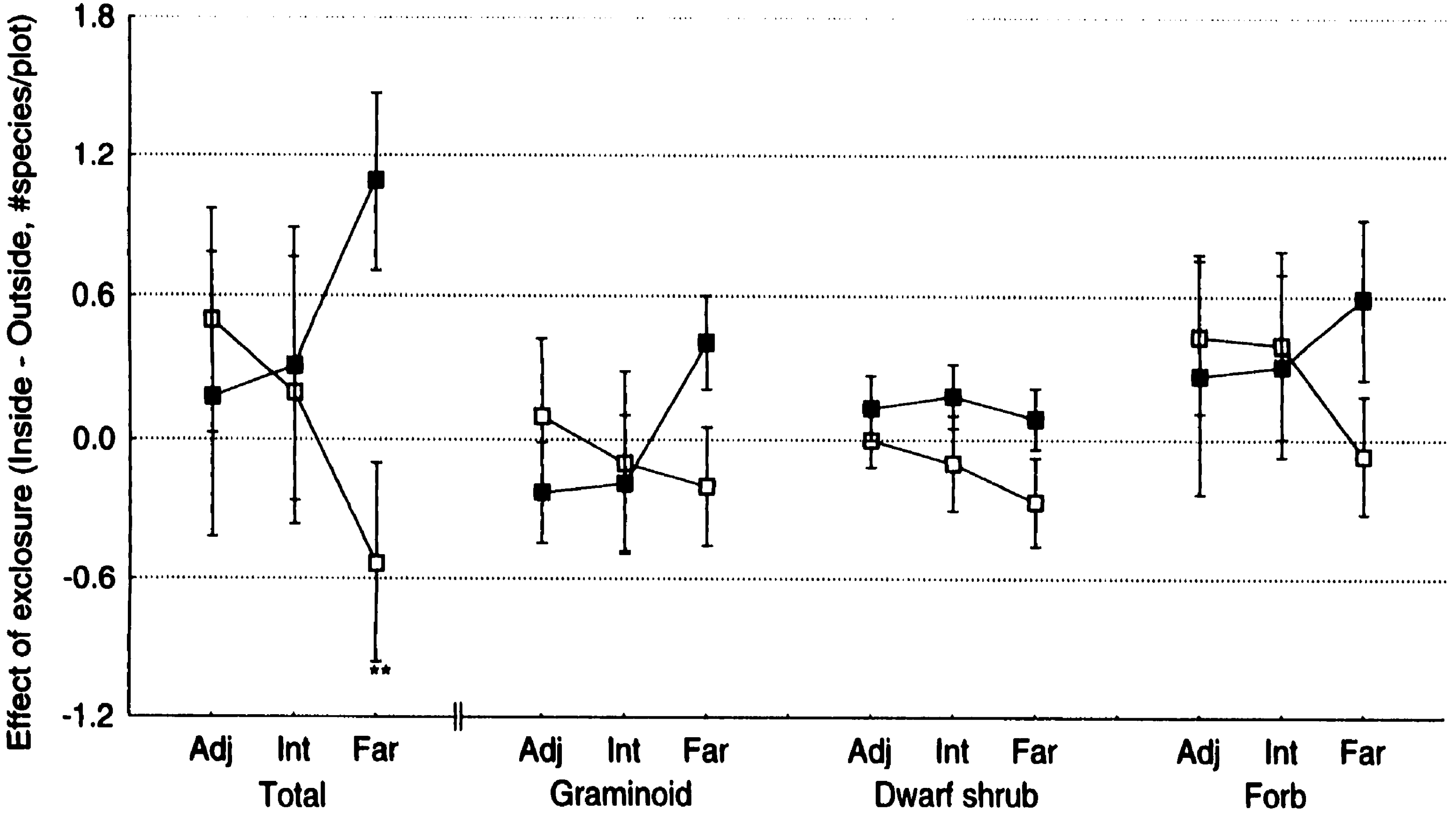
A few studies have observed that multiple levels of grazing intensity appear to create a unimodal response curve of plant abundances or plant growth of some species (McNaughton, 1979, 1986; Noy-Meir, Gutman and Kaplan, 1989; Hik and Jefferies, 1990). Several have predicted the same increased growth response pattern, often referred to as the grazing optimization hypothesis (Hilbert *et al.*, 1981). These studies suggest that at some intermediate level of grazing intensity, plants perform better—e.g., have greater aboveground production—or are more abundant than at lower or higher levels. Most studies corroborating this pattern have been conducted under controlled conditions, with experimentally imposed herbivores or plants (e.g., Williamson *et al.*, 1989). The value of examining naturally occurring herbivores and plants

Figure 2-11. Effect of site (Front Ranges [■] and Ruby Ranges [□]) on aboveground live biomass in two year exclosures (inside minus control plots), by distance from talus and life form, on 27 July (RR) and 29 July (FR) in 1998 (mean±S.E.). ANOVA results for DATE X DISTANCE effect are shown on each graph. Within each graph, all points that are significantly different from zero are indicated with asterisks (LSM, * $0.01<P<0.05$; ** $0.005<P<0.01$; *** $P<0.005$). Points within each graph that share lower case letters are non-significantly different (Tukey adjusted LSD, $P<0.05$).



Effect of exclosure (Inside - Outside, g·m^{-2})
80
60
40
20
0
-20
a***
a***
a***
b
b
b
a***
a
b***
a
a
a
a***
a***
ab*
abc
c
c*
a**
a
a
a
a
a
Adj
Int
Far
Total
Adj
Int
Far
Graminoids
Adj
Int
Far
Dwarf shrubs
Adj
Int
Far
Forbs

Figure 2-12. Effect of site (Front Ranges [■] and Ruby Ranges [□]) on species richness in 2-year exclosures, by life form group and distance from talus on 27 July (RR) and 29 July (FR), in 1998 (mean±S.E.). ANOVA results for DATE X DISTANCE effect are shown on each graph. Within life form groups that demonstrate a significant SITE effect, asterisks indicate where sites differ significantly (LSM, ** $0.005<P<0.01$).


Effect of exclosure (Inside - Outside, #species/plot)
1.8
1.2
0.6
0.0
-0.6
-1.2
**
Adj
Int
Far
Total
Adj
Int
Far
Graminoid
Adj
Int
Far
Dwarf shrub
Adj
Int
Far
Forb

has been emphasized because of the potential for past effects of grazing on the plants which is not captured in these types of experiments (Post and Klein, 1996; Lennartsson, Tuomi and Nilsson, 1997). Much controversy exists as to whether this optimization has been observed in terrestrial systems (Belsky, 1986, 1987; Detling, 1988), since many studies have not detected this pattern (Coppock *et al.*, 1983; Whicker and Detling, 1988; Belsky *et al.*, 1993; Zellmer *et al.*, 1993; Bergelson, Juenger and Crawley, 1996). In some sense, however, many of the disagreements have been philosophical (e.g., Belsky, 1986 and McNaughton, 1986b). In any case, appropriate nutrient levels must be available for optimization to occur (Hamilton *et al.*, 1998; de Mazancourt, Loreau and Abbadie, 1998), but little *in situ* evidence to support these models exists to date. Several other problems exist with many of these past studies, including a lack of consideration of within-season variability in grazing intensity, timing of grazing, water and nutrient availability.

One key distinction between some previous studies on plant optimization and the present study is the relative stability of the vegetation community. For instance, many studies on salt marshes in North America and Europe occur in communities that are under rapid successional change (e.g., Bazely and Jefferies, 1986), leading to theoretical investigations of the interactions between herbivores and successional change (Jefferies, Klein and Shaver, 1994; Drent and van der Wal, 1999). The alpine communities in southwestern Yukon Territory and specifically the meadows occupied by pikas in this study are relatively stable over centuries (D. Hik, in review). Thus, questions of how herbivores slow or accelerate community processes are superceded by questions of the maintenance and persistence of palatable communities.

Initial examination of the vegetation abundances along the naturally occurring grazing gradient emphasizes the importance of the timing of sampling as part of herbivory experiments. In our control plots (Fig. 2-2), depending on the sampling date, graminoids would appear to decrease in abundance along the grazing gradient (June and July), or show a unimodal peak at an intermediate level of grazing (August). Forbs and dwarf shrubs also show inconsistent biomass response patterns at the four sampling dates throughout the season, though mostly, they show a monotonically increasing aboveground live biomass with decreasing grazing intensity. Depending on the plant group and the time of season observed, all possible responses were observed along a gradient that ranges from virtually no herbivory to over 50% decrease of aboveground live biomass (see below). Huntly's (1987) simple model of vegetation abundance for *Ochotona princeps* in the Rocky mountains was a very poor predictor for graminoids and forbs in the Yukon at any date. She predicted peaks in graminoid abundances near and far from talus and monotonically increasing abundances of forbs with increasing distance from talus. She made these predictions primarily based on pika vegetation selectivity. It is possible that other mechanisms determining vegetation abundance are responsible for the pattern we observed here. For instance, one known compensatory mechanism among plant tolerance strategies is an increase in leaf longevity after leaf damage (McNaughton, 1979; Meyer, 1998). Studies which examine single dates within a season may not completely capture plant responses such as decreases in leaf senescence and may mask aboveground live biomass patterns that occur over the whole season—which may be more important for herbivores than peak biomass. Our control plots reflect many underlying mechanisms including the loss of vegetation due to pika herbivory itself, and only partially express the response of plants to the grazing gradient.

The difference in productivity between the temporary exclosures (actual productivity) and the control plots (apparent productivity) estimates the herbivore offtake, or the amount of vegetation removed by the pikas. Since the timing, intensity and specificity of vegetation removal likely contributes to a plant's ability to compensate for damage (Maschinski and Whitham, 1989), the late season grazing we observed suggests that it is unlikely that plants will overcompensate for the damage in the same year. These offtake values corroborate the behavioural observations of both species of North American pikas, which demonstrate that pika activity is greatest towards the end of the season (T. Bubela *et al.*, unpub. data). No studies on pikas to date have observed the high levels of grazing on graminoids we detected here and this pattern is apparently not determined by vegetation abundances since dwarf shrubs have comparable aboveground live biomass measures. Thus the pikas fed selectively, a process that has been documented in generalist herbivores (Dearing, 1996), however, the predictability of which plants would be selected remains unclear for small mammals in northern regions.

Theoretical and experimental attempts at predicting forage selectivity generally implicate nutrient availability or secondary compounds (Dearing, 1997a, 1997b; Hobbs, 1996). Little is known about late season nutrient levels in northern alpine graminoids and dwarf shrubs, though some species show monotonic declines in nutrients throughout the season (D. Hik, unpub. data). Secondary compound levels in the plants in our locations are also unknown. The most likely contribution to forage selectivity is late-season growth of leaf tissue; grazed plants of some species continue to produce new tissue late in the season (Ch. 3), lowering the average leaf age and leaf nutrient content (Whicker and Detling, 1988) and will continue to produce aboveground live biomass. It is likely that pikas will select those species which continue to produce new leaves late in the season, since evidence suggests that pikas can avoid the damaging effects of secondary compounds by storing vegetation (Dearing, 1997a).

2-year exclosures

Total aboveground live biomass shifts as a result of the 2-year exclosures indicate two important aspects of the pika-plant relationship. First, they reflect the current season losses of aboveground tissue to pika grazing. As such, they partially reflect the level and timing of pika grazing in the current season (short-term). Second, they are also a result of the consequences of shifts in photosynthetic capacity in the previous and current seasons as a result of release from pika grazing. The latter aspect reflects cumulative underlying physiological changes that occur when plants are released from herbivory (longer-term). Using 2-year exclosures like these, it is impossible to separate these two aspects of the plant-pika relationship; however, they do indicate composite short and long-term processes and any observed changes can be considered the "effect of pikas".

The aboveground live biomass patterns we observed strongly mirror the behavioural observations on pika foraging which suggest that pikas primarily forage near to talus (Huntly, Smith and Ivins, 1986; Huntly, 1987) and the intensity of foraging increases throughout the season (MacDonald and Jones, 1987; D. Hik unpub. data). First, we found no significant negative effect of grazing beyond 8m from the talus throughout the summer. Second, we observed an increasing effect of pikas throughout the summer, a pattern that has been reported only with behavioural data with no known record of the effect on plants. The increasing difference between inside and outside the exclosures likely reflects early season foraging bouts and past and current years' cumulative detrimental effects. Third, the difference between inside and outside the exclosures was not different between the intermediate and the adjacent exclosures until 14 August. Thus, not only did the effect increase throughout the summer, late season grazing affected plants near to talus significantly more than beyond 3 m. While peak aboveground live biomass in the control plots occurred in July for adjacent and far plots (Fig. 2-2), herbivore effect did not coincide with this and was strongest in mid-August adjacent to talus. As a result, studies examining the effects of an herbivore at peak season aboveground live biomass would not necessarily observe peak herbivore effect.

At the end of the growing season, the increased levels of aboveground live biomass within 2-year exclosures suggests that plants with a history of grazing (heavy or light) have a higher net annual production potential than plants with no grazing history. Since we observed this pattern in the second season of exclusion of pikas, we may be detecting latent positive effects of grazing to community production, which under constant annual grazing pressures are not realized and appear as negative effects of grazing over short term periods. This pattern was driven primarily by an increase in aboveground graminoid production suggesting that the graminoid growth form may allow for heightened response to an intermediate period of release from grazing. Thus while the short-term ability of graminoids to respond positively to grazing have been long reported (Owen and Wiegert, 1981, 1982; Brown and Stuth, 1993; Post and Klein, 1996), the conditions associated with pika herbivory appear to allow for relatively better performance when grazing pressures are sporadically removed. Since one or two year releases from grazing episodes may occur intermittently due to adult pika mortality and delayed haypile recolonization, the high potential for growth in years following temporary absence of grazing may promote the continued persistence of these highly palatable plant communities even with long-term grazing. To date, however, the frequency of occurrence of these episodic absences is unknown.

Separately, graminoid and dwarf shrub aboveground live biomass showed similar patterns to overall biomass. Both increased inside exclosures at both adjacent and intermediate locations. On 14 August, however, intermediate shrubs were not significantly affected by exclosures while graminoids are significantly affected. Aboveground live biomass of forbs was low, and the changes due to exclosures were not detectable in this coarse scale community analysis. In contrast to previous small mammal grazing studies (Coppock *et al.*, 1983; Huntly, 1987), graminoids in our sites persisted in the highly grazed areas but were not the dominant group. We observed the aboveground live biomass increases primarily in graminoids and dwarf shrubs, life forms which are reported to respond rapidly to removal of grazing pressure due to rapid regrowth of damaged leaves (Ch. 3; Archer and Tieszen, 1980) and release of dormant buds (Archer and Tieszen, 1980), respectively. Without examining individual species, it appears that in the second year following release from three different grazing intensities, there were no major shifts in vegetation composition, with both graminoids and shrubs increasing in abundance and forbs remaining in low abundance.

In contrast to a previous study on pikas in the Rockies where species richness increased outwards from talus (Huntly, Smith and Ivins, 1986), our study showed that species richness of all groups was greatest at an intermediate distance along the grazing gradient and lowest furthest from talus, consistent with Connell's intermediate disturbance hypothesis (Connell, 1978). Huntly, Smith and Ivins (1986) used distances that may not have been sufficiently far to detect the peak of species richness at intermediate distances, since they only measured species richness out to 5 m from talus. When we experimentally removed the effect of pikas, adjacent and intermediate exclosures showed an increase in species richness driven by the increase in forb species richness, and an overall decrease in species richness in far exclosures. Intermediate grazing level sites had the greatest species richness and showed the greatest increase when the pikas were excluded. This could be due to new detection of plants that were present but undetectable during grazing or this may suggest a dynamic influence of pika grazing on species richness possibly caused by a mosaic of small scale patches as a result of grazing (Connell, 1978), which cause a peak in species richness at intermediate levels of grazing. If grazing between 3 m and 7 m from talus has a greater foraging cost for pikas than grazing adjacent to talus, there is likely increased grazer selectivity resulting in spatially patchy distribution of herbivory and the observed increase in species richness (Olff and Ritchie, 1998). Due to the particular exclosure technique we used, however, we were not able to explicitly detect this pattern. Graminoids and dwarf shrubs do not appear to respond to the release from grazing, though this may be due to low species richness of these groups in our sites compared to forbs, which make up about 75% of the species (Appendix 1).

Effects of pikas on aboveground productivity

The productivity of the highly grazed plants in our sites is less than that of ungrazed plants (Fig. 2-9), indicating overall undercompensation within the same season (Belsky, 1983; McNaughton, 1983). This is not surprising for numerous reasons. First, pikas use latrines, so the direct nutrient inputs occasionally cited as an important factor enabling compensatory growth response (de Mazancourt, Loreau and Abbadie, 1998) do not occur. Second, pika grazing occurs most heavily in late summer, a condition under which few plants have ever shown compensatory growth as it has been measured (Maschinski and Whitham, 1989; Hik, Sadul, and Jefferies, 1991; Lennartsson, Nilsson and Tuomi, 1998). However, the reduction in productivity of highly grazed plants is not observed among graminoid and forb growth forms. The latter is likely due to low aboveground live biomass and thus low detectability, though, a leaf demographic study of one forb species (*Erigeron humilis*) in this same site (Ch. 3) showed that grazed plants were capable of high levels of leaf production and produced leaves that were larger than ungrazed plants. Not detecting a decrease in productivity among forbs, alternatively, may reflect the high levels of grazing tolerance among these alpine species.

Aboveground live graminoid biomass, on the other hand, is extensive in our sites and grazing is readily detectable using our sampling strategy. Among graminoids, peak aboveground live biomass was achieved in all plots by 10 July, as no further increase in aboveground live biomass was detected (Fig. 2-2). A leaf demography study showed that leaf production of a graminoid species occurred beyond this date but leaf senescence begins on or before 18 July (Ch. 3). This suggests that the productivity level of 0 $g \cdot m^{-2}$15-17day^{-1} that we observed here is likely a balance between senescence and aboveground productivity, rather than a termination of growth. As such, graminoid productivity, in spite of high levels of tissue loss late in the season, showed near exact compensation, demonstrating high grazing tolerance of these species and likely enabling the continued persistence of these plants.

Low productivity among dwarf shrubs following grazing was also found by Archer and Tieszen (1980). Their study on productivity suggests that in the absence of herbivore damage, dwarf shrubs had high and equivalent productivity to that of graminoids, but with herbivore damage, the productivity of the shrubs declined dramatically. Similarly, Klein (1987) found that following intensive overgrazing of St. Matthew Island by caribou, aboveground live graminoid biomass increased more rapidly than dwarf shrubs, however, with continued absence of grazing, graminoid abundances also declined. Leaf level studies on a shrub willow suggest that leaf damage had profound negative impacts on recovery (Houle and Simard, 1996). Henry and Gunn (1991) found that dwarf shrubs responded rapidly to grazing by caribou, however, the response of graminoids was more rapid. Our data support these previous findings as the ungrazed shrubs in the 2-year exclosures showed very high levels of aboveground productivity, though in the open control plots, productivity was very low before 27 July and highly negative during the early August growth period. The pattern of selective grazing observed here—higher offtake of graminoids compared to shrubs and forbs—coupled with graminoid persistence supports claims that tolerance is a viable strategy for community persistence (Rosenthal and Kotanen, 1994; Strauss and Agrawal, 1999). In addition, since pikas repeatedly graze sites and are capable of reducing the negative impacts of secondary compounds (Dearing, 1997a), defensive strategies could be unsustainable. Since evidence supports an increased relative abundance of shrubs in 2-year exclosed sites, grazing tolerance by more rapid short-term growth among graminoids is likely a beneficial strategy, as long as they can maintain these rates of production indefinitely.

Comparison of the effect of pikas at Front Ranges and Ruby Ranges

The overall effect of pika grazing at the two sites differs only at the intermediate exclosures and the difference is driven by graminoids. Graminoids are far less abundant in the Front Ranges than the Ruby Ranges and they were the most heavily consumed by pikas. The near absence of grazing effects beyond 2 m in the Front Ranges may be driven by the lack of graminoids and different shrub species beyond 2 m. In the Front Ranges, the majority of the aboveground live shrub biomass is *Dryas octapetala* which has very low nitrogen levels in aboveground tissue compared to other dwarf shrub species, especially in the later parts of the season (D. Hik, unpub. data). Since the exclosures beyond 2 m show no significant effect of pikas in the Front Ranges, it is likely that rather than forage outward from talus, the pikas forage greater distances laterally along the talus edge. The Front Range site appears to have a greater mosaic pattern of talus and meadow, providing a more elaborate edge area to forage. The lower distance from talus also reduces risk of predation and since less high quality vegetation occurs beyond 2 m, there is little benefit to foraging beyond. It is difficult to determine causality as the pattern of vegetation could be a function of pika selectivity. Graminoids may be less abundant beyond 3 m because pikas are not foraging there, and are therefore not removing the competitive dominant shrubs. Regardless of the mechanisms, the lack of effects beyond 3 m is more consistent with distances from talus traveled by *O. princeps* in the Rockies than the distances traveled by *O. collaris* in the Ruby Ranges (Huntly, Smith and Ivins, 1986; Huntly, 1987; Dearing, 1996). Vegetation availability, talus structure and other possible causes determine the foraging distance outward from talus of pikas, indicating that the effects of grazing may vary within a single species of herbivore depending on the physical and biological conditions of a site.

The effect of pikas on species richness only differs between the sites in the exclosures furthest from talus. In the far from talus exclosures, species richness increased in the Front Range exclosures and decreased in the Ruby Range exclosures, potentially reflecting diverse shifts in competitive interactions between the sites, in spite of almost no effect on aboveground live biomass in these far exclosures. There may be slight procedural effects of mesh exclosures on the local vegetation, which may affect competitive interactions between species, but that is not likely and these marginally significant results (P=0.05) may simply reflect a stochastic or spurious trend or other environmental factors.

General effects of pikas: combined spatial and temporal effects

At the end of the growing season in 1998, heavily grazed control (untreated) areas adjacent to talus had 45% less aboveground live biomass than intermediate sites and 40% less aboveground live biomass than far from talus areas. By the end of a second season of pika exclusion, total aboveground live biomass inside adjacent exclosures was 118% greater than adjacent controls, in intermediate exclosures total aboveground live biomass was only 44% greater than intermediate controls and far exclosures showed no increase and remained significantly depressed compared to the grazed exclosures. This effect changed throughout the season: it was greatest not at peak aboveground live biomass (27 July), but nearer the end of the season when the cumulative effects of grazing were strongest and the grazing intensity was highest. Different time scales of analysis produced significantly altered conclusions concerning plant response. Short-term aboveground productivity (15-17 day intervals) measured using temporary exclosures in highly grazed plots was far lower than short-term aboveground productivity in 2-year exclosures in the same highly grazed areas adjacent to talus, indicating that short-term aboveground productivity was not enhanced and remained very low in spite of short term release from pika grazing. Exclusion of pikas along a long-existent grazing gradient, on the other hand, showed that exclosed aboveground live biomass in heavily (adjacent) or lightly (intermediate) grazed areas was significantly greater than areas that had no history of grazing. Thus, by the end of the second season of pika exclusion, these plants from highly and lightly grazed sites had greater net aboveground production as compared to sites that had no history of grazing, suggesting that the historical grazing may have allowed for or caused enhanced growth. While these high levels of net aboveground production in areas adjacent to talus may be caused by inherently better quality habitat, these effects were not detected in the first season of herbivore exclusion (Fig. 2-6). Most exclosures were installed in linearly arranged trios to reduce heterogeneity of exclosure site choice. It is likely that the enhanced growth in exclosed yet historically grazed areas is due to the indirect effects of the pikas.

Generally the term overcompensation is applied to short-term or within-season relative increases in aboveground production compared to ungrazed controls and is usually detected by using temporary exclosures (McNaughton, 1983; Frank and McNaughton, 1993; McNaughton, Banyikwa, and McNaughton, 1997). In many ecosystems—particularly low productivity ecosystems—results of experimental work show that within-season exact- or overcompensation does not occur (Archer and Tieszen, 1980; Turner, Seastedt and Dyer, 1993; Ouellet, Boutin and Heard, 1994; Mulder and Harmsen, 1995). In this study, we found that plants in historically grazed areas had increased net aboveground production after two consecutive years without pika herbivory relative to plants with no history of pika herbivory. The immediate promotion of aboveground primary productivity in response to herbivory which has been detected elsewhere (Hik and Jefferies, 1990) did not occur here, likely because of the lack of nutrient returns directly to the soil via pika fecal and urine inputs. The plants may be allocating growth following release from grazing initially into underground reserves for enhanced nutrient uptake potential and for initial recovery from grazing damage, followed in the succeeding year by increased aboveground growth. Thus, indirect mechanisms may affect the observed pattern of delay followed by significant increase in net aboveground production in the following growing season. Tundra soils are known to have very low surface temperatures (Flanagan and Veum, 1974) creating very low nutrient mineralization rates. A reduction in standing leaf litter associated with grazing and the subsequent increase in daytime soil temperatures (Fig. 2-8) may promote soil nutrient mineralization (Chapin, 1983) or increased rate of litter decomposition (Vitousek *et al.*, 1994). This would cause an indirect and delayed nutrient increase in the extended period following grazing (Whicker and Detling, 1988). If this is a mechanism promoting the high levels of net aboveground production in the year following exclusion of pikas, it is likely that continued exclusion from herbivory would soon limit annual production with the increase in leaf litter build up. Other proposed mechanisms to account for the apparently higher net aboveground production in highly grazed areas include reductions in evapotranspiration leaving more moisture in the subsurface areas for root uptake, and a decrease in the soil C:N ratio followed by an increase in plant ability to outcompete microbes for available N (Whicker and Detling, 1988).

Most studies to date analyzing the conditions under which compensatory growth occurs have only examined single-season compensation and as a result, have proposed that late season herbivory will not allow for overcompensation (Maschinski and Whitham, 1989). Here, we measured late season vegetation removal by pikas and no compensatory growth within the year, yet within two-year exclosures, plants with a historical influence of grazing showed higher net annual production than those within identical exclosures with no historical influence of grazing. This examination of the effects of herbivory on production beyond a single season is important and relevant for long lived perennials with low productivity for which growth in the previous season is important in following seasons, particularly when there are periodic naturally occurring releases from herbivory. As predicted previously, but in the context of a single season of growth, we confirmed that the length of time for which herbivores are excluded changed the nature of what impact pikas had on vegetation (Mitchell and Wass, 1996).

The persistence of these plant communities under the high intensity grazing that we detected may result from the combined effect of both long-term grazing pressures—creating improved conditions for growth as well as species and genotypic assemblages which are highly palatable and have a high regrowth capacity—and an intermittent release from pika grazing caused by stochastic pika population processes. Because of the depressed short-term productivity in highly grazed meadows adjacent to talus, these communities are likely not traditional "grazing lawns" (McNaughton, 1979, 1984, 1985) being maintained and manipulated by the pikas (Drent and van der Wal, 1999). Rather, short-term processes cause declines in production, but the inter-year processes may be more important for the persistence of these highly grazed meadows, and thus pika grazing may increase the carrying capacity of these meadows (McNaughton, Banyikwa, and McNaughton, 1997).

Chapter 3 - Leaf demography of three alpine plant species under *in situ* collared pika grazing pressure: grazing history vs. current year defoliation

Abstract

We measured leaf births, leaf deaths and leaf length of *Kobresia myosuroides*, *Erigeron humilis* and *Oxytropis nigrescens* located in southwestern Yukon in response to two grazing histories (long/none) and two levels of current season grazing (present/absent) by collared pikas. All three species showed leaf responses indicating abilities to tolerate the removal of 58-61% of summer leaf production under natural conditions. We found that grazing history—plants located either <2m or >8m from talus piles with active and remnant haypiles—rather than current year grazing was the only significant factor determining shifts in leaf births and leaf deaths in response to pika herbivory. Only leaf length of *Kobresia* was reduced by current year herbivory. In response to grazing history, we detected several leaf morphological changes. Leaf length of historically grazed *Kobresia* were significantly taller on the first season census (30 June), but thereafter, they were shorter than historically ungrazed plants. Only historically grazed *Kobresia* responded by a strategy commonly observed elsewhere of increased new leaf production late in the season, though the response was small. Overall, the lack of late season leaf production likely reflected the late season increase of pika herbivory. Historically grazed *Oxytropis* differed from historically ungrazed plants by delaying end of season senescence and increasing the early season flush of new leaf production. Historically grazed *Erigeron* had slightly lower leaf births throughout the summer than historically ungrazed plants, but showed large and highly significant reduction in leaf senescence rate, particularly late in the season.

The responses of these plants and how these responses differ from the results of other studies can be largely understood as strategies to avoid the foraging behaviour of pikas: the

intensity of forage collection increases throughout the season due mostly to their haying behaviour. In addition, pikas do not return nutrients directly to the foraging meadows, so these plant species do not receive the benefits of grazing sometimes associated with direct additions of faecal nutrients. Our results demonstrate the morphological mechanisms by which these three plant species are able to tolerate and—more importantly for the herbivore—persist under heavy and chronic grazing. In general, there were few deleterious effects of current season pika grazing on within-season leaf births, leaf deaths and leaf length.

Introduction

Examining leaf demography—the birth, death and growth of individual leaves within a plant—is essential to understanding key morphological mechanisms of plant response to herbivory (Bazzaz and Harper, 1977; Chapman *et al.*, 1984; Hartnett and Bazzaz, 1984; Schmid *et al.*, 1988; Bazely and Jefferies, 1989; Houle and Simard, 1996; Suzuki, 1998; Meyer, 1998). Indeed, researchers have suggested that a plant's survival and growth depend critically on its ability to tolerate grazing events, often by altering morphological parameters (Briske, 1986; Butler and Briske, 1988; Rosenthal and Kotanen, 1994). Leaf level phenomena are particularly important to understand in long-lived perennials which dominate most arctic and alpine habitats and for which carbon gain within the season is essential for success in following years (McNaughton, 1984; Bazely and Jefferies, 1989; Schmid and Bazzaz, 1994).

Some documented plant level responses to herbivory include prostrate growth, shorter leaves, increased tillering, an extension of tiller recruitment period, and an increased rate of leaf production (McNaughton, 1976; Detling and Painter, 1983; McNaughton, 1984; Parsons and Penning, 1988; Butler and Briske, 1988; Bazely and Jefferies, 1989). Save for these few examples, much of the debate surrounding *whether* and *how much* plants tolerate and compensate for herbivore damage suffers from a lack of analysis into the morphological leaf level phenomena, particularly in long-lived perennial plants, leaving unanswered questions as to *how* compensatory growth following herbivory occurs within a plant (e.g., Belsky, 1986; Maschinski and Whitham, 1989; Dyer, Turner and Seastedt, 1993; Bergelson, Juenger and Crawley, 1996). More importantly, few studies have examined leaf demography while under the influence of native grazers and natural levels of grazing (e.g., Parsons, Johnson and Williams, 1988; Parsons and Penning, 1988; Zellmer *et al.*, 1993; Schmid *et al.*, 1988; Meyer, 1998). These features are not only important in the debate surrounding so-called beneficial aspects of grazing (Hartnett and Bazzaz, 1984; Belsky *et al.*, 1993), they may also cause qualitatively and quantitatively different effects than simulated grazing in controlled conditions (e.g., saliva; Dyer and Bokhari, 1976; tearing or shredding; Archer and Tieszen, 1980; Baldwin, 1990; Frank and McNaughton, 1993; Paige, 1999; see Baldwin, 1990). A prerequisite for this type of study is the knowledge of which plants will be grazed and how long they have been grazed for (Mulder and Harmsen, 1995).

Collared pikas (*Ochotona collaris*) are small rock-dwelling lagomorphs of high alpine regions. They show relatively stable interannual population levels (10-30% interannual fluctuations, D. Hik unpub. data) and as a result, they consistently graze the same patches in most years, potentially selecting for grazing tolerant plant genotypes (McNaughton, 1983; Herms and Mattson, 1992). Plants beyond a certain distance (>8 m) from the talus, which offers the pikas protection from predators, have undetectable levels of grazing (Huntly, 1987; Ch. 2). While significant and large effects of pikas have been detected adjacent to talus (Huntly, 1987; Ch. 2), it is unknown whether every individual plant in these highly grazed areas is grazed in every growing season. Other important ecological features distinguishing the effect of pikas from other small mammals include virtually no direct alteration of the physical structure of the area surrounding a haypile (e.g., burrowing animals; see Huntly, 1991), as well as gradual intensification of grazing late in the growing season in preparation for haypile formation (Ch. 2). Pikas use latrines within the rock piles for defecation and urination resulting in a very low rate of direct nutrient returns to the feeding areas (*O. princeps*; Aho *et al.*, 1998), eliminating a commonly observed beneficial return of herbivore grazing (McNaughton, 1985; Ruess and McNaughton, 1987). Due to repeated, predictable grazing, little physical disruption and low nutrient inputs, pikas are an excellent model organism to address questions about the response of plants to natural grazing levels both in the short-term and the long-term, while concurrently removing the effects associated with direct nutrient return.

Incorporating the temporal aspects of herbivory and plant growth is particularly important for studying leaf demography because of the potential for shifts in the timing of events such as photosynthetic rates, leaf births and deaths (Hartnett and Bazzaz, 1984; Kotanen and Jefferies, 1987; Houle and Simard, 1996; Suzuki, 1998). Some studies have shown that plants (especially Poaceae) increase tillering rate soon after grazing events (Bazely and Jefferies, 1989). Other studies have shown that leaf death rate is decreased after herbivory, leading to delayed leaf senescence (Meyer, 1998) and possible rejuvenation of remaining tissue resulting in increased photosynthetic capacity (Hodgkinson, 1974). Timing of herbivory events is also predicted to have important consequences for plant growth (Whitham *et al.*, 1991; Frank and McNaughton, 1993). Most data collected on plants which are able to compensate have been subject to early season grazing (Hik, Sadul and Jefferies, 1991; Frank and McNaughton, 1993) and theoretical predictions confirm that herbivory in later parts of the season will be more detrimental than early season grazing, especially in sites with low nutrient availability (Maschinski and Whitham, 1989; Lennartsson, Nilsson and Tuomi, 1998). Pika observations have shown that they tend to feed most heavily towards the end of a season (Ch. 2), suggesting that the rate of leaf removal may increase throughout the season. This may have severe effects on leaf demography as it has been reported that it is increasingly difficult to compensate for lost tissue increasingly later in the season (McNaughton, 1983; Maschinski and Whitham, 1989).

One understudied feature in plant-herbivore ecology concerns the potential selection pressures and adaptations that may occur in repeatedly grazed plants (McNaughton, 1979; Dyer, Turner and Seastedt, 1993; Sork, Stowe and Hochwender 1993). The existence of grazing tolerant ecotypes can be predicted theoretically (McNaughton, 1983) but are only partially documented (Detling, Painter and Coppock, 1986; Painter, Detling and Steingraeber, 1993). The response of grazing ecotypes is rarely contrasted with short-term release from grazing or longer term absence of grazing in arctic and alpine plants to address features of grazed and ungrazed plants. For instance, leaf production may be greatest in grazing tolerant plants which are not grazed in a current year because they do not have the immediate detrimental effects of the tissue removal, but there is less aboveground dead biomass which has been observed to decrease tissue production (McNaughton, 1979). In addition, herbivory tolerance and compensation may be tightly linked to the predictability of the grazing pressure (Crawley, 1987; Vail, 1992; Nilsson, Tuomi and Åström, 1996). Thus, testing for response to grazing without the context and knowledge of past grazing pressures may lead to unlikely and difficult to explain results (e.g., Paige and Whitham, 1987, criticized by Bergelson and Crawley, 1992a). Ideally, establishing a two-way factorial experiment of past history of grazing (Grazed or Ungrazed) with current year herbivory (Grazed or Ungrazed) would enable a closer examination into the different effects of short-term and long-term effects of grazing.

In the current study, we determined the seasonal leaf demography of three diverse plant taxa—*Kobresia myosuroides* (Cyperaceae), *Erigeron humilis* (Asteraceae), and *Oxytropis nigrescens* (Fabaceae)—in response to the natural grazing of the collared pika. Our primary objective was to examine the interaction between the effects of past history of grazing and current year grazing on leaf demography by contrasting plants at adjacent to talus plots (<2 m;

grazed history) and far from talus plots (>8 m; ungrazed history). Inherent within this objective, we analyzed herbivore effects at four equally spaced census periods throughout the growing season to examine temporal changes in morphology.

Methods

Study organisms and study site

We selected three species of plant that were common in our site and that were readily consumed by collared pikas. *Kobresia myosuroides*[1] (Vill.) Fiori & Paol. (Cyperaceae) is a common densely caespitose, dry area sedge. As with most other graminoids, this species has a basal meristem, allowing immediate leaf growth by means of extant leaf elongation after herbivore harvesting. Being caespitose, a commonly observed graminoid response to grazing of initiation of axillary meristems (Bazely and Jefferies, 1989) would not necessarily confer the presumed anti-herbivore form of more prostrate growth, and so may not be expected to occur. *Erigeron humilis* Graham (Asteraceae), a common composite, has a very different growth form with a basal rosette of leaves and erect single stalked flower. *Oxytropis nigrescens* (Pall.) Fisch. (Fabaceae), a high altitude legume, has a densely tufted caespitose growth form with large, nutritious seeds. Legumes have been often cited as being highly prized food for herbivores because of their nitrogen fixing abilities (see Ritchie and Tilman, 1995). Some studies have shown that they do not recover from grazing as well as graminoids (Hulme, 1996). Both dicotyledons must have growth strategies that favour new leaf initiation in response to grazed tissue rather than older leaf elongation because they have apical dominance. This latter method of regrowth is thought to require more plant resources to respond successfully to grazing (Mulder

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[1] Species names follow Cody (1996).

and Harmsen, 1995), and so depending on the timing of harvest, may have more adverse affects on the plants.

The collared pika (*Ochotona collaris*--Lagomorpha), a small lagomorph endemic to the mountain regions of south and central Yukon and central Alaska, is confined to talus slopes and consequently feeds near the edges of talus piles (MacDonald and Jones, 1987; Ch. 2). Pikas do not hibernate but instead collect and store enough food during the short summer (6-10 weeks) to support their needs for the rest of the year. As a result, pikas are central place foragers because they must return to a haypile after haying bouts (Andersson, 1978). They are also confined to areas near talus as a means of escaping predation risk (Huntly, 1987). This feeding in a short period and in a small area can be very intensive and extremely localized causing the vegetation surrounding talus patches to be heavily grazed, sometimes creating grazing “halos”. Pikas are also known to have very low adult dispersal rates, so the same bands of vegetation will be repeatedly grazed, year after year. These two factors contribute to the visually strong herbivore impacts on plants in the population. Most vegetation in our sites have either very few defense chemicals and are edible (though low in nutritional value; Batzli, White and Bunnell, 1981). Additionally, the overwinter decay of vegetation in pika haypiles may result in a reduction of secondary compounds to insignificant levels (Dearing, 1997a). In general, vegetation adjacent to pika talus piles will be repeatedly heavily grazed while vegetation beyond a certain distance will only be lightly grazed (ca. 3-7 m) or largely ungrazed (>8m) (Ch. 2).

At the Ruby Range site (RR: 61°13’N, 138°16’W), the pika population ranging from 65-100 individuals in a given year (D. Hik, unpub. data) shows only small interannual population fluctuations with no recorded population cycling occurring. As a result, evidence suggests low interannual variation in levels of pika grazing and rapid (0 to 2 years) recolonization of patches. This is a trend rarely observed in natural systems where areas, which are currently grazed, have a high probability that they have been regularly grazed for hundreds of years (or more). Our site has a very short growing season (6 – 10 weeks depending on microtopography) and generally low nutrient soils, so repeated intensive grazing in successive years may lead to low plant fitness, low productivity, and eventually high plant mortality.

Leaf demography

To examine plant morphological changes under *in situ* grazing pressure, we marked individual clusters of leaves of *Kobresia myosuroides* and *Oxytropis nigrescens* and individual plants of *Erigeron humilis* in order to measure timing and rate of leaf harvesting from naturally occurring herbivores as well as rate and timing of flower, fruit, leaf production, leaf deaths and leaf lengths. Both *Kobresia* and *Oxytropis* are caespitose species with hundreds of leaves within each genetic individual. Consequently, it was impossible to individually monitor every leaf of entire plants. Instead, we placed small circles of drab-coloured wire at the base of leaf clusters and monitored the fate of individual leaves and leaf births within that cluster. We minimized the number of marked clusters on any genet, and though some leaf clusters were likely part of the same plant, different parts of the same plant might be expected to respond independently from others (Haukioja, 1991). Individual plants of *Erigeron* are usually composed of a single basal rosette, so we placed a small drab-coloured wire marker immediately beside the single rosette and counted all leaves of a genetic individual.

In 1998, we selected two sets of three plots for each species, one set which was adjacent to talus ("adjacent"), the other at least 6 m from talus ("far"). Plots within each set were separated by at least 50m to eliminate spurious patterns due simply to selecting similar patches in a highly heterogeneous landscape. Though we attempted to locate plots in adjacent-far pairs, it was not always possible due to the patchy occurrence of these plants. It was not known prior to this experiment whether all plants in adjacent areas were grazed in each year nor how much individual plants in far plots are grazed by other species (though see below). It was known that adjacent plots are highly and regularly grazed over many years and far plots are undetectably grazed at a coarse community scale (Ch. 2). We assumed that plots adjacent to talus had long histories of intensive grazing because pikas show low population variability and low adult dispersal rates (*O. princeps*: Southwick *et al.*, 1986; *O. collaris*: Hik unpub. data). The plants in these adjacent areas require at least 2 years without grazers to show noticeably increased production whereas production levels in far plots show no change in production when exclosures are erected (Ch. 2). Plots that were far from talus were assumed to have very little history of grazing based on the same reasoning. Since it is possible for infrequent large mammal grazing in all plots—which could be destructive for individually marked plants—we erected 3 cm wire mesh exclosures over the far plots to attempt to eliminate overly damaging large vertebrate grazing for the duration of this study. These exclosures would not keep out very small mammal herbivores or insect herbivory.

While exclosures are an appropriate and particularly useful technique for understanding community response to grazing (Drent and van der Wal, 1999), for examining effects of within-season herbivory on individual plants they may not be ideal because not all plants are likely to be grazed. To determine response of plants to current season grazing, we chose not to erect exclosures in areas adjacent to talus because we suspected that not every plant in these areas would actually be grazed during a given summer. Thus, to distinguish between those plants which were or were not grazed in 1998, individual plants were considered "ungrazed" until the first date on which we detected grazing and were from that date onwards considered "grazed". Because a plant was considered ungrazed until it was actually grazed, our data do not reflect pika selectivity based on a preference for particular leaf traits (e.g., larger plants). Rather, our data reflects actual within-season plant response to being "grazed" or being "ungrazed".

Within each of the three plots we marked 25 individual plant clusters (*Kobresia* or *Oxytropis*) or plants (*Erigeron*), giving a total of 75 plants for each species under each grazing history. Within the sets of plots, plants were subject to natural levels of grazing providing our within season grazing treatment. Thus our four plant types in this experiment were either "adjacent-grazed" or "adjacent-ungrazed" and in far plots were "far-grazed" or "far-ungrazed". A consequence of this strategy of using the pikas as the experimenter was that sample sizes shifted throughout the season from large to small for currently ungrazed plants and vice versa for currently grazed plants.

We tagged plants and began leaf monitoring on 30 June, 1998. We sampled soon after snow had completely melted from all plots and at 3 more regular 15 – 17 day intervals (18 July, 5 August, 19 August). Each census period required 2-3 days, so we censused plots in the same order to reduce the variance of interval length between plots. At each sampling date, we counted number of adult leaves, number of recent leaf births, number of recent leaf deaths, number of grazed leaves (partially or fully), and leaf length. We also noted flower and fruit production, but in our samples so few plants flowered that formal analysis was not possible. This emphasizes that within-season flower production for long lived perennial plants is not a good measure of plant success or fitness (Doak, 1992). With black ink, we marked a single randomly selected leaf for measuring leaf length. We did not mark additional leaves because these plants had very small leaves and prevented accurate marking. In addition, we limited the amount of leaf level disturbance that was caused by the ink as we were attempting to address the response of the plants to disturbance. Leaves were considered new if they were visible but were not yet uncurled (*Erigeron* and *Oxytropis*) or less than 5 mm in length and were clearly newly produced vegetation rather than grazed (*Kobresia*). Completely dead leaves were gently snipped off with scissors so as not to recount them on later dates. From these data, we calculated cumulative number of leaf births and cumulative leaf deaths from 30 June, and also a standardized rate of leaf births and leaf deaths per 14 day period (not 15-18 days). To control for plant size, all analyses on leaf births, deaths and grazed numbers were standardized to the number of leaves on each plant at each date and are reported "per leaf". We did not standardize based on initial season leaf number because the small scale heterogeneity of these plants (e.g., timing of snow melt) caused us to suspect that some plots started growing later than others.

To measure leaf lengths, we marked a single randomly selected leaf of each tagged plant or plant cluster to follow its growth throughout the summer. If the marked leaf was heavily grazed or had died, we randomly chose a remaining leaf and remarked and measured it for the remainder of the life of that leaf. Leaf length, therefore, was a measure of a single randomly selected leaf and did not necessarily reflect leaf length of individual leaves that were grazed. A consequence of not marking all leaves with ink is that when a grazed leaf of *Kobresia* remained functional on subsequent sampling dates, it was counted on more than one occasion. Grazed leaves of *Erigeron* and *Oxytropis* would soon die and were not recensused. Levels of grazing reported here are based on the current number of leaves on each plant which are grazed and thus underestimate cumulative totals for *Kobresia*, particularly late in the season, but are a good estimate of actual rate for the two dicotyledons. Also, without marking individual leaves, we potentially underestimated leaf births and deaths, however, at each census date, we were able to account in number for every leaf from the previous census as dead, dying, grazed or untouched. Our technique for identifying new leaves (described above) as new recruits to the plant was confirmed as being appropriate for accounting for total leaf number.

Data analysis

We examined the effects of grazing history, current season grazing, and date on plants using a three-way repeated measures analysis of variance (GRAZING HISTORY, CURRENT GRAZING, DATE; RM-ANOVA; PROC MIXED, compound symmetry if circularity assumptions were met and unstructured covariance matrix otherwise; SAS INSTITUTE INC., 1998). In all data analyses, the effect of plot was nested within other main effects to test for pseudoreplication (Underwood, 1997). Thus variability among sites is shown by the nested effect of PLOT (DATE X CURRENT X HISTORY). As described above, pikas acted as the primary experimental agent for the effect of current season grazing. For each species, we tested the above effects on cumulative leaf births and leaf deaths, rate of leaf births and deaths, and leaf length. Natural log transformations normalized leaf lengths for the analysis, however, no transformation normalized the data on leaf births and deaths. Our sample sizes, however were generally quite large (Table 3-1) and thus our ANOVA analyses were likely quite robust to departures from normality (Box, 1953; Sokal and Rohlf, 1995; Underwood, 1997).

Results

Baseline values

Grazing levels on all three species in adjacent plots indicate very high levels of leaf loss to herbivores. 50%, 69% and 82% of all tagged *Kobresia*, *Erigeron*, and *Oxytropis* plants were grazed, respectively (Fig. 3-1). In plots far from talus, there was 5%, 22% and 40% grazing occurrence for *Kobresia*, *Erigeron*, and *Oxytropis*, respectively. Intensity of grazing on each plant in adjacent plots varied during the season, but continued throughout (Fig. 3-2). On 18 July, 58% of standing *Kobresia* leaves were grazed, while by the end of the season, 58% of *Erigeron* and 61% of all *Oxytropis* leaves produced had been grazed. In far plots, these numbers were 14%, 20% and 29% for *Kobresia, Erigeron* and *Oxytropis* respectively. We report cumulative proportion of grazed leaves for the two dicotyledons because after they are grazed, the leaves are no longer functional, whereas grazed *Kobresia* leaves persist and remain functional long after the grazing event. As a result, levels of grazing for *Kobresia* are a composite of grazing throughout the season with leaf senescence.

Table 3-1. Summary of sample sizes in all plots throughout the season. Plants with a grazed history were located within 2m of inhabited talus piles. Ungrazed sites were located beyond 8m from talus. Plants are considered grazed in the current season on and after the first date of detected grazing.

		Grazing history							
	Date	30 June		18 July		5 August		19 August	
Species	Current season grazing	Grazed	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed
Kobresia	Ungrazed	67	75	54	74	41	73	35	71
	Grazed	8	0	21	1	34	2	35	4
Erigeron	Ungrazed	36	69	24	61	25	59	21	57
	Grazed	39	6	43	14	43	16	46	16
Oxytropis	Ungrazed	61	71	36	54	18	47	13	45
	Grazed	15	4	35	19	55	28	58	30

Figure 3-1. Grazing occurrence in adjacent plots, measured as the proportion of tagged plants with some level of grazing, by species (*Kobresia* [◇], *Erigeron* [●] and *Oxytropis* [□]) and by date (mean±S.E.).

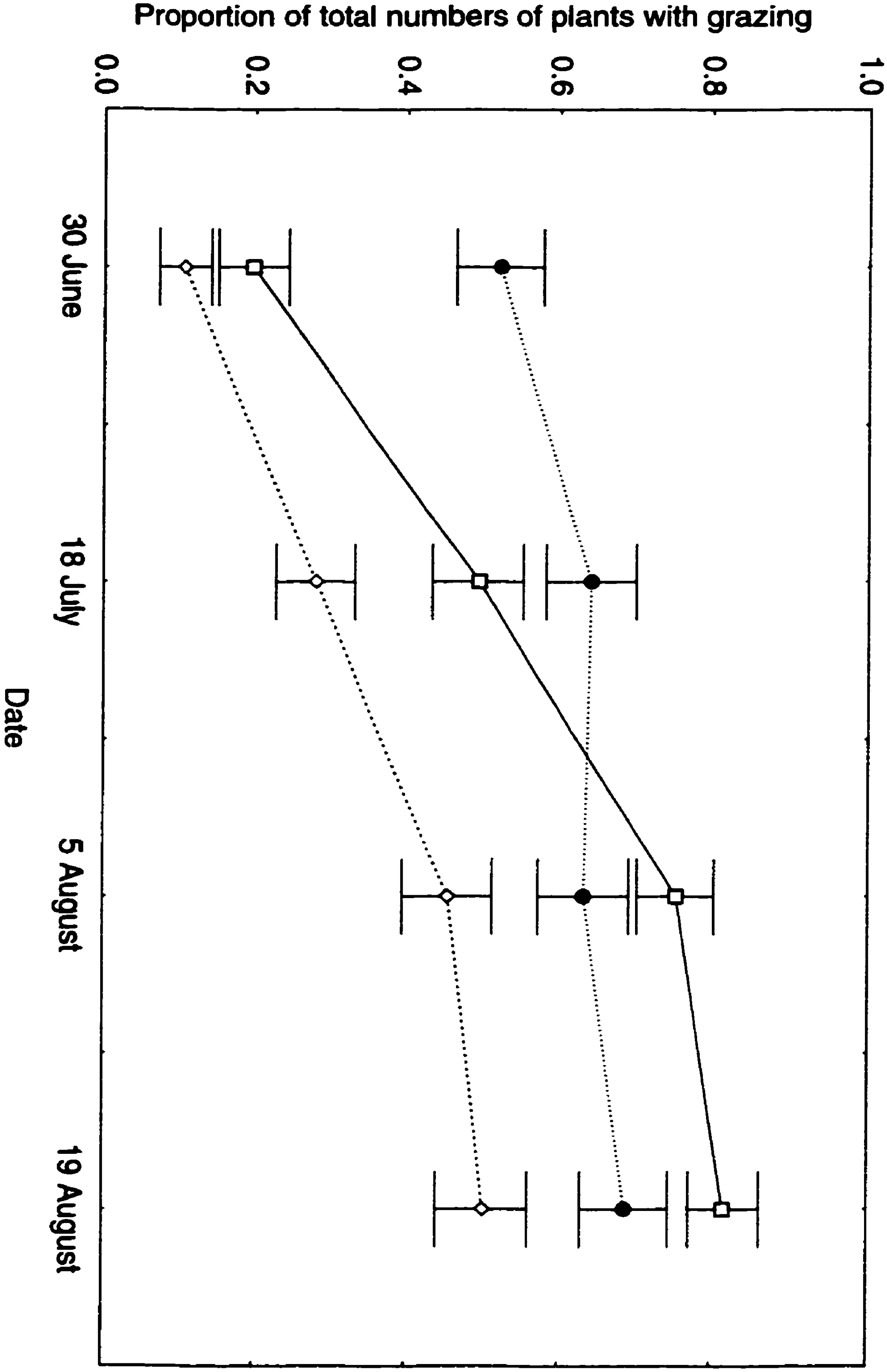
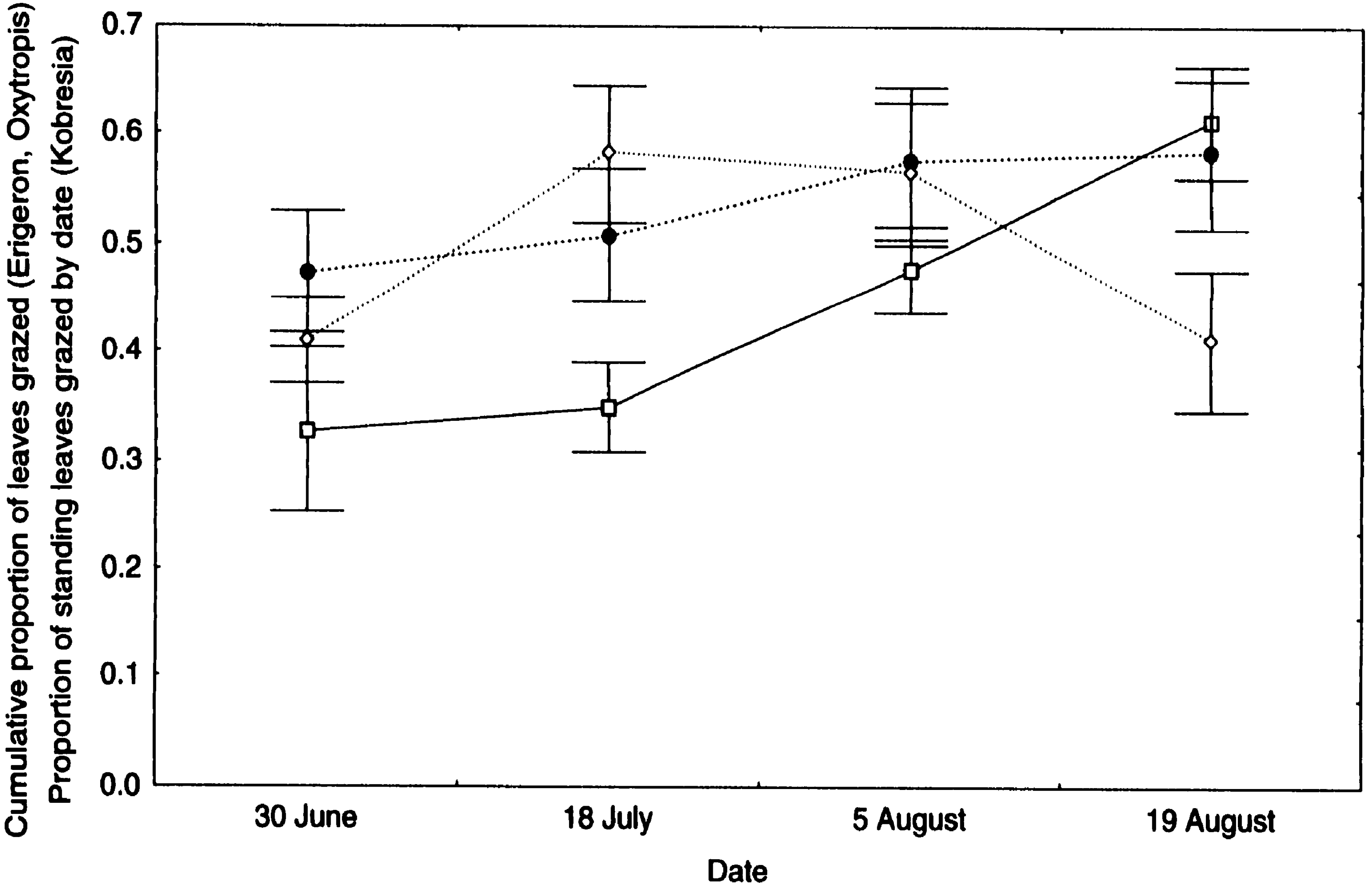

Proportion of total numbers of plants with grazing
0.0
0.2
0.4
0.6
0.8
1.0
30 June
18 July
5 August
19 August
Date

Figure 3-2. Intensity of grazing within grazed plants in adjacent plots (mean±S.E.). Values for *Erigeron* (●) and *Oxytropis* (☐) are cumulative proportions, whereas values for *Kobresia* (◇) are proportions at each date. See text for explanation.


Cumulative proportion of leaves grazed (Erigeron, Oxytropis)
Proportion of standing leaves grazed by date (Kobresia)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
30 June
18 July
5 August
19 August
Date

Across all plots—irrespective of grazing—cumulative and rate of leaf births were lowest among *Kobresia*, while *Erigeron* and *Oxytropis* had the most (Fig. 3-3). The two dicotyledons had at least twice the number of leaf births by the end of the summer as the monocotyledon (Fig. 3-3). During the large part of the growth season, the monocotyledon demonstrated very low rates of leaf births (<0.1 new leaves for each adult leaf for much of the season; see below). Cumulative leaf deaths were intermediate among *Kobresia* (0.38 per leaf), highest among *Erigeron* (0.61 per leaf), and *Oxytropis* had the least (0.28 per leaf). These total numbers of leaf births and leaf deaths likely influence the grazing response capabilities of these plants.

Current grazing

Generally, we detected virtually no effect of current season grazing on any growth parameters for any of the three species (Table 3-2). Log transformed leaf length in *Kobresia*, however, showed that grazed plants began the season at the same leaf length but did not continue to increase in size, while ungrazed plants increased (Fig. 3-4a). Leaf length in *Erigeron* was marginally (DISTANCE X GRAZING, P=0.07) affected by grazing, with early season plants showing increased leaf length, but this difference did not last throughout the summer (Fig. 3-4b). *Oxytropis* showed no significant effect of current year grazing (Fig. 3-4c).

Grazing history

Grazing history showed the most significant effects on plant growth parameters, particularly when examined across the growing season (GrHi X DATE, Table 3-2). Leaf length of historically grazed *Kobresia* plants was longer on 30 June, but thereafter historically ungrazed plants had much longer leaves (Fig. 3-5a). Historically grazed *Erigeron* plants had significantly shorter leaves adjacent to talus, while the interaction with date was not significant (Fig. 3-5b). *Oxytropis* leaf length was unaffected by grazing history (Fig. 3-5c).

Figure 3-3. Total cumulative number of leaf births and deaths by 19 August, 1998 (mean±S.E.).

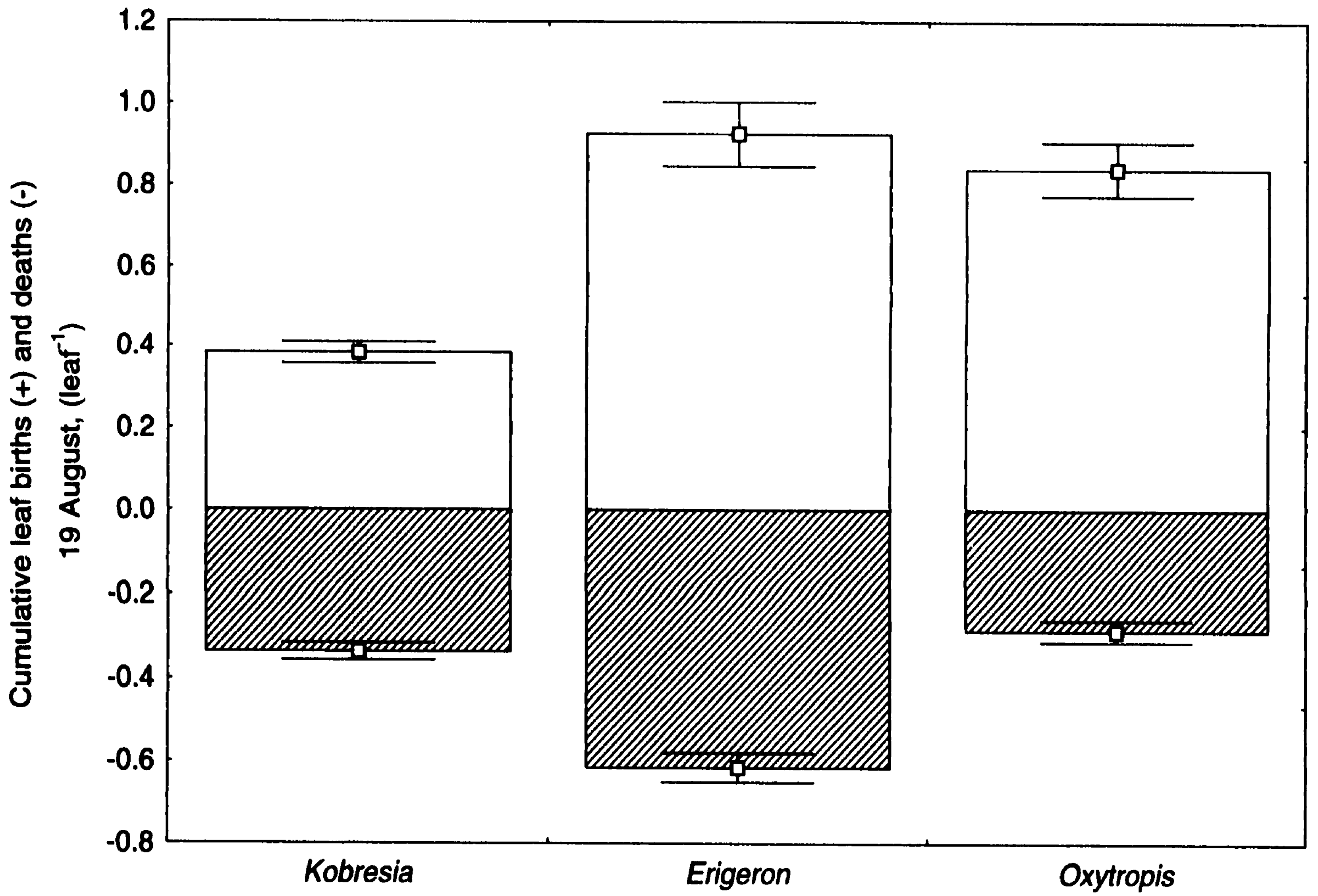

Cumulative leaf births (+) and deaths (-)
19 August, (leaf^{-1})
1.2
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
Kobresia
Erigeron
Oxytropis

Table 3-2. Summary of F-values from RM-ANOVAs for leaf demographic characters. Main effects are Grazing History (GrHi), Current season grazing (CurGraz), sample period throughout the summer (DATE) and PLOT (see methods). *: 0.05<P<0.01, **: 0.01<P<0.005, ***: P<0.005

	Cumulative leaf births		Cumulative leaf deaths		Rate of leaf births		Rate of leaf deaths		Leaf length (ln transf.)	
	$F_{(numdf,dendf)}$	P	$F_{(numdf,dendf)}$	P	$F_{(numdf,dendf)}$	P	$F_{(numdf,dendf)}$	P	$F_{(numdf,dendf)}$	P
Kobresia										
GrHi	$0_{(1,285)}$	0.9879	$0.25_{(1,414)}$	0.6151	$1.07_{(1,238)}$	0.3015	$0.79_{(1,311)}$	0.3733	$0.12_{(1,253)}$	0.7305
CurGraz	$0.41_{(1,318)}$	0.5222	$0.66_{(1,537)}$	0.4173	$0.21_{(1,294)}$	0.6508	$0.38_{(1,367)}$	0.5403	$11.12_{(1,296)}$	**0.001**
GrHi X CurGraz	$0.02_{(1,304)}$	0.8884	$1.8_{(1,536)}$	0.1798	$1.75_{(1,251)}$	0.1874	$1.23_{(1,339)}$	0.2682	$0.67_{(1,252)}$	0.4146
DATE	$34.17_{(3,272)}$	**<.0001**	$26.67_{(3,448)}$	**<.0001**	$2.64_{(3,281)}$	**0.0495**	$5.86_{(3,527)}$	**0.0006**	$21.54_{(3,200)}$	**<.0001**
DATE X GrHi	$1.67_{(3,242)}$	0.1733	$4.42_{(3,434)}$	**0.0045**	$3.06_{(3,210)}$	**0.0293**	$1.72_{(3,480)}$	0.1628	$7.25_{(3,183)}$	**0.0001**
DATE X CurGraz	$0.94_{(3,266)}$	0.4196	$1.33_{(3,448)}$	0.2649	$1.29_{(3,311)}$	0.2784	$1.65_{(3,529)}$	0.1775	$0.54_{(3,221)}$	0.6541
DATE X GrHi X CurGraz	$0.4_{(2,221)}$	0.6723	$1.07_{(2,439)}$	0.3447	$1.5_{(2,225)}$	0.2263	$1.65_{(2,506)}$	0.193	$3.15_{(2,169)}$	**0.0456**
PLOT(DATE X GrHi X CurGraz)	$1.45_{(24,180)}$	0.0905	$2.58_{(24,367)}$	**<.0001**	$1.47_{(24,147)}$	0.0875	$2.15_{(24,375)}$	**0.0015**	$4.08_{(24,167)}$	**<.0001**

Table 3-2 continued.

Erigeron										
GrHi	$4.34_{(1,156)}$	**0.0388**	$4.43_{(1,189)}$	**0.0367**	$1.73_{(1,171)}$	0.1901	$9.7_{(1,213)}$	**0.0021**	$3.68_{(1,201)}$	**0.0565**
CurGraz	$1.95_{(1,298)}$	0.1633	$0.82_{(1,475)}$	0.3646	$0.29_{(1,210)}$	0.5885	$0.7_{(1,240)}$	0.4021	$0.45_{(1,441)}$	0.5042
GrHi X CurGraz	$0.05_{(1,298)}$	0.8310	$1.45_{(1,475)}$	0.2292	$0.09_{(1,212)}$	0.7653	$1.03_{(1,243)}$	0.31	$0.02_{(1,439)}$	0.8767
DATE	$57.0_{(3,152)}$	**<.0001**	$142.73_{(3,395)}$	**<.0001**	$2.94_{(3,173)}$	**0.0346**	$37.81_{(3,447)}$	**<.0001**	$4.49_{(3,334)}$	**0.0042**
DATE X GrHi	$3.33_{(3,152)}$	**0.0212**	$6.73_{(3,395)}$	**0.0002**	$3.25_{(3,173)}$	**0.0231**	$3.46_{(3,447)}$	**0.0163**	$0.03_{(3,331)}$	0.9936
DATE X CurGraz	$1.16_{(3,178)}$	0.3284	$0.99_{(3,393)}$	0.3956	$0.5_{(3,197)}$	0.6818	$1.03_{(3,470)}$	0.3783	$2.3_{(3,334)}$	0.0774
DATE X GrHi X CurGraz	$2.3_{(3,179)}$	0.0791	$1.51_{(3,393)}$	0.2104	$1.36_{(3,198)}$	0.2578	$2.3_{(3,470)}$	0.077	$0.39_{(3,330)}$	0.7631
PLOT(DATE X GrHi X CurGraz)	$4.83_{(29,155)}$	**<.0001**	$2.94_{(29,375)}$	**<.0001**	$4.7_{(29,148)}$	**<.0001**	$5.4_{(29,342)}$	**<.0001**	$2.09_{(29,325)}$	**0.0085**
Oxytropis										
GrHi	$4.28_{(1,154)}$	**0.0402**	$3.27_{(1,232)}$	0.0721	$1.87_{(1,211)}$	0.1727	$0.75_{(1,254)}$	0.3862	$0.27_{(1,189)}$	0.602
CurGraz	$0.79_{(1,373)}$	0.3752	$0.09_{(1,426)}$	0.7692	$0.14_{(1,361)}$	0.7109	$0.46_{(1,358)}$	0.5004	$2.05_{(1,400)}$	0.1525
GrHi X CurGraz	$0.82_{(1,373)}$	0.3658	$2.36_{(1,426)}$	0.1253	$0.12_{(1,361)}$	0.7314	$0.57_{(1,358)}$	0.4495	$0.52_{(1,400)}$	0.4691
DATE	$24.52_{(3,175)}$	**<.0001**	$69.66_{(3,429)}$	**<.0001**	$21.72_{(3,187)}$	**<.0001**	$49.46_{(3,461)}$	**<.0001**	$6.54_{(3,179)}$	**0.0003**
DATE X GrHi	$1.77_{(3,175)}$	0.1541	$0.73_{(3,429)}$	0.5332	$1.03_{(3,187)}$	0.3823	$0.24_{(3,461)}$	0.8702	$1.29_{(3,179)}$	0.2798
DATE X CurGraz	$0.69_{(3,193)}$	0.5595	$0.24_{(3,442)}$	0.8719	$0.59_{(3,214)}$	0.6217	$0.42_{(3,493)}$	0.7403	$1.00_{(3,183)}$	0.393
DATE X GrHi X CurGraz	$0.69_{(3,193)}$	0.5600	$0.86_{(3,442)}$	0.4592	$0.76_{(3,214)}$	0.518	$0.38_{(3,493)}$	0.7657	$0.54_{(3,183)}$	0.6529
PLOT(DATE X GrHi X CurGraz)	$2.41_{(32,166)}$	**0.0002**	$1.66_{(32,444)}$	**0.0150**	$2.44_{(32,173)}$	**0.0001**	$1.79_{(32,519)}$	**0.0057**	$2.50_{(32,186)}$	**<.0001**

Figure 3-4. Effect of current season grazing (grazed [▲], ungrazed [□]) on leaf length values for all species, by date (mean±S.E.). (a) *Kobresia*, (b) *Erigeron*, and (c) *Oxytropis*.

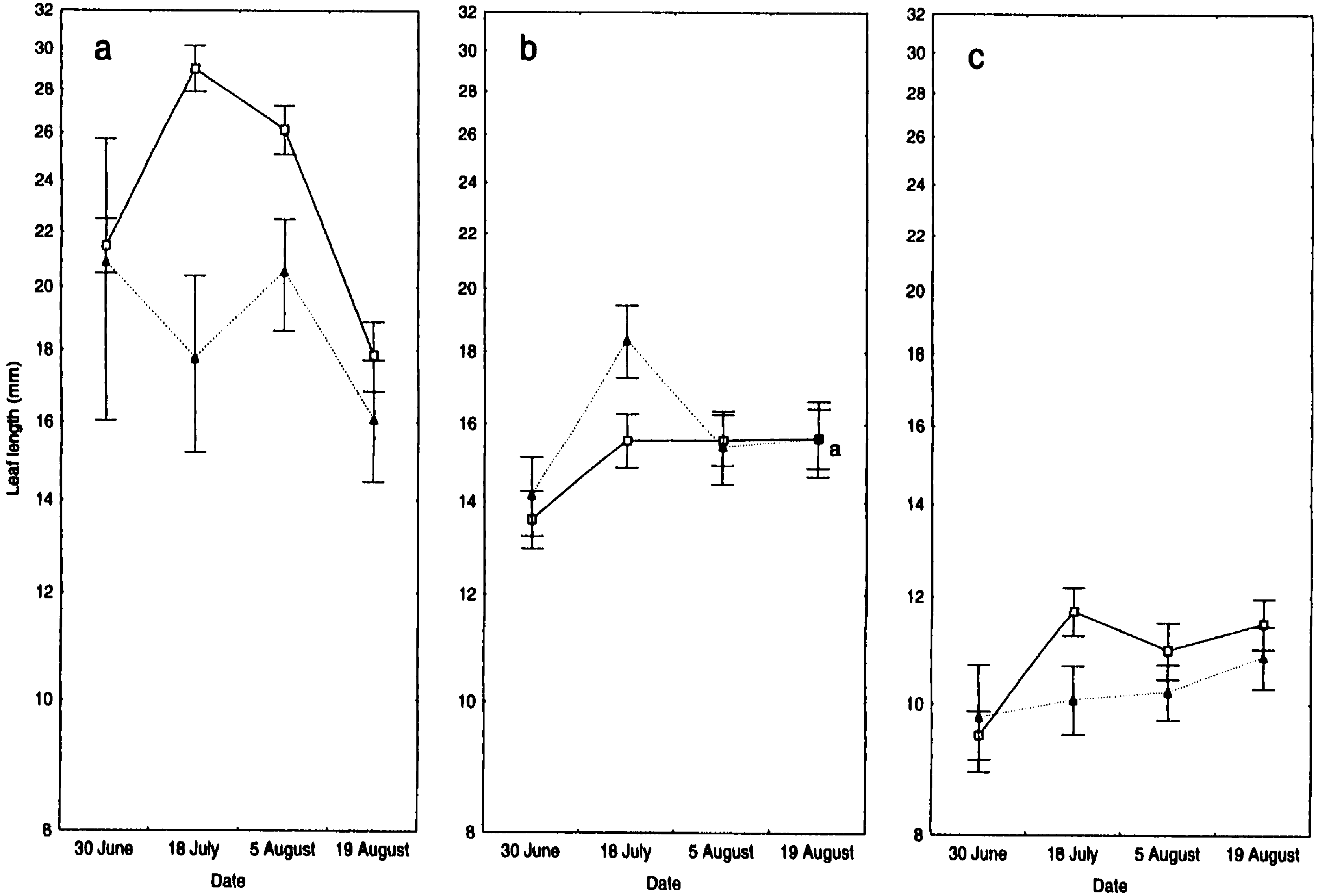
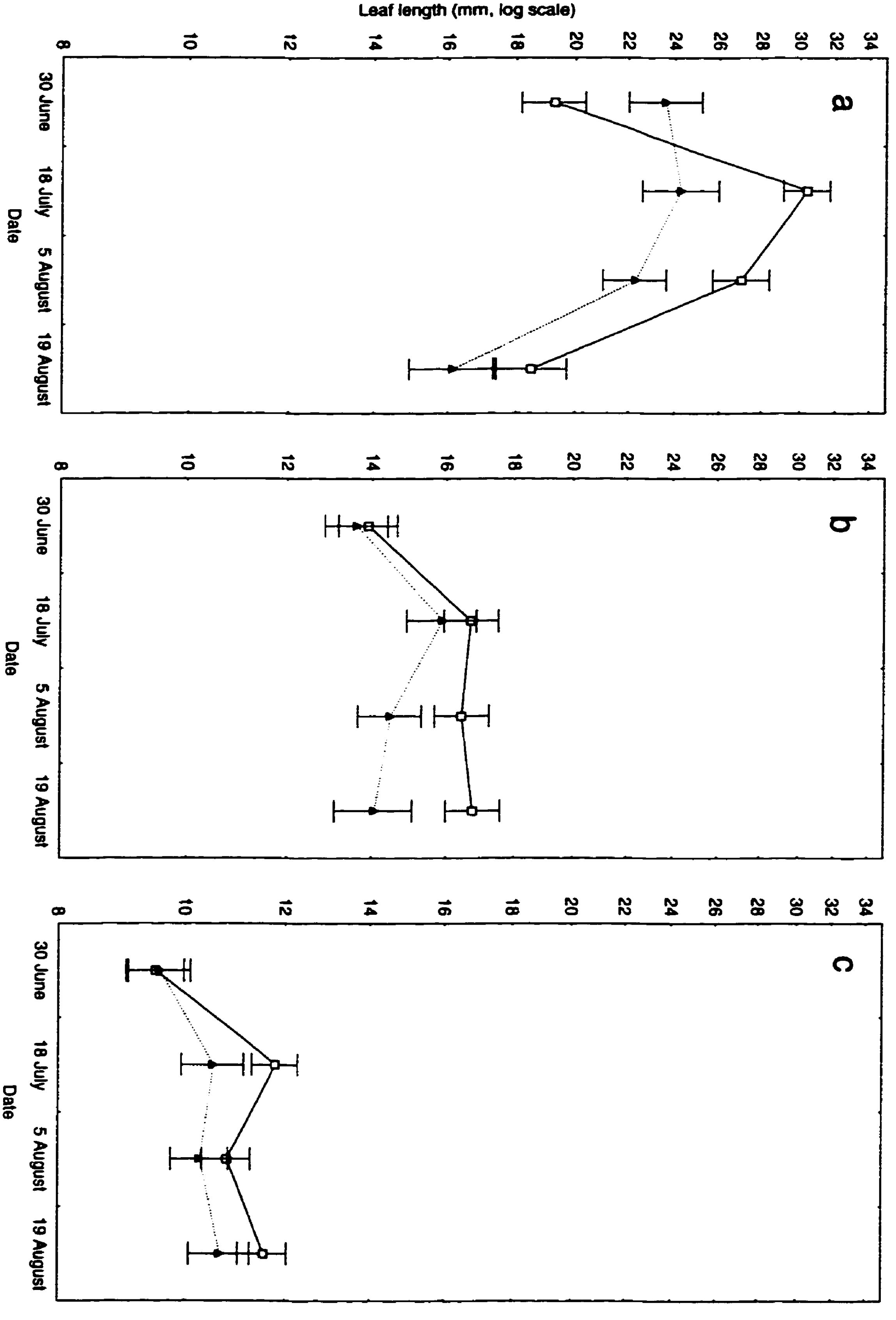

Leaf length (mm)
a
b
c
32
30
28
26
24
22
20
18
16
14
12
10
8
30 June
18 July
5 August
19 August
Date

Figure 3-5. Effect of grazing history (historically grazed [▲], historically ungrazed [□]) on leaf length values for all species, by date (mean±S.E.). (a) *Kobresia*, (b) *Erigeron*, and (c) *Oxytropis*.


a
b
c
Leaf length (mm, log scale)
8
10
12
14
16
18
20
22
24
26
28
30
32
34
30 June
18 July
5 August
19 August
Date

Cumulative leaf births were significantly affected by past history of grazing among *Erigeron* and *Oxytropis*, but not among *Kobresia* (Table 3-2; Fig. 3-6a-c). While historically grazed *Erigeron* plants had depressed leaf births compared to historically ungrazed plants—particularly later in the season—historically grazed *Oxytropis* plants showed increased leaf births compared to historically ungrazed plants (Fig. 3-6b, c). As for cumulative leaf deaths, historically grazed *Erigeron* showed significantly fewer deaths than historically ungrazed and significantly fewer as the summer progressed. Historically grazed *Oxytropis* showed a similar late season decline in cumulative leaf deaths, though was only significant at P=0.07. *Kobresia* showed a significant interaction between grazing history and date, however, this difference was driven by four historically grazed plants that had 100% mortality of standing leaves on 18 July (Fig. 3-6a). These plants were not removed from the original data analysis because new leaves were produced on these plants in subsequent censuses. When these plants were removed from the analysis, grazing history had no significant effect on *Kobresia* cumulative leaf deaths.

Rate of leaf births showed similar patterns to cumulative births for *Erigeron*, but among *Kobresia* plants, rate of leaf births picked up more detailed patterns (Table 3-2; Fig. 3-7a, b). Grazing history showed no significant effect on *Oxytropis* rate of leaf births (Fig. 3-7c). Among *Kobresia*, plants with a grazed history showed a depressed leaf production during the middle of the summer and a significant increase in leaf production late in the summer. The rate of leaf production among plants of historically ungrazed origin declined late in the season. The increased cumulative leaf births that was observed among ungrazed *Erigeron* is driven by a significant 18 July increase in the rate of leaf births. Generally, *Kobresia* and *Erigeron* show no monotonic increase or decrease in new leaf production but *Oxytropis* has significantly higher leaf production early in the season which declined until the two August censuses.

Rate of leaf death showed similar patterns to cumulative deaths: *Kobresia* and *Oxytropis* show variability in leaf death rate, though the differences are not significant, while *Erigeron*

Figure 3-6. Effect of grazing history (historically grazed [▲], historically ungrazed [□]) on cumulative leaf births and leaf deaths for all species, by date (mean±S.E.). (a) *Kobresia*, (b) *Erigeron*, and (c) *Oxytropis*.

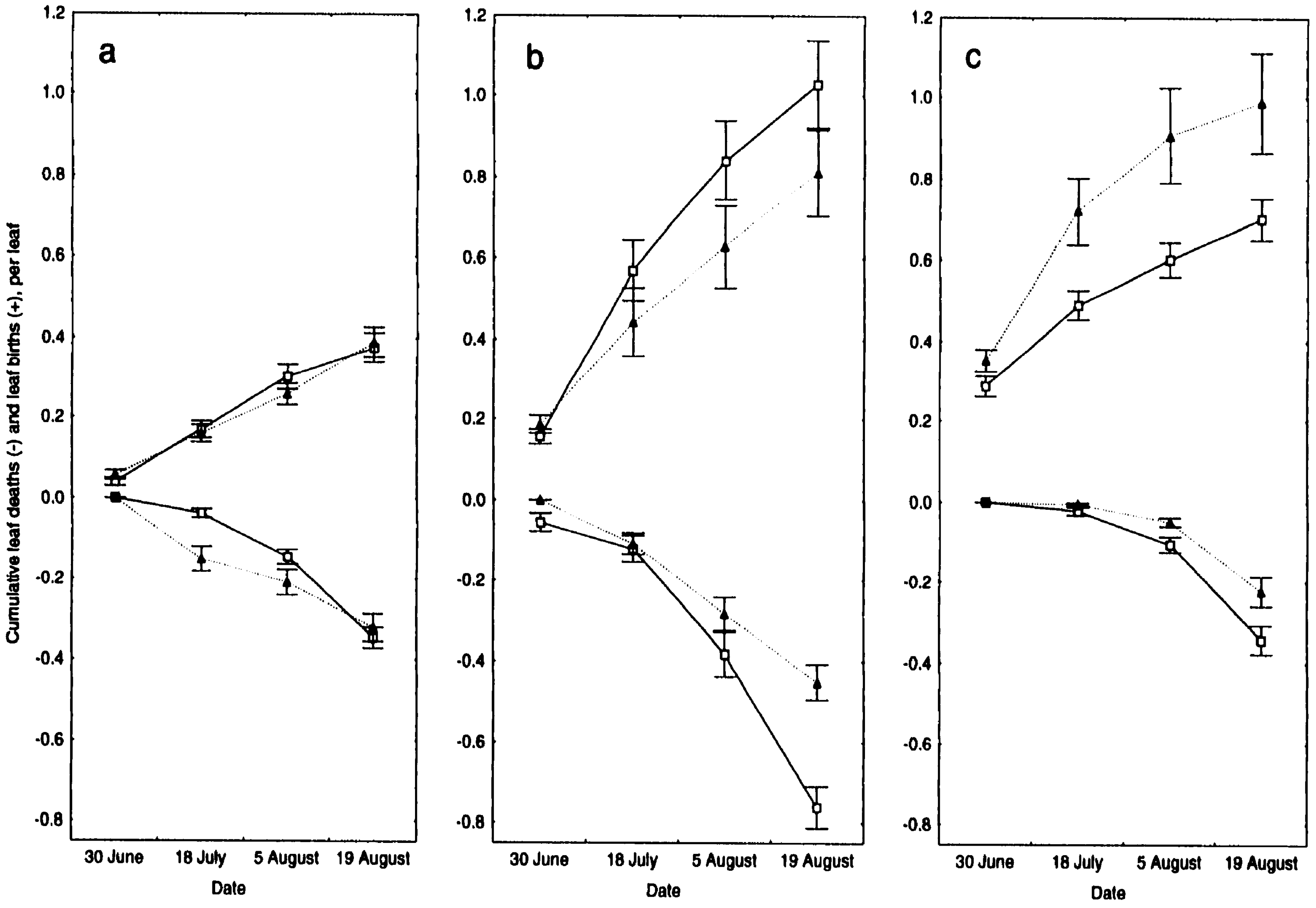
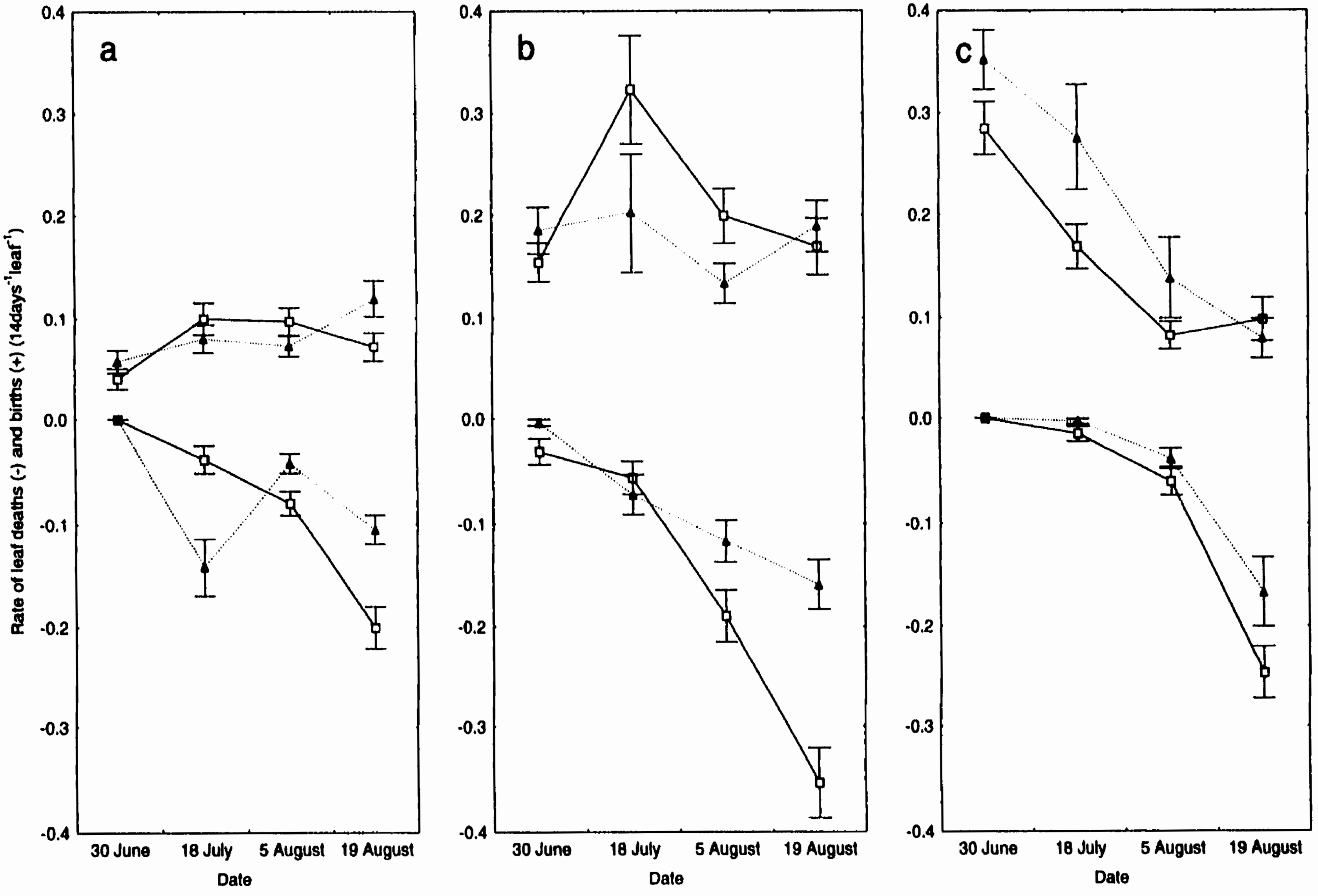

a
b
c
Cumulative leaf deaths (-) and leaf births (+), per leaf
1.2
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
30 June
18 July
5 August
19 August
Date

Figure 3-7. Effect of grazing history (historically grazed [▲], historically ungrazed [□]) on rate of leaf births and leaf deaths for all species, by date (mean±S.E.). (a) *Kobresia*, (b) *Erigeron*, and (c) *Oxytropis*.


a
b
c
Rate of leaf deaths (-) and births (+) (14days^{-1}leaf^{-1})
0.4
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
-0.4
30 June
18 July
5 August
19 August
Date

shows significantly fewer leaf deaths later in the season (Fig. 3-7a-c). Generally, the rate of leaf deaths increases monotonically for all species, except for adjacent *Kobresia* which had four plants with 100% leaf mortality in mid-season.

Discussion

Plant tolerance to herbivory, rather than other adaptations to herbivory that reduce consumption of plants, such as secondary defense chemicals, is a key means by which herbivores and plant communities may coexist and species can persist (Caldwell and Richards, 1986; Rosenthal and Kotanen, 1994; Strauss and Agrawal, 1999), particularly in low productivity ecosystems. Previous studies have demonstrated several physiological mechanisms for plant response to grazing: increased photosynthetic capacity via increased stomatal or mesophyll conductances (Painter and Detling, 1981; Nowak and Caldwell, 1984), reallocation of stored reserves to new leaf tissue (Bokhari, 1977; Richards, 1986), increase in intrinsic growth rates (Coley, Bryant and Chapin , 1985), and several others (McNaughton, 1979; Rosenthal and Kotanen, 1994). Addressing how plants respond morphologically to grazing pressures, is less studied under natural conditions and is one important aspect of understanding how tolerance is achieved.

In this study, individuals of three common high alpine plant species show remarkable ability to tolerate naturally occurring, sustained grazing levels of over 58% of aboveground leaves during the growing season—levels that have been considered heavy grazing across many habitats (McNaughton, 1986a; Holechek, Pieper and Herbel, 1989). Since the plants we selected were located <2m from talus and our recorded grazing incidence was 50%, 69% and 82% of leaves on all tagged plants, it is highly likely that these plants are chronically grazed in most years. In addition, we have shown elsewhere that collared pikas graze preferentially within a small band around talus and the intensity of grazing increases throughout the growing season

(Ch. 2). In contrast to many other herbivores that defecate and urinate directly on grazed vegetation, pikas use latrines within the talus, eliminating an important mechanism for the so called beneficial aspects of grazing (Bazely and Jefferies, 1985; Ruess and McNaughton, 1987; Hik and Jefferies, 1990; Day and Detling, 1990; Jaramillo and Detling, 1992; McNaughton, Banyikwa and McNaughton, 1997). This pattern of chronic grazing with little nutrient input has few analogues and is predicted to cause severe aboveground reductions (Archer and Tieszen, 1980; Ouellet, Boutin and Heard, 1994).

Previous studies on the effects of grazing on long lived perennials have observed a wide range of morphological changes in plant growth parameters. These have included an increase in production of axillary shoots in *Puccinellia phyganodes* in response to grazing and increased growth in old shoots in *Carex subspathacea* (Bazely and Jefferies, 1989; Kotanen and Jefferies, 1989). Other studies have demonstrated substantial ability for plants to compensate for leaf damage by rapid regrowth of lost tissue, but these are often associated with rapid recycling of nutrients due to *in situ* feces or urine deposition by the herbivore (Day and Detling, 1990; Steinauer and Collins, 1995; Frank and Evans, 1997; Tracy and Frank, 1998). In addition, it has been documented that plants which are lightly or moderately grazed can tolerate herbivore damage, but high levels of grazing tend to cause a decline in plant growth (Dyer, Turner and Seastedt, 1993; Turner, Seastedt and Dyer, 1993). What is considered light, moderate or heavy, clearly depends on the system involved. In our study, the natural levels of grazing during the growing season ranged from 58% to 61% of all leaves—levels from different herbivores that were considered high in studies in central Alaska (Molvar, Bowyer and Van Ballenberghe, 1993). These levels are not as high as some simulation studies in which plants have demonstrated remarkable abilities to regrow after near 100% removal of aboveground tissue (Archer and Tieszen, 1980), however, the same study shows that during chronic, repeated experimental clipping, all clipped plants underperform all control plants. Subjected to muskoxen grazing, *Oxytropis* plants show dramatic decreases in size, and were not regrazed for several years after the initial grazing events, allowing for substantial regrowth (Mulder and Harmsen, 1995). It has been reported that following grazing events, newly produced tissues have higher nutrient levels (Ouellet, Boutin and Heard, 1994), potentially promoting regrazing among animals that remain in the vicinity (i.e., are not migratory; Jefferies, Klein, and Shaver, 1994), and likely reducing the ability for plants to tolerate further damage, especially in habitats with low productivity. In our study, naturally occurring pika grazing affects not only a large proportion of plants, but also is repeated on the same plants throughout the growing season and likely into the next season. Few communities likely persist with such chronic levels of grazing, without nutrient inputs to maintain the production (Bazely and Jefferies, 1997).

The factors that allow these communities to persist can be understood by looking at morphological growth parameters. Across all plots and irrespective of grazing, both dicotyledons showed more cumulative leaf births than the monocotyledon, demonstrating strategies for potentially coping with grazing (Fig. 3-3). While the monocotyledon with its basal meristem can regrow older, grazed leaves, the dicotyledons must replace grazed leaves with new ones. With elevated leaf production rates compared to *Kobresia*, *Erigeron* and *Oxytropis* can potentially respond rapidly to grazing by means of new leaf production. Alternatively, we may have underestimated leaf births in *Kobresia* since sampling did not start immediately after snow melt in all sites due to heterogeneity of snow melt pattern. While there may have been early season (pre-30 June) leaf births in *Kobresia* that we did not measure, this is unlikely due to the haphazard pattern of plot location among the species. *Erigeron* had the greatest cumulative leaf deaths, suggesting that leaf longevity and leaf turnover rates among *Erigeron* plants are the shortest and fastest. *Kobresia* and *Oxytropis* had much fewer leaf deaths by the last census period, suggesting long leaf longevity, particularly for *Oxytropis*, which had high levels of leaf births.

Since all measures were standardized on a per leaf basis on each date, any effect of plant size and leaf number on growth has been minimized and thus our results are significant in spite of the leaf losses due to grazing. One consequence of this analysis, however, is that later season cumulative leaf births and deaths are not exactly equivalent to total leaves produced per leaf on starting plants. Rather, the values are more based on instantaneous plant size and are therefore not affected by plants that were at different stages during the first census period.

Current year grazing

None of the three species showed any significant decline or increase in cumulative or rate of leaf births or leaf deaths due to current season grazing. This suggests that these three diverse plant species with three very different growth forms do not respond to grazing by immediate alteration of new leaf production or leaf senescence. Neither *Kobresia* nor *Erigeron* showed a monotonically decreasing pattern in rate of leaf births throughout the duration of the growing season, demonstrating a potentially beneficial strategy for rapid response to grazing damage. With continued leaf births throughout the season, the damaging effects of leaf loss due to grazing may be mitigated because of already high leaf production. *Oxytropis* showed a significant decline in leaf births throughout the summer, conforming to a more common pattern of within-season new leaf production.

This study may underestimate the effects of current season clipping because the current grazing in far plots is relatively weak compared to the high intensity in the adjacent plots. To confirm whether this underestimate was important, we contrasted the effects of current year grazing within adjacent plots only, to examine the effect of current season high intensity grazing. We found that the only significant effect of within-season grazing was a slight delay in late season senescence in grazed *Erigeron* (19 August: 0.23 $\text{leaf}^{-1}\,14\text{days}^{-1}$ vs. 0.14 $\text{leaf}^{-1}\,14\text{days}^{-1}$, ungrazed vs. grazed; $0.05>P>0.01$).

The length of a single randomly chosen leaf differed significantly due to current year grazing among *Kobresia* and marginally among *Erigeron* plants. Currently grazed *Kobresia* had shorter leaves than ungrazed, and census date demonstrated that these plants were shorter only after 18 July. This suggested that the effect of grazing, which accumulates over the season, caused plants to be shorter, likely due to simple removal of taller leaf tissue. In contrast, we detected ($P=0.07$) currently grazed *Erigeron* plants to be marginally taller than ungrazed plants earlier in the season (18 July), but this difference disappeared as the season progressed. *Oxytropis* showed no change in leaf length due to grazing. These three different patterns likely reflect grazing from a terrestrial mammal and the three growth forms of the plants: the erect monocotyledon is grazed from above, reducing the length of an average leaf, and regrowth of old leaves is an important strategy. The increase in leaf length on 18 July among grazed *Erigeron* may be caused by a stimulating effect of early season (pre-18 July) grazing, cueing a rapid response of remaining leaves to compensate for the lost tissue. This response disappeared with continued grazing, though the early addition of photosynthetic tissue may have slightly increased carbohydrate fixation early in the season.

Grazing history

The location of plants adjacent to talus as compared to far from talus was far more important a factor determining leaf births and deaths than current year herbivory. In this study, we have assumed that plants adjacent to talus have a history of grazing due to the high levels of persistent and heavy grazing detected within a 2 m band of the talus Ch. 2). Earlier studies have shown and predict that long-term ecological factors create pressures that select for ecotypes or create long-term physiological patterns within plants that would override shorter term processes

(Clausen, Keck and Hiesey, 1948; McNaughton, 1979, 1983). Most studies concerning the effect of grazing history on plants have been on cultivated species (e.g., Kemp, 1937; Aarssen and Turkington, 1985) or using livestock (Peterson, 1962; Carman and Briske, 1985; Milchunas *et al.*, 1995; Varnamkhasti *et al.*, 1995). In natural systems, especially when grazing is heavy and the timing predictable (Crawley, 1987), long-term effects of herbivores may be very important. The difficulty in many systems is knowing the grazing history and thus the long-term impacts on the vegetation. In this study, we have directly contrasted the two usually confounding or unknown factors of current year grazing with past grazing history among *in situ* plants and with the naturally occurring grazer: the past history better determines leaf level morphological phenomena.

Plants adjacent to talus showed interesting patterns with respect to leaf length. *Kobresia* which grows vertically and was most affected by current season grazing, showed an early season (30 June) peak in leaf length and was taller than far plants, but was thereafter significantly shorter. It would be beneficial to maximize photosynthetic effort earlier in the season for *Kobresia* to avoid the later season grazing, but whether it is a strategy to maximize photosynthetic intake or a passive response to indirect alterations of other factors, such as decreased leaf litter, is not clear from this study. Historically grazed *Erigeron* demonstrated slightly smaller leaf lengths particularly later in the season, but this pattern is only marginally significant (P=0.06). Responses of adjacent *Oxytropis* were undetectably different from far *Oxytropis*. Since these two species must replace grazing induced tissue loss with new leaves—rather than by elongation of grazed leaves—it is interesting that the effect of grazing history was so dampened on leaf length compared to *Kobresia*. Physiologically, the dicotyledons may also be more constrained in terms of leaf length potential, preventing them from exploiting larger leaves as a strategy in ungrazed areas.

Cumulative leaf births were largely unaffected by grazing history among *Kobresia*. The removal of four outliers which had 100% leaf mortality on 18 July from the analysis, made cumulative and rate of leaf deaths also unaffected by grazing history. As a composite of leaf production and death throughout the season, the cumulative levels for *Kobresia* described here showed no enhancement or decline with grazing history. The significant late season (19 August) increase in rates of leaf births, however, suggests that *Kobresia* showed some positive response to grazing history to potentially offset some of the loss of photosynthetic tissue due to reduced leaf length.

Erigeron shows a different response to grazing history in terms of leaf births and deaths. While adjacent plants showed a significant decline in leaf births, both in terms of cumulative and rates of leaf births, they also demonstrated fewer leaf deaths and generally delayed leaf senescence during the period of censusing in this study. The lower levels of leaf births are primarily due to a large peak of leaf production in far *Erigeron* on 18 July, but the rates of leaf deaths in adjacent plots remained very low from 5 August onward. Thus, plants with a grazed history had minor reductions in leaf length and leaf births, but a highly significant reduction in leaf senescence, differing in response from *Kobresia*. Since all *Erigeron* plants had very high leaf births and deaths, the most likely response to grazing would be through alterations in leaf births and deaths, rather than leaf length. Regardless, like *Kobresia*, these plants showed morphological shifts that potentially offset the photosynthetic tissue loss due to grazing.

Oxytropis was the most unaffected overall by grazing history, though adjacent plants showed a positive response to both cumulative leaf births and delayed leaf senescence ($P=0.07$). Since these differences were due to very slight changes throughout the season, we did not detect them when analyzing leaf births and deaths as rates. *Oxytropis* was the only species of the three to show a monotonically declining level of leaf births throughout the season. This strategy of focussing leaf production early in the season would likely be highly beneficial given that the intensity of herbivory increases as the season progresses (Ch. 2). Thus, the overall lack of response to grazing history—in terms of leaf length, leaf births and leaf deaths—may be partially due to temporal avoidance of the heaviest herbivory. Because this species concentrates its leaf production early in these season, it may avoid energetically expensive new tissue loss late in the season. It is possible that *Oxytropis* is highly tolerant to late season pika grazing because of its early season flush of leaves. As a strategy to tolerate grazing, these plants may have more closely completed their entire season's photosynthetic needs than *Kobresia* or *Erigeron*, reducing the potentially detrimental effects of late season grazing. Adjacent *Oxytropis*, likely enhance their ability to persist by increasing leaf births and by decreasing leaf deaths throughout the season.

The delayed leaf senescence we observed among historically grazed plants may be a result of responses to extrinsic factors, such as release from shading, or shifts of intrinsic physiology as a response to past grazing pressures. In previous years, delaying leaf senescence would be advantageous to total plant photosynthesis, since maintaining older leaves requires very little energy reserves, and it is a strategy to compensate for lost photosynthetic tissue to herbivory. Thus, whether there has been selection due to grazing pressure, or *Erigeron* and *Oxytropis* are plastic for this trait, delaying leaf senescence likely reduces the detrimental effects of herbivory.

Species differences

Overall, *Erigeron* and *Oxytropis* plants had the highest number of leaf births during censusing period of the growing season, with cumulative values of 0.92 and 0.84 new leaves, respectively, for each leaf present on the plant. For these species to be tolerant to grazing, they must be readily capable of initiating new leaf growth, since that is it their only means of reestablishing pregrazing levels of photosynthesis. *Erigeron* in all sites had elevated levels of rate of leaf production which do not vary throughout the season. *Oxytropis*, rather than continue leaf births, focussed leaf production early in the season, and consequently showed very little leaf level response to grazing history or current year grazing. While *Erigeron* shows a slight decline in adjacent plots, *Oxytropis* increases its leaf births to higher levels. *Kobresia* plants, regardless of where they are growing and the presence of current year grazing, did not respond to grazing, except for a slight increase in late season births in adjacent plots. Monocotyledons with basal leaf meristems can respond to grazing by regrowing preexisting leaf tissue. Neither *Erigeron* nor *Oxytropis* responded to grazing by producing new leaves late in the season, a commonly observed compensatory response to leaf tissue loss (e.g., Crawley, 1983; Bazely and Jefferies, 1989; Kotanen and Jefferies, 1989; Whitham *et. al.*, 1991). The increase in late season production in *Kobresia* is only slight. Pika grazing intensifies later in the season (Ch. 2), so late season production of new, energetically expensive tissue would be potentially detrimental to the plants. Instead, increased production early in the season appears a better strategy in *Oxytropis* and alternate strategies are used in *Kobresia* and *Erigeron*.

Leaf death patterns of each species complemented the leaf birth responses to grazing history. *Oxytropis*, which showed a slight increase in leaf births, showed only a slight decrease in late season leaf senescence, whereas *Erigeron* showed a slight reduction in leaf births but a large (2.5 fold) and highly significant reduction in rate of leaf senescence on 19 August, suggesting that there are tradeoffs to each strategy of herbivore tolerance. Leaf senescence among *Kobresia*, though demonstrating variability between grazing histories, was not significantly affected. Previous studies have shown delayed senescence of leaf tissue in response to grazing (McNaughton, 1979; Meyer, 1998), but here we observed it strongly in a basal rosette composite, weakly in a legume and not a basal meristem sedge. *Oxytropis* leaves, across all plots, were maintained longer than the other species since there were large numbers of leaf births early in the season and a sharp decrease throughout the season; leaf deaths did not begin until later in the season. The shorter leaf lifespan in *Erigeron* may allow a more plastic response to leaf lifespan; senescence of the longer lived *Oxytropis* leaves cannot be delayed further, possibly due to growing season limitations. It is impossible in this study to determine whether these effects of grazing history are genetically based, but the differences between long-term grazing and short-term grazing is non-trivial. While these plants are physiologically capable of delaying senescence allowing for an extension of photosynthesis during the growing season, these delays only occur due to the longer term pressures of pika herbivory, regardless of the current season's grazing status.

Leaf length was strongiy affected by grazing among *Kobresia* and weakly among *Erigeron* and not at all among *Oxytropis*. While current year grazing caused a reduction in leaf height (*Kobresia*), grazing history caused a temporal shift which would lessen the detrimental effects of photosynthetic tissue loss (*Kobresia*). Since the generally observed grazing pattern of collared pikas shows that the intensity of grazing increases throughout the summer (Ch. 2; D. Hik, unpub. data), two possible explanations arise. First, it may be advantageous for the plants to focus photosynthetic activity earlier in the season to avoid peak grazing periods. The high predictability of pika grazing and relatively strong selective pressure placed on plants adjacent to talus to limit the damage due to grazing may create conditions suitable for this trend. The dangers of rapid early season growth, however, such as risk of late killing frost or depletion of stored reserves too early, would make it an unprofitable strategy for plants which have a low probability of being grazed. Alternatively, the removal of tissue in the previous season may result in reduced aboveground dead biomass which could limit photosynthesis of early, short leaves by shading (Monsi, Uchijima and Oikawa, 1973; McNaughton, 1979; Jefferies, Klein, Shaver, 1994). Current season grazing appeared to slightly increase leaf length in *Erigeron*, but this increase was not a long-term response, since historically grazed plants showed a slight overall reduction in leaf length. One possible explanation for the difference between the responses of the three species lies in their different leaf anatomies. Since individual grazed leaves of *Erigeron* and *Oxytropis* senesce almost immediately after being grazed and grazed *Kobresia* leaves continue to grow at a shorter length, grazing would more likely tend to decrease the length of standing leaves among *Kobresia*. *Erigeron* and *Oxytropis* likely have more constraints in leaf length and overall leaf shape than does *Kobresia*.

Kobresia myosuroides, *Erigeron humilis* and *Oxytropis nigrescens* are each highly grazed species by pikas, yet all persist even in highly grazed areas adjacent to talus. This study has demonstrated that when grazing is highly predictable and chronic in successive years, the long-term history of grazing affects leaf level responses more than whether a plant was grazed in the current year. The three different strategies of grazing tolerance demonstrated by these three species reflect their anatomy and physiological capabilities, but are each likely to reduce long-term detrimental effects of severe grazing.

Chapter 4 : The influences of grazing history and climate on the response to short-term simulated pika grazing on two alpine perennials.

Abstract

Using a common garden, we tested the influences of and interactions between history of grazing and climate history on responses of *Kobresia myosuroides* and *Erigeron humilis* to two levels of artificial clipping over 2 seasons. Grazing history was determined by the proximity of vegetation to talus piles inhabited by pikas, and our grazing treatments were selected to simulate pika herbivory. Light clipping treatment—removal of 1/3 of aboveground leaves at the end of July, 1997 and 1998—and heavy clipping treatment—removal of 1/3 of aboveground leaves on two occasions, end of July and mid August, 1997 and 1998—were performed late in the growing season to reflect the increasing intensity of pika foraging later in the season. Climate and site history of the plants was based on site of origin from one of three sites located along a 100km gradient characterized primarily by winter snowfall differences. Climate and site history influenced the starting values of transplanted individuals, but showed no effect on plant response to grazing treatments. Both levels of clipping caused increases in *Erigeron* overwinter survival compared to unclipped controls during 1997-8 and 1998-9, but had no effect on *Kobresia* overwinter survival. Grazing history interacted significantly with clipping treatment for three of four measured traits for *Kobresia*, but not for *Erigeron*. Historically grazed plants showed no change in leaf length, culm number, and level of senescence under light or heavy clipping compared to controls. Historically ungrazed *Kobresia* under heavy clipping had significantly increased leaf lengths, culm number and reduced leaf senescence compared to controls and light clipping, demonstrating highly positive responses to two successive years of heavy leaf removal, at least in the short term. Our data demonstrate remarkable abilities of these alpine species,

which grow in areas that have fewer than 90 growing days, to tolerate even heavy levels of herbivory, without direct nutrient inputs. We emphasize that variability in response to herbivory between species is important as different species use alternative strategies to tolerate grazing. Many studies ignore grazing history when examining response to grazing. We demonstrate that this may be very important to understanding response to current herbivory.

Introduction

Many experiments have attempted to examine the effects of herbivory on individual plants (Lee and Bazzaz, 1980; Bishop and Davy, 1984; Hartnett and Bazzaz, 1984; Crawley, 1997 and references therein) but the majority of these studies do not explicitly address the interaction between plant responses to short-term herbivory and ecotypic variation resulting from long-term processes (e.g., Paige and Whitham, 1987; Hik, Sadul and Jefferies, 1991; Bergelson and Crawley, 1992a; Turner, Seastedt and Dyer, 1993; Bergelson, Juenger and Crawley, 1996; Fox *et al.*, 1998). The body of literature on ecotypic variation is large and the effects on growth can be highly significant (Clausen, Keck and Hiesey, 1948; Gray and Scott, 1980), but addressing the influence of genetic background on response to grazing has been widely overlooked (Varnamkhasti *et al.*, 1995). Studies that do examine differential plant responses based on sites of origin often test for differences associated with different habitats (e.g., Open vs. Grass vs. Pine; Maschinski and Whitham, 1989). It is possible that within similar habitat types, however, plants are subjected to selective forces (Marquis, 1992) that may result in different responses to short-term experimental grazing depending on the ecotype (Detling, Painter and Coppock, 1986; Strauss, 1990; Dyer *et al.*, 1991; Painter, Detling and Steinberger, 1993; Milchunas *et al.*, 1995; Varnamkhasti *et al.*, 1995; Hobbs, 1996; Post and Klein, 1996; Järemo *et al.*, 1999).

Westoby (1989) distinguished between the short-term, ecological effects of grazing and the longer term, evolutionary effects of grazing and noted the larger magnitude of the longer term effects of grazing as compared to the former for the Lesser Snow Goose in a salt marsh habitat in Northern Canada. He warned, however, that in spite of the important distinction, the comparisons between these two temporal scales using Lesser Snow Geese data were gathered under different experimental conditions and designs and so should be cautiously interpreted. To date, there is little consensus of the interaction between the effects of long-term and short-term grazing on the performance of perennial herbs.

Climatic gradients have been shown to alter plant growth and performance, often creating distinct genetic ecotypes (Clausen, Keck and Hiesey, 1948; Galen, Shore and Deyoe, 1991; Oleksyn *et al.*, 1998). While the interaction between climate induced changes in plant growth and the influence of herbivores has been alluded to (Jonasson *et al.*, 1986; Galen, 1990; Galen, Shore and Deyoe, 1991), particularly among studies on insect herbivory (Ayres, 1993), little experimental work has attempted to understand this interaction due to mammalian herbivory. Evidence for a complex interaction between climate and herbivores does exist, however, though with few clear generalizations. For instance, Suzuki (1998) found that the low temperature and short growing season associated with a high altitude site was responsible for less herbivore damage than the lower site, in spite of a higher leaf quality. In terms of herbivory tolerance, Galen, Shore and Deyoe (1991) used transplants and found that plants originating from higher elevations with shorter growing seasons had lower resistance to aphids. While climate clearly has strong effects on plant performance in general, the influences of climatic history and grazing history on short-term plant response to clipping—the interaction between short and long-term responses—are poorly understood and are likely limited by the relative lack of transplant experiments.

Common garden experiments are often used to differentiate environmental effects on plant performance from genetic effects by subjecting plants to a single environment (Stowe, Sork and Farrell, 1994; Byers and Quinn, 1998) and their usefulness in examining genotype effects has been strongly emphasized (Marino, Cornell, and Kahn, 1993; Stowe, Sork and Farrell, 1994; Sibly, 1996). The range of characteristics tested in common garden experiments has been great, from variations in plant architecture (Skalova *et al.*, 1997) to water use efficiency (Anderson *et al.*, 1996) to altitudinal and latitudinal effects (Reich, Oleksyn and Tjoelker, 1996; Oleksyn *et al.*, 1998). Many of these studies indeed indicate local differentiation whereby plants grown in common gardens show ecotypic affinities to their site of origin by possessing genetically based characteristics which would seem to improve performance in their original location (e.g., date of bud set, Karhu *et al.*, 1996; high N-concentrations in cold derived plants, Oleksyn *et al.*, 1998). Collecting plants of known climatic and grazing origin and transplanting them into the common environment in a garden would allow direct examination of these influences on current year's growth and response to recent clipping.

Like other long-term ecological processes, grazing history—the consistent interannual presence or absence of herbivores in the area the plant originated from—would be expected to affect plant growth in the short-term. One possible reason for the lack of studies addressing the effect of grazing history on plant response to grazing is the difficulty in accurately determining the long-term grazing history of natural plant populations (but see livestock systems, e.g., Pearson, Sparrow and Lange, 1990; Miller and Halpern, 1998; Smith, 1998). The grazing patterns of collared pikas (*Ochotona collaris*), however, are relatively predictable. Pikas are small vertebrates (Order: Lagomorpha) that are restricted to talus piles at high elevations and latitudes in North America. They restrict their grazing to areas close to talus (<8m), largely due to predation risk further outwards from talus, and generally graze very intensively on areas closer to talus (*O. princeps*; Huntly, 1987; Dearing, 1996; *O. collaris*, Ch. 2 and 3). Due to the very slow meadow establishment in northern areas, areas far from talus piles remain distant from talus for many years (Price, 1971). The high levels of grazing observed close to talus by pikas (Ch. 2), create a very strong and long lasting selection gradient outwards from talus piles.

In the Yukon Territory, Canada, pikas inhabit areas of diverse growing season length, ranging from <6-8 weeks to 10-12 weeks. In many areas they are the dominant and most influential grazer of meadows near talus piles (Ch. 2). Finally, pika population size also shows limited interannual fluctuation (65 – 100 individuals per year in Ruby Range site; Hik unpub. data), enabling us to confidently determine the grazing history of plants in these areas (Southwick *et al.*, 1986; Hafner and Sullivan, 1995; Hik, 2000).

In this study, we used an *in situ* common garden design to examine the influence of grazing history and climatic history on the response of two common alpine perennials (*Kobresia myosuroides* [Cyperaceae] and *Erigeron humilis* [Asteraceae]) to simulated pika grazing. We contrasted the effects of climate with past grazing history by selecting plants from three distant sites differing in winter snowfall and growing season length and from highly grazed and ungrazed areas in each site. We hypothesize that the plants adapted to grazing will show more tolerance to clipping treatments (e.g., show little reduction in leaf production) than will plants with almost no history of grazing due to genetically based differences in grazing tolerance. In addition, plants originating from the site with a shorter growing season will be less likely to tolerate the heaviest clipping treatment due to the shorter time period of resource acquisition. Using a common garden, we were able to subject all plants to near identical environmental conditions and vary only the intensity of experimental clipping.

Methods

Study sites

Our three sites were selected to compare the effects of pikas under strikingly different environmental conditions. Sites were situated along a 100km NE-SW transect with the intermediate site occurring approximately midway between the two extremes. All sites were of similar altitude (1700-2300 m asl.) and were typical pika habitats with adequate areas of rock talus for location of a haypile and adequate areas of intact alpine vegetation, but differed in many important physical and climatic respects. The Icefields site (IF: 60°36'N 139°25'W) consists of isolated meadows, which are separated by large areas of ice and rock, that receive extreme amounts of winter snowfall (>8 m per year; Marcus and Ragle, 1970) creating a very compressed growing season (Hik, 2000). The Ruby Range site (RR: 61°13'N, 138°16'W) is described in detail elsewhere (Ch. 2), and is characterized by large continuous alpine meadows with patches of talus inhabited by pikas and very little winter precipitation (<0.6 m per year). The Front Range site (FR: 60°57'N, 138°32'W) is physically and climatically intermediate between the two with large portions of talus and fewer and smaller areas of alpine meadow (see Ch. 1). There is a high probability of mid-summer snowfall at IF and FR sites and a lower probability in the RR.

Common garden

Between 10 July and 17 July 1997, we collected and transplanted 216 individual plants of each of two common arctic and alpine plant species (*Kobresia myosuroides* (Vill.) Fiori & Paol. and *Erigeron humilis* Graham; Cody, 1996) into a local area common garden (situated in the RR site). *Kobresia* is a common densely caespitose, dry area sedge. As with most other graminoids, this species has a basal meristem, allowing immediate leaf growth by means of extant leaf elongation after herbivore harvesting. Being caespitose, a commonly observed graminoid response to grazing of initiation of axillary meristems (Bazely and Jefferies, 1989) would not necessarily confer the presumed anti-herbivore growth form of more prostrate growth, and so may not occur. *Erigeron*, a common composite, has a very different growth form with a basal rosette of leaves and erect single stalked flower. Upon collection, all plants were removed from their native ground and replanted in the garden as quickly as possible to reduce effects associated with transportation and transplanting. Before planting, a uniform patch of ground was selected in the Ruby Range site and was cleared of all native vegetation and roots to prevent any confounding effects of plant competition. Plants were planted in a randomized block design in the garden with a minimum distance between plants of 10 cm to eliminate any possibility of competition. All plants were in the ground by 18 July 1997. The dates of collection and planting represented the middle of the growing season when plants had very few senescent leaves. After planting, we allowed the plants 10-14 days to establish in garden before collecting the baseline data.

We collected equal numbers of plants (72) originating from each of the three physically separate and climatically different sites, the Icefields, the Front Ranges and the Ruby Ranges. Within each site, half of the plants were collected from locations that were either historically grazed (36; <2m from occupied talus) or historically ungrazed (36; >8m from occupied talus) in order to test for any ecotypic plant adaptations to pikas. Both of these species are readily grazed by pikas under natural conditions (Ch. 3). We determined areas to be historically grazed if they were near to talus and that talus contained extant pikas as well as signs (latrines) of a history of pika occupation. An area was selected to be historically ungrazed if it was at least 8m from a talus pile where there were extant pikas or from areas where there were no signs of pika occupation for some time (based on latrine occurrences). Up to two samples were collected from a given genet to minimize adverse impacts of collection.

Experimental clipping treatments were selected to simulate collared pika haying which occurs most heavily towards the end of the season (MacDonald and Jones, 1987; Huntly, Smith and Ivins, 1986; Ch. 2; D. Hik, unpub. data). The 36 plants of each description (IF-Ungrazed, IF-Grazed, FR-Ungrazed, FR-Grazed, RR-Ungrazed, RR-Grazed) were randomly assigned either to a control group with no artificial clipping (NONE), to a low level of artificial clipping (LIGHT) or to high level of artificial clipping (HEAVY). Low clipping level consisted of removal of approximately 1/3 of aboveground live biomass (AGB) once per season (1 August 1997 and 24 July 1998), while high clipping intensity treatment consisted of removal of approximately 1/3 of AGB in each of two periods in each season (1 August and 11 August 1997 and 24 July and 12 August 1998), in order to simulate more intensive grazing.

Measurements were made on plants immediately before treatments in 1997 to establish baseline levels and on three census dates in 1998 and were harvested on 14 July 1999. For *Kobresia*, at each census date we measured number of culms, height of the three longest leaves, number of fruits or flowers, and percent of aboveground tissue which is senescent (and conversely green). For *Erigeron*, at each census date, we measured number of green leaves, length of three longest leaves, height of flowering stalk, and number of recently dead leaves (since last census). For both species, overwinter survival was calculated as the proportion of individuals alive at the last census in the previous year surviving to the first spring census.

All plants were randomly allocated to clipping treatments and an ANOVA was conducted on plant traits soon after planting to confirm the design was random. Data collected in 1998 for all measured traits were analyzed using a full 4-way repeated measures analysis of variance (Main effects: SITE, GRAZING HISTORY, TREATMENT, DATE; SAS INSTITUTE INC., 1998; Proc Mixed, Repeated). Overwinter survival data for both 1997-8 and 1998-9 and final harvested biomass were analyzed using a 3-way ANOVA (SITE, GRAZING HISTORY, TREATMENT; SAS INSTITUTE INC., 1998; Proc GLM). We also used a 3-way Maximum Likelihood Generalized Linear Model (Proc GENMOD) in which we specified binomial family and a logit transformation. We found this to be less conservative, so we report here the results from the ANOVA. In all analyses, we focused on the main effect of treatment and the interactions between treatment and other main effects to determine how site of origin and grazing history affected the ability of a plant to respond to grazing. The design of using adult transplants (vs. seeds) in a common garden is not ideal for testing the main effects of site of origin and grazing history on growth characters because these main effects were significant factors affecting plant traits at time of planting (Table 4-1). The large reserves of arctic and alpine plants (Archer and Tieszen, 1980) provide growth inertia derived from the growing conditions of the sites of origin. We use the experimental clipping as a challenge to which the plants must respond.

On 14 July 1999, we destructively harvested all remaining plants for biomass measurements. Belowground portions were washed to remove all soil particles, so there was potential for loss of fine roots. Samples were dried at 60°C to constant mass and aboveground and belowground parts were separated and weighed. *Kobresia* did not survive past the second winter with enough numbers to examine all effects (TREATMENT, GRAZING HISTORY, and SITE), so in all analyses of final biomass on *Kobresia*, we eliminated the main effect of SITE, as it was not a significant influence in the previous summer. We analyzed final total biomass (aboveground and belowground) and final aboveground live biomass using analysis of covariance (ANCOVA) with number of leaves (*Erigeron*) or number of culms (*Kobresia*) at planting as the covariate. We also examined the effects of the garden treatments on aboveground:belowground ratios using ANOVA. Because we did not have measures for each plant upon planting and consequently could not use ANCOVA, we collected other plants from each site during to examine the "natural" ratios. We collected at least 20 plants of each group (SITE, GRAZING HISTORY, SPECIES; 243 plants total) between 5 July and 8 July 1999, washed belowground parts as above, dried them at 60°C to constant mass and aboveground and belowground parts were separated and weighed. We used these biomass values to examine aboveground:belowground ratios of untreated plants. It was not meaningful to use these absolute

Table 4-1. Summary of 3-way ANOVA of post transplant values for *Kobresia* and *Erigeron*. Main effects are TRMT (no clipping, light clipping or heavy clipping), SITE (Icefields, Front Ranges or Ruby Ranges) or GrHi (grazing history of the site where the plants were taken from) and interactions. F-values are reported with numerator and denominator degrees of freedom. Significant effects based on TRMT and interactions are shown in bold.

Erigeron	Leaf length		Number of leaves		Number of dead leaves	
Source	F	P	F	P	F	P
TRMT	$1.85_{(2,198)}$	0.1605	$0.03_{(2,198)}$	0.9687	$0.04_{(2,198)}$	0.9575
TRMT X GrHi	$1.42_{(2,198)}$	0.2453	$0.93_{(2,198)}$	0.3964	$1.02_{(2,198)}$	0.3617
TRMT X SITE	$0.4_{(4,198)}$	0.8108	$0.58_{(4,198)}$	0.6807	$0.64_{(4,198)}$	0.6343
TRMT X SITE X GrHi	$0.32_{(4,198)}$	0.8674	$1.64_{(4,198)}$	0.1651	$0.78_{(4,198)}$	0.5417
GrHi	$14.14_{(1,198)}$	0.0002	$14.32_{(1,198)}$	0.0002	$0.04_{(1,198)}$	0.8506
SITE	$6.7_{(2,198)}$	0.0015	$6.88_{(2,198)}$	0.0013	$1.88_{(2,198)}$	0.1547
SITE X GrHi	$1.38_{(2,198)}$	0.2531	$6.3_{(2,198)}$	0.0022	$0.07_{(2,198)}$	0.9281

Kobresia	Leaf length		Number of culms		Number of flowers		% Senescent	
Source	F	P	F	P	F	P	F	P
TRMT	$0.55_{(2,198)}$	0.5782	$4.79_{(2,198)}$	**0.0093**	$3.8_{(2,198)}$	**0.0241**	$1.00_{(2,198)}$	0.3708
TRMT X GrHi	$0.11_{(2,198)}$	0.8938	$0.82_{(2,198)}$	0.4406	$2.32_{(2,198)}$	0.1010	$0.41_{(2,198)}$	0.6626
TRMT X SITE	$1.66_{(4,198)}$	0.16	$0.47_{(4,198)}$	0.7597	$0.77_{(4,198)}$	0.5487	$1.35_{(4,198)}$	0.2545
TRMT X SITE X GrHi	$0.64_{(4,198)}$	0.633	$0.17_{(4,198)}$	0.9553	$0.65_{(4,198)}$	0.6308	$1.13_{(4,198)}$	0.3419
GrHi	$9.01_{(1,198)}$	0.003	$6.01_{(1,198)}$	0.0151	$0.45_{(1,198)}$	0.5008	$11.89_{(1,198)}$	0.0007
SITE	$6.77_{(2,198)}$	0.0014	$4.91_{(2,198)}$	0.0083	$1.75_{(2,198)}$	0.1769	$25.43_{(2,198)}$	<.0001
SITE X GrHi	$24.94_{(2,198)}$	<.0001	$10.6_{(2,198)}$	<.0001	$4.64_{(2,198)}$	0.0107	$3.81_{(2,198)}$	0.0238

biomass values as an indicator of the original size of the plants in the garden because only partial segments of *Kobresia* were originally planted in the garden as entire caespitose clumps were too large and overall variability in plant size of both species is enormous. Baseline biomass data was analyzed by two separate 2-way ANOVAs and compared to final harvest biomass ratio data.

Results

Overwinter survival

Results from the ANOVA for overwinter survival data are shown for *Kobresia* and *Erigeron* (Table 4-2). Overwinter survival of *Kobresia* was lower than *Erigeron* in both years (1997-8: 49% vs. 71%; 1998-9: 45% vs. 96%). Overwinter survival of *Erigeron* plants in 1997-8 and 1998-9 showed a significant positive effect of artificial grazing (Fig. 4-1; Table 4-2). Historical grazing had a similar positive and highly significant effect on *Erigeron* survival, but only over 1997-8 (Table 4-2; Grazed=81%, Ungrazed=58%). This beneficial effect of grazing history disappeared over the second winter. *Kobresia* overwinter survival in both 1997-8 and 1998-9, however, showed no significant effect of experimental clipping and neither grazing history nor site of origin influenced the survival rate of treatments differentially. *Kobresia* survival did show a significant three-way interaction in 1998 (Table 4-2) driven primarily by very low survival of two groups (Grazed, light clipping from Front Ranges and Ungrazed, light clipping from the Icefields—both had 2 of 12 plants survive). It is likely that this result is overly influenced by these low survival groups and we do not consider this to be meaningful variation rather a consequence of random low survival levels.

Measured traits

The effect of simulated grazing on measured traits in 1998 are shown for *Erigeron* (Table 4-3). There was no measurable effect of either low intensity or high intensity clipping on leaf

Table 4-2. Summary of 3-way ANOVA for overwinter survival. Data are taken from 4 July 1998 and 14 July 1999. Main effects are as in Table 4-1. Significant effects are shown in bold.

	Erigeron **1997-8**		***Erigeron*** **1998-9**		***Kobresia*** **1997-8**		***Kobresia*** **1998-9**	
Source	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**
TRMT	$6.94_{(2,176)}$	**0.0013**	$2.88_{(2,129)}$	**0.0596**	$1.73_{(2,198)}$	0.1796	$0.44_{(2,40)}$	0.6450
TRMT X GrHi	$0.87_{(2,176)}$	0.4195	$0.18_{(2,129)}$	0.8376	$0.93_{(2,198)}$	0.3953	$1.53_{(2,40)}$	0.2294
TRMT X SITE	$1.26_{(4,176)}$	0.2877	$0.26_{(4,129)}$	0.9053	$0.02_{(4,198)}$	0.9993	$1.68_{(4,40)}$	0.1730
TRMT X SITE X GrHi	$0.99_{(4,176)}$	0.4121	$1.79_{(4,129)}$	0.1342	$3.22_{(4,198)}$	**0.0138**	$0.83_{(4,40)}$	0.5125
GrHi	$6.16_{(1,176)}$	**0.0140**	$0.41_{(1,129)}$	0.5247	$0.08_{(1,198)}$	0.7829	$0.33_{(1,40)}$	0.5702
SITE	$2.42_{(2,176)}$	0.0915	$0.65_{(2,129)}$	0.5217	$0.93_{(2,198)}$	0.3953	$5.94_{(2,40)}$	**0.0055**
SITE X GrHi	$0.20_{(2,176)}$	0.8192	$4.83_{(2,129)}$	**0.0095**	$1.85_{(2,198)}$	0.1606	$0.19_{(2,40)}$	0.8269

Figure 4-1. Proportion of *Kobresia* and *Erigeron* plants surviving over 1997-8 and 1998-9 winters in the common garden as a function of clipping treatment (control [□], low [⚄], high [▨]). Points within year and species group that share lower case letters are non-significantly different (Tukey adjusted LSD, $P<0.05$). n.s. indicates that treatment was not a significant factor affecting survival.

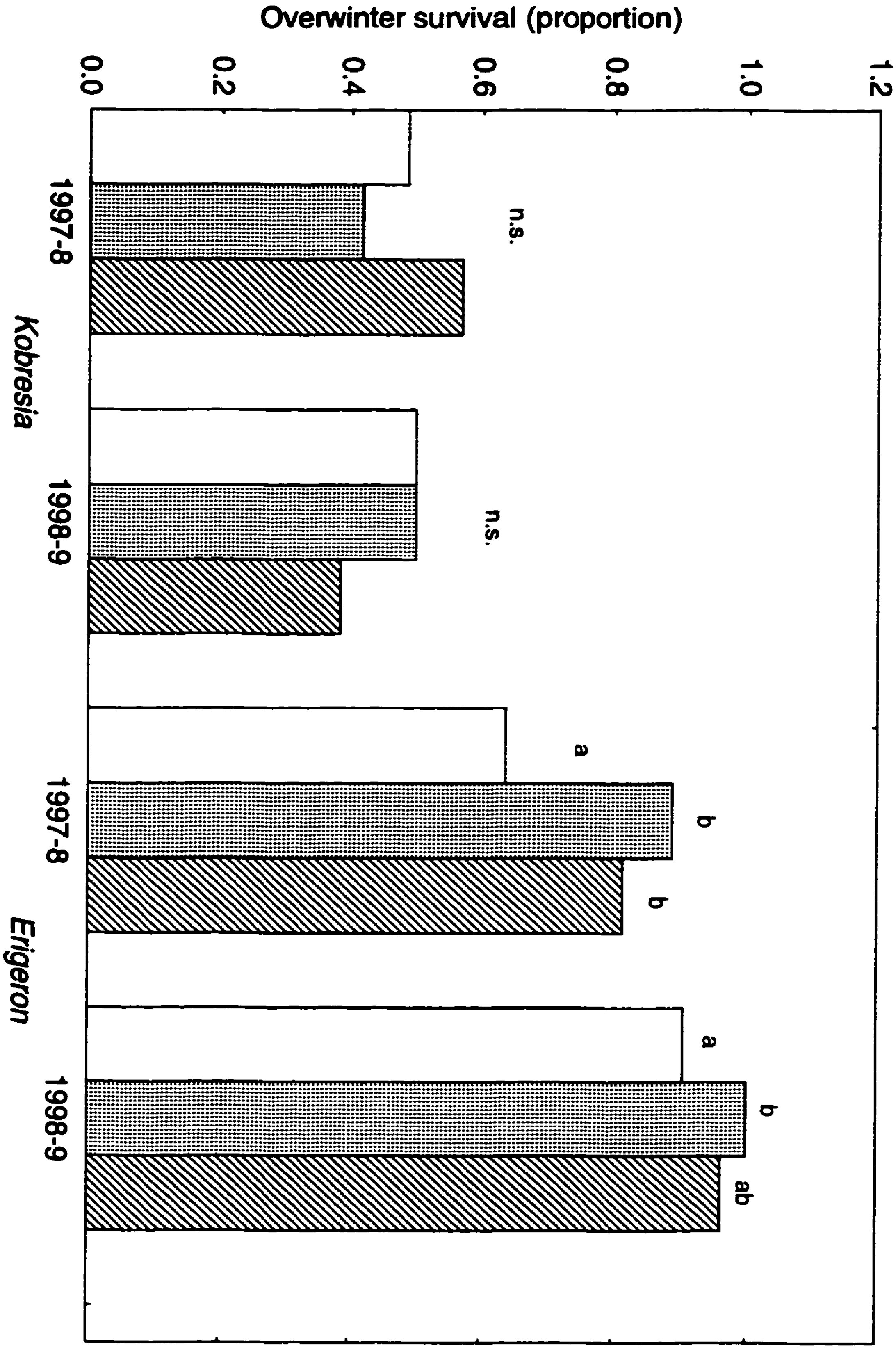

Overwinter survival (proportion)
0.0
0.2
0.4
0.6
0.8
1.0
1.2
n.s.
n.s.
a
b
b
a
b
ab
1997-8
1998-9
1997-8
1998-9
Kobresia
Erigeron

Table 4-3. Summary of 4-way RM-ANOVA for *Erigeron* character traits. Main effects are as in Table 4-1. Significant effects that include TRMT are shown in bold. Effects with TRMT are shown first for ease of viewing only.

Erigeron	Leaf length		# leaves		cumulative # dead		# dead leaves	
Effect	F	P	F	P	F	P	F	P
TRMT	0.71$_{(2,134)}$	0.4913	0.34$_{(2,135)}$	0.7113	0.36$_{(2,134)}$	0.7001	0.0$_{(2,136)}$	0.9975
TRMT X GrHl	0.76$_{(2,134)}$	0.4702	0.39$_{(2,135)}$	0.6766	0.17$_{(2,134)}$	0.8417	0.16$_{(2,136)}$	0.8495
TRMT X SITE	0.66$_{(4,134)}$	0.6240	0.34$_{(4,135)}$	0.8532	0.38$_{(4,134)}$	0.8212	0.33$_{(4,136)}$	0.8578
TRMT X DATE	2.02$_{(4,129)}$	0.0955	0.87$_{(4,132)}$	0.4812	0.62$_{(4,261)}$	0.6490	2.75$_{(4,265)}$	**0.0289**
TRMT X GrHl X DATE	0.02$_{(4,129)}$	0.9989	0.78$_{(4,132)}$	0.5412	0.07$_{(4,261)}$	0.9903	0.0$_{(4,265)}$	1.0000
TRMT X SITE X GrHl	1.47$_{(4,134)}$	0.2149	0.11$_{(4,135)}$	0.9774	0.57$_{(4,134)}$	0.6878	0.39$_{(4,136)}$	0.8132
TRMT X SITE X DATE	0.71$_{(8,134)}$	0.6819	1.26$_{(8,132)}$	0.2682	0.22$_{(8,261)}$	0.9879	0.31$_{(8,265)}$	0.9614
TRMT X SITE X GrHl X DATE	1.11$_{(8,129)}$	0.3583	1.11$_{(8,132)}$	0.3636	0.25$_{(8,261)}$	0.9802	0.31$_{(8,265)}$	0.9625
GrHl	0.2$_{(1,134)}$	0.6588	2.53$_{(1,135)}$	0.1141	2.31$_{(1,134)}$	0.1305	3.58$_{(1,136)}$	0.0605
SITE	5.46$_{(2,134)}$	0.0053	2.94$_{(2,135)}$	0.0564	0.45$_{(2,135)}$	0.6370	0.72$_{(2,136)}$	0.4865
SITE X GrHl	0.34$_{(2,134)}$	0.7140	10.42$_{(2,135)}$	<.0001	0.19$_{(2,134)}$	0.8245	1.35$_{(2,136)}$	0.2617
DATE	17.4$_{(2,129)}$	<.0001	104.59$_{(2,132)}$	<.0001	286.08$_{(2,261)}$	<.0001	123.9$_{(2,265)}$	<.0001
GrHl X DATE	2.05$_{(2,129)}$	0.1334	0.99$_{(2,132)}$	0.3728	4.05$_{(2,261)}$	0.0185	2.33$_{(2,265)}$	0.0993
SITE X DATE	1.42$_{(4,129)}$	0.2318	0.42$_{(4,132)}$	0.7973	1.21$_{(4,261)}$	0.3069	1.25$_{(4,265)}$	0.2896
SITE X GrHl X DATE	1.84$_{(4,129)}$	0.1248	1.02$_{(4,132)}$	0.3993	2.08$_{(4,261)}$	0.0839	2.87$_{(4,265)}$	0.0236

length, number of leaves, or cumulative number of dead leaves of *Erigeron* and neither site of origin nor grazing history of the plants affected their response to clipping. The TREATMENT X DATE interaction was significant for number of dead leaves (Fig. 4-2); end of season leaf senescence is slowed at both low and high clipping intensities compared to control plants.

Grazing history significantly altered the response of *Kobresia* to simulated grazing in 1998 (Table 4-4). In three of the four measured traits, the response pattern to clipping treatment of grazed plants was inverse to the response of ungrazed plants. For example, average leaf length of plants originating from grazed areas is highest at the low level of clipping, while plants originating from ungrazed areas have the longest average leaf length when subject to high clipping levels (Fig. 4-3a). This pattern is similar for culm number with a peak at low or no clipping for the grazed plants, and a peak at high clipping for ungrazed plants though this effect is only significant at P=0.07 (Fig. 4-3b). The level of aboveground senescence shows a similar but opposite pattern: plants of grazed origin have the lowest levels of senescence at low clipping intensities, while ungrazed plants show the least senescence at the highest levels of clipping (Fig. 4-3c). The apparent biphasic patterns for historically grazed plants are not statistically significant in multiple comparisons tests for any of the traits measured, thus there is no significant difference among historically grazed plants in response to treatments. The significant results that we obtained for the leaf length, culm number and senescence were driven primarily by the response of the historically ungrazed plants. In each case, the light clipping treatment caused a declining trend for all three traits, however, multiple comparisons tests showed that these were not significant. The heavy clipping treatment caused significant increases in leaf length, culm number and decreases in leaf senescence.

In spite of significant site differences (SITE main effect) in plant traits, neither species showed any influence of site of origin on response to clipping treatment for any trait (Table 4-2, 4-3 and 4-4). These traits differed among sites at time of transplanting (Table 4-1), so the

Figure 4-2. Effect on *Erigeron* of clipping treatment (control [▲], low [○], high [□]) on number of senesced leaves, by date (mean±S.E.). ANOVA results for TREATMENT X DATE effect is shown.

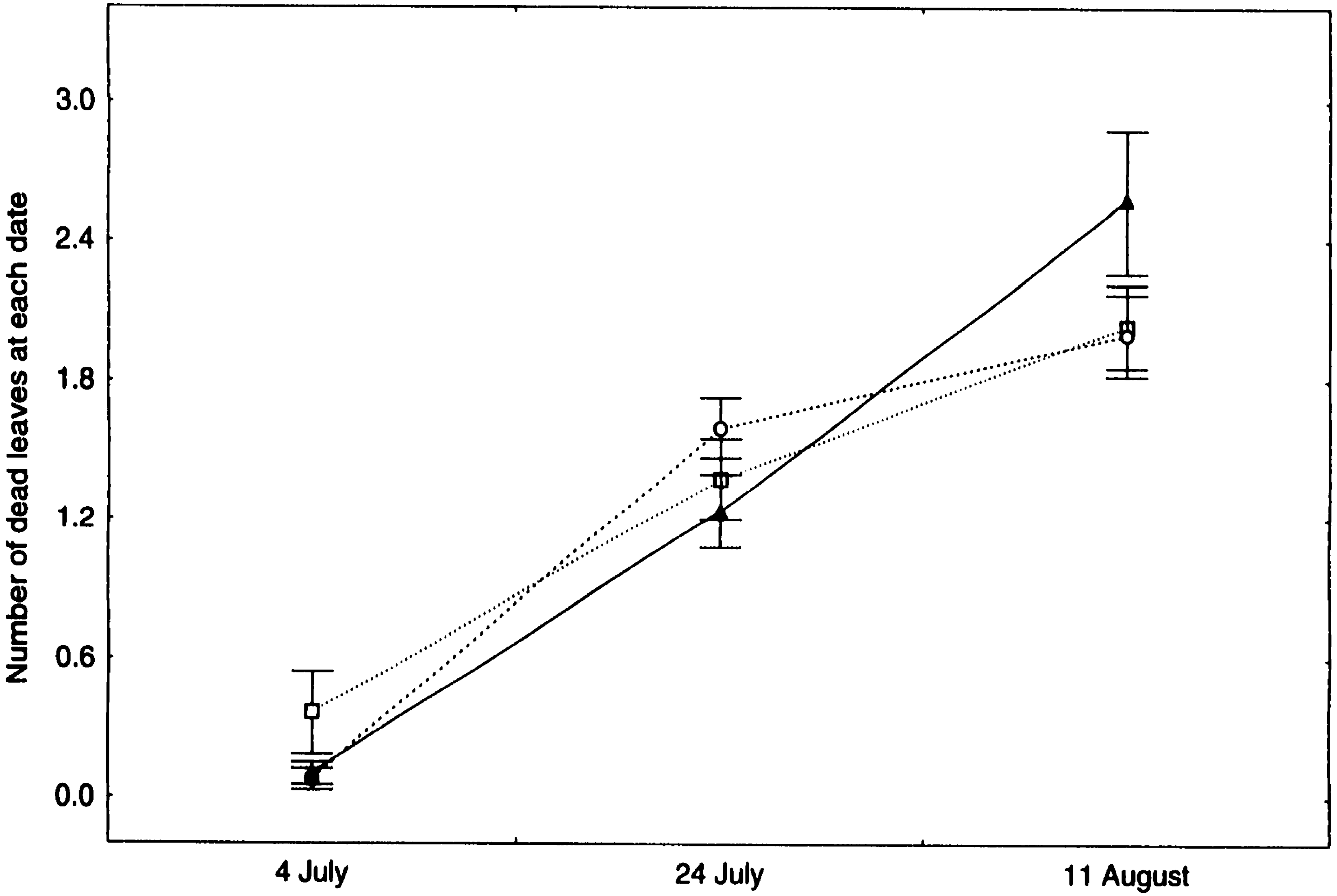
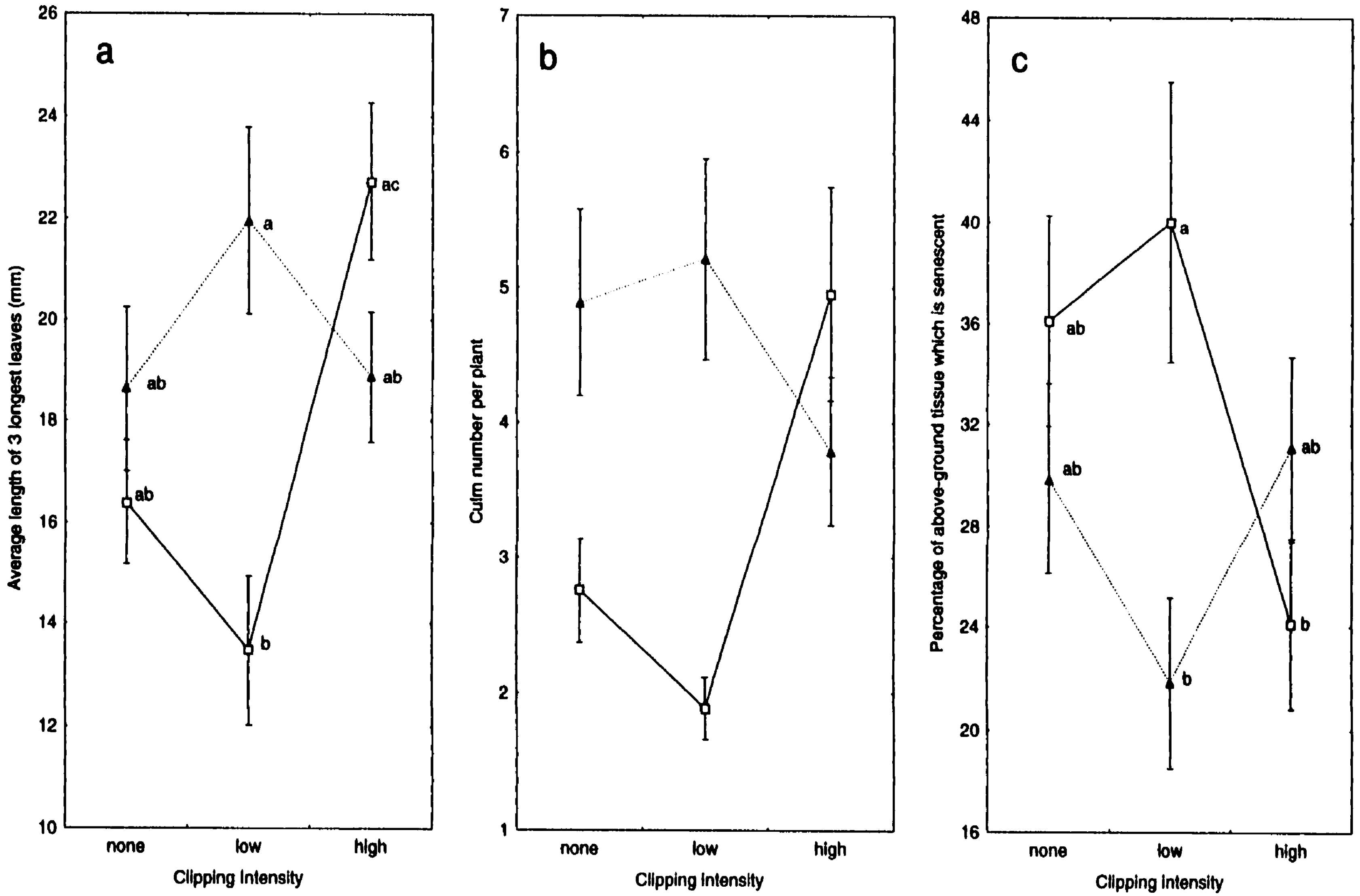

Number of dead leaves at each date
0.0
0.6
1.2
1.8
2.4
3.0
4 July
24 July
11 August

Table 4-4. Summary of 4-way RM-ANOVA for *Kobresia* character traits. See Table 4-3 for notes.

Kobresia	**Leaf length**		**# culms**		**# floral culms**		**% senescent**	
Effect	F	P	F	P	F	P	F	P
TRMT	$2.0_{(2,60)}$	0.1441	$0.67_{(2,76)}$	0.5144	$0.11_{(2,73)}$	0.8958	$0.96_{(2,37)}$	0.3907
TRMT X GrHi	$7.6_{(2,60)}$	0.0011	$2.69_{(2,76)}$	0.0745	$0.52_{(2,73)}$	0.5977	$6.88_{(2,37)}$	0.0029
TRMT X SITE	$0.24_{(4,60)}$	0.9155	$0.91_{(4,76)}$	0.4600	$0.99_{(4,73)}$	0.4183	$1.18_{(4,37)}$	0.3364
TRMT X DATE	$3.13_{(4,50)}$	0.0227	$1.29_{(4,49)}$	0.2887	$1.79_{(4,105)}$	0.1356	$0.34_{(4,37)}$	0.8525
TRMT X GrHi X DATE	$1.84_{(4,50)}$	0.1367	$0.48_{(4,49)}$	0.7493	$0.06_{(4,105)}$	0.9936	$1.22_{(4,37)}$	0.3190
TRMT X SITE X GrHi	$1.42_{(4,60)}$	0.2375	$0.47_{(4,76)}$	0.7556	$0.71_{(4,73)}$	0.5883	$0.58_{(4,37)}$	0.6771
TRMT X SITE X DATE	$1.0_{(8,50)}$	0.4511	$0.93_{(8,49)}$	0.5041	$0.82_{(8,105)}$	0.5860	$1.3_{(8,38)}$	0.2740
TRMT X SITE X GrHi X DATE	$0.73_{(8,50)}$	0.6619	$0.85_{(8,49)}$	0.5673	$0.43_{(8,105)}$	0.9014	$0.75_{(8,38)}$	0.6491
GrHi	$3.56_{(1,61)}$	0.0640	$1.7_{(1,77)}$	0.1959	$0.22_{(1,74)}$	0.6418	$5.22_{(1,37)}$	0.0281
SITE	$1.55_{(2,61)}$	0.2199	$10.98_{(2,77)}$	<.0001	$0.43_{(2,86)}$	0.6500	$3.2_{(2,87)}$	0.0454
SITE X GrHi	$2.51_{(2,61)}$	0.0896	$0.82_{(2,77)}$	0.4445	$0.43_{(2,74)}$	0.6493	$0.18_{(2,37)}$	0.8393
DATE	$13.1_{(2,50)}$	<.0001	$1.18_{(2,49)}$	0.3172	$1.0_{(2,106)}$	0.3725	$27.63_{(2,38)}$	<.0001
GrHi X DATE	$0.68_{(2,50)}$	0.5107	$0.49_{(2,49)}$	0.6159	$0.14_{(2,106)}$	0.8675	$0.7_{(2,38)}$	0.5006
SITE X DATE	$2.41_{(4,50)}$	0.0615	$0.58_{(4,49)}$	0.6785	$0.5_{(4,106)}$	0.7332	$0.48_{(4,38)}$	0.7503
SITE X GrHi X DATE	$0.2_{(4,50)}$	0.9363	$0.26_{(4,49)}$	0.9051	$0.47_{(4,106)}$	0.7550	$0.44_{(4,38)}$	0.7811

Figure 4-3. Influence of grazing history (ungrazed [□], grazed [▲]) on *Kobresia* response to clipping treatment (mean±S.E.). Points within each graph that share lower case letters are non-significantly different (Tukey adjusted LSD, $P<0.05$). Numbers within a graph indicate exact P-value of least squares difference for values that are close to $P=0.05$. a) Effect on leaf length of three longest leaves. b) Effect on number of culms. c) Effect on level of senescence.


a
Average length of 3 longest leaves (mm)
10
12
14
16
18
20
22
24
26
ab
ab
a
b
ac
ab
none
low
high
Clipping Intensity
b
Culm number per plant
1
2
3
4
5
6
7
none
low
high
Clipping Intensity
c
Percentage of above-ground tissue which is senescent
16
20
24
28
32
36
40
44
48
ab
ab
a
b
ab
b
none
low
high
Clipping Intensity

significant main effects in 1998 are not surprising. While census date had enormous effects on most measured plant traits (Table 4-2 and 4-3), *Kobresia* plants did not show any detectable TREATMENT X DATE effect indicating very little change over time in the effect of treatment on the plants.

Final harvest data show that two years of experimental clipping treatments had no effect on total biomass, aboveground biomass and aboveground:belowground biomass ratios for either *Erigeron* or *Kobresia* (Table 4-5). For *Erigeron*, the final biomass was solely a function of the covariate, starting leaf number. The data for *Kobresia* show largely non-significant effects, however, these are likely unreliable due to the low overall survival rate (25 of 216 individuals survived to harvest). Interestingly, both the baseline and the final harvest aboveground:belowground ratios for *Erigeron* indicated that site differences account for all the significant variation. Two years after transplanting into the garden, these ratios are still highly significantly different and the original patterns are maintained, though much lower: the Icefields having the highest and the Front Ranges having the lowest (Garden: IF: 0.67, RR: 0.48, FR: 0.43; Baseline: IF: 1.44, RR: 1.07, FR: 0.90).

Discussion

Studies examining the effect of grazing on plants rarely address the influence of past selective pressures on present grazing treatments. In this study, by collecting plants from areas both grazed and ungrazed by pikas and from 3 sites located along a 100km growing season gradient and planting them in a common environment, we were able to directly examine genetically based or long-term physiological influences on the short-term responses of two common alpine perennials to clipping. What few studies there are comparing the effects of long-term grazing and short-term grazing suggest that past grazing allows plants to respond more

Table 4-5. ANCOVA table of total biomass, aboveground biomass and ANOVA table of aboveground:belowground ratio at final harvest. ANOVA table of baseline biomass ratios.

	Total Biomass		Aboveground Biomass		Biomass Ratio			Baseline Ratio	
Erigeron	F	P	F	P	F	P		F	P
TRMT	$0.14_{(2,121)}$	0.8689	$0.0_{(2,121)}$	0.9974	$0.55_{(2,122)}$	0.5766			
TRMT X GrHi	$1.24_{(2,121)}$	0.2944	$0.33_{(2,121)}$	0.7223	$0.09_{(2,122)}$	0.9141			
TRMT X SITE	$0.8_{(4,121)}$	0.5299	$1.15_{(4,121)}$	0.3342	$0.35_{(4,122)}$	0.8416			
TRMT X SITE X GrHi	$1.39_{(4,121)}$	0.2422	$0.98_{(4,121)}$	0.4207	$0.24_{(4,122)}$	0.9180			
GrHi	$0.69_{(1,121)}$	0.4091	$0.07_{(1,121)}$	0.7971	$3.36_{(1,122)}$	0.0694	GrHi	$0.13_{(1,117)}$	0.7234
SITE	$1.76_{(2,121)}$	0.1769	$3.19_{(2,121)}$	**0.0449**	$7.53_{(2,122)}$	**0.0008**	SITE	$6.43_{(2,117)}$	**0.0022**
SITE X GrHi	$2.48_{(2,121)}$	0.0883	$2.33_{(2,121)}$	0.1012	$1.12_{(2,122)}$	0.3303	SITE*GrHi	$1.54_{(2,117)}$	0.2178
starting leaf number	$48.17_{(1,121)}$	**<.0001**	$36.59_{(1,121)}$	**<.0001**					

	Total Biomass		Aboveground Biomass		Biomass Ratio			Baseline Ratio	
Kobresia	F	P	F	P	F	P		F	P
TRMT	$0.38_{(2,18)}$	0.6882	$0.22_{(2,18)}$	0.8040	$2.00_{(2,19)}$	0.1626	GrHi	$5.42_{(1,114)}$	**0.0217**
TRMT X GrHi	$0.35_{(2,18)}$	0.7061	$0.19_{(2,18)}$	0.8254	$2.06_{(2,19)}$	0.1551	SITE	$20.76_{(2,114)}$	**<.0001**
GrHi	$2.3_{(1,18)}$	0.1469	$2.01_{(1,18)}$	0.1731	$0.11_{(2,19)}$	0.7481	SITE*GrHi	$4.4_{(2,114)}$	**0.0144**
starting culm number	$1.88_{(1,18)}$	0.1869	$1.91_{(1,18)}$	0.1834					

favourably to recent clipping events (e.g., with increased nitrogen concentrations, Milchunas, Varnamkhasti and Lauenroth, 1995). In this study, the common garden design enabled us to examine the influences of past grazing—genetic or latent physiology—on response to recent clipping.

Increased survival in *Erigeron* under light and heavy clipping treatments suggests a beneficial effect of simulated grazing. Since the erect flowering stalks of these plants were clipped (simulating pika grazing patterns) and control plants were left untouched, the survival gains of the clipped plants may be due to a shift in resource allocation from reproduction to storage necessary for overwinter survival. Most evidence, however, suggests that allocation to reproductive tissue accounts for only a small portion of production or biomass in most tundra plants (Chester and Shaver, 1982). Regardless, fitness gains in overwinter survival would likely be offset by reduced fitness from reduced seed set. Several other studies have shown that grazing rarely affects plant mortality (West, 1979; Jones and Harrison, 1980). The higher survival we observed among historically grazed plants may reflect an entirely different response. Belsky *et al.* (1993) and Mathews (1994) suggested that compensation in response to grazing may simply be a generalized response to reducing the impact of inflicted damage. Since the transplanting into the garden may act as a stress causing damage (Heschel and Paige, 1995), the plants with a history of grazing may be well adapted to recovery from damage, hence they experienced increased survival rates after transplanting.

In spite of predictions that climatic history would influence the response of plants to current year clipping, there was no significant interaction between site and treatment. Suzuki (1998) suggested that moderated damage inflicted on plants at higher altitudes may have been a result of decreased herbivore success in the colder temperatures, rather than a plant based resistance. Our data suggest that the different climatic histories characteristic of the different sites do not affect the plant response to clipping, in contrast to several previous studies (Galen, 1990; Galen, Shore, and Deyoe, 1991). Thus while there is ample evidence demonstrating that plants will adapt to local climatic conditions by altering physical or physiological characteristics (e.g., Karhu *et al.*, 1996), the differences between our sites (progressively shorter snow free periods, less soil establishment, etc.) have no detectable effect on the ability of these plants to respond to grazing. Pikas are active year round, regardless of their location (Conner, 1983; Huntly, Smith and Ivins, 1986), so their influence on the vegetation may not be affected by local climate.

What few studies have examined the interaction between long-term grazing and current year clipping, plant response has been shown to be predictable based on the assumption that plants originating from grazed areas will be better adapted to current year grazing. Plants originating from grazed sites have been shown to outperform plants from ungrazed locations when subjected to artificial current year clipping for numerous traits. Painter, Detling and Steingraeber (1989) showed that current year defoliation more adversely affected plants from long-term exclosures (ungrazed history) and Dyer *et al.* (1991) demonstrated that C-fixation rates were higher for grazing adapted plants following defoliation. Both of these studies, and several others (Briske and Anderson, 1992; Painter, Detling and Steingraeber, 1993), were limited in their generalized responses in that they tested only the responses of graminoids. In our study, the responses of the composite and the sedge differed markedly, emphasizing the different growth strategies of dicotyledons and monocotyledons.

Growth parameters of *Erigeron* were largely unaffected by clipping treatment suggesting a high capacity for this species to compensate for herbivore damage. We found no effects of 1/3 removal on one occasion or 1/3 removal on two occasions of leaf tissue on leaf length of three randomly chosen fully formed leaves, leaf number, cumulative number of dead leaves, or on total biomass, aboveground biomass, and aboveground:belowground biomass ratios based on final harvesting of samples on 14 July 1999. The only detectable effect was the temporal delay in number of dead leaves in response to clipping. We found similar results in another study on leaf demography of this same species that current season naturally occurring pika grazing had virtually no effect on leaf births and slight delays in late season leaf senescence and a slight decrease in leaf length (Ch. 3). Previous studies have demonstrated a delayed senescence in response to grazing as a means of recovering carbon gain capacity before the end of the season (Meyer, 1998). This response is not unexpected and indeed it provides a mechanism for the compensatory response. Importantly, the lack of influence of grazing history on current clipping suggests that *Erigeron* is a highly grazing tolerant species. *In situ* leaf demographic studies on this species indicate that there was no interaction between grazing history and current season grazing, and that all plants had a high leaf turnover rate throughout the season (Ch. 3), allowing these plants to respond quickly and easily to grazing events. Having a basal rosette of leaves, where the meristems are protected from damage by herbivores by being very low to the ground, is a recognized tolerance strategy which allows plants to easily compensate for damage (Archer and Tieszen, 1980; Rosenthal and Kotanen, 1994). Overall, low and high intensity clipping treatments in mid to late season, in the previous year and the current year caused no detectable change in leaf number, leaf length, cumulative number of dead leaves and number of dead leaves of *Erigeron*. This demonstrates the compensatory ability of this species and emphasizes a mechanism for its continued persistence following intense pika grazing (see Ch. 3).

In contrast, the monocotyledon *Kobresia* showed a significant influence of past grazing history on experimental clipping treatment. While control plants with no clipping showed no effect of grazing history, at low clipping intensity, historically grazed plants had significantly longer leaves, more culms and lower level of senescence than historically ungrazed plants. These patterns, whereby previously grazed plants perform markedly better than previously ungrazed plants, are consistent with earlier studies (Painter, Detling and Steingraeber, 1989; Dyer *et al.*, 1991). The finding that at high clipping intensity, plants originating from historically ungrazed sites showed a dramatic increase in leaf length, culm number per plant and a drop in senescence level is unexpected and suggests that these plants are stimulated in some aboveground traits by high levels of simulated clipping. To our knowledge, only one study has demonstrated increased growth and performance after a high intensity of simulated grazing in historically ungrazed plants (Knapp *et al.*, 1999), a pattern they attributed to high levels of reserves with which to respond to grazing. In our study, the observed increases in the growth parameters we measured only occurred above a certain level of grazing, suggesting that there was a critical damage threshold above which these plants shifted reserves into aboveground photosynthetic machinery. While previous studies have suggested that plants reallocated belowground reserves in an attempt to minimize the impacts of the damage on overwinter survival (McNaughton, 1983), our data show that this increased growth in the heavy clipping treatment did not adversely affect aboveground:belowground ratio or survival. Current theory and experiments suggest that overcompensation should only occur in plants that are damaged relatively early in the growing season (Maschinski and Whitham, 1989; Hik and Jefferies, 1990; Hik, Sadul and Jefferies, 1991; Lennartsson, Nilsson and Tuomi, 1998). The historically ungrazed plants in this study were clipped (1/3 aboveground biomass each time) in the previous season on 1 August and 14 August and in the current season on 24 July and 11 August and yet overcompensation of these aboveground growth parameters was measured. These plants overcompensated in aboveground parameters at high levels of grazing, an unexpected result that puts into question our understanding of compensatory mechanisms within perennial plants that possess large belowground reserves.

In addition, previously grazed *Kobresia* showed a consistent trend whereby the low clipping treatment caused a peak in performance for length of leaves and level of senescence, though the peak levels are not significantly higher than the control or higher intensity treatment. These plants compensated for the clipping damage in all measured traits at both levels of clipping, and do not show the same threshold response of historically ungrazed plants that could have long-term detrimental effects due to resource depletion. This pattern and the mechanisms by which this pattern is achieved are likely different from historically ungrazed plants. These grazed plants have regularly experienced levels of herbivory equivalent to those imposed in the experimental treatments and as a result, do not show any negative affect and appear marginally stimulated by light clipping. Additionally, high levels of clipping did not significantly affect leaf length, culm number, or senescence indicating that even with two events of 1/3 leaf removal, these plants can compensate tissue loss.

Our data suggest that aboveground:belowground biomass ratios are affected by site of origin. Both our baseline ratios from data collected in 1999 and the final garden ratios showed relatively low belowground reserves in the Icefields and highest in the Front Ranges. The consistency between these measures suggests that climate and site history selects for genotypes of particular biomass ratios. That neither species showed any effect of treatment or grazing history on biomass ratios suggests that reallocation is likely not a strategy of grazing tolerance in these two disparate species and other strategies are used instead. This is highly consistent with our other work on leaf demography that shows high grazing tolerance due to high levels of leaf turnover, delayed leaf senescence and rapid early season growth of leaves (Ch. 3).

Previous assumptions and experiments have proposed that historically grazed plants had increased capacity to respond positively to current grazing (Painter, Detling, and Steingraeber, 1989; Dyer *et al.*, 1991). Other studies have shown that past grazing has little effect on response to current grazing (Jaramillo and Detling, 1988; Post and Klein, 1996). In this study, *Erigeron humilis*, a composite with a basal rosette of leaves, is consistent with these latter studies in that it shows no influence of previous grazing on current simulated herbivory. Grazing history of *Kobresia myosuroides*, however, produces unexpected response patterns to simulated herbivory: previously grazed plants compensated better than ungrazed plants at low intensity clipping, but previously ungrazed plants responded equally or stronger than grazed plants at high intensity clipping and demonstrated overcompensation in aboveground tissue. Thus, the physiological responses of this perennial graminoid species are affected by past selection due to pika feeding, however, threshold levels of damage may exist beyond which different physiological strategies are utilized, depending on the grazing history. The underground reserves of these plants are large and the plants are well adapted to difficult climatic condition (Billings and Mooney, 1968; Archer and Tieszen, 1980; Chapin, Johnson and McKendrick, 1980; Shaver and Kummerow, 1992). As a result, it is feasible for arctic and alpine plants to reallocate resources, but the complex conditions under which this occurs as a response to herbivory and aboveground overcompensation results are poorly known. The most likely longer term results of these responses by historically ungrazed *Kobresia* would be either death or reduced allocation to belowground reserves. Our biomass data do not show this pattern, though the high overwinter mortality may have prevented detection of the reallocation of reserves due to low sample sizes. While it is difficult to conclude that the threshold herbivory overcompensation we observed is sustainable, we have emphasized the importance of knowing the grazing history of a plant in understanding response to current year herbivory.

Chapter 5: General Discussion

Summary of Results

There are seven primary results from the foregoing experiments. First, the influence of pika herbivory varies over a short-term temporal scale and short distance spatial scale. Due to the nature of central place haypiling, the effects of pikas on alpine vegetation increases monotonically throughout the summer and decreases monotonically outward from inhabited talus piles (Chapter 2). This peak of pika influence does not correspond with the peak in aboveground live biomass. Second, the effects on plant production of release from pika grazing are not measurable in the 15-17 day intervals or in the first 4 weeks following installation of exclosures in 1997. After nearly two seasons of pika exclusion, production in highly grazed areas increased by 118% compared to controls and was highly significantly greater than plots that are out of the influence of pika grazing. Third, these general patterns of pika effect vary between largely similar sites separated by only 50km. With more linear talus and different vegetation composition (fewer graminoids), the effect of pikas on aboveground production is undetectable beyond 2m from talus (Chapter 2). Fourth, in individual *Kobresia myosuroides*, *Erigeron humilis*, and *Oxytropis nigrescens* plants we detected that grazing history had a stronger influence on measured growth parameters than current season grazing (Chapter 3). Fifth, we measured 58%-61% current season leaf loss to herbivory—levels which likely reflect the chronic intensity of grazing—but we detected few negative effects of grazing. Plants from all species located in these highly grazed areas demonstrated positive growth in some parameters compared to historically ungrazed plants and demonstrated robust tolerance mechanisms (Chapter 3). Within-plant effects of pika herbivory demonstrate that three different life forms of vegetation differ in morphological leaf responses to naturally occurring pika grazing: historically grazed *Oxytropis* has early and enhanced leaf production and delayed late season leaf senescence;

historically grazed *Erigeron* had nearly continuous leaf production throughout the summer and showed greatly delayed late season leaf senescence; and in historically grazed *Kobresia*, leaf length maxima were shifted in time to late June, possibly reflecting a shift away from the heaviest grazing. Sixth, a common garden experiment demonstrated that plants originating from three sites of strikingly different climate, relief, and edaphic conditions responded indistinguishably to simulated pika grazing pressure (Chapter 4). Seventh, past history of grazing influenced the response of *Kobresia* plants to experimental clipping, but showed no effect on *Erigeron*. All *Erigeron* plants showed high tolerance to simulated clipping, including increased survival under low and high clipping treatments, while previously grazed or ungrazed *Kobresia* showed more complex biphasic response patterns (Chapter 4).

Limitations of using *in situ* grazers and simulated clipping

While the merits and strengths of using *in situ*, naturally occurring grazing and grazers have been emphasized in earlier chapters, I must point out some limitations. It is impossible to control the intensity of grazing pressure and to standardize the type of grazing (e.g., all leaves clipped to 2 mm, rather than a few grazed to 5 mm and others grazed to 0 mm). This clearly presents a problem in trying to compare responses of plants to grazing, since the plants may be receiving different grazing pressures. Also, as was seen in the open leaf demography plots (Chapter 3), it is not possible to determine *a priori* whether plants would be grazed or not when using naturally occurring grazing. My way around this was to use the pikas themselves as the experimenter. One inherent problem with this is that plants may show “responses to grazing” (particularly seen in examining leaf length) that may simply reflect a bias in the “experimenter choice”: pikas may not be causing early season peaks in grazed plants, they may be selectively grazing plants with longer leaves. I avoided this problem, however, by considering all plants ungrazed until a grazing event occurred. In chapter 2 and chapter 3, I decided that the responses of plants to naturally occurring grazing pressure are largely understudied, however, the benefits of examining the multiple compounding effects of natural grazers (saliva, tearing vs. cutting etc.) outweighed the drawbacks.

Similarly, there are limitations to using simulating herbivory by using scissors. The response of the plants will be based on mechanical damage and will miss other aspects of mammalian herbivory (e.g., saliva; Dyer and Bokhari, 1976; tearing or shredding; Archer and Tieszen, 1980; see Archer and Tieszen, 1986 and Baldwin, 1990). I attempted to mimic the pattern of pika grazing by removing 100% of 1/3 of the leaves—one mouthful—rather than removing 1/3 of 100% of the leaves. In instances where questions of regional variation are concerned—such as in my common garden—the only experimental technique is to use transplants. While an alternative to a common garden is to use reciprocal transplants, the practical limitations mean that not all combinations of sites would be tested and the experimental treatments would not be able to be performed simultaneously.

Herbivory tolerance and compensation

The ability of plants to tolerate herbivore damage is a final step in a sequence of strategies that begins with avoiding being grazed, continues with active or passive defense chemicals, and finally, when herbivory occurs, the best way to survive is to have numerous mechanisms to minimize the effects of the damage (McNaughton, 1979; Rosenthal and Kotanen, 1994). From the perspective of the herbivore, plants that readily tolerate grazing by producing new leaves, by delaying senescence in remaining leaves or by maintaining high levels of production are highly beneficial and arguably essential for the persistence of large populations of herbivores (McNaughton, Banyikwa and McNaughton, 1997). Plants with large investments in secondary compounds generally have lower productivity (Coley, Bryant and Chapin, 1985), so areas with plants that have relatively high productivity and high herbivory tolerance may be able to support higher herbivore numbers.

A specific type of tolerance strategy that is characterized by regrowth response (Rosenthal and Kotanen, 1994) is compensation, whereby the strength of the regrowth response after herbivory determines whether the plant undercompensates, exactly compensates or overcompensates. Literature on compensation after herbivory is abundant, intriguing, and heated (Dyer, 1975; McNaughton, 1976, 1979, 1983, 1986b; Hilbert *et al.*, 1981; Oksanen, 1983; Belsky, 1986, 1987; Verkaar, 1986; Parsons and Penning, 1988; Williamson *et al.*, 1989; Paige and Whitham, 1987; Chapin and McNaughton, 1989; Hik and Jefferies, 1990; van der Meijden, 1990; Paige, 1992; Vail, 1992, 1993; Alward and Joern, 1993; Belsky *et al.*, 1993; Bergelson, Juenger and Crawley, 1996; Lennartsson, Tuomi and Nilson, 1997; de Mazancourt, Loreau and Abbadie, 1998; Paige, 1999). Surprisingly, almost none of this literature discusses compensation as a multi-year process, perhaps because most of the research has focussed on highly productive systems or has focused on compensation as a fitness measure, rather than an herbage production indicator. Research interested in plant dynamics from the perspective of the herbivores, however, should by necessity be interested in measures of herbage production. If such is the case, then it is a logical—though apparently difficult—progression of thought to be interested in multi-year increases or decreases in vegetation production, particularly in habitats where there are resident herbivores and in generally low productivity. Clearly, in habitats such as arctic and alpine systems, where nutrient cycling is relatively slow, production is relatively low, and underground storage is a large factor in plant growth, responses to herbivory would not be expected to occur within the same season. Indeed, if time of response was standardized to absolute growth rates, two weeks of aboveground growth in temperate or tropical grasslands (up to 30 $g{\cdot}m^{-2}day^{-1}$, Serengeti; McNaughton, 1985; 80-600 $g{\cdot}m^{-2}year^{-1}$, North American grasslands;

Frank and McNaughton, 1993) would easily extend into two seasons of regrowth in habitats where the entire annual aboveground production is 30-150g$\cdot$m^{-2}.

In this study, we found that within-season short-term production of grazed vegetation inside temporary exclosures was much lower than similar ungrazed patches inside 2-year exclosures: vegetation showed undercompensation within the season in highly grazed areas adjacent to talus. The only way to analyze production of grazed vegetation after two years of herbivory exclusion is to compare it with production of ungrazed vegetation after two years of herbivory exclusion. Contrasting end of season aboveground live biomass of herbivore exclosed, grazed plots with herbivore exclosed, largely ungrazed plots far from talus after the second season of exclusion, we found that adjacent to talus, historically grazed plots showed aboveground live biomass values of 116 g$\cdot$m^{-2}, those with a light history of grazing in intermediate plots had values of 130 g$\cdot$m^{-2}, while ungrazed far plots only had 82 g$\cdot$m^{-2}. Contrasted with the previous year when all three plots had statistically indistinguishable aboveground live biomass levels (62 g$\cdot$m^{-2}, 78 g$\cdot$m^{-2}, and 68 g$\cdot$m^{-2}, respectively), these values suggest highly overcompensating vegetative production. This is highly relevant over-production for pika populations, yet would be entirely overlooked if only within-season production using temporary exclosures was measured. As a possible mechanism to account for this elevated production in historically grazed sites, the daytime temperatures of highly grazed plots were found to be higher than exclosed plots, potentially increasing nutrient mineralization rates (Flanagan and Veum, 1974; Chapin, 1983; Vitousek *et al.*, 1994). Because the rates of nutrient input are likely not high in any of these sites, the delay in response to this nutrient supply may be simply due to reduced plant resources due to removal of tissue by pika grazing.

The implications for this type of response to grazing are intriguing, given the nature of pika population dynamics, as they are currently understood. From research on the American pika (which may be different than the collared pika; Southwick *et al.*, 1986; Smith and Ivins, 1983; Peacock, 1997) and early data from the collared pika (D. Hik, unpub. data; E. McIntire, pers. obs.), there are two factors which may be important in the persistence of pika populations. First, populations sizes do not show cyclic fluctuations, like many northern small mammals, nor substantial population size fluctuations. Hypothesized benefits for plants due to the periodic release from grazing during population lows have been described as a means of plant recovery until the next herbivore population peak. With non-cyclic populations, this "off" time would not often occur. Second, while populations as a whole show little size variability, and individual adults are highly philopatric, there is some shifting of haypile locations between generations. Thus with small scale territorial vacancies and recolonizations, occurring on the time scale of individual pika lifetimes (2-5 years), individual patches of highly grazed vegetation may have one to two year releases from herbivory, enabling elevated production to occur and the vegetation community to persist without continued decay, due to stochastically driven metapopulation processes. There are still several questions that this hypothesis requires in order to falsify it, including separating out individual exclosure sets that do not have active haypiles next to them in a given year. In these plots, during these years, the control plot should approach the exclosed plot, since both would have had entire seasons without grazing. This will be tested with data in the future.

The analysis of leaf demography of *Kobresia*, *Erigeron* and *Oxytropis* complements the exclosure data, demonstrating that within-season grazing does not elicit a response from the vegetation, but the history of grazing—whether the plants are located within a small band surrounding talus piles—is a strong influence on leaf demography. Most importantly, however, these species used three different strategies demonstrating tolerance to long-term grazing.

In the common garden analysis, we tested for plant response to current season grazing and detected very little effect on measured plant performance traits. The history of grazing—consistent with the leaf demography study—was a significant effect on growth of *Kobresia*, with historically grazed plants showing virtually no effect of current year clipping, and historically ungrazed plants showing a significant positive threshold response on several plant performance traits at high levels of herbivory.

Species variation and grazing history: challenges and oversights

Our analyses on leaf demography and the common garden emphasize the importance of interspecific variation in strategies for herbivory tolerance. We used a legume, a composite, and a sedge to test for differences in response to the short-term and long-term effects of herbivory and found each species used a strategy consistent with its growth form, yet not highly predictable based on simply knowledge of its form. How to deal with this variability presents a problem for attempting to predict individual species responses to grazing in other studies. Extrapolating these data to community processes, such as species composition shifts due to herbivory, presents a particularly difficult challenge. One emergent pattern was that the traditional benefits of basal meristematic growth in response to grazing did not appear to outperform other strategies of altering leaf births and senescence utilized by the non-graminoids. That I observed detectable compensatory growth in response to long-term grazing in all three species (Ch. 3) corroborates the persistence of high species diversity in highly grazed meadows adjacent to talus (Ch. 2), with good representation of all three life forms.

Finally, in all three chapters, I found that grazing history had profound influences on the plants: on production, species composition, leaf demography and response to new clipping in a common environment. The consistent effect of grazing history I detected here potentially aids in contextualizing results from previous studies which attempted to understand response to grazing without controlling for grazing history (e.g., Paige and Whitham, 1987; Bergelson and Crawley, 1992a, 1992b; Paige, 1992, 1994, 1999; Lennartson, Nilsson and Tuomi, 1998; Meyer, 1998; Wegener and Odasz-Albrigtsen, 1998). Indeed, the effect of grazing history has been alluded to—in the context of high predictability of herbivory—as a means of explaining overcompensation (Crawley, 1987; Paige, 1992). In many ecosystems, the grazing history of plants may not be evident, however, a handful of studies from one research group has begun to address how the past history of grazing of native and naturally occurring herbivores influences plant growth (Painter, Detling and Steingraeber, 1989, 1993). As with the current study, these studies demonstrated that grazing history may be very important and most strongly predicted plant morphology in a common environment. In the current study, I found the long-term effects of a small, yet active herbivore to be profound on time scales much longer than a single year of examination. For a long-lived perennial that is subject to chronic grazing throughout its entire life, it is not surprising that the temporal snapshot of a single season of grazing was found to show little effect on plants. That so many studies have not attempted to reconcile the lifetime impacts of herbivory on long-lived perennials (see Doak, 1992) is troubling and limits the generality of many studies. Regardless, the diverse array of tolerance strategies I observed among a broad group of native species to long-term grazing by collared pikas are remarkable and emphasize the complex suite of processes that allow these highly utilized systems to persist indefinitely.

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Appendix 1. Species list for Ruby Ranges, Front Ranges and Icefields

RR	FR	IF	Life form	Family	Species
X		X	fern**	Aspidiaceae	Cystopteris fragilis (L.) Bernh.
X		X	fern**	Equisetaceae	Equisetum sp.
X			graminoid	Poaceae	Arctagrostis latifolia (R. Br.) Griseb. s.l.
X			graminoid	Poaceae	Festuca altaica Trin.
X	X		graminoid	Poaceae	Festuca brachyphylla Schultes & Schultes fil.
X			graminoid	Poaceae	Hierochloe alpina (Sw.) R. & S. ssp. alpina
X	X		graminoid	Poaceae	Poa alpina L.
X			graminoid	Poaceae	Trisetum spicatum (L.) Richt.
X	X	X	graminoid	Cyperaceae	Kobresia myosuroides (Vill.) Fiori & Paol.
X			graminoid	Cyperaceae	Carex podocarpa R. Br.
X	X		graminoid	Cyperaceae	Carex microchaeta Holm
X			graminoid	Cyperaceae	Carex lachenalii Schk.
X	X		graminoid	Cyperaceae	Carex rupestris All.
X	X		graminoid	Cyperaceae	Carex scirpoidea Michx.
X			graminoid	Cyperaceae	Carex misandra R. Br.
X		X	graminoid	Cyperaceae	Carex consimilis Holm
X			graminoid	Cyperaceae	Carex membranacea Hook.
X			graminoid	Cyperaceae	Carex vaginata Tausch
X	X		graminoid	Cyperaceae	Eriophorum angustifolium Honckn.
X	X		graminoid	Juncaceae	Luzula arctica Blytt spp. arctica
X	X		graminoid	Juncaceae	Luzula arcuata (Wahlenb.) Sw. ssp. unalaschkensis (Buc.) Hulten
X	X	X	graminoid	Juncaceae	Luzula spicata (L.) DC.
X	X		forb	Liliaceae	Lloydia serotina (L.) Rchb.
X	X	X	dwarf shrub	Salicaceae	Salix polaris Wahlenb.
X	X	X	dwarf shrub	Salicaceae	Salix reticulata L. ssp. reticulata
X		X	dwarf shrub	Salicaceae	Salix arctica Pall.
X	X		dwarf shrub	Salicaceae	Salix rotundifolia Trautv. ssp. dodgeana (Rydb.) Argus
X			dwarf shrub	Salicaceae	Salix sp. (shrub)
X			dwarf shrub	Salicaceae	Salix sp. (shrub)
X	X		forb	Polygonaceae	Oxyria digyna (L.) J. Hill
X			forb	Polygonaceae	Polygonum bistorta L. ssp. plumosum (Small) Hulten
X	X		forb	Polygonaceae	Polygonum viviparum L.
X	X		forb	Portulacaceae	Montia sarmentosa (C.A Mey.) Robins.
X			forb	Portulacaceae	Montia bostockii (A.E. Porslid) Welsh
X			forb	Portulacaceae	Claytonia tuberosa Pall.
X			forb	Caryophylaceae	Cerastium beeringianum Cham. & Schlect.
X	X	X	forb	Caryophylaceae	Stellaria longipes Goldie s.l.
X	X	X	forb	Caryophylaceae	Silene acaulis L. ssp. acaulis
X			forb	Caryophylaceae	Silene uralensis (Rupr.) Bocquet ssp. uralensis
X	X		forb	Caryophylaceae	Minuartia macrocarpa (Pursh) Ostenf.
X			forb	Ranunculaceae	Aconitum delphinifolium DC. ssp. delphinifolium
X	X		forb	Ranunculaceae	Anemone parviflora Michx.
X	X		forb	Ranunculaceae	Ranunculus sulphureus Sol.

X	X	X	forb	Papaveraceae	Papaver macounii Greene ssp. discolor (Hulten) Randel
		X	forb	Brassicaceae	Braya humilis (C.A. Mey.) Robins.
X			forb	Brassicaceae	Cardamine bellidifolia L.
X			forb	Brassicaceae	Cardamine purpurea Cham. & Schlecht.
X			forb	Brassicaceae	Draba crassifolia Grah.
X			forb	Brassicaceae	Draba stenoloba Ledeb.
X		X	forb	Brassicaceae	Draba sp.
X			forb	Brassicaceae	Eutrema edwardsii R. Br.
X			forb	Brassicaceae	Parrya nudicaulis (L.) Regel
X			forb	Crassulaceae	Rhodiola rosea L. ssp. integrifolia (Raf.) Hara
X		X	forb	Saxifragaceae	Saxifraga bronchialis L. ssp. funstonii (Small) Hulten
X			forb	Saxifragaceae	Saxifraga cernua L.
X			forb	Saxifragaceae	Saxifraga lyallii Engler ssp. hultenii (Calder & Savile) Caler & Taylor
X	X		forb	Saxifragaceae	Saxifraga flagellaris Willd. ssp. setigera (Pursh) Tolm.
X			forb	Saxifragaceae	Saxifraga hieracifolia Waldst. & Kit.
X	X	X	forb	Saxifragaceae	Saxifraga oppositifolia L. ssp. oppositifolia
X		X	forb	Saxifragaceae	Saxifraga nelsoniana D. Don s.l.
X	X		forb	Saxifragaceae	Saxifraga serpyllifolia Pursh
X			forb	Saxifragaceae	Saxifraga tricuspidata Rottb.
	X		forb	Saxifragaceae	Saxifraga razshivinii Zhmylev
		X	forb	Saxifragaceae	Saxifraga reflexa Hook.
X		X	forb	Rosaceae	Sibbaldia procumbens L.
X	X		dwarf shrub	Rosaceae	Dryas octapetala L.
X	X		forb	Rosaceae	Potentilla biflora Willd.
X			forb	Rosaceae	Potentilla diversifolia Lehm.
X			forb	Rosaceae	Potentilla uniflora Ledeb.
X		X	forb	Rosaceae	Potentilla villosa
X	X		forb	Fabaceae	Astragalus umbellatus Bunge
X	X	X	forb	Fabaceae	Oxytropis nigrescens (Pall.) Fisch. ssp. nigrescens
X	X		forb	Fabaceae	Oxytropis maydelliana Trautv.
X			dwarf shrub	Empetraceae	Empetrum nigrum L. ssp. hermaphrroditum (Lge.) Bocher
X			forb	Onagraceae	Epilobium angustifolium L. s.l.
X			forb	Onagraceae	Epilobium latifolium L.
X			forb	Pyrolaceae	Pyrola grandiflora Radius
X			dwarf shrub	Ericaceae	Ledum decumbens (Ait.) Lodd.
X			dwarf shrub	Ericaceae	Vaccinium vitis-idaea L. ssp. minus (Lodd.) Hulten
X			dwarf shrub	Ericaceae	Vaccinium uliginosum L. s.l.
X	X		dwarf shrub	Ericaceae	Cassiope tetragona (L.) D.Don
X			forb	Primulaceae	Dodecatheon frigidum C. & S.
	X		forb	Primulaceae	Androsace chamaejasme Host ssp. lehmanniana (Spreng.) Hulten
X			forb	Gentianaceae	Gentiana algida Pall.
		X	forb	Gentianaceae	Gentiana detonsa (Rottb.) Ma.
X			forb	Gentianaceae	Gentiana prostrata Haenke
X			forb	Gentianaceae	Gentianella propinqua (Richards.) J.M. Gillett ssp. propinqua
X		X	forb	Polemoniaceae	Polemonium acutiflorum Willd.
X			forb	Boraginaceae	Mertensia paniculata (Ait.)
X			forb	Boraginaceae	Myosotis alpestris Schm.
X	X		forb	Scrophulariaceae	Castilleja hyperborea Pennell

X	X		forb	Scrophulariaceae	Pedicularis capitata Adams
X	X		forb	Scrophulariaceae	Pedicularis langsdorfii Fisch. ssp. arctica (R. Br.) Pennell ex Hulten
X			forb	Scrophulariaceae	Valeriana capitata Pall.
X	X	X	forb	Campanulaceae	Campanula lasiocarpa Cham.
X	X		forb	Campanulaceae	Campanula uniflora L.
X	X	X	forb	Asteraceae	Antennaria monocephala DC.
X	X		forb	Asteraceae	Amica lessingii Greene
X	X		forb	Asteraceae	Artemisia norvegica Fries ssp. saxatilis (Bess. ex Hook.) Hall & Clem.
X	X	X	forb	Asteraceae	Erigeron humilis Graham
	X		forb	Asteraceae	Erigeron sp.
X			forb	Asteraceae	Petasites frigidus (L.) Fries ssp. frigidus
X	X		forb	Asteraceae	Saussurea angustifolia (Willd.) DC. ssp. yukonensis (A.E. Porsild) Cody
X	X		forb	Asteraceae	Senecio atropurpureus (Ledeb.) Fedtsch. ssp. frigidus (richards.) Hulten
X	X		forb	Asteraceae	Senecio tundricola Tolm.
X			forb	Asteraceae	Senecio lugens Richards.
	X		forb	Asteraceae	Senecio cymbalaria Pursh
X	X	X	forb	Asteraceae	Taraxacum lyratum (Ledeb.) DC.
	X	X	forb	Asteraceae	Solidago multiradiata Ait.

** Life form not present in any sample