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Plant response to defoliation in a subalpine green fescue community

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Abstract

This study was prompted by concerns that expansion of elk (*Cervus canadensus*) ranges upward into subalpine grasslands might be damaging green fescue (*Festuca viridula* Vasey) meadows in Mount Rainier National Park. Objectives of the study were to examine effects of season and intensity of defoliation on phytomass productivity and canopy cover of these subalpine dry meadows and to relate these observations to the degree of elk utilization actually occurring on 3 representative meadows. Grazing in all meadows was very light. Less than one 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. Only green fescue was grazed to any significant extent by elk. Defoliation treatments (0%, 25%, 50%, and 75% of aerial phytomass removed in either early-, mid-,or late-season 1986 and again in 1987) had little effect upon plant cover the following year. Total herbage production was greater for defoliated than for undefoliated control plots in 1987, but did not vary with season of defoliation. Reproduction of green fescue and *Lupinus latifolius* Agardh. tended to decline as defoliation intensity increased in 1987. Neither season nor intensity of defoliation affected any of the parameters measured in 1988, a year of very low plant production. Green fescue subalpine grasslands appear to be quite tolerant of defoliation. All treatment effects were small relative to yearly differences induced by climatic variation.

Key Words: elk, grazing, *Festuca viridula, Lupinus latifolius*, alpine climate

Resumen

Este estudio fue motivado por la preocupación de que la expansión del rango de apacentamiento del alce (*Crevus canadensus*) hacia pastizales subalpinos pudíera estar dañando las praderas de "Green fescue" (*Festuca viridula* Vasey) en el Parque Nacional Mount Rainier. Los objetivos de este estudio fueron examinar los efectos de la época e intensidad de defoliación en la productividad y cobertura aérea de estas praderas secas subalpinas y relacionar estas observaciones con el grado de utilización actual del alce en 3 praderas representativas. El apacentamiento en todas las praderas fue muy ligero. Menos de la mitad de todas las plantas examinadas mostraron alguna evidencia de haber sido apacentadas. Las plantas que fueron apacentadas típicamente tenían menos de 15% de las puntas removidas. Solo el "Green fescue" fue pastoreado en una cantidad significativa por el alce. Los tratamientos de defoliación (0%, 25%, 50% y 75% de remoción de la fitomasa aérea a inicio, medio y fin de la estación de 1986 y nuevamente en 1987) tuvieron poco efecto sobre la cobertura vegetal del siguiente año. En 1987, la producción total de forraje fue mayor en las parcelas defoliadas que en las no defoliadas (control), pero no varió por efecto de la época de defoliación. En 1987, la reproducción del "Green fescue" y Lupinus latifolius Agardh. Tendió a declinar conforme la intensidad de defoliación se incrementó. Ni la época ni la intensidad de defoliación afectaron los parámetros medidos en 1988, un año de muy baja producción vegetal. Los pastizales subalpinos de "Green fescue" parecen ser muy tolerantes a la defoliación. Todos los efectos de los tratamientos fueron pequeños en relación a las diferencias anuales inducidas por la variación climática.

Festuca viridula Vasey (green fescue) grasslands occur as mountain meadows or grassy slopes in the 1,000 to 2,000 m elevation zone throughout the western mountain ranges from British Columbia and Alberta south to central California and Colorado (Hitchcock and Chase 1971). Green fescue grasslands are relatively productive and palatable to large herbivores compared to other mountain vegetation. They were historically a major source of summer grazing for open-banded sheep (*Ovis aries*) in the Rocky, Willowa and Blue Mountain chains of the western U.S. The high mountains of the Cascade Range, in contrast, have generally supported relatively low populations of native ungulates and their ruggedness has discouraged domestic livestock grazing. Elk (*Cervus canadensus*) populations using mountain summer ranges have increased in many areas of Washington as a result of timber harvest patterns at lower elevations (Cooper 1987) and their introduction into areas of the Cascades which are not part of their historical range. Increasing summer use of high elevation meadows by ungulates is raising concern among national

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park managers about potential degradation of subalpine vegetation (Houston et al. 1994, Pfitsch 1981). The ability of plants in subalpine grasslands of the Cascades to tolerate increased defoliation by ungulates is largely unknown.

We sought to examine shifts in the structure (canopy cover) and phytomass productivity of a *Festuca viridula* grassland community attributable to known levels and seasons of defoliation, and to relate these findings to levels of defoliation which were actually occurring on similar subalpine green fescue grasslands in Mount Rainier National Park.

Materials and Methods

Study Area

Plant names used follow Garrison et al. (1976). Three green fescue stands located on the east side of Mount Rainier (latitude 47° N, longitude 122° W), at elevations of 1,750 to 1,920 m were used in this study. They are representative of the Subalpine Meadow Vegetation Zone as described by Henderson (1974), which covers approximately 10,000 ha of Mount Rainier National Park's 95,350 ha. This grassland is characterized by dominance of *Festuca viridula* on relatively dry, well-drained loamy soils, primarily derived from geologically young deposits of glacial till and volcanic ash. Other major plant species include *Lupinus latifolius* Agarah. (broadleaf lupine), *Potentilla flabellifolia* Hook.(fanleaf cinquefoil), *Polygonum bistortoides* Pursh (American bistort), *Veronica cusickii* Gray (Cusick speedwell), *Luzula* sp. (woodrush, predominately *L. glabrata* Desv.), *Ligusticum grayi* Coult. & Rose (licoriceroot), and *Carex spectabilis* Dewey (sedge). Visually, these meadows are a krummholz type of vegetation, consisting of open, low-growing, grass-forb meadow interspersed with patches of stunted subalpine fir (*Abies lasiocarpa* Hook. Nutt.).

Climate 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. Annual precipitation is approximately 3,000 mm, which occurs mostly as winter snow. Maximum annual snowpack varies from 250 cm to over 760 cm and occurs in March through April. Snow accumulation usually begins in mid-October to mid-November and remains until June or July. Annual air temperatures average only 3.4°C, with yearly high temperatures of around 30 °C usually occurring in late July. Weather in the subalpine zone characteristically varies dramatically from year to year (Weaver 1979). For example, Greene and Klopsch (1985) observed that the growing season for conifers near timberline on Mount Rainier varied from 58 to 116 days during a 3-year period. Diurnal temperature fluctuation during the growing season can also be large with differences between day and night temperatures often exceeding 26°C (Greene and Klopsch 1985).

Climatic Data

A standard U.S. Weather Service rain gauge and a recording hygrothermo-graph were used to record precipitation, air temperature, and relative humidity within Yakima Park throughout the 1986 and 1987 growing seasons. Total precipitation during the recording period (24 June 1986 to 15 September 1986 and 1 July 1987 to 13 September 1987) was 20 mm in 1986 and 71 mm in 1987. Night temperatures frequently were below 4°C while afternoon temperatures rarely reached 27°C. Dew formed most nights (relative humidity reached 100%), but humidity generally fell to below 50% by late afternoon. Subfreez-ing 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 0°C. These data are consistent with Weaver's (1979) description of the higher elevation, more mesic edge of typical mountain fescue grassland climates, where green fescue is most often found. High potential evaporation combined with relatively low summer season rainfall produce arid conditions during much of the growing season (Weaver 1979).

Utilization Sampling

Utilization of plants by herbivores was investigated in White River, Bear, and Yakima Parks using an ocular estimate technique (Bonham 1988). Four, 10-m line transects were randomly located in each study meadow. The species of each plant intersected by the line was recorded and it was assigned to 1 of 6 utilization classes; 0, 1 to 10, 11 to 25, 26 to 50, 51 to 75, or 76 to 100% of the current year's phytomass removed by grazers. Surveys were conducted in mid-growing season (August) of 1986 and 1987. Mean percentage utilization was calculated by plant species for each transect by averaging class mid-points of all grazed plants encountered.

Defoliation Experiment

Thirty, 9-m^2 plots were randomly assigned to 3 replications of 10 defoliation treatments within Yakima Park in 1986. Soil at Yakima Park is a geologically young surface developing from stony, well drained glacial drift (Henderson 1974). The resulting soil is coarse, well drained, and friable with relatively low soil moisture storage capacity (Henderson 1974). Large herbivores were excluded from experimental plots by electrified fencing. Treatments included all combi-nations of 3 defoliation times (early-, mid-, and late-growing season) and 3 intensities of defoliation (25, 50, and 75% of plant phytomass removed) plus undefoliated control plots.

Defoliation plots were hand clipped in late-July, mid-August, and early-September for early-, mid-, and late-season treatments, respectively, in 1986 and again in 1987. Defoliated plots were clipped to remove 0, 25, 50, or 75% of current aboveground phytomass, based upon experience gained from a preliminary clipping study adjacent to the plots. Clipped material was dried in a 50°C oven for 72 hours, then weighed. Plots were not clipped in 1988.

Canopy cover was estimated in early

July (prior to defoliation) in 1986, 1987, and in 1988, from twenty, 10-point frames (Sharrow and Tober 1979) per plot. Number of reproductive stems of Festuca viridula and Lupinus latifolius was counted within twenty, 10 × 20-cm quadrats per plot at the end of the growing season in early September 1986 and 1987.

Total aboveground phytomass standing crop was estimated at the end of the 1987 and 1988 growing seasons using a single probe electronic capacitance meter (Vickery et al. 1980). Thirty randomly placed capacitance readings per plot were converted to estimates of phytomass using a calibration equation ($r^2 = 0.79$ in 1987, 0.69 in 1988) derived on site each year from thirty, 78-cm^2 quadrats which were sampled with the meter, then clipped just prior to use of the capacitance meter for sampling plots. Phytomass at the end of the 1986 growing season was not measured due to early snowfall which prevented field sampling.

Statistical Analysis

Data were analyzed using analysis of variance techniques (Steel and Torrie 1980) at $P < 0.05$. Transects within the 3 meadows served as replication for utilization surveys. The Yakima Park defoliation study was analyzed as a completely randomized design with a 3 x 3 factorial arrangement of season and intensity of defoliation treatments, plus an untreated control. Control plots served as a zero defoliation intensity treatment. Analysis of variance was performed on the resulting 10 treatment combinations using a computer routine for unbalanced designs (Powerstat 1986). Separation of components of variance was obtained by initial expansion and paresing of the statistical model (Searle 1971) followed by fitting model components using a reversible sweep generator (Kennedy and Gentle 1980). This produced an orthogonal separation of variance into individual main effects, interactions, and residual error, similar to a conventional, balanced analysis of variance.

Means of significant treatment effects within each year were separated using Student-Newman-Keuls Multiple Range Test (Steel and Torrie 1980).

Results

Season by defoliation intensity interactions were not significant for any parameter measured, therefore, data interpretation focuses on main effects of season and intensity.

Utilization Transects

Consumption of lupine, Potentilla, Veronica, and Luzula by herbivores was low (Table 1). Generally, fewer than one half of the plants of these species showed signs of defoliation. Grazed plants typically had less than 10% of their phytomass removed. Although over one half of the Polygonum plants examined had been grazed, less than 15% of total biomass was removed. Only 42% of the green fescue plants examined had been grazed. Of the green fescue plants grazed, 74% of the plants in 1986 and 54% of the plants in 1987 had less than 25% of the current season's phytomass removed. No green fescue plants in 1986 and only approximately 3% of the green fescue plants in 1987 lost more than 75% of their current season's growth to herbivory.

Defoliation Experiment

Vegetation cover at Yakima Park prior to application of defoliation treatments in mid-July 1986 was 40% *Festuca viridula*, 23% *Lupinus latifolius*, 13% *Potentilla flabellifolia*, 7% *Polygonum bistortoides*, 7% *Veronica cusickii*, 2% *Luzula* sp., and 3% *Ligusticum grayi*. Defoliation intensity treatments were prescribed as a percentage of current season's plant phytomass at the time of defoliation. Therefore, the amount of phytomass removed by defoliation treatments varied seasonally as plants grew. Early-season treatments removed approximately 350 kg ha^{-1} less phytomass than did mid- and late-season defoliations, which were essentially equivalent. Average phytomass removed in 1986 was 410, 930, and 2,220 kg ha^2 for 25%, 50%, and 75% defoliation treatments, respectively. Material collected from the 1986 mid-season defoliation was hand sorted into component species. Approximately 82 to 94% of phytomass removed was *Festuca viridula* and *Lupinus latifolius* under all defoliation intensities. Phytomass removed from *Potentilla flabellifolia* and other low-growing perennial forbs increased as defoliation intensity increased, being 7, 8, and 18% of phytomass removed by 25%, 50%, and 75% defoliation treatments, respectively.

Total phytomass production did not vary with season of defoliation (Table 2) in either 1987 or 1988. Total annual production from 25% defoliation treatments was similar to unclipped

Table 1. Percentage of plants grazed (PG) and average total utilization (TU) observed in 3 parks on Mount Rainier in mid-summer 1986 and 1987. Data are utilization by both vertibrate and invertibrate herbivores ± standard error.

	Bear Park		White River Park		Yakima Park	
Year/Species	PG	TU	PG	TU	PG	TU
	- -	-	%-	- -		
1986						
Festuca viridula	62±2	14±12	7±6	5±1	24±1	2±1
Lupinus latifolius	5±3	1±1	0	0	0	0
Polygonum bistortoides	94±7	14±3	43±6	7±2	49±9	8±1
Potentialla flabellifoli	4±2	1±1	4±2	1±1	3±2	1±1
Veronica cusickii	25±10	6±3	29±11	5±2	15±2	1±1
Lusula sp	29±6	4±1	31±23	1±1	40±24	20±4
1987						
Festuca viridula	77±3	28±2	43±6	10±2	22±6	4±1
Lupinus latifolius	23±4	1±1	90±7	6±1	0	0
Polygonum bistortoides	46±20	4±1	53±14	6±1	57±7	4±1
Potentilla flabellifolia	6±4	1±1	10±5	1±1	9±1	1±1
Veronica cusickii	0	0	14±4	1±1	6±3	1±1
Luzula sp.	24±12	1±1	30±9	3±1	56±3	3±1

Table 2. Phytomass removed by clipping, final above ground phytomass, and total phytomass production in Yakima Park in 1987 and 1988 under differing season and intensity of defoliation applied in 1986 and again in 1987.

Item	Phytomass[1] removed 1987	Final[1] phytomass 1987	Total[1] phytomass 1987	Total[1] phytomass 1988
	----------	(kg ha^{-1})	----------	
Season				
Early	933[a]	1612[a]	2554[a]	421[a]
Mid	1278[ab]	1316[a]	2594[a]	468[a]
Late	1402[b]	1405[a]	2808[a]	481[a]
Intensity				
25%	373[a]	1592[a]	1965[a]	476[a]
50%	1120[b]	1461[a]	2582[b]	553[a]
75%	2120[c]	1288[a]	3409[c]	340[a]
Control	0[d]	2048[b]	2048[a]	650[a]
SE[2]	70	119	141	122

[1]Means within an item not sharing a common letter differ (P<0.05).
[2]SE is standard error of a mean.

control plots in both years. However, total phytomass production increased by 74% as defoliation increased from 25 to 75% of standing phytomass in 1987. Standing herbage phytomass at the end of the 1987 growing season was similar for 25%, 50%, and 75% defoliation treatments, but approximately 22% less than undefoliated plots. Averaged over all treatments, plant phytomass production in 1988 was only 20% of that observed in 1987.

Similar to plant production, sexual reproduction of the two major plant species in Yakima Park (Table 3) was low and did not differ among defoliation treatments in 1988. Number of reproductive stems of *Festuca viridula* and *Lupinus latifolius* in 1987 tended to decline with increasing defoliation above 25%. However, differences were not always significant at $P < 0.05$. Both species were particularly sensitive to early season defoliation, which reduced reproductive stems of Festuca viridula by 74% and *Lupinus latifolius* by 37%.

Average total plant canopy cover was similar in 1986 and 1987 (Table 4). 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 lower plant production that year. No differences in plant canopy cover could be attributed to either time or intensity of defoliation in 1986 or 1987 ($P > 0.05$). Likewise, no defoliation treatment effects were evident in 1988 with the exception of *Festuca viridula* canopy cover which was 9% on undefoliated control plots compared to an average 15% cover for defoliated plots.

Discussion

Fescue grasslands are common in the subalpine zone of western North America (Kuchler 1964). The subalpine zone is a challenging environment 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 the harshness and unpredictability of the mountain climate if they are to persist. In some ways, these conditions are similar to those experienced by other plants growing in harsh environments such as deserts where the effective growing season is also determined by brief, unpredictable events such as thundershowers. Chabot and Billings (1974) have 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 species (ie. *Festuca idahoensis*, *F. thurberi*) and adaptive strategies in common.

Although subalpine grasslands often are dominated by a few plant species, their flora is usually rich with many minor species using resources not captured by the dominants (Grabherr 1989). Few successional studies have been conducted. However, it is generally believed that green fescue together with broadleaf lupine are late seral or climax species (Henderson 1974, Franklin and Dyrness 1988) and that high amounts of other forbs are a sign of low seral status (Reid 1941). Green fescue dominates climax communities and may form almost pure stands (Pickford and Reid 1940, Johnson 1990). Plant community structure in our study (as indicated by canopy

Table 3. Average number of flowering stems of *Festuca viridula* and *Lupinus latifolius* in 1987 and 1988 under diffferent seasons and intensity of defoliation.

Item	*Festuca viridula*[1] 1987	*Festuca viridula*[1] 1988	*Lupinus latifolius*[1] 1987	*Lupinus latifolius*[1] 1988
	----------	Stems m^{-2}	----------	
Season				
Early	8a	5a	47a	2a
Mid	23a	3a	48a	5a
Late	29b	5a	79b	6a
Intensity				
25%	32a	6a	76a	5a
50%	16b	4a	62a	6a
75%	10b	3a	36b	2a
Control	22a	9a	74a	4a
SE[2]	4.1	8.9	1.7	1.7

[1]Means within an item and year not sharing a common letter differ (P<0.05).
[2]SE is standard error of a mean.

Table 4. Percentage canopy cover of the major plants growing in Yakima Park during early July, 1986-1988. Data are means ± standard error, averaged over all defoliation treatments each year[1].

Species	1986	1987	1988
		%	
Festuca viridula	32±3.8	35±4.5	15±2.1
Lupinus latifolius	18±4.3	18±3.8	2±1.4
Potentilla flabellifolia	11±3.2	11±2.8	12±1.6
Polygonum bistortoides	5±1.5	5±1.4	3±1.1
Veronica cusickii	5±1.4	5±1.4	3±1.0

[1]Species means within a year do not differ between defoliation treatments(P>.05).

cover) was unaffected by either season or intensity of defoliation treatments applied. Plant canopy cover was measured prior to the early season defoliation treatments each year. Therefore, any differences in canopy cover would be due to treatments applied during the previous year. Lack of response of the 2 dominant species, *Festuca viridula* and *Lupinus latifolius*, is surprising in light of the large amount of phytomass removed from them by the 75% utilization treatments in 1986 and again in 1987. Little phytomass was actually removed from the other plant species by our defoliations. This defoliation pattern was consistent with actual ungulate grazing occurring on our 3 study meadows as measured by forage utilization transects. Del Moral et al. (1985) suggested that subalpine fescue plants interfere with establishment and growth of subordinate plants and that preferential grazing may alter the competition sufficiently for subordinates to increase. Lack of response to defoliation in subdominant species suggests that competition between dominant and subdominant species for site resources was largely unaltered. This could be explained by the relative harshness of our site, which would tend to favor niche specialization of the plants present (Del Moral et al. 1985). Response of subdominant plant species to defoliation treatments would not be expected under these conditions.

Defoliation increased total phytomass produced in 1987. Clipped 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. The literature contains reports of both increases (Stohlgren et al. 1989) and decreases in subalpine graminoid production following defoliation (Stohlgren et al. 1989, Leigh et al. 1991, Ram 1992). Stohlgren et al.(1989) noted that in the Sierra Nevada Mountains, the most xeric graminoid communities had increased production while the more mesic communities had decreased phytomass production following clipping. This prompted them to speculate that xeric subalpine communities are more tolerant of defoliation than are more mesic ones. Henderson (1974) considered the green fescue communities to be the most xeric of the subalpine types present on Mount Rainier. Their presence on south facing slopes within the eastern rain shadow of the mountain and on coarse textured soils, makes them xeric communities within a generally mesic climatic zone.

Intensive ungulate grazing, repeated over a period of years can reduce green fescue cover. For example, 50 years of heavy grazing by domestic sheep (*Ovis aries*) in the Wallowa Mountains of Oregon (Reid et al. 1980) reduced green fescue, which was replaced over time by forbs and other xeric grass (*Stipa lettermanii* Vas.). However, the relative proportion of this retrogression attributable to defoliation compared to trampling damage by sheep is unclear. Our data suggest that 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. Oksanen and Ranta (1992) suggested that environmental stress and defoliation stress on mountain vegetation evoke similar adaptations in plants and that vegetation gradients often ascribed to environmental changes with elevation can as easily be explained by zonal differences in herbivory.

Subalpine plant communities provide habitat for a diverse array of native animals, including large and small mammalian herbivores, as well as many species of phytophagous insects (Thilenius 1975). Elk were the only large herbivores active in our study meadows. 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 on our transects was attributable to insects, particularly grasshoppers (predominately *Camnula pellucida*) which reached high numbers by mid-summer each year. Our observations are consistent with those of Wielgolaski (1975) who reported that invertebrates were a larger proportion of total animal phytomass 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 plant species (White 1974). Ungulate use of dry meadow vegetation was rather light. *Festuca viridula* was the only plant which was appreciably utilized by elk. Other plants, such as *Polygonum bistoroides*, were grazed by elk to only a minor degree, predominantly when growing within a *Festuca viridula* clump. This observation is consistent with that of range managers who consider green fescue to be a very palatable forage for livestock (Sampson 1924, Johnson 1990).

Several authors (Ram 1992, Leigh et al. 1991) have noted that subalpine grasslands are sensitive to season of defoliation. Interestingly, season of defoliation had no effect on total phytomass production in 1987. Apparently, the 1987 growing season was sufficiently long to support regrowth of plants, even those defoliated in early September. Phytomass 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 phytomass production was apparently predominantly constrained by climatic factors, it is difficult to deduce if defoliation effects did not carry over into 1988 or if any such effects were not sufficiently large to express themselves above the overriding impacts of climate. The 1988 phytomass data do display a numerical trend of decreasing total production with increasing level of past defoliation. Perhaps energy reserves were 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 dominates 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 trait probably reflects a need to flower very quickly at the beginning of the growing season to allow sufficient time to mature seed. However, sexual reproduction is potentially vulnerable to previous year's grazing.

Flowering of both *Festuca viridula* and *Lupinus latifolius* was reduced by defoliation. Greatest reduction in number of flowering stems was observed for early, intense defoliation. These results are consistent with reports of others who noted that defoliation reduced flowering in both subalpine grasses (Leigh et al. 1991) and forbs (Galen 1990). Galen (1990) has speculated that reduced sexual plant reproduction caused by increased grazing pressure in mountain environments with decreasing elevation may provide a mechanism which sets the lower elevational limits for some alpine and subalpine plants.

Our reproductive stem counts suggest that defoliation may have a more detrimental impact upon sexual reproductive potential than on vegetative growth of subalpine plants. Population dynamics of alpine and subalpine plant communities have not been extensively studied. Similar to deserts, subalpine meadows are dominated by long-lived perennial plants which, presumably, do not require annual seedling recruitment in order to maintain the stand. Colonization of new sites by fescues and lupines is, however, dependent upon seed production. Experience with areas where plants have been lost due to site disturbances such as overgrazing or trampling (Frank and Del Moral 1986, Reid et al. 1980), is that bare areas are slow to regenerate. Recovery of disturbed areas may take centuries (Brown et al. 1978).

Conceptually, then, green fescue grasslands are both robust and at the same time extremely fragile. They are vegetatively robust in the sense that the individual plants which comprise them are able to withstand considerable levels of periodic defoliation without apparent loss of vigor. Yet they are reproductively fragile in that established plants, once lost, are unlikely to be replaced for many years. Similar conclusions have been expressed by Oksanen and Virtanen (1996), who maintain that herbivory and other natural perturbances are an evolutionary force producing disturbance tolerance in many arctic and alpine plant communities. They state "The traditional view of the Arctic as a stress-influenced ecosystem with high sensitivity to disturbance and low capacity of recovery is only partially true". Clearly, much more must be learned about plant community dynamics and reproduction strategies of important subalpine plants if the long-term effects of herbivory are to be predicted and damaged areas are to be successfully rehabilitated.

Conclusions and Specific Implications

Our data do not support the view that green fescue stands on Mount Rainier are particularly sensitive to defoliation. Plant community scale data (cover) were unaffected by repeated single yearly defoliation events with as high as 75% of standing phytomass removed. Although plant phytomass 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 the most lenient defoliation treatment (25% utilization) was substantially above levels of defoliation occurring naturally in the 3 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.

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