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Effects of Weather on Caribou Forage Productivity and Nutrition within the Range of the Chisana Herd

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RESEARCH FINAL REPORT

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STUDY TITLE: Effects of Weather on Caribou Forage Productivity and Nutrition Within the Range of the Chisana Herd

AUTHOR: Elizabeth A Lenart

PERIOD: 1 January 1996-30 June 1997

Editor's Note: The author's report includes additional herd trend information and her Master's of Science thesis, which is the appendix to this final report. References to this report should indicate the date on the report cover, spanning the entire project from 1 May 1994 to 30 June 1997.

SUMMARY

Beginning in 1989 the Chisana Caribou (*Rangifer tarandus*) Herd in the northern Wrangell Mountains of Alaska substantially declined in size and productivity. Summers were significantly warmer and slightly drier during years of population decline. In the subarctic tundra, we increased air temperature and decreased precipitation with a plastic tent, decreased light intensity with a shade cloth, and increased precipitation by adding water to determine climatic effects on nutrient content and biomass of caribou forage during summer 1994 and 1995. We determined that short-term variations in climate can affect nutrient quality, particularly nitrogen content, in above-ground biomass of caribou forage. The warmer, drier summers may have adversely affected the Chisana population by increasing insect harassment and decreasing nitrogen content in caribou forage. The decline of the Chisana Caribou Herd was most likely influenced by a combination of factors such as weather, forage quality, insect harassment, and predation.

Key words: Alaska, caribou, Chisana, digestibility, forage productivity, forage quality, nitrogen, weather.

CONTENTS

BACKGROUND

The Chisana Caribou (*Rangifer tarandus*) Herd ranges in the Nutzotin and north Wrangell Mountains from the Nabesna River east into the Yukon Territory, Canada (Kelleyhouse 1990). In the early 1960s, Skoog (1968) thought the Chisana Herd numbered approximately 3000 caribou. During the late 1970s, however, the herd was estimated to be < 1000 animals (Kelleyhouse 1980). Between 1981 and 1988, the herd increased to 1900 caribou; calf:cow ratios in October ranged from 34:100 to 43:100. Recently, the Chisana Caribou Herd declined in both size and productivity. The herd decreased from 1900 animals in 1989 to 1300 in 1992; calf:cow ratios in autumn declined from 31:100 in 1988 to < 1:100 in 1992, the lowest recorded for any caribou herd in Alaska. In 1992 adult mortality increased substantially, and the bull:cow ratio approached the minimum management objective of 30:100 established by the Alaska Department of Fish and Game (Gardner 1993). In March 1993 only 50% of the adult females were pregnant. By 1994 and 1995 pregnancy rates increased to 86% and 95%, respectively. No data exists for pregnancy rates before 1993.

From 1984 through 1989, the average annual harvest of the Chisana Caribou Herd was 44 bulls; 50% to 60% of this harvest was taken by nonresidents guided by local outfitters and 9% to 12% by local residents. Beginning in 1990, a voluntary harvest restriction initiated by local guides and outfitters in response to the herd's decline resulted in an average take of 22 bulls. In 1993 the Alaska Board of Game established a registration permit system allowing a maximum harvest of 20 bulls (Craig Gardner, pers commun). It is unlikely this small harvest influenced the decline of the herd.

Staff biologists studying the Delta and Fortymile caribou herds (in Interior Alaska) reported high adult mortality, low calf recruitment, and significantly lower body weights of calves from 1989 through 1992 (Valkenburg 1992). They hypothesized that warm, dry summers and heavy snow in winter the last few years may have depressed forage quality, quantity, or availability and, hence, body condition of caribou in Interior Alaska (Pat Valkenburg, pers commun). Factors limiting productivity in the Delta and Fortymile caribou herds also may be affecting the Chisana Caribou Herd.

GOAL

My goal was to investigate the effects of summer temperature, precipitation, and variable sunlight on forage production and nutrient content within the summer range of the Chisana Caribou Herd. In addition, I examined relationships between historical weather patterns and parameters of the caribou population. This study may increase our understanding of how weather influences forage quality and availability in Interior Alaska and, in particular, the Chisana caribou range. In conjunction with other studies, a knowledge of weather effects may help explain the widespread decline of Interior Alaska caribou herds. Thus, weather data may become useful in predicting or explaining variations in productivity of caribou populations.

OBJECTIVES

PLANT RESPONSE TO TREATMENT EFFECTS

To determine the effects of simulated variation in sunlight intensity, precipitation, temperature on nutrient quality, biomass, and digestibility of forages within the summer range of the Chisana caribou, I tested the following null hypotheses:

- Changes in available sunlight do not affect forage nutrient quality, biomass, and digestibility.
- Changes in amount of precipitation do not affect forage nutrient quality, biomass, and digestibility.
- Changes in temperature do not affect forage nutrient quality, biomass, and digestibility.
- Changes in temperature and precipitation combined do not affect forage nutrient quality, biomass, and digestibility.

- Changes in sunlight availability and precipitation combined do not affect nutrient quality, biomass, and digestibility.

HISTORICAL WEATHER PATTERNS AND CARIBOU POPULATION PARAMETERS

To determine relationships between calf production and survival and weather patterns in the Chisana caribou range, I tested the following null hypotheses:

- During the period of caribou decline (1989-1993), patterns of summer rainfall, summer temperature, and winter snowfall were not different from previous years when the herd was stable or increasing.

STUDY AREA

This study was conducted in the eastern portion of Wrangell-St. Elias National Park and Preserve at Solo Mountain (61°50'N, 141°50'W) in Interior Alaska during summer 1994 and 1995. The study site was located at an elevation of 1524 m in an area where Chisana caribou are found from postcalving through summer. The Chisana Herd ranged at elevations from 800 to 2000 m (Gardner 1997). Calving is restricted to higher elevations (1460–2000 m) with parturient females sequestering themselves away from other caribou (Gardner 1997). During 1990-1995 postcalving aggregations of 300 to 500 animals were found at Solo Mountain.

Predators within the range of the Chisana Herd include wolves (*Canis lupus*), grizzly bears (*Ursus arctos)*, and coyotes (*Canis latrans*). Ungulates other than caribou in the study area include Dall sheep (*Ovis dalli dalli*) and Alaskan moose (*Alces alces gigas*).

Regional vegetation is a mosaic of white and black spruce (*Picea glauca* and *P. mariana*) at lower elevations (700 to 900 m), alpine tundra (predominately a *Carex-Dryas* community) at intermediate elevations (1000–1550 m), and heath (*Cassiope*) and bare ground and rugged talus slopes at higher elevations (1600 to 2000 m). Willows (*Salix*) follow the riparian drainages. Mountain sides are dominated by willow (*Salix*), shrub birch (*Betula nana*), and blueberry (*Vaccinium vitas-idaea*).

The climate is typical of the subarctic with long, cold winters and a short growing season. For summer (15 Jun–15 Aug 1981-1995), mean total precipitation was 139 mm, mean maximum temperature was 17.8° C, and mean temperature was 11.5° C (Nabesna Weather Station; Fig 2). Snowfall in the winter range averages 28.9 cm (1 Oct –1 May, 1980-1995; Northway Weather Station).

METHODS

TUNDRA-MAT EXPERIMENTAL DESIGN

A 48 m by 60 m grid consisting of 30 treatment plots was established in a traditional postcalving area of the Chisana Herd. Each plot contained 8 subplots, making a total of 240 vegetation subplots, each 0.25 m^2. Five replicates of 6 treatments (including controls) were applied to simulate a cloudy summer; a cloudy, wet summer; a warm, dry summer; and a warm, wet summer. The 6 treatments included: 1) unaltered control, 2) control with supplemental watering, 3) clear plastic only (to increase temperature by 3° to 4°C and decrease precipitation), 4) clear plastic with supplemental watering (to increase temperature by 3° to 4° C), 5) shade only (50% shade tarp), and 6) shade with supplemental watering (50% shade tarp). Temperature, precipitation, and amounts of supplemental watering under control, shaded, and clear plastic plots were recorded. In addition, a local weather station recording ambient temperature, sunlight availability, and rainfall was established.

The clear tarps and shade tarps are 1.8 m by 3.6 m. One 0.25 m^2 subplot was clipped during the 4 time periods (9 Jun, 26 Jun, 20 Jul, 9 Aug) in 1994 and 1995. Beginning 22 June 1994 through 8 August 1994 and 20 June 1995 through 5 August 1995, 30 liters of water was added once a week to those treatments requiring water. From 14 June 1994 through 8 August 1994 and 10 June 1995 through 10 August 1995, a data logger, recording temperature every 1.6 hour, and a rain gauge were placed at 1 of the 5 replicates for each of the 6 treatments. On 16 July 1994 and 15 July 1995, soil core samples were collected from each plot. This design allows me to look at plant response to 2 seasons of treatment.

SHRUB HABITAT EXPERIMENTAL DESIGN

Five replicates of 3 treatments (including controls) were applied to plots in a community consisting mainly of *Salix pulchra*. These plots were not treated until 10 July 1994 due to weather and time constraints. Treatments were removed 5 August 1994 and reestablished 25 June 1995 through 6 August 1995. The treatments included: 1) unaltered control, 2) clear plastic tarp, and 3) 50% shade tarp. The tarps are 3.6 m by 3.6 m and cover 4 to 5 willow plants or the clonal plant. A data logger and rain gauge were placed at 1 of the 5 replicates for each of the 3 treatments. Approximately 25 annual shoots were clipped from each site on 2 August 1994, 12 July 1995, and 8 August 1995.

PLANT ANALYSES

Forage vegetation samples were analyzed for percent nitrogen, percent in vitro dry matter digestibility, and percent tannin concentration (in willows) at University of Alaska Fairbanks. Above-ground biomass was estimated in the tundra-mat experiment.

DIET COMPOSITION AND FECAL SAMPLES

Fecal pellets were collected from nearby caribou groups throughout summer 1994 and summer 1995. Pellets were analyzed to identify forage fragments from microhistological characteristics, determine diet composition (Dearden et al. 1975), and percent nitrogen at Washington State University Laboratory.

HISTORICAL DATA

Historical weather data (e.g., annual averages for summer temperature, summer precipitation, snow depth, and snow-free days) were obtained from Nabesna and Northway weather stations. Chisana caribou population parameters (e.g., calf:cow ratios, population abundance) were obtained from the Alaska Department of Fish and Game survey-and-inventory reports.

RESULTS AND DISCUSSION

VEGETATION ANALYSES

Cloudy summers may decrease growth of forbs, especially during July and August, because above-ground biomass of live forbs was lower in the shaded plots (Appendix:Table 2). In addition, there was some indication that water would limit growth in forbs during a dry summer. Biomass in graminoids (i.e., *Carex bigelowii*) also was lower in the shaded plots during late spring (28 June) 1995 (Appendix:Table 2). Similarly, Chapin and Shaver (1985) reported that shade reduced growth of *C. bigelowii* in a wet tussock tundra, and Bø and Hjeljord (1991) concluded that growth of graminoids in southeastern Norway was delayed in a cloudy, wet June. We detected no differences in biomass among treatments in prostrate willows in 1994 or 1995, and we did not estimate biomass in the *S. pulchra* experiment; however, Chapin and Shaver (1985) reported that warmer temperatures increased growth in *S. pulchra*.

Although a cloudy summer may decrease above-ground biomass in some plants, it increases nitrogen concentration (Appendix:Fig 7 and 8). Other studies also have reported higher protein content in *S. pulchra* and *Betula nana* grown in shade relative to full sunlight (Bø and Hjeljord 1991; Molvar et al. 1993) and higher nitrogen concentration in *Eriophorum* growing in cooler temperatures compared with warmer temperatures (Jonasson et al. 1986). In contrast, Chapin et al. (1995) reported higher nitrogen concentration in their greenhouse plots. Chapin et al. (1995) suggested that indirect effects of warmer temperatures could potentially increase rates of mineralization in the soil, hence increasing availability of nutrients. The tundra-mat plots had a thick layer of moss and litter, which insulated the soil and retarded rates of decomposition and nitrogen mineralization. Yet, there is some evidence that soil moisture may be higher in a cloudy summer because shaded plots were significantly higher in percent soil moisture compared with greenhouse plots during the 1994 sampling. Although our shade treatment may have been extreme (i.e., 50% shade for the entire summer), we hypothesize that as long as temperatures remain high enough for plant growth (≥ 5°C), a cloudy summer should produce higher nitrogen concentrations in above-ground live biomass of caribou forage than a clear summer in this type of vegetation.

Although there is good evidence that a cloudy summer is favorable for increasing nitrogen concentration in caribou forage, there is some indication from our experiments that it would have a negative effect on percent digestibility (Appendix:Fig 8 and 9). In the tundra-mat experiment, percent digestibility was lower in shade plots near the end of the season for graminoids, forbs, and prostrate willows in 1994 and 1995 (Appendix:Fig 7 and 9). This trend also occurred in the *S. pulchra* experiment. We suggest that in the greenhouse plots, sugars (i.e., soluble carbohydrates) accumulated in the plant by the end of the season because of higher photosynthetic rates due to higher temperatures (Appendix:Table 1). There is some evidence, however, of higher percent digestibility being associated with shade. Molvar et al. (1993) reported higher in vitro dry matter digestibility and nitrogen concentration in *S. pulchra* in natural shady versus sunny sites. These sites, however, were frequented by moose which probably contributed nutrients to the soil via feces and urine (Molvar et al. 1993), thereby influencing digestibility. Other factors (e.g., sex and age of plant, secondary compounds;

Bryant et al. 1983; Klein and Bay 1994; Reichardt et al. 1990) also may be influencing digestibility and interacting with or masking the effects of climate.

Tannin concentration was lower in shaded plots in the *S. pulchra* experiment in 1995 (Appendix:Fig 8). Similarly, Jonasson et al. (1986) and Bø and Hjeljord (1991) reported lower concentrations of secondary metabolites in a cooler summer compared with a warmer summer. Differences were not detected in the tundra-mat experiment, which had different species (*S. arctica, S. reticulata*).

DIET COMPOSITION AND FECAL ANALYSES

Chisana caribou used a greater percent of graminoids after the postcalving period than reported in other herds of caribou. Over the 2 summers, fecal samples had 20% to 30% graminoids compared with < 15% in other herds (Appendix:Fig 6; Boertje 1984; Russell et al. 1993). Shrubs constituted 20% to 64% of the diet as estimated from fecal analyses, which is comparable to other diets of caribou in summer (Appendix:Fig 6; Boertje 1984; Kelsall 1968; Thompson and McCourt 1981). Percent nitrogen was slightly higher in June 1995 compared with June 1994.

HISTORICAL WEATHER

Summers were substantially warmer and slightly drier during years in which the Chisana Herd was declining compared to years when the herd was stable or increasing (Appendix A:Fig 5). Warm, dry summers tend to favor insect outbreaks (Mattson and Haack 1987). Our index of insect harassment indicates that severity of insect harassment was higher during the years the herd was declining ($P = 0.01$). Stress from insects can increase energy expenditure of caribou (Russell et al. 1993), decrease time spent foraging (Russell et al. 1993; White et al. 1975), and decrease forage availability by caribou having to escape to higher elevations where insects are less abundant. These effects combine to reduce energy intake, which can negatively affect body condition and reproductive success of female caribou (Couturier et al. 1988; Thomas and Kilaan 1990). Warm, dry summers also can affect fecundity of female caribou by affecting quality and abundance of forage on summer ranges. Crete and Huot (1993) and Reimers (1983) concluded that poor summer range adversely influenced the George River caribou and Norwegian reindeer populations, respectively; yet, the effects of climate on plant productivity and nutrient content within these ranges were not determined. In our plant experiments, we determined that cloudy summers could increase nitrogen concentration per bite size in forage of caribou compared with clear summers; however, above-ground live biomass probably would be lower during cloudy summers.

Snow depth in winter probably did not contribute substantially to the population decline because we detected no significant differences or trends in means of snow depth between years when the herd was stable or increasing and years when the herd was declining (Appendix:Fig. 4). In addition, there is some indication that winter range for the Chisana Herd was good, at least during the early 1990s, because fecal pellets collected in winter 1994 were composed of at least 70% lichens, which is comparable to other caribou herds (Russel et al. 1993). The Chisana caribou wintered in the same area in 1991 and 1993 (Gardner 1997). Therefore, weather and range condition in winter probably did not greatly influence the decline of the Chisana Herd.

As observed in the plant experiments, temperature and irradiance can influence nitrogen content in caribou forage, with higher nitrogen concentration in above-ground biomass with lower irradiance and temperature. Therefore, during a cloudy summer, caribou may be able to acquire more nitrogen in fewer bites, but they also are probably acquiring more dead matter (particularly in graminoids) from the previous year and possibly expending more energy foraging because there is less available green biomass (Boertje 1990). Thus, there could be a trade-off between nitrogen and biomass (and perhaps digestibility) as nutritional requirements change throughout the summer. Indirect effects of weather via insect harassment also may influence foraging conditions and, thus, a cloudy summer could decrease insect harassment, which would allow more time for foraging.

See Appendix for further details on Results and Discussion.

PRESENTATIONS

I presented a poster paper at the annual Alaska Cooperative Fish and Wildlife Research Unit meeting on 1 March 1995 and 1996, the Second International Arctic Ungulate Conference on 13-17 August 1995, and the 76th Society of Mammalogists on 21-24 June 1996. I presented a Master's of Science thesis at University of Alaska Fairbanks in May 1997.

CONCLUSIONS

We determined that short-term variation in climate can affect nutrient quality, particularly nitrogen content, in above-ground biomass of caribou forage. This outcome is only meaningful, however, when considered in relation to the availability of forage for individual caribou. Summers were substantially warmer and slightly drier during declining years (Appendix:Fig 4). Thus, the decline of the Chisana Herd was probably influenced by adverse summer weather by affecting the nutrition of caribou. The low pregnancy rates in 1993 (50%) indicate a contributing nutritional effect, at least initially, which is probably related to forage quality and abundance. By 1994, however, pregnancy rates increased to > 85%, yet recruitment remained low. It is possible that predation by wolves (*Canis lupus*), grizzly bears (*Ursus arctos*), and coyotes (*Canis latrans*) exacerbated the decline of the Chisana caribou population. Boertje et al. (1996) suggested that direct and indirect effects of adverse weather increased vulnerability to predation and influenced the population size in caribou herds (Delta, Denali, and Macomb) in Interior Alaska during the early 1990s. These circumstances are similar to the Chisana Herd.

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fecals; and editing manuscripts. I also appreciate research design assistance from J Ver Hoef, C Gardner, D Reed, T Bowyer, R Ruess, P Valkenburg, R DeLong, K Jenkins, and B Route. Pilots P Zaczkowski flew in technical assistance, T Overly flew in all field gear from Chisana, and J Coady and P Valkenburg flew field gear from Fairbanks to Chisana.

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APPENDIX Climate and Caribou: Effects of Summer Weather on the Chisana Caribou Herd

CLIMATE AND CARIBOU: EFFECTS OF SUMMER WEATHER ON THE CHISANA CARIBOU HERD

A

THESIS

Presented to the Faculty

of the University of Alaska Fairbanks

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for the Degree of

MASTER OF SCIENCE

By

Elizabeth A. Lenart, B.S.

Fairbanks, Alaska

August 1997

ABSTRACT

In 1989, the Chisana caribou (Rangifer tarandus) herd in the northern Wrangell Mountains, Alaska declined substantially in population size and productivity. Summers were significantly warmer and slightly drier during years the herd was declining (1989-1995) compared with years when the herd was stable or increasing (1981-1988). We increased air temperature and decreased precipitation with a plastic tent, decreased light intensity with a shade cloth, and increased precipitation by adding water to determine climatic effects on nutrient content and biomass of caribou forage during summer in 1994 and 1995 in the subarctic tundra. We determined that short-term variations in climate affected nutrient quality, particularly nitrogen content, in above-ground biomass of caribou forage. The warmer, drier summers (1989-1995) may have affected the Chisana population adversely by increasing insect harassment and decreasing nitrogen content in their forage.

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INTRODUCTION

Caribou (Rangifer tarandus) herds in Alaska and Canada experience short and long-term fluctuations in population size and occasionally undergo dramatic changes in numbers (Adams et al., 1996; Messier et al., 1988; White et al., 1981). Factors influencing these fluctuations include adverse weather, forage quality and availability, intraspecific competition, insect harassment, and predation (Bergerud, 1980; Boertje et al., 1996; Dale et al. 1994; Leader-Williams, 1980; Russell et al., 1993; Skogland, 1985; White, 1983). Beginning in 1989, the Chisana Caribou Herd in the northern Wrangell Mountains of Alaska declined markedly in both size and productivity (Fig. 1). Other caribou herds in interior Alaska also experienced high mortality of adults, low rates of calf recruitment, and significantly lower body mass of calves during 1989-1992 (Valkenburg et al., 1996). Such a widespread decline in population sizes of caribou herds in interior Alaska suggested that poor nutrition was possibly depressing numbers of caribou (Valkenburg et al., 1996). One factor contributing to these observed changes may have been a decline in the quality and availability of forage as affected by climate change.

In spring and summer, caribou forage selectively, choosing plants high in nutrients and avoiding plants high in secondary compounds (Klein, 1970; Kuropat and Bryant, 1980; White, 1983). Forage quality and availability directly influence body condition of female caribou, which, in turn, affects production of young (Leader-Williams, 1980; Reimers, 1983; Skogland 1985, 1986). For example, Cameron et al. (1993), Cameron and Ver Hoef (1994), and Gerhart et al. (1996) noted significant positive correlations between body weights of female barren ground caribou (R. t. granti) in autumn and their subsequent rate of parturition. Pregnancy rate also varied directly with dressed body weight of females in wild Norwegian reindeer (Reimers, 1983). In George River caribou (R. t. caribou), summer nutrition and increasing population density likely regulated the population through a combination of decreased fecundity and survival (Crete and Huot, 1993). Despite evidence for positive relationships between nutritional status and reproductive performance in caribou, there are few data on range quality and, specifically, how it is affected by climate. Thus, data on relationships among climate, range quality, and population density are a necessary component for understanding the dynamics of caribou populations.

Annual variation in climate, including irradiance, temperature, and precipitation, may influence forage quality by altering nutrient concentrations and anti-herbivore defenses in above-ground biomass of plants and can affect forage availability by influencing plant growth. For example, short term ($\leq$ 3 yrs) field experiments involving simulated environmental changes (i.e., increased temperature, reduced irradiance) on tundra vegetation showed variable effects on plant growth and nutrient content in some species of graminoids and deciduous shrubs in Arctic-tussock and wet-meadow tundra, and at polar sites (Chapin and Shaver, 1985; Chapin et al., 1995; Shaver et al., 1986; Wookey et al., 1993). In Arctic tussock and wet-meadow tundras, shading reduced growth in Carex bigellowii, Eriophorum vaginatum, E. angustifolium and Betula nana and elevated air temperature increased growth in Salix pulchra, but decreased growth in E. angustifolium (Chapin and Shaver, 1985). In a low-alpine heath, warmer air temperatures decreased nutrient concentrations and increased phenolic content in above-ground shoots of E. vaginatum, Rumex acetosa, and Solidago virgaurea (Jonasson et al., 1986). Bowyer et al. (in press) documented that nitrogen content of Salix

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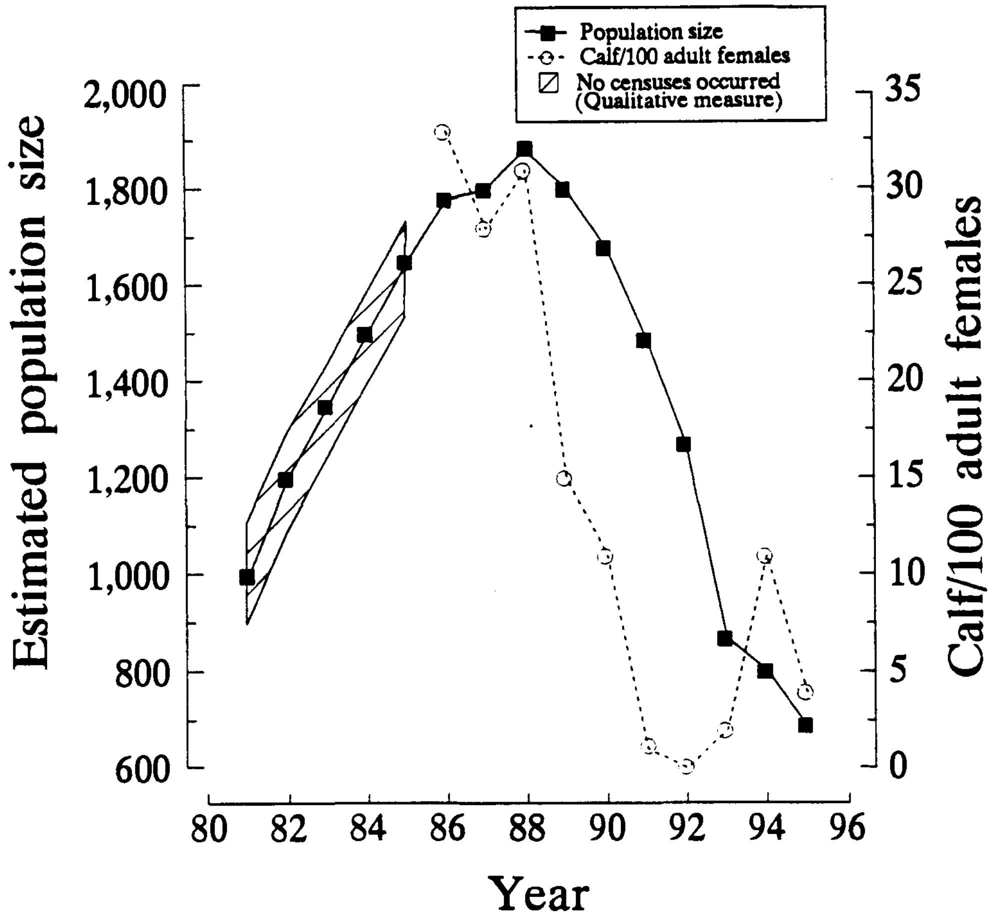

Fig. 1. Estimated population size and calf:100 adult females in the Chisana caribou herd, Solo Mountain, Alaska, 1981-1995.

pulchra declined more rapidly during an unusually warm spring in interior Alaska compared with years when the nitrogen decline was closer to seasonal averages.

Variation in annual precipitation, temperature, and irradiance also can affect plant growth and forage quality indirectly through soil properties (Chapin, 1983). Because tundra ecosystems in the Arctic and subarctic are strongly limited by nutrient availability (Chapin and Shaver, 1985; Haag, 1974; Ruess et al., 1997), the indirect effects of warmer temperatures on rates of soil nitrogen mineralization, and thus availability of nutrients, may be more important than the direct effects of temperature on plant growth (Chapin, 1983). In addition, low soil moisture has been shown to limit net primary productivity and nitrogen content in some species of tundra plants (Chapin et al., 1988; Webber, 1978). In contrast, Carex aquatilis exhibited reduced growth in a higher water table (Peterson et al., 1984). Consequently, there is potential for annual variation in climate to affect summer quality of forage for caribou.

Besides annual variation in climate, long-term changes in climate are expected to occur through global warming (Chapin et al., 1992). Global warming is predicted to have the largest effects on tundra, boreal forests, and polar deserts with temperature and precipitation expected to change substantially (Maxwell, 1992). At latitudes > 64° N (Lashof and Ahuja, 1990), summer temperature is predicted to increase an average of 3.5°C over the next 50 years (Maxwell, 1992). Simulation models show more variability in the predictions for precipitation, with most projecting increases of 1-10% (Etkin, 1990; Maxwell, 1992). Undoubtedly, effects of climate change will vary seasonally and on a localized spatial scale. Chapin et al. (1995) suggested that regional climatic warming already may be occurring in the moist tussock tundra in northern Alaska.

With the exception of Eastland and White (1991) and Bowyer et al. (in press), little consideration has been given to the effects of climate change on populations of large mammals. To determine if differences in climate could be detected between years in which the Chisana caribou herd was stable or increasing and years when the population was declining, we investigated relationships between climatic variables and population size of Chisana caribou. We tested the null hypotheses that summer temperature, summer rainfall, and snow depth were not different between years the population was declining (1989-1995) and years the herd was stable or increasing (1981-1988). We predicted that years the herd was declining would have higher summer temperatures, lower summer precipitation, and higher snow depth compared with years the herd was stable or increasing because these climatic factors are thought to reduce quality and quantity of forage for caribou.

To determine effects of annual variation in climate on forage quality, we used field experiments to determine whether altered light, temperature, or water availability influenced the nutrient content of caribou forage within the range of the Chisana herd. We tested the null hypotheses that the following conditions did not affect nitrogen (N) content, above-ground biomass, in vitro dry matter digestibility, or tannin content: 1) changes in available sunlight; 2) changes in amount of precipitation; 3) changes in ambient temperature; 4) changes in temperature and precipitation combined; and 5) changes in available sunlight and precipitation combined. We predicted that plants receiving reduced irradiance and thus lower temperature would have lower above-ground biomass, higher nitrogen concentration and digestibility (Salisbury and Ross, 1985), and less tannin content (Bryant, 1983) compared with plants grown at higher temperatures. We expected that reduced irradiance would decrease photosynthetic rates and thus total biomass, but increase percent nitrogen due to increases in the ratio of N:biomass. Percent digestibility also would be higher because there would be less structural carbohydrate due to less growth. The tannin content should be lower because there would be less available carbon allocated to defenses (Bryant, 1983). We predicted that for plants grown at higher temperatures, supplemental water would increase both biomass and percent nitrogen.

MATERIALS AND METHODS

Study area.--This study was conducted in the eastern portion of Wrangell-St. Elias National Park and Preserve at Solo Mountain (61° 50'N, 141° 50' W) in interior Alaska during the summers of 1994 and 1995. The study site was located at an elevation of 1,524 m in an area where Chisana caribou occur from post-calving through summer (Fig. 2). The Chisana herd ranges in the Nutzotin and north Wrangell Mountains from the Nabesna River east into the Yukon Territory, Canada (Fig. 2) at elevations ranging from 800 to 2,000 m (C. Gardner, in litt). Calving is restricted to higher elevations (1,460-2,000 m) with parturient females sequestering themselves away from other caribou (C. Gardner, in litt.). During 1990-1995, post-calving aggregations of 300-500 animals occurred at Solo Mountain.

Hunting pressure on the Chisana herd has remained relatively low since the 1980's, at which time the average harvest was 44 adult males/year. By 1990, this harvest was reduced to 22 adult males, and in 1994 and 1995 no permits for harvest were issued.

Predators within the range of the Chisana herd include wolves (Canis lupus), grizzly bears (Ursus arctos), and coyotes (Canis latrans). Ungulates other than caribou in the study area include Dall's sheep (Ovis dalli dalli) and Alaskan moose (Alces alces gigas).

Regional vegetation is a mosaic of white and black spruce (Picea glauca and P. mariana) at lower elevations (700-900 m), alpine tundra (predominately a Carex - Dryas community) at intermediate elevations (1,000-1,550 m), and heath (Cassiope) and bare ground and rugged talus slopes at higher elevations (1,600-2,000 m). Willows (Salix) follow the riparian drainages. Mountain sides are dominated by willow (Salix), shrub birch (Betula nana), and blueberry (Vaccinium vitas-idaea).

The climate is typical of the subarctic with long, cold winters and a short growing season. For summer (15 June-15 August 1981-1995), mean total precipitation was 139 mm, mean maximum temperature was 17.8° C, and mean temperature was 11.5° C (Nabesna Weather Station; Fig. 2). Snowfall in the winter range averages 28.9 cm (1 Oct -1 May, 1980 - 1995; Northway Weather Station).

Historical data on caribou and weather.--We obtained maximum, minimum, and average-daily temperature and daily precipitation for 15 June - 15 August 1981 - 1995 from the Nabesna weather station located 90 km northwest of the study site at an elevation of 915 m (Fig. 2). A crude index of severity of insect harassment was estimated from the number of days the average temperature was $\geq$ 13°C during 1 July - 15 August (Russell et al., 1993). Because our index does not include information on wind speed, and mosquitoes (Culcidae) and oestrid flies (Cephenemyia, Hypoderma) are often active only when wind $<$ 6 m/s and $<$ 9

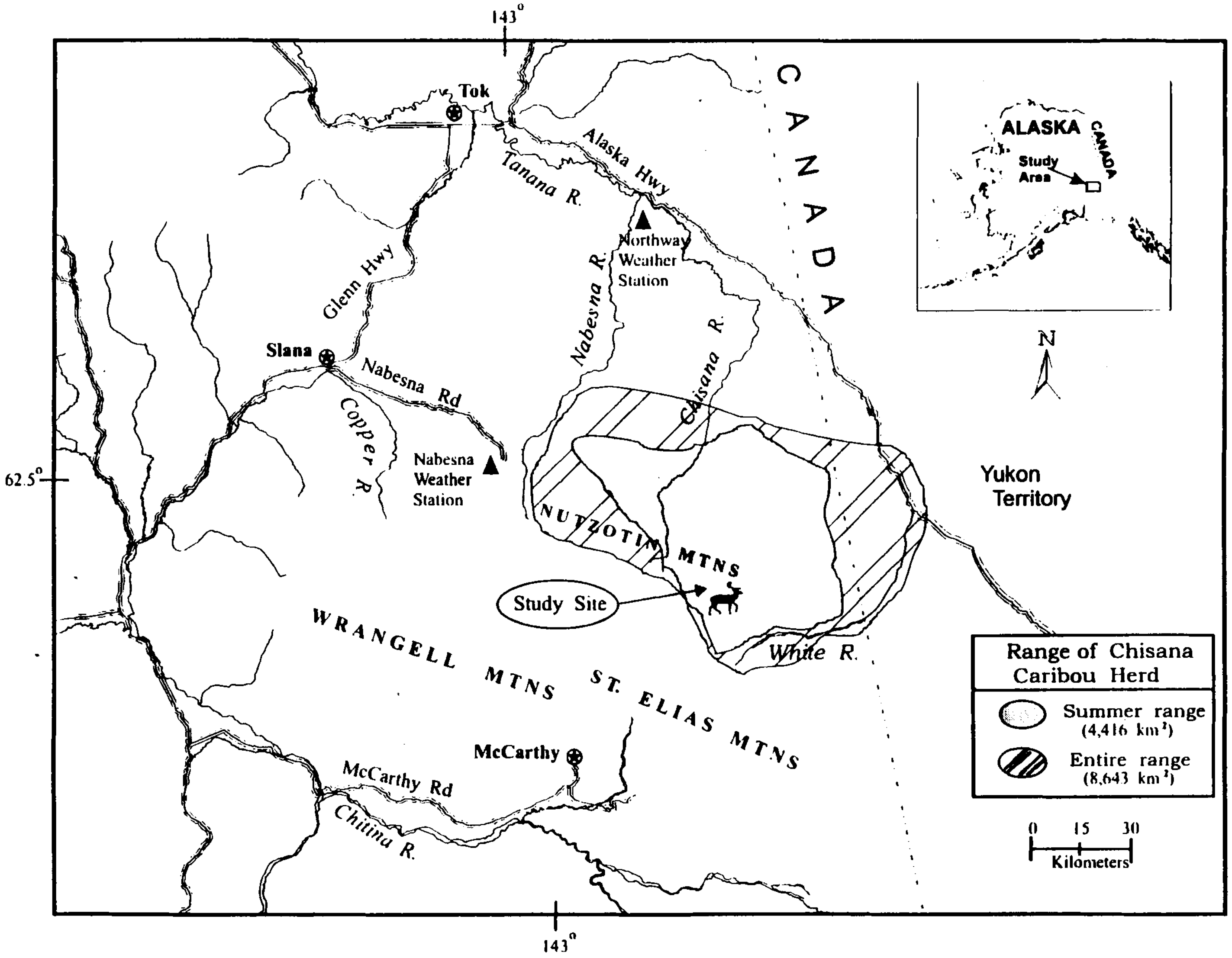

Fig. 2. Range of Chisana caribou herd and location of study site for summer 1994 and 1995.

m/s (respectively; Russell et al., 1993), our calculations may yield an overestimate of actual levels of insect harassment. Snow depth and average winter temperature from 1 October - 30 April were obtained from the Northway weather station, located 90 km north of the study site at an elevation of 535 m (Fig. 2). Population parameters (ratios of calf:adult female, population size, and pregnancy rates) for the Chisana caribou herd were obtained from the Alaska Department of Fish and Game Survey & Inventory reports from 1981 - 1995 (D. O. Kelleyhouse, in litt.; C. Gardner, in litt.).

Experimental designs and field procedures.--Two experimental designs were implemented in an area of representative habitat where Chisana caribou occur from post-calving (19-26 June) through summer. The experiment involving tundra-mat habitat was conducted in a tundra community of sedge and Dryas (slope <5%) consisting mainly of Carex bigelowii, Dryas octopetala, Salix reticulata, S. arctica, Lupinus arctica, and moss, with few lichen (Cladina). An experiment involving Salix pulchra was located on a mountainside (slope ca. 20%) in a shrub community consisting mainly of S. pulchra, Betula nana, and Vaccinium vitas-ideas. All plant nomenclature follows Hultén (1968).

In tundra-mat habitat, a 48 by 60-m grid, consisting of 30 (1.8 by 3.6 m)treatment plots, was established in June 1993 (Fig. 3). Percent cover of each species was estimated for all plots during 1993 prior to applying treatments to the plots in 1994. A principal-components analysis (PCA) was performed on percent cover estimates and these factor scores were used to compute a variogram that identified spatial autocorrelation in the grid. Based on the estimated autocorrelation in the variogram, treatments were assigned to plots by using a simple genetic algorithm (Goldberg, 1989) with simulated annealing (Geman and Geman, 1984), to obtain an optimal spatial pattern that allowed maximum statistical power for detecting treatment effects (Ver Hoef and Cressie, 1993).

Six treatments (including one control) were applied to the 30 vegetation plots in the tundra-mat habitat to simulate changes relative to extant summer conditions: a warmer, drier summer; a warmer, wetter summer; a cloudy, drier summer; and a cloudy, wetter summer. The six treatments were: 1) greenhouse (clear plastic tarp); 2) greenhouse with additional water; 3) shade (50% shade tarp); 4) shade with additional water; 5) unaltered control (no tarp); and 6) no tarp with additional water. There were five replicates per treatment. The shade tarps allowed 40 - 70% of natural precipitation to pass through; the greenhouse plots prevented natural precipitation from reaching the plot. Thirty liters of water were added once each week to the treatment plots requiring additional water to mimic above average rainfall.

Treatments were applied during 14 June - 8 August 1994 and 13 June - 5 August 1995 on each plot in both years. Each treatment plot included eight subplots, each 0.25 m^2. Treatment plots were spaced 7.5 m apart horizontally and 9.8 m apart vertically (Fig. 3). Subplots were spaced 28.5 cm apart horizontally, 18 cm apart vertically and were 28 cm from the edge of the tarp. Clear and shade tarps were 1.8 by 3.6 m and covered an entire plot. The tarps were suspended ca. 25-35 cm above the plant canopy in a tent-like fashion and opened at the sides to allow circulation of air and to prevent humidity from increasing above natural conditions. Clear tarps were made from 0.5 ml polyethelene plastic. Shade tarps were made from 50% ALUMINET (Hummert International, St. Louis). We implemented a design that sampled plots in close proximity to one another to help reduce variance among plots. We selected this design over one that randomly located plots widely across the landscape so that effects of treatments could be detected. We acknowledge that this reduces the area of

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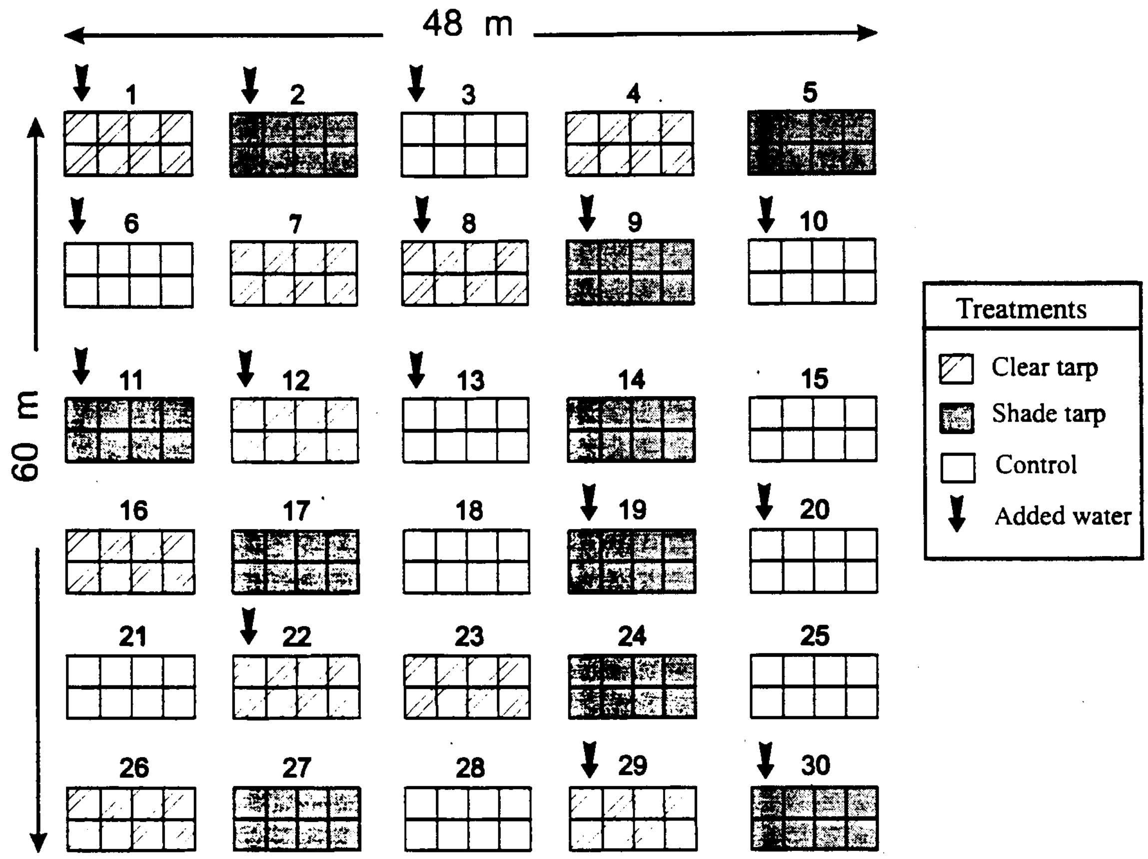

Fig. 3. Tundra-mat experimental design at Solo Mountain, Alaska, in the summer range of the Chisana Caribou Herd, 14 June - 8 August 1994 and 13 June - 5 August 1995. Each treatment plot consists of eight 0.25m^2 subplots.

inference for our experiment, but this methodology was essential to test effects of climatic variables on forages because of the variable nature of plant communities in areas inhabited by caribou.

To assess above-ground biomass, four subplots were clipped in 1994 and four were clipped in 1995. All vegetation in one 0.25 m^2 subplot per treatment plot was clipped to the ground-level on the following dates: 10-11 June, 26-28 June, 19-22 July, and 8-12 August during 1994, and 5-8 June, 27-30 June, 20-22 July, and 6-9 August during 1995. Clipping dates varied slightly between years in an attempt to clip plants at the same phenological stage in both years. Clipping in the first time period did not occur until plants were green (green-up) and there was sufficient above-ground biomass to obtain adequate samples (> 2 g dry weight) for forage analyses. The second clipping occurred when plants had been growing for approximately 2 weeks and was defined as late spring (based on plant phenology, not day length), the third clipping occurred during peak season biomass, and the last clipping occurred during of senescence. Treatments were applied following the first clipping in both years. Clippings were placed in paper bags, and these paper bags into plastic bags, and stored on the ground in the shade to keep them cool until sorting. Sorting plants began immediately after clipping and would take up to 12 days.

Samples were sorted into live and dead, with live plants sorted further into three plant categories: forbs (e.g., Lupinus arctica, Dryas octopetala , Astragulus, Thalictrum alpinum, Pedicularis capitata, Oxytropis nigrescens were the dominant species), graminoids (Carex bigellowi was the dominant species), and prostrate willows (Salix reticulata and S. arctica). Although percent cover of mosses and lichens was estimated, we removed moss from analyses because it is not an important forage for caribou in summer (Boertje, 1984) and its intake by caribou is usually incidental. Lichens also were removed from analyses because there was not adequate material for forage analyses. After sorting, plants were air-dried for 2-5 days and then stored in paper bags. In addition to above-ground biomass, percent cover of species was estimated visually on each subplot and ranked as: 1 (<1%), 2 (1 - 5%), 3 (6 - 10%), 4 (11 - 25%), 5 (26 - 50%), 6 (51-75%), 7 (76 - 100%).

Ambient air temperature was recorded every 1.6 h from 14 June - 8 August 1994, and 13 June - 5 August 1995 for one replicate per treatment using HOBO data loggers (ONSET Instruments, Pocassett, PA). The HOBO-TEMP was placed approximately 25 cm above the ground in the center of the plot. Precipitation (± 1 mm) was recorded using a rain gauge for one replicate per treatment. One soil core (4 cm diameter by 10 cm deep) was collected from the center of each treatment plot on 16 July 1994 and again on 14 July 1995. Cores were placed in plastic bags and stored in the field in a cooler with snow for 1 day, then air-freighted to Fairbanks and frozen for later analyses.

Five replicates of three treatments were applied to 15 plots in S. pulchra habitat. Treatments included: 1) greenhouse (clear plastic tarp); 2) shade (50% shade tarp); and 3) control (no tarp). Treatments were established randomly during 10 July - 2 August 1994, and 20 June - 1 August 1995. Each treatment plot included four to five willow ramets and was divided into four 0.25 m^2 subplots. Clear tarps and shade tarps were 3.6 by 3.6 m and covered an entire plot. Tarps were suspended ca. 1-1.5 m above the ground.

Approximately 15 - 25 twigs of current annual growth for S. pulchra were clipped from one 0.25 m^2 subplot per treatment plot on the following dates: 3-5 August 1994, 11 July 1995, and 2-3 August 1995. Samples were placed into paper bags and air dried.

Fresh samples of caribou feces were collected to determine diet composition and confirm that the plants in the experiments were included in the diet of Chisana caribou. Each composite sample contained three fecal pellets from each fresh defecation. Fecal pellets were collected on the following dates (number in parentheses indicates the estimated number of caribou in a group from which feces were gathered): 2 June (13), 24 June (200), 3 July (120), 26 July (35), and 7 August (75) in 1994, and 20 June (300), and 29 June (250) in 1995. Fecal pellets were air dried until removal from the field and then stored frozen. Diet composition was assessed from the fecal samples by identifying forage fragments from microhistological characteristics (Dearden et al., 1975). Analysis of fecal samples was conducted at the Habitat Laboratory at Washington State University. Percent diet composition was based on epidermal fragments of plants in 100 microscope views per composite sample and was identified to species. Nitrogen concentration in caribou feces was determined by combustion in a LECO CNS 2000 autoanalyzer at Washington State University.

Plant analyses.--For the tundra-mat experiment, each vegetation sample was oven-dried at 58°C for 48 h to constant weight and weighed to the nearest 0.01 g to estimate above-ground biomass. Leaves and flowers were included in the analyses of forbs. Leaves and early buds were removed from prostrate willows, re-dried and weighed. Woody material was not included because it seldom is summer forage for caribou (Boertje, 1984). Biomass was not estimated for the S. pulchra experiment.

Prior to weighing, the litter layer was removed from each soil core. Cores were weighed frozen and weighed after oven-drying for 48 h to estimate percent soil moisture. Percent soil moisture was calculated as (frozen weight - dry weight)/frozen weight.

Samples of forbs (including leaves, stems, and flowers), graminoids, and prostrate willows (leaves and early buds), and leaves and early buds from the S. pulchra experiment, were each ground in a Wiley mill through a 20-mesh (0.12 mm; for in vitro dry matter digestibility analysis) and 40-mesh (0.06 mm; for N analysis) screen. The ground samples were stored in a tightly sealed plastic bag.

Nitrogen concentration in plant tissue was determined by combustion in a LECO CNS 2000 autoanalyzer at the Forest Soils Laboratory at the University of Alaska Fairbanks (Bremner and Mulvaney, 1982). In vitro dry matter digestibility (IVDMD) was determined at the Institute of Arctic Biology at University of Alaska Fairbanks using the Tilley and Terry (1963) technique with modifications recommended by Person et al. (1980). Rumen liquor was obtained from a fistulated reindeer that ranged free in the pasture at the Large Animal Research Station at the University of Alaska Fairbanks and was supplemented with a barley and corn based concentrate with crude protein $\geq$ 16% (Quality Textured Ration, Alaska Mill and Feed, Anchorage).

An assay for proanthocyanidin (condensed tannin) was performed at the Institute of Arctic Biology, University of Alaska Fairbanks following procedures outlined in Martin and Martin (1982). Tannin analyses were conducted on leaves of all samples (ground to 0.12 mm) collected from the S. pulchra experiment and on 120 samples of prostrate willows (S. reticulata, S. arctica, S. hybrid) collected from the tundra experiment (20 July and 10 August 1994, and 21 July and 8 August 1995). The standard (reference sample) for all tannin assays was condensed tannin from S. pulchra.

Statistical analysis.-- We performed a principal-components analysis on a correlation matrix (i.e., the variables were standardized because of different units of measurement). We used 14 variables for summer weather (degree days > 5° C, snow-free days, monthly mean and maximum temperature, monthly precipitation, summer mean and maximum temperatures, total summer precipitation) to determine which variables explained most of the variation. Another principal-components analysis was performed on factors 1 and 2 to generate two 95% C. I. ellipsoids on the bivariate mean (Johnson and Wichern, 1982) to compare patterns of summer weather for years the Chisana herd was stable or increasing with years the herd was declining. We performed a multivariate analysis of variance (MANOVA) on the two variables that explained most of the variation in the first PCA to test for differences at $\square < 0.05$ (Johnson and Wichern, 1982). We used a *t* test on average summer temperature, July temperature, and precipitation to test these variables individually in accordance with our hypotheses. These same tests (PCA, MANOVA) were applied to winter variables (snow-depth index, snow depth on 15 November and 1 April, average winter temperature, average November temperature, and average April temperature). We also conducted a *t*-test on average depth of snow for 15 November-1 April. In addition, we performed a PCA on both summer and winter variables combined. To examine the combined role of population density and weather on the decline of the Chisana herd, we also included population size in the summer and winter PCA's.

Biomass, percent N, percent soil moisture, IVDMD, and tannin content from the spatially designed experiment (Fig. 3) were analyzed using the gls-variogram method (Ver Hoef and Cressie, 1993) to detect differences among treatments. To analyze biomass from the tundra-mat habitat, we modified the gls-variogram for use with covariates, similar to analysis of covariance. We performed principal-components analysis (PCA) on medians of cover classes for each species and used factor 1 as a covariate for the biomass analyses to correct for changes in species composition across the grid. The gls-variogram uses the underlying spatial variation (autocorrelation) to estimate treatment contrasts with greater precision than classical ANOVA (Ver Hoef and Cressie, 1993). Ver Hoef and Cressie (1993) suggested comparing the test statistic to a standard normal distribution. Because of our small sample sizes, however, we simulated the null distribution for the gls-variogram for a variety of autocorrelation values and obtained a significant level of $\underline{Z} = 2.4$ versus the traditional 1.96 from the standard normal distribution. We used the following model: $Y_{ijkm} = R_{ij} + E_{ijkm}$, where is R_{ij} treatment effect: $i = 1$ (add H_2O), 2 (no H_2O); $j = 1$ (shade), 2 (greenhouse), 3 (control); and E_{ijkm} is a spatially-explicit error term; $k =$ rows 1, 2, 3, 4, 5, 6, and $m =$ columns 1, 2, 3, 4, 5.

We tested the following contrasts: 1) main effects of water ($R_{11} + R_{12} + R_{13} - R_{21} - R_{22} - R_{23}$); 2) main effects of control versus shade ($R_{13} + R_{23} - R_{11} - R_{21}$); 3) main effects of control versus greenhouse ($R_{13} + R_{23} - R_{12} - R_{22}$); 4) main effects of shade versus greenhouse ($R_{11} + R_{21} - R_{12} - R_{22}$); 5) control shade for watered plots ($R_{13} - R_{11}$); 6) control versus greenhouse for watered plots ($R_{13} - R_{12}$); 7) shade versus greenhouse for watered plots ($R_{11} - R_{12}$); 8) control versus shade for no-watered plots ($R_{23} - R_{21}$); 9) control versus greenhouse for no-watered plots ($R_{23} - R_{22}$); 10) shade versus greenhouse for no-watered plots ($R_{21} - R_{22}$); 11) shade versus greenhouse interaction for watered plots ($R_{11} - R_{12} - R_{21} + R_{22}$); 12) shade with water versus vs. shade with no watered plots ($R_{11} - R_{21}$); 13) greenhouse with water versus greenhouse with no watered plots (R_{12} - R_{22}); and 14) control with water versus control with no watered plots (R_{13} - R_{23}). We recognize that we performed multiple tests, but our inference is not dependent on all of these tests because we also were examining patterns in these data. By using a Bonferroni, we would not have enough power to detect differences because our P-value would equal 0.001 to be significant. Thus, because there is a 1/20 chance of a test being significant ($P < 0.05$), and there were 168 tests, we proposed the following rules when interpreting the data: if only one contrast per plant category per analysis (N, biomass, IVDMD) per clipping period was significant or if only one contrast of the 14 was significant for only one time period, we attributed these outcomes to chance.

For the S. pulchra experiment, we used ANOVA to test for differences among treatments for N, IVDMD, and tannins. We only applied contrasts two, three, and four as described previously because there was no water treatment.

RESULTS

Caribou population dynamics and climate.--During the mid to late 1970's, the Chisana caribou herd decreased to <1,000 animals from an estimated 3,000 animals in the early 1960's (D. Kelleyhouse, in litt.). Between 1981 and 1988, the herd increased to 1,900; calf:adult female ratios in October ranged from 34:100 to 43:100 (D. Kelleyhouse, in litt.; Fig. 1). In 1989, herd size and calf recruitment began to decline steadily, and in autumn 1992 ratios of calf:adult female were <1:100 (C. Gardner, in litt.; Fig. 1). In March 1993, only 50% of adult females were pregnant. In 1994 and 1995, pregnancy rates were 86% and 95%, respectively. No data exist for pregnancy rates prior to 1993. Thus, caribou were stable or increasing from 1981 to 1988 and declined markedly thereafter (Fig. 1).

Snow depth did not vary significantly between years the Chisana caribou population was declining compared with years the herd was stable or increasing. Results of principal-components analysis on the winter weather indicated that 40% of the variation was explained by the first factor with snow-depth (1 Oct - 1 May) having a positive weight in contrast to average temperature with a negative weight. Thus, a higher mean depth of snow was related to a lower mean temperature in winter. The second factor explained 29% of the variation with average April temperature having a positive weight in contrast to snow depth on 1 April, which possessed a negative weight. Thus, after accounting for the first factor, high April temperatures were correlated with low snow depth on 1 April. The 95% C. I. ellipsoids of the bivariate mean from factor 1 and 2 showed that there was some overlap in variables related to winter weather between years the herd was stable or increasing and years the herd was declining (Fig. 4). The MANOVA between stable and declining years using the two most influential variables, snow-depth index and average winter temperature, was not significant ($F = 2.86$, d.f. = 11, $P = 0.10$). Likewise, the t-test on snow depth between stable and declining years was not significant ($t = 1.61$, d.f. = 12, $P = 0.13$).

Summers tended to be warmer and slightly drier during years the caribou population was declining compared with years the herd was stable or increasing. Results of principal components analysis for the summer weather indicated that 38% of the variation was explained in the first factor with variables related to summer temperature having positive weights and precipitation variables (1 July - 15 August) possessing negative weights. Thus, in

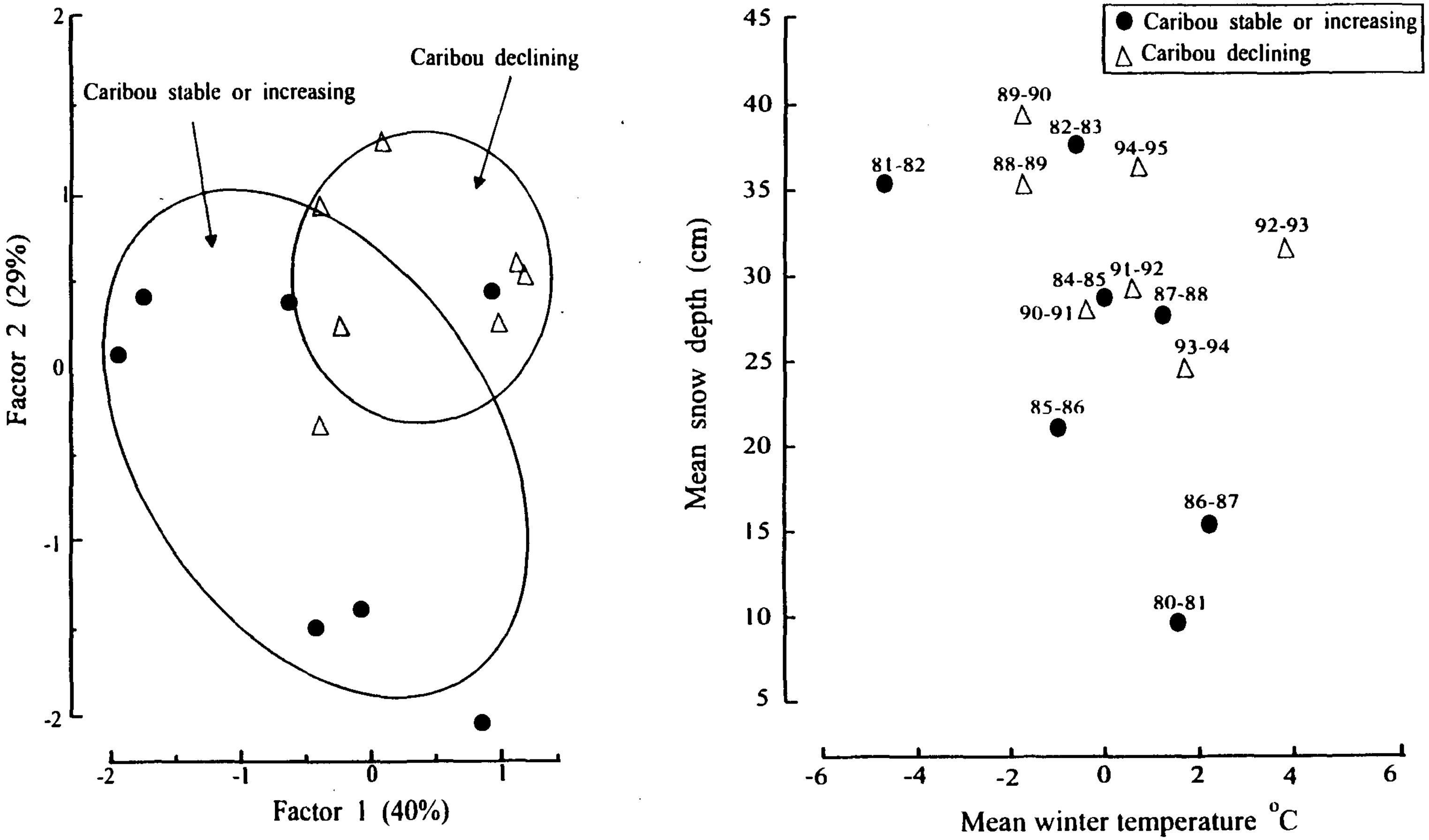

Fig. 4. (Left) Results of principal-components analysis showing 95% C.I. of the bivariate mean using winter weather variables from years the Chisana caribou herd was increasing or stable compared with years the herd was declining, Solo Mountain, Alaska. (Right) Mean winter temperature (1 Oct - 1 April) and mean snow depth from Northway Weather Station, Alaska 1981-1995. Number above marker indicates year.

general, higher summer temperatures were correlated with lower precipitation (Fig. 5). The second factor explained 18 % of the variation with June temperature having positive weight in contrast to June precipitation, and July and August temperatures with negative weights. Thus, after accounting for the first factor, a warmer June was correlated with low June precipitation and cooler temperatures in July and August. The 95% C. I. ellipsoids on the bivariate means generated from factors 1 and 2 showed that there was some overlap in summer weather between years when the herd was stable or increasing and years when the herd was declining (Fig. 5). The MANOVA for differences between these periods (variables were summer temperature, 15 Jun - 15 Aug, and precipitation, 1 July - 15 Aug) was marginally nonsignificant ($F = 3.5$, d.f. = 11, $P = 0.06$) indicating that differences likely occurred (Fig. 5). The t-test indicated there was a significant difference ($t = 2.5$, d.f. = 12, $P = 0.027$) in mean summer temperature between years the Chisana herd was stable or increasing ($\overline{X}$ ± SD= 11.3°C ± 0.9; 1981 - 1988) and years the population was declining ($\overline{X}$ ± SD = 12.3°C ± 0.5; 1989-1995). Differences were marginally nonsignificant for precipitation (1 July-15 Aug; t = 1.97, d.f. =12, $P = 0.07$).

Results of the PCA for summer and winter weather variables combined indicated that 44% of the variation was explained in the first factor with variables related to summer temperature and snow depth having positive weights and precipitation variables (1 July-15 August) possessing negative weights. Thus, deeper snows in winter tended to be followed by warmer and drier summers. The second factor explained 17% of the variation with June precipitation having a positive weight and June temperature possessing a negative weight. Thus, a higher precipitation in June was correlated with cooler temperatures in June.

Including population size in the summer and winter PCA's did not alter the outcomes substantially. For the PCA in winter, factor 1 explained 34 % of the variation and factor 2 explained 26% of the variation. For the PCA in summer, factor 1 explained 33 % of the variation and factor 2 explained 21% of the variation. Interpretation of these data for both PCA's was the same as without including population size in these analyses.

We indexed severity of insect harassment as the number of days the average temperature was ≥ 13°C during 1 July - 15 August. The t-test indicated a significant difference ($t = 3.16$, d.f. = 12, $P = 0.015$) between years the population was stable or increasing ($\overline{X}$ ± SD =14.3 ± 4.5; 1981-1988) and years the population was declining ($\overline{X}$ ± SD = 21.8 ± 5.5; 1989-1995).

Diet composition.--Chisana caribou used a large percent of graminoids after the post-calving season (18 - 26 June; Fig. 6). Over both summers, fecal samples were composed of 20 -35 % graminoids (mainly *Carex*; Fig. 6). Shrubs (mainly *Salix*) constituted 20 - 46% of plant material in feces in 1994 and 41 - 64% in 1995. There was a higher percent of moss and lichens in June 1994 diet than June 1995; whereas June 1995 diet composition had a higher percentage of shrubs than June 1994 (Fig. 6). Percent fecal nitrogen was higher in June 1995 than June 1994; but, because of small sample sizes, we were unable to test for differences (Fig. 6).

Plant experiments.--At the study site, total precipitation was higher in 1995 than 1994, and maximum mean temperature was higher in 1994 than in 1995 (Table 1). Green-up occurred approximately 5-7 days earlier in 1995 than 1994. Relative to controls, air

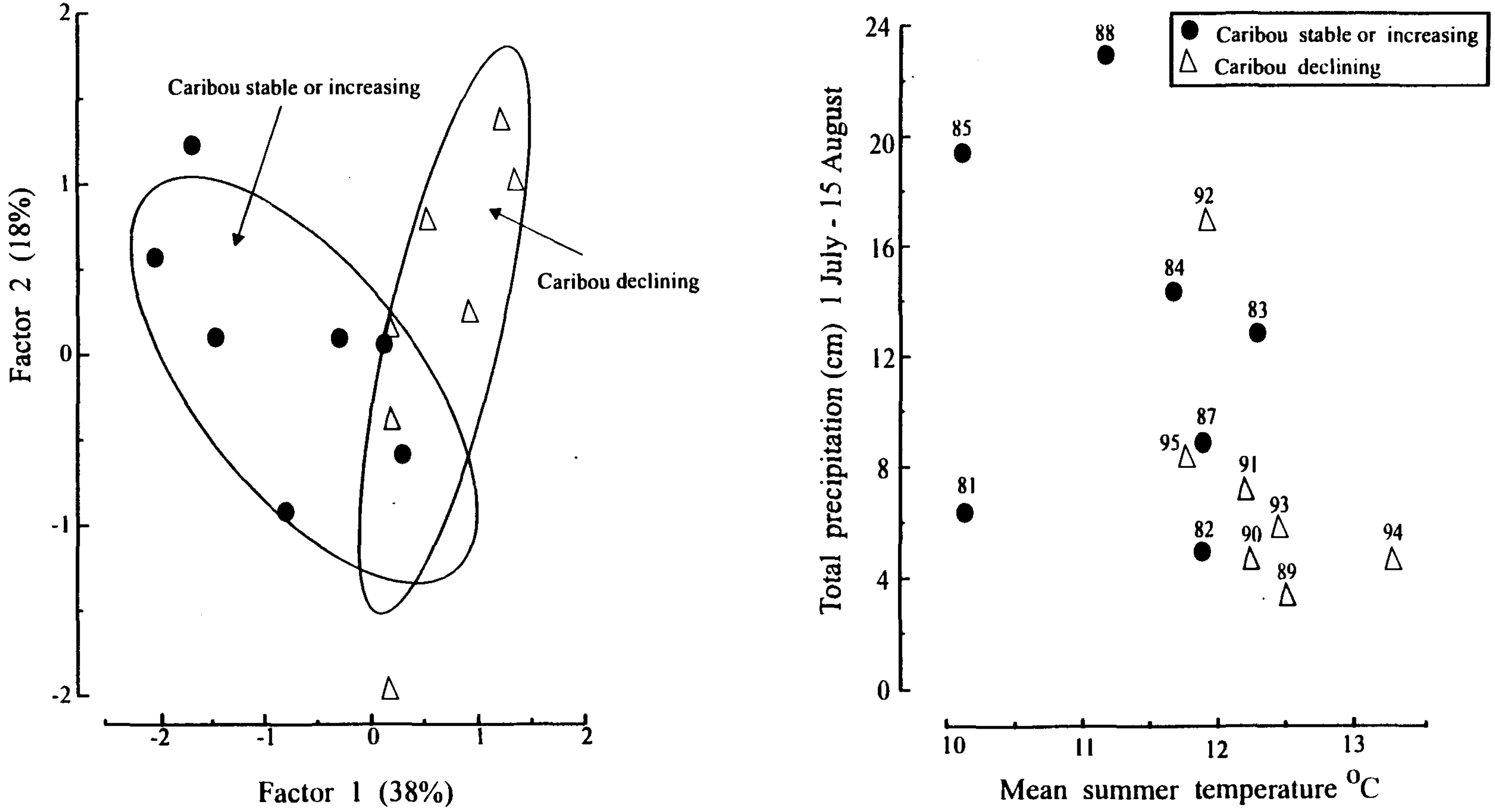

Fig. 5. (Left) Results of principal-components analysis showing 95% C.I. of the bivariate mean using summer weather variables from years the Chisana caribou herd was increasing or stable compared with years the herd was declining, Solo Mountain, Alaska. (Right) Mean summer temperature (15 Jun - 15 Aug) and total precipitation (1 July - 15 Aug) from Nabesna Weather Station, Alaska 1981-1995. Number above marker indicates year. No data were available for 1986.

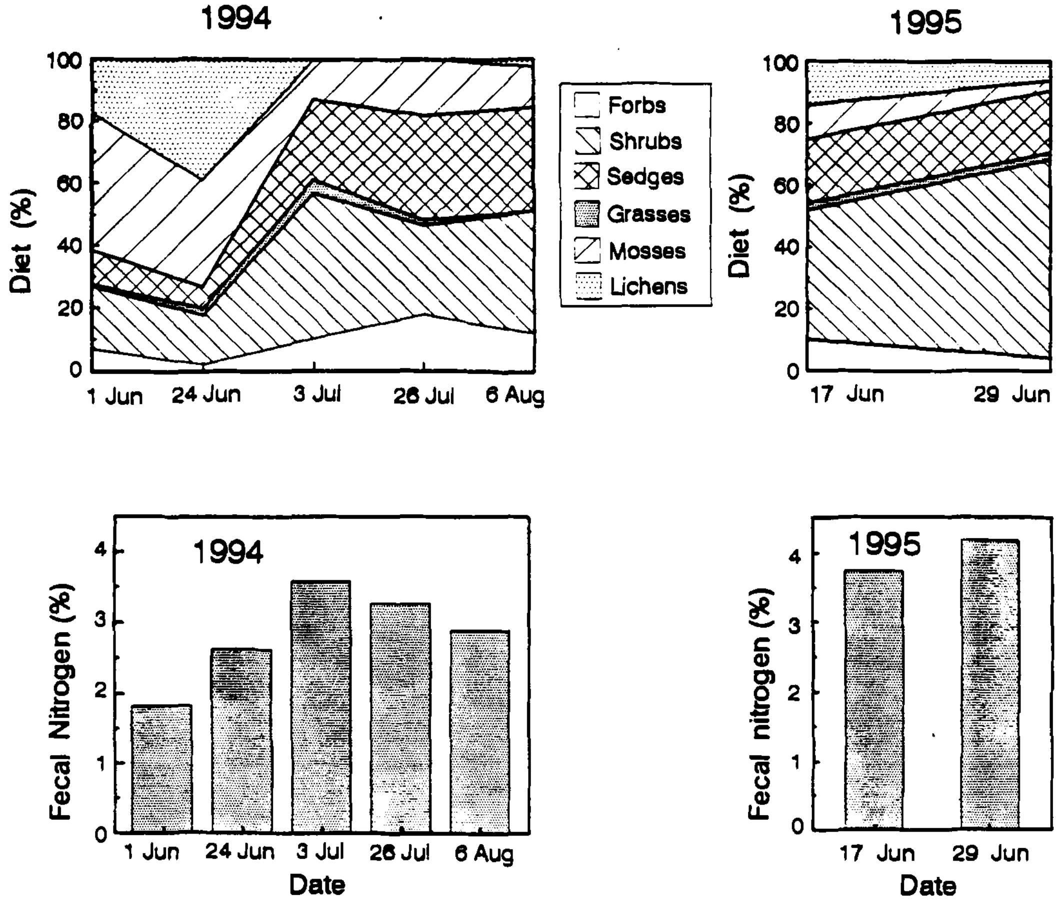

Fig. 6. Percent of diet composition and nitrogen estimated from plant fragments in caribou feces collected near Solo Mountain, Alaska during summer 1994 and 1995.

Table 1.--Sum of daily mean, maximum, and minimum and mean, average maximum, and average minimum temperature[a], degree days > 5°C, and total precipitation[b] collected from one shade, one greenhouse, and one control plot, Solo Mountain, Alaska.

Environmental parameters	Summer 1994			Summer 1995		
	Shade	Greenhouse	Control	Shade	Greenhouse	Control
Air Temperature °C						
Σ Daily Mean	527	665	587	479	587	516
Σ Daily Maximum	884	1267	1021	845	1128	900
Σ Daily Minimum	158	171	166	107	107	105
Mean	9.6±3.2	12.3±3.8	10.8±3.5	8.9±2.9	10.9±3.3	9.5±3.2
Average Maximum	16.0±4.6	24.0±6.9	18.5±5.3	5.6±4.6	20.9±5.4	16.7±4.7
Average Minimum	2.8±2.8	2.8± 2.9	2.7±2.9	1.7±2.7	1.7±2.7	1.6±2.8
Degree days > 5°C	245	385	305	209	317	245
Total Precipitation (mm)	40.6	0.0	97.0	118.9	0.0	163.3

[a] Temperature was collected from 14 June - 6 August (n = 54 days).

[b] Precipitation was collected from 14 June - 13 August (n = 61 days).

temperatures increased in the greenhouse plots ($\bar{X}$ = 11.9 ± 3.8 °C) and decreased in the shade plots ($\bar{X}$ ± SD = 9.6 ± 3.2 °C; Table 1) over the 2 years.

In the tundra-mat experiment, results are reported as contrasts from main effects (i.e., includes both water and unwatered plots per tarp treatment), unless otherwise noted. A complete description of all contrasts is provided in Appendices A-F.

In the tundra-mat experiment, no significant differences occurred among treatments in above-ground biomass for graminoids in 1994 (Table 2). During the late spring sampling (28 June) in 1995; however, the main effects of greenhouse plots were significantly higher ($P < 0.05$) than both shaded and control plots, and greenhouse with water was higher than greenhouse without water. Forb biomass in the shaded plots was significantly lower compared with greenhouse and control plots during both peak biomass and senescence in both 1994 and 1995 (Tables 2, 3). In 1994, greenhouse with water was significantly higher in biomass than greenhouse without water during the 20 July sampling and control with water was higher than control without water during the 9 August sampling ($P < 0.05$). Greenhouse with water also was higher than greenhouse without water during the 28 June 1995 sampling, similar to the graminoids. Although 1995 was a wetter summer, most precipitation occurred in July and August. For the prostrate willows, some differences were detected during the first sampling in 1994, which was prior to treatment and also during the second sampling, which was unexpected because the treatments had been applied for a short time (ca. 2 weeks). Thus, such differences later in summer should be viewed with caution. In 1995, no significant differences occurred (Table 3). Shaded plots had significantly higher soil moisture compared with greenhouse plots during the 1994 sampling (Table 4). No significant differences among treatments occurred in 1995, nor were there any differences between years for the controls. A complete description of all means ± 1 SD for biomass, N, and tannin analyses is provided in Appendices F-M.

Shading tended to increase nitrogen content relative to the greenhouse treatment in both experiments. In the tundra-mat experiment, the main effects (water and unwatered plots combined) of shaded plots were significantly higher in nitrogen ($P < 0.05$) than greenhouse plots in all plant categories on all but one sampling date in 1995 and for prostrate willows and forbs during senescence in 1994 (Table 3, Fig. 7). In addition, shaded plots were higher in nitrogen than control plots in several clippings, and control plots were occasionally significantly higher when compared with greenhouse plots (Table 3, Fig. 7). For prostrate willows, control without water was significantly higher in nitrogen than control with water on 7 August 95. In the *S. pulchra* experiment, shaded plots were also significantly higher in nitrogen ($P < 0.05$) than either the greenhouse or control plots on the second (11 July 1995) and third (5 August 1995) dates of sampling (Fig. 8).

Analyses of *in vitro* dry matter digestibility (IVDMD) in the graminoids indicated that IVDMD was significantly higher ($P < 0\ .05$) in greenhouse plots than in shaded plots during onset of senescence in 1994 and 1995 (Table 3, Fig. 9). In addition, during senescence, IVDMD also was higher in the control plots than shaded plots in 1994 and higher on greenhouse plots than the control plots in 1995. For forbs, there was a main effect of water, and control with water was higher in IVDMD than control without water during senescence in 1994 ($P < 0.05$). No significant differences in IVDMD were detected in 1995; however, greenhouse plots were higher in IVDMD compared with shaded plots during most of the

Table 2.-- Biomass means ± 1 SD (g/0.25m^2) for tundra-mat experiment, Solo Mountain, Alaska. Different letters indicate significant differences ($P < 0.05$) within each sampling period and 'H' indicates a main effect of water. Statistical results obtained from gls-variogram and principle components analysis which corrected for species composition changing across the grid.

	Clipping period			
Plant/Treatment	10 Jun 1994	26 Jun 1994	20 July 1994	9 Aug 1994
Prostate willows		H		
Greenhouse	3.52 ± 2.16	6.22 ± 2.73	7.76 ± 3.65^{b}	16.06 ± 15.53
Shade	3.64 ± 3.83	10.37 ± 5.54	10.65 ± 5.02^{b}	13.79 ± 9.76
Control	4.49 ± 3.64	9.62 ± 4.58	16.29 ± 11.49^{a}	11.48 ± 3.79
Graminoids		H		
Greenhouse	1.00 ± 0.90	2.05 ± 1.49	4.64 ± 3.48	3.30 ± 2.41
Shade	1.32 ± 0.65	3.32 ± 2.42	4.99 ± 1.10	3.87 ± 1.96
Control	0.64 ± 0.37	2.31 ± 1.49	3.85 ± 2.79	4.16 ± 2.52
Forbs				
Greenhouse	7.32 ± 3.38	12.02 ± 7.57	30.39 ± 14.60^{a}	30.19 ± 10.87^{a}
Shade	6.80 ±3.06	13.30 ± 6.67	19.83 ± 6.95^{b}	16.39 ± 7.43^{b}
Control	6.96 ± 2.89	19.45 ± 8.17	29.93 ± 7.44^{a}	28.08 ± 14.04^{a}
	6 Jun 1995	28 Jun 1995	22 July 1995	7 Aug 1995
Prostate willows				
Greenhouse	12.14 ± 10.70	14.53 ± 6.62	18.80 ± 10.76	13.94 ± 5.76
Shade	8.53 ± 4.81	13.85 ± 5.74	17.66 ± 16.15	13.02 ± 7.88
Control	6.31 ± 4.11	15.13 ± 7.69	12.91 ± 4.36	13.87 ± 6.00
Graminoids				
Greenhouse	1.86 ± 1.30	4.46 ± 2.12^{a}	4.50 ± 2.12	3.87 ± 2.71
Shade	1.79 ± 0.68	3.70 ± 1.65^{b}	5.98 ± 3.10	4.81 ± 2.45
Control	1.34 ± 0.89	2.78 ± 1.47^{b}	4.26 ± 2.62	3.60 ± 2.34
Forbs				
Greenhouse	12.50 ± 7.48	26.12 ± 10.46	32.70 ± 16.85^{ab}	40.73 ± 1348^{a}
Shade	8.61 ± 3.26	21.77 ± 6.75	26.20 ± 9.30^{a}	20.17 ± 10.03^{b}
Control	11.25 ± 5.61	22.37 ± 8.62	37.21 ± 10.33^{b}	31.93 ± 8.76^{b}

Table 3.--Significance of gls-variogram ($P < 0.05$, $n = 10$ per mean) in biomass, percent nitrogen, and percent digestibility analyses of the three plant categories in response to shade (S), greenhouse (G), and control (C) in 1995 tundra-mat experiment, Solo Mountain, Alaska. NS indicates no significant difference.

Plant category and clipping period[a]	Above-ground biomass	% nitrogen	In vitro dry matter digestibility
Prostrate willows			
Green-up	NS	NS	NS
Late spring	NS	S > G; S > C	NS
Peak biomass	NS	S > G; S > C	NS
Senescence	NS	S > G; S > C	G > S
Graminoids			
Green-up	NS	S > G	NS
Late spring	G > S; G > C	S > G; C > G	NS
Peak biomass	NS	S > G; S > C	NS
Senescence	NS	S > G	G > S; G > C
Forbs			
Green-up	NS	S > G	NS
Late spring	NS	S > G; C > G	NS
Peak biomass	C > S	S > G; S > C	NS
Senescence	G > S; G > C	S > G; S > C	NS

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[a] Plants were collected at green-up (6 June 1995), late spring (28 June 1995), peak biomass (22 July 1995), and senescence (7 August 1995).

Table 4.--Percent soil moisture (mean ± 1 SD) for three treatments in tundra-mat experiment, Solo Mountain, Alaska. Different letters indicate significant differences ($P < 0.05$).

	Sampling period	
Tarp treatment	16 July 1994	14 July 1995
Greenhouse	32.7 ± 4.9^{b}	31.2 ± 6.0
Shade	36.6 ± 4.1^{a}	32.5 ± 4.4
Control	34.2 ± 4.0^{b}	35.3 ± 7.2

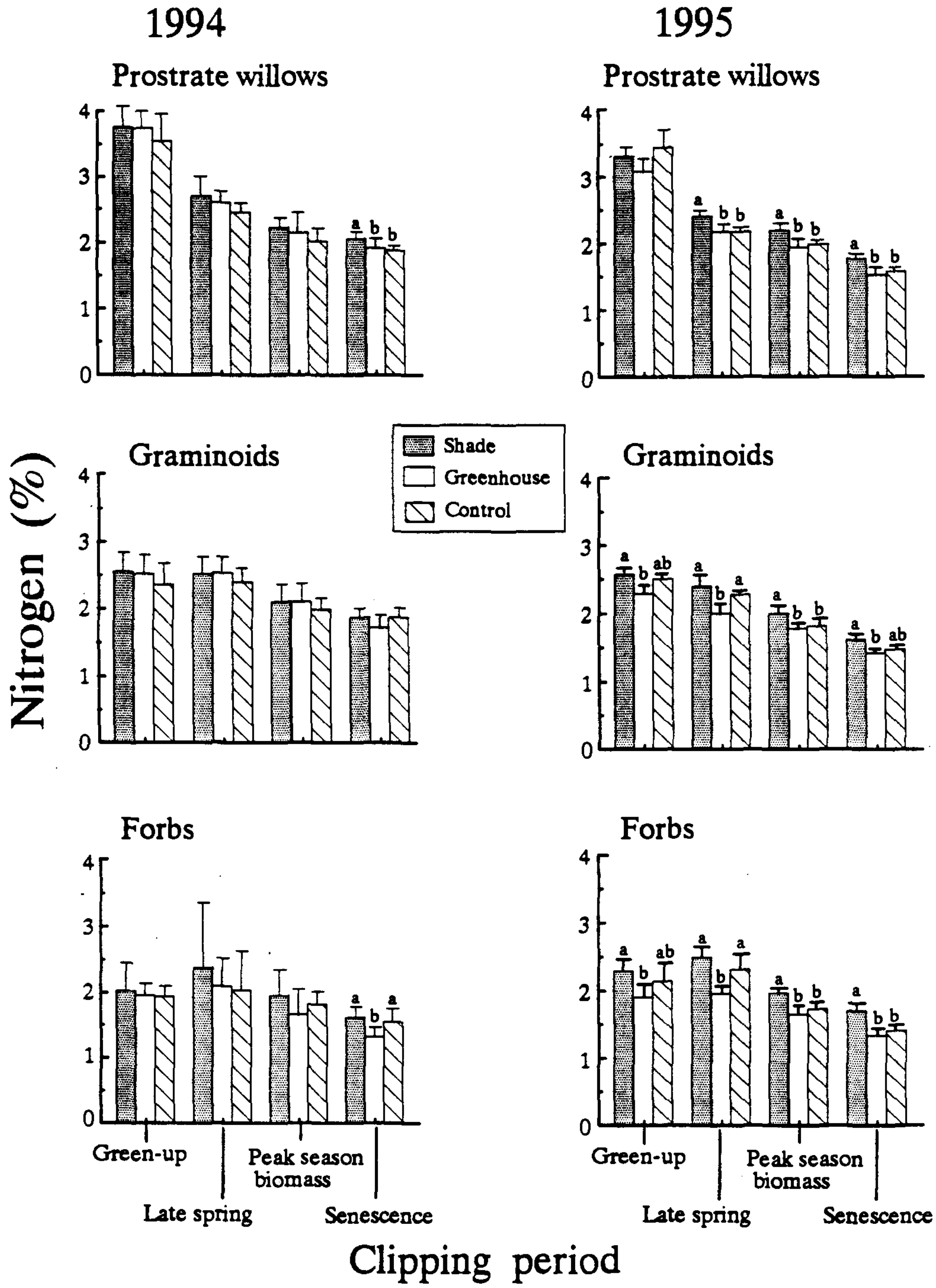

Fig. 7. Means + 1 SE (n = 10) for 1994 and 1995 tundra-mat experiment for percent nitrogen by plant category in response to shade, greenhouse, and control. Plants were collected at green-up (10 Jun 94; 6 Jun 95), late spring (26 Jun 94; 28 Jun 95), peak season biomass (20 July 94; 22 July 95), and senescence (9 Aug 94; 7 Aug 95). Treatments were established 14 June - 8 August 1994 and 13 June - 5 August 1995. Different letters above bars indicate significant differences ($P < 0.05$) within each sampling period.

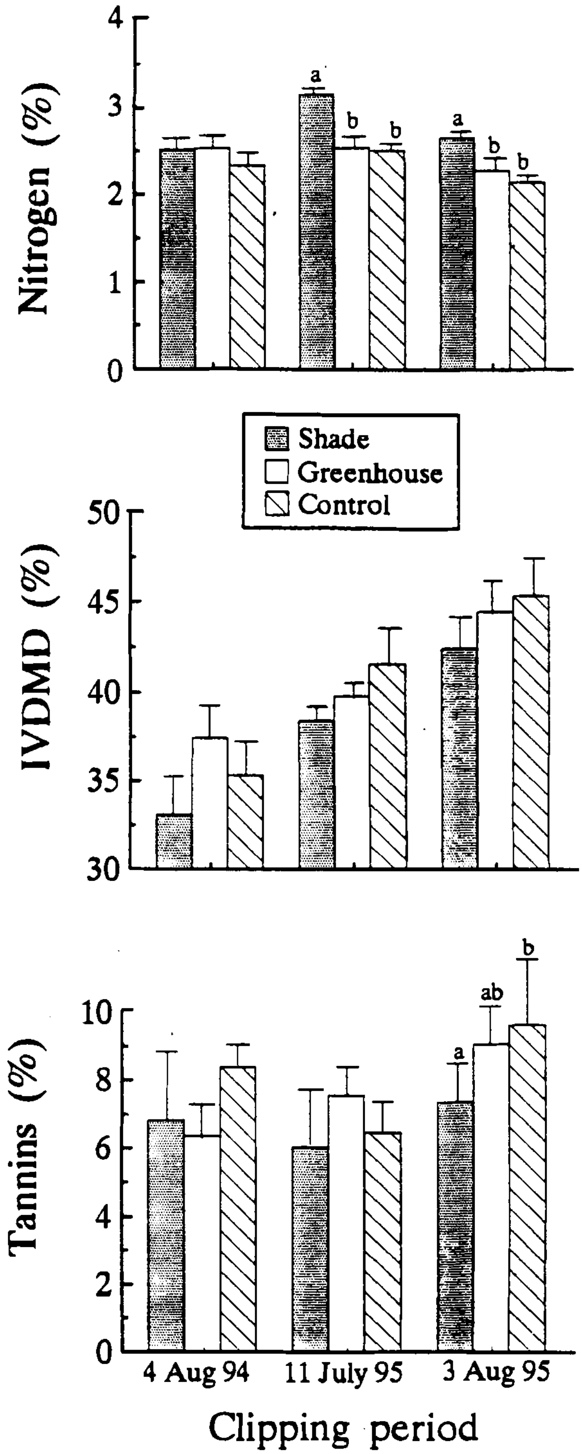

Fig. 8. Means + 1SE ($n = 5$) for Salix pulchra experiment for percent nitrogen, IVDMD, and percent tannin in response to shade, greenhouse, and control for all clipping periods. Treatments established 10 July - 2 August 1994 and 20 June - 1 August 1995. Different letters above bars indicate significant differences ($P < 0.05$) within each sampling period.

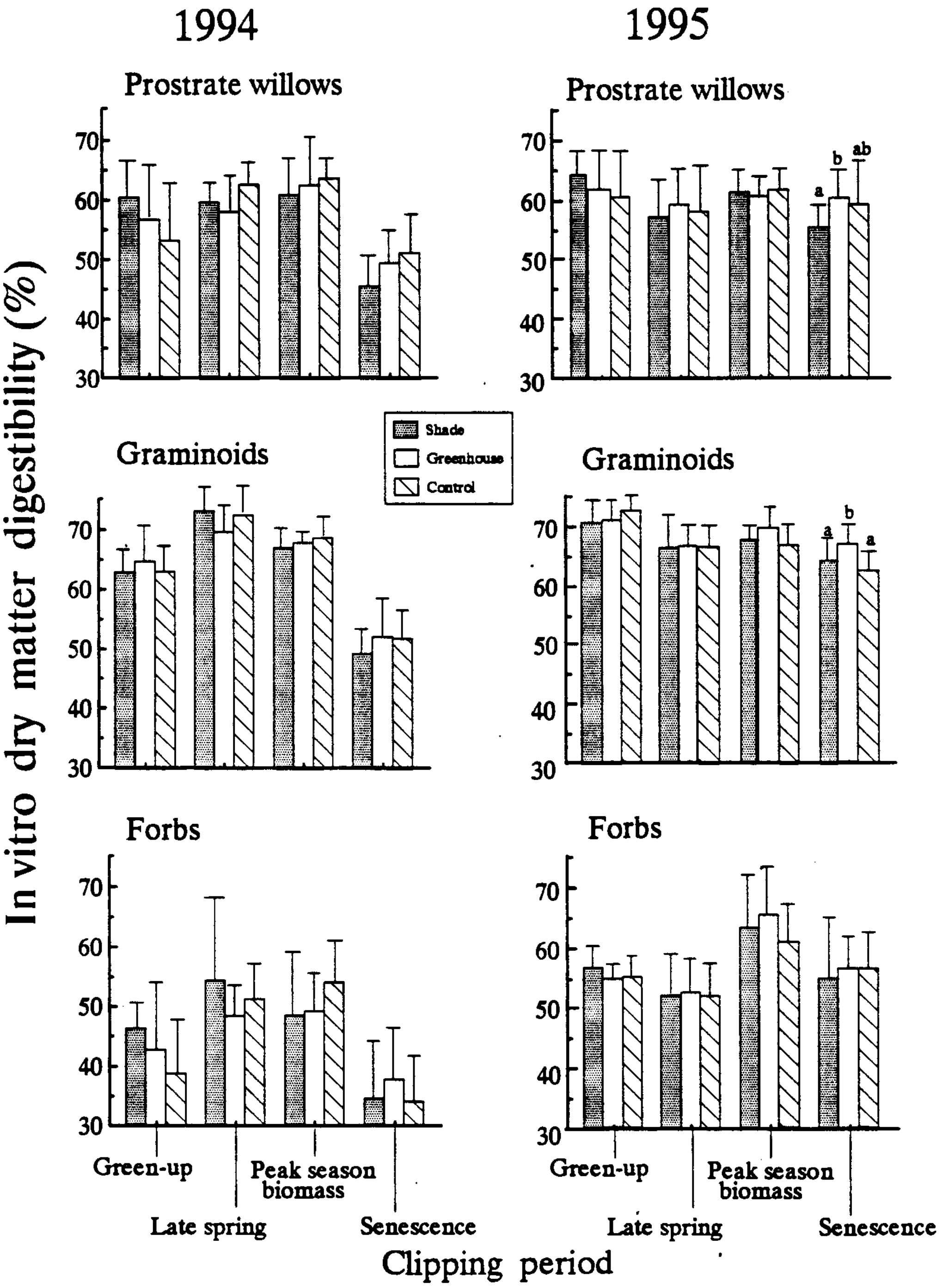

Fig. 9. Means + 1 SE ($\underline{n}$ = 10) for 1994 and 1995 tundra-mat experiment for IVDMD by plant category in response to shade, greenhouse, and control. Plants were collected at green-up (10, Jun 94; 6 Jun 95), late spring (26 Jun 94; 28 Jun 95), peak season biomass (20 July 94; 22 July 95), and senescence (9 Aug 94; 7 Aug 95). Treatments were established 14 June - 8 August 1994 and 13 June - 5 August 1995. Different letters above bars indicate significant differences ($\underline{P}$ < 0.05) within each sampling period.

summer (Fig. 9). In the prostrate willows, the main effect of control plots was significantly higher in IVDMD than shaded plots during senescence in 1994 and there also was a main effect of water ($P < 0.05$; Table 3). In addition, control with water was significantly higher in IVDMD than control without water, and greenhouse with water also was higher in IVDMD than greenhouse without water during senescence in 1994, which was similar to the forbs. Control plots were significantly higher in IVDMD than shaded plots during late spring in 1994. In 1995, IVDMD in both greenhouse and control plots was significantly higher than shaded plots during senescence ($P < 0.05$). In the *S. pulchra* experiment, no significant differences occurred among treatments for IVDMD; however, mean IVDMD in shaded plots was consistently lower than in either the greenhouse or control plots (Fig. 8).

Tannin content was significantly higher in the control plots than in the shaded plots ($P < 0.05$) during the last sampling for the *S. pulchra* experiment (Fig. 8). In the tundra-mat experiment, no significant differences in tannin content occurred among treatments for samplings during 20 July and 10 August 1994 and 22 July and 5 August 1995.

DISCUSSION

Population trends and climate.--The Chisana caribou herd experienced substantial declines in both population size and calf recruitment beginning in 1989 (Fig. 1). Although deep snow can reduce forage availability, increase energy expenditure, and influence calf survival (Fancy and White, 1985), the 95% *C.I.* in the winter PCA showed a wide range of climatic values during years the herd was stable or increasing, suggesting that Chisana caribou could withstand such variability in winter weather (Fig. 4). Furthermore, snow depth in winter probably did not contribute substantially to the population decline because we detected no significant differences or trends in means of snow depth between years when the herd was stable or increasing and years when the herd was declining (Fig. 4). Although snow depth reached 66 cm (70 cm is considered severe) at the Northway Weather Station in March 1990, snow depth in the remaining years during the population decline never exceeded 40 cm. If Chisana caribou were in poor physical condition entering winter, however, the lower snow depths, hard packed snow (Fancy and White, 1985), or poor winter range (i.e., low abundance of lichens; Skogland, 1986) could have had a negative effect. For example, Thomas (1982) reported that adult female caribou (*R. t. peary*) were unable to replenish reserves sufficiently to sustain reproduction the following season after a severe winter. Skogland (1985) also determined that at high population density, wild reindeer were regulated mainly through food limitation in winter. Nonetheless, there is some indication that winter range for the Chisana herd was good, at least during the early 1990's, because fecal pellets collected in winter 1994 were composed of at least 70% lichens, which is comparable to other caribou herds(Russel et al., 1993), The Chisana caribou wintered in the same area in 1991 and 1993 (C. Gardner, in litt.). Therefore, weather and range condition in winter probably did not greatly influence the decline of the Chisana herd.

Summers were substantially warmer and slightly drier during years in which the Chisana herd was declining compared with years when the herd was stable or increasing (Fig. 5). Warm, dry summers tend to favor insect outbreaks (Mattson and Haack, 1987). Our index of insect harassment suggests that severity of insect harassment was higher during the years the herd was declining (P = 0.01). Insect harassment of caribou usually occurs during July and August and includes both mosquitoes (Culicidae) and oestrid flies (Cephenemyia, Hypoderma; Russell et al., 1993). Stress from insects can increase energy expenditure of caribou (Russell et al., 1993), decrease time spent foraging (Russell et al., 1993; White et al., 1975), and decrease forage availability by caribou having to escape to higher elevations where insects are less abundant. These effects combine to reduce energy intake, which can negatively affect body condition and reproductive success of female caribou (Couturier et al., 1988; Thomas and Kilaan, 1990). Warm, dry summers also can affect fecundity of female caribou by affecting quality and abundance of forage on summer ranges. Crete and Huot (1993) and Reimers (1983) concluded that poor summer range adversely influenced the George River caribou and Norwegian reindeer populations, respectively; yet, the effects of climate on plant productivity and nutrient content within these ranges were not determined. In our plant experiments, we determined that cloudy summers could increase nitrogen concentration per bite size in forage of caribou compared with clear summers; however, above-ground live biomass likely would be lower during cloudy summers.

Plant experiments.--Although we detected some differences between watered and unwatered plots; in general, we detected no consistent main effects of water in the tundra-mat experiment. This outcome may have been influenced by the differences in summer weather between 1994 and 1995. Summer 1994 was substantially drier and warmer than summer 1995 (Table 1, Fig. 5). To consistently detect a difference in effects of water, we may have needed to add more water during 1994, and in 1995 there may have been adequate precipitation to saturate the soil adjacent to our plots, thereby providing subsurface water (Table 1, Fig. 5). In addition, green-up occurred approximately 5 days later in 1994 than in 1995.

Chisana caribou used a greater percent of graminoids after the post-calving period than reported in other herds of caribou. Over the two summers, fecal samples had 20-30% graminoids compared with < 15% in other herds (Fig. 6; Boertje, 1984; Russell et al. 1993). Shrubs constituted 20 - 64% of the diet as estimated from fecal analyses, which is comparable to other diets of caribou in summer (Fig. 6; Boertje, 1984, Kelsall, 1968, Thompson and McCourt, 1981). Moss occurred in the feces at a greater percentage in 1994 (range: 13-34%) compared with approximately the same sampling periods in 1995 (range: 3-11%; Fig. 6). This suggests that caribou were in areas of less available forage in 1994, perhaps at higher elevations to escape insect harassment. Most (ca. 95%) of the plant species that occurred in the feces of caribou were represented in the experiments, suggesting that our manipulations of plants would have relevance to caribou populations.

Cloudy summers may decrease growth of forbs, especially during July and August, because above-ground biomass of live forbs was lower in the shaded plots (Table 2). In addition, there was some indication that water would limit growth in forbs during a dry summer. Biomass in graminoids (i.e., Carex bigelowii) also was lower in the shaded plots during late spring (28 June) in 1995 (Table 2). Thus, during an earlier, warmer spring, C. bigelowii may be able to increase live biomass for 3-4 weeks before other species. Similarly, Chapin and Shaver (1985) reported that shade reduced growth of C. bigelowii in a wet tussock tundra, and BØ and Hjeljord (1991) concluded that growth of graminoids in southeastern Norway was delayed in a cloudy, wet June. Likewise, Rachlow and Bowyer (1994) noted that a cool, short summer resulted in a lower quality diet for Dall's sheep. We detected no differences in biomass among treatments in prostrate willows in 1994 or 1995, and we did not estimate biomass in the S. pulchra experiment; however, Chapin and Shaver (1985) reported that warmer temperatures increased growth in S. pulchra.

Although a cloudy summer may decrease above-ground biomass in some plants, it increases nitrogen concentration (Figs. 7,8). Other studies also have reported higher protein content in S. pulchra and Betula nana grown in shade relative to full sunlight (BØ and Hjeljord, 1991; Molvar et al., 1993) and higher nitrogen concentration in Eriophorum growing in cooler temperatures compared with warmer temperatures (Jonasson et al., 1986). In contrast, Chapin et al. (1995) reported higher N concentration in their greenhouse plots. Chapin et al. (1995) suggested that indirect effects of warmer temperatures could potentially increase rates of mineralization in the soil, hence increasing availability of nutrients. The tundra-mat plots had a thick layer of moss and litter, which would insulate the soil and retard rates of decomposition and nitrogen mineralization. Yet, there is some evidence that soil moisture may be higher in a cloudy summer because shaded plots were significantly higher in percent soil moisture compared with greenhouse plots during the 1994 sampling. Although our shade treatment may have been extreme (i.e., 50% shade for the entire summer), we hypothesize that as long as temperatures remain high enough for plant growth (≥ 5°C), a cloudy summer should produce higher nitrogen concentrations in above-ground live biomass of caribou forage than a clear summer in this type of vegetation.

Although there is good evidence that a cloudy summer is favorable for increasing nitrogen concentration in caribou forage, there is some indication from our experiments that it would have a negative effect on percent digestibility (Fig. 8, 9). In the tundra-mat experiment, percent digestibility was lower in shade plots near the end of the season for graminoids, forbs, and prostrate willows in 1994 and 1995 (Fig. 7,9). This trend also occurred in the S. pulchra experiment. We suggest that in the greenhouse plots, sugars (i.e., soluble carbohydrates) accumulated in the plant by the end of the season because of higher photosynthetic rates due to higher temperatures (Table 1). Percent digestibility, however, was substantially lower in all plant categories during senescence in 1994 (the dry summer) than in 1995 (Fig. 8, 9). Thus, a very warm summer may have negative effects on IVDMD (Table 1). This may be especially so for prostrate willows and forbs because some watered plots were higher in IVDMD compared with unwatered plots. There is some evidence, however, of higher percent digestibility being associated with shade. Molvar et al. (1993) reported higher IVDMD and N concentration in S. pulchra in natural shady versus sunny sites. These sites, however, were frequented by moose which likely contributed nutrients to the soil via feces and urine (Molvar et al., 1993), thereby influencing digestibility. Other factors (e.g. sex and age of plant, secondary compounds; Bryant et al., 1983; Klein and Bay, 1994; Reichardt et al., 1990) also may be influencing digestibility and interacting with or masking the effects of climate.

Secondary compounds, particularly tannins, also may reduce digestion and intake of some foods in herbivores (Bryant et al., 1983; Robbins et al., 1987) by binding to proteins and inhibiting absorption (Zucker, 1983). The carbon-nutrient balance hypothesis predicts that in a nutrient-limited environment, plants growing in the shade would have a lower concentration of secondary compounds than plants growing in the sun because the plants in the sun would allocate the excess carbon to defenses (Byrant et al., 1983). As predicted by the carbon-nutrient hypothesis, shaded plots were lower in tannin concentration in the S. pulchra experiment in 1995 (Fig. 8). Similarly, Jonasson et al. (1986) and Bø and Hjeljord (1991) reported lower concentrations of secondary metabolites in a cooler summer compared with a warmer summer. Differences were not detected in the tundra-mat experiment, which had different species (S. arctica, S. reticulata). These willow species may not have high concentrations of tannins and the cloudy summer in 1995 may have naturally reduced tannin concentrations and masked effects of treatments. Few data exist on the effects of tannins on ruminant digestion and the extent of these compounds affecting foraging strategy by caribou. McArthur et al. (1993), however, determined that mule deer (Odocoileus hemionus) selected forage with lower tannin phenolics when given a choice. Because caribou are selective feeders (Klein, 1970), they may be able to prevent accumulating a high concentration of phenolics by avoiding those plants high in secondary compounds. Nonetheless, results from the S. pulchra experiment and other studies (Bø and Hjeljord, 1991; Jonasson et al., 1986) suggest that a cloudy summer would be more favorable for caribou, resulting in lower tannin concentrations in their forage.

Nutritional effects.-- Forage quality and availability during summer can affect physical condition and reproduction in reindeer and caribou (Cameron et al., 1993; Gerhart et al., 1996; Reimers, 1983) and thereby influence population size (Crete and Huot, 1993; Leader-Williams, 1980). Caribou are nitrogen deficient at the end of winter (McEwan and Whitehead, 1970) similar to other Arctic ungulates (Rachlow and Bowyer 1991, 1994). Female caribou need to replenish their reserves throughout the summer to conceive that autumn (Cameron et al., 1993; Reimers, 1983; Skogland, 1985; White, 1983). This short period in which to replenish fat and protein reserves is influenced by climate. As observed in the plant experiments, temperature and irradiance can influence nitrogen content in caribou forage, with higher nitrogen concentration in aboveground biomass with lower irradiance and temperature. Therefore, during a cloudy summer, caribou may be able to acquire more nitrogen in fewer bites; but they also are probably acquiring more dead matter (particularly in graminoids) from the previous year and possibly expending more energy foraging because there is less available green biomass (Boertje, 1990). Thus, there could be a trade-off between nitrogen and biomass (and perhaps digestibility) as nutritional requirements change throughout the summer. Indirect effects of weather via insect harassment also may influence foraging conditions, and thus, a cloudy summer could decrease insect harassment, which would allow more time for foraging.

Obviously, poor quality and low abundance of forage are not always independent of density-dependent effects. Food limitation may result from high population density relative to carrying capacity (McCullough, 1979). Because pregnancy rates in the Chisana herd were low in 1993 and the numbers had been declining for four years, this herd may have exhibited adverse effects of high population density by 1989 and during the early 1990's if damage to forage persisted for several years. Furthermore, Skogland (1985) suggested that most evidence indicates that density-independent factors, specifically climatic ones, cannot regulate populations unless their influence is excessive or is experienced in conjunction with a high population. Nonetheless, including population size in the PCA's did not influence the results. Population size, however, may not be important over the size of populations sampled, but size relative to carrying capacity is a crucial factor and still could be involved. Increasing population density would reduce per capita availability of forage and also further exacerbate negative effects of declining quality of forage (McCullough, 1979).

We have determined that short-term variation in climate can affect nutrient quality, particularly nitrogen content, in above-ground biomass of caribou forage. This outcome is only meaningful, however, when considered in relation to the availability of forage for individual caribou. Summers were substantially warmer and slightly drier during years when the herd was declining than previous years (Fig. 4). Thus, we hypothesize that the decline of the Chisana herd was influenced by adverse summer weather by affecting the nutrition of caribou. The low pregnancy rates in 1993 (50%) suggest a contributing nutritional effect, at least initially, which is probably related to forage quality and abundance. By 1994, however, pregnancy rates increased to > 85%, yet recruitment remained low (Fig. 1). Thus, it is possible that predation by wolves, grizzly bears, and coyotes exacerbated the decline of the Chisana caribou population. Boertje et al. (1996) suggested that direct and indirect effects of adverse weather increased vulnerability to predation and influenced the population size in other caribou herds in interior Alaska during the early 1990's. Predation has been reported as regulating ungulate populations in Arctic ecosystems (Van Ballenberghe and Ballard, 1994; Gasaway et al., 1983, 1992) and may affect the population dynamics of caribou (Adams et al,. 1996; Bergerud, 1980; Crete and Desrosiers, 1995; Dale et al., 1994; Whitten, 1992).

Caribou, forage, and global warming.-- Global warming is predicted to have more pronounced effects at northern latitudes (Lashof and Ahuja, 1990). Effects of annual variation in weather compared with long-term changes in climate, however, will likely result in different outcomes. For example, Chapin et al. (1995) determined that short-term responses (3 year) were poor predictors of longer-term changes at least for composition of plant communities. This was most likely due to warming of the soils and increases in nutrient cycling (Chapin et al., 1995; Nadelhoffer et al., 1992). Increased nutrient cycling could cause species composition to change rapidly within tundra ecosystems with fast-growing species with high nutrient requirements expanding (Berendse and Jonasson, 1992). Thus, in general, a mosaic of taiga forest and shrubland would eventually displace Arctic tundra (Bryant and Reichardt, 1992), which would likely adversely affect caribou populations by creating competition with browsing ungulates and eliminating food sources, especially in winter. Nonetheless, the effects of global warming on forage quality and abundance and insect harassment in summer, and snow conditions in winter and early spring, and their influence on caribou populations would likely be manifested long before composition of plant communities changed. Tracking these weather variables, even short-term responses, could provide transitional information on possible responses of caribou populations to effects of global warming. Because productivity in caribou populations is strongly related to their forage, global warming holds great potential to alter the population dynamics of these large mammals. Indeed, Bowyer et al. (in press) argued that climate change would likely affect populations of arctic ungulates long before it brought about changes in the composition of plant communities. Our data support this contention and suggest that more research on the relationship between climate change and population dynamics of large mammals is needed.

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APPENDIX A. Results of tests of contrasts obtained from gls-variogram for 1994 above-ground biomass analysis for the tundra-mat experiment, Solo Mountain, Alaska. Only significant ($P < 0.05$) differences are listed. * indicates a main effect of water; C = Control; S = Shade; G = Greenhouse; A = add water; N = no water.

Plant/Contrast Variables	Clipping period Green-up	Late Spring	Peak Biomass	Senescence
Prostrate willows				
Main effects of water	*	*		
Main effects of Control vs. Shade			C > S	
Main effects of Control vs. Greenhouse		C > G	C > G	
Main effects of Shade vs. Greenhouse	G > S			
Control, no water vs. Shade, no water			C > S	
Conrol, no water vs. Greenhouse, no water			C > S	
Shade, no water vs. Greenhouse, no water	G > S			
Control, add water vs. Shade, add water	C > S			
Control, add water vs. Greenhouse, add water		C > G	C > G	
Shade, add water vs. Greenhouse, add water		S >G		
Control, no water vs. Control, add water	CN >CA	CN > CA		
Shade, no water vs. Shade, add water				
Greenhouse, no water vs. Greenhouse, add water				
Shade vs. Greenhouse interaction for water				
Graminoids				
Main effects of water		*		
Main effects of Control vs. Shade				
Main effects of Control vs. Greenhouse				
Main effects of Shade vs. Greenhouse				
Control, no water vs. Shade, no water				
Control, no water vs. Greenhouse, no water				
Shade, no water vs. Greenhouse, no water				
Control, add water vs. Shade, add water				
Control, add water vs. Greenhouse, add water				
Shade, add water vs. Greenhouse, add				

APPENDIX Continued

Plant/Contrast Variables	Clipping period			
	Green-up	Late Spring	Peak Biomass	Senescence
water				
Control, no water vs. Control, add water				
Shade, no water vs. Shade, add water				
Greenhouse, no water vs. Greenhouse, add water				
Shade vs. Greenhouse interaction for water				
Forbs				
Main effects of water				
Main effects of Control vs. Shade			C > S	C > S
Main effects of Control vs. Greenhouse				
Main effects of Shade vs. Greenhouse			G > S	G > S
Control, no water vs. Shade, no water				
Control, no water vs. Shade, no water				
Control, no water vs. Greenhouse, no				
Shade, no water vs. Greenhouse, no water				
Control, add water vs. Shade, add water			C > S	C > S
Control, add water vs. Greenhouse, add water			G > S	
Shade, add water vs. Greenhouse, add water				G > S
Control, no water vs. Control, add water				CA > CN
Shade, no water vs. Shade, add water	SN >SA			
Greenhouse, no water vs. Greenhouse, add water			GA > GN	
Shade vs. Greenhouse interaction for water				

APPENDIX Continued

APPENDIX B. Results of tests of contrasts ($P < 0.05$) obtained from gls-variogram for 1995 above-ground biomass analysis for the tundra-mat experiment, Solo Mountain, Alaska. Only significant ($P < 0.05$) differences are listed. * indicates a main effect of water; C = Control; S = Shade; G = Greenhouse; A = add water; N = no water.

	Clipping period			
Plant/Contrast Variables	Green-up	Late Spring	Peak Biomass	Senescence
Prostrate willows				
Main effects of water				
Main effects of Control vs. Shade				
Main effects of Control vs. Greenhouse				
Main effects of Shade vs. Greenhouse				
Control, no water vs. Shade, no water				
Control, no water vs. Greenhouse, no water				
Shade, no water vs. Greenhouse, no water				
Control, add water vs. Shade, add water				
Control, add water vs. Greenhouse, add water				
Shade, add water vs. Greenhouse, add water				
Control, no water vs. Control, add water				
Shade, no water vs. Shade, add water				
Greenhouse, no water vs. Greenhouse, add water				
Shade vs. Greenhouse interaction for water				
Graminoids				
Main effects of water				
Main effects of Control vs. Shade				
Main effects of Control vs. Greenhouse			G > C	
Main effects of Shade vs. Greenhouse			G > S	
Control, no water vs. Shade, no water				
Control, no water vs. Greenhouse, no water				
Shade, no water vs. Greenhouse, no water				
Control, add water vs. Shade, add water	G > C	G > C		
Control, add water vs. Greenhouse, add water	G > S	G > S		
Shade, add water vs. Greenhouse, add water				

APPENDIX Continued

	Clipping period			
Plant/Contrast Variables	Green-up	Late Spring	Peak Biomass	Senescence
Control, no water vs. Control, add water				
Shade, no water vs. Shade, add water				
Greenhouse, no water vs. Greenhouse, add water		GA > GN		
Shade vs. Greenhouse interaction for water				
Forbs				
Main effects of water				
Main effects of Control vs. Shade			C > S	
Main effects of Control vs. Greenhouse				G > C
Main effects of Shade vs. Greenhouse				G > S
Control, no water vs. Shade, no water				
Control, no water vs. Shade, no water				
Control, no water vs. Greenhouse, no				
Shade, no water vs. Greenhouse, no water				G > S
Control, add water vs. Shade, add water				C > S
Control, add water vs. Greenhouse, add water				G > C
Shade, add water vs. Greenhouse, add water				G > S
Control, no water vs. Control, add water				
Shade, no water vs. Shade, add water				
Greenhouse, no water vs. Greenhouse, add water		GA > GN		
Shade vs. Greenhouse interaction for water		*		

APPENDIX C. Results of tests of contrasts ($\underline{P} < 0.05$) obtained from gls-variogram for 1994 nitrogen analysis for the tundra-mat experiment, Solo Mountain, Alaska. Only significant ($\underline{P} < 0.05$) differences are listed. * indicates a main effect of water; C = Control; S = Shade; G = Greenhouse; A = add water; N = no water.

	Clipping period			
Plant/Contrast Variables	Green-up	Late Spring	Peak Biomass	Senescence
Prostrate willows				
Main effects of water				
Main effects of Control vs. Shade		S > C	S > C	S > C
Main effects of Control vs. Greenhouse				
Main effects of Shade vs. Greenhouse				S > G
Control, no water vs. Shade, no water				S > C
Control, no water vs. Greenhouse, no water				
Shade, no water vs. Greenhouse, no water				S > G
Control, add water vs. Shade, add water				S > C
Control, add water vs. Greenhouse, add water				
Shade, add water vs. Greenhouse, add water				
Control, no water vs. Control, add water				
Shade, no water vs. Shade, add water				
Greenhouse, no water vs. Greenhouse, add water				
Shade vs. Greenhouse interaction for water				
Graminoids				
Main effects of water				
Main effects of Control vs. Shade				
Main effects of Control vs. Greenhouse				
Main effects of Shade vs. Greenhouse				
Control, no water vs. Shade, no water				
Control, no water vs. Greenhouse, no water				
Shade, no water vs. Greenhouse, no water				
Control, add water vs. Shade, add water				
Control, add water vs. Greenhouse, add water				
Shade, add water vs. Greenhouse, add water				

APPENDIX Continued

	Clipping period			
Plant/Contrast Variables	Green-up	Late Spring	Peak Biomass	Senescence
Control, no water vs. Control, add water				
Shade, no water vs. Shade, add water				
Greenhouse, no water vs. Greenhouse, add water				
Shade vs. Greenhouse interaction for water				
Forbs				
Main effects of water				
Main effects of Control vs. Shade				C > G
Main effects of Control vs. Greenhouse				S > G
Main effects of Shade vs. Greenhouse				
Control, no water vs. Shade, no water				
Control, no water vs. Shade, no water				
Control, no water vs. Greenhouse, no				
Shade, no water vs. Greenhouse, no water				S > G
Control, add water vs. Shade, add water				
Conrol, add water vs. Greenhouse, add water				
Shade, add water vs. Greenhouse, add water				
Control, no water vs. Control, add water				
Shade, no water vs. Shade, add water				
Greenhouse, no water vs. Greenhouse, add water				
Shade vs. Greenhouse interaction for water		*		

APPENDIX Continued

APPENDIX D. Results of tests of contrasts (P < 0.05) obtained from gls-variogram for 1995 nitrogen analysis for the tundra-mat experiment, Solo Mountain, Alaska. Only significant (P < 0.05) differences are listed. * indicates a main effect of water; C = Control; S = Shade; G = Greenhouse; A = add water; N = no water.

	Clipping period			
Plant/Contrast Variables	Green-up	Late Spring	Peak Biomass	Senescence
Prostrate willows				*
Main effects of water				
Main effects of Control vs. Shade		S > C	S > C	S > C
Main effects of Control vs. Greenhouse				
Main effects of Shade vs. Greenhouse		S > G	S > G	S > G
Control, no water vs. Shade, no water		S > C	S > C	
Control, no water vs. Greenhouse, no water	C > G			
Shade, no water vs. Greenhouse, no water		S > G	S > G	S > G
Control, add water vs. Shade, add water		S > C		S > C
Control, add water vs. Greenhouse, add water				
Shade, add water vs. Greenhouse, add water				S > G
Control, no water vs. Control, add water				CN > CA
Shade, no water vs. Shade, add water				
Greenhouse, no water vs. Greenhouse, add water				
Shade vs. Greenhouse interaction for water				
Graminoids				
Main effects of water				
Main effects of Control vs. Shade			S > C	S > C
Main effects of Control vs. Greenhouse		C > G		
Main effects of Shade vs. Greenhouse	S > G	S > G	S > G	S > G
Control, no water vs. Shade, no water				S > C
Control, no water vs. Greenhouse, no water				
Shade, no water vs. Greenhouse, no water		S > G		S > G
Control, add water vs. Shade, add water			S > C	
Control, add water vs. Greenhouse, add water		C > G		
Shade, add water vs. Greenhouse, add water	S > G	S > G	S > G	S > G

APPENDIX Continued

	Clipping period			
Plant/Contrast Variables	Green-up	Late Spring	Peak Biomass	Senescence
Control, no water vs. Control, add water				
Shade, no water vs. Shade, add water				
Greenhouse, no water vs. Greenhouse, add water				
Shade vs. Greenhouse interaction for water				
Forbs				
Main effects of water				
Main effects of Control vs. Shade	S > C		S > C	S > C
Main effects of Control vs. Greenhouse				
Main effects of Shade vs. Greenhouse	S > G	S > G	S > G	S > G
Control, no water vs. Shade, no water				
Control, no water vs. Shade, no water	S > C			S > C
Control, no water vs. Greenhouse, no		C > G		
Shade, no water vs. Greenhouse, no water	S > G	S > G		S > G
Control, add water vs. Shade, add water	S > C			S > C
Control, add water vs. Greenhouse, add water				
Shade, add water vs. Greenhouse, add water			S > G	S > G
Control, no water vs. Control, add water				
Shade, no water vs. Shade, add water				
Greenhouse, no water vs. Greenhouse, add water				
Shade vs. Greenhouse interaction for water				

APPENDIX E. Results of tests of contrasts ($P < 0.05$) obtained from gls-variogram for 1994 in vitro dry matter digestibility analysis for the tundra-mat experiment, Solo Mountain, Alaska. Only significant ($P < 0.05$) differences are listed. * indicates a main effect of water; C = Control; S = Shade; G = Greenhouse; A = add water; N = no water.

	Clipping period			
Plant/Contrast Variables	Green-up	Late Spring	Peak Biomass	Senescence
Prostrate willows				*
Main effects of water				
Main effects of Control vs. Shade				
Main effects of Control vs. Greenhouse		C > S		C > S
Main effects of Shade vs. Greenhouse				
Control, no water vs. Shade, no water				
Control, no water vs. Greenhouse, no water				
Shade, no water vs. Greenhouse, no water				
Control, add water vs. Shade, add water		C > S		
Control, add water vs. Greenhouse, add water				
Shade, add water vs. Greenhouse, add water				
Control, no water vs. Control, add water				CA > CN
Shade, no water vs. Shade, add water		SA > SN		
Greenhouse, no water vs. Greenhouse, add water				GA > GN
Shade vs. Greenhouse interaction for water				
Graminoids				
Main effects of water				
Main effects of Control vs. Shade				C > S
Main effects of Control vs. Greenhouse				
Main effects of Shade vs. Greenhouse				G > S
Control, no water vs. Shade, no water				
Control, no water vs. Greenhouse, no water				G > C
Shade, no water vs. Greenhouse, no water				G > S
Control, add water vs. Shade, add water				
Control, add water vs. Greenhouse, add water				
Shade, add water vs. Greenhouse, add water				

APPENDIX Continued

Plant/Contrast Variables	Clipping period Green-up	 Late Spring	 Peak Biomass	 Senescence
Control, no water vs. Control, add water				
Shade, no water vs. Shade, add water				
Greenhouse, no water vs. Greenhouse, add water				
Shade vs. Greenhouse interaction for water				
Forbs				
Main effects of water				*
Main effects of Control vs. Shade				
Main effects of Control vs. Greenhouse				
Main effects of Shade vs. Greenhouse				
Control, no water vs. Shade, no water				
Control, no water vs. Shade, no water				
Control, no water vs. Greenhouse, no				
Shade, no water vs. Greenhouse, no water				
Control, add water vs. Shade, add water				
Control, add water vs. Greenhouse, add water				
Shade, add water vs. Greenhouse, add water				
Control, no water vs. Control, add water				CA > CN
Shade, no water vs. Shade, add water				
Greenhouse, no water vs. Greenhouse, add water				
Shade vs. Greenhouse interaction for water				

APPENDIX Continued

APPENDIX F. Results of tests of contrasts ($P < 0.05$) obtained from gls-variogram for 1995 in vitro dry matter digestibility analysis for the tundra-mat experiment, Solo Mountain, Alaska. Only significant ($P < 0.05$) differences are listed. * indicates a main effect of water; C = Control; S = Shade; G = Greenhouse; A = add water; N = no water.

	Clipping period			
Plant/Contrast Variables	Green-up	Late Spring	Peak Biomass	Senescence
Prostrate willows				
Main effects of water				
Main effects of Control vs. Shade				
Main effects of Control vs. Greenhouse				
Main effects of Shade vs. Greenhouse				G > S
Control, no water vs. Shade, no water				
Control, no water vs. Greenhouse, no water				
Shade, no water vs. Greenhouse, no water				G > S
Control, add water vs. Shade, add water				
Control, add water vs. Greenhouse, add water				
Shade, add water vs. Greenhouse, add water				
Control, no water vs. Control, add water				
Shade, no water vs. Shade, add water				
Greenhouse, no water vs. Greenhouse, add water				
Shade vs. Greenhouse interaction for water				
Graminoids				
Main effects of water				
Main effects of Control vs. Shade				
Main effects of Control vs. Greenhouse				G > C
Main effects of Shade vs. Greenhouse				G > S
Control, no water vs. Shade, no water				
Control, no water vs. Greenhouse, no water				G > C
Shade, no water vs. Greenhouse, no water				G > S
Control, add water vs. Shade, add water				
Control, add water vs. Greenhouse, add water				
Shade, add water vs. Greenhouse, add water				

APPENDIX Continued

	Clipping period			
Plant/Contrast Variables	Green-up	Late Spring	Peak Biomass	Senescence
Control, no water vs. Control, add water				
Shade, no water vs. Shade, add water				
Greenhouse, no water vs. Greenhouse, add water				
Shade vs. Greenhouse interaction for water				
Forbs				
Main effects of water				
Main effects of Control vs. Shade				
Main effects of Control vs. Greenhouse				
Main effects of Shade vs. Greenhouse				
Control, no water vs. Shade, no water				
Control, no water vs. Shade, no water				
Control, no water vs. Greenhouse, no				
Shade, no water vs. Greenhouse, no water				
Control, add water vs. Shade, add water				
Control, add water vs. Greenhouse, add water				
Shade, add water vs. Greenhouse, add water				
Control, no water vs. Control, add water				
Shade, no water vs. Shade, add water				
Greenhouse, no water vs. Greenhouse, add water				
Shade vs. Greenhouse interaction for water				

APPENDIX Continued

APPENDIX G. Above-ground biomass (g/0.25m^2) means ± 1 SD for tundra-mat experiment in 1994.

	Plant category					
Date/Treatment	Graminoids	Forbs	Prostrate willows	Leaves only prostrate willows	Lichen	Dead
10 June 1994						
Greenhouse, add water	0.95 ± 1.14	6.70 ± 4.35	2.77 ± 2.35	1.40 ± 0.95	1.74 ± 1.40	57.15 ± 17.39
Greenhouse, no water	1.05 ± 0.73	7.94 ± 2.41	4.27 ± 1.89	2.06 ± 0.68	1.64 ± 1.38	76.06 ± 15.08
Shade, add water	1.09 ± 0.78	6.13 ± 2.48	2.85 ± 1.54	1.63 ± 0.59	0.86 ± 0.74	58.90 ± 8.73
Shade, no water	1.55 ± 0.44	7.47 ± 3.72	4.43 ± 5.40	2.22 ± 1.98	1.13 ± 1.27	71.93 ± 12.22
Control, add water	0.54 ± 0.29	8.41 ± 2.65	6.30 ± 4.30	3.36 ± 2.40	1.71 ± 0.89	70.00 ± 8.28
Control, no water	0.65 ± 0.45	5.33 ± 2.90	1.92 ± 0.63	1.31 ± 0.48	1:18 ± 0.86	88.82 ± 35.37
26 June 1994						
Greenhouse, add water	1.56 ± 1.25	13.46 ± 7.58	5.76 ± 2.19	4.21 ± 2.54	1.51 ± 1.47	51.10 ± 23.43
Greenhouse, no water	2.53 ± 1.69	10.64 ± 8.17	6.67 ± 3.38	4.34 ± 2.64	1.99 ± 1.65	61.35 ± 21.45
Shade, add water	2.25 ± 1.13	12.27 ± 6.65	11.19 ± 4.36	8.00 ± 2.50	1.11 ± 1.14	70.50 ± 35.39
Shade, no water	4.39 ± 3.00	14.32 ± 7.30	9.55 ± 5.07	6.61 ± 3.64	0.67 ± 1.00	86.60 ± 22.24
Control, add water	1.36 ± 0.82	21.09 ± 6.89	12.39 ± 5.03	8.29 ± 3.01	1.31 ± 1.13	63.32 ± 22.60
Control, no water	3.26 ± 1.43	17.81 ± 9.80	6.84 ± 1.65	5.25 ± 1.15	1.13 ± 1.34	58.12 ± 48.36
20 July 1994						
Greenhouse, add water	4.71 ± 4.82	36.98 ± 12.66	6.96 ± 2.89	4.68 ± 1.97	2.17 ± 1.20	68.76 ± 14.06
Greenhouse, no water	4.57 ± 2.23	22.15 ± 13.84	8.77 ± 4.69	5.82 ± 3.87	1.31 ± 0.77	62.74 ± 17.19
Shade, add water	4.86 ± 1.88	22.18 ± 3.98	12.30 ± 2.40	7.92 ± 0.70	0.40 ± 0.33	55.38 ± 20.61
Shade, no water	5.06 ± 0.57	17.48 ± 8.89	9.34 ± 6.41	5.71 ± 3.54	0.79 ± 1.12	45.12 ± 12.64
Control, add water	3.50 ± 2.43	31.78 ± 8.47	14.66 ± 9.43	8.81 ± 3.58	1.00 ± 0.57	64.07 ± 27.27
Control, no water	4.29 ± 3.51	28.07 ± 6.66	18.33 ± 14.95	9.44 ± 3.66	1.64 ± 0.93	58.43 ± 15.23
9 August 1994						
Greenhouse, add water	2.65 ± 3.07	33.04 ± 10.44	18.04 ± 16.78	9.07 ± 6.02	2.24 ± 1.62	97.44 ± 38.43
Greenhouse, no water	3.96 ± 1.59	27.33 ± 11.68	14.08 ± 15.85	7.95 ± 7.29	2.48 ± 1.40	92.23 ± 29.12
Shade, add water	3.40 ± 1.59	19.37 ± 6.85	12.01 ± 6.60	6.89 ± 1.54	0.85 ± 0.82	81.11 ± 35.00
Shade, no water	4.33 ± 2.35	13.40 ± 7.43	15.57 ± 12.76	7.24 ± 4.22	0.47 ± 0.64	77.66 ± 9.09
Control, add water	2.84 ± 2.39	37.11 ± 7.81	10.61 ± 3.85	7.45 ± 1.62	2.50 ± 0.96	101.14 ± 35.66
Control, no water	5.47 ± 2.05	19.04 ± 13.36	12.35 ± 3.94	7.90 ± 2.70	1.20 ± 1.23	58.86 ± 32.47

APPENDIX Continued

APPENDIX H. Above-ground biomass (g/0.25m^2) means ± 1 SD for tundra-mat experiment in 1995.

	Plant category					
Date/Treatment	Graminoids	Forbs	Prostrate willows	Leaves only prostrate willows	Lichen	Dead
7 June 1995						
Greenhouse, add water	1.74 ± 1.50	15.61 ± 7.12	13.46 ± 13.60	6.04 ± 6.62	1.49 ± 1.47	70.73 ± 40.30
Greenhouse, no water	1.97 ± 1.25	9.38 ± 7.15	10.82 ± 8.25	3.43 ± 2.09	0.85 ± 0.68	66.34 ± 27.22
Shade, add water	1.39 ± 0.50	9.40 ± 1.80	6.92 ± 2.52	3.61 ± 0.87	0.77 ± 0.45	50.46 ± 14.18
Shade, no water	2.18 ± 0.63	7.81 ± 4.37	10.54 ± 6.59	3.84 ± 1.34	0.93 ± 1.73	58.81 ± 19.26
Control, add water	0.84 ± 0.74	12.22 ± 2.89	8.12 ± 4.88	3.88 ± 2.47	1.72 ± 1.25	53.44 ± 23.59
Control, no water	1.84 ± 0.77	10.28 ± 7.75	4.50 ± 2.43	1.77 ± 1.10	1.46 ± 1.24	56.96 ± 15.58
28 June 1995						
Greenhouse, add water	4.49 ± 3.11	30.85 ± 11.79	14.82 ± 6.74	8.88 ± 3.81	2.34 ± 1.39	75.92 ± 25.79
Greenhouse, no water	4.43 ± 0.68	21.39 ± 7.18	14.24 ± 7.27	7.93 ± 4.07	1.42 ± 0.55	57.21 ± 16.25
Shade, add water	3.29 ± 1.79	22.98 ± 3.75	14.21 ± 4.13	8.53 ± 2.26	2.25 ± 1.36	46.08 ± 7.14
Shade, no water	4.11 ± 1.58	20.57 ± 9.21	13.49 ± 7.54	8.40 ± 4.24	1.00 ± 1.38	47.11 ± 17.48
Control, add water	1.66 ± 0.85	25.17 ± 6.89	14.29 ± 6.16	7.75 ± 2.78	1.76 ± 1.06	64.10 ± 17.13
Control, no water	3.89 ± 1.01	19.56 ± 9.99	15.96 ± 9.67	8.55 ± 4.62	1.39 ± 1.14	57.01 ± 30.04
22 July 1995						
Greenhouse, add water	3.67 ± 2.44	40.12 ± 18.41	19.52 ± 12.40	10.23 ± 5.95	1.88 ± 1.26	74.28 ± 40.14
Greenhouse, no water	5.33 ± 1.57	25.28 ± 12.74	18.08 ± 10.28	10.48 ± 6.54	2.15 ± 0.65	56.11 ± 24.18
Shade, add water	4.88 ± 2.85	26.82 ± 6.01	12.48 ± 2.03	7.53 ± 1.25	1.09 ± 1.01	51.37 ± 15.28
Shade, no water	7.08 ± 3.24	25.28 ± 12.55	22.84 ± 22.70	11.01 ± 9.23	0.87 ± 0.96	41.36 ± 15.48
Control, add water	3.05 ± 2.39	42.69 ± 10.98	11.97 ± 4.98	6.87 ± 2.88	2.40 ± 1.87	71.64 ± 38.76
Control, no water	5.47 ± 2.47	31.73 ± 6.66	13.86 ± 3.98	8.23 ± 2.33	1.41 ± 1.05	66.28 ± 6.25
9 August 1994						
Greenhouse, add water	3.79 ± 3.01	40.24 ± 16.92	15.02 ± 5.48	7.58 ± 2.75	0.92 ± 0.89	55.82 ± 22.68
Greenhouse, no water	3.94 ± 2.72	41.22 ± 6.47	12.87 ± 6.47	6.75 ± 3.10	2.70 ± 1.66	48.81 ± 19.15
Shade, add water	4.53 ± 2.37	20.99 ± 10.36	13.48 ± 6.64	7.53 ± 3.52	1.08 ± 1.45	44.15 ± 13.73
Shade, no water	5.08 ± 2.78	19.35 ± 10.83	12.56 ± 9.76	6.36 ± 4.12	0.46 ± 0.70	35.25 ± 10.55
Control, add water	1.65 ± 1.23	36.63 ± 6.66	14.00 ± 2.97	7.47 ± 1.62	1.05 ± 0.64	43.60 ± 13.05
Control, no water	5.54 ± 1.16	27.23 ± 8.55	13.74 ± 8.50	7.05 ± 4.12	1.05 ± 0.76	47.51 ± 10.32

APPENDIX I. Tundra mat nitrogen means ± 1 SD in 1994.

	Clipping dates			
Plant/Treatment	6/10/94	6/26/94	7/20/94	8/9/94
Prostate willows				
Greenhouse, add water	3.75 ± 0.34	2.70 ± 0.21	2.11 ± 0.23	1.93 ± 0.15
Greenhouse, no water	3.76 ± 0.15	2.51 ± 0.17	2.19 ± 0.39	1.93 ± 0.16
Shade, add water	3.78 ± 0.37	2.69 ± 0.39	2.15 ± 0.16	2.05 ± 0.07
Shade, no water	3.76 ± 0.16	2.72 ± 0.18	2.29 ± 0.12	2.07 ± 0.13
Control, add water	3.61 ± 0.39	2.44 ± 0.17	1.96 ± 0.13	1.91 ± 0.06
Control, no water	3.47 ± 0.31	2.49 ± 0.17	2.11 ± 0.20	1.88 ± 0.09
Graminoids				
Greenhouse, add water	2.57 ± 0.34	2.53 ± 0.30	2.06 ± 0.13	1.72 ± 0.33
Greenhouse, no water	2.49 ± 0.31	2.56 ± 0.24	2.16 ± 0.47	1.74 ± 0.18
Shade, add water	2.48 ± 0.39	2.47 ± 0.26	2.12 ± 0.02	1.89 ± 0.15
Shade, no water	2.64 ± 0.14	2.58 ± 0.13	2.11 ± 0.23	1.87 ± 0.15
Control, add water	2.25 ± 0.28	2.33 ± 0.33	1.98 ± 0.22	1.88 ± 0.09
Control, no water	2.51 ± 0.43	2.46 ± 0.23	2.03 ± 0.13	1.88 ± 0.19
Forbs				
Greenhouse, add water	1.95 ± 0.20	2.13 ± 0.50	1.52 ± 0.22	1.33 ± 0.17
Greenhouse, no water	1.97 ± 0.17	2.07 ± 0.40	1.82 ± 0.48	1.33 ± 0.13
Shade, add water	1.85 ± 0.11	2.47 ± 1.08	1.92 ± 0.26	1.57 ± 0.09
Shade, no water	2.20 ± 0.55	2.28 ± 0.86	1.99 ± 0.50	1.66 ± 0.23
Control, add water	1.91 ± 0.14	1.85 ± 0.23	1.79 ± 0.22	1.50 ± 0.18
Control, no water	1.97 ± 0.18	2.22 ± 0.81	1.84 ± 0.21	1.59 ± 0.27

APPENDIX J. Tundra-mat nitrogen means ± 1 SD in 1995.

Plant/Treatment	Clipping dates 6/6/95	6/28/95	7/22/95	8/7/95
Prostate willows				
Greenhouse, add water	3.23 ± 0.58	2.17 ± 0.20	1.98 ± 0.26	1.52 ± 0.25
Greenhouse, no water	2.95 ± 0.15	2.19 ± 0.23	1.91 ± 0.19	1.54 ± 0.13
Shade, add water	3.27 ± 0.18	2.36 ± 0.13	2.13 ± 0.19	1.77 ± 0.07
Shade, no water	3.39 ± 0.39	2.46 ± 0.17	2.26 ± 0.19	1.77 ± 0.13
Control, add water	3.19 ± 0.36	2.14 ± 0.12	1.97 ± 0.18	1.44 ± 0.11
Control, no water	3.70 ± 0.74	2.19 ± 0.20	2.02 ± 0.12	1.63 ± 0.12
Graminoids				
Greenhouse, add water	2.21 ± 0.35	1.90 ± 0.36	1.74 ± 0.05	1.44 ± 0.11
Greenhouse, no water	2.37 ± 0.40	2.19 ± 0.13	1.84 ± 0.13	1.43 ± 0.08
Shade, add water	2.52 ± 0.20	2.33 ± 0.14	2.01 ± 0.17	1.60 ± 0.13
Shade, no water	2.64 ± 0.16	2.48 ± 0.42	2.00 ± 0.14	1.65 ± 0.10
Control, add water	2.49 ± 0.13	2.21 ± 0.15	1.77 ± 0.21	1.50 ± 0.08
Control, no water	2.51 ± 0.10	2.35 ± 0.10	1.87 ± 0.09	1.49 ± 0.13
Forbs				
Greenhouse, add water	1.81 ± 0.25	2.01 ± 0.28	1.70 ± 0.15	1.40 ± 0.14
Greenhouse, no water	2.02 ± 0.57	1.93 ± 0.14	1.66 ± 0.32	1.30 ± 0.10
Shade, add water	2.20 ± 0.15	2.48 ± 0.22	2.02 ± 0.21	1.69 ± 0.13
Shade, no water	2.43 ± 0.35	2.54 ± 0.36	1.94 ± 0.19	1.76 ± 0.24
Control, add water	2.01 ± 0.32	2.07 ± 0.20	1.74 ± 0.16	1.40 ± 0.12
Control, no water	2.31 ± 0.88	2.60 ± 0.79	1.76 ± 0.22	1.45 ± 0.12

APPENDIX K. Tundra-mat in vitro dry matter digestibility means ± 1 SD in 1994.

	Clipping dates			
Plant/Treatment	6/10/94	6/26/94	7/20/94	8/9/94
Prostate willows				
Greenhouse, add water	54.03 ± 9.13	59.58 ± 6.19	63.12 ± 7.07	52.55 ± 5.47
Greenhouse, no water	59.12 ± 8.04	56.60 ± 5.00	61.87 ± 9.77	46.49 ± 3.53
Shade, add water	60.39 ± 4.60	57.44 ± 3.38	63.14 ± 7.53	47.18 ± 3.45
Shade, no water	60.80 ± 8.48	62.45 ± 2.28	59.36 ± 3.81	44.04 ± 6.17
Control, add water	54.22 ± 10.14	64.08 ± 3.05	64.50 ± 2.99	54.75 ± 4.78
Control, no water	52.47 ± 9.22	61.31 ± 3.98	62.78 ± 2.46	47.75 ± 5.01
Graminoids				
Greenhouse, add water	62.74 ± 4.49	70.41 ± 5.86	67.30 ± 1.79	54.73 ± 4.45
Greenhouse, no water	66.95 ± 7.53	69.22 ± 4.38	68.72 ± 0.87	50.03 ± 6.93
Shade, add water	62.37 ± 5.42	71.28 ± 4.55	68.34 ± 2.82	51.31 ± 3.15
Shade, no water	63.53 ± 1.61	75.21 ± 1.40	66.31 ± 3.51	47.33 ± 3.63
Control, add water	65.03 ± 1.17	71.38 ± 4.35	70.63 ± 2.25	54.62 ± 3.82
Control, no water	61.77 ± 5.54	73.83 ± 3.55	67.00 ± 3.12	49.66 ± 4.09
Forbs				
Greenhouse, add water	39.00 ± 13.82	48.53 ± 5.72	44.30 ± 3.83	42.33 ± 8.02
Greenhouse, no water	46.77 ± 8.82	48.07 ± 5.56	54.22 ± 5.71	33.42 ± 7.22
Shade, add water	47.07 ± 3.96	53.70 ± 13.25	46.51 ± 6.45	36.26 ± 8.73
Shade, no water	45.81 ± 6.30	55.32 ± 15.72	50.67 ± 15.40	33.21 ± 11.36
Control, add water	41.44 ± 9.57	48.80 ± 3.40	53.44 ± 8.29	39.24 ± 6.08
Control, no water	36.28 ± 9.24	53.93 ± 7.26	54.88 ± 7.54	29.16 ± 6.65

APPENDIX L. Tundra-mat in vitro dry matter digestibility means ± 1 SD in 1995.

	Clipping dates			
Plant/Treatment	6/6/95	6/28/95	7/22/95	8/7/95
Prostate willows				
Greenhouse, add water	61.48 ± 7.06	61.43 ± 4.38	61.15 ± 1.90	58.73 ± 4.97
Greenhouse, no water	62.51 ± 6.62	57.28 ± 7.67	60.42 ± 4.71	62.44 ± 4.22
Shade, add water	62.95 ± 3.75	56.85 ± 6.02	60.18 ± 3.63	56.42 ± 3.81
Shade, no water	66.32 ± 5.43	57.67 ± 7.57	63.69 ± 1.89	54.50 ± 4.22
Control, add water	61.35 ± 10.54	60.28 ± 4.61	61.84 ± 3.09	60.45 ± 6.12
Control, no water	60.09 ± 3.62	56.43 ± 10.29	62.04 ± 2.74	58.33 ± 8.35
Graminoids				
Greenhouse, add water	70.94 ± 3.54	65.85 ± 3.98	69.85 ± 4.29	67.71 ± 4.48
Greenhouse, no water	71.88 ± 4.08	67.65 ± 5.03	70.19 ± 2.73	67.02 ± 1.47
Shade, add water	70.57 ± 6.28	66.89 ± 5.19	67.28 ± 2.69	66.16 ± 1.65
Shade, no water	71.53 ± 1.61	66.37 ± 5.69	68.91 ± 1.34	62.99 ± 4.10
Control, add water	74.84 ± 1.67	66.22 ± 3.62	67.15 ± 2.59	64.35 ± 2.82
Control, no water	71.48 ± 1.99	67.46 ± 5.37	67.01 ± 3.57	61.06 ± 1.80
Forbs				
Greenhouse, add water	55.46 ± 2.85	53.29 ± 6.11	66.74 ± 5.59	57.58 ± 4.81
Greenhouse, no water	54.41 ± 2.25	52.12 ± 5.19	64.52 ± 9.93	55.94 ± 6.26
Shade, add water	57.10 ± 4.48	52.34 ± 6.64	62.94 ± 11.07	52.56 ± 7.57
Shade, no water	56.65 ± 2.10	52.27 ± 6.92	63.88 ± 6.10	57.50 ± 12.33
Control, add water	56.65 ± 5.05	53.35 ± 6.46	61.17 ± 3.05	52.86 ± 5.72
Control, no water	53.47 ± 3.84	50.89 ± 3.73	61.23 ± 9.15	60.59 ± 4.23

APPENDIX M. Salix pulchra nitrogen, in vitro dry matter digestibility (IVDMD), and tannin means ± 1 SD, 1994 and 1995.

	Clipping period		
Analysis/Treatment	8/4/94	7/11/95	8/3/95
Nitrogen (%)			
Greenhouse	2.54 ± 0.18	2.55 ± 0.17	2.27 ± 0.20
Shade	2.52 ± 0.20	3.15 ± 0.12	2.65 ± 0.12
Control	2.34 ± 0.20	2.50 ± 0.11	2.14 ± 0.06
IVDMD (%)			
Greenhouse	37.44 ± 3.32	39.75 ± 1.19	44.47 ± 3.53
Shade	33.07 ± 3.84	38.39 ± 1.55	42.24 ± 3.55
Control	35.29 ± 3.92	41.52 ± 3.92	45.39 ± 4.08
Tannins (μg/ml)			
Greenhouse	127.60 ± 21.49	155.35 ± 17.90	182.24 ± 22.69
Shade	136.67 ± 38.11	116.81 ± 32.31	149.68 ± 21.83
Control	156.23 ± 27.28	151.57 ± 50.08	192.05 ± 33.46

Alaska's Game Management Units