

Response of arctic sedges to release from grazing: leaf elongation in two species of *Carex*

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Abstract

We have used demographic methods to determine whether increased rates of leaf elongation occur in two sedges, *Carex subspathacea* Wormsk and *Carex xflavicans* Nyl., when heavily grazed by Lesser Snow Geese (*Chen caerulescens caerulescens* (L.)) at La Perouse Bay, Manitoba. Rates of elongation of leaves declined as leaves aged. Most comparisons between grazed and ungrazed plots indicated that rates of elongation of leaves of grazed shoots were not significantly greater than corresponding rates for ungrazed shoots. No trends were evident. As reported elsewhere, increased production and turnover of leaves accounted for most of the regeneration of photosynthetic area following grazing in both species.

Introduction

Much of the resistance of grasses and sedges to the deleterious effects of grazing is attributable to the positions of their meristems. The basal (intercalary) meristem of a graminoid leaf is located close to the shoot; this meristem often escapes damage by grazers, so that regrowth of clipped leaves is possible following grazing (Hyder 1972; Dahl and Hyder 1977; Harper 1977; Crawley 1983; McNaughton 1983). In some grasses and sedges, increased rates of elongation of leaves following grazing are an important intrinsic (physiological) mechanism, whereby a tiller regenerates its photosynthetic surface area after grazing (McNaughton 1983; McNaughton et al. 1983; Coughenour 1985; Wallace et al. 1985).

The sedges, *Carex subspathacea* Wormsk² and *Carex xflavicans* Nyl. grow respectively in saline and freshwater habitats at La Pérouse Bay, Manitoba. Both species are heavily grazed during the summer by a breeding colony of 7000 pairs of Lesser Snow Geese (*Chen caerulescens caerulescens* (L.)) and their offspring.

In 1980, comparisons of grazed and ungrazed plots indicated that the summer foraging activities of the geese increased the net aboveground primary production of a grazing lawn of *Carex subspathacea* by 60 to 80% (Cargill and Jefferies 1984b). This increase was a consequence of the geese increasing the availability of nitrogen for plant growth in this nitrogen-limited environment (Cargill and Jefferies 1984a, 1984b; Bazely and Jefferies 1985, 1989; Jefferies 1988). Much of the increased production is a consequence of an increase in the number of births of leaves and in the turnover rate of leaves; significant short-term changes in the demography of shoots do not occur in response to grazing (Kotanen and Jefferies 1987). *Carex X flavicans* also responds to grazing within one season with an increase in the births of leaves, but not of shoots (Kotanen 1987; Kotanen and Jefferies 1989).

The purpose of this study was to determine whether shoots of *Carex subspathacea* and *Carex X flavicans* show increased elongation of leaves when grazed, in addition to the increased natality of leaves. If so, this would be a further mechanism contributing to the observed increase in aboveground net primary production when swards are grazed. Rates of elongation of leaves were compared between plants in plots subject to grazing and plants in plots from which geese were excluded.

Materials and methods

The study area

The extensive tidal flats at La Pérouse Bay (58°04'N, 94°03'W) on the shores of Hudson Bay are dominated by a stoloniferous grass, *Puccinellia phryganodes*, and by a rhizomatous sedge, *Carex subspathacea* (Jefferies *et al.* 1979). Beyond the high-water mark, the landscape consists of freshwater ponds, moss carpets which surround many of the ponds, and shrub tundra vegetation. *Carex x flavicans* Nyl., a hybrid of *Carex subspathacea* and *Carex aquatilis* Wahl. grows in shallow fresh water and in moss carpets.

On arrival at La Pérouse Bay in May, Lesser Snow Geese (*Chen caerulescens caerulescens*) grub for roots and rhizomes of graminoid plants on the tidal flats and eat the swollen basal portion of developing shoots of *Carex x flavicans* and *C. aquatilis* in freshwater ponds (Jefferies 1988). The remainder of the severed shoot is discarded. About 7000 pairs of geese nest inland beyond the tidal flats and after the hatching of 30 000 goslings in late June (Cooke *et al.* 1982), families feed intensively on the leaves of both saltwater and freshwater graminoids which have started aboveground growth by that time. In tidal areas the geese uniformly crop the vegetation to 2.5 cm or less in height. Although very patchy, herbivory by the geese can be intense in stands of *Carex x flavicans* where swards may be maintained at a height of less than 5 cm. The geese begin their southward migration in mid-August.

The growth habits of Carex subspathacea and Carex Xflavicans The morphology of the two sedges resembles that of *Carex aquatilis*, described by Shaver and Billings (1975), Billings *et al.* (1978) and Shaver *et al.* (1979). Leafy shoots are produced in clusters from sub-terranean rhizomes. Vegetative tillers of *C. subspathacea* may reach 20 cm in height in ungrazed areas, although shoots of plants growing in the intertidal flats rarely exceed 3 cm in height. Ungrazed tillers of *Carex Xflavicans* are commonly 15-20 cm tall. Throughout the summer leaves develop sequentially from an apical meristem that is concealed at the centre of each shoot near the ground surface. Even after a young leaf elongates sufficiently to be visibly exerted from the centre of a tiller, its base remains concealed by the bases of older leaves which surround it. Leaves of intertidal *C. subspathacea* live for 30-45 days (Kotanen and Jefferies 1987). The life expectancy of leaves of *Carex Xflavicans* is in excess of 1 year. Flowering occurs in both species, but at a low frequency. Swards of both species consist of a mosaic of rhizomes produced by different ramets.

The morphology and ecology of these species are described in Cayouette and Morisset (1985, 1986), Kotanen (1987), and Kotanen and Jefferies (1987).

Measurement of leaf elongation

In late May and early June, 1986, before the onset of the intense grazing during the post-hatch period, one pair of plots (0.5 x 0.5 m) was established in each of three haphazardly chosen swards of *Carex subspathacea* (sites 1, 2, and 3) and one of *Carex xflavicans* (site 4). Wire netting (0.6 x 0.6 m, 0.5 m tall) was placed around one plot of each pair (the ungrazed plot); the remaining plot of each pair was not enclosed (the grazed plot). Another pair of plots was established at each of two additional *Carex xflavicans* sites (sites 5 and 6) at the beginning of July, following hatch. These swards of *Carex Xflavicans* had suffered some grazing, but the erection of exclosures prevented further foraging by geese in the ungrazed plot of each pair. Individual plots of each pair were within 3 m of each other, and sites were at least 100 m apart.

Immediately after hatch, when swards in unexclosed plots had been grazed by adult geese and goslings, experimental shoots in each plot were marked with a small ring of thin, coloured wire set in the sediment around each shoot. The shoot closest to each of the 25 intersections of crosswires of a removable 0.5 X 0.5m metal quadrat, strung with thin wire at intervals of 10 cm, was selected for the study. The least distance between any marked shoot and the edge of a plot was about 10 cm. All leaves on each shoot were marked with distinctive patterns of small dots of India ink in order to allow easy identification. After each leaf was marked, its length from the apex to the surface of the sediment was measured to the nearest millimetre. Both the ungrazed and grazed plots were then exclosed to prevent geese from removing tissue before the next examination of the leaves.

Shoots were reexamined and leaves remeasured 1 week later. After the measurements had been completed, new grazed plots were established. Shoots were selected and ringed in each of these plots and their leaves marked and measured as described above. These grazed plots were exclosed until the next sampling date. The

grazed plots from the previous week were abandoned, but the same shoots in the same set of ungrazed plots were followed for the duration of the study.

The procedure outlined above was repeated 5 times before the end of August at intervals of 6- 10 days for plots of *C. subspathacea*. On the fifth occasion only 15 shoots were selected per plot, and one pair of plots was abandoned because of damage by caribou. Elongation of each leaf was calculated as the increment in its measured length between samplings. Comparison of lengths of senescent leaves between samplings indicated that measurements were accurate to within 1-2 mm for a 10-20 mm leaf.

New grazed plots of *Carex xflavicans* were established and enclosed and increments in leaf lengths were measured at intervals of 9 to 19 days, depending on the date of sampling. The accuracy of measurements was in the order of 2-3 mm for a 20-30 mm leaf. Four, three and two sets of measurements of leaf elongation were made in paired plots at sites 4, 5, and 6, respectively, during the season.

Leaves in ungrazed plots of both species that had been grazed or damaged before the plots were enclosed were excluded from all analyses. Leaves that appeared or died between two samplings were also excluded from the analysis of that sampling interval.

Statistical methods

Since different pairs of plots were established at different times, the sampling intervals varied in duration, and sample sizes were not equal, analysis by a single multifactor ANOVA or MANOVA was impractical. Consequently data for each site and for each sampling interval were treated separately to test whether rates of elongation varied with the age of a leaf and to define homogeneous sets of leaves for statistical analysis of grazing effects. Leaves were grouped into age classes which were considered separately. In each analysis, class 1 consisted of the youngest leaf of each shoot at the beginning of that sampling interval. Class 2 consisted of leaves that had been produced immediately before the youngest leaves, as indicated by their positions on each shoot. Similarly, leaves were placed in older age classes on the basis of their positions on each shoot. However, because leaves of the older age classes elongated little, they were grouped together in class 3 for *C. subspathacea* and class 4 for *Carex Xflavicans*. Excluding overwintering leaves, the mean ages of successive classes of leaves differed by 10- 14 days for *C. subspathacea* and by 13- 19 days for *Carex xflavicans*. On the first sampling date, some class 2 and possibly some class 1 leaves of both species had been produced during the previous year, as well as many older leaves.

No attempt was made to distinguish between grazed and ungrazed leaves in grazed plots, since this would have made the analysis very complex. Few tillers in grazed swards escape clipping by geese.

Where data could be transformed to approach a normal distribution and to pass the F_{MAX} - test for homogeneity of variance, a one-way analysis of variance was used to test for significant differences. If no effective transformations could be found, the two-tailed nonparametric Wilcoxon test was employed (corrected for ties; Sokal and Rohlf

1981) to test for significant distributional differences between treatments. Other statistical tests were used as indicated. The statistical analyses assumed that shoots behaved independently. Although this assumption cannot be proven, there was no reason to suspect the existence of significant interdependence between shoots.

Cumulative error is a problem when conducting multiple tests of significance (Kirk 1982). As well, although paired plots were chosen to be as similar as possible initially, and although previous experiments have found the effects of treatment (erection of enclosure) to be much stronger than between-plot variation, any pair of plots might still have differed from each other because of factors other than the treatments. Consequently, among the multiple tests reported below, isolated significant results have been treated with suspicion. Highly significant results and consistent trends in significance are more useful in the interpretation of collections of multiple statistical tests. Since the 36 tests of the effects of grazing that were performed for each species were nonindependent, the overall cumulative error rate for each of these two collections of tests is difficult to calculate. However, it can be shown (Kirk 1982, pp. 101- 103) that by considering as significant only results less probable than 0.1%, the overall error rate for each species would be limited to less than 5%.

Results

Carex subspathacea

Rates of elongation of leaves of *C. subspathacea* declined with age in both grazed and exclosed plots (Fig. 1). Average rates of elongation for the youngest class of leaves (class 1 leaf) ranged between 1.7 and **0.3**mm per day. Rates for the next youngest class of leaves (class 2) were between 1 and **0.1** mm per day, while rates of elongation of older leaves (class 3 leaves) were generally less than **0.3**mm per day. Elongation of a leaf was essentially complete by the time it was considered class 3 (i.e., age **30** to 42 days).

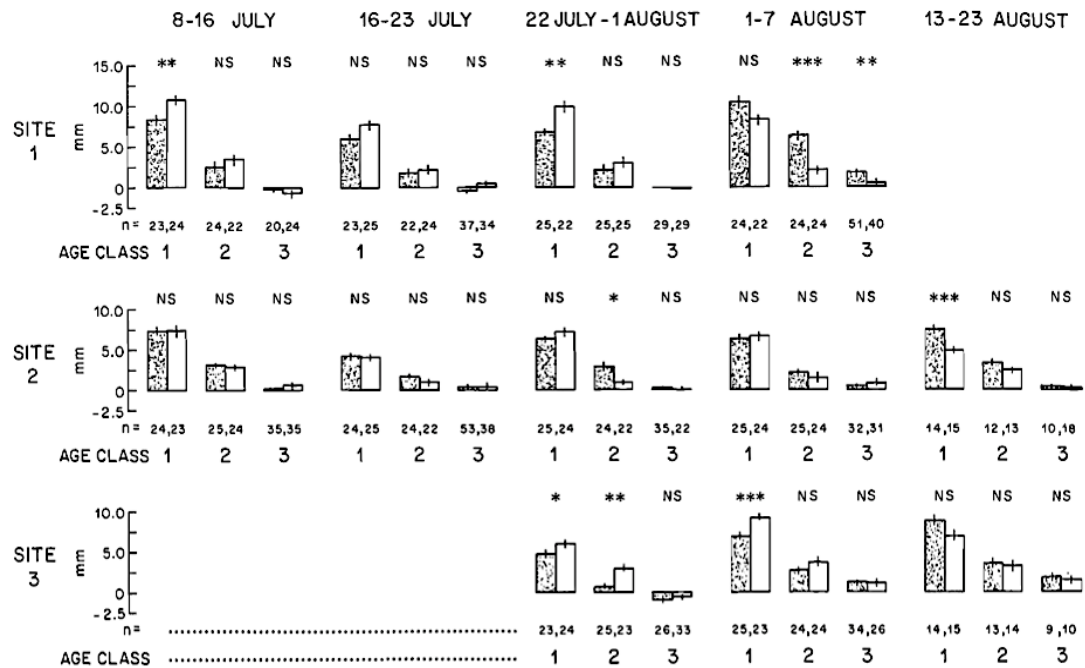


FIG. 1. Means \pm SE and sample sizes (n) of the measured elongation (mm) between 8 July and 23 August 1986 of leaves of *Carex subspatheca* at sites 1, 2, and 3 in an intertidal marsh at La Pérouse Bay, Man. Results of analyses of variance or two-tailed Wilcoxon rank tests comparing data from grazed plots (shaded bars) and ungrazed plots (open bars) are also given. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

Grazing did not have consistently significant effects upon the elongation of leaves. Out of 36 comparisons of paired plots, only in 4 cases did the elongation of leaves in the grazed plot significantly exceed that in the ungrazed plot ($p < 0.001$ in 2 cases), and in 5 instances this trend was significantly reversed ($p < 0.001$ in 1 case) (Fig. 1). Grazing significantly increased elongation in only one comparison of class 1 leaves; the other 3 cases occurred in class 2 and 3 leaves in which the absolute difference between treatments was relatively small. Of the cases in which grazing significantly decreased elongation, four occurred in class 1 leaves. When the mean value of the leaf elongations at each site and at each sampling interval was treated as a replicate, it was possible to perform a nonparametric sign test for each age class of leaves (Sokal and Rohlf 1981). These tests were used to examine the null hypothesis that the mean elongations for the grazed plots did not differ significantly from the means for the ungrazed plots with which they were paired. The three tests failed to demonstrate a significant difference between grazed and ungrazed plots for the elongation of any age class of leaves ($p > 0.05$). When all age classes were treated as replicates as well, a nonparametric sign test also failed to demonstrate a significant difference between treatments ($p > 0.05$). since neither means for the same plot at different times, nor means for different age classes of leaves in the same plot are likely to be independent, these sign tests must be treated as approximate. A posteriori examination of the comparisons between paired plots (Fig. 1) suggested that leaf elongation might have been reduced by grazing early in the season, but enhanced later in the year. This

hypothesis can only be tested approximately, since the comparisons involved might be expected to be mutually nonindependent (see above). An approximate test was performed as follows. Comparisons between paired plots were grouped in two classes: early season (July 9 to August 1) and late season (August 1 to August 23). A two-way X^2 test was used to test whether the proportion of comparisons between paired plots in which mean elongation for an age class of leaves was greater in the grazed plot varied with the season (early or late). The resulting test was not significant ($X^2 = 2.86$, 1 df; $p = 0.09$), suggesting that the effect of the grazing treatment did not vary over time.

Carex xflavicans

Rates of elongation of leaves of *Carex x flavicans* declined with age in both grazed and ungrazed plots (Fig. 2). Average rates of elongation of leaves per day ranged from 3.5 to 0.6 mm for class 1 leaves, from 2.5 to 0.5 mm for class 2 leaves, and between 0.6 and 0 mm for class 3 leaves. Older leaves elongated very little; averages were less than 0.3 mm per day. Elongation of a leaf extended over at least 52 to 76 days.

As in the case of *C. subspathacea*, grazing did not have consistently significant effects upon the elongation of leaves. Out of 36 comparisons of paired plots, in 4 cases elongation of leaves in grazed plots significantly exceeded that in ungrazed plots ($p < 0.001$ in 1 case), while in 7 cases this trend was significantly reversed ($p < 0.001$ in 1 case). Only two of the cases in which grazing significantly increased elongation involved class 1 or 2 leaves; the others involved class 3 or 4 leaves, in which the absolute differences between treatments were relatively small. Of the cases in which grazing significantly decreased elongation, all but one involved class 1 or 2 leaves. Approximate nonparametric sign tests failed to demonstrate a significant difference between the grazed plots and the ungrazed plots for the elongation of any age class of leaves, when the mean value for each site at each sampling interval was treated as a replicate ($p > 0.05$). When age classes were also treated as replicates, an overall nonparametric sign test still failed to demonstrate a significant difference between treatments ($p > 0.05$).

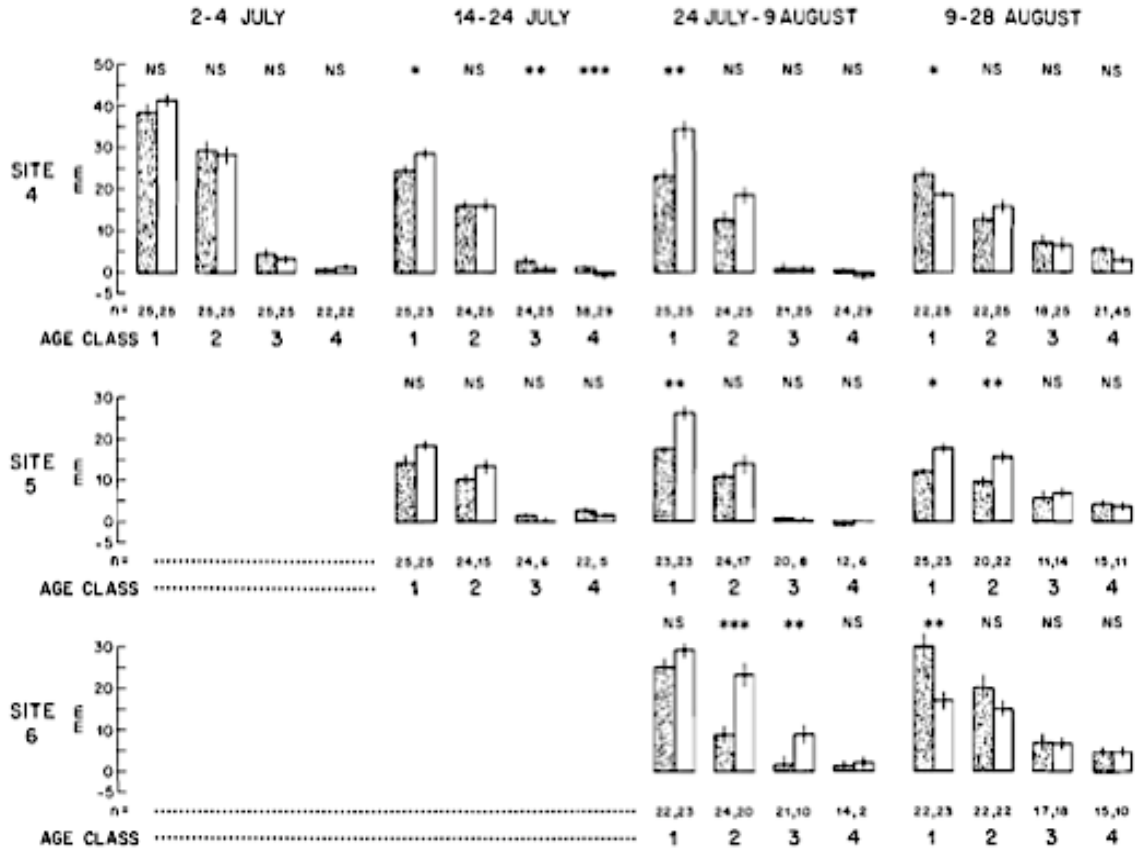


FIG. 2. Means \pm SE and sample sizes (n) of the measured elongation (mm) between 2 July and 28 August 1986 of leaves of *Carex x flavicans* at sites 4, 5, and 6 in a freshwater marsh at La Pérouse Bay, Man. Results of analyses of variance or two-tailed Wilcoxon rank tests comparing data from grazed plots (shaded bars) and ungrazed plots (open bars) are also given. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

As for *C. subspathacea*, a posteriori examination of the data (Fig. 2) suggested that grazing might have reduced leaf elongation during the first three sampling intervals (July 2 to August 10), while increasing elongation during the final interval (August 9 to August 28). An approximate two-way X^2 test was performed to test whether the proportion of comparisons between paired plots in which mean elongation for an age class of leaves was greater in the grazed plot varied with the season (first three samplings versus the last sampling). The resulting test was not significant ($X^2 = 2.73$, 1 df; $p = 0.1$), suggesting that the effect of the grazing treatment did not vary over time.

Discussion

Rates of elongation of leaves of both species of *Carex* declined as leaves

aged. It was estimated that leaves of *C. subspathacea* continued to elongate measurably for approximately 30 to 42 days following their exertion. As the life expectancy of new leaves of this sedge ranges from 30 to 47 days during the summer at La Pérouse Bay (Kotanen and Jefferies 1987), these results suggest that elongation continued at a diminishing rate throughout most of the life of each leaf. Leaves of *Carex xflavicans* were estimated to elongate for at least 52 to 76 days. These results suggest that leaves of *Carex xflavicans* produced early in July, a few weeks after spring thaw, were still elongating at the return of sub-zero daytime temperatures in September. Such a long period of growth is consistent with the observation that the average life span of a leaf of this hybrid is in excess of one growing season (Kotanen 1987). There is circumstantial evidence that leaves produced late in the summer continued to elongate during the following summer, as mature leaves present at the first sampling date continued to elongate during July and August, despite having obviously overwintered. These patterns of growth resemble those described for leaves of other arctic members of the Cyperaceae (Johnson and Tieszen 1976; Archer and Tieszen 1980; Jonasson and Chapin 1985). Although the effects on the vegetation of foraging by geese tend to be unevenly distributed in both space and time (Kotanen 1987; Jefferies 1988), all study sites were intensely grazed between the hatch of goslings in late June and the departure of the geese in mid-August. At least 49% of the leaves of *Carex subspathacea* that were produced in 1984 at sites near the experimental plots on the intertidal flats were clipped by geese before the final sampling date in September of that year (Kotanen and Jefferies 1987). The corresponding figure for leaves of *Carex xflavicans* was 76% in 1985 (Kotanen 1987). On average, new leaves of *C. subspathacea* were grazed at about 19 days of age in 1984, while rapid elongation was still occurring (Kotanen and Jefferies 1987). Although the equivalent figure is not available for *Carex Xflavicans*, the long duration of elongation of leaves of this hybrid suggests that most of these leaves were grazed while they were still extending. Since geese rarely destroyed the intercalary meristems, leaves of these species continued to extend following grazing, reestablishing their photosynthetic surface areas. Unless average rates of elongation of leaves were greater in grazed shoots than in shoots that escaped herbivory, this regrowth of leaves would not maintain the photosynthetic surface area of a grazed tiller at the same value as that of an ungrazed tiller. The tropical graminoids *Kyllinga nervosa* Steud., *Panicum coloratum* L., and *Themeda triandra* L. have revealed significantly increased rates of elongation of leaves in response to simulated grazing (Wallace 1981; McNaughton *et al.* 1983; Coughenour 1985; Wallace *et al.* 1985). In contrast, this study at La Pérouse Bay stimulation of growth of grazed leaves. Rates of elongation were not significantly different in most statistical comparisons, indicating that grazing had no consistent effect on the elongation of leaves. These conclusions were not altered if only plots established before hatch were considered. Although study sites were chosen to be as similar as possible, the few significant differences that occurred may have

been the spurious products of uncontrolled environmental differences between paired plots. In addition, 1 in 20 statistical tests might be expected to have been significant at the 5 % level, even if grazing truly had no effect upon elongation.

In summary, shoots of neither *Carex subspathacea* nor *Carex xflavicans* respond within one season to herbivory by geese with increased rates of elongation of leaves. Although grazed leaves may continue to elongate at rates similar to ungrazed leaves, replacement of the aboveground tissue removed by geese primarily occurs through enhancement of production of new leaves (Kotanen 1987; Kotanen and Jefferies 1987).

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