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Source: *Oecologia*, Vol. 58, No. 1 (1983), pp. 92-102
Published by: Springer in cooperation with International Association for Ecology
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Oecologia (Berlin) (1983) 58:92–102

Oecologia

Effects of simulated grazing on foliage and root production and biomass allocation in an arctic tundra sedge (*Eriophorum vaginatum*)

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Summary. *Eriophorum vaginatum* is a tussock-forming member of the Cyperaceae, widespread in the arctic tundra, and a common food item for grazing herbivores on the Alaskan North Slope. Populations of this sedge at Atkasook, Alaska, were subjected to a variety of simulated grazing experiments to determine tiller responses to frequent and intensive defoliation.

The initial, short-term response of *Eriophorum* to defoliation was an increase in leaf production at the expense of belowground structures. Multiple defoliations, however, resulted in proportionately greater reductions in leaf weight than leaf area. Leaf blades of defoliated plants weighed 0.71 mg/cm of length, compared to an average weight/length ratio of 0.91 mg/cm in control plants. Declines in leaf production were accompanied by weight losses in stem base and sheath components and a curtailment of root growth. Root initiation was reduced by 28 and 63%, respectively, after one and two seasons of multiple defoliations, and the depth of penetration of these annual roots was reduced substantially. Total root biomass was reduced 24% in the least severe defoliation treatment and 85% in the most severe treatment. The allocation of dry matter into new tillers on defoliated plants, relative to new tiller production of control plants, was reduced by 75% after two seasons of defoliation, although equivalent numbers of tillers were initiated. The reduced biomass of daughter tillers was restored to levels observed in control plants during the season of rest following the season of multiple defoliation. Sexual reproduction was significantly depressed in the most severe defoliation treatment and stimulated by the least severe treatment. Defoliation treatments of intermediate severity had no significant impact on flower initiation.

Over 80% of the tillers subjected to complete defoliation at 10-day intervals for one entire growing season survived, overwintered and initiated growth the following season. Recovery from multiple defoliations was partially achieved by the stimulated growth and extended longevity of older leaves on the tiller, although one season of rest was not enough to fully replenish weight losses of storage organs. Tillers were capable of withstanding more defoliation events when clipping was initiated early in the growing season. Biomass of storage organs of tillers subjected to multiple defoliations imposed at 10-day intervals for two entire growing seasons was 34% above the estimated minimum biomass necessary for tiller survival. The data suggest that *Eriophorum* tillers can survive 100% leaf removal at 10-day intervals for 50 to 75% of their estimated three to four year lifespan.

Introduction

Eriophorum vaginatum L. is a rhizomatous, perennial, tussock-forming graminoid in the Cyperaceae. The autecology and physiological ecology of this widespread arctic tundra sedge was reviewed by Wein (1973) and Chapin et al. (1979), respectively. Chapin et al. (1980) documented seasonal nutrient allocation patterns in *E. vaginatum*, while trends in leaf growth and photosynthesis have been examined by Johnson and Tieszen (1976). However, the responses of *E. vaginatum* specifically, and arctic plants in general, to biotic features of their environment are little known.

E. vaginatum commonly occurs where grazers, such as caribou (*Rangifer*), lemmings (*Lemus* and *Dicrostonyx*), ground squirrels (*Citellus*), ptarmigan (*Lagopus*), and geese (several genera) in Alaska (Batzli and Brown 1976) and domestic sheep (*Ovis*) in Scotland (Grant et al. 1976) are abundant. The early growth of *E. vaginatum* (Tieszen and Johnson 1968; Chapin et al. 1980) makes it an important early season forage for caribou on calving grounds (Kelsall 1968). Monocots supplied from 55 to 80% of the brown lemming's (*Lemus trimucronatus*) diet at Barrow, Alaska (Batzli and Pitelka 1975), and species of *Lemus* and *Microtus* showed strong preferences for *E. vaginatum* at the Atkasook site in northern Alaska (Batzli and Jung 1980). Krebs (1964) observed that *Lemus* and *Dicrostonyx* lived in tussock vegetation and utilized *E. vaginatum* around Hudson's Bay, Canada. Tikhomirov (1959) reported that feeding geese consumed 40 to 80% of the *Eriophorum* shoots in test plots. While the accumulation of standing dead shoots may serve to deter herbivores, it has been observed that once this litter is removed by grazing, caribou will repeatedly and preferentially return to regraze the tussocks (White and Trudell 1980).

Cody (1964, 1965) observed overgrazing of *E. vaginatum* by reindeer (*Rangifer*) during the summer months to the point of killing this plant in Canada's Reindeer Grazing

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Preserve. Grant et al. (1976) made similar observations of overgrazing by sheep on *Eriophorum* ranges in western Scotland. Thus, it is likely that *E. vaginatum* is subjected to intense grazing pressures at frequent and regular intervals in northern Alaska. However, these grazing periods will vary with time of season and herbivore population cycles and patterns of movement.

Although Bliss (1975) and Batzli (1975) reviewed both positive and negative environmental impacts of herbivores on tundra plants and soils, little detailed information concerning the physiological responses of plants in tundra grazing systems is available (Mattheis et al. 1976; Tieszen and Archer 1979). The present experiments were initiated to determine effects of simulated, intense, and chronic grazing on *E. vaginatum* tussocks of an inland arctic tundra site near Meade River (Atkasook), Alaska. Treatments were designed to determine the degree to which *E. vaginatum* tillers could tolerate extensive, frequent defoliation and to determine how various defoliation regimes might influence leaf production, root growth, biomass of storage tissue, and vegetative and sexual reproduction patterns.

Material and methods

Site description

Field work was conducted at the Meade River Field Station ($70^1/_4$ 28′ N, $157^1/_4$ 26′ W, 15 m elevation) of the Naval Arctic Research Laboratory, near Atkasook, Alaska, approximately 110 km southwest of Barrow, Alaska. The general pattern of weather, soils, and vegetation at Atkasook are described in Batzli and Brown (1976), Haugen and Brown (1980), Everett (1980) and Komarkova and Webber (1980). Plant nomenclature follows Hultén (1968).

Defoliation treatments

Twenty individual *E. vaginatum* tussocks of comparable age and vigor, from similar micro- and macrohabitats, were selected at 15-day intervals over the course of the 1976 growing season and subjected to chronic defoliation treatments. One tiller was monitored on each tussock. Tillers that were monitored were comparable in leaf number, stature, orientation, vigor, and stage of development for each point in time. Selected tillers, and all other tillers on the tussock, were clipped to moss level (8 to 15 mm above apical meristems).

Defoliation regimens were first initiated on June 18, 1976, and were subsequently initiated at 15-day intervals for the remainder of the growing season (Table 1). In the text, "early spring" refers to that group of plants initially defoliated on June 18; "fall" refers to those tillers or tussocks initially defoliated on July 28, etc.

Leaf growth

Leaf regrowth on tillers of each defoliation regimen was clipped back to moss level, dried, and weighed at 10-day intervals during the 1976 growing season. In the subsequent field season (1977), we randomly subdivided the tussocks within each seasonal defoliation treatment into two subgroups of 10 each (Table 1). We continued defoliation in one group at 10-day intervals; the other subgroup was not clipped. Leaf growth measurements were also made on tillers recovering from multiple defoliations.

Leaves of selected individual tillers were consecutively numbered from the first green leaf to emerge (and thus the oldest living leaf) to the last leaf to emerge. The length of leaf tissue exserted on selected tillers was measured at 10-day intervals. Because of high correlations between leaf length and leaf area ($r = 0.90$) leaf widths were not recorded. Leaf widths were checked periodically and found to be quite constant regardless of time of season and type of defoliation treatment. At the end of the 1977 growing season, all leaf material from the recovering tillers was harvested for biomass determinations.

On June 27, 1977, we chose five additional tussocks for multiple defoliation. Tussocks in this treatment (referred to as the chronic 1977 treatment) (Table 1) were subjected to periodic leaf removal as described above. The purpose of this additional treatment (similar to the early spring clipping regime) was to provide samples of belowground structures and tiller components for biomass analysis from plants subjected to a single, full season of chronic leaf removal.

Tiller survivorship and reproduction

At the time of the initial defoliation the number of actively growing adult tillers per tussock in the early spring and fall defoliation regimens were counted. The number of tillers per tussock was again counted in mid-June and late August of the subsequent season.

At the end of the 1977 field season, tussocks from the early spring and fall defoliation treatments were destructively sampled and the number of adult tillers (flowering and non-flowering) and vegetatively propagated daughter tillers were recorded. Daughter tillers were divided into two age classes, V0 and V1. Tillers classified as V0 were rhizomatous phytomers in their first year of belowground growth. They were typically achlorophyllous and had not yet produced leaves. V1 tillers were daughter tillers in their first season of aboveground production and typically had one or two partially developed and exserted leaves.

Tiller biomass and root production

Tussocks of control (undefoliated), early spring, fall, and chronic 1977 treatments were harvested during the last week of August, 1977. Tillers were counted and subdivided into leaf, sheath, stem base, and root components (Fig. 1). Individual sheath and stem base components were randomly subsampled for population biomass estimates.

Three tussocks from the early spring chronic defoliation treatment were covered with an opaque plastic tarp to prevent photosynthesis between clipping dates. These tussocks, termed "black bag" in figures, were checked periodically for leaf growth. When leaf production ceased, the tussocks were destructively sampled for the stem base and sheath components. The biomass of these structures, after leaf production ceased, was assumed to represent the approximate minimum dry weight biomass necessary for tiller growth and maintenance.

At the end of the second growing season (1977) tussocks from the early spring and fall defoliation treatments, along with control tussocks, were excavated down to permafrost to document the effects of the various treatments on root initiation, elongation, and distribution. The annual roots of *E. vaginatum* extended outward and downward beneath

Table 1. Dates of initial defoliation of *Eriophorum vaginatum*, treatment descriptions, and the number of clippings made before the final harvest in August, 1977

Date of initial defoliation		Multiple defoliation treatments and rest periods	Number of clippings			Parameters measured				
			1976	1977	total	Leaf growth	Below ground biomass	Reproduction	Survivorship	Root initiation and elongation
		Controls	0	0	0	x	x	x	x	x
1976	18 June	Early spring chronic – 2 yrs	6	6	12	x	x	x	x	x
		Early spring recovery – 1 yr rest	6	0	6	x	x	x	x	x
	3 July	Late spring chronic – 2 yrs	5	6	11	x				
		Late spring recovery – 1 yr rest	5	0	5	x				
	14 July	Summer chronic – 2 yrs	4	6	10	x				
		Summer recovery – 1 yr rest	4	0	4	x				
	28 July	Fall chronic – 2 yrs	2	6	8	x	x	x	x	x
		Fall recovery – 1 yr rest	2	0	2	x	x	x	x	x
1977	27 June	Chronic, 1977 – 1 yr	0	6	6	x	x	x	x	x

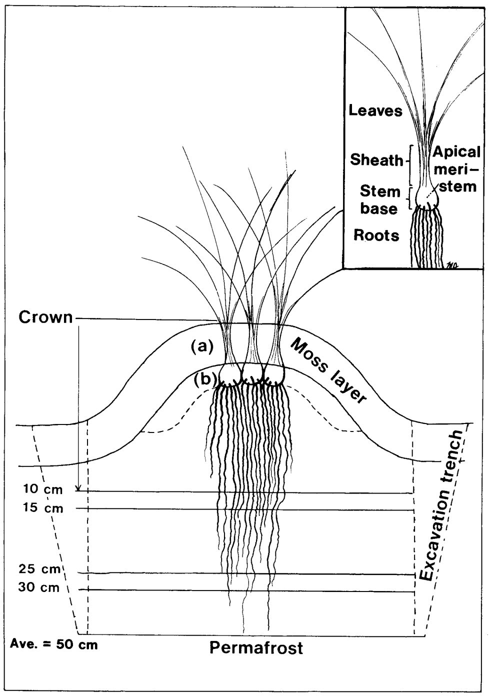

Fig. 1. A diagramatical, longidtudinal cross section of an *E. vaginatum* tussock. Apical meristems were protected by a layer of moss 8 to 15 mm deep *a*. Stem bases formed a nearly continuous layer at the moss-mineral soil interface *b*. Insert depicts a vegetative tiller illustrating how plant parts were separated for biomass determinations. Tussocks were excavated to permafrost and the number of roots penetrating from 10 to 15 and 25 to 30 cm below the tussock top (crown) were counted

the tussock, advancing behind the retreating permafrost, and were contained in an area that only slightly exceeded the aboveground tussock area. Roots of *E. vaginatum* were white, unbranched, and readily distinguished from roots of all other species in the community. The white color of these annual roots made it easy to distinguish between live and dead roots associated with each tussock. Large root diameters (0.8 to 1.0 mm) insured that nearly all *E. vaginatum* roots were removed from the soil.

The number of live roots per tiller was recorded for a subsample of 20 tillers from each tussock within each defoliation treatment. An estimate of root elongation and distribution throughout the soil profile was obtained by counting the number of roots passing through the soil horizons 10 to 15 and 25 to 30 cm below the tussock crown (Fig. 1). By dividing the number of roots counted in each layer by the number of tillers in the tussock crown, the mean number of roots per tiller at each of the two depth increments was determined. Total root biomass was estimated for four tussocks of each destructively sampled treatment. The entire cylinder of soil beneath each tussock, down to 30 cm, was removed. All *E. vaginatum* roots found were cleaned, rinsed, dried and weighed.

A Student's t-ratio (Haber and Runyon 1973) was utilized to test for significant differences between means. Significant differences were accepted at the 0.05 level of probability unless otherwise stated.

Results

Leaf production: chronic treatments

Leaf production following defoliation events during the first season were more a function of the time of season of initial clipping than the number of clipping events. Tillers that were defoliated early in the season produced less cumulative leaf biomass and more cumulative leaf length than did plants defoliated late in the season or control plants (Fig. 2). All defoliated tillers exserted significantly more cumulative leaf length than controls; however, only in the fall defoliation treatment was leaf biomass production significantly stimulated. By the time of the third defoliation in early season clipping treatments, tillers had produced only 50 to 58% of the amount of cumulative leaf biomass of control plants in spite of exserting 18 to 56% more cumulative leaf length. Plants within the fall defoliation treatment at the time of the third defoliation had produced 50% more cumulative leaf biomass per tiller and 12% more cumulative leaf length per tiller than control plants (Fig. 2). Trends in the cumulative leaf biomass of entire tussocks were nearly identical to trends for individual tillers (data not shown).

Leaf production in tillers subjected to multiple defolia-

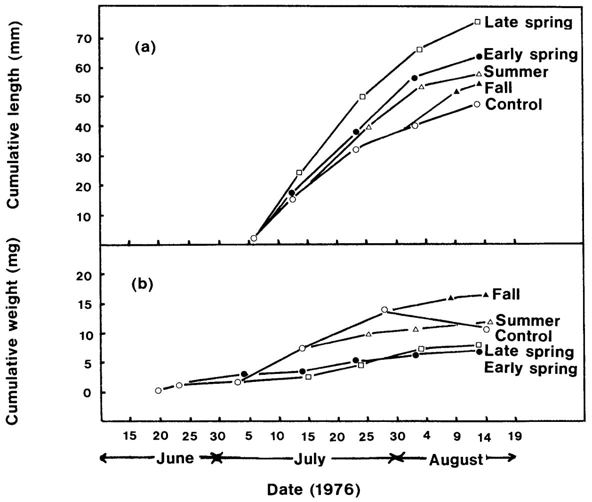

Fig. 2a, b. Mean cumulative change in leaf length **a** and weight **b** of control and tillers subjected to multiple defoliation during the first growing season (1976) ($n = 20$). Standard errors (omitted for clarity) averaged 4.8% and 7.4% of the mean values shown for length and weight determinations, respectively, and did not exceed 7.4% and 10.1%, respectively

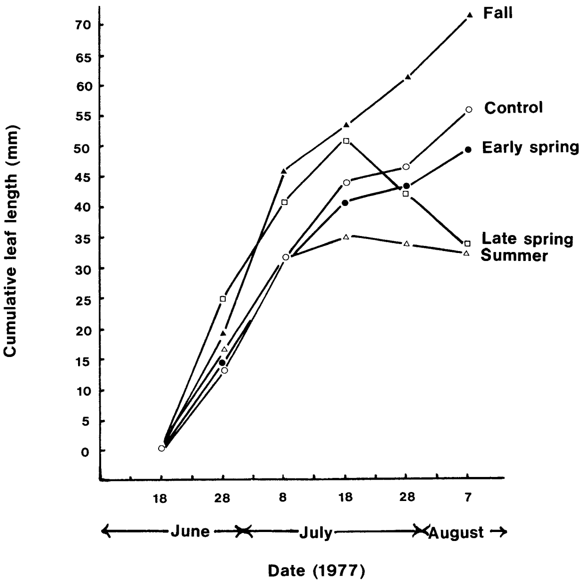

Fig. 4. Mean cumulative change in length of green leaf blades for *E. vaginatum* tillers repeatedly defoliated in 1976 and then allowed to recover in 1977 ($n = 10$). Standard errors (omitted for clarity) averaged 10.9% of the mean values shown and did not exceed 14.2%

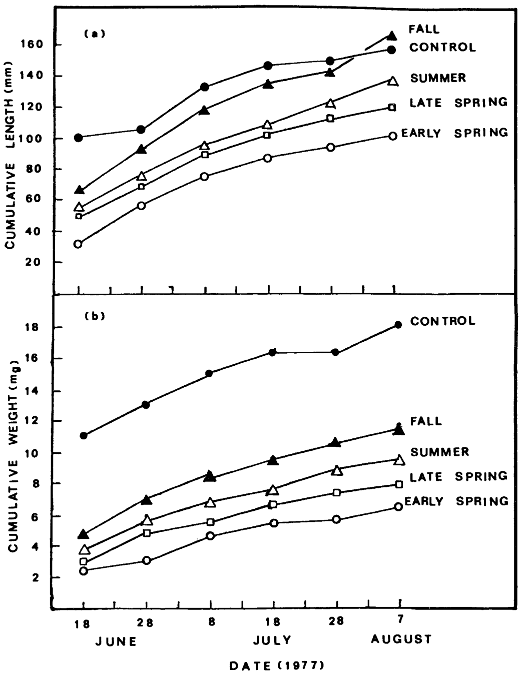

Fig. 3a, b. Cumulative amount leaf material exserted from individually selected tillers defoliated for the second successive growing season compared with undefoliated control tillers ($n = 10$). Standard errors (omitted for clarity) averaged 6.8% of the mean values shown and did not exceed 10.2%

tions in 1976 was markedly reduced during the second growing season. When clipping treatments were terminated on August 7, 1977, chronically defoliated tillers had 38 to 66% less leaf biomass and as much as 35% less leaf length than control tillers (Fig. 3). Trends in leaf biomass of entire tussocks were also comparable with trends described for individual tillers (data not shown). Leaf biomass per tussock was reduced by 56 and 46% in early spring and fall chronic defoliations, respectively. Tussocks defoliated in late spring and summer had intermediate quantities of leaf biomass.

Leaf production in defoliated tillers more closely approached that of controls in cumulative leaf length than in biomass. This indicated that leaf weight per unit length was reduced in tillers subjected to multiple defoliations. To examine this relationship more closely, recently exserted leaf material was collected on July 28 of the second season from tillers in the early spring clipping treatments and from control tillers ($N = 100$). Each leaf segment was measured for length and width, dried and weighed. Leaf widths of all samples were essentially equal, but recently exserted control leaf blades weighed an average of 0.91 mg/cm, whereas leaves from plants in the early spring treatment weighed 0.71 mg/cm. These differences were highly significant ($P < 0.01$).

Leaf production: recovery treatments

Trends in recovery, as indicated by leaf length measurements, varied markedly depending upon the time of season that defoliation was initiated (Fig. 4). The length of leaf tissue exserted by tillers subjected to multiple defoliation since early spring of the first growing season was comparable to the length of leaf tissue exserted by control plants. Tillers on which multiple defoliations were initiated later in the season (fall treatment) had stimulated leaf growth during the subsequent season of rest. Length of leaf blades exserted during the season of rest (1977) was depressed in plants from treatments that were initiated in the middle to latter part of the 1976 growing season. All previously

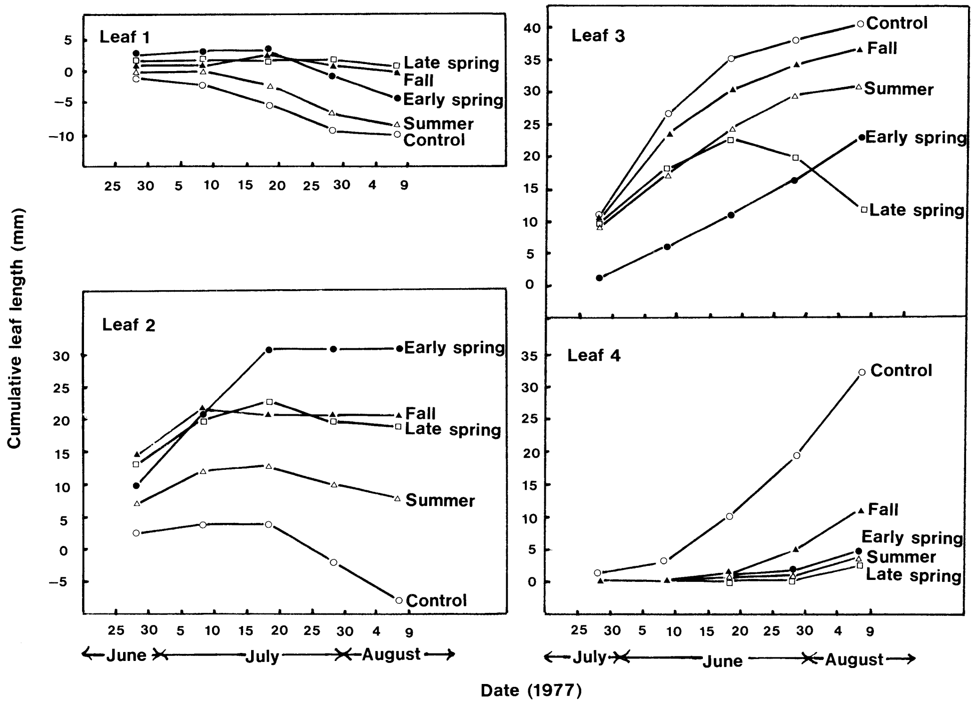

Fig. 5. Mean cumulative change in length of green leaf blades for *E. vaginatum* tillers defoliated and then allowed to recover in 1977 ($n=10$). Standard errors (omitted for clarity) averaged 9.6% of the mean values shown and did not exceed 12.1%

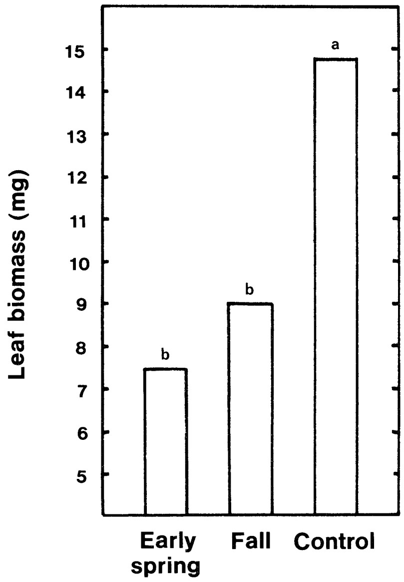

Fig. 6. Leaf biomass at the end of 1977 for control tillers and tillers recovering from multiple defoliations imposed the previous growing season (1976) ($n=20$). Standard errors averaged 8.2% of the mean values shown. Columns with the same letter above are not significantly different at $P<0.05$

clipped tillers, regardless of time of initial defoliation, retained older leaves longer than did control tillers (Fig. 5). However, growth and production of younger leaves (leaves 3 and 4) was inhibited and retarded.

Estimates of leaf biomass per tiller were obtained in mid-August at the time of final sample collection for the early spring, fall, and control treatments. Tillers that had been subjected to multiple defoliations since early spring or fall of the previous season had 48 and 41% less leaf biomass, respectively, than did control tillers (Fig. 6). Thus,

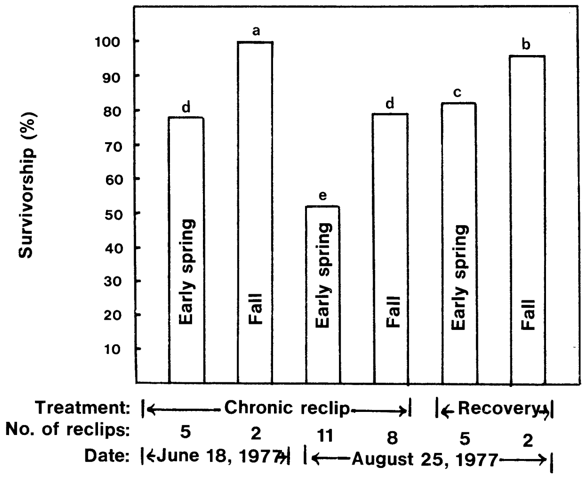

Fig. 7. Percentage of tillers on tussocks defoliated in 1976 that overwintered, then initiated and maintained growth at the beginning and end of the 1977 season ($n=10$ tussocks). Survivorship in a group of non-defoliated tillers (not graphed) was 98%. Standard errors averaged 0.27% of the mean values shown. Columns with the same letter above are not significantly different at $P<0.05$

the discrepancy that was noted between weight and length of leaf tissue exserted in tillers from the chronic treatments also existed in tillers that had received one year of rest.

Tiller survivorship

Of the tillers that were clipped beginning in the early spring, an average of 78% survived the first season, overwintered, and initiated growth the following spring (Fig. 7). All tillers in the fall chronic defoliation treatment survived the first year's defoliation. During the subsequent growing season, the number of tillers surviving repeated defoliation continued to decline. By the end of the second season of multiple

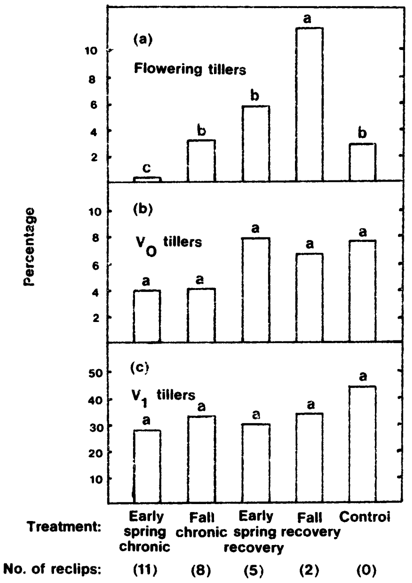

Fig. 8. Mean percentage of adult tillers initiating new (V0) or maintaining older (V1) daughter tillers or flowering buds at the end of the second season of clipping ($n = 80$). Standard errors averaged 30% of the mean values shown for flowering tillers and did not exceed 50%. Standard errors averaged 35% and 64% of the mean values for the V0 and V1 components, respectively, ranging up to 75% and 80%. Columns with the same letter above are not significantly different at $P < 0.05$

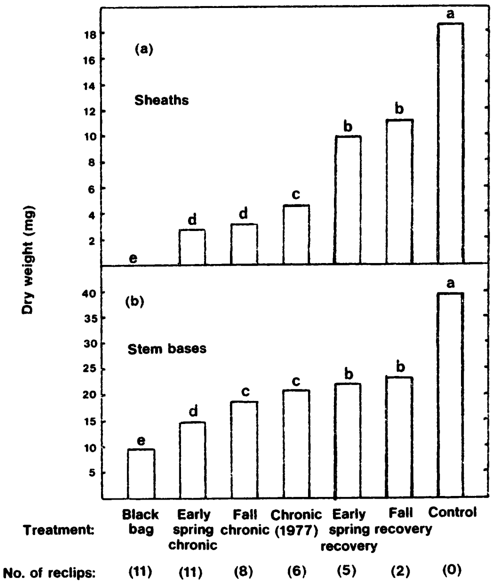

Fig. 9. Mean dry weight of live tissue in the sheath and stem base compartments at the end of the second season of clipping treatments ($n = 80$). Standard errors averaged 4.9% and 8.4% of the mean values shown for the sheath and stem base components, respectively. Columns with the same letter above are not significantly different at $P < 0.05$

Table 2. Effect of defoliation and subsequent recovery upon vegetative reproduction of *Eriophorum vaginatum*

Treatment	Daughter tiller production	
	Number/Parent	weight (mg/tiller)
Control	0.43a*	11.9a
Early spring		
Chronic	0.35a	2.9b
Recovery	0.38a	11.4a

* Column means followed by the same letter are not significantly different at $P < 0.05$

defoliation only 53% of the tillers in the early spring chronic treatment were producing or maintaining leaf-sheath tissue, compared to 79% in the fall chronic treatment (Fig. 7). Plants clipped only during the first season stabilized during the second season and no additional mortality was noted.

Tiller reproduction

Older (V1) daughter tillers were found on approximately 43% of the adult control tillers examined at the end of the second season of defoliation (Fig. 8). The percentage of defoliated adult tillers with this V1 age class of tillers ranged from 27% in the early spring chronic treatment to 33% in the fall recovery treatment. Recently initiated V0 daughter tillers were present on 7% of the control tillers and occurred on 4 to 8% of the defoliated adult tillers (Fig. 8). Although the production of V0 and V1 age classes of daughter tillers was lowest for defoliated tillers, the observed differences were not significant. Weights of daughter tillers were, however, substantially lower in tussocks subjected to multiple defoliations (Table 2).

Flower buds had formed on 2.5% of the control tillers examined. The percentage observed in controls was significantly greater ($P < 0.01$) than the percentage obtained in plants from the early spring chronic defoliation treatment (Fig. 8). The percentage of flowering tillers in the fall recovery treatment was significantly higher than the percentage observed for control tillers ($P < 0.01$) (Fig. 8). Tillers from the early spring recovery treatment also had a higher percentage of flowering individuals than controls. The observed difference was, however, significant only at $P = 0.10$.

Tiller biomass

Total production of *E. vaginatum* tillers was determined at the end of the second growing season by adding the mean cumulative leaf weight to the mean stem base and sheath weights. Defoliation treatments resulted in weight losses ranging from 70% in the early spring chronic treatment to 34% in the fall recovery treatment. Defoliated tillers produced less leaf biomass (Fig. 3) and had less weight in stem base and sheath components (Fig. 9). In general, the longer a tiller had been without leaves, the greater the weight loss.

Three tussocks from the early spring chronic treatment were covered with an opaque plastic tarp at the beginning of the second season (1977) to prevent photosynthesis in leaf tissue generated between clipping dates. By August 2, 1977, leaf production of plants in this treatment had ceased. The mean dry weights of these stem bases, 9.9 mg, was significantly lower ($P < 0.01$) than stem base weights from plants from any other treatment (Fig. 9). The stem base biomass at the time leaf production ceased probably repre-

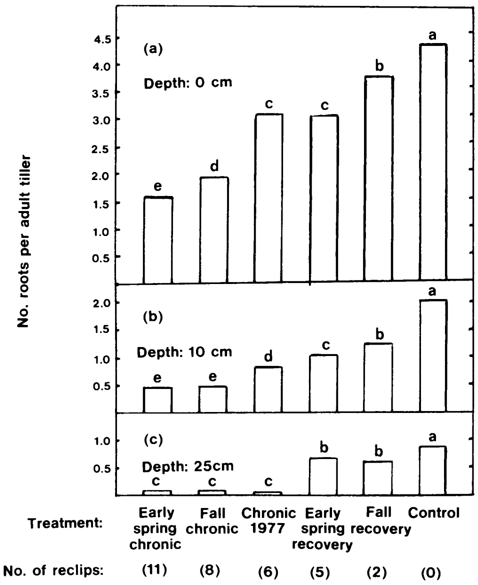

Fig. 10. Average number of roots per adult tiller initiated (depth = 0 cm) and penetrating to depths of 10 and 25 cm below the top of the tussock ($n = 20$ tillers for root initiation; $n = 10$ tussocks for depth of root penetration). Standard errors averaged 18.3%, 3.5%, and 3.0% of the mean values shown for the respective depths of 0, 10, and 25 cm. Columns with the same letter above are not significantly different at $P < 0.05$

sented the minimum stem base dry weight at which an *E. vaginatum* tiller could produce and maintain leaf tissue. In terms of percentages, this suggests that the average adult *E. vaginatum* tiller could lose as much as 75% of its normal stem base dry weight before failing to produce new leaf tissue. Sheath structures by this time had died (Fig. 9). Stem bases of plants in the early spring chronic clipping treatments were nearly 34% above this critical minimum level at the end of the second full season of multiple defoliations. Tillers from the fall chronic defoliation treatments were 46% above this critical level and stem bases of tillers defoliated for one entire growing season could have conceivably tolerated an additional 52% reduction in stem base dry weight.

Root production

Multiple defoliations significantly reduced root initiation, elongation, and biomass in *E. vaginatum* tillers. Control tillers had an average of 4.3 roots at the end of the growing season. After one or two seasons of multiple defoliation the average number of roots initiated per tiller declined to 3.1 and 1.6, respectively, reductions of 28 and 63%. Less severe defoliation treatments resulted in plants having intermediate numbers of roots (Fig. 10). Of those roots initiated and maintained by control tillers at the end of the season, 48% reached a depth of 10 cm, and 20% extended to 25 cm. In contrast, only about 25% of the roots of tillers subjected to multiple defoliation reached a depth of 10 cm and less than 5% penetrated to 25 cm (Fig. 10b and c).

Total root biomass per tussock was significantly lower in clipped tussocks than in unclipped tussocks. Root biomass was lowest in tussocks subjected to two entire season of leaf removal. These tussocks suffered an 85% reduction in root biomass. Tussocks in the least severe treatment, the fall recovery treatment, sustained a 24% reduction in root biomass (Table 3).

Table 3. Mean root biomass of *Eriophorum vaginatum* tussocks subjected to various defoliation treatments ($n = 4$). Differences in tussock size were standardized by proportioning root biomass to the number of tillers counted in the tussock crown

Treatment	Root biomass (g/tussock)
Control	1.65a*
Fall recovery	1.25b
Early spring recovery	0.72c
Chronic 1977	0.78c
Fall chronic	0.54d
Early spring chronic	0.24e

* Means followed by the same letter are not significantly different at $P < 0.005$

Discussion

Leaf production

Clipping experiments at Barrow, Alaska, showed that arctic graminoids were quite tolerant of chronic defoliation (Mattheis et al. 1976). Our results further suggest that tundra graminoids are capable of withstanding multiple, intensive, and frequent defoliation events. The initial, short-term response of *E. vaginatum* to a single defoliation was an increase in leaf production at the expense of belowground structures. In the first year of this study, despite multiple defoliation, production of leaf area remained higher than normal, although biomass of leaf tissue declined below that of controls. During the subsequent season of continued multiple defoliation, leaf growth and weight were depressed from 25 to 50% of control values depending upon the date when clipping was initiated. Declines in leaf production were accompanied by substantial weight losses in the stem base and sheath components, and a severe curtailment of root growth. Despite the severity of the clipping treatment, stem base weights were well above the apparent minimum mass necessary to sustain leaf production. Reserves might, however, have been depleted to the extent that overwinter survivorship would have been extremely low (McCarty and Price 1942; Smith 1964; Mooney and Billings 1965; Owensby et al. 1970).

Overall survivorship was quite high in all but those plants subjected to chronic defoliation for two consecutive growing seasons. Nearly 80% of the *E. vaginatum* tillers clipped for one and one-half growing seasons survived the treatment. Tillers clipped at 10-day intervals for one entire growing season and not at all the subsequent growing season did not sustain any additional mortality during the season of recovery. Goodman and Perkins (1968) dated ungrazed *E. vaginatum* tillers within tussocks in Wales and found that leaf production continued for three or four years, after which time the tiller initiated a terminal inflorescence and died. Given this chronology, it is conceivable that an *E. vaginatum* tiller can withstand severe defoliation pressures for 50 to 75% of its normal lifespan.

An examination of leaf growth dynamics suggests several ways in which the impact of defoliation on an *E. vaginatum* tiller might be minimized. Removal or damage to the apical meristematic tissue of graminoids typically results in a cessation of production and death of at least the aboveground portions of the tiller (Hyder 1972). Vegetative *E. vaginatum* tillers with apical meristems located 8 to 15 mm beneath the moss surface (Fig. 1) are likely to avoid such injury. In addition, the culmless growth habit of *E. vaginatum* insures that the apical meristem will not be elevated above the moss level. In years of high lemming population densities or in the case of heavy trampling by caribou, the moss cover may be disturbed and the apical meristems exposed. Meristem vulnerability will normally, however, be limited to flowering tillers which comprised less than 3% of the populations sampled.

In addition to the strategic location of the apical meristem, which enables vegetative *E. vaginatum* tillers to continue to produce leaf tissue regardless of the time of season of defoliation, the sequential pattern of leaf exsertion observed in *E. vaginatum* (Johnson and Tieszen 1976) may also be adaptive. By maintaining only a few living leaves at any one time, the tiller exposes a minimum investment of nutrients and energy to possible loss by grazing. Leaf replacement in *E. vaginatum* and other graminoids with similar strategies has been shown to be more rapid and efficient than leaf replacement in other growth forms following defoliation (Archer and Tieszen 1980).

While Mattheis et al. (1976) noted a shift in production toward younger leaves in *Dupontia fischeri* following defoliation, we observed a preferential growth and an extended longevity of older leaves in defoliated *E. vaginatum* tillers and a relative decline in the production of younger leaves (Fig. 5). The extended longevity of older leaves on the tillers may benefit plants recovering from defoliation in several ways. Older leaves export more photosynthate and nutrients than younger leaves (Williams 1964; Davidson and Milthorpe 1966; Wardlaw 1968), and their maintenance may be more metabolically economical than the biosynthesis of new leaf material, especially if the normal decline in photosynthetic rate typically associated with leaf aging were postponed (Hopkinson 1966; Hodgkinson et al. 1972; Gifford and Marshall 1973). Photosynthetic rates of these older leaves may even be rejuvenated to rates comparable to those of younger leaves. Detling et al. (1979, 1980) found that leaves remaining or produced after defoliation of blue grama (*Bouteloua gracilis*) tillers had higher photosynthetic rates than leaves of control plants. Also, older leaves are usually less palatable than younger plant parts (Kamstra et al. 1968; Rockwood 1974). Therefore, the probability of the tiller being regrazed during the recovery period might be significantly reduced.

The low leaf weight to length ratio of regenerated foliage suggests that defoliated *E. vaginatum* tillers allocated less of their stored reserves and photosynthate to structural leaf materials such as cell walls and lignin, thus maintaining a relatively high leaf area with a decrease in mass. Superficially, such a conservation measure would appear to result in the production of leaves that might be more palatable to herbivores. In addition, nitrogen, phosphorus, and potassium concentrations were higher in new leaves produced after defoliation than in newly initiated leaves of control tillers (Chapin 1980). Unless the desirability of regenerated foliage were offset by increased levels of secondary compounds, previously grazed tillers might have a higher probability of being regrazed at a later date. We have observed a 30 to 40% increase in the phenolic content of regenerated foliage of previously clipped *Carex aquatilis*, another arctic graminoid (Rhodes and Archer, unpublished). However, a preliminary screening of leaf tissue from previously clipped *E. vaginatum* tillers revealed that the phenolic content of this regenerated foliage was only 2 to 4% higher than levels observed in control tillers.

Reproduction

The rate of vegetative tiller production was not significantly depressed by even two years of chronic defoliations (Table 2, Fig. 8). In contrast, most studies in which grass plants were clipped or grazed have shown that vegetative tillering was markedly reduced (Troughton 1957; Ellison 1960; Jameson 1963) and quantitatively related to the severity of clipping (Davis 1960; Baker and Hunt 1961). Stimulation of tillering might be expected if apical meristematic tissue were disturbed (Youngner 1972). However, all apical meristems remained intact in our treatments. Allocation of carbon to tillers nevertheless was affected.

The average weight of daughter tillers produced by plants in the early spring chronic defoliation treatment was only 25% that of the controls (Table 2). Such low daughter tiller biomass suggests that the success of vegetative reproduction following multiple defoliations might be quite low. One season of rest was, however, sufficient to restore biomass production of the vegetative propagules to levels comparable to those observed in the control tillers.

The results of this study also suggest that under extreme defoliation pressures, populations of *E. vaginatum* may experience an indirect loss of sexual reproduction because of lowered plant vigor and depletion of stored energy and nutrient reserves. In this regard, Tikhomirov (1959) and Smirnov and Tokamakova (1971, 1972) observed that lemming grazing suppressed flowering in several arctic graminoids. In addition, direct losses of reproductive primordia because of preferential grazing may occur. Spetzman (1959) noted that *E. vaginatum* was utilized by caribou, especially during the flowering period, and Pearsall (1950) mentioned that deer and sheep grazed young flowering shoots of *Eriophorum*. In an environment such as the arctic tundra, where sexual reproduction is already severely limited, such grazing, induced losses may be of some significance.

The stimulation of flowering noted in less severe defoliation treatments (Fig. 8) may be of some adaptive significance and the result of an interaction between the time of season of defoliation and the level of reserves and nutrients in storage tissue. When reserve levels decline to a certain level, the remaining reserves may be diverted toward flower initiation rather than to leaf tissue. Such a change in allocation patterns would serve to perpetuate the species. The short-term growth of the individual tiller would be sacrificed if, as a result of grazing or other biotic or abiotic factors, the environment were chronically unsuitable for vegetative growth for some period of time. However, such a depletion of nutrients and reserves presumably would have to occur at a time in the growing season when photoperiod or light intensity would facilitate floral induction (Teeri 1974). The altered patterns of leaf and root growth and development observed in *E. vaginatum* following defoliation may have upset hormonal balances in favor of flower initiation if defoliations occurred at critical periods in the growth stage of the tiller. Damage to the plant parts is one of many factors that can alter sexual expression in plants (Helsop-Harrison 1957) and result in a variety of compensatory reproductive responses (Hendrix 1979). Perhaps defoliations imposed at certain intensities and frequencies can cause *E. vaginatum* tillers to change from a vegetative to a sexually reproductive mode. Struik (1967) has also noted that for several forb species, individuals subjected to various degrees of grazing had a higher percentage of floral initiation than did ungrazed plants.

Root production

Cessation of root growth and substantial decreases in root respiration and nutrient uptake rates following defoliation have been shown in several glasshouse studies (Jameson 1963; Davidson and Milthorpe 1966; Evans 1972; Bokhari 1977) and have been interpreted as a consequence of a shift in allocation of reserves to shoot growth to restore a favorable root/shoot ratio. In *E. vaginatum*, substantial reductions in root initiation and elongation (Fig. 10) and biomass accumulation (Table 3) resulted from chronic defoliation treatments. In addition, Chapin and Slack (1979) noted decreased root weight per unit length for *E. vaginatum*. Thus, roots of defoliated *E. vaginatum* tillers responded somewhat like leaves, in that relatively high surface areas were maintained despite a decrease in biomass.

The decreased elongation of roots would seem to be especially deleterious to *E. vaginatum* tillers. Typically, the annual roots of *E. vaginatum* follow the retreating permafrost (Wein 1968; Wein and Bliss 1974; Chapin et al. 1979). In so doing, the roots are in a position to more effectively absorb soil nutrients released by the alternating freezing and thawing at the soil-permafrost interface or to absorb nutrients accumulated in water draining along the permafrost surface. Multiple clippings eventually prohibited the normal downward extension of *E. vaginatum* roots and in so doing, might have resulted in nutrient limitations for plant growth and recovery. Grazing simulations at Barrow, Alaska, suggest that leaf growth following defoliation may deplete nutrient reserves more than carbohydrate reserves (Chapin 1977). Thus, root activity and associated nutrient uptake following defoliation must be maintained if photosynthetic leaf tissue is to be successfully reestablished. In fact, shoots that regrew following defoliation had even higher nutrient concentrations than newly initiated leaves of control tillers (Chapin 1980). As it turns out, the initial response of *E. vaginatum* roots to foliage removal was an icreased weight-specific respiration rate, accompanied by an increased rate of nutrient uptake (Chapin and Slack 1979). Only after four defoliations spaced at 10-day intervals did root nutrient uptake rates decrease to below control levels. It was at this same intensity that root tip mortality was observed to increase from 35 to 90%.

Tiller biomass: chronic defoliations

The more often plant foliage was removed, the longer the tillers went with reduced photosynthetic input. Thus, tiller response over the longer term became a function of the number of defoliations rather than the time of season for treatment initiation. The longer the plant went with reduced photosynthetic input, the greater the weight losses in storage organs (Fig. 9). Such weight losses represent expenditures of stored reserves (Hickman and Pitelka 1975; Buwai and Trlica 1977). As reserves were expended, root initiation and elongation (Fig. 10) and leaf production (Fig. 3) declined. Tiller weight losses continued until the stem base lost about 75% of its weight. By this time the sheath had died and leaf production had ceased. However, even after defoliation at 10-day intervals for two growing seasons (12 clippings), *E. vaginatum* stem bases were still 34% above the apparent minimum weight necessary to sustain tiller growth and maintenance. Tillers defoliated for one and one-half seasons or for one season were 46 and 52%, respectively, above this critical minimum biomass (Fig. 9).

Tiller biomass: recovery treatments

Tillers subjected to late season defoliations (those initiated in mid to late July) were impacted to the same degree as tillers subjected to early season defoliations (those initiated in early June), even though the tillers of late season regimes had been subjected to three fewer clipping events. One season of rest was not sufficient time for any of the defoliated tillers to completely regain the biomass losses resulting from defoliation (Fig. 6 and 9; Table 3). Trlica et al. (1977) found that blue grama plants receiving three heavy defoliations (90% leaf removal) required two years of rest to regain vigor ratings and total nonstructural carbohydrate levels comparable to those of control plants. Tillers receiving six heavy multiple defoliations did not fully recover in the two-year rest period. Neither group of tillers fully recovered herbage yields during the two-year rest period. In this study, tiller mortality was generally higher for plants clipped early in the growing season (Fig. 7), but those tillers that did survive initiated growth early and recovered nearly as well as did tillers that were clipped only later in the growing season. Neither group, however, achieved total recovery during one growing season of rest. Leaf biomass (Fig. 6) and sheath and stem base weights (Fig. 9) were quite comparable for tillers defoliated early and late in the growing season. However, root initiation and elongation (Fig. 10) and biomass (Table 3) were more severely impacted by early season defoliations.

In terms of leaf biomass and the biomass of storage organs, it appears that *E. vaginatum* can withstand more defoliation events when those events are initiated early in the growing season. Compared to June defoliations (six clippings), acute and chronic leaf removal near the end of July (three clippings) had a comparable impact on tillers and their ability to recover the following season. Because the seasonal course of carbohydrate storage is generally inversely related to herbage growth (see review by Trlica and Singh 1979), defoliations that occur at the end of peak leaf production may occur before reserve stores have been replenished. If leaf tissue is removed at this time, a further depletion of reserves would result if regrowth occurs, and carbohydrate levels may not be replenished before the end of the growing season. The following spring, the tiller must then initiate growth with lower than normal reserve levels. Coyne (1969) studied seasonal trends in total available carbohydrates with respect to phenological stage of development and concluded that plant vigor depends upon the amount of carbohydrate reserves stored at the end of the growing season. Trlica and Cook (1971, 1972) and Menke (1973) found that severe defoliation of several semi-arid range species was especially detrimental if defoliations occurred when plants were rapidly replenishing their reserves, usually near maturity. Plants defoliated near the time of maximum leaf exsertion usually produced little regrowth, hence little photosynthetic tissue was present during the normal period for carbohydrate storage.

Finally, we postulate that defoliations that occur later in the growing season, for example August, should have a lesser impact than June and July defoliations. By August, reserves expended to generate leaf tissue earlier in the season would have been largely replenished. Trlica et al. (1977) defoliated blue grama and western wheatgrass (*Agropyron smithii*) tillers during several stages of phenological development and found that defoliations imposed very late in the growing season, during quiescence, had the least effect on herbage yield and vigor in subsequent growing seasons. However, removal of leaves before nutrients could be translocated out prior to fall die back may adversely affect tiller growth the following season.

Acknowledgements. This work was supported by NSF Grant DPP-7512944 as part of the RATE (Research on Arctic Tundra Environments) program. The outstanding field assistance provided by G. Archer, M. Slack, D. Smith and J. Trudell is very much appreciated. We also thank F.S. Chapin and Douglas Johnson for their active collaboration and J.K. Detling and M.J. Trlica for their critical review of the manuscript.

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Received June 12, 1982