EFFECTS OF REMOVAL OF NEIGHBORING SPECIES ON GROWTH, NUTRIENTS, AND MICROCLIMATE OF *ERIOPHORUM VAGINATUM*

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ABSTRACT

The effect of removal of moss and low-growing shrubs on the growth of the tussock-forming cotton sedge *Eriophorum vaginatum* was studied at Eagle Creek in central Alaska. Shrubs and/or moss were removed from heavily infested tussocks with greater or lesser amounts of self-shading. Removal of moss produced little effect. Removal of shrubs resulted in an increase in the irradiance at the tussock surface and increases in tussock temperatures on afternoons of clear days. Tussocks with less self-shading also received more irradiance and showed higher temperatures. Tussocks from which shrubs had been removed produced many more daughter tillers and had smaller adult tillers than did the controls. Tussocks with less self-shading produced more daughter tillers than tussocks with more self-shading.

Shrub removal caused increases in concentration of potassium in tillers, but did not change the concentration of nitrogen, phosphorus, magnesium, calcium, total nonstructural carbohydrates, and micronutrients.

The results of the experiment indicate that shrub removal did not greatly affect the nutrient regime of the tussocks. Instead, most of the results of shrub removal can be attributed to alterations of the radiation regime of the tussocks. Increased tiller production probably resulted from changes in light quantity, light quality, or the direct effect of increased temperatures in the meristematic region.

The combination of shading by shrubs and self-shading may have important effects on the vegetative demography of *E. vaginatum* and on macro- and microsuccession in tussock tundra.

INTRODUCTION

The effects of competition on plants that live in stressful environments are poorly known. Grime (1979) discussed the competitive ability of plants that grow in stressful environments vs. plants that do not, but did not address the question of competition between plant species that have apparently equal abilities to survive unfavor-

able conditions. Most research on competition in stressful environments has focused on desert plant communities (Woodell et al., 1969; Yeaton and Cody, 1976). These studies demonstrated the possibility of interference between neighboring plants through competition for water. Fonteyn and Mahall (1981) showed that plants of *Larrea tridentata* and *Ambrosia dumosa* growing in the Mojave Desert had a negative effect on the water potentials of

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their neighbors. They concluded that interference between neighboring plants could have important effects on the structure of desert communities.

Much less is known about competition in arctic or alpine ecosystems. Savile (1960) suggested that competition was insignificant in the sparse vegetation of the Canadian Arctic Archipelago. However, Griggs (1956) found striking differences in the capacity of cushion plants of alpine tundra of Colorado to invade and eventually take over the sites occupied by other species. The present study examined the interaction between cotton sedge, *Eriophorum vaginatum* L., a dominant sedge of tussock tundra in northern Alaska, and neighboring plant species. Recently disturbed areas are first colonized by *E. vaginatum* which forms tussocks composed of many closely packed tillers (Chapin and Chapin, 1980). Later, the tussocks are colonized by a mixture of mosses and low-growing shrubs. *Eriophorum vaginatum,* however, remains an important component of the plant community (Wein and Bliss, 1973, 1974). This sequence contrasts with succession in old fields of temperate zones where the pioneer species disappear soon after initial colonization.

The first objective of this study was to determine the effect of colonization by other species on the growth and tiller demography of *E. vaginatum.* The second objective was to understand the mechanisms responsible for the changes in growth and demography. Two hypotheses were formulated: (1) Availability of mineral nutrients would be reduced as a consequence of the colonization by shrubs and mosses. Reduced nutrient availability would reduce growth of *E. vaginatum.* Mineral nutrients, particularly nitrogen and phosphorus, have been shown to limit primary productivity of *E. vaginatum* as well as other tussock tundra species (Shaver and Chapin, 1980). The shrubs would compete in the root zone with the roots of *E. vaginatum,* while the mosses would intercept nutrients brought in by precipitation or by leaching (Van Cleve et al., 1981). (2) Colonization by shrubs or moss would reduce the amount of solar radiation reaching the tussocks and thereby reduce tussock temperature as well as the amount of light available for photosynthesis. Both of these changes would be expected to reduce growth. Furthermore, decreased temperatures because of shading would reduce decomposition and thereby reduce nutrient availability to the tillers.

To test these hypotheses, a removal experiment was set up in June 1978, in tussock tundra in central Alaska. The experiment was followed for three growing seasons until August 1980 to allow time for the treatments to have an effect. Such experiments have been used to evaluate interspecific competition (Fowler, 1981), community response in old fields (Pinder, 1975; Allen and Forman, 1976; Hils and Vankat, 1982), and competition for water in the Mojave Desert (Fonteyn and Mahall, 1981).

METHODS

The study was performed near Eagle Creek in central Alaska. Descriptions of the site are given by Shaver and Chapin (1980) as well as in Chapin et al. (1979), Wein and Bliss (1974), and Shaver and Cutler (1979). In addition to the graminoids *E. vaginatum* and *Carex bigelowii* Torr., the shrubs *Vaccinium vitis-idaea* L., *V. uliginosum* L., *Rubus chamaemorus* L., *Ledum palustre* ssp. *decumbens* L., and *Betula nana* L. are also abundant. Common mosses include *Sphagnum* spp., *Dicranum* spp., and *Polytrichum* spp.

The experiment was performed on tussocks of Class III and IV (Fetcher and Shaver, 1982). Class III tussocks have 10 to 50% cover of moss and shrubs, while Class IV tussocks have 50 to 97% cover. Tussocks of Classes I and II (<10% cover of moss and shrubs) did not have enough moss and shrubs to be included in the experiment, while tussocks of Class V (>97% cover of moss and shrubs) did not have enough *E. vaginatum.*

In early June 1978, 16 Class III and 16 Class IV tussocks of *E. vaginatum* were assigned randomly to one of four treatments: control, shrub removal, moss removal, or both shrub and moss removal. The experimental design was a three-way factorial analysis of variance with initial tussock class (III or IV), shrub removal, and moss removal as factors. Four replicate tussocks were used in each cell of the design. Moss was carefully removed by hand plucking, while shrubs were cut off at the surface of the tussock (Figure 1). Tillers of *C. bige-* *lowii* and lichens were removed from all the tussocks, so that all tussocks received some amount of disturbance. A slice 20 cm deep was made with a serrated knife around the outside of the tussocks from which shrubs had been removed to sever roots and rhizomes of shrubs whose tops were outside the tussock. The slice was made at the beginning of the growing season before any of the current-year roots of *E. vaginatum* had penetrated to the region of the slice (Chapin et al., 1979). When regrowth of shrub or moss shoots occurred, the regrowth was removed.

In each tussock, ten tillers were chosen haphazardly and tagged in early June 1978. A pencil was poked into the tussock and the nearest adult tiller (Figure 2a) was tagged. Adult tillers were identified by the presence of a brown senescence band on one or more leaves indicating that the tiller had survived at least one winter (Fetcher and Shaver, 1983). Approximately equal numbers were tagged in the center and edge regions of each tussock. Length of the longest leaf and the number of green leaves were recorded in early June and early August of 1978, 1979, and 1980. Leaf length was measured from the top of the leaf sheath to the top of the green portion of the blade. Length of any senescent portion of the leaves was recorded. At the end of each growing season, the number of daughter tillers produced by each tagged tiller was recorded, as well as the number of tillers that had formed inflorescence buds (Figure 2b) or died.

In 1979 and 1980, total growth in length of leaves was

measured from the top of plastic sticks that were stuck in the tussock next to each tiller. A ruler was placed on the top of each stick and the length of each leaf was measured in early June, early July, and early August. The sticks penetrated 5 cm into the tussock and were held firmly by a barbed point. Thus they were unlikely to have changed position over the growing season. Gartner (1982) found that toothpicks placed in different microsites in tussock tundra at Toolik Lake in northern Alaska were infrequently disturbed between late May and late September.

An index of tiller size was calculated as the product of the number of green leaves and the length of the longest leaf. This index was highly correlated with dry mass of tillers ($r = 0.90$, $p < 0.0001$).

In August 1980, 25 adult tillers (sheaths and green leaves only) were harvested from the center of each tussock following methods of Chapin et al. (1979) and Shaver and Chapin (1980). All daughter tillers and tillers with inflorescence buds that were encountered while harvesting 25 adults were also harvested (Goodman and Perkins, 1968; Chapin et al., 1979; Shaver and Chapin, 1980). The tillers were dried at 65°C and weighed. The following quantities were recorded or calculated: mean mass of adult tillers, inflorescence buds, and daughter tillers and number of buds produced per 25 adults.

Two indices of daughter tiller production were calculated. The first was the number of daughter tillers per adult tiller (N_D/N_A). The second was mean mass of daughters divided by mean mass of adults ($M_D N_D^{-1}/M_A N_A^{-1}$), which was a measure of the size of the average daughter tiller as a fraction of the size of the mother. Tillers that produced inflorescence buds were added to the 25 adult tillers for calculation of the various indices because tillers with buds could also produce daughter tillers.

The 25 adult tillers from each tussock were ground in a Wiley mill and analyzed for concentrations of total nonstructural carbohydrates (TNC), nitrogen, phosphorus, potassium, calcium, magnesium, and micronutrients on a dry weight basis. Total nonstructural carbohydrates were determined using the 0.02 N H_2SO_4 extraction (Smith, 1969). Nitrogen was determined using the micro-Kjeldahl method. After converting to dry ash, the residue was dissolved in concentrated hydrochloric acid, and phosphorus was determined colormetricly as the phosphomolybdate complex. Potassium was determined with flame emission photometry, while calcium, magnesium, manganese, zinc, copper, and iron were determined with atomic absorption spectrophotometry (Donohue and Gettier, 1980).

Tussock temperature was measured using a single copper-constantan thermocouple inserted at the base of the tillers 4 cm below the surface of each tussock (Figure 2c). Additional measurements were made at a depth of 16 cm. Temperatures were measured in July and August 1980 on several days with different sky conditions.

Light profiles were measured for each tussock under clear sky conditions (Figure 2c). Readings were taken for
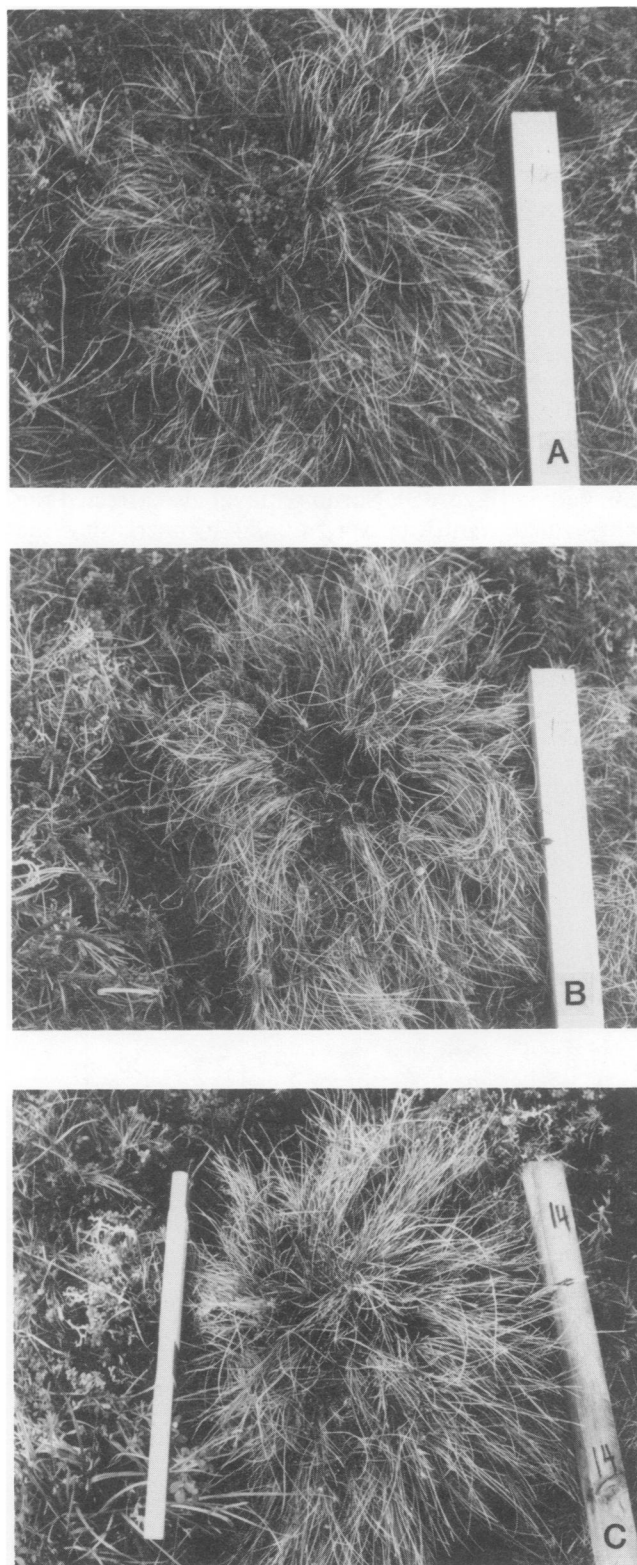

FIGURE 1. (a) Class III tussock of *Eriophorum vaginatum* in June 1978 before removal of shrubs and moss. (b) Same tussock immediately after removal of shrubs and moss. (c) Same tussock in August 1980 before final harvest.

26 tussocks beginning at 1230 solar time and ending at 1500 solar time 19 July 1980. The remaining six tussocks were measured between 0900 and 0940 on 20 July 1980. A ruler was placed perpendicular to the surface of each tussock and photosynthetic photon flux density (PPFD) was measured at heights of 15, 10, 5, and 2 cm above the tussock with a sensor for photosynthetically active radiation (Licor, Inc.). The sensor was pointed directly at the sun. Two profiles were measured for each tussock. The proportion of PPFD received at heights of 10, 5, and 2 cm was calculated by dividing the values for PPFD measured at those heights by the value measured at 15 cm, which was above the tussock canopy.

RESULTS

MICROENVIRONMENTAL MEASUREMENTS

There was a significant ($p < 0.05$) effect on light profile of the class to which tussocks belonged before treatments were applied (hereafter called initial tussock class). Class III tussocks with or without shrubs had a greater reduction in PPFD than did Class IV tussocks because the longer leaves of Class III tussocks produced greater self-shading (Figure 3). Shrub removal also affected the light profile significantly ($p < 0.05$) by increasing the amount of PPFD that penetrated to lower levels of the canopy of both Class III and Class IV tussocks (Figure 3). Because the amounts of PPFD and total solar irradiance are highly correlated, shrub removal allowed more irradiance to strike the tussock surface.

Temperatures at 4 cm depth were significantly higher on most occasions in Class IV tussocks than in Class III tussocks (Table 1). The longer leaves of the Class III tussocks intercepted more irradiance, which resulted in cooler tussock temperatures. This effect was observed whether or not shrubs were present. Shrub removal increased temperatures in both Class III and IV tussocks (Table 1). Differences between treatments were greater on the sunny days of 11 August and 18–19 July than on the overcast day of 13 August. No significant difference was found between treatments for temperatures at a depth of 16 cm (Table 1).

GROWTH OF TAGGED TILLERS

Analysis of covariance was used to analyze the growth of tagged tillers. The initial value of length of the longest leaf in June 1978 was used as a covariate for analyses of leaf length in August of 1978, 1979, and 1980. Similarly, the initial value for the tiller size index (length of longest leaf × number of leaves) was used as a covariate for the analyses of tiller size index.
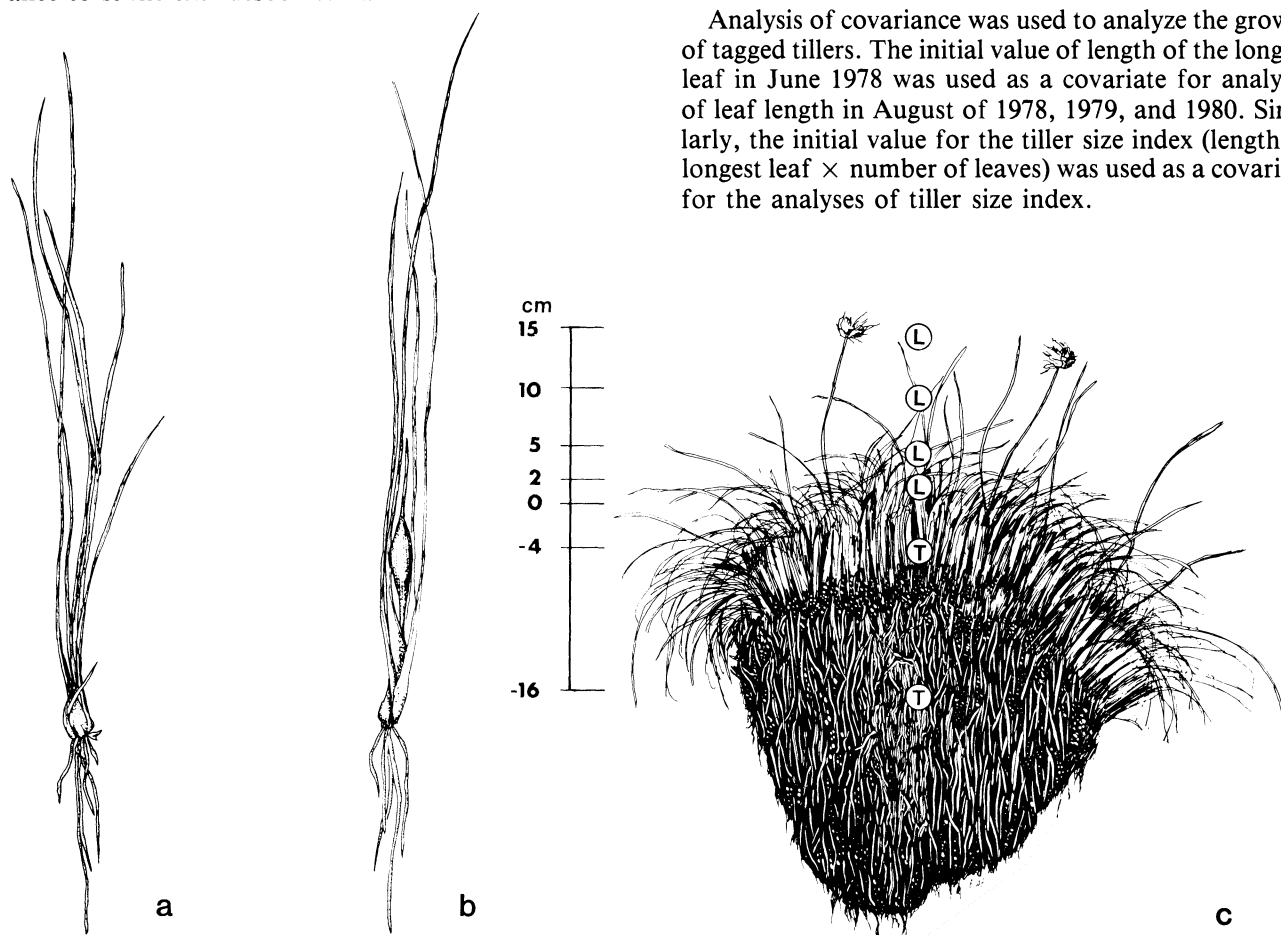

FIGURE 2. (a) Adult tiller of *Eriophorum vaginatum* with daughter tiller. (b) Inflorescence bud of *Eriophorum vaginatum*. (c) Cross-section of tussock of *Eriophorum vaginatum* showing location of temperature measurements (T) and light measurements (L).
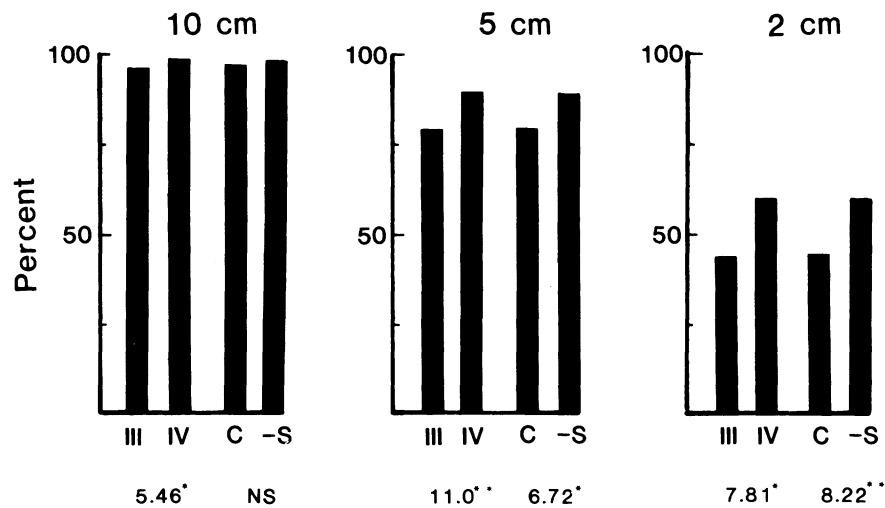
FIGURE 3. Means for main effect of initial tussock class and shrub removal on photosynthetic photon flux density (PPFD) at 10, 5, and 2 cm in the canopy of tussocks of *Eriophorum vaginatum* as a percentage of the PPFD measured at 15 cm. Each mean for main effect of initial tussock class includes control tussocks, shrub removal tussocks, moss removal tussocks, and shrub and moss removal tussocks. Similarly, each mean for main effect of shrub removal includes Class III tussocks with moss, Class III tussocks without moss, Class IV tussocks with moss, and Class IV tussocks without moss. III, Class III tussocks; IV, Class IV tussocks; C, tussocks with shrubs; -S, tussocks from which shrubs had been removed. Numbers below each pair of bars are the F-ratios for that effect from analysis of variance. $*p<0.05$; $**p<0.01$.

TABLE 1

Means for main effect of initial tussock class and shrub removal on temperature (°C) at depths of 4 and 16 cm in tussocks of E. vaginatum *on 18 and 19 July and 11 and 13 August 1980*[a]

Solar time (depth)	Class III	Class IV		Control	Shrub removal	
18 July						
0915 (4 cm)	12.2	13.9	(5.47*)	12.4	13.7	(NS)
1155 (4 cm)	14.6	16.3	(9.02**)	14.5	16.4	(9.67**)
1325 (4 cm)	14.9	16.4	(9.44**)	14.7	16.6	(15.7***)
1405 (16 cm)	8.0	8.9	(NS)	8.4	8.6	(NS)
19 July						
1005 (4 cm)	13.8	15.6	(7.49*)	13.8	15.6	(7.24*)
1335 (4 cm)	15.8	17.6	(10.8**)	15.3	17.9	(24.9****)
1625 (4 cm)	15.1	16.3	(12.3**)	14.8	16.7	(32.0****)
11 August						
0900 (4 cm)	14.4	17.3	(5.77*)	15.2	16.6	(NS)
1200 (4 cm)	19.1	22.7	(9.49**)	19.4	22.0	(6.16*)
1500 (4 cm)	17.5	19.6	(19.2***)	17.7	19.4	(12.9***)
1800 (4 cm)	15.3	15.8	(NS)	15.1	16.0	(9.67**)
1230 (16 cm)	10.2	11.1	(NS)	10.4	10.8	(NS)
13 August						
0905 (4 cm)	11.3	12.0	(NS)	11.6	11.8	(NS)
1200 (4 cm)	12.2	13.0	(8.89**)	12.3	12.8	(NS)
1455 (4 cm)	11.4	11.8	(6.58*)	11.4	11.8	(6.58*)
1755 (4 cm)	10.2	10.1	(NS)	10.1	10.2	(NS)
1230 (16 cm)	9.0	9.0	(NS)	9.2	8.8	(NS)

[a]F-ratio and level of significance are shown next to pairs of means. $*p<0.05$; $**p<0.01$; $***p<0.001$; $****p<0.0001$; NS, not significantly different.

Class III tussocks had longer leaves in June 1978 than Class IV tussocks (89 mm vs. 81 mm, $F = 4.35, p<0.05$). After adjusting for the initial size of the tagged tiller, I found that initial tussock class did not greatly affect length of the longest leaf and the tiller size index. In other words, the effect of initial tussock class on tiller size did not change greatly over the course of the experiment, although there was a general decline in the size of tillers of all tussocks. Only in August 1979 was there a significant effect of initial tussock class on length of the longest leaf ($F = 10.6, p<0.01$). At that time, Class III tussocks had longer leaves than Class IV tussocks.

In August of all three years, length of the longest leaf in both Class III and IV tussocks was reduced as a result of shrub removal (Figure 4). Shrub removal reduced the tiller size index in both Class III and IV tussocks in August 1979 and 1980. Analysis of covariance showed

a statistically significant interaction ($F = 4.96, p<0.05$) between initial tussock class and shrub removal in August 1980. Mean difference between length of the longest leaf in June 1978 and August 1980 was 55 mm for Class III tussocks with shrubs and 27 mm for Class IV tussocks with shrubs. For tussocks from which shrubs had been removed the mean difference was 3.3 and 3.6 mm for Class III and Class IV tussocks, respectively. Hence, the interaction was the result of a greater reduction in length of the longest leaf for Class III tussocks than for Class IV tussocks.

Extension growth, defined as the total length of new leaves per tiller, was significantly reduced as a result of shrub removal in both 1979 ($F = 17.0, p<0.01$) and 1980 ($F = 13.0, p<0.01$). Mean extension growth in 1979 was 168 mm for tussocks that did not have shrubs removed and 114 mm for tussocks that had shrubs removed. In 1980 extension growth was 188 mm and 149 mm for tussocks with and without shrubs, respectively.

Number of green leaves was not affected by any of the treatments. This result is consistent with earlier observations that leaf production rates of *E. vaginatum* are remarkably constant (Fetcher and Shaver, 1983). Moss removal did not affect the growth of tillers at any time in the experiment.

DEMOGRAPHY OF TAGGED TILLERS

Number of daughter tillers per tagged tiller was calculated for 1978, 1979, and 1980, while number of dead tillers per tagged tiller was calculated for 1979 and 1980. In 1978 there was a statistical interaction between tussock class and removal of moss (Table 2); production of daughter tillers was highest in Class IV tussocks from which moss had been removed. In 1979, there was a three-way interaction between initial tussock class, shrub removal, and moss removal for production of daughter tillers (Table 2), but the overall pattern was for higher tillering rates to be found in tussocks from which shrubs were removed. In 1980 the only significant effect was associated with shrub removal, which resulted in increased tillering.

Tiller mortality in 1979 was affected by a three-way interaction between initial tussock class, shrub removal, and moss removal (Table 2). In 1980, tiller mortality increased as a result of shrub removal (Table 2). In general, there was an increase in tiller mortality due to shrub removal. When combined with the results for tillering, these results show that shrub removal increased the rate of turnover of the tiller population. Furthermore, the net rate of increase (number of daughter tillers minus number of deaths) was greater in tussocks from which shrubs had been removed than in control tussocks or those from which moss alone had been removed.
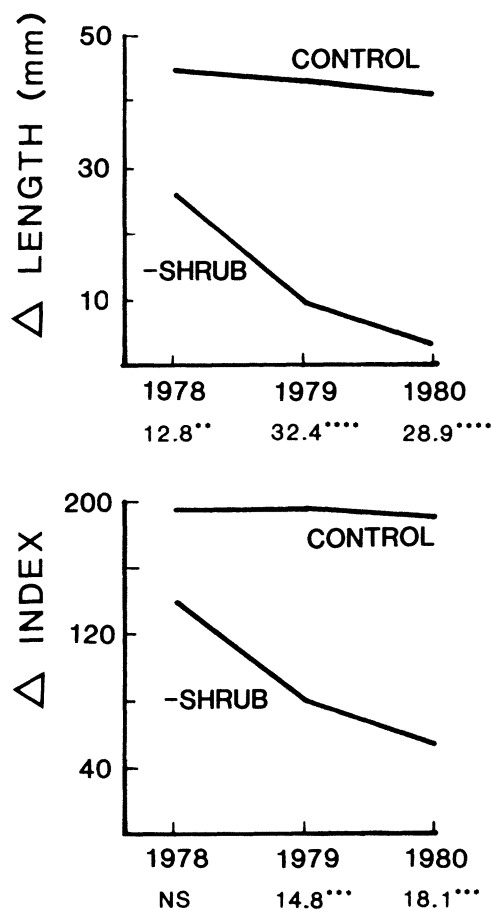

FIGURE 4. Mean differences between the length of the longest leaf of *Eriophorum vaginatum* tillers in August of 1978, 1979, and 1980 and the length in June 1978 ($\triangle$ LENGTH) and between the tiller size index (length of the longest leaf × number of leaves) in August 1978, 1979, and 1980 and the value in June 1978 ($\triangle$ INDEX) as a result of the main effect of shrub removal. Control, tussocks with shrubs; -Shrubs, tussocks from which shrubs had been removed. Numbers below each point are F-ratios for the effect of shrub removal from analysis of covariance. $**p<0.01$; $***p<0.001$; $****p<0.0001$.

HARVEST RESULTS

Total mass of adult tillers plus daughters and buds was not significantly affected by any of the factors. Mean mass of adult tillers, on the other hand, was affected significantly by initial tussock class ($F = 4.93, p<0.05$) and

shrub removal ($F = 6.92$, $p < 0.05$). Mean mass of adult tillers was 77 mg in Class III tussocks vs. 59 mg in Class IV tussocks. Similarly, it was 79 mg in control tussocks vs. 57 mg in tussocks from which shrubs had been removed. Mean mass of daughters and of inflorescence buds was not significantly affected.

There was a significant ($F = 20.8$, $p < 0.0001$) interaction between the effects of shrub and moss removal on the number of buds encountered while harvesting 25 adult tillers. The interaction was the result of greater production of buds in tussocks subjected to either shrub removal (3.5 buds/25 tillers) or moss removal (2.9 buds/25 tillers)

as compared to control tussocks (0.9 buds/25 tillers) or tussocks from which both shrubs and moss had been removed (1.1 buds/25 tillers). This result is an exception to the general rule of no effect of moss removal on tillers of *E. vaginatum*.

Number of daughter tillers per adult tiller (N_D/N_A) increased significantly as a result of shrub removal in both Class III and IV tussocks (Figure 5). In Class IV tussocks N_D/N_A was higher than in Class III tussocks (Figure 5). On the other hand, mean mass of daughter tillers divided by mean mass of adult tillers showed no response, being approximately 0.25 for all treatments (Figure 5). Therefore, the effect of initial tussock class and shrub removal was to reduce the size of tillers and to increase the rate of daughter tiller production, but the mean mass of daughter tillers as a fraction of the mass of adults was unaffected.

The effect of shrub removal was to change the allocation patterns for vegetative propagation. Instead of a few
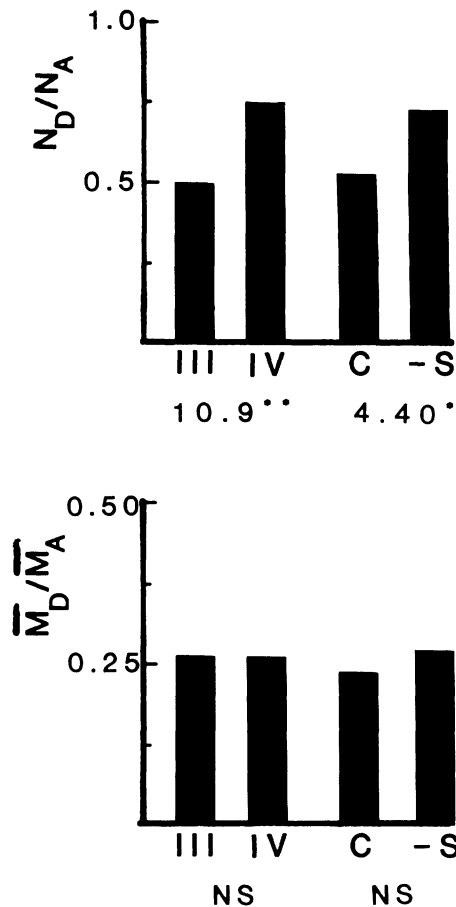
TABLE 2

Mean rates of daughter tiller production and tiller mortality as affected by initial tussock class, shrub removal, and moss removal in 1978, 1979, and 1980 for tagged tillers of Eriophorum vaginatum

Daughters/Adult		
1978		
Two-way interaction between initial tussock class and moss removal (6.03*)[a]		
	Class III	Class IV
Control	0.24	0.14
Moss removal	0.16	0.38

1979				
Three-way interaction between initial tussock class, shrub removal, and moss removal (6.29*)				
	Class III		Class IV	
	Control	Shrub removal	Control	Shrub removal
Control	0.44	0.32	0.20	0.80
Moss removal	0.34	0.53	0.59	0.73

1980	
Main effect of shrub removal (4.32*)	
Control	Shrub removal
0.62	0.99

Dead tillers/Adult				
1979				
Three-way interaction between initial tussock class, shrub removal, and moss removal (6.53*)				
	Class III		Class IV	
	Control	Shrub removal	Control	Shrub removal
Control	0.02	0.17	0.02	0.00
Moss removal	0.02	0.02	0.02	0.07

1980	
Main effect of shrub removal (5.95*)	
Control	Shrub removal
0.08	0.18

[a]Values in parentheses are F-ratios for a particular effect. $*p < 0.05$.

FIGURE 5. Means for main effects of initial tussock class and shrub removal on number of daughters per adult tiller (N_D/N_A) and mean mass of daughter tillers divided by mean mass of adults ($\bar{M}_D/\bar{M}_A$) for *Eriophorum vaginatum* tussocks. III, Class III tussocks; IV, Class IV tussocks; C, tussocks with shrubs; -S, tussocks from which shrubs had been removed. $*p < 0.05$; $**p < 0.01$; $****p < 0.0001$.

large daughter tillers being produced by large adult tillers, many small daughters were produced by smaller adults. Class III tussocks had lower values for N_D/N_A, but the absence of any significant interactions between initial tussock class and shrub removal indicated that the response of N_D/N_A to shrub removal was not mediated by the amount of shrub and moss cover initially present.

NUTRIENT CONCENTRATIONS

Of the macronutrients, only potassium appeared to be significantly ($F = 5.33$, $p < 0.05$) changed by the treatments. Its concentration increased from 0.53 to 0.62% in response to shrub removal, whereas the concentrations of Its concentration increased from 0.53 to 0.62% in response to shrub removal, whereas the concentrations of nitrogen, phosphorus, calcium, magnesium, and copper were unchanged. Total nonstructural carbohydrates were also unaffected.

Tillers from Class IV tussocks had significantly higher concentrations of the micronutrients zinc ($F = 4.47$, $p < 0.05$) and manganese ($F = 8.30$, $p < 0.01$) than tillers from Class III tussocks. In addition, there were significant interactions between initial tussock class and moss removal on concentrations of manganese ($F = 4.85$, $p < 0.05$) and iron ($F = 4.37$, $p < 0.05$). Oechel et al. (1983) found that several micronutrients including iron and molybdenum limited photosynthesis of vascular plants in tussock tundra at Eagle Creek. At present it is difficult to interpret the results for micronutrient concentrations that I found. Future studies may show that micronutrients play an unexpectedly important role in tussock tundra.

DISCUSSION

For the *E. vaginatum* tussocks in this study, most of the effects of removal of shrubs and mosses could be attributed to the removal of shrubs alone. The removal of shrubs caused significant changes in the amount of irradiance reaching the tussocks, the temperature regime, and tiller demography, whereas removal of moss appeared to affect the outcome of the analyses infrequently. For both Class III and Class IV tussocks, removal of shrubs caused the production of smaller, shorter tillers that produced more daughters of smaller size. In other words, the shrub removal treatment resulted in a decrease in the mean size of the tillers and an increase in their number such that overall production of biomass was unchanged. Similar results were reported by McGraw (1982) who found that removal of neighboring species increased the number of new shoots produced by *Dryas octopetala* growing on a fellfield near Eagle Creek, Alaska. However, McGraw (1982) did not find any changes in shoot size in response to removal.

Initial tussock class also had an effect on the outcome of some analyses. Class IV tussocks reached higher daytime temperatures than Class III tussocks, presumably because shorter leaves of *E. vaginatum* in Class IV tussocks allowed more incoming radiation to penetrate to the surface of the tussock. The effect of tussock class on tiller size and tussock temperature was the same whether or not shrubs were present. Thus, Class IV tussocks experienced less self-shading than Class III tussocks. The effect of less self-shading on tiller demography was similar to the effect of shrub removal. Class IV tussocks produced more daughter tillers than Class III tussocks.

The amount of vegetative cover appears to play a significant role in the temperature regime of a tussock, regardless of the type of cover. Both self-shading and shading by shrubs caused decreases in tussock temperature during the day. Self-shading and shading by shrubs caused equal reductions in temperature as shown by the lack of interaction between initial tussock class and shrub

removal. Thus, Class IV tussocks with shrub removal had the least shading and the highest temperatures, followed by Class III tussocks without shrubs and Class IV tussocks with shrubs, which had roughly the same temperature. Class III tussocks with shrubs were the coldest.

SHRUB REMOVAL AND PHYSIOLOGY OF *E. VAGINATUM*

What physiological factors contributed to the increased production of daughter tillers in the tussocks from which shrubs had been removed? The hypothesis that root competition from shrubs would reduce the availability of nutrients was not supported. Nitrogen and phosphorus concentrations did not change as a result of shrub removal. Furthermore, total production and shoot mass did not increase. Concentration of potassium did increase as a result of shrub removal. But potassium is not a limiting nutrient whereas nitrogen and phosphorus limit productivity of *E. vaginatum* at Eagle Creek (Shaver and Chapin, 1980).

On the whole, the results suggest that there were no changes in the availability of limiting nutrients. The possibility remains that the increase in concentration of potassium came about because all nutrients became more available, and that nitrogen and phosphorus were utilized by the tillers while potassium, which was not limiting, simply increased in concentration. However, such a pattern of utilization should have led to increased total production so the possibility appears somewhat remote.

The hypothesis that tussock growth would be reduced by shrub and moss colonization causing reduced temperature and light for photosynthesis was partially supported. Removal of shrubs increased the amount of total irradiance reaching the tussock, increased tussock temperature, and altered the rate of daughter tiller production.

At least three explanations are possible for the mechanism whereby changes in the radiation regime altered the pattern of vegetative propagation. (1) Increased light could have resulted in increased net photosynthesis, which would cause total production of TNC to increase as a re-

sult of shrub removal. This was not observed for the aboveground part of the plant, hence the explanation appears unlikely. (2) The increased temperatures found near the meristematic region could have increased metabolic rates and directly stimulated production of daughter tillers. The fact that tillering rate increased in this study without increases in concentration of nitrogen and phosphorus in adult tillers suggests that temperature acted directly. Total production of biomass of adult plus daughter tillers was not affected by any of the treatments. In other words, total primary production was not changed, instead photosynthates were shifted from the production of large tillers to the production of more, smaller tillers. In contrast, when tussock tundra was fertilized the size of adult tillers increased as well as the number of daughter tillers (Shaver and Chapin, 1980). (3) An altered radiation regime could affect vegetative propagation through changes in light quality. Deregibus et al. (1983) found that plants of *Lolium* spp. produced more tillers when exposed to light with a higher red/far-red ratio (R:FR). Increases in the red/far-red ratio could have produced the decreased leaf length of *E. vaginatum* tillers and the increased production of daughter tillers that was observed when shrubs were removed. Changes in light quality may also have been responsible for the increases in flowering when moss or shrubs were removed. Further investigation will be necessary before the relative importance of changes in light quality vs. changes in temperature regime can be established.

A possible mechanism that was proposed in the introduction is that increased temperature increased decomposition and made more nutrients available to the tillers and stimulated tillering. This hypothesis is not supported for the same reasons that the root competition hypothesis is not supported; namely, there was no change in the concentration of the limiting nutrients nitrogen and phosphorus as a result of shrub removal.

In conclusion, most of the evidence from this experiment suggests that, of the mechanisms examined, the direct effects of temperature or changes in light regime are most likely to be responsible for the altered production of daughter tillers. Apparently, colonization by shrubs decreases the growth rate of the tussock by reducing the production of daughter tillers through changes in the amount or kind of solar radiation that reached the tussock.

RADIATION REGIME AND SUCCESSION IN TUSSOCK TUNDRA

This result has several implications for the analysis of macro- and microsuccession in tussock tundra. Macrosuccession is defined here as restoration of the original composition of the community after some form of heavy disturbance such as fire (Wein and Bliss, 1973) or scraping with a bulldozer (Chapin and Chapin, 1980). The macrosuccessional sequence is marked by decreasing dominance of *E. vaginatum* (Wein and Bliss, 1973; Fetcher et al., 1984) and by decreases in the rate of turnover of tillers of *E. vaginatum* (Fetcher and Shaver, 1983). That is, tillers die at younger ages and produce daughter tillers at younger ages in disturbed tussock tundra than in undisturbed tussock tundra. This phenomenon may be the result of decreased nutrient availability (Wein and Bliss, 1974). The results of the present study suggest that changes in light quality and intensity and low temperatures that result from self-shading and shading by other species may further reduce the turnover rate for *E. vaginatum* tillers.

The results further indicate that self-shading and shading by shrubs have equal effects on light penetration, tussock temperature, and tiller demography of *E. vaginatum*. The lack of statistical interaction between initial tussock class and shrub removal means that self-shading and shading by shrubs are additive in their effect on the properties listed above. Therefore, it appears that either self-shading or shading by shrubs can cause the reduction in tiller turnover rate found by Fetcher and Shaver (1983).

Microsuccession refers to vegetative microcycles as described by Watt (1947). In microsuccession, a given patch of ground is occupied by a plant which goes through juvenile, mature, and degenerate stages. After the plant dies the patch may be reoccupied by the juvenile stage. Fetcher and Shaver (1982) proposed that tussock classes I to V formed a sequence, with Class I being the juvenile stage, Class II being a mature stage, and Classes III to V being degenerate stages. Class V tussocks had lower tillering rates than tussocks of Classes I and III (Fetcher and Shaver, 1982). According to the scheme described above, heavily colonized tussocks should eventually disappear under a blanket of shrubs and moss. But some tussocks show regions of regrowth where relatively rapid production of new tillers is taking place (Figure 6). Class IV tussocks are warmer than Class III tussocks because of less self-shading even though they have more cover by shrubs and mosses (Table 1). Hence, a mechanism for regeneration can be postulated; namely, increased temperature stimulates tillering at one part of a Class IV tussock with the result that a new tussock of Class I is formed. This tussock grows, passing through Classes II and III until self-shading changes light intensity and quality, lowers temperature, and slows the tillering rate. Shrubs and mosses colonize the tussock and reduce tillering further. At this point the shrubs and mosses may bury the tussock completely or the tussock may regenerate in the manner described above.

TEMPERATURE MODIFICATION AND COMPETITION

The results of this experiment indicate that plants can influence the pattern of growth and, presumably, the fitness of their neighbors by modifying the temperature regime in the meristematic region. This mechanism has not been considered previously. Harper (1977) provided a list of possible ways in which a plant can influence its neighbors. He included microclimatic alterations such as "reducing light intensity," "changing the humidity profile," and "changing light quality" but did not consider modification in the temperature regime of neighboring plants.

FIGURE 6. Cross section of Class IV tussock from Eagle Creek showing regrowth of *Eriophorum vaginatum*.

Most previous studies of the mechanism of competition (e.g., Donald, 1958; Black, 1960) have taken place in the temperate zones where temperature is less likely to limit plant growth than light, water, or mineral nutrients. Since the present study is one of the first of this type that has been carried out in the Arctic, it is not surprising that the mechanism of temperature modification has remained undetected. However, this mechanism may be significant early in the growing season of many species in the temperate zones. If certain plants can shade the meristems of their neighbors so that they are cooled and thus growth rate is reduced, the plants that are doing the shading may gain an initial advantage in size. Once the initial advantage is achieved it often persists throughout the life cycle of the plant (Harper, 1977).

COMPETITION IN STRESSFUL ENVIRONMENTS

Interference from neighboring shrubs appears to affect significantly the growth habit of *E. vaginatum*, which suggests that competition is taking place in tussock tundra. Savile's (1960) hypothesis that biological competition is not important in the arctic was not supported, although the tussock tundra at Eagle Creek is a closed community quite unlike the sparsely vegetated communi-

ties discussed in his paper. Even sparsely vegetated communities may have competition, however, as shown by Griggs (1956). The results of the present study when combined with those of Fonteyn and Mahall (1981) for desert shrubs and Griggs (1956) and McGraw (1982) for alpine tundra indicate that competition can be an important factor in the life cycle of plants of stressful environments.

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