Biomass allocation in a subantarctic clonal plant (*Acaena magellanica*) under grazing by introduced reindeer

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Abstract: Biomass allocation and growth by the clonal plant *Acaena magellanica* were characterized for three populations grazed by introduced reindeer on the subantarctic island of South Georgia. Annual growth markers (internode lengths) were used to divide each rhizome into current year's shoots, one-year-old and two-year-old rhizome segments. Total dry weights were significantly smaller in grazed than in ungrazed populations. Leaf biomass of current year's shoots was very much lower in grazed shoots. Rhizome length and number of leaves were less affected than dry weight by grazing, and the reindeer grazing thus seems to mainly influence biomass accumulation rather than morphology in *Acaena*. Interactions with *Festuca contracta* in both grazed and ungrazed areas were also studied in a two-year competition experiment. No apparent release of soil resources (as measured by an increase in plant growth) was apparent in plots where *Festuca* was removed, but the current year's shoots of *Acaena* were smaller and more numerous in these plots than in controls, especially in the ungrazed area.

Introduction

Clonal, rhizomatous plants are a common and often dominant plant group in subarctic/arctic areas (Billings & Mooney 1968, Bliss 1971, Callaghan 1989), as well as in subantarctic areas (Smith & Walton 1975). A specific feature of clonal plants growing in these seasonal environments is the formation of annual growth markers, analogous to annual growth rings in trees (Callaghan & Collins 1976). The types of annual markers may differ: *Lycopodium annotinum* L. and *Polytrichum commune* Hedw., for instance, produce compressed microphylls and smaller leaves, respectively, at the beginning and end of each growing season (Callaghan *et al.* 1978, Callaghan 1980),*Hylocomium splendens* (Hedw.) B.S.G. typically grows as a layered mat in subarctic areas with each layer representing one year's growth due to winter conditions damaging the apex of the shoots (Callaghan *et al.* 1978), whilst in the subantarctic *Acaena magellanica* (Lam.) Vahl produces shorter internodes at the beginning and end of each growing season (Walton 1976). These annual markers may persist for ten years or more in some species due to a low decomposition rate in the tundra, and can thus be used as historical records of growth (Callaghan & Collins 1976, Havström *et al.* 1995).

Callaghan (1989) argues that abiotic factors, such as short cool summers, strong winds and infertile soils, provide the major selection pressures for clonal plants in tundra environments. However, herbivores may also have a large impact on plant community structure, and may act as a major selection pressure on clonal plants, in both subarctic

(Andersson & Jonasson 1986, Moen *et al.* 1993, Oksanen & Moen 1994) and subantarctic areas (Leader-Williams 1988, Lawrence & McClintock 1989). This may be especially important in subantarctic areas where all the vertebrate herbivores are introduced species. Many studies have examined the growth and morphology of clonal plants under a variety of environmental conditions (see Hutchings & Mogie 1990 and references therein), but none to our knowledge have compared grazed and ungrazed, non-graminoid, clonal plants by using annual markers. The aim of this study was to quantify long-term grazing effects on biomass and growth of several populations of *Acaena magellanica* using annual markers to divide the rhizome into yearly increments.

Materials and methods

Study site

South Georgia is a mountainous, subantarctic island (53°56'–54°55'S, 34°45'–38°15'W) over half of which is covered with permanent ice and snow, confining the vegetation mainly to coastal areas. The vascular flora is impoverished with only 26 native and an additional 30 or so introduced species, most of which have a very limited distribution (Walton & Smith 1973, Greene & Walton 1975).

In 1925, seven reindeer were introduced to Husvik Harbour on South Georgia by Norwegian whalers. The animals (three males and four females) were brought from Norway to provide sport and additional meat for the personnel at the

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whaling stations in Stromness Bay. The introduction was successful, and the herd had increased to c. 800 animals when last counted in 1973 (Leader-Williams 1988). The herd has continued to expand its range (Moen & MacAlister 1994), and the reindeer have caused significant impacts on the plant communities (Leader-Williams et al. 1987).

Study species

The genus *Acaena* (Rosaceae) is largely restricted to the Southern Hemisphere, and *Acaena magellanica* is found on the southern part of South America and several cool temperate and subantarctic islands (Walton 1979a). *A. magellanica* (hereafter called *Acaena*) is a semi-decumbent, suffruticose rhizomatous perennial, with deciduous pinnate leaves, and flowers grouped in terminal capitula carried above the leafy canopy (Walton 1976). It is one of the four or five species that may form closed swards on South Georgia, and is tolerant of a wide variety of edaphic conditions, occupying a similar niche to ericacaeous dwarf-shrubs in Arctic vegetation (Walton 1976). Characteristics of ungrazed populations of *Acaena* on South Georgia have been published (Walton 1976, 1977a, 1977b, 1979b). However, due to its high leaf nitrogen content and easy digestibility *Acaena* is a preferred food species during the summer for the introduced reindeer (Leader-Williams 1988) and introduced rats which may consume large quantities in near-shore locations (Pye & Bonner 1980, Moen personal observation), but no data characterizing grazed populations exists. Due to reindeer grazing, flowering shoots are almost totally absent in grazed plant communities, and this study will thus deal exclusively with vegetative shoots.

The rhizome of *Acaena* has a sympodial growth form with branching from leaf axils. Internode length is a function of the growth rate, and the winter period is clearly defined on the rhizomes by very short internodes (usually <1 mm as compared to 2–10 mm in summer). The species is effectively deciduous, but leaf abscission does not occur, and the leaf laminae usually decay *in situ*. Petioles and leaf scars can usually be seen even on rhizome parts several years old until the epidermis has decayed. The short internodes were used as markers to delimit each year's growth (Walton 1976). In the following, "shoots" will be used for current year's growth including both rhizomes and photosynthetic leaves, while "rhizomes" will be used for older parts of the clone. "Rhizome systems" will denote the excavated parts of the clone.

Sampling of rhizomes

Rhizome systems of *Acaena* were collected around the Stromness Bay area on South Georgia between 16–26 February 1993. Three different habitats were chosen for comparisons between grazed and ungrazed populations:

a) Fellfield: The gravel flood plain in the lower valley of Husdal. Vegetation consisted mostly of *Festuca contracta* T. Kirk and *Acaena magellanica*, with scattered *Phleum alpinum* L., *Rostkovia magellanica* (Lam.) Hook. f. and a variety of moss species. Rhizome systems from a reindeer exclosure erected in March 1974 (Kightley & Smith 1976, Leader-Williams et al. 1987), and <10 m from the sampled grazed rhizomes, were chosen as ungrazed controls.

b) Bog: The north-facing side of Husdal with a thick layer of wet peat (>5 m thick). Vegetation consisted of *Festuca contracta, Rostkovia magellanica, Acaena magellanica* and an extensive moss cover of *Tortula robusta* Hook. et Grev. together with *Sanionia uncinata* (Hedw.) Loeske, *Riccardia (=Aneura) georgiensis* (Steph.) Hassel and *Dicranoloma hariotii* (C. Muell.) Par. Rhizome systems from a small unnamed bay between Enten Bay and Carlita Bay c. 8 km from Husdal (Moen & MacAlister 1994) were chosen as ungrazed controls since no similar ungrazed areas could be found any closer.

c) Pioneer: Scattered plants growing in gravel in the abandoned whaling station in Husvik. Plants protected from the reindeer by fallen debris etc. in the whaling station were chosen as ungrazed controls.

In each habitat, a plot of c. 2 × 2 m was marked and a current year's vegetative shoot of *Acaena* was randomly chosen within that plot. The rhizome system, starting with the current year's shoot, was excavated until parts of the rhizome without an epidermis layer were found. The process was repeated a number of times in each habitat. The only exceptions were the exclosure population where current year's shoots had to be randomly chosen from a smaller plot due to limited area of the exclosure, and the ungrazed pioneer plants where individuals of similar size as the grazed samples were chosen from those ungrazed plants that could be found.

Each rhizome system was centripetally divided up into year classes (Bell 1991:284) as far as it was possible to accurately determine the age of the rhizome. The age-classes will hereafter be called "C" for current year's shoots, "C+1" for one-year-old segments etc. However, only current year's shoots were sampled from the pioneer plants as the heavily grazed rhizomes had a club-shaped form (resembling pollarded trees) and the internodes for previous years' growth could not be accurately defined. In all grazed populations, only year classes with no obvious grazing signs were analysed: e.g. current year's shoots that were damaged and where the number of internodes could not be accurately measured were not included except as a marker for the next year class. Each current year's shoot was divided into leaves and rhizomes (except from the grazed fellfield population where leaves and rhizomes were weighed as a unit), the number of leaves was counted, and the length of the internodes was measured. Only the rhizome measurements were taken from older segments, together with the number of leaf scars. All leaves

and rhizomes were dried at 50°C for three days and weighed. The branching angle was also measured before the side branches were cut from the main rhizome. Data on internode lengths, branching angles and branching potential will be used in a future computer simulation of growth.

All equivalent shoot parts of the same year-class from the same population were used as replicates in the analyses. Ideally the analyses should have been done on a genet basis, but it proved impossible to excavate entire rhizome systems in any of the populations. Table I shows the sample sizes for all populations and measurements. All comparisons were by student t-tests.

Interactions with Festuca

In February 1991, a removal experiment designed to study the interaction of and competition between *Acaena* and *Festuca contracta* was initiated. Twenty 50 × 50 cm plots were marked in a grazed *Festuca-Acaena* grassland (Husdal), and twenty on an ungrazed island in Stromness Bay (Grass Island). In each habitat, *Festuca* was removed by hand from 10 randomly chosen plots and the other 10 were left as untreated controls. In January–February 1993, the above-ground biomass (current year's shoots for *Acaena* including both rhizomes and leaves) from the central part of each plot (40 × 40 cm) was harvested. Two plots from Husdal had to be omitted as one could not be found (missing corner pegs) and one was extremely trampled by reindeer. The *Acaena* shoots were dried at 80°C for 1 h and weighed (leaves and rhizomes not separated).

The data were tested by two-way ANOVA using Habitat

Fig. 1. Total shoot weight (mean±SE) of current year's shoots in three different habitats. G=grazed, U=ungrazed.
*** = *P*<0.0001 (t-test).

(grazed vs. ungrazed) and Treatment (hand-weeded vs. controls) as fixed factors. The data were examined for deviations from the assumptions of the test by checking the residuals, and an appropriate transformation was done (log-transformation for total weight and number of shoots, while the individual weights were square-root transformed).

Results

Biomass and growth

Total *Acaena* shoot weight (rhizomes and leaves) of current year's shoots from grazed populations were much smaller than shoots from ungrazed populations in all three habitats (Fig. 1). It is noteworthy that the grazed fellfield shoots had only *c.* 4% of the dry weight of the ungrazed shoots even though the plants were separated only by a few metres. The proportional dry matter allocation to rhizomes and leaves did not differ between the bog populations, while grazed pioneer shoots allocated significantly more to rhizomes than the ungrazed shoots (Table II). The ungrazed fellfield shoots had also a relatively high allocation to rhizomes.

Rhizome weight differed significantly in both current year's shoots and the two older age-classes between the bog populations (Fig. 2). The heaviest rhizomes occurred in the

Table 1. Sample sizes for all populations, age-classes and measurements. - = no measurements were taken. C = current year's segments of the rhizomes, C+1 = one-year-old segments, C+2 = two-year-old segments.

Population and age-class	Dry weight	Shoot length	No. of leaves
Fellfield, ungrazed			
C	49	49	49
C+1	11	11	11
C+2	-	-	-
Fellfield, grazed			
C	85	-	87
C+1	32	26	30
C+2	9	9	9
Bog, ungrazed			
C	59	59	59
C+1	19	19	14
C+2	3	3	1
Bog, grazed			
C	27	25	25
C+1	15	16	18
C+2	6	6	5
Pioneer, ungrazed			
C	61	61	61
Pioneer, grazed			
C	59	58	57

Table II. Percentage allocation of dry weight to rhizomes or leaves for current year's shoots (mean and se). - = no data available, ns = non-significant, *** =*P*<0.0001 (Student's t-test on arcsine-transformed proportions).

Populations	Grazed				Ungrazed		
	Rhiz.	Leaves	SE		Rhiz.	Leaves	SE
Fellfield	-	-			23.9	76.1	1.7
Bog	18.6	81.4	2.6	ns	17.0	83.0	1.3
Pioneer	28.0	72.0	1.8	***	17.4	82.6	0.9
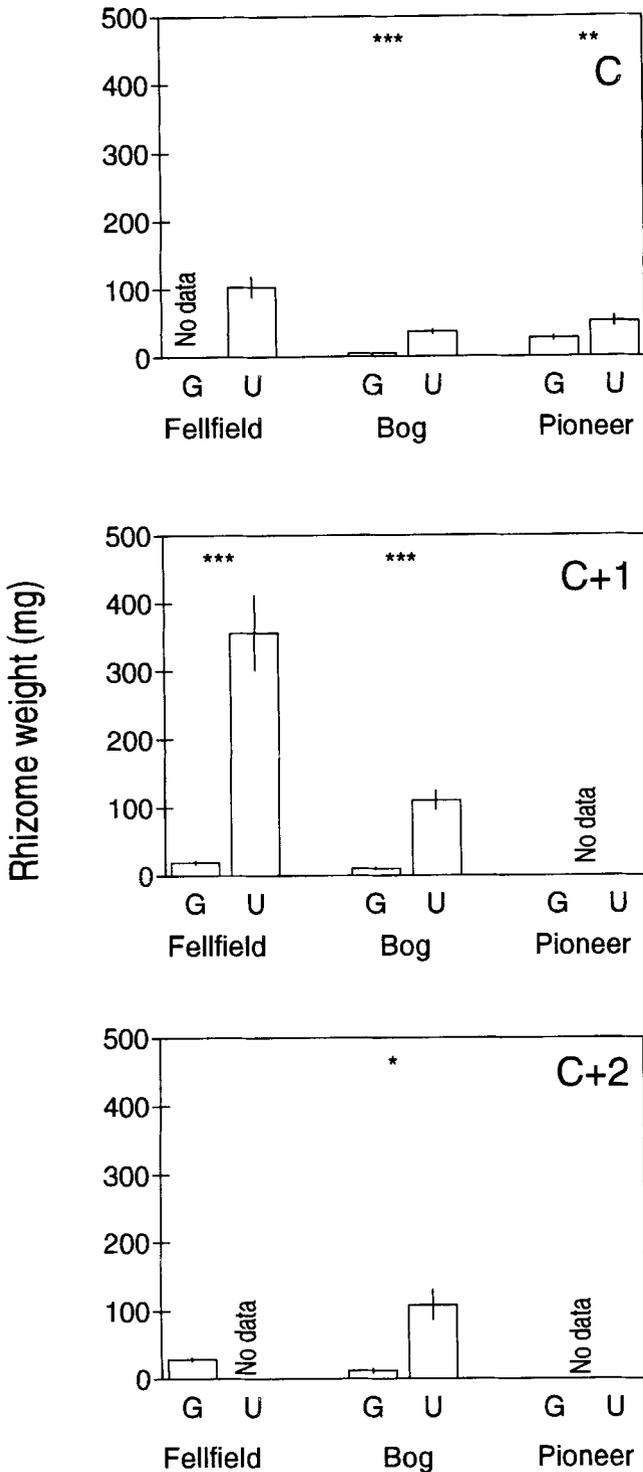
Fig. 2. Rhizome weight (mean±SE) in three habitats for three age-class segments. G=grazed, U=ungrazed. * = P<0.05, ** = P <0.01, *** = P <0.0001 (t-test).

C+1 segment of the ungrazed fellfield shoots.

The total rhizome length did not differ in current year's shoots in any habitat, but was significantly higher in the ungrazed C+1 segments in both the fellfield and the bog
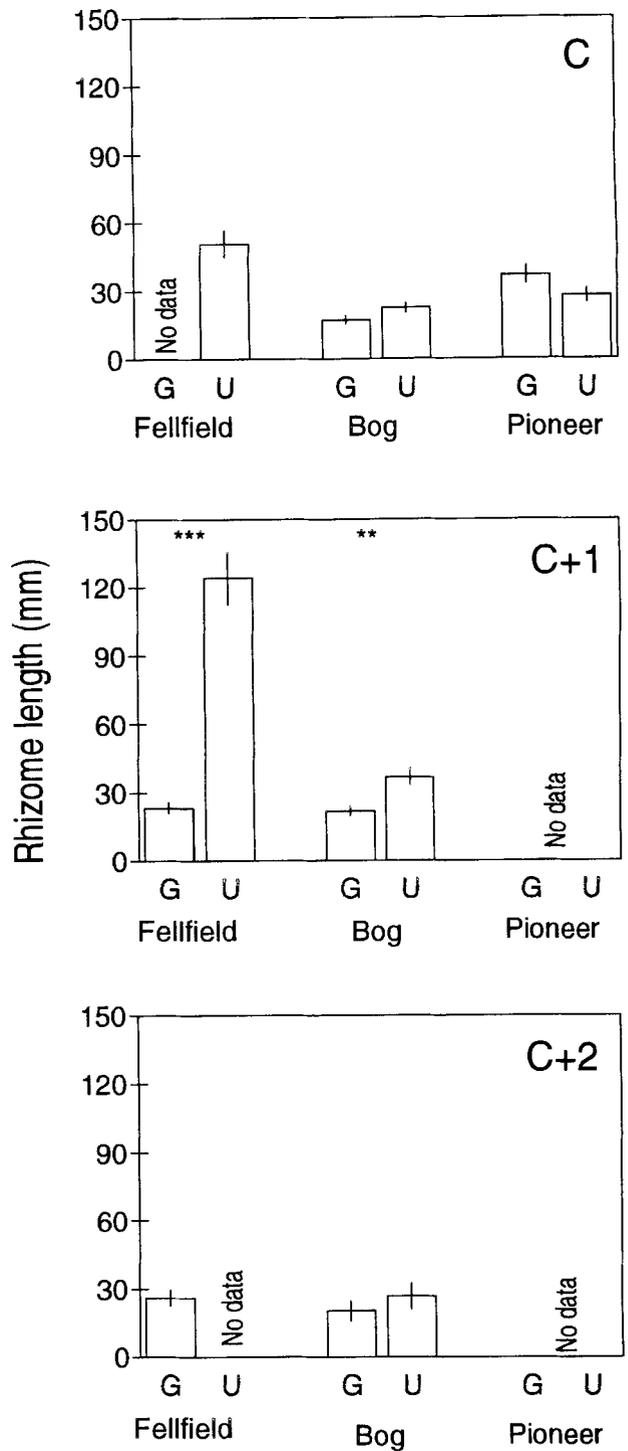
Fig. 3. Rhizome length (mean±se) in three habitats for three age-class segments. G=grazed, U=ungrazed. ** = P <0.01, *** = P <0.0001 (t-test).

habitat (Fig. 3).

The number of leaves was significantly lower in ungrazed current year's shoots in the pioneer habitat, while the number of leaf scars was significantly higher in ungrazed C+1
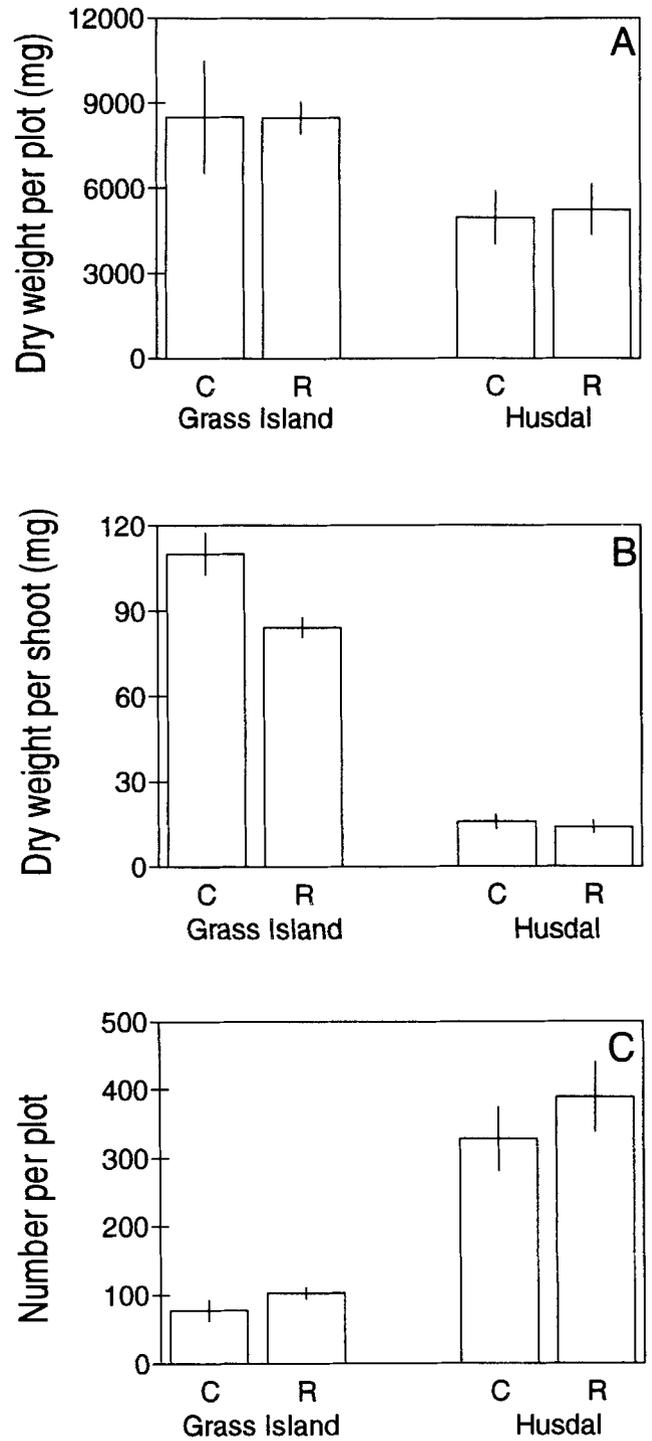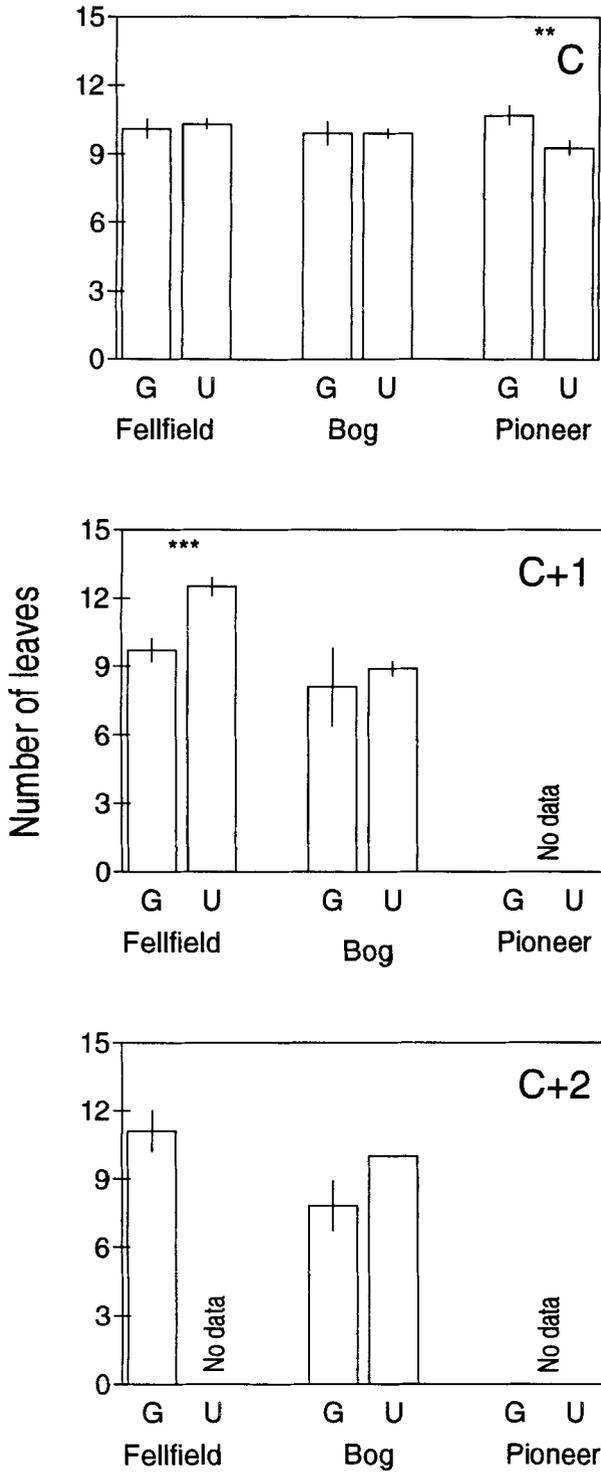
Fig. 4. Number of leaves (or leaf scars for C+1 and C+2 segments; mean±se) in three habitats for three age-class segments. G=grazed, U=ungrazed. ** = *P* <0.01, *** = *P* <0.0001 (t-test).

Fig. 5. Mean±se for current year's shoots of *Acaena* in Husdal (grazed) and Grass Island (ungrazed). C=Controls, R=*Festuca* removed. See ANOVA test in Table III. a. Total dry weight per plot (mean ± se). b. Dry weight per individual shoot (mean ± se). c. Number of shoots per plot (mean ± se).

Table III. Interactions with *Festuca contracta*. Analyses of variance using Habitat (grazed vs. ungrazed) and Treatment (*Festuca* hand-weeded vs. controls) as fixed factors. Total weights and numbers of shoots were log-transformed, while individual weights were square-root transformed.

Source	SS	df	F	p
A. Total weight				
Habitat	0.51	1	13.14	0.001
Treatment	0.02	1	0.60	0.44
H x T	0.00	1	0.01	0.91
Error	1.33	34		
B. Individual weight				
Habitat	341.92	1	470.34	<0.0001
Treatment	5.26	1	7.24	0.01
H X T	2.71	1	3.72	0.06
Error	24.72	34		
C. Number of shoots				
Habitat	3.47	1	107.91	<0.0001
Treatment	0.16	1	4.83	0.04
H x T	0.01	1	0.46	0.50
Error	1.09	34		

Table IV. Comparisons of ungrazed current year's shoots from this study with data from Walton (1976). Mean values (± se) are shown.

Population	Dry weight (mg)	No. of leaves
Walton (1976)		
Moist peat	803±68	14.0±0.2
Dry scree	649±38	12.8±0.2
Pioneer	1916±148	16.0±0.3
Bog	366±26	12.4±0.2
This study		
Fellfield	389.4±33.3	10.3±0.2
Bog	223.4±15.4	9.9±0.2
Pioneer	268.2±35.0	9.3±0.3

segments in the fellfield habitat (Fig. 4).

Interactions with Festuca

Removal of *Festuca contracta* did not have any effect on total dry weight per plot of current year's shoots of *Acaena* in either of the habitats (Fig. 5a, Table III). The control plots in Husdal had only approximately half of the biomass of the ungrazed plots on Grass Island, and the mean individual weight of the shoots was much smaller in Husdal but the number per plot was higher (Fig. 5b & c).

However, the morphology seemed to change as a response to the removal treatment, especially on the ungrazed Grass Island. *Acaena* shoots in hand-weeded plots were smaller and more numerous than in the control plots even though total biomass was very similar (Fig. 5, Table III). The same trend was seen in Husdal although the differences were smaller.

Discussion

Reindeer grazing had a profound effect on the *Acaena* populations as was expected: most of the measured characteristics were significantly smaller for grazed shoots than for ungrazed ones. Continuous defoliation will deplete the resource reserve of plants and thus decrease biomass production (Chapin 1980). Rhizome weight (Fig. 2) was also more affected than rhizome length (Fig. 3) in current year's shoots and C+2 segments. However, the proportional allocation to leaves and rhizomes was similar, at least for the bog populations (Table II). The reindeer grazing thus reduces biomass accumulation in both rhizomes and leaves, while relative allocation of resources and annual length

increments is less influenced.

Sometimes grazed shoots had initiated new side branches on older parts of the rhizome, indicating a reserve of dormant buds on the rhizome. The initation of side branches could be a response to broken apical dominance as has been shown for other clonal plants, e.g. *Carex bigelowii* Torr. (Jónsdóttir & Callaghan 1988), and *Lycopodium annotinum* (Svensson & Callaghan 1988). Other studies have also shown a substantial translocation of resources from physiologically integrated parts of the rhizomes to defoliated shoots (Pitelka & Ashmun 1985, Slade & Hutchings 1987, Jónsdóttir & Callaghan 1989, Marshall 1990). It is not known to what extent resources are translocated within rhizome systems of *Acaena*, but preliminary studies (Walton 1982) have shown that in ungrazed rhizome systems leaf bases are used for temporary carbohydrate storage and sideshoots are primarily dependent on the leaves subtending them. At least in the short term it appears that each current year's shoots acts as a relatively self-contained unit, retaining most of the carbohydrate produced. Older rhizome segments must eventually depend on carbohydrates from photosynthetic leaves in the youngest segment, and the use of annual segments as replicates, rather than entire rhizomes, is a limitation of this study. However, if each branch system of the rhizome is seen as an integrated physiological unit (*sensu* Watson & Caspar 1984), each unit would respond independently to the grazing and could thus be treated as replicates. This assumption appears to be supported by the limited ^{14}C translocation studies on *Acaena* (Walton 1982).

Walton (1976) investigated the biomass allocation in ungrazed *Acaena* rhizomes. The sampling was done in the Grytviken area (*c.* 18 km southeast of Husvik) in the austral summer of 1973/74. Four populations were studied: monospecific stands of *Acaena* on moist peat and dry scree, isolated plants on dry gravel in Grytviken whaling station, and scattered plants in a *Rostkovia-Tortula* mire. Comparisons with ungrazed current year's vegetative shoots in the present study show that his plants were larger and had a higher number of leaves (Table IV). This may be attributable in part to a later date (March) for the harvest, to what is believed to be a generally warmer and more protected local

climate around Grytviken than around Husdal in any year, to the variability in production between years which is evident in Fig. 3, and to the greater carbohydrate reserves which must accumulate in a favourable environment.

Interactions with Festuca

The lack of response in total dry weight per plot of *Acaena* shoots when *Festuca* was removed (Fig. 5), seems to show that, at least on a two year timescale, *Acaena* and *Festuca* do not show any detectable signs of competition for soil resources in these two habitats. An excavation of roots in an *Acaena-Festuca* grassland in Husdal showed that the two species have different rooting depths (Moen, personal observation) which could serve as a niche separation between the species: *Festuca* had very shallow roots, most of which were in the top 10 cm of soil, while *Acaena* rhizomes extended far deeper. Walton (1979a) recorded *Acaena* rhizomes throughout a peat profile to depths of up to 1.5 m.

However, the removal of neighbours caused a morphological response in *Acaena*, which also differed between the grazed and the ungrazed area. One explanation for the change in morphology may be that the removal of *Festuca* increased the amount of light reaching the ground, and thus changed the red/far-red ratio (Novoplansky *et al.* 1990, Schmitt & Wulff 1993). This ratio has been shown to be important in determining internode growth versus lateral bud growth in other clonal plants (Hutchings & Mogie 1990, Dong 1993). If a change in the red/far-red ratio induced lateral bud growth in *Acaena*, together with no apparent release of soil resources as indicated by the lack of response in total biomass, then a higher number of shoots using the same amount of resources would result in smaller individual shoots. The morphological response in the grazed plots was not of the same magnitude as in the ungrazed ones (Fig. 5), possibly because grazing had already induced bud growth in these rhizomes. Thus, the plants did not have the same potential for responding to neighbour removal. An alternative explanation for the morphological response is that in the process of removing the *Festuca*, the rhizomes of *Acaena* were damaged and this may have induced lateral bud growth. However, the removal was done very carefully, and no broken or damaged rhizomes were seen.

Acknowledgements

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