The Effect of Mountain Goats on the Subalpine Plant Communities of Klahhane Ridge, Olympic National Park, Washington.

by

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A thesis submitted in partial fulfillment
of the requirements for the degree of

Master of Science

University of Washington

1981

Approved by Lawrence C Bliss
(Chairperson of Supervisory Committee)

Program Authorized
to Offer Degree Botany Department

Date December 11, 1980

Master's Thesis

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Abstract

The effect of mountain goats on the subalpine plant communities of Klahhane Ridge, Olympic National Park, Washington

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The population of mountain goats on Klahhane Ridge has reached a level that is exerting significant pressure on the food resource of their habitat. The environmental and habitat requirements of the goats concentrate the pressure especially in cooler regions that recieve heavy use in the middle of the summer.

The response of each plant community to the grazing pressure and physical disturbance of the mountain goats varies according to the nature of the plant community, and the intensity of goat use. Environments which are physically limiting to the survival of plants will respond to mountain goat pressures by a decline in species density. More moderate environments may respond to selective grazing of dominant species and light trampling levels by increasing in species density. High levels of physical disturbance

change species composition to an early successional stage.

The changes in plant community composition induced by mountain goats are different for each community. In all cases, however, the change is toward a reduction in the abundance and production of preferred forage species. This will result in a decline in the population of mountain goats that the ridge can support.

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ACKNOWLEDGMENTS

I want to express my sincere appreciation to Dr. Lawrence C. Bliss for his guidance and encouragement in all stages of this work. I also thank the other members of my supervisory committee, Dr. Robert Cleland, Dr. Charles Driver, and Dr. Fiorenzo Ugolini for their advice on the design and execution of this study.

I especially thank my trusty rusty field assistant, Peter Rapp, whose botanical skills and indefatigable energy made the long hours of field work a pleasure, and doubly productive; and Susan Foster for much needed early season field help, as well as moral and intellectual support.

The contributions of the following people are also much appreciated: my fellow graduate students for contributing ideas and support; Edd Schreiner, Doug Pike, and John Harter, for stimulating conversations; Dr. Roger del Moral for technical advice on field and computer methodology; Bruce Moorhead and the staff of the Olympic National Park Office of Science and Technology, for their interest and logistical support; and Victoria Stevens, Mike Hutchins, and goat ropers too numerous to name for companionship in the field, and insight into the ways and means of the mountain goat.

I gratefully acknowledge the National Park Service, U.S. Department of the Interior for providing the funds for this research.

INTRODUCTION

The introduction and establishment of populations of large herbivores has resulted in changes in plant community species composition and productivity in many areas of the world. A classic example of this is the loss of endemic plant species and the increase in non-native species which has occurred in Hawaii under the influence of feral goats (Yocum, 1967; Baker and Reser, 1972). Similar loss of species is attributed to feral goat activities in the California islands, the Galapagos, and in New Zealand (Coblenz, 1978). New Zealand has seen considerable changes in plant communities after the introduction of sheep (Whittaker, 1976), feral pigs (Challis, 1975), deer (Holloway, 1950; Mark and Baylis, 1975), and Himalayan thar (Caughley, 1970). In Grand Canyon National Park, feral burros have been held responsible for distruction of desert plant communities by grazing and trampling (U.S. Dept. Int. U.S.N.P.S.,1980). Digging activities of the European wild boar have resulted in a loss species from mountain meadows in Smoky Mountain National Park (Bratton, 1974; Howe and Bratton, 1976; Howe, Singer, and Ackerman, 1979). Eruption of ungulate populataion levels following introduction has characteristically resulted in the over-use and distruction of the food resource, and the ultimate decline of the

population (review by Caughley, 1970). Intelligent management of introduced herbivore populations requires a complete understanding of the ecological life history of the animal and its habitat.

This study was undertaken to contribute to the understanding of the relationship of the mountain goat and its environment in the Olympic Mountains, Washington. Mountain goats (Oreamnos americanus) were introduced to the Olympic Mountains in the 1920's. The introduced population has grown and spread throughout the alpine and subalpine areas of the Olympic Peninsula (Moorhead, 1977). The population size is currently estimated to be 500-700 animals (Stevens, pers. comm.). Most of the mountainous habitat favored by the goats is within Olympic National Park, where the goats have been protected from hunting since the Park's establishment in 1938.

The highest density of goats occurs on Klahhane Ridge in the northeast part of Olympic National Park. Approximately 170 goats share a summer range of about 10 km^2. This concentration of 17 animals/km^2 compares with figures of 2.8 (Chadwick, 1977) and 0.48 (Singer, 1975) goats/km^2 for natural populations in different areas of Glacier National Park. Chadwick (1977) attributes the differences in density in Glacier to the relative abundance of rocky terrain. The more gentle subalpine areas studied

by Singer (1975) supporting the lower density of animals. Differential densities of mountain goats occur in the Olympic Mountains as well, the abundance of animals in an area is related to the availability of steep rocky terrain and other essential habitat components. Stevens (1979) summarized the major habitat requirements for mountain goats in Olympic National Park. They include the following: 1) steep rocky cliffs for escape and cover; 2) open subalpine or alpine meadows to provide forage; and 3) thermoregulatory habitat, principally cool areas in which the animals can escape the summer heat.

Chadwick (1977) proposes that populations of mountain goats are limited primarily by extrinsic abiotic factors, climate and primary (geomorphic) succession. Biotic influences seemed to be of secondary importance in the native populations of Glacier National Park. In an area with concentrated populations such as Klahhane Ridge, biotic factors (i.e. competition for food resources) may be expected to be more important in maintaining population levels. The high level of use of the food resource in such an area can also be expected to have implications on the overall vigor of the plant communities.

Objectives of this study

The objective of this research has been to determine the effect of mountain goat activities on the plant

communities of the Olympic Mountains. This study has been concerned with the plant communities of Klahhane Ridge. Vegetation changes in the Klahhane Ridge area which have been attributed to mountain goat activities have been noticable for at least ten years (Moorhead, pers. comm.) but were first reported by Olmsted (1976).

The goals of this study were the following:

1) To document the important plant communities of Klahhane Ridge. These baseline data on species composition and productivity can be used in long term studies of the effect of mountain goats on the plant communities.
2) To determine the ways that the goats may be changing the plant communities. This information, together with an understanding of the factors controlling plant distribution, can be used to formulate hypotheses on the direction and magnitude of goat induced changes.
3) To assess the habitat factors which limit the Klahhane Ridge mountain goat population, and to formulate a model which can be used to help understand the magnitude of population pressures on the vegetation of Klahhane Ridge.

THE STUDY AREA

Geology

The Olympic Mountains form the center of the Olympic Peninsula in northwest Washington. The mountains were uplifted by plate tectonic processes during the Cascadian revolution (late Pliocene - early Pleistocene). Oceanic sediments deposited in the Eocene-Miocene (55-15 m.y.b.p.) make up the sandstones, siltstones, and shales that dominate the central core mountains. The peripheral Crescent Formation is a horseshoe of mountains formed when basaltic rock of the sea floor was sheared off and piled up as the oceanic plate moved under the continental plate (Tabor, 1975) (Figure 1).

Fluvial and glacial processes have been important in shaping the Olympic landscape. Four major glacial periods have occurred, filling the Puget Lowlands with at least six different continental ice sheets. Alpine glaciers occurred during the Salmon Creek and Fraser Periods (Crandell, 1965). The periods of continental and alpine glaciations were staggered so that there has been land free from ice in the Olympic Mountains at all times. The glaciers are responsible for deep U-shaped valleys with sharp ridges and steep north cirques. The erosive action of water has steepened the topography. Eleven major rivers radiate from

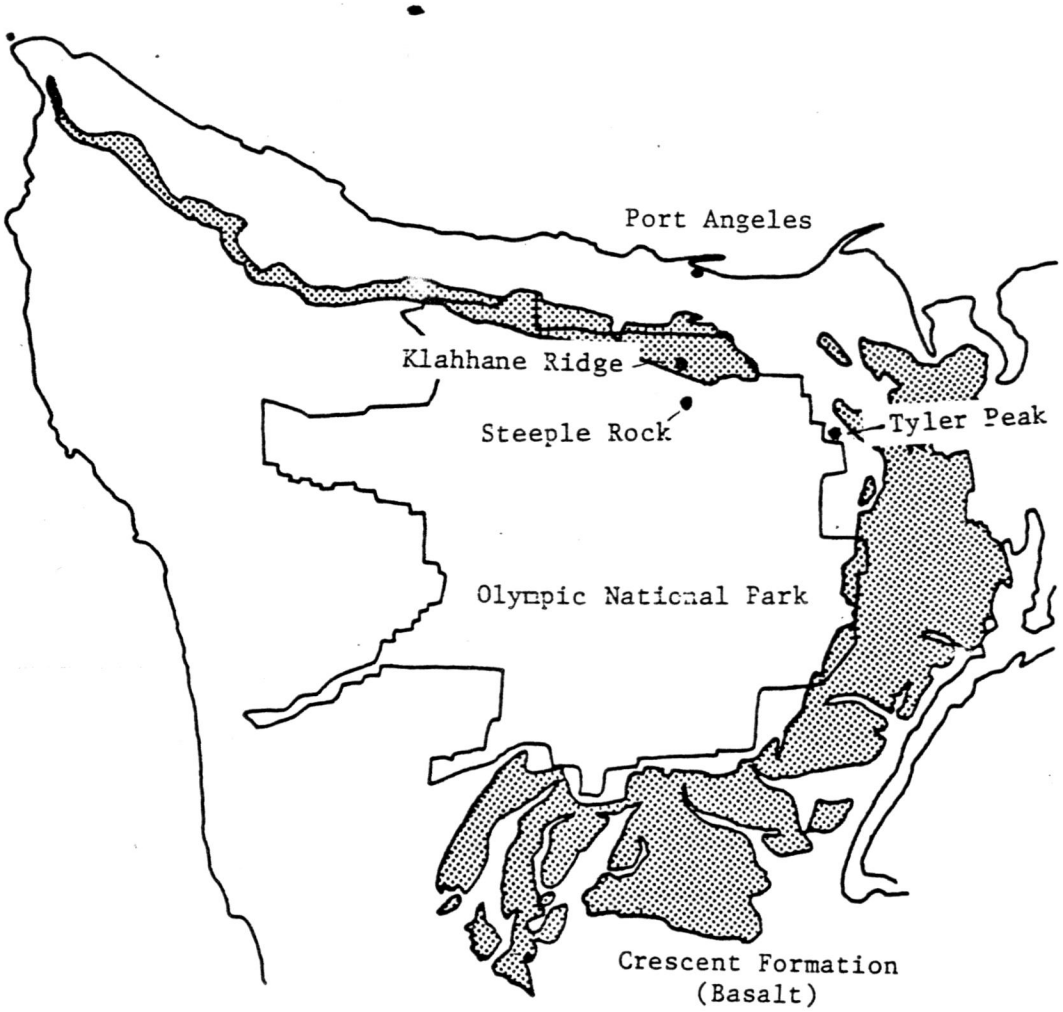


Figure 1. Map of the Olympic Peninsula showing locations mentioned in the text.

the central core mountains.

Climate

The climate of the Olympic Peninsula is dominated by the maritime influence of the Pacific Ocean. Winters are mild and wet, summers warm and dry. Klahhane Ridge is in the rain shadow of the main crest of the Olympics. Most of the precipitation in this area falls as snow during the winter months. The nearest weather station is in Port Angeles, 13 km to the north and at sea level. Weather data for Port Angeles are presented in Figure 2.

Study site

Klahhane Ridge is in the northeast part of Olympic National Park (lat. 47°59'30"N, long.123°27'30"W). It is bounded by Mt. Angeles (1967 m) on the west and by Rocky Peak (1895 m) on the east. The ridge top averages about 1800 m in elevation, and study areas included sites from 1520 m to 1830 m. Klahhane Ridge is located in the Crescent Formation; parent materials are interbedded basaltic and sedimentary rock. The topography varies from stable meadows with sedimentary substrate to unstable scree slopes and steep rocky outcrops generally underlain by weathering resistant basaltic rock.

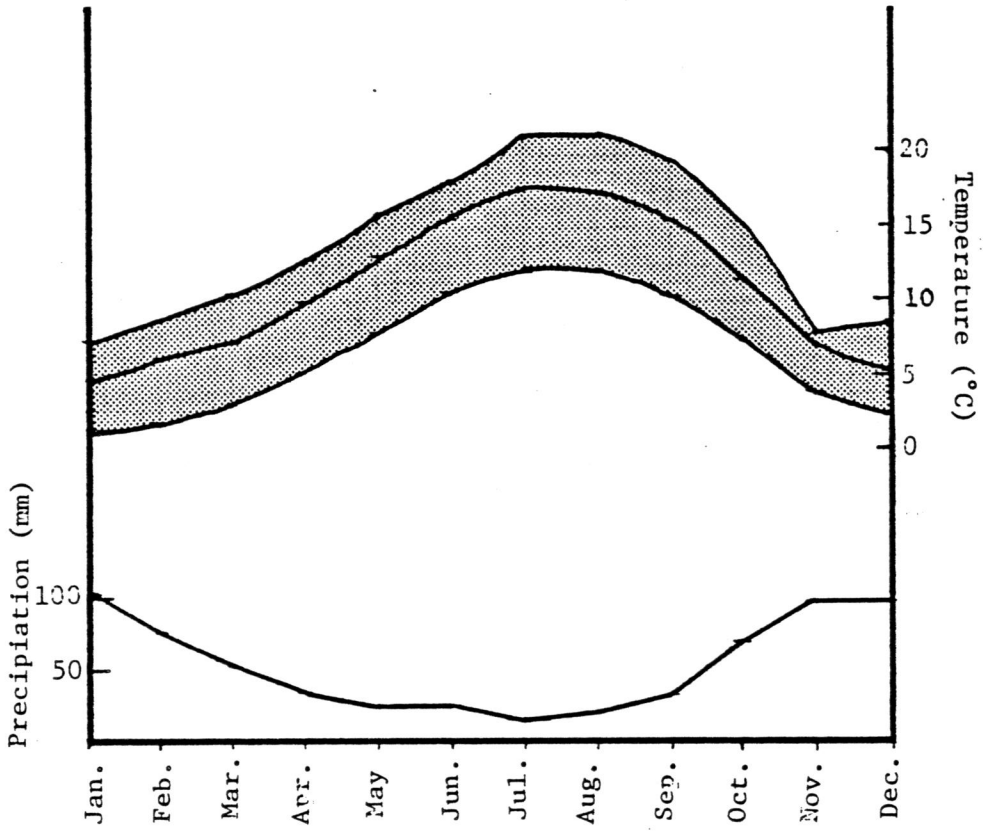


Figure 2. Environmental data for Port Angeles, Washington. Monthly average precipitation, maximum, minimum, and mean temperatures. NOAA data, averages from 1941-1970.

THE PLANT COMMUNITIES OF KLAHHANE RIDGE

The subalpine herbaceous plant communities of the Olympic Mountains have been described by Kuramoto and Bliss (1970). They were able to relate general community patterns to the major environmental factors determining the distribution of plant species. While the same broad environmental patterns occur throughout the subalpine regions of the Olympics, community composition in any area is subject to local environmental and historical factors, and can be extremely variable within a community type.

Documentation of the plant communities in an area of heavy goat use serves the following three purposes. 1) It provides baseline data to be used in future studies of the effect of the mountain goats on their habitat. 2) An understanding of the important environmental parameters which determine local community pattern is necessary to be able to understand and predict the potential changes in plant communities due to mountain goat activities. 3) Quantification of the amount of potential forage and determination of a carrying capacity will provide insight into the magnitude of population pressures exerted by the goats on the plant communities.

The plant communities of Klahhane Ridge were sampled in

1979 to provide such documentation. Estimates of composition of vascular plant species, grazing preference, and net above ground production were made for the important plant communities within mountain goat habitat. In 1980, potential above ground primary productivity (production over time) was determined in 5 plant communities, and an estimate was made of the amount of forage consumption for important species.

Methods - 1979

Field

The ridge was surveyed and 20 areas were selected for sampling. Selection of areas to be sampled was intended to express the range of plant communities on the ridge. Each area was chosen on the basis of uniform physiognomy and floristic pattern. One 10m x 10m plot was established in each area, located so that obvious environmental gradients and ecotones were avoided. Two diagonal corners of each plot were permanently marked with 1cm steel reinforcing rod. A stratified random sampling procedure was employed. Each plot was subdivided into 10, 2m x 5m subplots. One $1m^2$ quadrat was randomly located in each subplot to be sampled (total sample size = 10% of total plot area) (Figure 3). In order to determine the vegetational composition of each plot, total cover of each species was visually estimated to the nearest 1%. An estimate of grazing was made for each

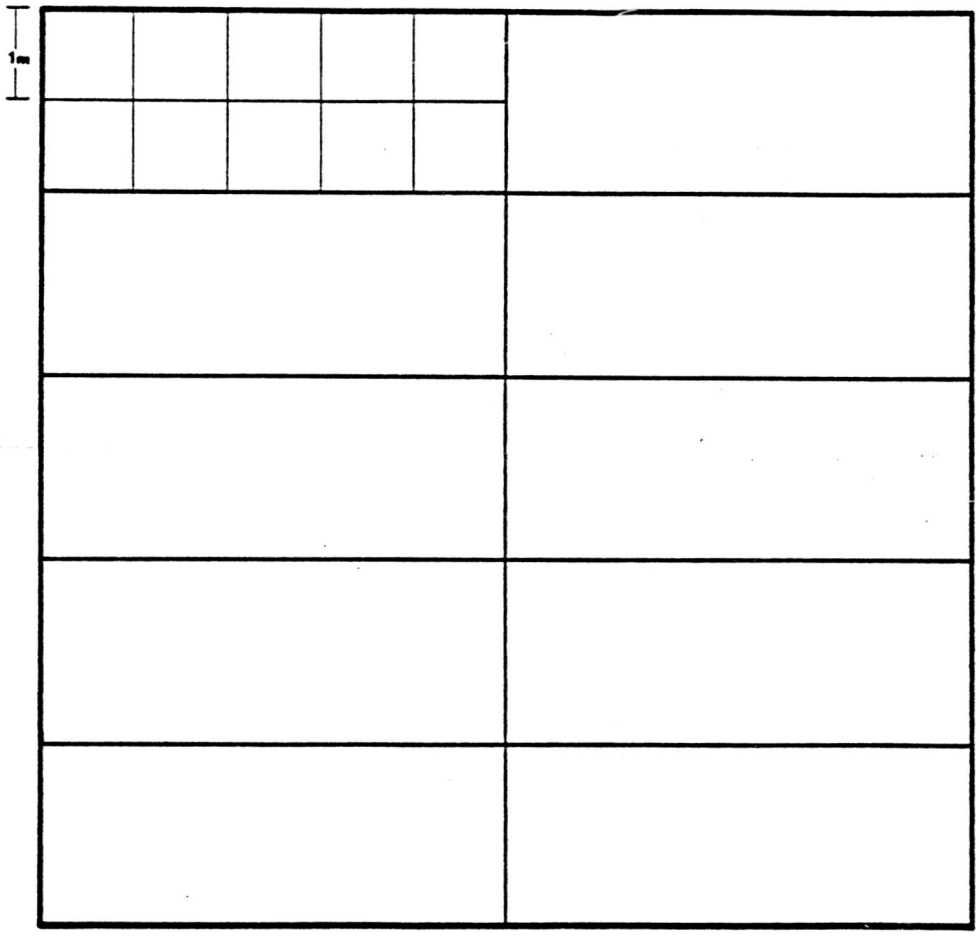


Figure 3. Diagram of the 10 x 10 m sample plots used in 1979. Subplots are 2 x 5 m and quadrats sampled are 1 x 1 m. One quadrat was randomly selected for sampling in each subplot.

species in each plot, 1 being 1-25% of the individuals of a species showing evidence of grazing; 2, 26-50%; 3, 51-75%; 4, 76-100%. One $0.25m^2$ subquadrat was randomly selected in each quadrat for production estimates. Herbaceous plants were clipped at ground level and the material sorted to include only plant material produced that year. Cover estimates were made for shrubby species and some cushion plant species which were not harvested. The samples were dried at 65^oC and weighed.

Analytical

Two computer programs, ORDIFLEX (Gauch, 1977), and CLUSTAN (Wishart, 1975), were used to aid in the analysis of the plant community data (cover values for each species in each plot). Computer analysis was done on the University of Washington's CDC 6400 computer.

The clustering program CLUSTAN, produces dendrograms which help define important plant communities (see Clifford and Williams, 1973, for a description of the use of clustering programs). An hierarchical subprogram was used which operates by evaluating all of the plots in a sample, and combining the two most similar plots into one. It then considers the new set of plots, determines the two that are most similar and joins them, successively until all of the plots are joined. The level at which the groups formed are meaningful is subjectively determined.

Polar ordination is one of the ordination techniques that is available in the ORDIFLEX program. Polar ordination provides a means by which important environmental gradients determining the distribution of plant communities can be indirectly determined. This technique was first developed and used by Bray and Curtis (1957). The polar ordination program operates on the principle of similarity and dissimilarity of plots. The two most dissimilar plots form the endpoints of the first axis. Subsequent axes are defined by the two plots that are most unlike the first two endpoints and each other. The rest of the plots are then arranged according to their similarities to the reference endpoints.

Plant community types were defined by these techniques and the ridge was surveyed to determine their distribution. A map of the plant communities was made with reference to areal photos. The areal extent of the different communities was estimated by cutting them out of the map and weighing, using paper weights of standard areas as a reference.

Methods - 1980

Exclosures (10m x 10m) paired with vegetation plots 1, 2, 11, 14, and 20, were constructed as soon as possible after snow-melt. The exclosures were divided into two equal areas, one to be reserved for non-distructive vegetation sampling and the other to be used for harvesting and

production estimates (Figure 4) The paired unexclosed plots were treated in the same way. Production harvests were carried out at 3 or 4 times during the summer, June 11-15, June 29-July 2, July 17-21, and August 24-September 5. Seven quadrats ($0.25m^2$) were harvested each time. The quadrats were located within the exclosure in a stratified random procedure, 1 in each of the 6, 1m x 4m subplots and another 1 in a randomly selected subplot. Different sample quadrats were harvested each time.

Important forage species were selected as target species in each plot. Total plant cover, and cover of each target species were visually estimated to the nearest 0.5%. All plants were clipped at ground level and sorted to include only current season production, dried at 65°C to a constant weight, and weighed. The target species were harvested seperately and the number of individuals harvested was recorded. For Festuca idahoensis and Poa incurva, an "individual" was a clump with a standard basal area ($4.5cm^2$). Cover estimates were made for Phlox diffusa and Juniperus communis; the plants were not harvested. In the June and July harvests, 7 quadrats ($1m^2$) were randomly located in the non-exclosed plot. An appropriate number of individuals of the target species were randomly located in each quadrat and clipped at ground level. Biomass per individual was calculated for target species inside and

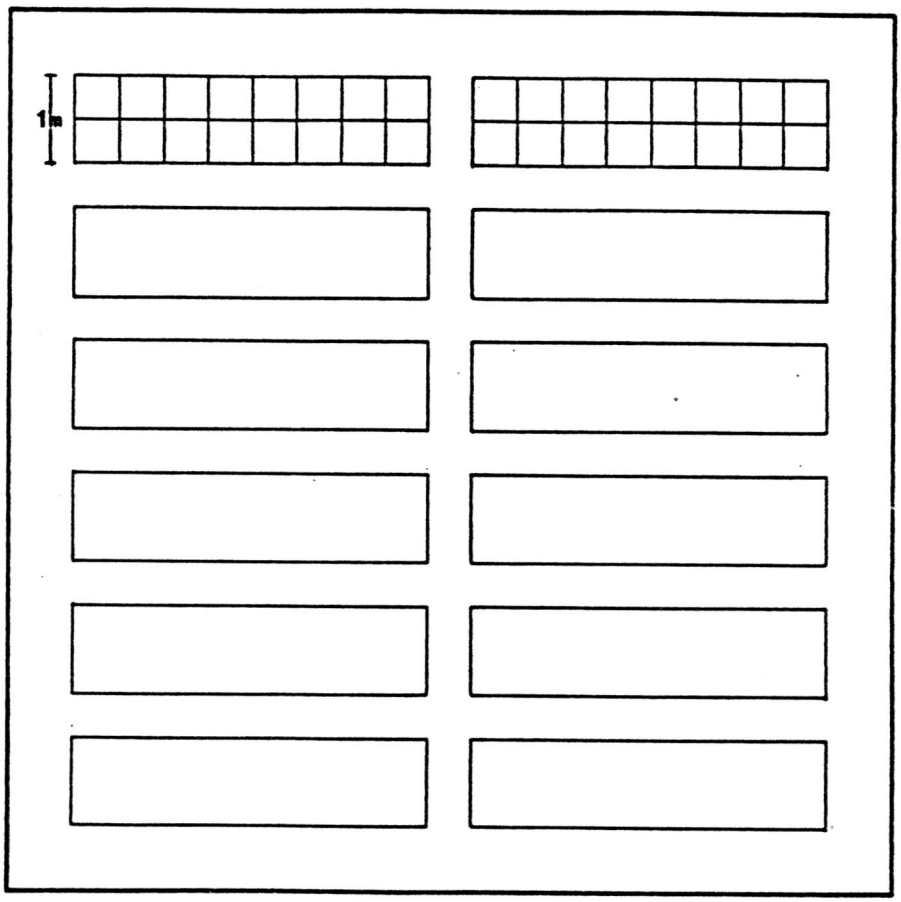


Figure 4. Diagram of the 10 x 10 m exclosure sampled in 1980. Subplots are 1 x 4 m with 0.5m walkways provided. One half of each exclosure was used for production harvests. Quadrats harvested are 0.5 x 0.5 m. One quadrat was randomly selected for harvest in each subplot and in one additional randomly chosen subplot.

outside the exclosures. In the final harvest, cover estimates were made for each species, individuals of the target species were counted, the plants (including Phlox) were clipped at ground level, seperated to species, dried and weighed. The exclosure and non-exclosed plots were treated the same in the final harvest.

Plant Community Results

The 20 communities sampled can be grouped into 9 distinct plant community types. The degree of relatedness of the communities sampled is indicated by the height at which they are joined in the dendrogram produced by CLUSTAN (Figure 5). There are three basic "families" of communities, the first being those meadows that are included in the broad range of Community Type 1 (CT 1), that generally occur on fairly stable slopes with the snow cover melting early in the season (mid-May to early June). The second includes plots limited to unstable substrates (CT's 2 and 3), and the members of the third group are communities in stable areas with late snow melt (CT's 4, 5, 6, and 7). Two communities are very dissimilar from the others, CT 8 is a moist site at low elevation which has some species found in other types, but also has a number unique to this type. The ridge top community (CT 9) has many species that are not found in other areas that are adapted to the harsh, more alpine conditions of this site.

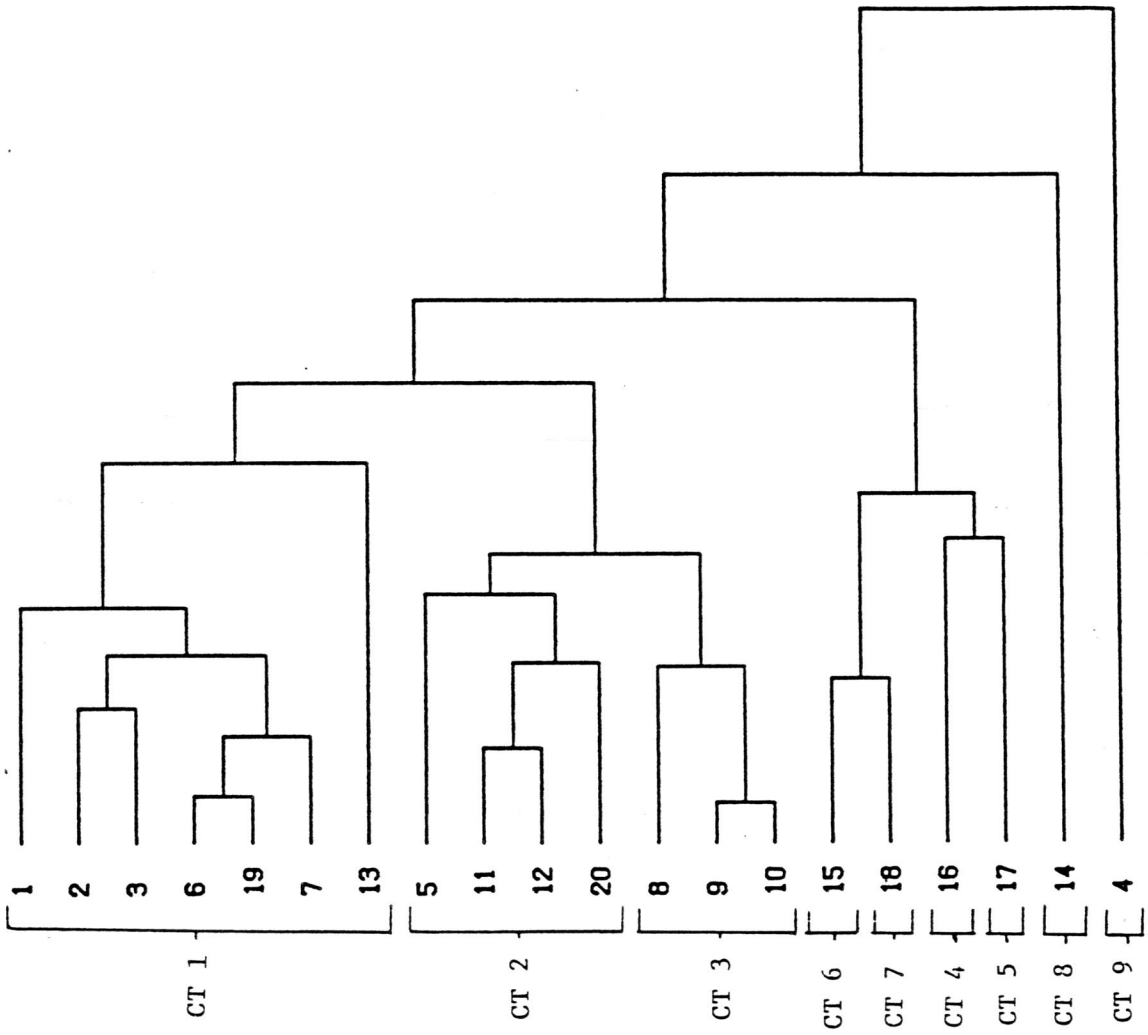


Figure 5. Classificatory dendrogram of 20 plots sampled on Klahhane Ridge. Community types are indicated by brackets.

The axes of an indirect ordination are usually interpreted as environmental gradients important in determining the distribution of species and hence that of communities. The dominant gradients are frequently not single environmental factors, more often they are groups of factors which change together. Microenvironmental measurements were not made in each of the plots sampled in this study, therefore the gradients must be inferred from apparent macro-environmental differences. Axis 1 is best interpreted as a scale of substrate stability (Figure 6). Stability decreases from left to right on the plot, from the late snow plots which have virtually no erosion potential, to the scree plots in which the substrate is actively moving. The second axis is not so easily interpreted. Time of snow melt appears to be an important factor, with the plots at the top of the ordination having late snow melt and those at the bottom relatively early. This creates a multiple gradient which includes the length of the growing season and the amount of available soil moisture.

Community type 1, Phlox-fescue meadow.

This plant community type dominates many areas of Klahhane Ridge. It occurs on stable substrate on slopes from 5°-30°. It is most abundant on southern aspects, but also occurs on stable areas on the ridge top and on east facing slopes in the north cirque. These communities are

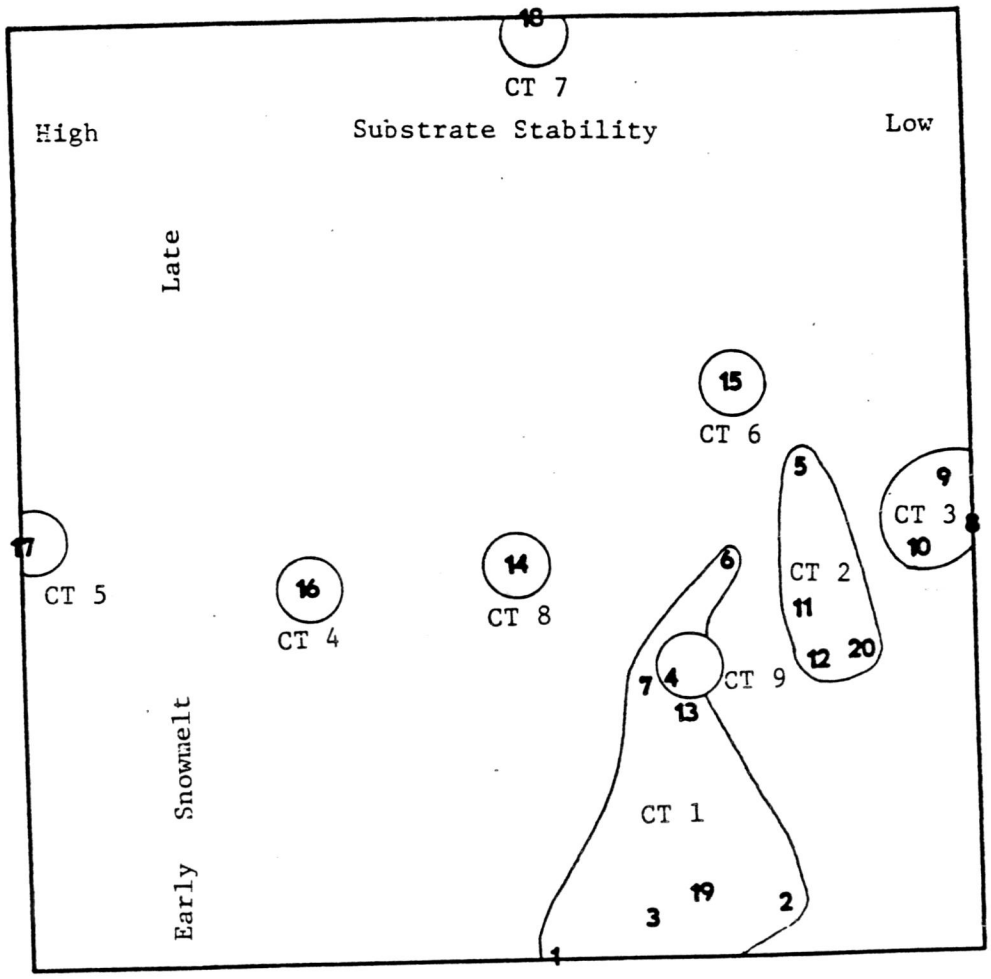


Figure 6. Two dimensional polar ordination of 20 plots sampled on Klahhane Ridge. Lines enclosing plots delimit community types.

elements of the mesic grass forb meadow type described by Kuramoto and Bliss (1970). There is considerable variability in species composition depending on elevation and the duration of snow cover. There is a gradient of snow release times, with the majority of the meadows being released in early to mid-May. These meadows are dominated by Phlox diffusa, Festuca idahoensis, and Arenaria capillaris. In the lee of tree groups, where snow remains longer (early June), large herbs such as Lupinus latifolius and Hydrophyllum fendleri join the other dominants. In more level areas which hold snow until the middle of June, elements of late snow melt meadows (e.g. Carex spectabilis, and Erigeron perigrinus) begin to replace some other species (e.g. Phlox diffusa, Erigeron subtrinervis). At low elevations, Festuca idahoensis becomes quite dominant, while Arenaria capillaris is rare. At high elevations this community type grades into the ridge top fellfields (CT 9), with the appearance of mats of Juniperus communis and associated more alpine species (e.g. Oxytropis campestris, Solidago multiradiata etc.). The meadows are extremely species rich (54 spp. total, average 24 spp./plot), many species have a high frequency but relatively low cover (e.g. Achillea millefolium, Viola adunca, Agoseris spp., Orthocarpus imbricatus, Silene parryi, and others). Average above ground production was about 165 g/m^2 (Table 1).

Table 1. Above-ground net primary production in plant communities sampled in 1979.

Community Type	Plot #	Production Mean (g)	S.D.	n
Phlox-	1	148.6	45.1	9
fescue	2	147.7	63.6	10
meadow	3	187.3	56.7	10
	6	233.4	70.9	10
	7	234.0	109.0	10
	13	70.0	14.4	10
	19	156.0	46.5	10
CT 1 Average		168.1±15		69
Unstable	5	211.1	151.5	9
herb	11	192.8	75.1	9
meadow	12	76.0	44.4	10
	20	no sample		
CT 2 Average		160.0±28		28
Scree	8	9.2	7.0	10
	9	33.4	26.4	10
	10	89.9	40.4	10
CT 3 Average		44.2±15		30
Heather CT 4 (herbs only)	16	19.2±6	8.8	10
Late snow CT 5	17	118.8±54	74.8	10
Lupine-sedge CT 6	18	222.0±38	53.2	10
Luetkea drainage CT 7	15	34.1±17	30.9	15
Tall sedge, grass, herb CT 8	14	113.2±26	36.4	10
Ridge top fell field CT 9	4	no sample		

Many species show evidence of grazing. Festuca, Phlox, Silene, Lomatium nudicaule, Erigeron spp., Aster paucicapitatus, Bromus sitchensis, and Polygonum bistortoides appear to be the most preferred, although average grazing estimates indicate that none were grazed more than 25% of the time when the plots were sampled. The fescue dominated lower elevation meadows had very little evidence of grazing during the growing season. The goats use the south side meadows during the periods of cool weather early in the season, and again in the fall. They avoid this area during the hottest part of the summer. The meadows in this community type which are on cooler east slopes are grazed during the hot time in the middle of the summer.

Community type 2, Unstable herb meadows.

This meadow type occurs on the south-facing slopes on the ridge, below basaltic outcrops, as well as on an east-facing slope in the north cirque. The substrate is extremely unstable and slopes are steep (30-36°). The vegetation is similar to the dry grass forb meadow type of Kuramoto and Bliss (1970). Dominant species change with the amount of available moisture. The exposed areas on the south side which melt in early May, are dominated by Eriophyllum lanatum, and Artemesia ludoviciana, with Phacelia heterophylla and Achillea millefolium. East-facing

slopes which melt in mid-May have no Eriophyllum and less Artemesia. Cirsium edule becomes more important and Phacelia and Achillea remain important. In sheltered sites on the south side with early June snow melt, the dominants are Cirsium and Phacelia. Elements of the lower elevation mesic Saussaurea forb community (Kuramoto and Bliss, 1970) also make an appearance in these areas (e.g. Saussaurea americana, Aster paucicapitatus and Bromus sitchensis). Hydrophyllum fendleri is important in all areas but was senescent at the time of sampling in most plots. Phlox and Festuca are common in some areas, though not nearly as abundant as in CT 1. Community types 1 and 2 share many minor herbaceous elements.

Net above ground production is quite variable, according to the abundance and stature of the tall herbs. Estimates from two plots in the same meadow were 90g/m^2 and 200g/m^2 (Table 1, Plots 12 and 11). Plant cover in these plots was 36% and 43% respectively. Grazing was heavy in this community type, with nearly all species showing some grazing evidence. Species which were heavily used (more than 25% of the individuals were grazed) are Festuca, Silene, Erigeron, Bromus, Eriophyllum, Artemesia, Campanula, Aster, Hedysarum, Poa, Valeriana, and Elymus. The dominant species, especially Phacelia, Hydrophyllum, and Cirsium, escaped serious defoliation from grazing. The areas were

used all summer, but heavy use occurred in the east-facing meadows during the hottest parts of the summer, July to mid-August. During these times these areas are shaded more than meadows on the south side.

Community type 3, Scree.

This community type is associated with actively moving steep (35-40°) scree slopes. Plant cover is sparse (15±15%) and is usually dominated by large herbs. Senecio neowebsteri is abundant in areas of late snowmelt in the north facing cirque. Areas on the north side which are snow free earlier in the season are dominated by Phacelia heterophylla, along with Delphinium glareosum. Achillea millefolium occurs with relatively high frequency, though it is not as tolerant of active soil movement as the more robust herbs. Small herbs and grasses are found in the lee of large plants and boulders. Net above ground production was low, and extremely variable depending on local plant cover (10-90g/m^2, see Table 1). Despite the low productivity, these areas were quite heavily used by the goats for forage. Phacelia heterophylla, the dominant species in many areas of this community type, was not seriously grazed. Many of the associated grasses and herbs are significantly grazed, Achillea millefolium, Bromus sitchensis, Aster paucicapitatus, Hedysarum occidentalis, Erigeron perigrinus, and Valeriana sitchensis individuals

were all grazed 26-50% of the time. Poa incurva and Sitanion hystrix were grazed 76-100% of the time. The goats forage in the north-facing scree areas as the shadows move across them during the hot days of the summer.

Community type 4, Heather.

This plant community occurs on relatively gentle north-facing slopes that become snow free in early June. This type fits well into the heather shrub type described by Kuramoto and Bliss (1970). The meadows on Klahhane are dominated by Cassiope mertensia, with a cover of about 30-40%. Phyllodoce empetriformis is of secondary importance, its cover averaging about 10%. Luetkea pectinata, Carex spectabilis, and C. nigricans have a high frequency and low cover. Herb above ground production averaged about 20g/m^2. Carex spectabilis and Polygonum bistortoides are moderately (less than 25%) grazed.

Community type 5, Late snow dwarf sedge.

Communities of this type occur in protected basins where snow accumulation is high and release from snow cover does not occur until early to mid-July. There is nearly a continuous mat of vegetation and decomposing plant litter. Carex nigricans, and C. spectabilis share dominance in the plot sampled, each with a cover of about 30%. Antennaria lanata is important in areas that are marginal to the late snow basins. Phleum alpinum, Potentilla flabellifolia, and

Polygonum bistortoides are frequent associates with low cover values. Above ground production in this community was measured at about 120g/m^2. This compares with estimates for this wide-spread community type of 155±35g/m^2 in both 1966 and 1967 (Kuramoto and Bliss, 1970). Carex spectabilis is by far the preferred forage species in this habitat, showing evidence of grazing on more than 50% of the individuals. Carex nigricans, Polygonum bistortoides and Erigeron perigrinus are moderately (less than 25%) grazed.

Community type 6, Lupine-sedge meadow.

This plant community is restricted in distribution to well-drained north-facing slopes with very late snow melt. It is a subset of the tall sedge type that has widespread distribution in the Olympic Mountains (Kuramoto and Bliss, 1970). Plant cover is about 70%. On Klahhane, the community is dominated by Lupinus latifolius, with a cover of about 60%. Carex spectabilis is second in abundance with a cover of less than 10%. Other species of minor importance include Veronica cusickii and Luetkea pectinata. Net production in this community averaged about 220g/m^2, the bulk of which was Lupinus and C. spectabilis. This is substantially less than the estimates from the sedge dominated tall sedge type with production of 320±66g/m^2 in 1966, and 395g/m^2 in 1967 (Kuramoto and Bliss, 1970). Significant grazing occured on C. spectabilis, with more

than 50% of the plants being heavily grazed. Poa cusickii was also heavily grazed (more than 25%) while Veronica cusickii and Lupinus showed grazing of less than 25%.

Community type 7, Luetkea drainage.

This community type is related to both the heather and the late snowmelt basin (Figure 5). It occurs in drainages on gentle north-facing slopes. Plant cover is about 30%. Luetkea pectinata, a low growing herbaceous species that spreads vegetatively by lateral shoots, is the most important species with an average cover of about 15%. Carex nigricans and C. spectabilis are also relatively abundant. Luzula piperi, Juncus drummondii, and Veronica cusickii have a high frequency and low cover. Net above ground production was quite low in this community, averaging about 34g/m^2. More than 75% of the Carex spectabilis individuals were grazed. Other species, C. nigricans, Juncus drummondii, and J. mertensiana showed moderate grazing (less than 25%). Most species in this community showed no evidence of grazing.

Community type 8, Tall sedge, grass and herb meadow.

This plant community is restricted to a moist area below a waterfall in the north cirque. Total plant cover is about 60%. It is dominated by several species of tall graminoids. Carex spectabilis is the most important species (cover 14%) while the grasses Bromus sitchensis, Deschampsia

caespitosa, Poa incurva, Trisetum spicatum, Phleum alpinum, and Festuca idahoensis cover about 10%. Large herbs are also important, Arnica spp. and Cirsium edule cover about 10 and 4% respectively and occur with high frequency. Net production in this area was about 115g/m^2 in 1979, and 160g/m^2 in 1980. The cool waterfall area is heavily used by goats during the hot part of the summer. Nearly all species showed some evidence of grazing, and a number were heavily grazed, Carex spectabilis, Phleum alpinum, Bromus sitchensis, Poa incurva, and Deschampsia caespitosa individuals were all grazed more than 25% of the time. There was substantial surface soil disturbance in some areas of this community.

Community type 9, Ridge top fellfield.

Cushion and mat forming plants dominate the windswept ridge top areas on Klahhane. The same growth form also makes up an understory in the uppermost krumholtz on the top of the ridge. The community type is a subset of the cushion plant type which is common on dry windy ridges in the northeast part of the Olympic Mountains (Kuramoto and Bliss, 1970). The ridge top is kept snow free much of the winter by strong winds. The soil is very thin and rocky, and vegetation is low growing. Plant cover in the plot sampled was about 40%, with the most important plants being the low mat forms of Juniperus communis and Phlox diffusa.

Many of the species are held in common with CT 1, with which this community intergrades at an elevation of 1800-1830m. The distinguishing feature is the occurance of alpine species which are not found at lower elevations. Among these are Arenaria rubella, Erigeron compositus, Solidago multiradiata, Oxytropis campestris, and Smelowskia calycina. No plant production estimates were made in this area. Evidence of grazing was not abundant in this community though the ridge top was used all summer by the goats while traveling. Species which were significantly grazed were Oxytropis campestris and Solidago multiradiata (less than 25%). Phlox, Festuca, Viola adunca, and Anemone sp. were also moderately grazed (less than 25%). It appears that the ridge top community is probably not an important source of forage for the goats during the growing season while other more productive areas are available.

Community types - Discussion

The environmental factors which are most important in determining the distribution of plant species, and therefore the distribution of plant communities on Klahhane Ridge are the stability of the substrate, and the time of release from snow cover (with its implications on the length of the growing season, temperature, and the amount of available soil moisture during the growing season). Other studies in the subalpine areas of the Olympic Mountains have found

similar gradients to be important in determining the distribution of plant communities. Canaday and Fonda (1974) found a correlation between community distribution and microenvironmental patterns imposed by snowbanks. They described a gradient of snow melt times and plant communities, in order of increasing snow cover, from snow free windswept ridgetops, to mesic grass communities, to tall sedge communities, to dwarf sedge communities released from snow quite late in the summer. These community patterns are quite similar to those found in this study. Belsky (1979) found that substrate stability and soil moisture were the two most important environmental gradients determining community distribution in subalpine and alpine sites at Deer Park (O.N.P.). Kuramoto and Bliss (1970) identified the dominant gradients as air temperature and soil moisture. These are both elements of the time of snow melt gradient identified as being important on Klahhane. Communities that melt out later in the season occupy more sheltered areas that are not as subject to the heating and dessicating influence of the sun as the open communities of the south and east-facing slopes. They will therefore have a cooler mean temperature and will not dry out until later in the season. It is important to note that the range of community types described by Kuramoto and Bliss (1970) is much broader than those described in this study.

GRAZING AND DISTURBANCE

A large grazing animal exerts two primary pressures on the plants in a community, defoliation due to grazing, and the physical disturbance of trampling, pawing and digging (Harper, 1977). The potential changes in plant community composition as a result of grazing and physical disturbance are dependent on the following factors: 1) the selectivity of grazing or "predation"; 2) susceptability of different species to predation or disturbance; and 3) competitive nature of the community.

While large herbivores tend to be generalists, preferences for certain food items can normally be demonstrated. Factors which influence the choice of one plant species over another include the following: a) relative nutritional value and digestability of different plants or plant parts; b) presence of plant defences, either chemical (alkaloids, tannins, etc.) or physical (thorns, spines, etc.); c) phenology of the plants will influence both of the preceeding factors; d) the mode of grazing; some animals can be much more precise in their bite than can others. The growth form of the plants will influence the ability of an herbivore to profitably consume it; e) intensity of use of an area; selectivity of forage items

decreasing with increasing use of an area; and f) the whim of the individual animal (Stoddart and Smith, 1955; Harper, 1977)

While most plants are detrimentally affected by the loss of resources due to grazing and trampling, plant response to defoliation and physical disturbance differs between species. Some plant species can tolerate levels of grazing or disturbance harmful to others. The growth form of a plant influences how it is affected by both defoliation and physical disturbance. Plants which have their growing point at or near the ground level are more resistant to defoliation (Harper, 1977) and trampling (Schreiner, 1974), Plants with an upright form and terminal growing point can lose most of their reserves to a single grazing event, and are more susceptable to fragmentation by trampling. Plants which evolved with heavy grazing pressure may actually function more efficiently if they are grazed than if not (McNaughton, 1979).

The competitive nature of the community is important in determining how grazing and disturbance pressures affect the balance of species. Biotic interactions are very important in shaping community pattern in environments that are not physically limiting to the growth of plants. In severe environments, the distribution of species is more dependent on tolerance to limits imposed by the environment.

Competition will therefore play a smaller role in shaping the community's response to the actions of a large herbivore.

If grazing is uniformly heavy, the competitive hierarchy of a community will be shifted to favor those species which are tolerant of defoliation by grazing. Selective predation can change the composition of plant communities by altering the competitive status of the plants. If competitive dominants are preferred forage species, normally supressed species can be released from competitive exclusion. Unpalatable species can gain a competitive advantage and dominate an area. There are many range land examples of reduction of preferred grasses and increased abundance of unpalatable shrubs as a result of heavy grazing pressure (Mueggler, 1950; Buffington and Herbal, 1964; Pearson, 1965; Laycock, 1967; and others). The species richness of the British chalk grassland is attributed to intensive grazing of the dominant grasses by sheep and rabbits (Hope-Simpson, 1940; Thomas, 1960; 1963). Data presented by Pearson (1965) suggest that the abundance of many species of herbs is greater in grazed versus ungrazed range lands in Idaho. The "deterioration" of range lands due to grazing pressure may result in a more species rich assemblage of plants. Grazing prevents a natural succession towards scrub vegetation, followed by woodland in

the British Chalk (Tansley and Adamson, 1925), and slows the successional progress of mid-grass prairie toward tall grass prairie with woody vegetation (Penfound, 1964). Choice of food items by different species of herbivore results in grazed meadows of different composition. Pastures grazed by cattle are dominated by a high proportion of forbs, while grazing by sheep results in meadows dominated by grasses (Norman, 1957).

If subordinant species are preferred, the competitive hierarchy is enhanced, and a decline in diversity is to be expected, as preferred forage items are consumed to local extinction. This is possible with a selective generalist, as the animal can survive on less favored forage items and continue to prey upon the preferred when encountered (Harper, 1977).

The theoretical relationship of non-selective predation or physical disturbance, and diversity of plant communities is fairly well accepted (Odum, 1963; Harper, 1969; Grubb, 1977; Grime, 1979). As disturbance increases, sites are opened in the community which can be exploited by colonizing plants. The increase in species density continues until the severity of the physical environment limits the ability of many species to survive. A model proposed by Grime (1973) graphically presents the above concept (Figure 7). Communities in environments which are physically limiting to

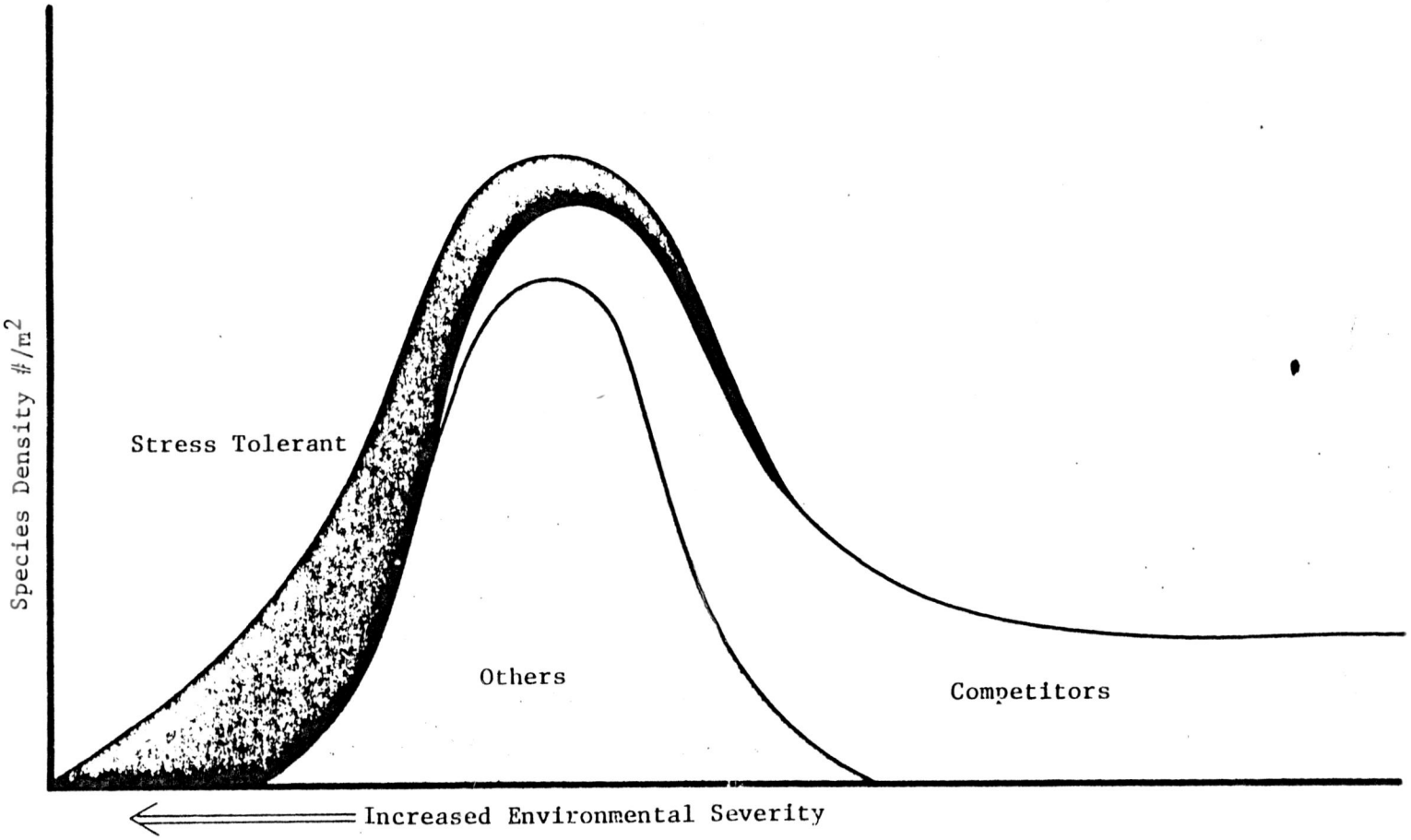


Figure 7. Model of relationship of plant species density and physical disturbance. Redrawn from Grime, 1973.

the survival of plants will decrease in species density as a result of the increased stress imposed by a grazing animal.

Grazing preference

In order to be able to predict the effect of the mountain goats on the plant communities of Klahhane Ridge the following questions about their foraging activities must be answered:

1) Are the goats selective or general in their choice of food items?

2) If they are selective, what is the status of their preferred and non-preferred forage species in the plant community, dominants, potential dominants, or subordinants?

Methods

The forage species used by the goats were determined by estimating the proportion of grazed plants of each species in each plant community sampled in the vegetation analysis. It was relatively easy to determine whether most species had been grazed, by the presence or absence of evenly clipped plants or plant parts. This method does not seperate grazing activities of other mammalian herbivores from that of the mountain goat, but the density of goats on the ridge, compared to other herbvivore densities is sufficient to hold them responsible for the majority of observed defoliation. These data were supplemented by observations made of

mountain goat foraging activities. This method provides a general impression of feeding, although it was usually quite difficult to determine exactly which plants were being grazed in the low growing vegetation. The methods employed provide sufficient resolution to be able to answer the questions posed above.

Results and Discussion

The mountain goats of Klahhane Ridge are selective generalists in their choice of forage items. There are very few species which show absolutely no grazing evidence (Appendix A). The majority of species occasionally showed evidence of grazing. There are a number of preferred forage species that are grazed a high proportion of the time, and another group which are rarely taken (Table 2).

Observation of mountain goat feeding activities support the contention that they are selective generalists. The goats snuffle along in the plants, appearing quite random in their selection of food items. Selection appears to be based more on smell or taste than sight. Frequently, they will graze up to and around a large clump of a non-preferred species. Other times the goats will apparently selectively forage for certain plant species, generally only if the species is abundant in the area. It must be noted that on several occasions goats were seen to selectively graze species which were normally not preferred (i.e. Phacelia

Table 2. Plant species which are preferred mountain goat forage, and species which are generally avoided.

Preferred forage species	Family
Festuca idahoensis	Graminae
Poa incurva	"
Elymus glaucus	"
Bromus sitchensis	"
Carex spectabilis	Cyperaceae
Artemesia ludoviciana	Compositae
Erigeron subtrinervis	"
Erigeron perigrinus	"
Eriophyllum lanatum	"
Aster paucicapitatus	"
Senecio neowebsteri	"
Silene parryi	Caryophyllaceae
Silene douglasia	"
Polygonum bistortoides	Polygonaceae
Campanula rotundifolia	Campanulaceae
Hedysarum occidentalis	Leguminosae
Oxytropis campestris	"
Avoided species	
Hydrophyllum fendleri	Hydrophyllaceae
Phacelia heterophylla	"
Cirsium edule	Compositae
Lupinus latifolius	Leguminosae
Cassiope mertensianus	Ericaceae
Phyllodoce empetriformis	"

heterophylla and Cirsium edule).

Many of the species which are grazed far less frequently than their abundance in the community would predict, are low-growing species which may be difficult to profitably consume (e.g. mats of Phlox diffusa, Arenaria capillaris, A. rubella,, rosettes of Erysimum arenicola, Geum triflorum). The most obviously non-preferred species are large herbs (i.e. Phacelia heterophylla, Hydrophyllum fendleri, Cirsium edule).

Most of the species which are preferred forage are not dominant or potential dominants in their respective plant communities. These species can be expected to decline in abundance as a result of selective grazing. There are two cases where dominant species may be losing importance in their preferred communities due to heavy grazing. These are Festuca idahoensis and Carex spectabilis. In the case of F. idahoensis, many subordinant species may be benifitting from the decline in vigor of this species due to heavy grazing in the stable meadows of CT 1. The low mat plants Phlox diffusa and Arenaria capillaris (co-dominants with fescue in CT 1) are not heavily grazed, but do not seem to be gaining importance in this community type, probably because of their slow growth and mat plant form. The communities in which Carex spectabilis is a dominant are areas of late snow melt and hence a restricted growing season. The number of

species which are able to exploit the reduction in vigor of this dominant species is small. Co-dominant species which are not heavily grazed (e.g. Lupinus latifolius) will increase in importance. The abundance of Lupinus in the meadow sampled (CT 6) could be a product of this selective pressure compared with other meadows where Carex clearly dominates, meadows that experience a much lower goat density.

Senecio neowebsteri is a dominant species in some scree areas and recieves significant grazing pressure. While this species may be suffering from selective predation (Pike, 1981), there are no other species able to tolerate the extreme growing conditions to take advantage of the reduced vigor.

The major non-preferred species are outstanding in that many of them are dominants in their respective communities (e.g. Phacelia heterophylla, CT's 2 and 3; Cirsium edule, CT 2; Hydrophyllum fendleri, CT 2; Lupinus latifolius, CT 7; Phyllodoce empetriformis and Cassiope mertensiana, CT 4). These species stand to gain in competitive advantage due to the selective foraging of the goats.

While it was not the objective of this study to quantitatively determine the composition of the diet of the mountain goats on Klahhane Ridge, these results do allow some generalizations to be made. The summer diet of the

goats on Klahhane is composed primarily of grasses, sedges, and herbs. Shrubby species are unimportant, perhaps due to the dearth of appropriate species (i.e. Vaccinium or Arctostaphylos spp., etc.). A goat will occassionally be seen eating large amounts of conifer foliage (Abies lasiocarpa), but this is unusual. This diet compares with summer diet compositions ranging from shrub dominance reported by Anderson (1940) in the Cascade Mountains, to other areas where grasses and herbs make up the bulk of the forage (Saunders, 1955; Hibbs, 1967; Smith, 1976). A summary of the literature values for summer diet composition is presented in Table 3.

The success of introduced and native populations of mountain goats in a number of different areas with widely varied plant species compostion suggests that the species' requirement of habitat conditions relies more on the presence of steep rocky outcrops than it does on the presence of specific forage items. The goats are able to adapt their feeding preferences to the forage available in an area.

Community effects - Grazing

Two efforts were made to determine how mountain goat grazing may be affecting the important plant communities of the south side of Klahhane Ridge (CT 1). The first, carried out during the summer of 1979, was an extensive survey of

Table 3. Summer mountain goat diet composition (Adapted from Hjeljord, 1971).

Area	Composition					Reference
	Grass	Forbs	Ferns	Conif	Shrub	
Cascades	12	18	-	-	70	Anderson, 1940
Alberta	63	14	-	-	23	Cowan, 1944
Montana	76	18	3	1	2	Saunders, 1955
Colorado	82	14	-	T	4	Hibbs, 1967
Alaska	36	14	-	-	-	Hjeljord, 1971
Montana	32	44	-	T	24	Chadwick, 1973
Montana	72	26	-	T	2	Smith, 1976

all components of the plant community. The second, carried out in 1980, was an intensive study of the production response of Festuca idahoensis to simulated grazing. The two studies will be dealt with independently.

Big south meadow - Survey

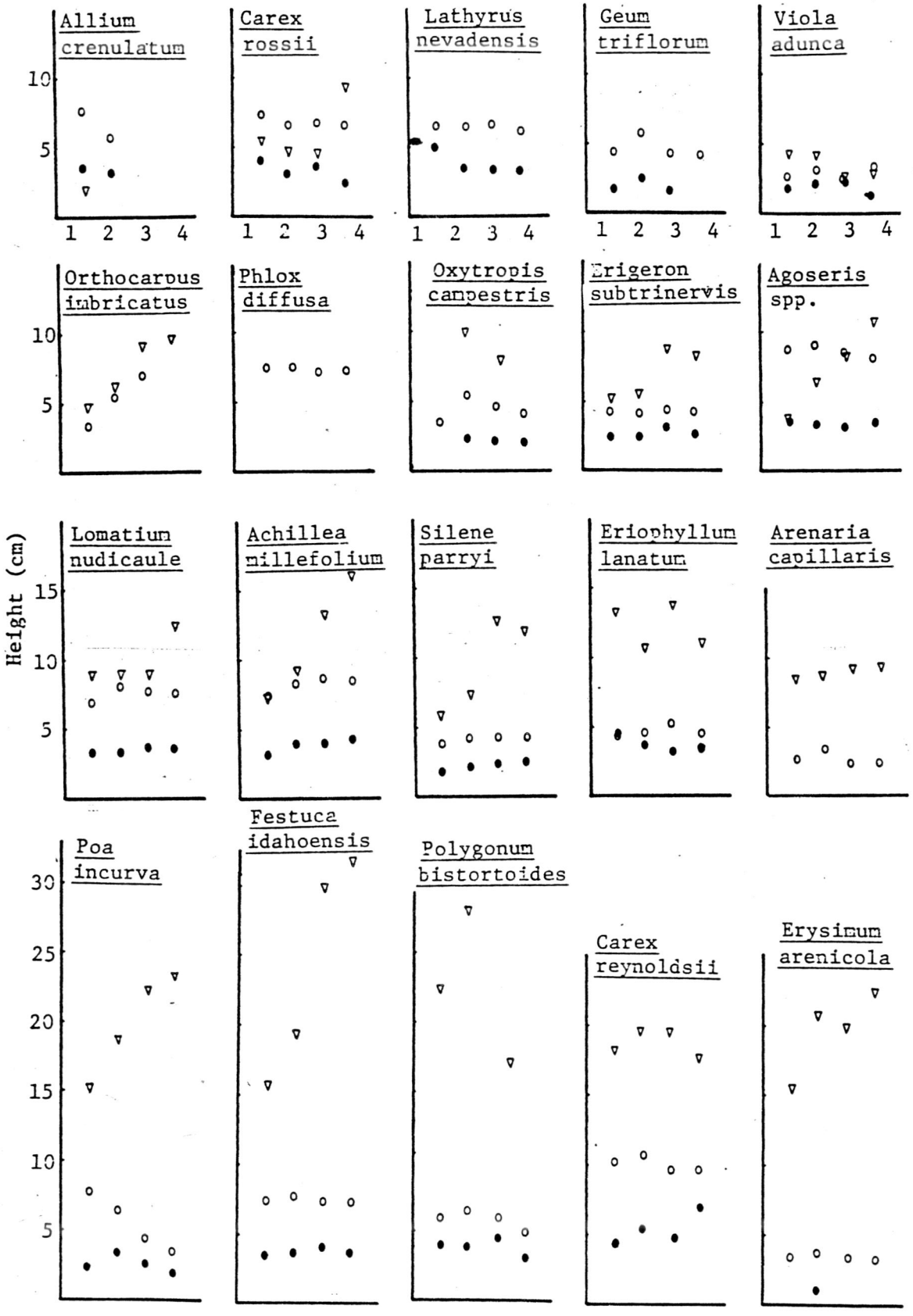
Methods

A large south-facing meadow near the top of Klahhane Ridge was selected as the site for the extensive study of community response to mountain goat grazing. Plots (43, $0.5m^2$) were located randomly on a grid in unexclosed areas of the meadow. Two plots were randomly located within each of five large (4m x 4m) exclosures to be used as a control sample. Diagonal corners of each plot were permanently marked with pins, to enable repositioning a 0.5m x 1m frame. Unexclosed plots were sampled four times (late June, mid-July, late July, and late August). The exclosure plots were not sampled at the end of August due to time constraints. Cover, phenology, and intensity of grazing were recorded for each species. Measurements were made of the average height of grazed leaves, average height of ungrazed leaves, and the average height of an ungrazed stem or flower.

Results

Vegetative growth had essentially ceased and flowering had begun for most of the species by the first sample time (Figure 8). Figure 9 shows that the level of grazing

Figure 8. Mean leaf length (ungrazed - 0; grazed - 0) and flower height (V) for 20 important species in 43 plots in a south facing meadow on Klahhane Ridge. Sample periods 1-4 are on the x-axes. Sample period 1, late June; 2, mid-July; 3, late July; and 4, late August.


Allium crenulatum
Carex rossii
Lathyrus nevadensis
Geum triflorum
Viola adunca
Orthocarpus imbricatus
Phlox diffusa
Oxytropis campestris
Erigeron subtrinervis
Agoseris spp.
Lomatium nudicaule
Achillea millefolium
Silene parryi
Eriophyllum lanatum
Arenaria capillaris
Poa incurva
Festuca idahoensis
Polygonum bistortoides
Carex reynoldsii
Erysimum arenicola
Height (cm)
1 2 3 4

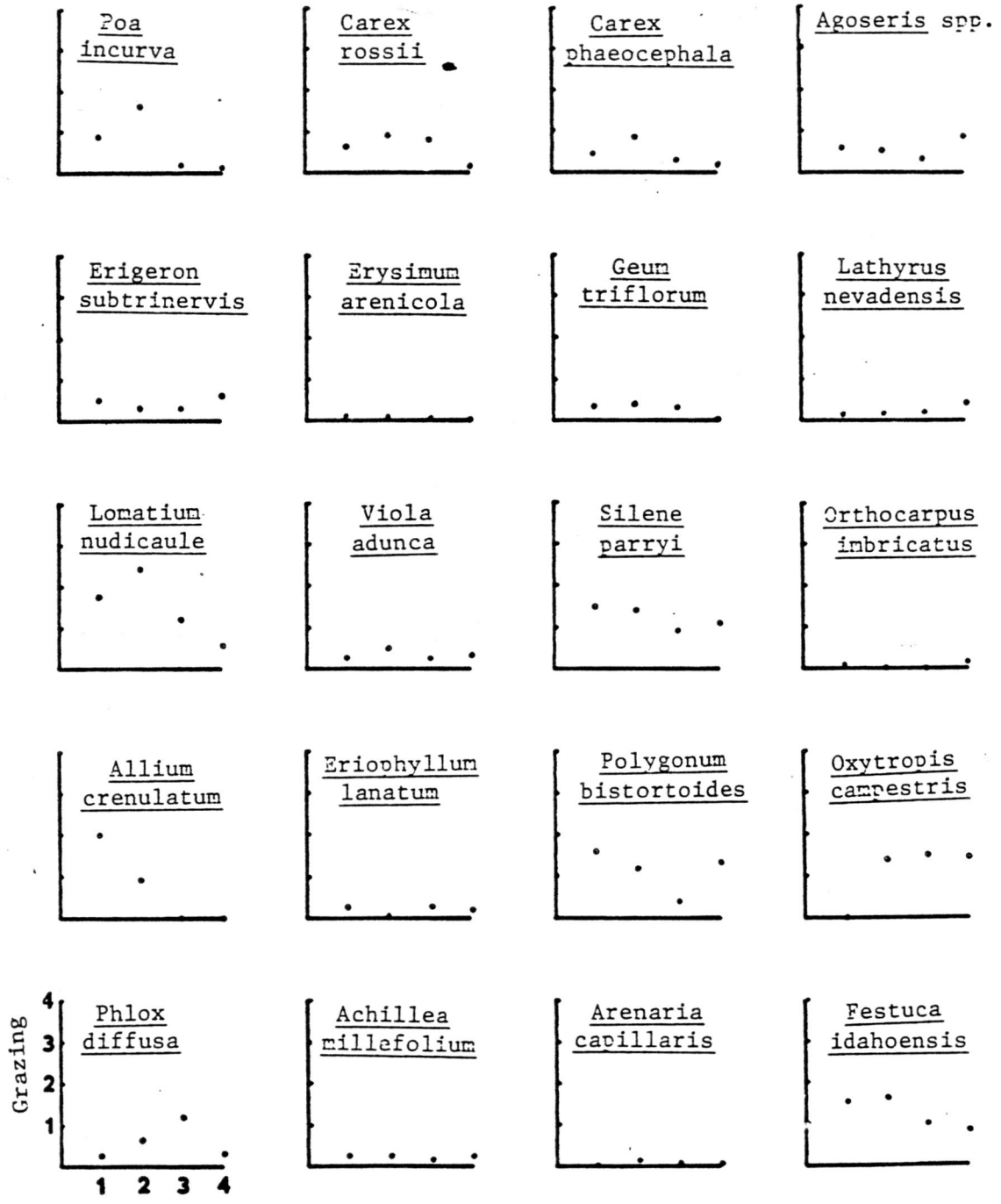


Figure 9. Mean grazing values for important species in 43 plots in a south facing meadow on Klahhane Ridge. Sample period 1, late June; 2. mid-July; 3, late July; and 4, late August.

changed very little for all species during the time period sampled. Most of the grazing had occurred in this meadow prior to the initiation of sampling. This is supported by direct observations that the goats did not forage in the south-facing meadows to any great extent during the hot part of the summer (July and early August). By late August, the goats were using these meadows on cool days but evidently the level of use was not sufficient to be detected in our sampling.

Evidence of grazing was recorded on most species. Many species showed more than 25% of the individuals grazed, Festuca idahoensis, Silene parryi, Lomatium nudicaule, Poa incurva, Allium crenulatum, and Oxytropis campestris. Other species were frequently grazed (less than 25%) Phlox diffusa, Carex rossii, C. reynoldsii, Agoseris spp., Polygonum bistortoides. Oxytropis is outstanding in that it was not grazed until the second week of July. Nearly every individual of this species observed on the ridge showed evidence of heavy grazing by the end of the summer.

Many species show more vigorous growth and advanced phenology inside the exclosures (Table 4). The differences are more pronounced in species which are significantly grazed (i.e. Festuca idahoensis, Poa incurva, Agoseris spp., Lomatium nudicaule, and Polygonum bistortoides), but not all species which are grazed show this response. Plant species

Table 4. Species which show advanced phenology and/or greater leaf length or flower height inside exclosures. Species which recieve significant grazing pressure are indicated with an asterisk.

Advanced Phenology	Flower Height	Leaf Length
Festuca idahoensis*	Festuca idahoensis*	Festuca idahoensis*
Arenaria capillaris	Arenaria capillaris	
Poa incurva*	Poa incurva*	
Erigeron subtrinervis*	Erigeron subtrinervis*	
Eriophyllum lanatum	Eriophyllum lanatum	
Erysimum arenicola		
Polygonum bistortoides*		
Lomatium nudicaule*		
Geum triflorum		
	Danthonia intermedia*	
	Orthocarpus imbricatus	
	Antennaria microphylla	
	Achillea millefolium	
		Carex rossii*
		Agoseris spp.*
		Lathyrus nevadensis

which do not recieve significant grazing pressure also show more vigorous growth and advanced phenology inside the exclosures. These plants are probably responding favorably to the removal of disturbance by trampling.

It is also conceivable that the enhancement of growth and acceleration of phenology within the exclosures may be due to the creation of a more favorable environment due to the presence of the fence around the exclosure plots. These areas retain more snow and may be subject to less wind than the open meadow. This could result in an enhanced moisture regime which might be responsible for the growth response. These effects are minimized by the construction of large exclosure areas, and by using fencing material with large mesh which minimizes wind reduction.

While the general vigor of a number of species in this plant community has declined, probably as a result of mountain goat activities, there are no apparent changes in community composition as a result. It is concievable that the grazing and trampling pressure may depress some species enough that others may be more able to survive. A long term study of the exclosed and unexclosed areas of this meadow is necessary in order to quantitatively determine the nature of community changese due to mountain goat activities.

Simulated grazing on Festuca idahoensis

The response of important community members to

defoliation must be understood, in order to be able to help predict the effect of grazing on a plant community. To this end we examined the production response of Festuca idahoensis to simulated grazing. This bunch grass is a dominant species in the south-facing meadows on Klahhane Ridge, it is also an important forage species for the mountain goats.

Methods

Sixty Festuca idahoensis plants with a similar basal area ($75cm^2$) were located in a subalpine meadow near Steeple Rock, an area of very low goat use. The plants were randomly assigned to 1 of 4 treatments, the control plants, which were not clipped during the growing season, and three levels of "grazing" intensity, clipped once, twice, or three times during the growing season. Simulated grazing was carried out at a height of 2-3cm (determined to be the average height of goat-grazed plants on Klahhane). All of the plants were cut at ground level at the end of the growing season. The harvested parts were dried to a constant weight and weighed. Total production of each plant was determined by summing the different harvest amounts. A one-way ANOVA was carried out to determine if the mean total above-ground production was significantly different between treatments. A Stewart-Newman-Kuels test was used to determine the means that were significantly different at the

5% level (Sokal and Rohlf, 1969).

Results

The abovground production of ungrazed plants was significantly greated than that of any of the grazing treatments. While a trend toward reduced production with increasing frequency of clipping was indicated, none of the grazed samples differed significantly (Table 2.5). None of the grazed plants successfully produced flowers, while 36% of the control plants did.

Table 2.5. Results of simulated grazing study on Festuca idahoensis.

Component	Clipped 3 times	Clipped 2 times	Clipped 1 time	Control no graze
Mean total production (g)	4.01	4.15	4.53	5.13*
Flowers Initiated (at first clip)	47%	64%	53%	57%
Successful Flrs. (final harvest)	0%	0%	0%	36%

*Means are significantly different $F_{0.05,3,40}=2.84$

Underlined values are not significantly different (5%) (SNK)

Discussion

Festuca idahoensis is a bunch grass common to grasslands and sagebrush desert, to dry and rock mountain slopes and meadows from British Colombia to Sierran California and east to Alberta and Colorado (Hitchcock and Cronquist, 1973). It is an important species in many

rangelands throughout the Great Basin and into northern California. Defoliation of Idaho fescue has resulted in a loss of "vigor" in this and other studies (Pond, 1969; Hormay and Talbot, 1961). Hormay and Talbot (1961) reported that clipping during active growth reduced total herbage yield, reduced basal area 49% the following year, increased mortality, and reduced flower stalk production. In areas that had been heavily grazed by cattle they observed 21% fewer F. idahoensis plants, the plants were 42% smaller in size resulting in 68% less yield than in ungrazed areas. They concluded that the observed patterns could be explained by the nature of carbohydrate storage in the plants. Defoliation is harmful at any time, but it is especially harmful during periods of rapid growth, when stored reserves are at a minimum.

Pond (1960) showed a similar reduction in vigor in grazed versus ungrazed samples. An edaphic effect was noted, with the plants on granitic soils apparently suffering from a lighter level of grazing than plants on more nutrient rich sandstone soils. He found that average leaf length was as good an indicator of plant vigor, and more easily measured, than basal area or total dry weight.

As stated above, F. idahoensis is one of several species which showed more robust growth inside exclosures than it did in areas subjected to goat grazing and

trampling. Ungrazed leaf length and flower height were both greater inside exclosures, and plant phenology was accelerated (Figure 10).

Grazing is concentrated in the south side meadows during the early summer and again in the cool periods of the late summer and fall. Much of the grazing of fescue occurs before the initiation of flowering. As F. idahoensis is a truely caespitose, non-rhizomatous perrenial, it cannot rely on asexual propagation for proliferation, it therefore must successfully flower and set seed in order to maintain its population. According to Hormay and Talbot (1961), and supported by the findings in this study (Table 5), grazing nearly eliminates flowering success during the year of defoliation, and decreases it in subsequent years. The smaller flower stalk height in the unexclosed meadow is an indication that the amount of energy allocated to sexual reproduction is less than in the undisturbed meadow. It is not known whether the reduction in apparent vigor has resulted in less seed production in the grazed meadow. It is also not known how much of a reduction in seed production would have a significant effect on the number of plants that are able to establish, and hence on the vigor of the population as a whole. It is concievable that the population of Idaho fescue on Klahhane Ridge that is subject to heavy goat use is suffering a loss of vigor. A longer

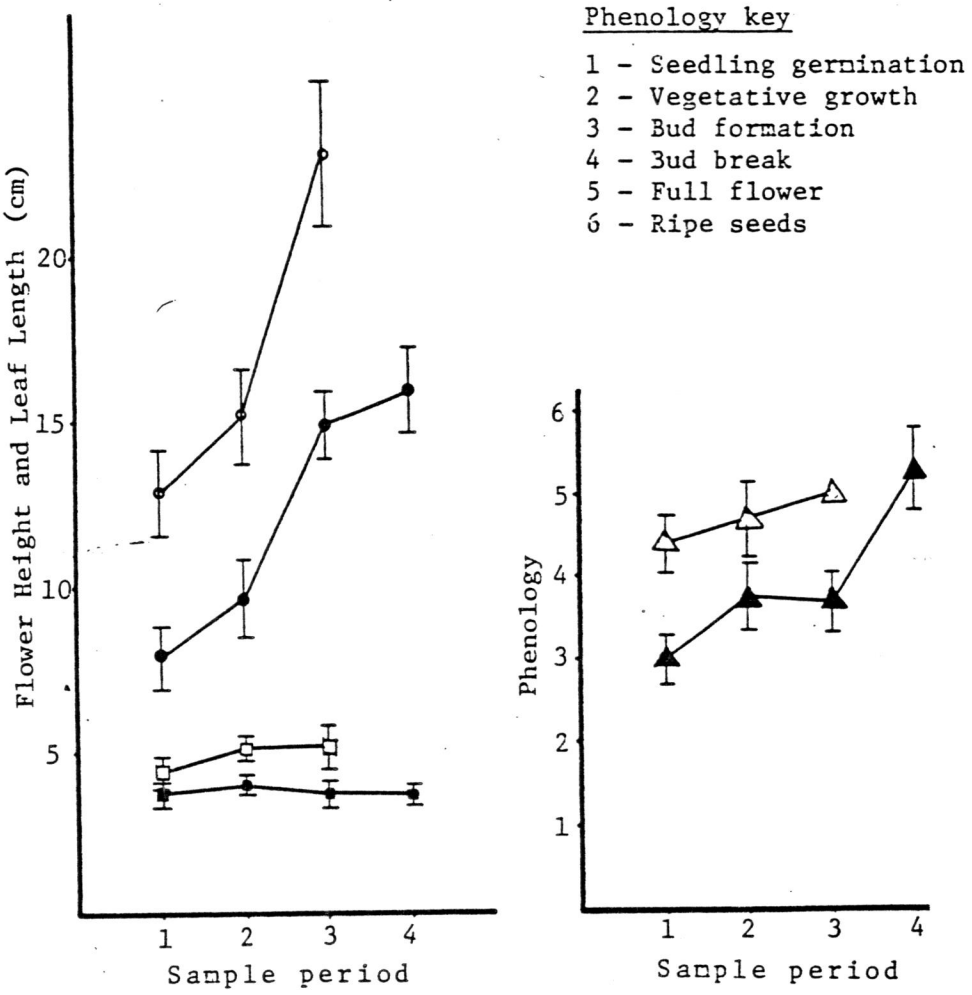


Figure 10. Mean phenology (Δ), flower height (O), and leaf length (□) for Festuca idahoensis plants in exclosures (open figures), and in unexclosed meadow (solid figures). Bars indicate ± 1 standard error. Sample period 1, late June; 2, mid-July; 3, late July; and 4, late August.

term investigation of the biology of this species is necessary to conclusively determine whether its status in the community is severely threatened by mountain goat influences.

The seasonality of goat foraging activities on Klahhane may be causing less damage to the population of Festuca idahoensis than if grazing were not seasonal. Grazing is especially heavy during the later periods of the summer when the vegetative portions of the plants are senescent. While any herbage removal is detrimental to the future health of the plant, grazing at this time has the least effect, as carbohydrate reserves have been translocated for storage in the roots. It is concievable that the areas near the top of the ridge sampled in the extensive study (10% cover) once were dominated by F. idahoensis more like in lower elevation meadows which recieve little grazing pressure during the growing season (25% cover). As many environmental variables change along this elevational gradient, it is impossible to ascribe any observed differences to differential grazing pressure alone. A long term study of the exclosed areas will hopefully reveal the former nature of the meadow community at the top of the ridge.

Mountain goat disturbance

Olmsted (1976) ranked the damage of mountain goat

activities to the environment in the following order: trampling - dust-bathing - bedding - feeding. A casual hiker can easily see that some areas on the ridge have been very disturbed by the goats. The intensity of physical disturbance can range from occasional trampling during grazing activities, to concentrated trampling and trailing in areas of more frequent use, to active pawing and digging during dust bathing or wallowing.

Light trampling

The most notable effect of general light trampling is the loss of species and life forms which are particularly susceptable to this form of disturbance. This is especially notable in the apparent loss of lichen and moss cover in the relatively stable meadows on the south side of Klahhane Ridge. Klahhane's south side meadows were compared with similar meadows on the south side of Tyler Peak, an area of low goat use. Moss and lichen occur within 86% of 22 plots ($0.5m^2$) on Tyler, versus 33% of 43 plots ($0.5m^2$) on Klahhane. On Tyler, moss and lichen have combined cover of about 10%, while on Klahhane their cover is only about 1%. The presence of fragments of well developed lichen and moss ground cover in some areas on Klahhane suggest that the observed difference cannot merely be explained by environmental differences between the two areas. That lichen is extremely susceptable to physical distruction by

trampling has been shown by Schreiner (1974). Kunze (1980) notes that areas with a high level of animal activity (deer and marmot) have low lichen cover.

It is possible that light trampling in relatively stable meadows could open areas for colonization, providing numerous microenvironments to be exploited by a diversity of species. Many of the species growing in the subalpine meadows have life history tendancies which allow them to exploit small openings in the canopy (i.e. active asexual propagation or successful seedling establishment). Some stable communitites may respond to light disturbance with an increase in species diversity. Other areas on less stable substrate will decline in diversity as trampling merely increases the severity of an extreme physical environment. This is the case in the herb meadows on basaltic substrate, where plants of the more stable meadows (e.g. Phlox, Festuca, Arenaria, Viola, etc.) are clinging to isolated patches of stable substrate. These clumps are easily removed by a single footfall. In these areas, even light disturbance by trampling will result in a loss of species.

Concentrated trampling

When trampling becomes more concentrated, sensitive species are lost and plant cover reduced (Bell and Bliss, 1971; Schreiner, 1974). Trails have ben formed in all areas

of Klahhane Ridge by the activities of mountain goats and black tailed deer. The effect of concentrated trampling can be seen at a heavily used area (by humans as well as mountain goats) at the saddle of the ridge. Plant cover is less and Achillea millefolium, an active colonizing species is more abundant.

Wallowing and digging

One activity of the mountain goat that directly alters the composition of the vegetation, is the creation of open areas by dustbathing or wallowing. The goats wallow apparently in order to help thermoregulate, and to control insects (Stevens, 1979). Wallows are present in many areas of the ridge, but are especially abundant in the fine textured sandstone soils of the south side. Seventy wallows larger than $1m^2$ were counted in a reconnaissance of one large meadow (200m x 200m). Of these, 47 (67%) showed an apparent change in plant community composition in the margin and immediately below the open area. In addition to changes in plant species' abundance, the areas are noticably greener than the normal meadow vegetation from the end of July to the middle of August.

A shift in community composition toward an abundance of efficient colonizing species is expected in any area where the plant cover is disturbed. In addition to this shift, it was hypothesized that removal of plant cover has altered the

moisture regime of the immediate surroundings. This could be due to reduction of evaporation because of the lack of a transpiring canopy of vegetation and/or to changes in the soil characteristics due to wallowing activities. The resulting abundance of available moisture for the plants in the immediate vicinity explains the lush vegetation adjacent to the open areas. It may also help explain why species which normally are not important elements of the stable meadow communities of the south side can effectively colonize disturbed sites in this area.

Methods

Three wallows with an apparent change in the surrounding plant community composition were selected for sampling. Transects were run at 2m or 3m intervals perpindicular to a line that was dropped from the top of the wallow to the bottom of the area covered with soil that has been displaced from the wallow. The transects started at the edge of the wallow and consisted of 32 contiguous 1 dm^2 quadrats (Figure 11). Cover classes were recorded for eleven important species in each quadrat, 0, not present; 1, + to 10% cover; 2, 11 to 25%; 3, 26 to 50%; and 4, 51 to 100%. Average cover values were computed for each species at each quadrat distance from the wallow margin by weighting the cover scores, 1=5%, 2=17.5%, 3=37.5%, 4=75%.

Percent soil moisture was calculated by gravimetic

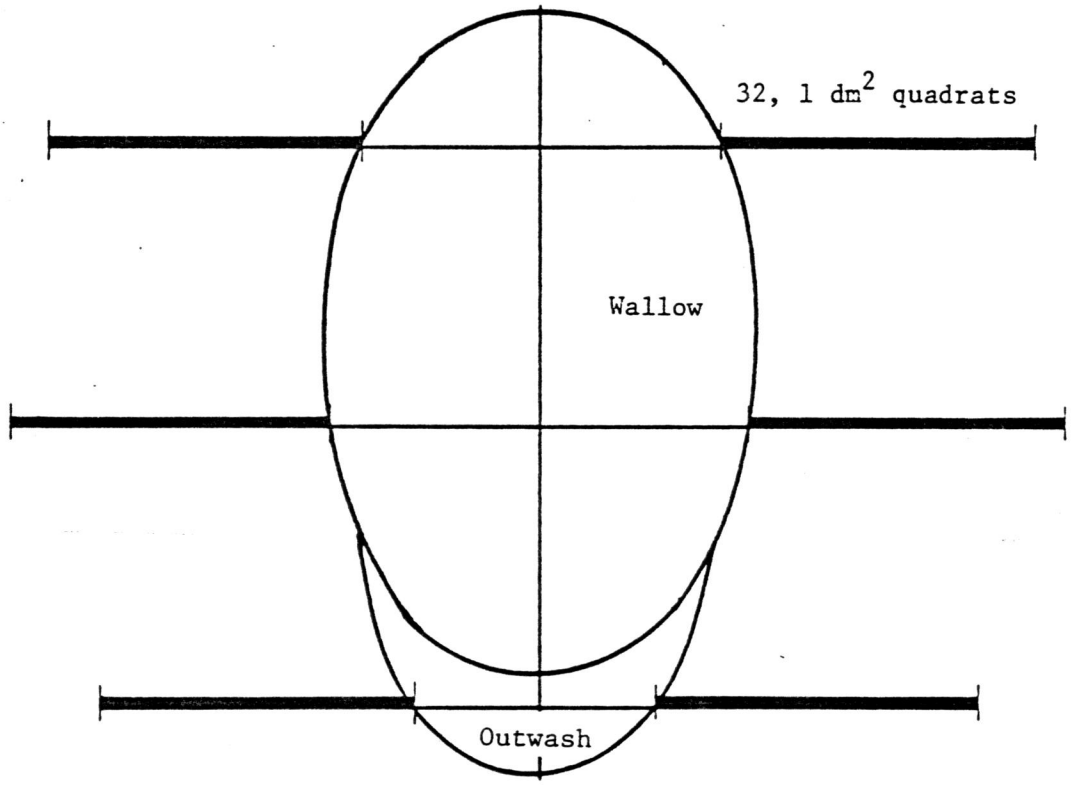


Figure 11. Diagram of method used to sample the vegetation adjacent to goat wallows. Heavy lines represent 32 contiguous 1dm^2 quadrats.

analysis at 3-5 times during the summer in two of the wallows eventually used for documentation of vegetation change, and adjacent undisturbed meadow vegetation on the south side (Plots 1 and 2, CT 1), as well as for meadow soil from plots 11 and 5, areas of naturally high levels of soil movement (CT 2). Three soil samples were collected from the main rooting zone (20-25cm depth) for soil water determination (gravimetric method). Soil texture was determined by the Bouyoucous method (Day, 1965), and percent organic matter by the loss on ignition method.

Results

Three trends of plant cover values occur as the margin of the wallows is approached (Figure 12). Species which show little variation in average cover (Festuca and others), species which decrease in average cover close to wallows (Phlox and Arenaria), and those that increase in abundance close to wallows (Achillea, Artemesia, and Phacelia). Soil moisture curves of the wallow soils are more similar to the soils of the unstable herb community than they are to the soil of the adjacent undisturbed meadow (Figure 13). The stable soils have a higher percent moisture throughout most of the growing season, ending the season at a slightly lower percent than the wallow soils or the soils in the unstable herb meadows. Particle size analysis indicates that the wallow and unstable herb meadow soils have a greater

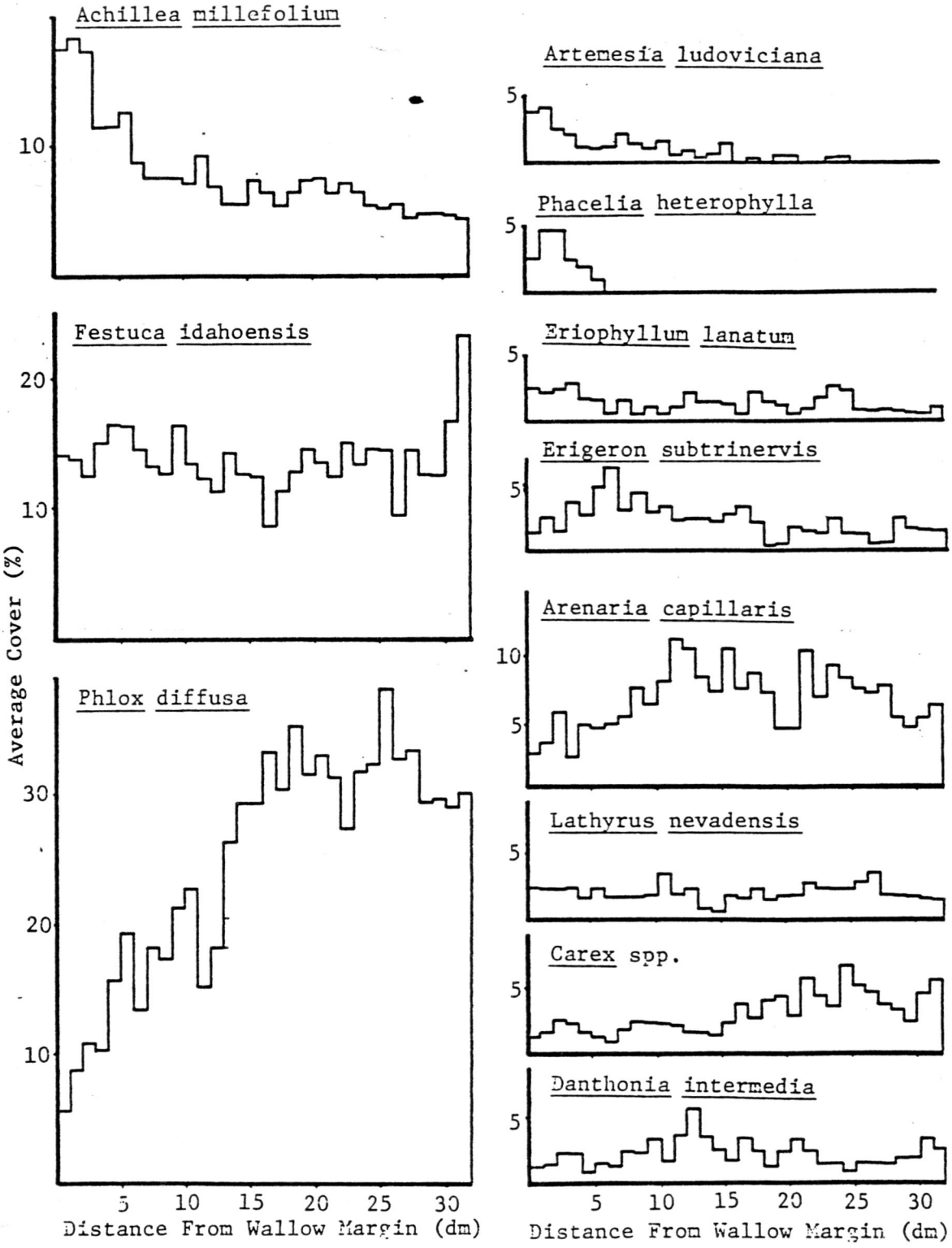
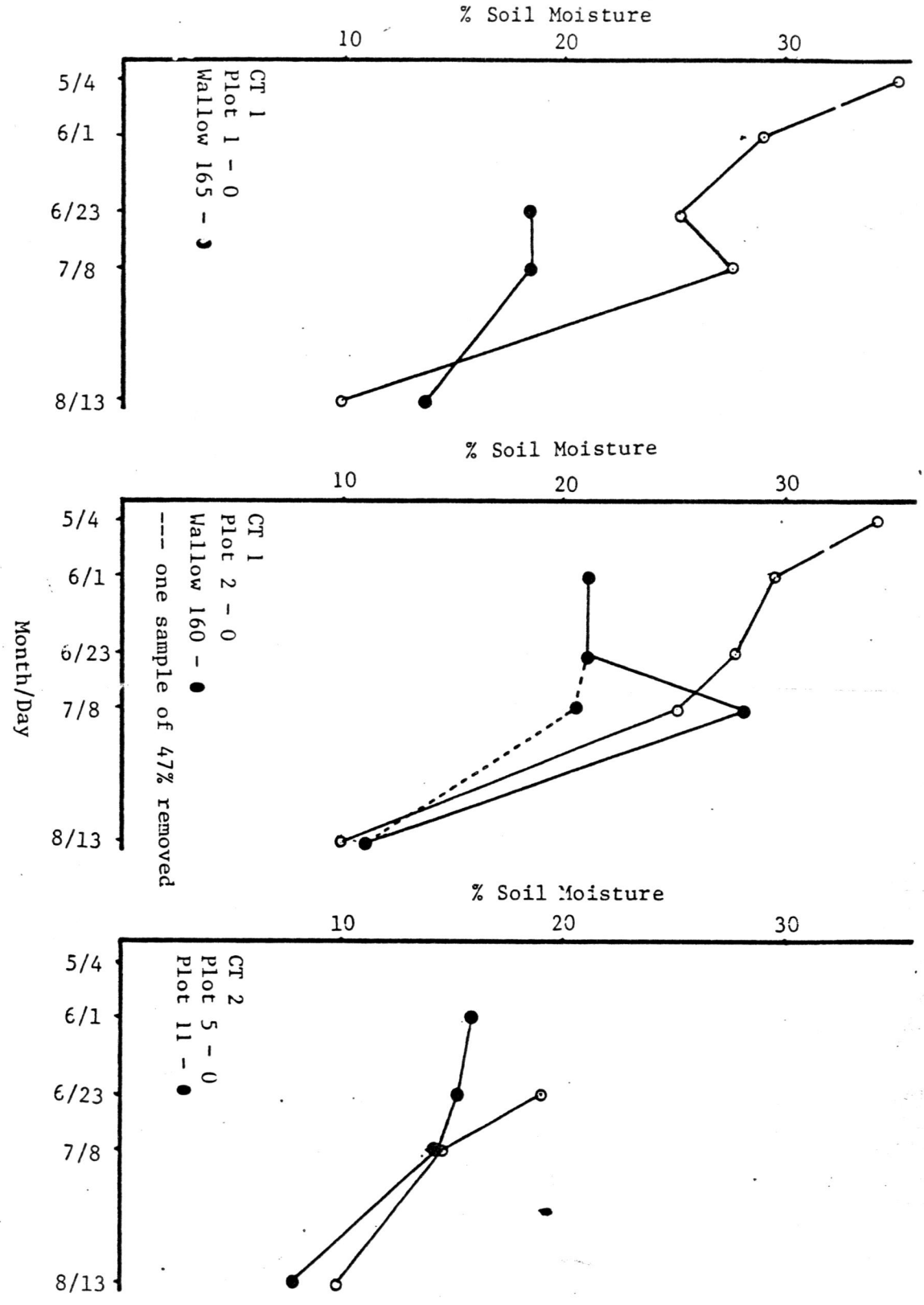


Figure 12. Histograms of mean cover values for eleven species at 1dm intervals from the margins of goat wallows.

Figure 13. Seasonal trends in percent soil moisture for meadow (CT's 1 and 2) and wallow soils.


% Soil Moisture
10
20
30
5/4
6/1
6/23
7/8
8/13
CT 1
Plot 1 - 0
Wallow 165 - ●
% Soil Moisture
10
20
30
5/4
6/1
6/23
7/8
8/13
CT 1
Plot 2 - 0
Wallow 160 - ●
--- one sample of 47% removed
% Soil Moisture
10
20
30
5/4
6/1
6/23
7/8
8/13
CT 2
Plot 5 - 0
Plot 11 - ●
Month/Day

proportion of sand while the undisturbed meadow soils have more silt and clay (Table 6). The loss on ignition of the wallow soils indicates that they have less organic matter than is present in either of the meadow soils (Table 6).

Discussion

Species which are active colonists and that can tolerate significant amounts of substrate instability are more abundant near the wallows than in undisturbed vegetation (Achillea, Artemesia, Phacelia). Achillea is common in the undisturbed meadow, and is an active colonist of open areas. Phacelia and Artemesia are not important members of the surrounding undisturbed meadow community. They occur primarily in areas of active soil movement (i.e. localized disturbed areas and in CT's 2 and 3). The character of these two herbaceous species is different from the surrounding undisturbed vegetation. They are potentially large leafy herbs, while most of the species in this area are quite low growing. It was this observation and the observation stated above, that the margins of the wallows are obviously greener than the surrounding vegetation during the dry period at the end of the summer, that led to the hypothesis that the goat wallows were isolated patches with an altered moisture regime. The more mesic environment adjacent to the wallows allows species which cannot successfully compete for moisture in this

Table 6. Soil characteristics from undisturbed meadow (CT 1), wallow (CT 1), and unstable meadows (CT 2).

	Sand (%)	Silt (%)	Clay (%)	Loss on Ignition (%)
CT 1				
Plot 1	71	16	13	12.9
Plot 2	67	19	14	12.7
Wallow 160	76	13	11	9.3
Wallow 165	71	15	14	11.5
CT 2				
Plot 5	75	13	12	10.9
Plot 11	78	13	9	14.1

Table 7. Physical properties of soils from Kuramoto and Bliss, 1970.

Community	Horizon	Texture Clay (%)	Silt (%)	Sand (%)	Soil moisture .033 mPa	1.5 mPa
Dry grass-forb	A	72.6	14.1	13.3	23.2	8.8*
	AC	73.9	11.7	14.3	18.1	6.6*
	C	69.4	14.0	16.6	17.8	7.1
Mesic grass	A	63.5	20.3	16.2	44.1	29.3*
	B_1	67.8	14.8	17.4	26.2	15.0*
	B_2	68.3	18.7	14.0	21.8	7.4

*Main rooting zone

community to establish themselves. It was felt that reduced transpiration demand due to the lack of plant cover could result in patches of soil with more water available for the surrounding vegetation.

It can be seen from the percent moisture curves of the wallow soils and the meadow soils that the moisture regime of the wallows is indeed different from that of the normal meadow (Figure 13). It appears that the wallows have less moisture than the undisturbed soils for most of the summer, and while the amount of moisture in the soil is greater at the end of the summer, a difference of 1 or 2 percent is not too substantial. It must be remembered that the important aspect of soil moisture for the plants is not the total amount of water in the soil, rather it is the amount of available moisture in the soil that determines the plants' response. Available moisture is water that is present in the soil at water potentials greater than the wilting point water potential of the plants. Kuramoto and Bliss (1970), obtained moisture release values for the soils from their mesic grass community (of which the phlox-fescue communities on the south side of Klahhane are members) and their dry grass forb meadow (similar to the unstable herb meadows on Klahhane). They found that the moisture release values for the rooting zones of the two soils were quite different, and that the soils of the dry grass community were

physiologically wetter than those of the mesic grass community (Table 7). This means that if a mesic grass community soil has 15% water, the soil is at the wilting point (-1.5 mPa), while the soil of the dry grass community would still have a large amount of available moisture. The dry grass community soils do not reach the wilting point until they reach about 7% water.

The difference in moisture retention between two soils is generally due to particle size and/or organic matter content differences. Soils with lots of fine clay particles and/or organic matter will hold water tighter than will soils of a more coarse texture. It was hypothesized that the activities of the wallowing goats, and the removal of the cover of vegetation resulted in a soil that had characteristics more like those of the unstable meadows where Phacelia and Artemesia are abundant, than those of the surrounding undisturbed vegetation.

This hypothesis is supported by our results, in that both wallow soils and soils of the unstable herb meadow have a higher percetage of sand than do the undisturbed meadow soils (Table 6). The wallow soils appear intermediate between the two meadow soils in this regard. The amount of organic matter of the wallow soils is less than in either meadow soil. This could serve to further increase the difference between the moisture retention properties of the

meadow and wallow soils. It therefore appears that while the wallow soils are coarser and should therefore drain more rapidly than the undisturbed soils, the wallow soils have the same or more moisture at the end of the growing season. This water is more available to the surrounding plants than the water that is tightly bound to the clay particles and organic matter of the meadow soil. This increased availability of moisture allows plants which normally cannot compete for moisture in this community to successfully invade open areas created by goat wallowing.

In addition to helping to understand plant colonization patterns in areas of localized disturbance, this information also provides some insight into successional processes that occur in this area. An unstable slope is colonized by large taprooted herbs (Phacelia heterophylla and Senecio neowebsteri) that are tolerant of active substrate movement. As these herbs begin to stabilize areas of the slope, other species can become established in their lee. Species such as Achillea millefolium and Artemesia ludoviciana are especially efficient colonists in this regard because they do not need to rely on the uncertain prospects of sexual reproduction in this severe environment. They can spread vegetatively as long as soil movement is not too active. As the slope is further stabilized, species which are not tolerant of physical disturbance can become established

(Phlox, Arenaria, Festuca, and many others). With increasing vegetation cover, finer soil particles are trapped and organic matter accumulates. In an environment which recieves its major input of precipitation during the melt of winter snows, the result of increasing clay and organic content in the developing soil is to make soil moisture less available to the plants during the dry period of the growing season. Plants which need abundant moisture to survive are replaced by those which are able to tolerate the more xeric conditions.

The resistance of basaltic substrate to weathering slows the progress of this process. Basaltic substrate that has become stabilized (usually on more gentle slopes) has given rise to the same kind of plant community that occurs on the sedimentary substrates.

Community effects - Conclusions

Each plant community will respond to the influences imposed by the mountain goats in different ways. The severity of the physical environment and the nature and intensity of goat activities will determine each community's response. The following hypotheses can be proposed about the response of the plant communities of Klahhane Ridge.

1) In physically limiting environments (ridge top, late snow, and unstable substrates), any goat activity will further increase the environmental demands on

plant growth and survival. The number of species able to survive declines as stress is increased. The selectivity of grazing focuses impact on the preferred species, while others are spared. Trampling pressures favor species which are tolerant to physical disturbance.

2) In moderate environments, supression of a dominant species by trampling or preferential grazing will result in a release of subordinant species and a subsequent increase in species diversity, or the increased dominance of a co-dominant species if it is capable of rapid growth, and if it is resistant to goat pressure.

These general hypotheses can be used to predict the direction of change for each plant community. Predictions for the nine plant community types important on Klahhane Ridge are summarized below.

CT 1. Selective grazing of a potential dominant (Festuca idahoensis) and light trampling on relatively stable substrates, coupled with the absence of a rapidly growing potential dominant (in most areas) will result in maintenance of high densities of plant species. Other preferred forage species may decline, further increasing the available room for subordinants. Extreme physical disturbance will result in the loss of plant cover and the

creation of patches of early successional species

CT 2 and CT 3. Preferential grazing of subordinant species and avoidance of dominants, as well as increased substrate instability will result in a loss of subordinant species and a decline in species density.

CT 4. General light use, avoidance of dominants, and substrate stability indicate that this community type will change little.

CT 5. The extremely short growing season due to late snow melt, and a nearly complete mat of vegetation and litter make these areas difficult to successfully colonize. Preferential grazing of the co-dominant (Carex spectabilis) will favor the proliferation of associated species. Community response will be slow as plant growth is quite slow.

CT 6. Late snow and an unstable substrate create an environment where biotic interactions are minimized. Species present are adept at colonization in stressful situations, little change in species composition will result from continued goat activity.

CT 7. Preferential grazing of an important species (Carex spectabilis) may favor nearly total dominance by Lupinus latifolius. Breaks in the lupine canopy could be colonized by a number of subordinant species.

CT 8. Uniformly heavy grazing on large plants may

favor lower growing species and an increase in species density, but species with less biomass.

CT 9. The extreme ridge-top environment will decrease in species density as trampling and grazing continues.

CARRYING CAPACITY - A MODEL

Carrying capacity (K) is defined as the population level of an organism at which an equilibrium is attained with the resources provided by the environment (Ricklefs, 1979). A population that exceeds the level of resource availability will decline until a new population level is attained that is in balance with the resources available. Similarly, a population which is not using all of the available resources can be expected to increase until the carrying capacity is reached. The critical limiting resource depends upon the biology of the system, but generally it has two main components, space, and energy or food. Food is frequently considered the major limiting resource for herbivore populations (White, 1978).

It is possible for a population to be maintained below the level of available resources in an area by biotic and/or abiotic factors. The primary non-resource related biotic factor important in maintaining ungulate populations is predation (Pimlott, 1967). Abiotic factors are elements of the environment that cause mortality independent of population levels. In a mountain environment these include such "objective mountain hazards" as rockfall, avalanche, deep snow, loss of footing on steep cliffs, and lightning

bolts.

Populations which are actually limited by food may remain well below the apparent level of food production in an area, "starving in the midst of plenty." Leafy vegetation can be a comparitively low quality food resource in that it has low protein levels, and a high proportion of undigestable material and toxic organic compounds (Wittaker and Feeney, 1971). It may be that populations are not limited by the amount of forage available, but rather by the ability to process the forage efficiently. Populations may be limited by resource requirements at specific stages in their life cycle, high nutrient requirements of rapidly growing young animals are especially important in limiting many populations (White, 1978). The amount of resources available may be limiting during a critical season, especially during late winter when the animals have low energy reserves.

The abundance of all three essential elements of mountain goat habitat (rocky bluffs for cover, open meadows for forage, and thermoregulatory habitat) can potentially limit populations of goats in an area. Given an area of steep rocky outcrops and associated open meadows, it is interesting to ask what size mountain goat population can be supported in the habitat. The question of a carrying capacity for goats on Klahhane Ridge was addressed in the

hopes that it would provide insight into the potential mountain goat population size on Klahhane, and that the model could be generalized to predict population levels in other areas of the Olympic Mountains. This information is important in that it will help gain an understanding of the magnitude of potential changes in habitat due to mountain goat activities.

Results and Discussion

The total net production of each community type (mean net production x areal extent) was calculated from the 1979 production estimates. This provides an estimated total production of about 155,000 kg for the meadow communities on Klahhane Ridge (Table 8). This underestimates the total amount of forage available to the goats as it does not include forage produced in the rocky outcrop, the forested, or the ridge top fellfield areas. Of the time spent in foraging activities on Klahhane Ridge, 87% is spent in open meadows or scree slopes (Stevens, 1979).

The 1980 estimates of production over time (Figure 14) provide an idea of the amount of forage available in important meadow communities at different times during the summer. The meadows in community type 1 have relatively little increase in biomass as the summer progresses compared with those in community types 2 and 8. In the latter areas the plants are primarily large herbs and grasses, while in

Table 8. Total above ground production by community type.

Community type #	Name	Areal extent (m^2)		Production (g/m^2)	Total Production (kg)
1	Phlox-fescue	532,004	46%	168.8±58	8.980×10^4
2	Unstable herb	151,167	13%	160.0±73	2.419×10^4
3	Scree	298,667	26	44.2±41	1.320×10^4
4	Heather	80,166	7%	19.2±9	1.523×10^3
5	Late snow	17,333	1.5	118.8±74	2.063×10^3
6	Luetkea	13,666	2%	34.1±31	1.523×10^2
7	Lupine-sedge	8,666	1	222.0±53	1.924×10^3
8	Tall sedge,grass	8,500	1	113.2±36	9.605×10^2
9	Ridge top	36,000[1]	3%	-	-
	Saussaurea forb	57,000		365.0±106[2]	2.08×10^4
TOTAL PRODUCTION		1,146,169 m^2 (1.14 km^2)			1.54935×10^5

[1]no production estimate
[2]Kuramoto and Bliss, 1970

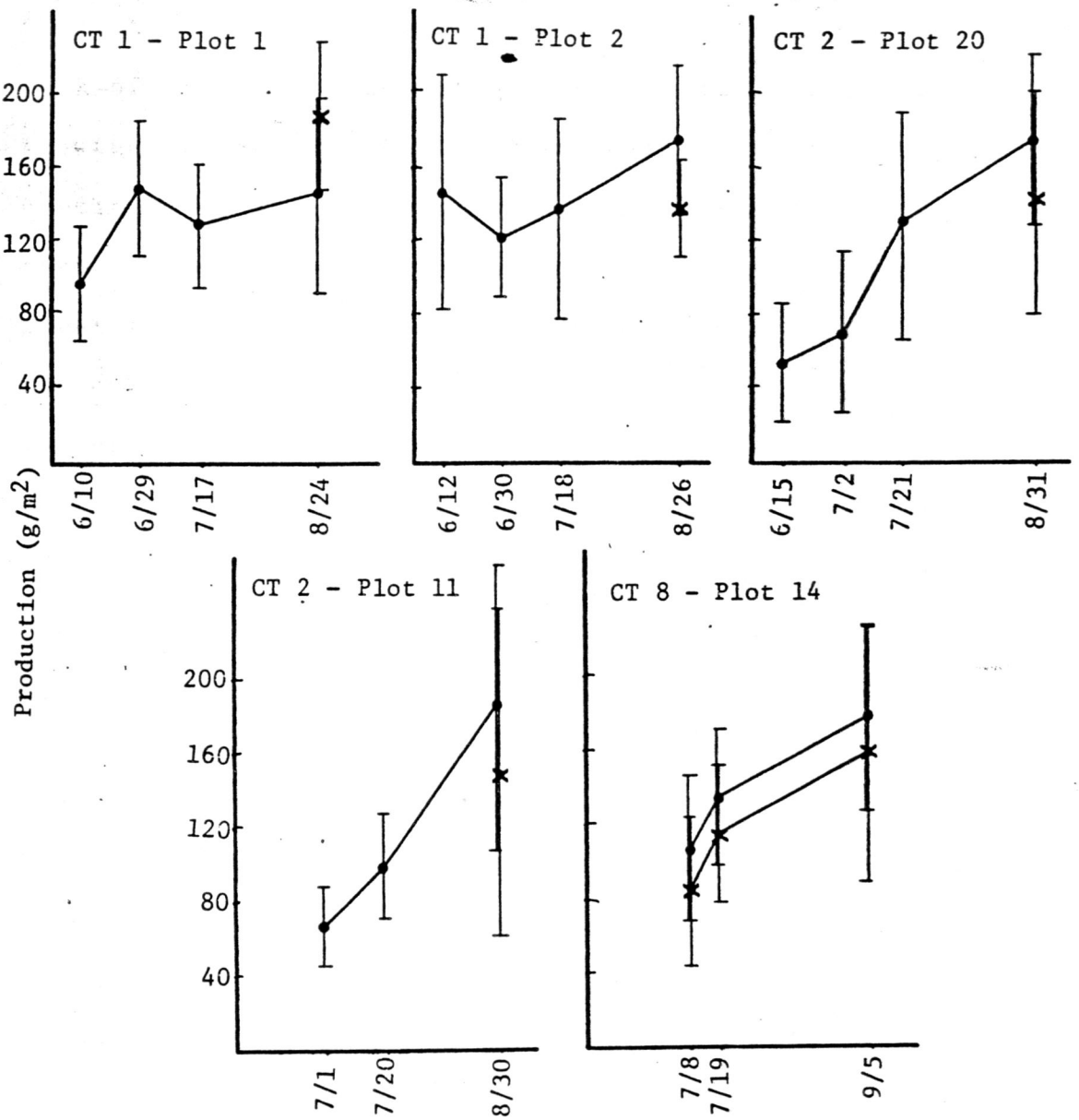


Figure 14. Seasonal trends in net aboveground production in 5 plots (•, inside exclosures; x, outside exclosures) sampled in 1980. Bars indicate ± 1 standard error.

CT 1, herbs and grasses are small and mat plants make up the bulk of the plant biomass. These plants do most of their growing quite early in the season while the taller plants continue to grow though the season. The variability in plant species composition and production within plots is too great to attribute the differences between grazed and exclosed plot production to an estimate of grazing influence.

The amount of forage removed by grazing is estimated for the target species in Table 9. Variability is quite high, but significant differences are obtained for Festuca idahoensis in plots 1, 2, and 11, Poa incurva in plot 1, and Silene parryi in plots 1, 2, and 11. The amount of biomass removed is between 30 and 50% of the total. It is important to note that the sample period(s) where significant differences occurred were early in the season for CT 1, and in the middle of the season for CT 2. These times correspond to the periods of concentrated use in the different areas.

While these results indicate that a substantial amount of biomass of important forage species is being removed, they do not provide an estimate of the total amount of forage being consumed by the goats. This question is very difficult to approach directly as the variability in species composition and productivity is extremely high in all

Table 9. Production per individual of target forage species inside and outside of exclosures at different times during the summer. Values which are significantly different at the 5% level (t-test) are indicated with an asterix, percent difference is indicated for values which are significantly different.

Plot # Species	Date	wt/ind (g) in	wt/ind (g) out		% diff	Plot #	Date	wt/ind (g) in	wt/ind (g) out		% diff
Plot 1	6/10	0.20	0.20			Plot 1	6/10	0.016	0.025		
Festuca	6/29	0.40	0.28	*	29	Silene	6/29	0.024	0.016	*	33
idahoensis	7/17	0.52	0.43			parryi	7/17	0.024	0.024		
	8/24	0.58	0.49				8/24	0.045	0.022		
Plot 1	6/10	0.035	0.033			Plot 1	6/10	0.15	0.09		
Lomatium	6/29	0.056	0.099			Poa	6/29	0.23	0.15	*	35
nudicaule	7/17	0.086	0.074			incurva	7/17	0.47	0.22	*	53
	8/24	0.076	0.063				8/24	0.36	0.33		
Plot 2	6/12	0.36	0.19	*	47	Plot 2	6/12	0.032	0.026		
Festuca	6/30	0.39	0.31	*	20	Silene	6/30	0.033	0.021		
idahoensis	7/18	0.73	0.47			parryi	7/18	0.032	0.032		
	8/26	0.78	0.61				8/26	0.048	0.025	*	48

Table 9 continued.

Plot # Species	Date	wt/ind (g) in	out		% diff	Plot #	Date	wt/ind (g) in	out		% diff
Plot 11	7/1	0.17	0.18			Plot 11	7/1	0.026	0.019		
Festuca	7/20	0.37	0.23	*	38	Silene	7/20	0.030	0.028		
idahoensis	8/30	0.58	0.52			spp.	8/30	0.043	0.024	*	44
Plot 11	7/1	0.52	0.25			Plot 20	7/2	0.027	0.031		
Polygonum	7/20	0.18	0.22			Bromus	7/21	0.064	0.041	*	37
bistort.						sitchensis	8/31	0.103	0.116		
Plot 20	6/15	0.23	0.19			Plot 20	6/15	0.034	0.045		
Festuca	7/2	0.28	0.27			Artemesia	7/2	0.047	0.059		
idahoensis	7/21	0.44	0.36			ludoviciana	7/21	0.099	0.157		
	8/31	0.58	0.50				8/31	0.340	0.260		

communities sampled. The problem of the extent of mountain goat pressure on the food resource was therefore approached indirectly by determining the total amount of available forage on Klahhane Ridge through the growing season, and determining how many goats that it would support. This figure can then be compared with the current population size on Klahhane Ridge for an indication of the extent of the population pressures on the plant communities.

The simplist form of an equation for calculating an area's carrying capacity for a food limited herbivore is to estimate the amount of forage produced in an area and divide that by the amount of forage necessary to support an animal for the time period under consideration: K=P/R/T, where K is the carrying capacity, P is forage production, R is the forage required to support one animal for one day, and T is the number of days in question. Using the data from Table 8 (total production = 155,000 kg) and an estimated average mountain goat daily requirement of 0.92kg of forage per day (2.2% of 42kg average mountain goat body weight, calculated for the Klahhane Ridge population by a weighted average of mean adult nanny, billy, juvinile, and kid weights), the calculated summer (180 days) carrying capacity for Klahhane Ridge is 935 animals. This is considerably greater than the observed population of about 170 goats on the ridge, and assumes that all of the aboveground production is harvested

each year.

A more reasonable estimate of carrying capacity can be obtained if one considers two other important aspects of mountain goat biology: 1) that of thermoregulation, and the abundance of available forage at different times during the summer; and 2) the percentage of forage that can be harvested on an annual basis without serious deterioration to species compostion and net annual productivity. Stevens (1979) noted that the aspect on which mountain goats foraged on Klahhane Ridge was well correlated with temperature. Hot days were spent on north-facing aspects, while cool days are spent on southern aspects. The critical temperature appeared to be about 12-13°C. It must be energetically unfavorable for the goats to forage on the south side when the weather is hot. This is supported by observations that during the hot periods of both 1979 and 1980 summers (early July to mid-August) the goats were rarely seen on the south side of the ridge, their daily foraging activities being carried out on the cooler areas of the ridge. It must be noted that the preference for north side forage during this time may be due to the fact that the areas have been more recently released from snow cover, and therefore may have more young protein-rich shoots, and plants with a high water content, factors that may influence the goats' choice of forage areas.

A modified calculation of carrying capacity for Klahhane Ridge would therefore take into consideration three time periods, the first being early summer, when south side meadows are snow free and the weather is cool (Figure 15), the second being the hot period in the middle of the summer when all areas of the ridge are open, but the northern aspects are favored (Figure 16), and the third being the late summer and autumn) when the entire ridge is available for foraging activities (Figure 17). A seperate carrying capacity can be calculated for each. The time period with the smallest amount of available forage would be the critical period, when the goats are most concentrated on the food resource.

The limiting time period in terms of available forage is clearly the hot summer period. The total amount of plant material available during this time is about 25% of that available during the early summer, and 13% of that available during the late summer and fall (Table 10).

If all of the plant material produced each year was to be consumed, the health of the plant community and the mountain goat population would decline in subsequent years. Thilenius (1975) quotes a "reasonable" stocking density in alpine range lands to be one where 20-30% of the forage is consumed each year. This is reasonable in that it allows sufficient vegetation recovery from year to year to be able

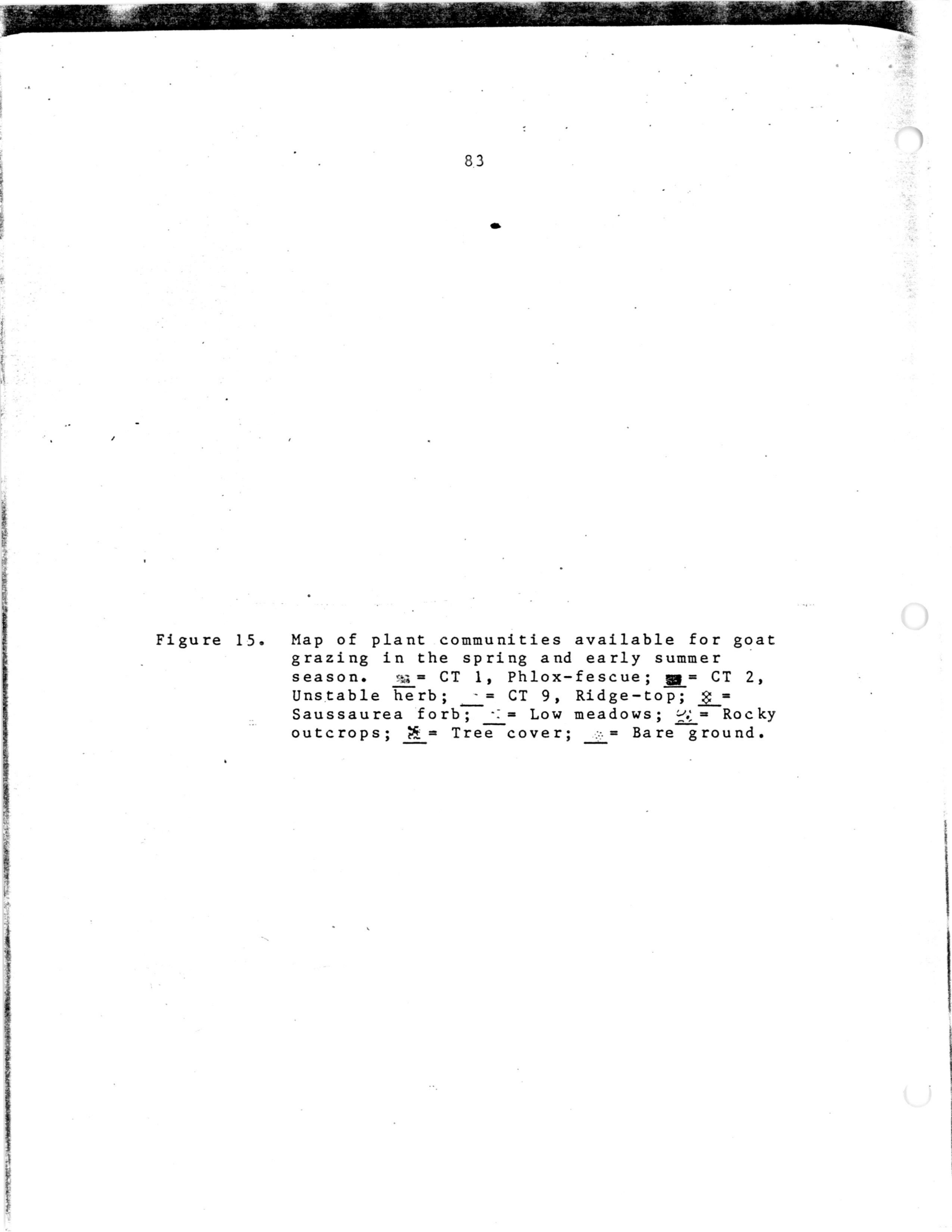


Figure 15. Map of plant communities available for goat grazing in the spring and early summer season. = CT 1, Phlox-fescue; = CT 2, Unstable herb; = CT 9, Ridge-top; = Saussaurea forb; = Low meadows; = Rocky outcrops; = Tree cover; = Bare ground.

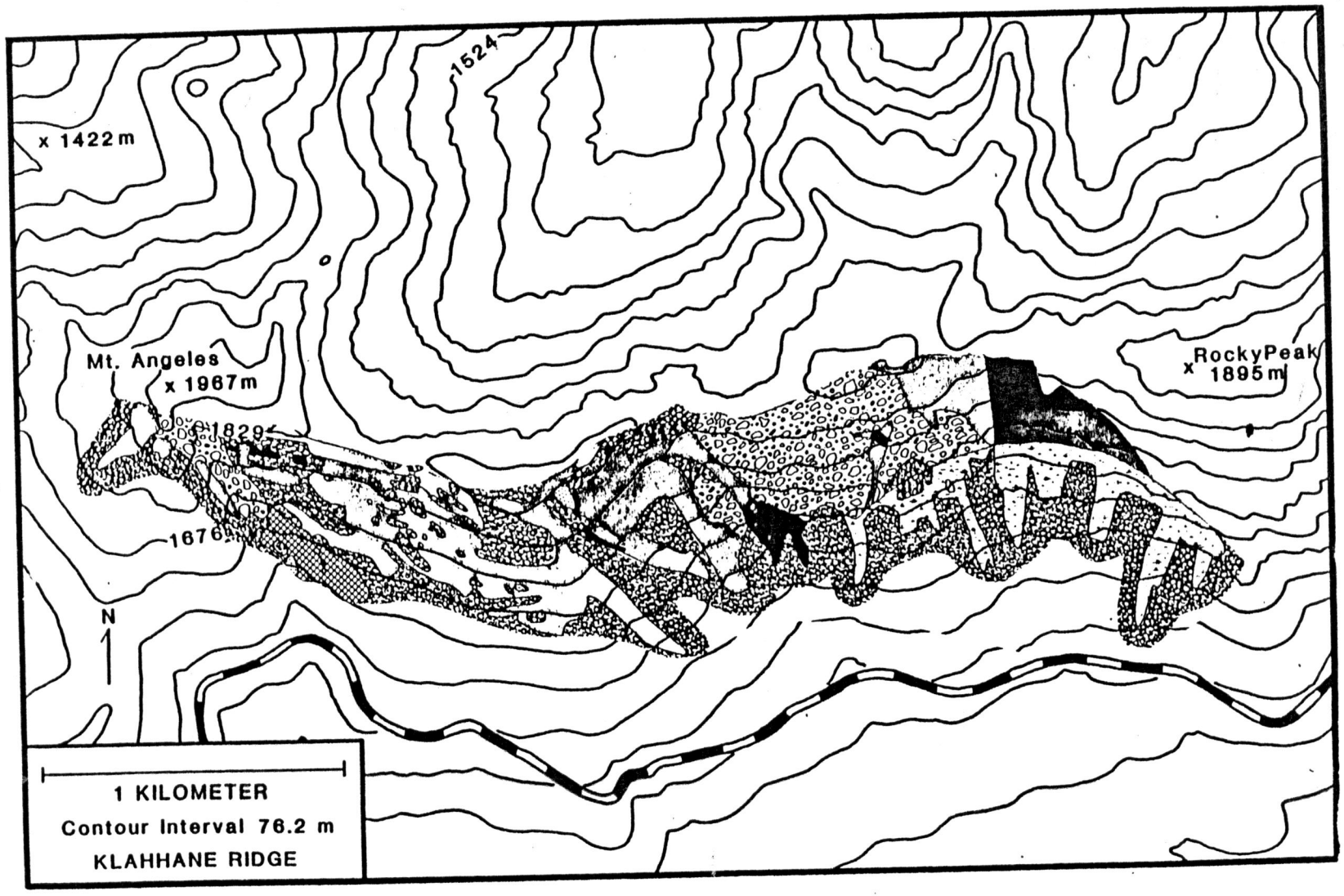
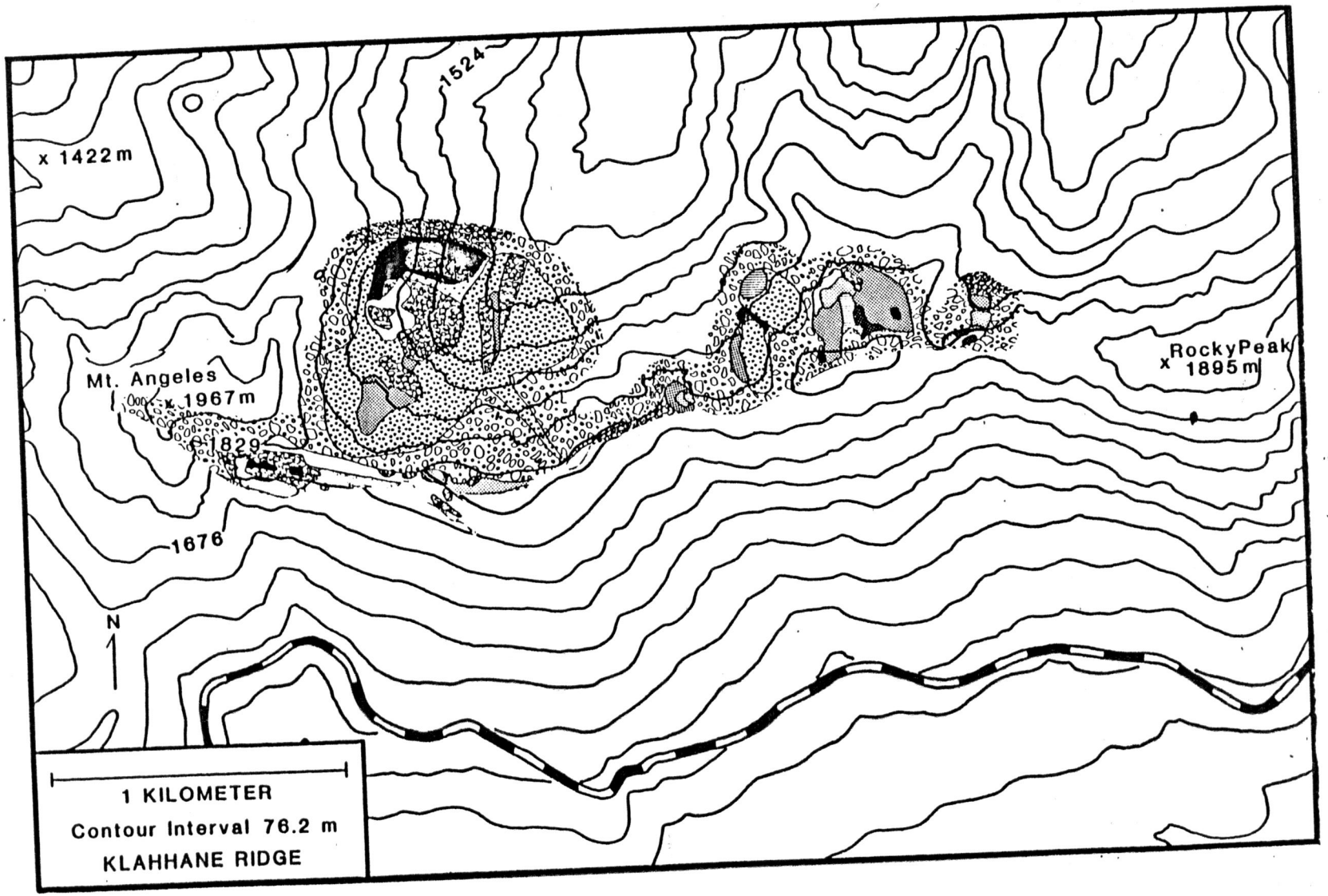

x 1422m
1524
Mt. Angeles
x 1967m
1829
1676
Rocky Peak
x 1895m
N
1 KILOMETER
Contour Interval 76.2 m
KLAHHANE RIDGE

Figure 16. Map of plant communities available for goat grazing in the middle of the summer season. = CT 1, Phlox-fescue; = CT 2, Unstable herb; = CT 3, Scree; = CT 4, Heather; = CT 5, Late snow; = CT 6, Luetkea; = CT 7, Lupine-sedge; = CT 8, Tall sedge, grass, herb; = CT 9, Ridge-top; = Rocky outcrops; = Tree cover.


x 1422 m
1524
Mt. Angeles
x 1967 m
1829
1676
RockyPeak
x 1895 m
N
1 KILOMETER
Contour Interval 76.2 m
KLAHHANE RIDGE

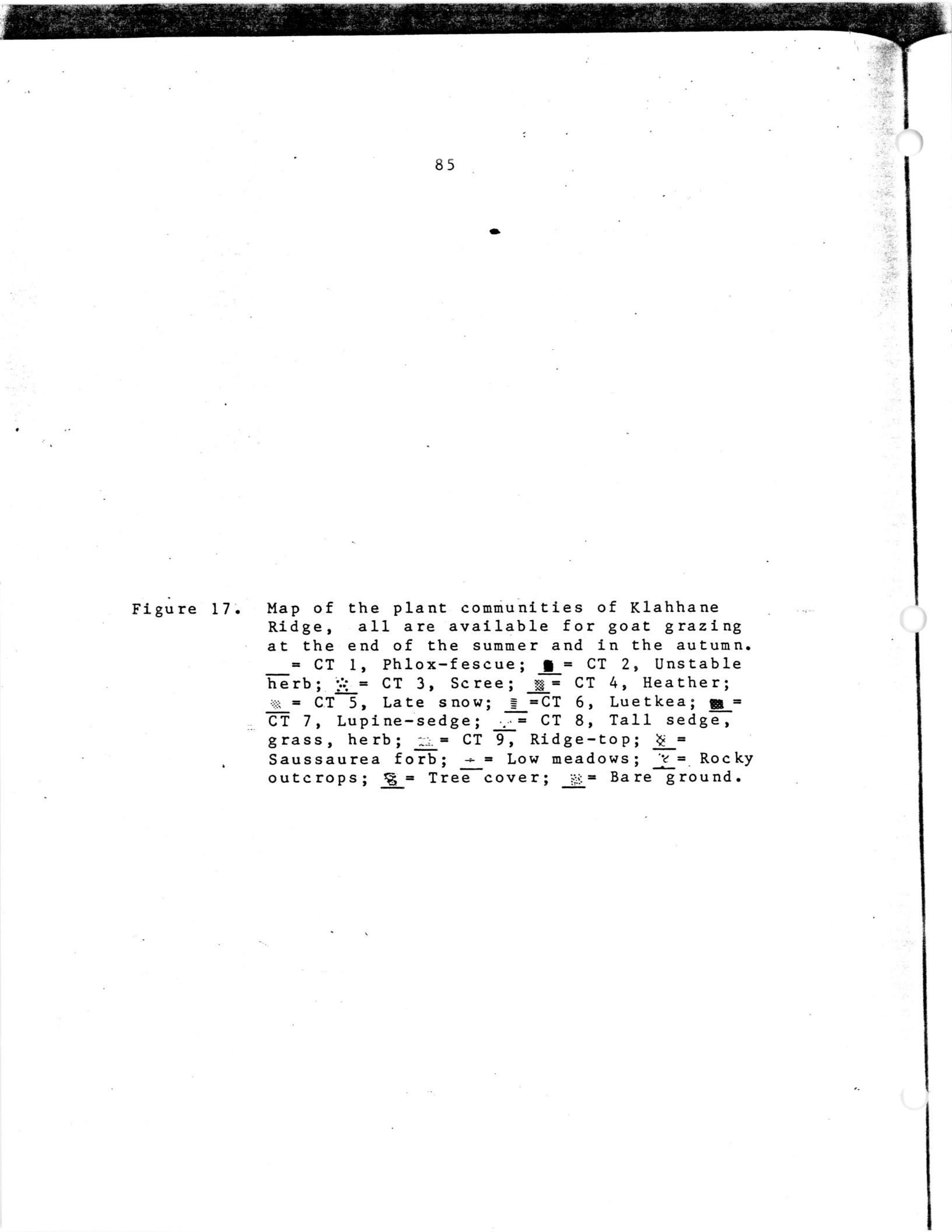


Figure 17. Map of the plant communities of Klahhane Ridge, all are available for goat grazing at the end of the summer and in the autumn. = CT 1, Phlox-fescue; = CT 2, Unstable herb; = CT 3, Scree; = CT 4, Heather; = CT 5, Late snow; =CT 6, Luetkea; = CT 7, Lupine-sedge; = CT 8, Tall sedge, grass, herb; = CT 9, Ridge-top; = Saussaurea forb; = Low meadows; = Rocky outcrops; = Tree cover; = Bare ground.

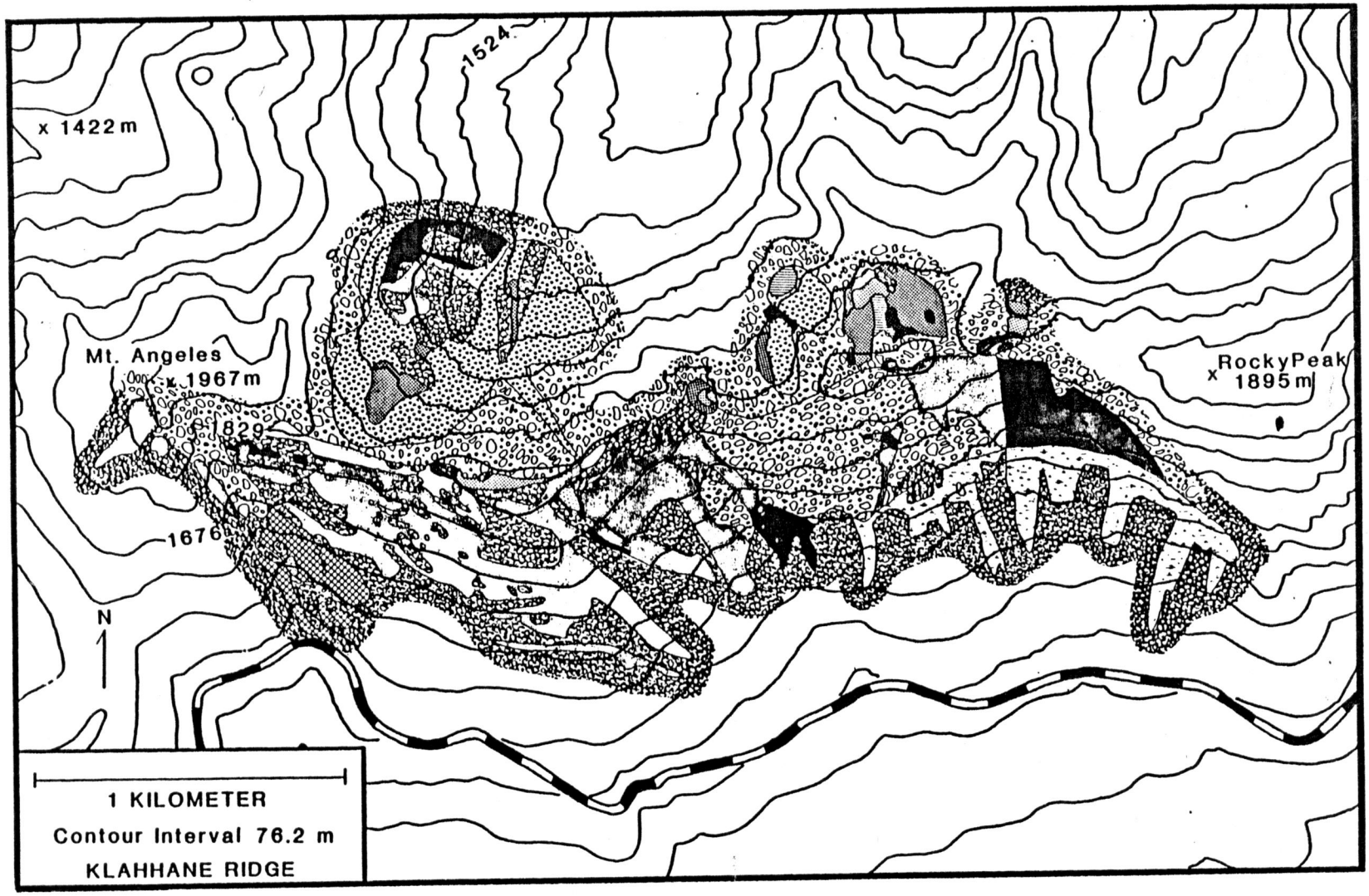

x 1422m
1524
Mt. Angeles
x 1967m
1829
1676
RockyPeak
x 1895m
N
1 KILOMETER
Contour Interval 76.2 m
KLAHHANE RIDGE

Table 10. Calculation of carrying capacities of 3 summer time periods. Production estimates (CT 1 and 2) for the first two time periods are averages of early season (June 29-30) and mid-season (July 18-20). Values for the final time period and for other community types are end of season net production averages.

Time #	Community type Name	Areal extent m^2	Prod. g/m^2	Total Prod. (g)	TP days days avail.	Available forage (kg)
			Spring and Early Summer			
1	Phlox-fescue	26,000	169	4.39×10^6	55/180	1,340
1	"	462,837	169	7.82×10^7	55/135	31,870
2	Unstable herb	115,667	160	1.85×10^7	55/135	7,590
	Saussaurea forb	39,500	365*	1.44×10^7	55/135	5,870
1	TOTAL AVAILABLE FORAGE					46,620
55 days						
			Mid-Summer			
1	Phlox-fescue	26,000	169	4.33×10^6	45/180	1,100
1	"	28,500	169	4.82×10^6	45/125	1,730
2	Unstable herb	35,000	160	5.60×10^6	"	2,020
3	Scree	298,667	44	1.32×10^7	"	4,750
4	Heather	80,166	19	1.52×10^6	"	550
5	Late snow	17.333	119	2.06×10^6	"	740
6	Luetkea	13,666	34	4.65×10^5	"	170
7	Lupine-sedge	8,666	222	1.92×10^6	"	690
8	Tall sedge grass	8,500	113	9.61×10^5	"	350
2	TOTAL AVAILABLE FORAGE					12,100
45 days						

Table 10 continued.

Time	Community type #	Name	Areal extent m^2	Prod. g/m^2	Total Prod. (g)	TP days / days avail.	Available forage (kg)
			Late Summer and Autumn				
	1	Phlox-fescue	14,667	169	2.48×10^6	80/80	2,480
	1	"	462,837	"	7.82×10^7	80/135	46,350
	1	"	28,500	"	4.82×10^6	80/125	3,080
	1	"	26,000	"	4.39×10^6	80/180	1,950
	2	Unstable herb	115,667	160	1.85×10^7	80/135	10,960
	2	"	35,500	"	5.68×10^6	80/125	3,640
	3	Scree	298,667	44	1.32×10^7	80/125	8,450
	4	Heather	80,166	19	1.52×10^6	80/125	970
	5	Late snow	17,333	119	2.06×10^6	80/125	1,320
	6	Luetkea	13,666	34	4.65×10^5	80/125	300
	7	Lupine-sedge	8,666	222	1.92×10^6	80/125	1,230
	8	Tall sedge grass	8,500	113	9.61×10^5	80/125	620
		Saussaurea forb	39,500	365*	1.44×10^7	80/135	8,530
		"	17,500	"	6.39×10^6	80/80	6,390
3		TOTAL AVAILABLE FORAGE					96,270

80 days

*Kuramoto and Bliss, 1970

to maintain the same stocking density. Potential changes in community composition are maintained at the level where populations of important forage species are not being detrimentally reduced. This factor is dependent on the ecology of the system in question.

Assuming that a reasonable stocking density removes 20-30% of the annual production (aboveground) on Klahhane Ridge, the sustainable carrying capacity, based upon spring to fall available forage, would then be calculated at 190-280 goats, considering the production of the entire ridge. These figures may be considered a reasonable estimate of the maximum population level supportable on the ridge before environmental deterioration occurs. The amount of forage available during the hot summer season is much less than is available at other times during the summer. At this time the goats are most concentrated on their food resource. The mountain goat population which would remove 20-30% of the total forage available in the northern meadows used at this time can be calculated from the data presented in Table 11 to be 112-167 goats. This population of goats would be at a level which could be sustained without undue damage to the food resource during the season when they are most concentrated on that resource. The population which could be supported without damage by the south side meadows would be much greater than that which can be supported

Table 11. Calculation of the percent forage removed from the north and south sides of Klahhane Ridge by the current goat population. Assumptions: One goat=42kg, consumes 0.92kg forage/day; there are 170 goats on Klahhane Ridge.

Time Period	# of Days	Forage Removed (kg)	Forage Available (kg)	% Removed
Early summer(1)	55	8,602	46,620	18
Mid-summer (2)	45	7,038	12,100	58
Late summer (3)	80	12,512	94,310	13

Area	Time period	# of days	Forage available (kg)	% removed	Forage removed (kg)
North side	2	45	11,000	58	6,380
	3	80	19,610	13	2,549
TOTAL		125	30,610	29	8,929
South side	1	55	45,280	18	8,150
	3	80	65,840	13	8,559
TOTAL		135	111,120	15	16,709
High south side	1	55	1,340	18	241
	2	45	1,100	58	638
	3	80	1,950	13	254
TOTAL		180	4,390	26	1,133
Low south side	3	80	8,870	13	1,153
GRAND TOTAL			154,990	18	27,924

without damage to the north side meadows.

The current population of 170 goats on Klahhane Ridge is removing about 18% of the total forage produced. While this level is below the sustainable level of 20-30% forage removed, grazing is concentrated due to mountain goat habitat preferences for high meadows near the ridge top, and in north side meadows during the hot middle of summer season. The north side meadows are losing nearly 30% of their total production to grazing, the high meadows on the south side that are used all summer long are losing about 25%, while the rest of the south side meadows suffer only about 15% defoliation (Table 11). The north side meadows produce about 20% of the total Klahhane Ridge aboveground production, yet they supply about 32% of the mountain goat forage (Table 12).

The selective grazing of the goats concentrated the defoliation on preferred forage species, resulting in the fact that preferred species supply a disproportionate amount of forage. This is reflected in the levels of grazing apparent on target forage species, both on the north side and in heavily used high south side meadows where 30-50% of the total production is removed (Table 9). This is especially important in the meadows on much of the north side where a good deal of the total production is made up of

Table 12. Total production, total forage removed by the current population of 170 goats, and percentages of the totals for the different areas on Klahhane Ridge.

Area	Total production (kg)	% of total	Forage removed (kg)	% of total
North side	30,610	20	8,929	32
South side	111,120	71	16,709	60
High south side	4,390	3	1,133	4
Low south side	8,870	6	1,153	4

large, generally avoided, herbs. A further refinement of this model would take the relative amount of forage supplied by preferred species and non-preferred species, compared to the relative proportions of each in the total production.

From these calculations, it is evident that the areas used during the hot time period in the middle of the summer are subject to more concentrated grazing intensity than are the areas used during the other time periods. This is supported by our grazing estimates in the different communities, the intensity of grazing on preferred species is much higher in the cooler areas. The lower level of use on the south side is reflected in observations that there are areas at lower elevations on the south side (available time periods 1 and 3) that are dominated by the preferred forage species Festuca idahoensis that have very little evidence of grazing. Differential concentration of grazing intensity has profound implications for the health of the individual plant communities on the ridge. The areas subject to concentrated grazing activities can be expected to be the first to decline in vigor, and to be most subject to compositional changes.

Conclusions

This study has provided evidence, directly and indirectly, that the population of mountain goats on Klahhane Ridge is exerting a significant pressure on their

summer food resource. A substantial grazing pressure on important forage species (Festuca idahoensis, Poa incurva, and Silene parryi) is indicated by the removal of approximately 30-50% of the above ground annual production. This level of use is severe enough that a reduction of population vigor can be expected and no doubt has already occurred in some meadows. This direct evidence of grazing intensity supports earlier visual estimates of grazing intensity in the important meadows of community types 1 and 2. The data also suggest that other species (i.e. Carex spectabilis) sustain considerable defoliation due to goat grazing.

The high variability of plant community composition and production in the subalpine meadows makes the direct determination of forage consumption from the whole community extremely difficult. It was possible to indirectly estimate the magnitude of population pressures by considering the amount of plant material available to the goats and the daily forage requirements of an individual goat. The results obtained in this manner indicate that the current population of goats present on the ridge removes about 16% of the total amount of net annual production yearly. While this figure is well within the amount of forage removal considered to be allowable on alpine range lands (Thileneus, 1975), environmentally induced habitat requirements do not

result in grazing that is evenly distributed throughout the meadows of the ridge. The amount of forage available to the goats during the hot period of the summer when the goats are concentrated in the cooler areas, is probably the most limiting factor during the growing season.

Changes in plant community composition have undoubtedly occurred and will continue to occur as long as grazing and trampling pressures remain. As outlined above, the predicted direction of change in all plant communities, and especially in those that recieve substantial grazing pressure, is toward a habitat with less available forage. Grazing and physical pressures reduce the levels of preferred forage species and favor unpalatable species and species resistant to physical disturbance. The population level of the goats will decline as they significantly modify their food resource, as has occurred in many other populations of introduced ungulates (Caughley, 1970). There is evidence that the population on Klahhane has already started to decline (currently about 170) with a peak population level of more than 200 animals occurring in 1977 (Stevens, pers.comm.). The ultimate sustainable level will depend on the abundance of available food resources in specialized habitats and at critical seasons, rather than on the level of forage available on the ridge as a whole.

Summary

1. The major environmental factors determining the distribution of plant communities on Klahhane Ridge are the time of snowmelt and stability of the substrate. Nine plant community types are described, ranging from ridge-top fellfields which are snow free in April, through phlox and fescue dominated meadows on southern aspects from which the snow melts in May, to a group of communities in protected areas that become snow free in late June to early July. Substrate stability deceases from late snow basins through fairly steep but stable meadows on sandstone substrate and steep, unstable herb meadows generally on basaltic substrate to actively moving very steep scree slopes.

2. The goats use all of the different plant communities during the summer season. The phlox-fescue meadows and the unstable herb meadows provide the bulk of the available forage. The goats are selective generalists in terms of forage preference; most species are grazed occassionally, a few are preferred, and a few are avoided. Festuca idahoensis and Carex spectabilis are two preferred species which are dominant members of different plant communities. The majority of the species which are rarely grazed (Phacelia heterophylla, Cirsium arvense, Hydrophyllum fendleri, Lupinus latifolius, Cassiope mertensiana and Phyllodoce empetriformis) are dominants or potential

dominants in their respective communities.

3. Festuca idahoensis, an important member of south side plant communities, is preferentially grazed. Simulated grazing experiments indicate that this species is susceptable to damage from defoliation. Total production is significantly less for plants that are clipped during the growing season than for unclipped controls. Flowering success is also significantly reduced. Festuca idahoensis is one of several species which has more vigorous growth inside exclosures than outside in a meadow subject to heavy goat grazing.

4. Digging and wallowing activities of the goats have created many bare areas in the different meadow communities on Klahhane Ridge. The colonists of such openings in south-side meadows are able to exploit local patches of abundant available moisture. The altered moisture regime allows plant species which cannot successfully compete for moisture in the undisturbed meadow to become established.

5. Hypotheses as to the direction of goat induced changes in plant communities vary according to the severity of the physical environment, and the intensity and type of goat activity. Species density will decline in severe environments with continued grazing and trampling by mountain goats. Moderate environments may be maintained at high levels of species density by selective grazing and

general light trampling. At high levels of use, species density will decline.

6. The mountain goat population currently present on Klahhane Ridge is exerting significant pressure on the food resource of their habitat. The environmental and habitat requirements of the goats concentrate the pressure especially in cooler regions that recieve heavy use during the middle of the summer. The habitat is expected to decline in abundance and productivity of important forage species, resulting in a decline in the population of mountain goats that the ridge can support.

7. This very preliminary model predicts that the spring to fall meadows can support a sustained population of 112-167 goats. However at these population levels there will continue to be severe soil disturbance in the form of dusting and thermoregulation wallows.

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APPENDIX A. Mean percent cover, percent frequency ( ), and grazing estimate for species in the nine plant community types sampled on Klahhane Ridge. Grazing estimates are indicated by superscripts, ' = a trace of grazing, * that 1-25% of the individuals of a species showed evidence of grazing, ** that 26-50%, *** that 51-75%, and **** that 76-100%.

Species	Community type								
	1	2	3	4	5	6	7	8	9
Phlox diffusa	18.8* (83)	2.6* (47)							8.5 (100)
Festuca idahoensis	11.8* (100)	2.1*** (78)						0.5* (40)	0.7 (91)
Arenaria capillaris	5.1' (82)	0.2 (10)							
Achillea millefolium	2.2' (66)	4.3* (70)	2.1** (60)			0.01 (10)		1.6* (70)	2.4' (91)
Carex rossii	1.5* (60)	0.4* (32)							0.6' (55)
Silene spp.	1.1* (74)	0.4*** (45)						0.4* (50)	0.1 (09)
Erigeron subtrinervis	0.6* (27)	0.3** (45)							
Lathyrus nevadensis	0.8' (56)	0.3' (58)							
Danthonia intermedia	0.5* (24)		0.9' (50)						

Appendix A continued.

Species	Community type								
	1	2	3	4	5	6	7	8	9
Carex phaocephala	0.4* (22)					0.3' (30)			
Orthocarpus imbricatus	0.9' (71)	0.1 (15)		0.4' (40)					
Lomatium nudicaule	0.4* (31)								
Geum triflorum	0.1 (09)								
Carex hoodii	0.8 (06)	0.2 (10)							
Allium crenulatum	0.03 (09)								
Sedum stenopetalum	0.03 (04)								
Sanicula graveolens	0.06 (13)								
Castilleja miniata	0.04' (04)								
Polygonum bistortoides	0.6* (39)	0.3* (38)		0.3* (30)	0.7* (90)			0.8* (70)	

Appendix A continued.

Species	Community type								
	1	2	3	4	5	6	7	8	9
Thalictrum occidentales	0.2* (09)								
Luzula spicata	0.7' (15)								0.4' (63)
Hydrophyllum fendleri	1.1 (13)	2.3 (65)							
Bromus sitchensis	0.9 (24)	0.7** (30)	0.07** (10)					4.2** (100)	
Polemonium pulcherimum	0.2* (02)								
Eriophyllum lanatum	0.5' (28)	1.6** (45)							
Cirsium edule	0.1' (07)	6.7' (81)						3.9' (100)	
Artemesia ludoviciana	0.3' (14)	5.4** (65)	0.07* (13)					0.4* (10)	
Lomatium martindalei	0.04* (07)	0.3* (53)	0.3* (46)						
Campanula rotundifolia	0.3* (15)	1.1** (50)						0.1* (10)	

Appendix A continued.

Species	Community type								
	1	2	3	4	5	6	7	8	9
Polygonum minimum	0.04 (04)	0.2' (30)							
Arenaria macrophylla	0.03 (03)	0.1* (11)						0.1 (10)	
Pachistema myrsinites		0.4* (25)							
Stipa occidentalis		0.2' (20)							
Agoseris spp.	1.5* (89)		0.1* (13)		0.01 (10)	0.5* (50)		0.3* (50)	
Vicia americana	0.3 (28)	0.6 (42)							
Saussaurea americana		0.3** (10)							
Orobanche fasciculata		0.03 (05)							
Aster paucicapitatus	0.3** (08)	0.8*** (65)	1.3** (17)						
Phacelia heterophylla	0.6' (21)	8.2' (90)	7.8* (66)						

Appendix A continued.

Species	Community type								
	1	2	3	4	5	6	7	8	9
Phacelia sericia			0.3* (13)						0.2 (27)
Senecio neowebsteri			0.9* (25)						
Delphinium glareosum	0.3 (03)		1.3' (38)						
Elmera racemosa			0.2* (03)						
Epilobium alpinum			0.2* (48)	0.01 (10)		0.3 (30)	0.2 (53)		
Sedum divergens			0.4' (40)			0.01 (07)			
Senecio flettii		0.02 (05)	0.1* (16)			0.2' (20)			
Douglasia laevigata			0.003 (03)						
Viola adunca	1.3* (83)	0.1* (13)	0.1* (13)						0.8* (91)
Penstemon procerus	0.2 (06)	0.02 (02)							0.01 (09)

Appendix A continued.

Species	Community type								
	1	2	3	4	5	6	7	8	9
Hedysarum occidentale		0.5** (50)	0.1** (07)						
Erigeron perigrinus	1.3* (14)		0.1** (07)	0.4 (70)	0.9* (60)	0.2* (20)	0.3 (33)		
Veronica cusickii	0.3' (14)			0.8' (70)	0.7' (60)		1.0' (100)	1.0' (80)	
Ranunculus eschscholtzii	0.1' (13)						0.2 (20)	0.8 (50)	
Poa incurva	0.3* (25)	0.1*** (10)	0.3**** (23)					1.6** (90)	
Arnica spp.	0.3* (13)							10.5* (90)	
Aster foliaceus	0.1* (07)							3.7* (60)	
Epilobium angustifolium	0.1* (07)	0.01 (05)						0.8* (50)	
Valeriana sitchensis	0.1 (07)	0.02** (02)	0.2** (17)					1.5* (90)	
Elymus glaucus	0.02 (02)	0.5** (08)						0.7*** (20)	

Appendix A continued.

Species	Community type								
	1	2	3	4	5	6	7	8	9
Galium sp.								0.4 (30)	
Deschampsia caespitosa								2.9** (50)	
Arabis spp.						0.3 (50)	0.1 (20)	0.3* (40)	
Trisetum spicatum	0.1* (16)	0.02 (02)			0.01 (10)	0.4 (40)	0.1 (07)	1.8* (90)	
Potentilla spp.	0.1' (13)	0.1' (10)			6.4 (90)		0.01 (07)	0.5 40)	0.2' (27)
Cassiope mertensiana				41.6 (100)	0.1 (10)		0.2 (07)		
Phyllodoce empetriformis				10.9 (100)					
Luetkea pectinata				4.9 (100)		1.9 (40)	13.6 (93)		
Carex nigricans				2.1' (90)	32.6* (100)	0.6 (30)	7.7* (93)		
Carex spectabilis				1.3* (90)	27.5*** (100)	7.5*** (100)	2.1**** (93)	13.9** (100)	

Appendix A continued.

Species	Community type 1	2	3	4	5	6	7	8	9
Hieracium gracile				0.2' (60)		0.1' (20)	0.1 (27)		
Deschampsia atropurpurea				0.2 (50)		0.1 (20)	0.1 (13)		
Phleum alpinum	0.1* (16)	0.1** (10)			3.5' (100)	0.2 (20)	0.1 (27)	0.6* (60)	
Antennaria spp.	0.03 (07)	0.02 (02)		2.3 (100)	0.4 (40)	0.3 (10)	0.3 (40)		0.4 (45)
Juncus drummondii						0.1 (10)	1.6 (87)	0.3* (20)	
Arenaria rossii							0.01 (07)		
Luzula piperi				1.3 (80)		0.9' (60)	0.8* (87)		
Lupinus latifolius	5.7' (28)					59.4* (100)			
Poa cusickii						0.2** (30)			
Erysimum arenicola	0.3 (41)	0.6' (57)	0.6' (60)						0.8 (100)

Appendix A continued.

Species	Community type 1	2	3	4	5	6	7	8	9
Collinsia parviflora	0.2 (02)								0.01 (09)
Juniperus communis	0.03 (03)							0.01 (10)	14.6 (100)
Arenaria rubella									2.1 (100)
Anemone sp.									1.0* (100)
Erigeron compositus									0.7 (82)
Agropyron caninum									0.6' (64)
Solidago multiradiata									0.6* (27)
Oxytropis campestris									0.3* (21)
Sitanion hystrix		0.002' (02)	0.002**** (03)						0.3' (55)
Saxifraga tolmei						0.01 (10)	0.8 (53)		

Appendix A continued.

Species	Community type 1	2	3	4	5	6	7	8	9
Saxifraga caespitosa									0.1 (09)
Smelowskia calycina									0.3 (36)
Saxifraga ferruginea							0.01 (14)		
Polysticum lonchitus								0.1 (10)	
Lichen/moss	0.9 (49)	0.02 (02)	0.2 (30)	3.4 (100)	4.5 (90)	0.7 (70)	1.7 (100)	0.6 (20)	1.6 (100)
Litter	4.0 (98)	2.5 (100)	0.1 (27)	20.6 (100)	17.5 (90)			8.2 (100)	4.0 (100)
Rock (greater than 7cm)	1.3 (47)	3.7 (67)		0.1 (10)	0.2 (10)	8.3 (90)	12.7 (100)	1.4 (70)	16.8 (100)
Bare ground cover	33.5	53.2	83.1	9.5	5.6	22.5	55.2	35.6	40.6
Plant cover	63.4	45.5	16.5	56.9	72.8	74.0	30.0	54.6	35.7
Number of species	55	41	22	15	11	22	23	29	23