LEAF AND SHOOT DEMOGRAPHY OF AN ARCTIC STOLONIFEROUS GRASS, \textit{PUCCINELLIA PHRYGANODES}, IN RESPONSE TO GRAZING

D. R. BAZELY* AND R. L. JEFFERIES†

Department of Botany, University of Toronto, Toronto, Ontario, Canada M5S 1A1

SUMMARY

(1) Swards (\text{<} 2.5 \text{ cm in height}) of \textit{Puccinellia phryganodes} are heavily grazed by lesser snow geese (\textit{Chen caerulescens caerulescens}) on intertidal flats on the shores of Hudson Bay. This paper describes the morphological changes that account for the increased net primary production due to grazing.

(2) Demographic techniques were used in 1983 to monitor the births and deaths of leaves and shoots in grazed and ungrazed swards (exclosures) between mid-June (‘spring melt’) and early September (before ‘freeze-up’).

(3) Overall, the mean number of axillary shoots produced per main shoot of \textit{Puccinellia} was significantly higher in grazed plots (2.03) than that in ungrazed plots (1.47). Shoots remained alive beyond one growing season.

(4) There was no significant difference in the mean number of leaves produced per main shoot by plants from grazed and ungrazed swards. Leaf births per axillary shoot were significantly greater in grazed plots compared with ungrazed plots. Overall 64\% of all leaves produced between June and September were grazed or partially grazed.

(5) Within-season cumulative deaths were 6.9 and 6.0 leaves per main shoot and 2.2 and 1.1 leaves per axillary shoot, respectively, in grazed and ungrazed plots. Life expectancies for leaves exerted between June and early August were as follows: partially grazed leaves 24.9–30.2 days, ungrazed leaves in grazed plots 27.5–34.4 days, leaves in ungrazed plots 32.7–42.5 days. This indicates a rapid turnover of leaves in this arctic salt marsh. Leaves produced late in the season survived the winter but died in early summer of the following year.

(6) These results are compared with those of \textit{Carex subspathacea}, the other important forage species. In \textit{C. subspathacea} the greater net primary production in response to grazing is achieved by the growth of existing shoots and not by the production of new shoots.

INTRODUCTION

Herbivores have conspicuous effects on plant growth and form (McNaughton 1976, 1979a, b, 1983). The effects include a reduction in canopy height and increased tillering, leading to a prostrate, dense canopy that has been called a ‘grazing lawn’ (McNaughton 1984). Typically, grasses of grazed swards are smaller and consist of short-lived repeating, modular morphological units with intercalary meristems. Besides the stimulation of tillering in grasses as a result of grazing (Wade 1979; Gray & Scott 1980; Jones, Collett & Brown 1982; Parsons \textit{et al.} 1983; Ruess, McNaughton & Coughenour 1983; Belsky 1986), heavy grazing may increase the rate of leaf production as well (Grant, Barthram & Torvell 1981). The different growth responses of graminoid plants to grazing can be examined

* Present address: Edward Grey Institute of Field Ornithology, Department of Zoology, South Parks Road, Oxford OX1 3PS.
† Correspondence author.
using demographic methods to determine leaf and shoot turnover and survivorship of individual ramets.

*Puccinellia phryganodes* (Trin.) Scribn. & Merr., a stoloniferous grass, is widespread in arctic salt marshes, where it is a colonist of intertidal sediments and an important source of forage for lesser snow geese (*Chen caerulescens caerulescens* L.). At La Pérouse Bay, Manitoba (58°04'N, 94°03'W) on the shores of Hudson Bay, a breeding colony of approximately 7000 pairs of geese and 20000 goslings feed intensively on the graminoid plant communities of the salt-marsh flats from mid-June to mid-August, when the birds start their southward migration (Cooke *et al.* 1982). The geese consume up to 80% of the net above-ground primary production (NAPP), and grazing significantly increases NAPP (Cargill & Jefferies 1984). The increase reflects the response of the graminoid forage species to the addition of nutrients from goose faeces (Bazely & Jefferies 1985). The rapid growth response of the grass to available nutrients within the post-hatch period more than compensates for the adverse effects of defoliation on production (Sadul 1987). Increased biomass production and tillering as a result of nitrogen fertilization have also been recorded in *Eriophorum vaginatum* from Alaska (Shaver, Chapin & Gartner 1986) and in the East African sedge *Kylinda nervosa* (Ruесс, McNaughton & Coughenour 1983).

In this investigation, changes in the growth of shoots that enable *Puccinellia phryganodes* to achieve a significant increase in NAPP when grazed were determined. Using demographic techniques, we measured the production and turnover of shoots and leaves of *Puccinellia* in swards subjected to grazing, in which faeces accumulated, and in swards protected from grazing. The second objective of the study was to compare these results with those of the production and turnover of shoots of the sedge *Carex subspathacea* Wormsk., the other important graminoid species of the salt marsh (Kotanen & Jefferies 1987).

**MATERIALS AND METHODS**

*The site*

A description of the salt marsh and a summary of the La Pérouse Bay snow goose project have been presented elsewhere (Jefferies, Jensen & Abraham 1979; Cooke *et al.* 1982; Jefferies 1988a, b). Briefly, the inter-tidal flats at La Pérouse Bay are dominated by *Puccinellia phryganodes* and *Carex subspathacea*, a rhizomatous sedge. Dicotyledonous species present at low frequency include *Potentilla egedii* Wormsk., *Plantago maritima* L., *Ranunculus cymbalaria* Pursh. and *Stellaria humifusa* Rottb. The existence of the graminoid community in its present form is strongly dependent upon herbivory. Each year the geese crop the vegetation of the flats to a height of 2·5 cm or less. When exclosures were erected, rapid changes in the species composition of the sward occurred during successive seasons and the standing crop increased five-fold within two seasons (Bazely & Jefferies 1986).

*The growth habit of Puccinellia phryganodes*

This perennial grass is strongly stoloniferous and produces axillary and extra-axillary (infra-nodal) branches iteratively. Plants are low-growing and mat-forming. The sward on the tidal flats consists of an interwoven mat of shoots produced by different clones. Although plants grow vigorously, flowering is rare, particularly in grazed sites. Seed set has never been observed anywhere in the Arctic (Sørensen 1953; Dore & McNeill 1980).
TABLE 1. Locations of paired grazed and ungrazed plots (approximately 2 m apart) dominated by Puccinellia phryganodes, and the mean number of axillary shoots produced per main shoot of Puccinellia in each plot, from June to September 1983 at La Pérouse Bay, Manitoba. Not all shoots initially marked survived and \( n \) refers to intact main shoots at the end of the summer.

<table>
<thead>
<tr>
<th>Site in estuary</th>
<th>Quadrat code</th>
<th>Grazed plots</th>
<th>Ungrazed plots</th>
</tr>
</thead>
<tbody>
<tr>
<td>Island</td>
<td>G1</td>
<td>81</td>
<td>1.31 (72)</td>
</tr>
<tr>
<td>Tidal flats</td>
<td>G2</td>
<td>81</td>
<td>1.72 (36)</td>
</tr>
<tr>
<td>in south</td>
<td>G3</td>
<td>81</td>
<td>3.11 (36)</td>
</tr>
<tr>
<td>part of Bay</td>
<td>G4</td>
<td>81</td>
<td>—</td>
</tr>
<tr>
<td>Tidal flats</td>
<td>G5</td>
<td>81</td>
<td>1.81 (42)</td>
</tr>
<tr>
<td>in east part</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Bowden (1961) has reported that plants from eastern North America are sterile triploids (\( 2n = 21 \)), a finding confirmed by Sadul (1987).

**Demographic methods**

Three sites in La Pérouse Bay were selected for demographic studies of Puccinellia shoots in 1983. These were an island in the outer estuary of the Mast River on the southwest side of the Bay, and the tidal salt marsh in the southern and eastern parts of the Bay. Geese had been observed grazing intensively at all sites in 1982. The following plots were established in late June (end of ‘spring melt’): on the island, a pair of grazed and ungrazed plots; in the southern tidal flats, three paired grazed and ungrazed plots; and on the tidal flats in the eastern part of the Bay, a pair of grazed and ungrazed plots (Table 1). Paired plots were located approximately 2 m from each other in uniform swards of Puccinellia. Disturbance of the geese by observers across the entire marsh was minimal, because the sites were approximately 1.5 km apart.

The size of the plots was 0.5 m × 0.5 m. Ungrazed plots were enclosed with wire mesh (0.75 m × 0.75 m × 0.75 m), while the grazed plots were unprotected, thereby allowing the geese access to the plots. Individual shoots were located in each plot with the aid of a 0.5 m × 0.5 m metal quadrat, strung at 5-cm intervals with thin wire to form a grid of eighty-one intersections. The quadrat was placed over permanent corner pegs set into the ground, and the individual shoots were identified by a ring of coloured wire, pushed into the ground around the base of the Puccinellia shoot closest to each of the eighty-one cross-wire intersections on the first sample date. The loops did not interfere with grazing, because they sat flush with the sediment. Less than 0.5% of all loops could not be located during the season. In addition, leaves present at the start of the season and all new leaves on main and axillary shoots were marked with a distinctive pattern of small Indian ink dots applied with a fine brush. The technique enabled patterns of leaf development and senescence to be determined for each shoot during the summer of 1983.

The demography of leaves and shoots in all plots was recorded on five occasions: 25–29 June, 7–11 July, 19–22 July, 4–10 August and 30 August–1 September 1983, except for a pair of grazed and ungrazed plots (G, UG 4; Table 1) where no measurements were made during early August. As a consequence, data from these plots were excluded from the
analyses of the production of axillary shoots and of cumulative births and deaths of leaves, because unrecorded demographic events between 12 July and 30 August 1983 may have led to biased cumulative values. The mean intervals between the midpoints of all sample dates for the remainder of the plots were between 7.5 and 21 days. On each sampling occasion, the observations on all plots took 2–6 days to complete. Leaves could not be marked when wet, and the presence of polar bears also restricted sampling in August. Existing leaves and shoots were identified, and new leaves and branch shoots marked. The condition of all leaves, whether alive, partially grazed, missing, or dead, was recorded on each occasion.

The survival of leaves and shoots that were marked in September 1983 and leaves that were produced between September 1983 and June 1984 were recorded in June 1984, immediately after the spring melt.

Statistical analysis of data

In some analyses, data from the first sampling in 1983 have been excluded, because the ages of leaves and shoots could not be determined accurately. Statistical comparisons of births and deaths of leaves and shoots in grazed and ungrazed plots were based on cumulative births and deaths for each pair of plots, unless otherwise stated. Analyses of the number of leaves produced per shoot and the number of leaf deaths per shoot were important exceptions; these were based on twenty randomly selected shoots per plot. The truncation of sample size was necessary in order to avoid unequal sample sizes from each cohort. All data passed the $F_{\text{max}}$ test for the homogeneity of variance (Kirk 1982).

Expected leaf lifespans and grazing schedules during the field season were calculated from the survivorship of marked leaves produced between June and early August. These leaves failed to survive beyond the end of the growing season. Because the survivorship of leaves differed between plots subject to the same treatment, the results for each plot were analysed separately. Although the dates of births, deaths and grazing of individual leaves occurred at unknown times within each sampling interval, values were adjusted by assuming all events occurred at the midpoint of the appropriate interval. To obtain large enough samples for the estimation of lifespans, survivorship data were pooled for cohorts of leaves produced between June and early August for each plot. This approach is valid only if the populations from each cohort are stationary (i.e., the populations have a stable age distribution and population numbers do not differ appreciably between cohorts) (Pielou 1969). This assumption is approximately true for leaf lifespans over this period.

Paired $t$-tests or analyses of variance (ANOVA) based on a split-plot design were used to make statistical comparisons of the demographic data of leaves and shoots from paired grazed and ungrazed plots. Comparisons between paired plots constitute an example of pseudoreplication, where the effects of site and treatment may be confounded. As mentioned earlier, the paired plots were within approximately 2 m of each other. At each site the sward was homogeneous and there were no apparent differences between plots at the start of the study.

RESULTS

Production of axillary tillers

In grazed plots in 1983 a total of 613 axillary shoots were produced by 324 main shoots of Puccinellia (mean = 1.89 axillary shoots per main shoot); the corresponding number for ungrazed plots was 1.48 axillary shoots per main shoot ($n = 321$). The greater production
of axillary shoots by main shoots from grazed plots was highly significant but there was also significant site-to-site variation (ANOVA: $F_{\text{treatment}} = 43.03$, d.f. = 1.3; $F_{\text{site}} = 111.55^{***}$, d.f. = 3.3) (Table 1). Axillary shoots recorded during the first sampling period in late June 1983 were not included in the analysis because their ages could not be determined.

There was very little shoot mortality in ungrazed plots of *Puccinellia* during the summer of 1983. In grazed plots, although the bulk of the main shoot was removed from a number of individual shoots, the basal meristems were left intact and it was still possible to record the production of axillary shoots at the base of the grazed main shoot. Twenty-nine percent of all shoots (both main and axillary) were grazed in this manner during the season, although most of the damage to these shoots occurred from mid- to late August, after the colony of lesser snow geese had migrated southwards. In individual plots, numbers of damaged main or axillary shoots, as a percentage of all shoots of each type, ranged from twelve to sixty-five and from eight to twenty-seven, respectively.

**Cumulative leaf births and deaths**

Leaves produced by shoots in grazed and ungrazed plots are shown in Fig. 1. The number of leaves produced by shoots in grazed plots includes leaves that had been removed by the geese, which could be identified because the leaf sheath remained attached to the shoot. The combined cumulative leaf births for main and axillary shoots from grazed plots were not significantly different from the corresponding totals for shoots from ungrazed plots (paired $t$-test: $t = 0.57$, N.S., d.f. = 3).
The cumulative number of leaves that died in grazed plots included leaves that were removed by grazing and those that died of other causes. Total cumulative leaf deaths for both main and axillary shoots were significantly higher in grazed plots than in ungrazed plots (paired one-tailed t-test: \( t = 2.75 \), d.f. = 3) (Fig. 1). In grazed plots in early July, cumulative deaths on main shoots increased more rapidly than cumulative births in grazed plots because of the removal of leaves by geese. By the end of the season, however, there was no significant difference in the cumulative number of leaf deaths on main shoots in grazed and ungrazed plots (paired one-tailed t-test: \( t = 0.29 \), N.S., d.f. = 3). In contrast, cumulative deaths on axillary tillers were substantially higher in grazed plots compared with values for ungrazed plots (Fig. 1) (paired one-tailed t-test: \( t = 2.62^* \), d.f. = 3).

The effect of grazing on the mean net number of live leaves per quadrat (MNNLL) differed for axillary v. main shoots (Fig. 2). In ungrazed sites, MNNLL on axillary shoots increased between June and September, while in grazed plots the increase was only maintained until early August, after which MNNLL declined. By September MNNLL on axillary shoots was similar in both grazed and ungrazed plots. When the numbers of partially grazed live leaves were subtracted, the net number of intact leaves on axillary shoots in grazed plots was lower than that in ungrazed plots on all sampling occasions. The MNNLL for the eighty-one main shoots in ungrazed plots fluctuated around 270 leaves throughout the summer, while corresponding values for MNNLL in grazed plots declined from 260 to 100 live leaves as summer progressed (Fig. 2). The combined net number of ungrazed and partially grazed leaves in grazed plots and the number of ungrazed leaves in ungrazed plots were analysed in relation to season, treatment and site (G, UG plots 1–5). The results of the ANOVA based on a hierarchial design indicated a strong seasonal effect, but the effects of treatment and site were not significant (ANOVA: \( F_{\text{treatment}} = 0.92 \), N.S., d.f. 1:4; \( F_{\text{site}} = 0.83 \), N.S., d.f. 1:4; \( F_{\text{season}} = 17.21^{**} \), d.f. = 4:16). The interaction terms were not significant. The exclusion of partially grazed leaves from the analysis failed to alter the statistical findings.
Overall, 39% of the cumulative number of leaves produced on main and axillary shoots from June to September 1983 were removed by the geese, ranging from 28% to 52% for individual plots. When partially grazed leaves are included, the cumulative proportion of leaves produced during this period that were grazed increased to 64% ranging from 45% to 84% for the different plots.

*Births and deaths of leaves on surviving shoots*

A series of statistical analyses was carried out to determine whether grazing affected numbers of leaf births and deaths on main and axillary shoots that survived the summer intact (i.e. not removed). Because relatively few shoots fell into this class, the data were severely truncated. Twenty main and twenty axillary shoots from each plot were selected at random out of twenty-eight available shoots (the maximum number common to all plots). Live leaves present on the first sampling date in June 1983 were not included in the analysis. There was considerable variation in the number of leaf births per main shoot in the different plots at both grazed (5-4-6-4 leaves) and ungrazed (5-2-6-3 leaves) sites. When differences in cumulative leaf births per main shoot were compared for variation caused by site and treatment (grazed or ungrazed), neither factor was significant (ANOVA: \( F_{\text{site}} = 1.14, \text{ N.S., d.f.} = 3 \); \( F_{\text{treatment}} = 0.39, \text{ N.S., d.f.} = 1 \)). Axillary shoots which were recorded for the first time on the final sample date were excluded from the analysis of leaf births and deaths. Twenty shoots were selected at random from the remaining axillary shoots in each plot. The overall mean number of leaf births per axillary shoot ranged between 4-4 and 5-2 in grazed plots and between 3-4 and 3-8 in ungrazed plots. The total number of cumulative leaf births for the twenty axillary shoots during July and the first half of August was significantly greater in grazed plots (ANOVA: \( F_{\text{treatment}} = 24.76^*, \text{ d.f.} = 1 \)). The effect of site was not significant.

The mean number of leaf deaths on main shoots between July and September 1983 ranged from 5-5 to 6-7 in ungrazed plots and from 6-4 to 7-7 in grazed plots. When the effects of site and grazing treatment on cumulative leaf deaths were tested, both factors were significant (ANOVA: \( F_{\text{site}} = 134.9^*, \text{ d.f.} = 3 \); \( F_{\text{treatment}} = 264.7^***, \text{ d.f.} = 1 \)). Thus, cumulative leaf deaths per shoot, which include totally grazed leaves, were significantly higher on main shoots in grazed plots compared with corresponding values for ungrazed plots. Mean cumulative deaths on axillary shoots varied from 1-9 to 2-8 in grazed plots and from 1-1 to 1-7 in ungrazed plots. A similar ANOVA test to the above indicated that there was a significant effect of grazing treatment on the values for mean cumulative deaths (\( F_{\text{treatment}} = 58.9^*, \text{ d.f.} = 1 \)). The effects of site on the cumulative leaf deaths were not significant.

The mean number of leaf deaths per axillary shoot in ungrazed plots was significantly lower than the corresponding number of leaf births per axillary shoot (ANOVA: \( F_{\text{births/deaths}} = 984.51^***, \text{ d.f.} = 1 \); \( F_{\text{site}} = 8.81, \text{ N.S., d.f.} = 3 \)). Results for the mean number of leaf deaths per axillary shoot in grazed plots were also less than the mean number of births per shoot (ANOVA: \( F_{\text{births/deaths}} = 108.89^*, \text{ d.f.} = 1 \); \( F_{\text{site}} = 1.64, \text{ N.S., d.f.} = 3 \)). In contrast, the mean cumulative number of leaf deaths on main grazed shoots was significantly higher than the mean cumulative number of leaves produced (ANOVA: \( F_{\text{births/deaths}} = 13.83^*, \text{ d.f.} = 1 \); \( F_{\text{site}} = 3.62, \text{ N.S., d.f.} = 3 \)).

*Leaf life expectancies*

Life expectancies of leaves on main shoots in grazed plots varied from 29-0 to 34.1 days, while those on main shoots in ungrazed plots had life expectancies of 32.7–38.2 days. The
Response of an arctic grass to grazing

Table 2. Life expectancies of leaves of grazed* and ungrazed main and axillary shoots of *Puccinellia phryganodes.* Values are based on records of leaves produced between June and early August 1983 (n = number of leaves).

<table>
<thead>
<tr>
<th>Quadrat number</th>
<th>Estimated life expectancy (days)</th>
<th>n</th>
<th>Quadrat number</th>
<th>Estimated life expectancy (days)</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Main shoots</td>
<td></td>
<td></td>
<td>Ungrazed plots</td>
<td></td>
<td></td>
</tr>
<tr>
<td>G1</td>
<td>34·1 (33·9)</td>
<td>116</td>
<td>UG1</td>
<td>38·2 (35·0)</td>
<td>453</td>
</tr>
<tr>
<td>G2</td>
<td>30·5 (29·3)</td>
<td>143</td>
<td>UG2</td>
<td>33·9 (30·9)</td>
<td>467</td>
</tr>
<tr>
<td>G3</td>
<td>29·0 (28·6)</td>
<td>91</td>
<td>UG3</td>
<td>32·7 (27·0)</td>
<td>572</td>
</tr>
<tr>
<td>G4</td>
<td>29·4 (26·8)</td>
<td>143</td>
<td>UG4</td>
<td>36·9 (33·1)</td>
<td>398</td>
</tr>
<tr>
<td>Axillary shoots</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>G1</td>
<td>30·6</td>
<td>90</td>
<td>UG1</td>
<td>34·9</td>
<td>119</td>
</tr>
<tr>
<td>G2</td>
<td>27·5</td>
<td>83</td>
<td>UG2</td>
<td>34·2</td>
<td>206</td>
</tr>
<tr>
<td>G3</td>
<td>29·1</td>
<td>103</td>
<td>UG3</td>
<td>36·0</td>
<td>324</td>
</tr>
<tr>
<td>G4</td>
<td>34·4</td>
<td>150</td>
<td>UG4</td>
<td>42·5</td>
<td>181</td>
</tr>
</tbody>
</table>

* Leaves on shoots in quadrats in grazed plots that escaped grazing by lesser snow goose.
† Values in parentheses are obtained from the analysis of only the first cohort and are provided for comparison with the estimates based on pooled data.

latter values were significantly greater based on paired comparisons (Table 2) (ANOVA: F_{treatment} = 24·08**, d.f. = 1·3; F_{site} = 5·57, N.S., d.f. = 3·3). The life expectancies for leaves in grazed plots were based on ungrazed leaves. The life expectancies of ungrazed leaves on axillary shoots in grazed plots varied from 27·5 to 34·4 days, while those of leaves on axillary shoots in ungrazed plots varied from 34·2 to 42·5 days (Table 2). Again, the ages of leaves from ungrazed plots were significantly greater in paired comparisons (ANOVA: F_{treatment} = 66·69***, d.f. = 1·3; F_{site} = 17·31*, d.f. = 3·3).

When a leaf was partially grazed, it survived for up to twenty-one days after being clipped. Estimated life expectancies of partially grazed leaves ranged from 24·9 to 29·0 days on main shoots and from 25·8 to 30·2 days on axillary shoots. The estimated life expectancy of partially grazed leaves (mean = 26·2 days, n = 634) on main shoots was not significantly lower than that of intact leaves (mean = 30·6 days, n = 544) (ANOVA: F_{treatment} = 9·2, N.S., d.f. = 1·3; F_{site} = 1·04, N.S., d.f. = 3·3). In the case of axillary shoots, the estimated life expectancy of partially grazed leaves (mean = 27·3 days, n = 331) was also not significantly different from the corresponding value for ungrazed leaves (mean = 30·1 days, n = 516). (ANOVA: F_{treatment} = 3·49, N.S., d.f. = 3·3; F_{site} = 2·4, N.S., d.f. = 3·3).

In calculating the mean age at which leaves were grazed, leaves that were partially grazed were combined with those that were completely removed. The mean age at which leaves on main shoots were grazed between June and September 1983 varied from 13·2 to 17·9 days between plots, while leaves on axillary shoots were grazed between the ages of 15·1 and 18·6 days between plots.

Survival of shoots between September 1983 and June 1984

When plots were re-examined in June 1984, immediately after spring melt, 244 shoots (n = 108 from grazed plots and n = 136 from ungrazed plots) were relocated out of a total of 927 shoots marked in the late summer of 1983. During the previous nine months, a large amount of silt was deposited on plots. Recognizable ink spots were detected on
leaves of thirty-two shoots. A higher percentage of marked shoots from ungrazed plots (18%) had died than from grazed plots (6%). In addition, a far higher percentage of shoots (26%) in grazed sites had produced three or four live leaves approximately eight days after the spring melt, compared with the 1% in ungrazed plots. Some live shoots in both grazed and ungrazed plots were devoid of live leaves, which had been removed by snow buntings (Bazely 1987). The oldest live leaf on each shoot was usually light green in colour with yellow patches; it appeared to have been produced in 1983.

DISCUSSION

Previous studies have shown that grazing by lesser snow geese resulted in a significant increase in the NAPP of grazed Puccinellia swards compared with corresponding values for ungrazed swards. In 1979 and 1980 the increases were 36% and 46%, respectively (Cargill & Jeffries 1984), while in 1982 and 1983 the increases were 80% and 106%, respectively (Bazely 1984). In 1983 the summer was exceptionally late. The increase of 106%, based on measurements of differences in above-ground standing crop from June to October, corresponded to an estimated above-ground production of (dry weight) biomass of 159 g m⁻². The estimate of above-ground production of biomass in 1982 was 114 g m⁻² (Bazely 1984). Aside from differences in weather between years, measurements of cumulative biomass in 1983 were made over a period of 16.5 weeks rather than twelve weeks, as in 1982. Lesser snow geese grazed 89% of NAPP in 1982 and 60% in 1983 (Bazely 1984). Levels of consumption of 60% and above are high for terrestrial ecosystems and have generally only been observed in grassland areas grazed by large mammals (Campbell 1966; Frame 1966; Wiegert & Evans 1967). Schultz (1969) reported that lemmings grazed from 20% to 90% of the NAPP of arctic graminoid plant communities, although intensive grazing was very localized.

The increase in the production of axillary shoots largely accounted for the increased NAPP of grazed Puccinellia swards. The activation of shoots in response to grazing has been observed in temperate salt marshes (Gray & Scott 1980), African grasslands (Vesey-Fitzgerald 1973; McNaughton 1976) and agricultural grasslands (Jones, Collett & Brown 1982; Parsons et al. 1983). Unlike P. phryganodes, the other heavily grazed graminoid species at Le Pérouse Bay, Carex subspathacea, showed no significant differences in shoot production between grazed and ungrazed plots (Kotanen & Jeffries 1987). An increase in the number of leaves on existing shoots accounted for the increase in NAPP of grazed swards C. subspathacea.

The geese do not graze all areas of the marsh to the same degree. Two sets of paired plots (G3/UG3; G4/UG4) were located on the tidal flats in the west part of the Bay, close to an area of willows that marked the landward limit of the tidal flats. Field observations indicated a reluctance of geese to feed in this locality for any length of time, possibly because of the inability of the birds to command a wide field of view at a time when adults were moulting and goslings were not fully fledged. In such locations the birds were particularly vulnerable to attacks from predators.

As indicated earlier, 29% of all shoots were damaged. Most of the damage occurred during the second half of August. At this stage of the season very few (< 50) lesser snow geese remained on the marsh, and most of the geese present were migratory Canada geese Branta canadensis L. The Canada geese were never present on the tidal grazing flats in large numbers, except during the spring and fall migrations. Canada geese are more destructive than snow geese in their grazing habits. Lesser snow geese rarely take entire
shoots; instead, the birds either clip or remove leaves. Where leaves were only clipped, basal meristems remained intact, thereby ensuring continued growth of clipped leaves. Likewise, axillary shoots were able to develop from the main shoot. The demography of the shoots indicated that shoot turnover was slow compared with that of leaves. The detection of a difference in the pattern of mortality between shoots of grazed and ungrazed plots was not possible, given the longevity of shoots and the short duration of the study.

The production of new leaves and the turnover of existing leaves or shoots of *Puccinellia phryganodes* were more rapid than corresponding values reported for the sedge *Eriophorum vaginatum* growing in arctic and sub-arctic environments (Johnston & Tieszen 1976; Robertson & Woolhouse 1984). Main shoots of *Puccinellia* in both grazed and ungrazed sites produced a new leaf once every eleven days, on average, during the summer. There was no significant difference in cumulative birth of leaves of shoots from grazed and ungrazed plots. As mentioned earlier, in 1983 the summer was late, so that the expected increase in above-ground production in grazed plots did not become evident until the last sample date in October, six weeks after the demographic study stopped. If it had been possible to record numbers of births during September and October, we predict that the number would have been significantly greater in grazed plots.

There was also a rapid turnover of leaves in *C. subspathacea*; shoots in grazed plots produced significantly more leaves than those in ungrazed plots (Kotanen & Jefferies 1987). The estimated life expectancies of *Puccinellia* leaves in ungrazed plots were between 32-7 and 38-2 days, in contrast to corresponding values for *Carex* leaves of between 44-6 and 45-8 days. Life expectancies of ungrazed leaves on grazed shoots of *Puccinellia* and *Carex* were similar to each other (*Puccinellia*: 29-0-31-1 days; *Carex*: 29-3-35-0 days) and significantly (*P < 0·001*) shorter than the life expectancies of leaves on ungrazed shoots. The life expectancies of partially grazed leaves and ungrazed leaves of grazed shoots of both *Puccinellia* (partially grazed leaves: 24-9-29-0 days; *n* = 103–146 leaves measured on main shoots in different plots) and *Carex* (Kotanen & Jefferies 1987) were not significantly different. The mean age of leaves of *Puccinellia* when grazed (13–19 days) corresponds well with similar data for *C. subspathacea* (Kotanen & Jefferies 1987). In both species, the mean age of leaves when grazed coincides with the full expansion of leaves.

The variation in the growth of shoots and the turnover of leaves between plots subjected to the same treatment appeared to be a consequence of different grazing intensities and the prevailing conditions of the habitat. Plants of *P. phryganodes* showed a high degree of phenotypic plasticity in response to grazing. Shoots in grazed plots tended to be prostrate with short, wide leaves, while in ungrazed plots, the shoots were upright, with long thin leaves. Similar morphological changes have been observed in other grazed systems (Gray & Scott 1980; Belsky 1986). Rates of leaf appearance have also been found to vary in *Lolium perenne* in response to different cutting treatments (Vine 1983).

The results given in this paper, together with those for *C. subspathacea* (Kotanen & Jefferies 1987), provide a basis for interpreting the morphological changes which occur when plants of these two graminoid species are grazed, and which account for the increase in NAPP at a time when most needed by the geese. Although the growth patterns of plants of the two species when grazed and fertilized are different, the rapid leaf turnover and the low life expectancies of leaves which do not overwinter are common to both species. The low life expectancy of leaves, particularly in an arctic environment, was unexpected and requires further investigation.
ACKNOWLEDGMENTS

We thank Jo-Anne Rzadki, Thor Thorleifson and Robin Labatt for field assistance, and students and staff at La Pérouse Bay Tundra Biology Station and members of the Churchill Northern Studies Centre for logistic support. Dr S. H. C. Marriott gave us valuable statistical advice. Peter Kotanen and David Hik and the anonymous referees made a number of very helpful suggestions and improvements concerning the manuscript. We gratefully acknowledge financial support from the Natural Sciences and Engineering Research Council of Canada, the Canadian Wildlife Service (Environment Canada) and the Department of Indian and Northern Affairs. Miss B. Wheatley kindly typed the manuscript.

REFERENCES


Response of an arctic grass to grazing


*(Received 7 January 1988; revision received 17 April 1989)*