SUBALPINE GREEN FESCUE COMMMUNITY ECOOGY: REACTION TO DEFOLIATION

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Fescue grasslands are common in the subalpine zone of western North America (Kuchler 1964). 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). Green fescue (<u>Festuca viridula</u> Vasey) grasslands occur as mountain meadows or grassy slopes in the 1,000 to 2,000 m 3300 to 6700 ft) elevation zone throughout the western mountain ranges from British Columbia and Alberta south to central California and Colorado (Hitchcock and Chase 1971). Green fescue dominates these communities and may form almost pure stands (Pickford and Reid 1940, Johnson 1990). Although few successional studies have been conducted, it is generally believed that green fescue together with broadleaf lupine (<u>Lupinus latifolious</u> Agardh.) are late seral or climax species (Henderson 1974, Franklin and Dyrness 1988) and that high amounts of other forbs is a sign of low seral status (Reid 1941). For example, fifty years of heavy grazing by sheep in the Wallowa Mountains (Reid et al. 1980), reduced green fescue, which was replaced over time by forbs and other xeric grass (<u>Stipa lettermanii</u> Vas.). The relative proportion of this retrogression attributable to defoliation compared to trampling damage by sheep is unclear.

Subalpine plant communities provide habitat for a diverse array of native animals, including both large and small mammalian herbivores, as well as many species of herbivorous insects (Thilenius 1975). Subalpine grasslands in the Rocky Mountains of the United States and Canada have traditionally been summer foraging areas of deer (<u>Odocoileus hemionus</u>), elk (<u>Cervus canadensus</u>), mountain goats (<u>Oreamnos americanus</u>), and bighorn sheep (<u>Ovis canadensis</u>), as well as domestic sheep (<u>Ovis aries</u>). Green fescue grasslands are relatively productive and palatable to livestock compared to other mountain vegetation. They were historically a major source of summer grazing for open banded sheep 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 populations using mountain summer ranges have increased in many areas of Oregon and Washington as a result of land management practices at lower elevations (Cooper 1987). In addition, elk and mountain goats have been introduced into areas of the Cascades which, arguably, have not been part of their historical range (Pfitsch 1981). Increasing summer use of high elevation meadows by elk and mountain goats is raising concern about impacts upon subalpine vegetation in Mount Rainier and Olympic National Parks. The ability of plants in subalpine grasslands of the Cascades to tolerate increased defoliation by ungulates is largely unknown. Vegetation monitoring is greatly hampered by lack of a diagnostic understanding of plant community response to defoliation.

Our study was one facet of a larger study conducted by the United States National Park Service to examine the extent and impacts of elk grazing in Mount Rainier National Park. Our objectives were:

(1) to determine the degree of elk grazing that was actually occurring on subalpine green fescue grasslands of Mount Rainier.

(2) to examine shifts in a the structure (canopy cover) and productivity of a green fescue grassland community attributable to known levels and seasons of defoliation.

METHODS

Study Area

Plant names used follow Garrison et al. (1976). Three green fescue meadows (Yakima Park, Bear Park, and White River Park) located on the east side of Mount Rainier at elevations of 1750 to 1920 m (5800 to 6400 ft.) were used in this study. They are representative of the Subalpine Meadow Vegetation Zone as described by Henderson (1974), which covers approximately 10,000 hectares (25,000 acres) of Mount Rainier National Park's 95,350 hectares (236,000 acres). This grassland is characterized by dominance of green fescue on relatively dry, well-drained sites. Other major plant species include broadleaf lupine, Potentilla flabellifolia Hook.(fanleaf cinquefoil), Polygonum bistortoides Pursh (American bistort), Veronica cusickii Gray (Cusick speedwell), Luzula sp. (woodrush), 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.).

Annual precipitation is approximately 3000 mm (118 inches), which occurs mostly as winter snow (Henderson 1974). Snow accumulation usually begins in mid-October to mid-November and remains until June or July. Maximum annual snowpack varies from 250 cm to over 760 cm (8 to 25 ft.) and occurs in March through April. Summer precipitation is generally less than 25 cm (10 inches.) Annual air temperatures average only 3.4 °C (38 °F), with yearly high temperatures of around 30 °C (86 °F) 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 three-year period. Diurnal temperature fluctuation during the growing season can also be large with differences between day and night temperatures often exceeding 26 °C (80 °F).

A standard U.S. Weather Service rain gauge and a recording hygrothermograph 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 - 15 September 1986 and 1 July 1987 - 13 September 1987) was 20 mm (0.8 inches) in 1986 and 71 mm (2.8 inches) in 1987. Night temperatures frequently were below 4°C (39^0F) while afternoon temperatures rarely reached 27°C (80°F). Dew formed most nights, but humidity generally fell to below 50% by late afternoon. 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 were above freezing. 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).

Actual levels of Defoliation

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 one of 6 utilization classes; 0, 1-10, 11-25, 26-50, 51-75, or 76-100% of current year's herbage removed by grazers. Surveys were conducted in mid-growing season (August) of 1986 and 1987.

Consumption of lupine, Potentilla, Veronica, and Luzula by herbivores was relatively low (Figures 1 and 2). Generally, fewer than half of these plants showed signs of any defoliation. Grazed plants typically had less than 10% of their weight removed. Although over half of the Polygonum plants examined had been grazed, less than 15% of total biomass was removed. Only 42% of the green fescue plants

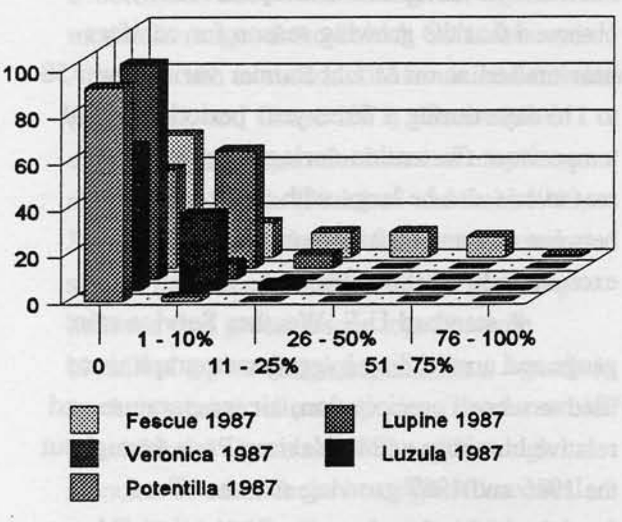

Figure 1. Percent of plants within each of 6 utilization classes. Classes are based upon % of current growth removed by herbivores. Data are average of 3 meadows.

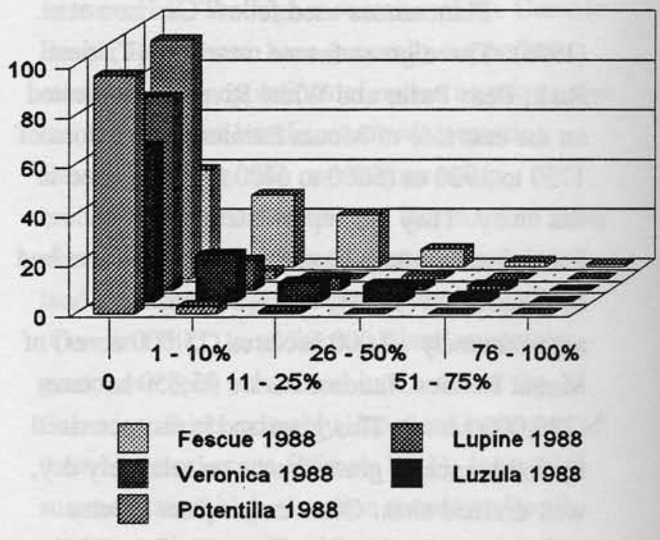

Figure 2. Percent of plants within each of 6 utilization classes. Classes are based upon % of current growth removed by herbivores. Data are average of 3 meadows.

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 their current season's growth removed. 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 Study

Effects of known levels of defoliation on plant community structure and productivity were studied at Yakima Park. Three replications of all combinations of three defoliation times (early, mid, and late growing season) and three intensities of defoliation (25, 50, and 75% of plant weight removed) plus undefoliated control plots were applied to 3m x 3m plots. Defoliated 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. Plots were clipped to remove 0, 25, 50, or 75% of current aboveground plant biomass, based upon experience gained from a preliminary clipping study adjacent to the plots. Large herbivores were excluded from experimental plots by electrified fencing. 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 1988, from twenty 10-point frames (Sharrow and Tober 1979) per plot. Number of reproductive stems of green fescue and lupine were counted within twenty 10x20 cm quadrats per plot in early September 1986 and 1987. Total aboveground herbage was estimated at the end of the 1987 and 1988 growing seasons using a single probe electronic capacitance meter (Vickery and Nicole 1982). Herbage at the end of the 1986 growing season was not measured due to early snowfall which prevented field sampling. Data were analyzed each year by Analysis of Variance as a factorial arrangement of treatments within a completely randomixed design with three replications.

RESULTS

Season by defoliation intensity interactions were not significant ($P < 0.05$) for any parameter measured, therefore, data interpretation centers around main effects of season and intensity.

Vegetation cover at Yakima Park prior to application of defoliation treatments in mid-July 1986 was 40% green fescue, 23% lupine, 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 growth at the time of defoliation. Therefore, herbage removed by defoliation treatments varied seasonally as plants grew. Early season treatments removed approximately 350 kg/ha less herbage than did mid and late season defoliations which were essentially equivalent. Average herbage removed was approximately 410, 930, and 2220 kg/ha for 25%, 50%, and 75% defoliation treatments, respectively. Material collected from the 1986 mid-season defoliation was hand sorted into its component species. Similar to actual levels of use measured on utilization transects, approximately 82 to 94% of herbage removed by clipping was green fescue and lupine under all defoliation intensities. Weight removed from

Potentilla flabellifolia and other low growing perennial forbs increased from 7 to 18% of herbage removed as defoliation intensity increased from 25 to 75% of herbage present.

Total herbage production in 1987 did not

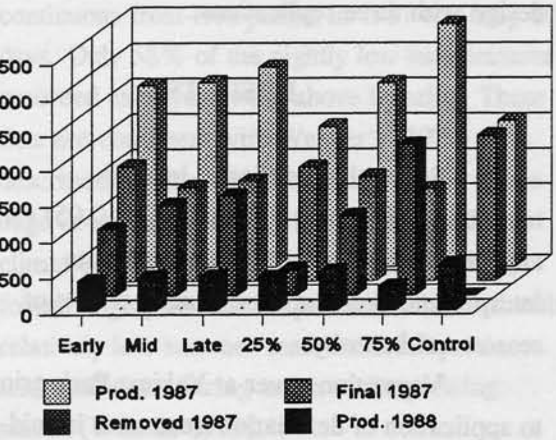

Figure 3. Herbage mass (kg/ha) under early-, mid-, and late seasons of defoliation to remove 25%, 50%, and 75% of current year's growth in Yakima Park.

vary with season of defoliation (Figire 3) in either 1987 or 1988. Annual production from 25% defoliation treatments was similar to unclipped control plots. Total herbage production increased by 74% as defoliation increased from 25 to 75% of standing weight in 1987. Herbage 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, herbage production in 1988 was only one fifth that observed in 1987.

Like plant production, sexual reproduction of the two major plant species in Yakima Park (Figure 4) was relatively low and did not differ among defoliation treatments in

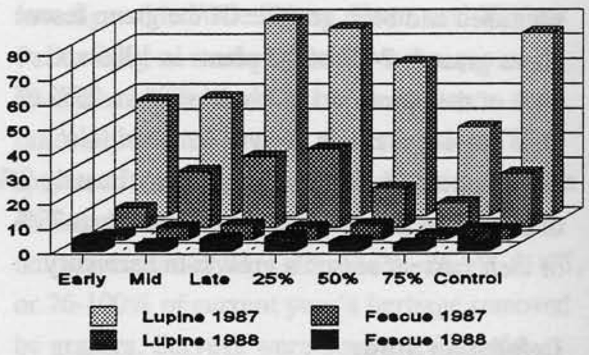

Figure 4. Number of flowering stems per m^2 under early-, mid-, and late season defoliation which removed 25%, 50%, or 75% of current year's herbage in Yakima Park.

1988. Number of reproductive stems of both green fescue and lupine in 1987 tended to decline with increasing defoliation above 25%. However, differences were not always statistically significant at $p < 0.05$. Both plants were particularly sensitive to early season defoliation, which reduced reproductive stems of green fescue by 74% and lupine by 37%.

Average total plant canopy cover was similar in 1986 and 1987 (Table 1). 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. No differences in plant canopy cover could be attributed to either time or intensity of defoliation.

DISCUSSION

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 sunlight 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 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 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 species (ie. Festuca idahoensis, F. thurberi) and adaptive strategies in common.

Plant community structure (as indicated by canopy 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. Any differences in canopy cover would be due to treatments applied during the previous year. Lack of response of the two dominant species, green fescue and lupine, is surprising in light of the large amount of herbage removed from them by the 75% utilization treatments in 1986 and 1987. Little herbage was actually removed from the other plant species by our defoliations. This defoliation pattern was consistent with actual ungulate grazing occurring on our 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 herbage 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 plant 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, on coarse textured soils makes them xeric communities within a generally mesic climatic zone.

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) suggest that environmental stress and defoliation stress on mountain vegetation evokes 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.

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 which reached high population numbers by midsummer each year. Our observations are consistent with those of Wielgolaski (1975) who reported that invertebrates were a larger proportion of total animal mass 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. Green fescue was the only plant which displayed appreciable utilization by elk. Other plants, such as Polygonum bistoroides, were grazed by elk to only a minor degree, predominately when growing together with a green fescue plant. This observation is consistent with those of range managers who consider green fescue to be a very palatable forage for livestock (Sampson 1924, Johnson 1990).

Several authors (Ram 1991, Leigh et al. 1991) have noted that subalpine grasslands are sensitive to season of defoliation. Interestingly, season of defoliation had no effect on total herbage production in 1987. Apparently, the 1987 growing season was sufficiently long to support regrowth of plants, even those defoliated in early September. Herbage 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 herbage production was apparently predominately constrained by climatic factors, it is difficult to deduce if defoliation effects did not carryover into 1988 or if any such effects were not sufficiently large to express themselves above the overriding impacts of climate. The 1988 production data do display a numerical trend of decreasing total production with increasing levels 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 green fescue and lupine 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 data suggest that defoliation may have a more detrimental impact upon sexual reproductive potential than it does 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 recruitment in order to maintain the stand. Colonization of new sites by fescue and lupine 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, 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. 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 if damaged areas are to be successfully rehabilitated.

ACKNOWLEDGMENTS

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Table 1. Plant canopy cover (%) from Yakima Park plots defoliated in early (E), mid (M), or later season (L) to levels of 0 (C), 25% (1), 50% (2), or 75% (3) biomass removal. Means in a column for each plant not sharing a common letter differ ($P < .05$).

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

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