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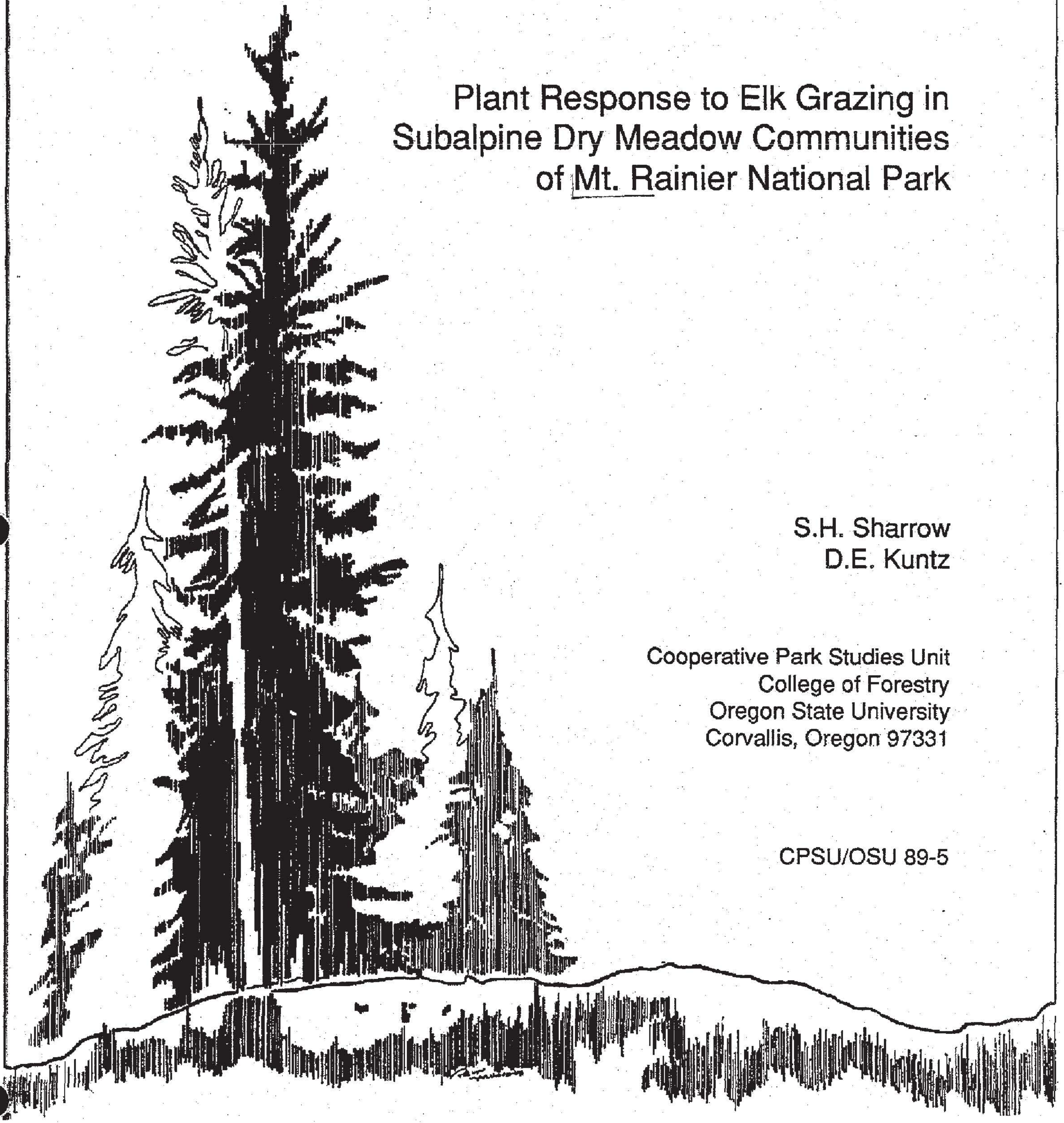

Plant Response to Elk Grazing in Subalpine Dry Meadow Communities of Mt. Rainier National Park

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EXECUTIVE SUMMARY

This study was conducted in 1986-1988 in support of the elk monitoring project in Mount Rainier National Park. Objectives of the study were to supplement the vegetation monitoring portion of the elk study by:

(1) determining the degree of elk utilization occurring on three of the seven vegetation monitoring sites.

(2) examining the effects of season and intensity of grazing (defoliation) on a subalpine dry meadow.

Four utilization transects per meadow were examined in Yakima, Bear, and White River Parks in mid-summer 1986 and 1987. Grazing in all of these meadows was very light. Less than half of the plants examined showed any evidence of having been grazed. Plants which were grazed typically had less than 15% of their tops removed. Insects appeared to be the predominant grazers on the meadows studied. Only green fescue (*Festuca viridula*) was grazed to any significant extent by elk.

The effects of season (early-, mid-, and late-season) and intensity (0%, 25%, 50%, and 75% of aerial biomass removed in 1986 and again in 1987) of defoliation was studied at Yakima Park during 1986-1988. Defoliation treatments had little effect upon plant frequency, cover, or final plant biomass each year. Reproduction of green fescue and lupine (*Lupinus latifolius*) did, however, tend to decline as defoliation intensity increased. Considering the severity of our defoliation treatments compared to the amount of elk grazing measured in the utilization surveys, it is unlikely that defoliation of vegetation by elk is having any detrimen-

tal effect. We suspect that elk use of these meadows would have to more than triple before short-term changes in plant community composition would occur as a result of defoliation by elk. This conclusion does not necessarily pertain to physical damage caused by trailing, wallowing etc. Although we do not see any immediate impacts of elk grazing on the study meadows, a reduction in reproductive potential of the two dominant dry meadow plants in our defoliation studies is a potential concern. Much more needs to be known about plant population dynamics and reproduction in subalpine meadows before the long-term implications of grazing on their vegetation can be predicted and areas damaged by humans and/or wildlife consistently rehabilitated.

INTRODUCTION

Observations of increasing size of elk herds using Mount Rainier National Park have raised concerns about possible damage to subalpine plant communities by increased elk grazing and trampling in these potentially fragile plant communities. A monitoring system was established in 1979 to determine the impact of increased elk grazing on seven subalpine meadows representative of the Festuca-Lupinus-Potentilla habitat type (Hanley et al 1979) in Mount Rainier National Park. Frequency data collected for this study during 1979-1984 did not support the conclusion that grazing by elk was having any impact upon the vegetation of the meadows studied (Motazedian and Sharrow 1984). However, reservations were expressed concerning the appropriateness of frequency data for this use and the lack of suitable ungrazed reference areas to aid in interpretation of data. In addition, interpretation of vegetation monitoring data was hampered by lack of background information about forage selection by elk and plant community response to grazing in similar subalpine meadows.

The goal of this study was to provide information in support of the on-going monitoring project by:

(1) determining the degree of elk grazing that was actually occurring on monitored meadows.

(2) examining shifts in plant community structure (cover and frequency) attributable to different levels of defoliation .

(3) examining the effects of defoliation on productivity and reproduction of the two dominant subalpine dry meadow plants,green fescue (*Festuca viridula*) and broadleaf lupine (*Lupinus latifolius*).

STUDY AREA

Three of the seven subalpine meadows being monitored by the National Park Service as part of an elk management evaluation were used in this study. These meadows (Yakima Park, Bear Park, and White River Park) are located on the east side of Mount Rainier at elevations of 5840 to 6400 feet (1750 to 1920 m). They are representative of the Subalpine Meadow Vegetation Zone as described by Henderson (1974), which covers approximately 24,600 acres (10,000 hectares) of Mount Rainier Park's 235,612 acres (95,350 hectares). This Dry-Grass Vegetation Type is characterized by dominance of *Festuca viridula* (green fescue) on relatively dry, well-drained sites in the northeastern portion of Mount Rainier. Other major plant species include *Lupinus latifolius* (broadleaf lupine), *Potentilla flabellifolia* (fanleaf cinquefoil), *Polygonum bistortoides* (American bistort), *Veronica cusickii* (Cusick speedwell), *Luzula sp.* (woodrush), *Ligusticum grayi* (licoriceroot), and *Carex sp.* (sedge). Visually, these meadows were a Krummholz type of vegetation, consisting of open, low-growing grass-forb meadow interspersed with patches of stunted subalpine fir (*Abies lasiocarpa*). Numerous mammalian herbivores have been reported to use such areas in the mountains of the Pacific Northwest (Reichel 1986), including pocket gophers (*Thomomys sp.*), ground squirrels (*Spermophilus sp.*), voles (*Clethrionomys sp.*), mountain goats (*Ovis canadensis*), deer (*Odocoileus hemionus*) and Elk (*Cervus elaphus*).

Relatively little weather data are available from the subalpine zone, perhaps because of inaccessibility and the harsh climatic conditions which prevail there. Weather data for the subalpine zone of Mount Rainier were summarized by Henderson (1974) for 1930-1970, Greene and Klopsch (1985) for 1978-1980, and by Motazedian and Sharrow (1984) for 1979-1984. Data used in these summaries were collected at Paradise (elevation 5550 ft , 1680 m) which supports mostly heath-shrub and lush herbaceous vegetation compared to the dry meadow vegetation type which dominates our primary research site at Yakima Park (elevation 6400 ft., 1920 m). Nevertheless, Paradise is the most similar reporting station available. Annual precipitation at Paradise averages 118 inches (300 cm), which occurs mostly as winter snow. Maximum annual snowpack varies from 100 inches (250 cm) to over 300 inches (760 cm) and occurs in March through April. Snow accumulation usually begins in mid-October to mid-November and remains until June or July. Summer precipitation is approximately 10 inches (25 cm.). Annual air temperatures average only 38 ^{o}F (3.4 ^{o}C), with yearly high temperatures of around 85 ^{o}F (30^{o} C) usually occurring in late July. Weather in the subalpine zone characteristically varies dramatically from year to year. Greene and Klopsch (1985), for example, observed that the growing season for conifers at Paradise varied from 58 to 116 days during a three year period. Diurnal temperature fluctuation during the growing season can also be large with differences between day and night temperatures often exceeding 80 ^{o}F (26 ^{o}C) at Paradise (Greene and Klopsch). Clearly, the subalpine climate is a challenging one for plants because of both the brevity and unpredictability of the growing season.

METHODS AND PROCEDURES

Of the seven sites previously monitored by the Park Service on Mount Rainier, Bear Park, White River Park, and Yakima Park were selected for our vegetation utilization study because they best represented the dry meadow vegetation type. Yakima Park was selected for defoliation studies because of its relatively uniform stand of vegetation and its accessibility. Temporary electrified fencing was used in Yakima Park to exclude large herbivores from an area approximately 66 ft x 74 ft (20 m x 22 m) in size during the 1986 and 1987 growing seasons. A total of 30 individual 100 $ft.^2$ (9 m^2) plots were randomly assigned to 3 replications of 10 defoliation treatments within this exclosure. Treatments included all combinations of three defoliation times (early, mid, and late growing season) and three intensities of defoliation (25, 50, and 75% of plant biomass removed) plus undefoliated control plots. A standard U.S. Weather Service rain gauge and a recording hygrothermograph were placed within the exclosure to record precipitation, air temperature and relative humidity throughout the 1986 and 1987 growing seasons. Treatments corresponding to 0, 25, 50, and 75% biomass removal were applied to the appropriate plots by hand clipping in late-July, mid-August, and early-September for early, mid, and late season treatments , respectively, in 1986 and 1987. Actual clipping was based upon stubble heights of 6, 4, and 2 inches (15, 10, 5 cm) for 25, 50, and 75% treatments, respectively, as a preliminary clipping study adjacent to the plots suggested that these stubble heights best corresponded to the desired levels of biomass removal. All material removed from plots was ovendried at 50 °C for 72 hours, then weighed. Plots were not clipped in 1988. Plant canopy cover was estimated in early July (prior to application of treatments) in 1986 , 1987, and 1988, from twenty systematically placed 10-point frames (Sharrow and Tober 1979) per plot. Plant frequency was measured in early September 1986 and 1987, and in mid-July 1988 using 20 systematically placed nested quadrats per plot. Nested quadrats contained areas of 5x10 cm, 10x20 cm, and 20x50 cm to facilitate analysis of changes in the amount of both rare and common plants. Number of reproductive stems of _Festuca viridula_ and _Lupinus latifolius_ per 10x20 cm plot were also recorded during frequency sampling. Total aboveground plant biomass was estimated at the end of the 1987 and 1988 growing seasons using a single probe electronic capacitance meter. Thirty randomly placed capacitance readings per plot were converted to estimates of herbage biomass using a calibration equation derived on site each year from thirty 78 cm^2 quadrats which were sampled with the meter, then clipped (r^2=0.79 in 1987, 0.69 in 1988).

Utilization of plants by herbivores was investigated in White River , Bear, and Yakima Parks using a modified percent-of-plants grazed technique. Four 33 ft (10 m) line transects were randomly located in each study park. The species of every plant intersected by the line was recorded and it was assigned to one of 6 utlilzation classes , 0, 1-10, 11-25, 26-50, 51-75, or 76-100% of current year's biomass removed by grazers. Surveys were conducted in mid-growing season (August) of 1986 and 1987.

Data were analyzed using analysis of variance techniques at $p<.05$. Transects within sites served as replication for utilization surveys. The Yakima Park defoliation study was examined as a factorial arrangement of two factors (season and intensity of defoliation) in a completely randomized design with 3 replications. Means of significant treatment effects each year were separated using Student-Newman-Kuels Multiple Range Test (Steel and Torrie 1980).

RESULTS AND DISCUSSION

Climate

Weather data collected during the 1986 and 1987 growing season (Figures 1 and 2) indicate that conditions are cooler and dryer at Yakima Park than the averages previously reported from the Paradise weather station. Dew formed most nights (relative humidity reached 100%), but humidity generally fell to below 50% by late afternoon. Total precipitation during the recording period (24 June 1986 - 15 September 1986 and July 1987 - 13 September 1987) was only 0.8 inches (20 mm) in 1986 and 2.8 inches (71 mm) in 1987. Night temperatures frequently were below 40 ^{o}F (4 ^{o}C) while afternoon temperatures rarely reached 80 ^{o}F (27 C). Subfreezing temperatures may occur any night of the year. Frost free period in 1986 was approximately 30 days, while the longest continuous frost free period in 1987 was only 10 days. Only 58% of the nightly low temperatures recorded each year exceeded 32 ^{o}F (0 ^{o}C).

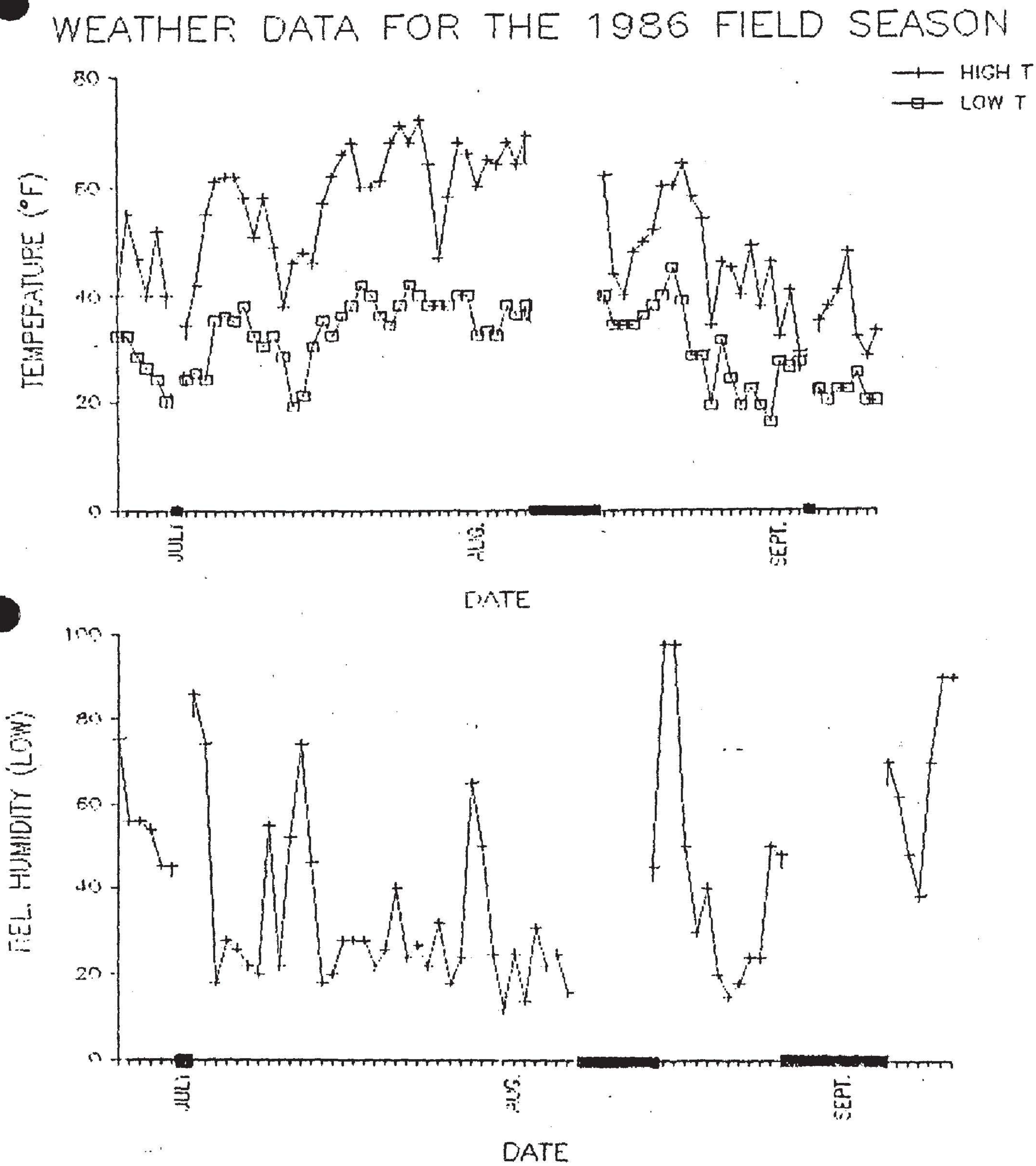

Figure 1. Weather measurements collected at Yakima Park, Mount Rainier National Park.

■ -Indicates data not collected.

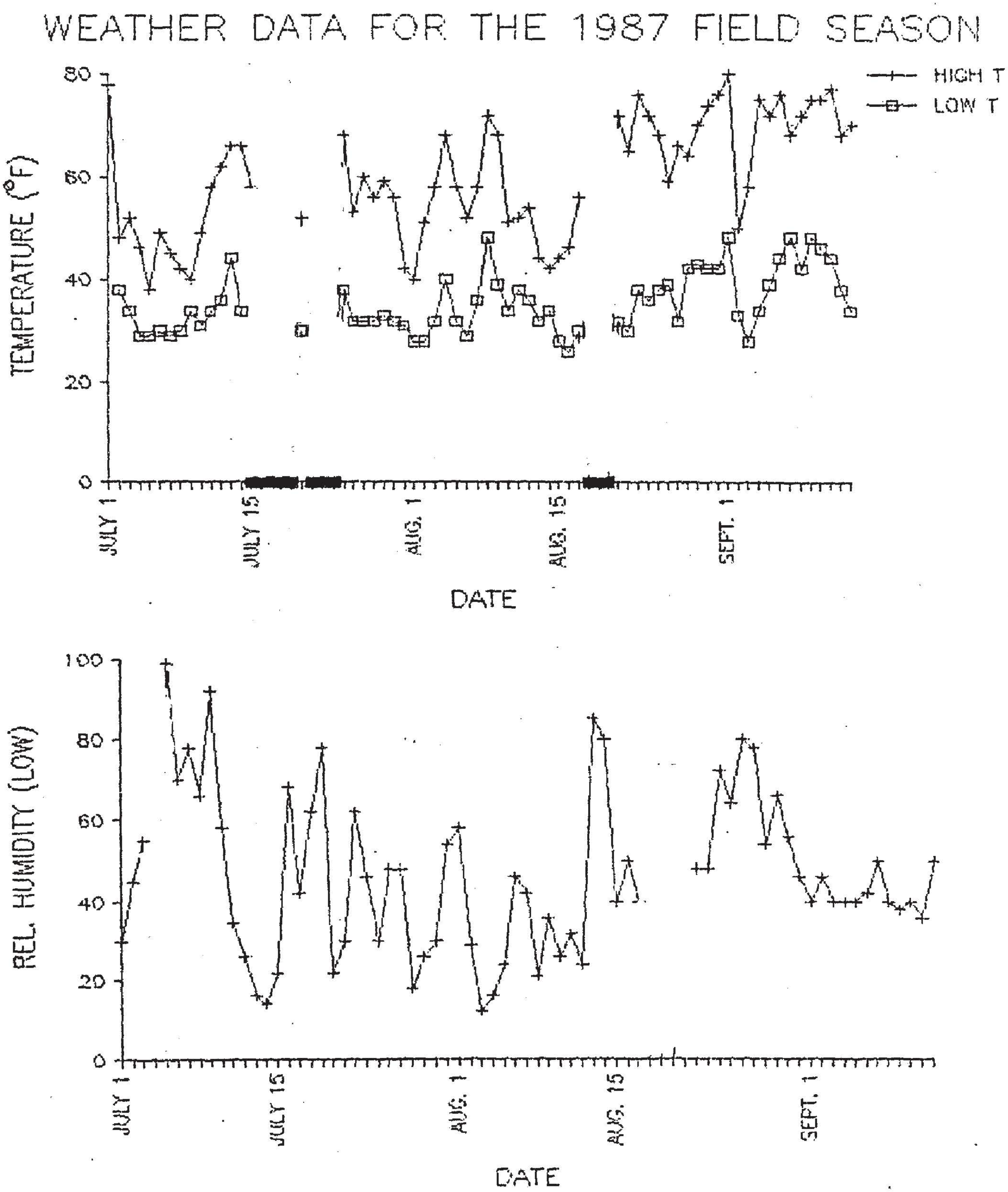

Figure 2. Weather measurements collected at Yakima Park, Mount Rainier National Park.

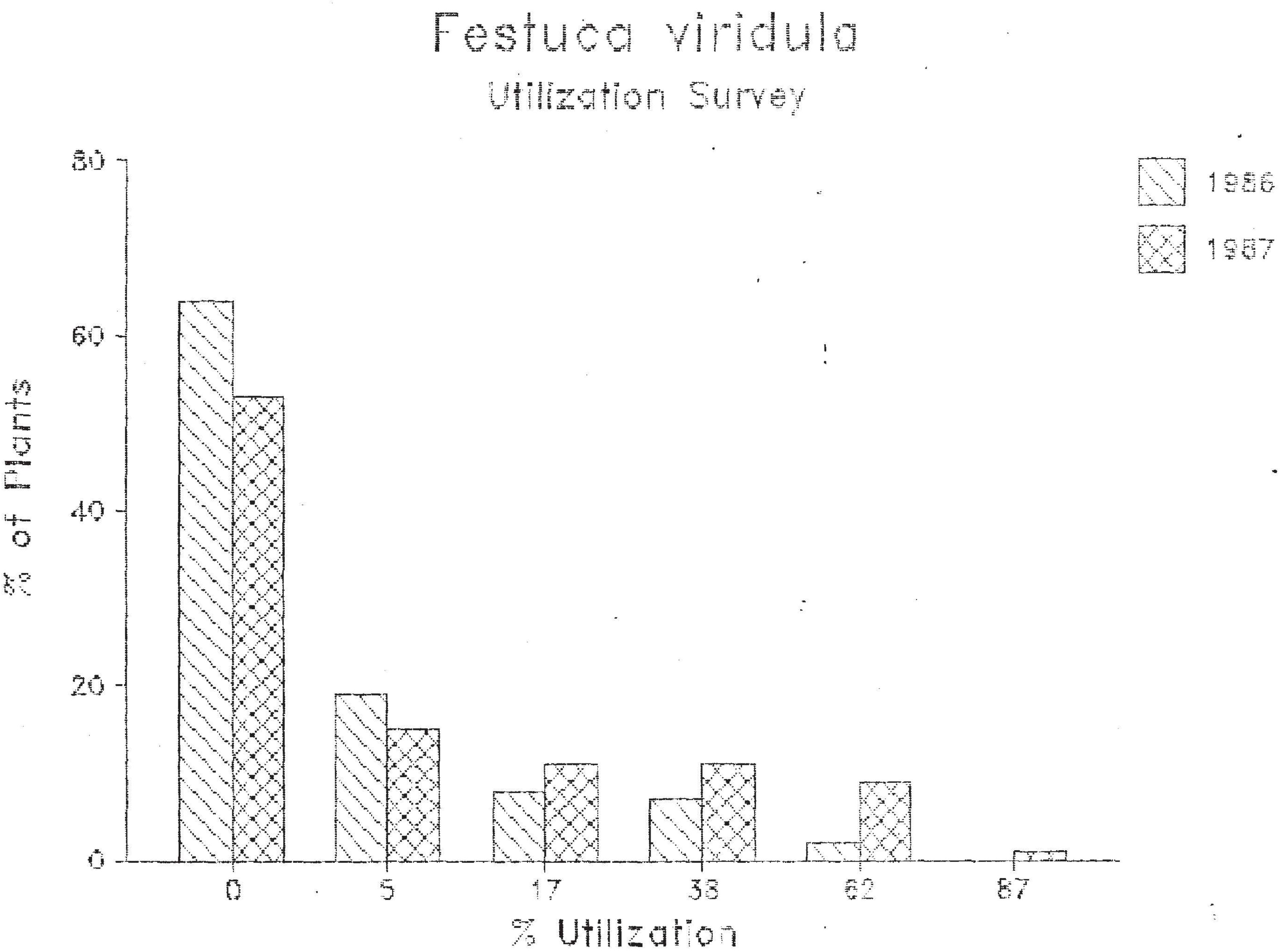

Figure 3. Percent total plant aboveground biomass removed by herbivores (% utilization). Data are the average of surveys made in Yakima, Bear, and White River Parks, Mount Rainier National Park.

Utilization Transects

Results of the utilization surveys are summarized in tables 1 and 2. Our data are total utilization, including consumption of forage by both vertibrate and invertibrate herbivores. Consumption of Lupine, Potentilla, Veronica, and Luzula by herbivores was relatively low. Generally, less than half of these plants showed signs of any defoliation. Grazed plants typically had less than 10% of their biomass removed. Although over half of the Polygonum plants examined had been grazed, total amount of biomass removed was less than 15%. Careful examination of the edges of grazed tissue together with the size and pattern of bites taken allowed us to partition grazing by large ungulates such as elk from that of smaller herbivores. Most of the utilization of forbs was attributable to insects, particularly grasshoppers which reached high population numbers by midsummer each year. Our observations are consistent with those of Wielgolaski (1975) who reported that invertebrates were a far larger proportion of total animal biomass of Norwegian alpine communities than were vertebrates. Insects , such as grasshoppers, are low-volume but selective grazers which may exert considerable defoliation pressure on individual alpine plants (White 1974). Ungulate use of dry meadow vegetation was rather light. Festuca viridula was the only plant which displayed appreciable utilization by elk. Other plants were grazed by elk to only a minor degree, predominately when growing together with a Festuca viridula plant. Only 42% of the fescue plants examined had been grazed. Of the fescue plants grazed,

Table 1. Percent of plants grazed (% PG) and average total utilization (% TU) observed in three parks on Mount Rainier in midsummer 1986.

Plant Species	Bear Park		White River Park		Yakima Park	
	% PG	% TU	% PG	% TU	% PG	% TU
Festuca viridula	62	14	27	5	24	2
Lupinus latifolius	5	<1	0	0	0	0
Polygonum bistortoides	94	14	43	7	49	8
Potentilla flabellifolia	4	<1	4	<1	3	<1
Veronica cusickii	25	6	29	5	15	1
Luzula sp.	29	4	31	1	40	20

Table 2. Percent of plants grazed (% PG) and average total utilization (% TU) observed in three parks on Mount Rainier in midsummer 1987.

Plant Species	Bear Park		White River Park		Yakima Park	
	% PG	% TU	% PG	% TU	% PG	% TU
Festuca viridula	77	28	43	10	22	4
Lupinus latifolius	23	1	------		90	6
Polygonum bistortoides	46	4	53	6	57	4
Potentilla flabellifolia	6	<1	10	<1	9	<1
Veronica cusickii	0	0	14	<1	6	<1
Luzula sp.	24	1	30	3	56	3

Table 3. Canopy cover (%) and species composition (%) of the Yakima Park site immediately prior to application of defoliation treatments in mid-July 1986.

Plant Species	Percent Canopy Cover	Percent Composition
Festuca viridula	32.5	43
Lupinus latifolius	18.3	24
Potentilla flabellifolia	10.8	14
Polygonum bistortoides	5.2	7
Veronica cusickii	5.3	7
Luzula sp.	1.9	2
Ligusticum grayi	2.4	3

74% of the plants in 1986 and 54% of the plants in 1987 had less than 25% of their current season's biomass removed (Figure 3). No fescue plants in 1986 and only approximately 3% of the fescue plants in 1987 lost more than 75% of their current season's growth to herbivory.

Defoliation Experiment

Festuca viridula, Lupinus latifolius, and Potentilla flabellifolia together comprised most of the vegetation at Yakima Park (Table 3). Defoliation intensity treatments were prescribed as a percentage of current season's plant biomass at the time of defoliation. Therefore, plant biomass removed by defoliation treatments varied seasonally as plants grew (Table 4). Early season treatments removed approximately 350 kg/ha less biomass than did mid and late season defoliations which were essentially equivalent. Overall, average biomass removed was approximately 410, 930 , and 2220 kg/ha for intensities 1 (25% utilization), 2 (50% utilization), and 3 (75% utilization), respectively. Material collected from the 1986 mid-season defoliation was handsorted into its component species (Table 5). The majority of biomass removed was Festuca viridula and Lupinus latifolius under all defoliation intensities. Biomass removed from Potentilla flabellifolia and other low growing perennial forbs increased as defoliation intensity increased (stubble height decreased).

Frequency measured using the mid-sized quadrat (5X10 cm) was

Table 4. Average amount of herbage removed (kg/ha) from Yakima Park plots defoliated in early (E), mid (M), or late season (L) to levels of 0 (C), 25% (1), 50% (2), or 75% (3) biomass removal.

Defoliation Treatment		Year	
Season	Intensity	1986	1987
C	0	0	0
E	1	310	160
E	2	1020	790
E	3	2160	1860
M	1	600	490
M	2	1510	1360
M	3	2630	1990
L	1	400	480
L	2	1030	1220
L	3	2090	2620

Table 5. Percentage of weight removed by species for each clipping intensity applied at Yakima Park in mid-season 1986.

Intensity	Festuca virdula	Lupinus latifolius	Potentilla flabellifolia	OTHER
Light (1)	71.6	21.7	0.0	6.7
Moderate (2)	46.1	45.7	0.0	8.2
Heavy (3)	53.9	27.7	5.7	12.7

Table 6. Plant Frequency (%) from Yakima Park plots defoliated in early (E), mid (M), or late season (L) to levels of 0 (C), 25% (1), 50% (2), or 75% (3) biomass removal.

Season	Intensity	Yearly Means[1] 1986	1987	1988
		Festuca viridula		
C	C	90a	92	87a
E	1	78a	87a	87a
E	2	82a	87a	87a
E	3	77a	88a	88a
M	1	77a	82a	77a
M	2	80a	80a	78a
M	3	78a	85a	83a
L	1	88a	87a	83a
L	2	87a	88a	88a
L	3	83a	92a	72a
		Sy=4.6	Sy=3.5	Sy=6.9
		Lupinus latifolius		
C	C	66.7a	68a	32a
E	1	63a	55a	28a
E	2	76.7a	60a	17a
E	3	81.7a	58a	13a
M	1	85a	65a	37a
M	2	75a	72a	27a
M	3	51.7a	43a	15a
L	1	73a	82a	37a
L	2	60a	60a	27a
L	3	63a	68a	28a
		Sy=9.1	Sy=8.6	Sy=8.1
		Potentilla flabellifolia		
C	C	73a	75a	72a
E	1	60a	58a	52a
E	2	61a	67a	62a
E	3	70a	63a	52a
M	1	32a	48a	32a
M	2	40a	43a	40a
M	3	63a	65a	55a
L	1	55a	60a	52a
L	2	60a	62a	57a
L	3	48a	40a	40a
		Sy=10.9	Sy=9.3	Sy=11.5

[1] Means in a column for each plant not sharing a common letter differ (P<.05). Sy = Standard error.

Season	Intensity	Yearly Means 1986	1987	1988
		Ligusticum grayi		
C	C	28a	30a	25a
E	1	33a	33a	33a
E	2	38a	30a	23a
E	3	20a	38a	33a
M	1	35a	47a	23a
M	2	12a	17a	12a
M	3	25a	22a	23a
L	1	20a	17a	20a
L	2	43a	38a	38a
L	3	27a	28a	22a
		Sy=7.5	Sy=7.2	Sy=7.4
		Aster alpigenus		
C	C	28a	20a	22a
E	1	22a	22a	13a
E	2	25a	18a	12a
E	3	28a	23a	12a
M	1	25a	22a	22a
M	2	25a	25a	10a
M	3	17a	25a	20a
L	1	32a	23a	23a
L	2	10a	22a	15a
L	3	17a	15a	20a
		Sy=6.2	Sy=7.8	Sy=7.3
		Erigeron peregrinus		
C	C	30a	35a	28a
E	1	26.7a	27a	17a
E	2	25a	18a	15a
E	3	15a	22a	17a
M	1	20a	18a	15a
M	2	27a	22a	22a
M	3	30a	30a	22a
L	1	5a	28a	13a
L	2	28a	27a	13a
L	3	15a	15a	10a
		Sy=7.4	Sy=6.6	Sy=6.4

Season	Intensity	Yearly Means 1986	1987	1988
		Polygonum bistortoides		
C	C	37a	50a	52a
E	1	35a	47a	40a
E	2	23a	23a	35a
E	3	63a	43a	45a
M	1	65a	35a	30a
M	2	17a	37a	28a
M	3	27a	38a	35a
L	1	35a	30a	25a
L	2	17a	48a	38a
L	3	30a	42a	35a
		Sy=7.4	Sy=8.7	Sy=9.7
		Veronica cusickii		
C	C	70a	55a	65a
E	1	43a	42a	32a
E	2	52a	60a	43a
E	3	38a	67a	48a
M	1	57a	55a	43a
M	2	48a	50a	42a
M	3	67a	57a	50a
L	1	43a	70a	47a
L	2	65a	52a	50a
L	3	58a	65a	43a
		Sy=8.6	Sy=7.5	Sy=9.5
		Luzula sp.		
C	C	77a	70a	63a
E	1	37a	37a	28a
E	2	43a	48a	45a
E	3	30a	28a	27a
M	1	8a	12a	13a
M	2	7a	3a	2a
M	3	33a	40a	30a
L	1	30a	28a	25a
L	2	35a	37a	28a
L	3	28a	30a	27a
		Sy=19.0	Sy=19.4	Sy=17.5

Table 7. Plant canopy cover (%) from Yakima Park plots defoliated in early (E), mid (M), or late season (L) to levels of 0 (C), 25% (1), 50% (2), or 75% (3) biomass removal.

Season	Intensity	Yearly Means[1] 1986	1987	1988
		Festuca viridula		
C	C	36a	40a	9b
E	1	29a	27a	17ab
E	2	29a	29a	18ab
E	3	28a	34a	14ab
M	1	30a	40a	14ab
M	2	37a	36a	14ab
M	3	31a	36a	14ab
L	1	41a	38a	14ab
L	2	35a	42a	23a
L	3	30a	32a	16ab
		Sy=3.8	Sy=4.5	Sy=2.1
		Lupinus latifolius		
C	C	17a	19a	5a
E	1	18a	15a	2a
E	2	16a	10a	4a
E	3	18a	9a	1a
M	1	18a	20a	1a
M	2	22a	22a	1a
M	3	16a	10a	3a
L	1	15a	27a	1a
L	2	18a	18a	1a
L	3	24a	26a	4a
		Sy=4.3	Sy-3.8	Sy=1.4
		Potentilla flabellifolia		
C	C	11a	11a	15a
E	1	15a	12a	11a
E	2	12a	15a	13a
E	3	11a	10a	16a
M	1	10a	6a	13a
M	2	7a	7a	10a
M	3	16a	17a	9a
L	1	10a	10a	9a
L	2	10a	12a	12a
L	3	5a	5a	11a
		Sy=3.2	Sy=2.8	Sy=1.6

[1] Means in a column for each plant not sharing a common letter differ ($P<.05$).

Season	Intensity	Yearly Means 1986	1987	1988
		Ligusticum grayi		
C	C	1a	3a	0.3a
E	1	1a	2a	0.3a
E	2	2ab	3a	0.3a
E	3	3ab	2a	0.2a
M	1	2ab	2a	0.2a
M	2	2ab	1a	1.3a
M	3	2ab	2a	0.2a
L	1	2ab	2a	0.3a
L	2	6b	3a	0.2a
L	3	3ab	4a	0.3a
		Sy=2.7	Sy=3.9	Sy=2.8
		Polygonum bistortoides		
C	C	9a	8a	5a
E	1	6a	4a	3a
E	2	4a	4a	3a
E	3	5a	7a	4a
M	1	4a	5a	3a
M	2	5a	5a	3a
M	3	6a	5a	3a
L	1	4a	3a	3a
L	2	5a	6a	3a
L	3	5a	4a	4a
		Sy=1.5	Sy=1.4	Sy=1.1
		Veronica cusickii		
C	C	6a	6a	4a
E	1	7a	5a	3a
E	2	6a	6a	4a
E	3	8a	8a	1a
M	1	7a	5a	3a
M	2	3a	4a	3a
M	3	4a	7a	2a
L	1	3a	5a	2a
L	2	4a	3a	3a
L	3	5a	5a	3a
		Sy=1.4	Sy=1.4	Sy=1.0

Season	Intensity	Yearly Means 1986	1987	1988
		Luzula sp.		
C	C	3a	2a	0.2a
E	1	1a	3a	0.5a
E	2	6a	4a	0.2a
E	3	2a	2a	0.2a
M	1	0a	0a	0.2a
M	2	0a	0a	0.7a
M	3	3a	1a	1.3a
L	1	3a	2a	0.2a
L	2	1a	1a	0.3a
L	3	1a	1a	0.5a
		Sy=1.6	Sy=1.5	Sy=0.37

selected to study plant community response to defoliation as it appeared to have the best sensitivity for the major plant species encountered. Neither intensity nor season of defoliation affected frequency of any plant monitored (Table 6). Lack of changes in plant frequency are understandable in light of the short-term nature (3 years) of this study. Substantial changes in plant community structure are often required for treatment-induced changes in frequency to be apparent above naturally occurring variation within plant communities.

Average plant canopy cover was similar in 1986 and 1987 (Table 7). Lower cover values in 1988 compared to 1986 or 1987 reflect data collection at a slightly earlier plant phenological stage in 1988 together with generally low plant production that year. Similar to frequency, no differences in plant canopy cover could be attributed to either time or intensity of defoliation. Plant canopy cover was measured prior to application of the early season defoliation treatments each year. Any differences in canopy cover would likely be due to treatments applied during the previous year. Lack of response of the two main species, _Festuca viridula_ and _Lupinus latifolius_, is surprising in light of the large amount of biomass removed from them by the 75% utilization treatments in 1986 and again 1987. Little biomass was actually removed from the other plant species by our defoliations. Presumably, lack of response to defoliation by the two dominant species means that competition between dominant and subdominant species for site resources was largely unaltered. Response of subdominant plant species to defoliation treatments would not be expected under these conditions.

Total net plant biomass production (standing biomass at the end of the growing season plus biomass removed by clipping) in 1987 varied among defoliation intensity treatments (Table 8). Production from 25% defoliation treatments was similar to unclipped control plots. Biomass production increased by 74% as defoliation increased from 25 to 75% of standing biomass in 1987. This corresponds to approximately 29 kg/ha increased forage production for each additional 1% defoliation above 25%. Standing herbage biomass at the end of the 1987 growing season was similar regardless of defoliation treatment applied. Apparently, defoliated plants responded by replacing the leaf tissue removed. This is a common reaction of herbaceous plants to defoliation and forms the basis of McNaughton's (1984) grazing lawn hypothesis concerning plant-herbivore interactions. Interestingly, season of defoliation had no effect on plant growth in 1987. Apparently, the 1987 growing season was sufficiently long to support regrowth of plants, even those defoliated in early September. Plant production in 1988 was substantially lower than in 1987. Neither intensity nor season of defoliation affected total net plant production that year. Since plots were not clipped in 1988, any treatment effects detected that year would be carryover effects from the 1986 and 1987 treatments. Because 1988 plant production was apparently predominately constrained by climatic factors, it is difficult to deduce if defoliation effects did not carryover into 1988 or if

Table 8. Aerial plant biomass production (kg/ha) from Yakima Park plots defoliated in early (E), mid (M), or late season (L) to levels of 0 (C), 25% (1), 50% (2), or 75% (3) biomass removal.

		1987			1988
Season	Intensity	Removed	Ending Biomass	Total[1]	Total[1]
C	C	0	2048	2048a	650a
E	1	156	1757	1914a	550a
E	2	788	1711	2499ab	536a
E	3	1855	1395	3250bc	176a
M	1	487	1482	1969a	504a
M	2	1357	1357	22714	379a
M	3	1990	1109	3100b	522a
L	1	476	1537	2014a	374a
L	2	1216	1317	2533ab	746a
L	3	2516	1362	3879c	322a
				Sy=215	Sy=130

[1] Means in a column not sharing a common letter differ (P<.05).

any such effects were not sufficiently large to express themselves above the overriding impacts of climate on growth of subalpine plants. The 1988 plant production data do display a numerical trend of decreasing total production with increasing levels of past defoliation. Such a relationship would be understandable in light of the possible needs for energy reserves to be used for immediate replacement of leaf tissue removed in 1987 instead of stored to support plant growth the following year. Growth from buds set the previous year dominants early spring growth of most perennial plants. Size and number of buds set in previous seasons should be important determinants of growth potential for perennial plants existing in short season environments such as alpine and subalpine meadows. Many alpine plants set flower primordia during the year previous to flowering (Mark 1970). This adaptation probably reflects a need to flower very quickly at the beginning of the grazing season if sufficient time is to remain to develop seed. It does, however, make sexual reproduction potentially vulnerable to previous year's grazing.

Like plant production, sexual reproduction of the two major plant species in Yakima Park (Table 9) was relatively low and did not differ among defoliation treatments in 1988. Number of reproductive stems of both Festuca viridula and Lupinus latifolius in 1987 tended to decline with increasing defoliation above 25%, however, differences were not always statistically significant at $p<.05$. Both plants tended to be especially sensitive to early season defoliation, but differences were again not always statistically significant.

Table 9. Number of *Festuca viridula* and *Lupinus latifolius* reproductive stems (stems/m^2) in Yakima Park plots defoliated in early (E), mid (M), or late season (L) to levels of 0 (C), 25% (1), 50% (2), or 75% (3) biomass removal.

Defoliation		*Festuca viridula*[1]		*Lupinus latifolius*[1]	
Season	Intensity	1987	1988	1987	1988
C	0	22ab	9a	74a	4a
E	1	18ab	8a	59a	1a
E	2	3b	5a	67a	3a
E	3	1b	2a	15a	2a
M	1	46a	7a	58a	7a
M	2	16ab	2a	69a	6a
M	3	6ab	1a	18a	1a
L	1	33ab	4a	111a	7a
L	2	29ab	6a	52a	8a
L	3	26ab	6a	76a	4a
		Sy=8.8	Sy=2.6	Sy=23.6	Sy=2.6

[1] Means in a column not sharing a common letter differ (P<.05).

DISCUSSION AND CONCLUSIONS

Clearly the subalpine environment is a challenging one for plants. Growing seasons are often short and can vary substantially from year to year. Within a year, wide fluctuations in temperature, moisture, and insolation can occur rapidly as different air masses pass over the mountains. Plants must deal with both the harshness and unpredictability of the mountain climate if they are to persist. In some ways, these condition are similar to those experienced by other plants growing in harsh environments such as deserts where the effective growing season is determined by brief, unpredictable rainfall events such as thundershowers. Chabot and Billings (1974) have, in fact, postulated that alpine vegetation of the Sierra Nevada Range was derived from upward migration of cold desert vegetation over geologic time. Not surprisingly, they share several adaptive strategies in common. Both areas are dominated by long-lived perennial plants. Perennality is very useful in areas with short, highly variable growing seasons as it allows plants to carry nutrients and energy from year to year, thus reducing the impacts of climatic variability on plant growth. Perennality is also important in reducing the need for annual reproductive success. Although relatively little is understood about the reproductive dynamics of alpine or subalpine plants, it is probably similar to desert perennials which only successfully reproduce either sexually or asexually during atypically favorable climatic patterns involving several growing seasons. Successful reproduction typically requires a favorable growing season for production of reproductive disseminules (ie. seeds, rhizomes, stolons etc.) followed by one or more especially favorable growing seasons for new plants to become established. Under such conditions, plant populations consist of a set of generational cohorts corresponding to flushes of reproduction interspersed by nonreproductive periods.

Taken in total, our data do not support the view that subalpine dry meadow vegetation on Mount Rainier is very sensitive to defoliation. Plant community scale data (frequency and cover) were unaffected by defoliation levels as high as 75% of standing biomass removed. Although plant biomass present at the end of the growing season in 1987 was reduced by defoliation, the magnitude of this reduction was small compared to the yearly fluctuation in plant standing crop observed between 1987 and 1988. Even our most lenient defoliation treatment (25% utilization) was substantially above levels of defoliation occurring in the three meadows monitored. Motazedian and Sharrow (1984) concluded that monitoring data collected from these meadows during 1976-1984, did not support the view that vegetational change was occurring as a result of increased elk grazing . Our data are consistent with this view and further suggest that substantial increases in herbivore use (perhaps as much as 4 fold) could occur without short-term changes in the plant community. Apparently, subalpine dry meadow plants are able to tolerate severe periodic defoliation. This is not surprising when one considers that (1) plants may effectively be defoliated by freezing at any time during the normal growing season and (2) the dry meadow plant community evolved in the presence of native herbivores such as insects and small mammals which can exert considerable grazing pressure on plants in localized areas. Our reproduction data suggests that defoliation may have a more detrimental impact upon reproductive potential than it does on vegetative growth of subalpine plants. Population dynamics of alpine and subalpine plant communities have not been extensively studied. Experience with areas where plants have been lost by elk or human trampling is that these areas are slow to regenerate. Recovery of disturbed alpine areas may take centuries (Brown et al. 1978). Conceptually , then, alpine and subalpine plant communities are both robust and at the same time extremely fragile. They are vegetatively robust in the sense that the individual plants which comprise it are able to withstand considerable levels of defoliation without apparent loss of vigor. Yet they are reproductively fragile in that potential reproduction is sensitive to defoliation and once lost, individual plants are unlikely to be replaced for many years. Clearly, much more must learned about the population dynamics and reproduction strategies of important alpine and subalpine plants if the long-term effects of herbivory are to be predicted and/or if damaged areas are to be successfully rehabilitated.

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