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Reviewed work(s):

Source: *Journal of Ecology*, Vol. 71, No. 1 (Mar., 1983), pp. 131-147

Published by: [British Ecological Society](#)

Stable URL: <http://www.jstor.org/stable/2259967>

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## LIFE HISTORIES OF TILLERS OF *ERIOPHORUM VAGINATUM* IN RELATION TO TUNDRA DISTURBANCE

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### SUMMARY

(1) Life-tables were constructed for vegetative tillers of *Eriophorum vaginatum* from undisturbed and disturbed tussock tundra in Alaska. Life-tables were also constructed for tillers from tundra that had been fertilized with N, P and K. The life-tables were used to estimate population parameters and to construct constant coefficient matrix models of tiller demography.

(2) Tiller survival was lower in disturbed than it was in undisturbed tundra, and daughter tillers were produced sooner. Addition of nutrients (as fertilizer) produced no change in tiller survival and in the age distribution of daughter tiller production in the first year following fertilization. The shapes of the survival curves were intermediate between Deevey Type I and Deevey Type II curves.

(3) The generation time for tillers in undisturbed tundra was 5.3 years—about twice as long as in disturbed tundra—while the annual rate of increase of tillers did not differ greatly. Fertilization produced large increases in the annual rate of increase, but the generation time was shortened only slightly.

(4) Reproductive values, defined as the expected number of daughter tillers from tillers of a given age relative to the expected number from a tiller aged 0, fell into one of three patterns: (i), decline from maximum value at age 0; (ii), increase from age 0 followed by a monotonic decline; (iii), increase from age 0 followed by a gradual, irregular decline and a plateau in the older age classes. The peak in reproductive value for patterns (ii) and (iii) occurred 2–4 years after the onset of tillering at age 1 or 2 years; this result was attributed to increases in age-specific tillering rate with tiller age.

(5) Sensitivity analysis of the matrix models revealed that sensitivity of the annual rate of increase to changes in tillering rate and survival declines with age. The annual rate of increase was equally sensitive to changes in tillering rate and survival from age 0 to age 3. In the older age classes the annual rate of increase was more sensitive to changes in tillering rate than to changes in survival.

### INTRODUCTION

*Eriophorum vaginatum* L. (cottonsedge) is a tussock-forming sedge that is a dominant member of many plant communities of northern Alaska, Canada, and Eurasia (Britton 1957; Wein & Bliss 1974; Chapin, Van Cleve & Chapin 1979; Wein 1973; Bliss 1981). At the same time, *E. vaginatum* is conspicuously successful as an invader of disturbed areas, both natural and man-made (Wein & Bliss 1973, 1974; Chapin & Chapin 1980; Chapin & Shaver 1981). It is unusual for one species to be so successful in both disturbed and undisturbed habitats, particularly over such a wide geographic range.

The purpose of this work was to compare the demography of vegetative growth of *E. vaginatum* from several disturbed and undisturbed sites in Alaska. We viewed the tussock

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as a population of tillers (Harper & White 1974; Bazzaz & Harper 1977; White 1979; Harper 1980). Specifically, we were interested in comparing life histories of tillers as described by age-specific rates of tiller survival and daughter tiller production. We were also interested in several summary statistics derived from the age-specific rates including gross and net reproductive rates of tillers, generation time of tillers, the rate of increase in tiller populations, and the sensitivity of the rate of increase to changes in age-specific rates (Caswell 1978). The principal question we tried to answer was: are there patterns in the demography of individual tillers which could account for the dominance of *E. vaginatum* in such diverse habitats?

In tussock tundra, physical disturbance is associated with an increase in primary productivity and nutrient content of *E. vaginatum* (Wein & Bliss 1973, 1974; Chapin & Van Cleve 1978; Chapin & Chapin 1980; Chapin & Shaver 1981). Productivity and nutrient content of *E. vaginatum* can also be increased by direct addition of nutrients (Tamm 1954; Goodman & Perkins 1968a, b; Shaver & Chapin 1980). The similar responses of productivity and nutrient content to fertilization and to physical disturbance suggest that the demographic response of *E. vaginatum* tillers may be similar as well. Therefore, we studied the demography of tillers in tussocks from undisturbed tundra, from two types of physically disturbed tundra, and from fertilized tundra.

#### STUDY SITES

The studies were made at two sites in Alaska: Eagle Creek (65°26'N, 145°30'W; 730 m altitude), and Toolik Lake (68°38'N, 149°25'W; 719 m altitude). The Eagle Creek site was south of the Brooks Range; Toolik Lake was north of it. Both sites were typical cottontsedge-tussock tundra as described by Britton (1957). Detailed site descriptions are given for Eagle Creek by Wein & Bliss (1974) and Shaver & Cutler (1979). Total primary production at Eagle Creek averaged about 75 g m<sup>-2</sup> year<sup>-1</sup> (Wein & Bliss 1974). The species with highest net primary productivity were *Eriophorum vaginatum* L., *Vaccinium vitis-idaea* L., *Ledum palustre* L., *V. uliginosum* L. and *Carex bigelowii* Torr. (Wein & Bliss 1974). Other important vascular species were *Andromeda polifolia* L., *Betula nana* L., *Empetrum nigrum* L. and *Rubus chamaemorus* L. Mosses covered approximately 45% of the surface (Alpert & Oechel, 1982). Common moss species at Eagle Creek were *Dicranum elongatum* Schleich. ex Schwaegr., *Polytrichum commune* Hedw., *Sphagnum balticum* (Russ.) Russ. ex C. Jens, and *S. lenense* H. Lindb. ex Pohle (Alpert & Oechel 1982). At Toolik Lake the vegetation was similar except that there was less moss, *Vaccinium uliginosum* was less abundant, and *Betula nana* was more abundant.

Soils at Eagle Creek consisted of 20–30 cm of peat underlain by silty, frozen loess. Maximum thaw depth was about 40 cm below the moss surface. There was no sign of cryoturbation. At Toolik Lake, frost activity was apparent, and the peat layer was thinner (0–20 cm). Plant cover was nearly complete (B. Lachenbruch, personal communication).

At both Eagle Creek and Toolik Lake, control sites were compared with sites that had been manipulated in various ways. At Eagle Creek, the undisturbed tundra was compared with (i) a vehicle track that had been in intermittent use for about 15 years prior to sampling, and (ii) a site that had been scraped clear of vegetation with a bulldozer in June 1970 (Chapin & Van Cleve 1978; Chapin & Chapin 1980). These two disturbed sites are referred to as the 'vehicle track' and the 'scraped' sites, respectively. At Toolik Lake the undisturbed tundra was compared with a site that had been fertilized in July 1978 with NH<sub>4</sub>NO<sub>3</sub>, 25 g m<sup>-2</sup>; superphosphate, 25 g m<sup>-2</sup>; and K<sub>2</sub>O, 31.6 g m<sup>-2</sup>. The fertilizer was

applied in the way described by Shaver & Chapin (1980); the rates of application were chosen for comparison with similar experiments by Tamm (1954) in Sweden, Goodman & Perkins (1968a, b) in Britain, and Shaver & Chapin (1980) in Alaska. This site was termed the 'fertilized' site.

### GROWTH HABIT OF *ERIOPHORUM VAGINATUM*

General descriptions of the growth habit of *Eriophorum vaginatum* can be found in Goodman & Perkins (1968a), Wein (1973), and Chapin, Van Cleve & Chapin (1979). Here we describe some of the characteristics of *E. vaginatum* that facilitated demographic analysis.

Tussocks of *E. vaginatum* in undisturbed tundra generally consist of 300–600 live tillers (Fetcher & Shaver 1982). Live tillers are those which have one or more green leaves that appear to be healthy. During the growing season a tiller produces one to four new leaves in sequence. At the end of the season the whole length of oldest leaves dies. The tips of the youngest leaves die, but the basal portions of the leaves survive through the winter. These leaves resume growth the following year, and the point to which the leaves had died appears as a dark band. Thus it is possible to distinguish current-year (new) live leaves from those which survived from the previous year. Observations of marked tillers support this interpretation of the pattern of leaf production (N. Fetcher, unpublished). Because decomposition is slow, completely dead leaves are retained on the tiller and are readily distinguished and counted, and it is possible to determine the total number of leaves produced by a tiller in its lifetime.

In the present paper, we focus on the patterns of vegetative growth, deferring a presentation of flowering biology to a later paper. During the course of a growing season a tiller can produce one, two, or three daughters intravaginally. It may also produce an inflorescence bud, which will be exerted in the following year. Some tillers can form both inflorescence buds and daughter tillers but others form either inflorescence buds or tillers but not both. If a tiller forms an inflorescence bud, it will die after flowering the next year.

### METHODS

#### *Determination of tiller age*

Accurate measurement of tiller age was crucial to estimation of all of the life-history parameters used in this study. For tillers of *E. vaginatum*, the only usable index of age was the total number of leaves produced by a tiller over its lifetime. Tiller age was calculated by dividing total leaf number by the mean number of leaves produced per year (Shaver & Billings 1975; Callaghan 1976). The accuracy of this procedure depends on the year-to-year variation in leaf production rate and the variation of leaf production rate with total leaf number. We investigated both of these.

The number of new leaves produced per tiller per year, or leaf production rate, was determined by counting the number of leaves that did not have a dead, overwintered tip. The total number of leaves on a tiller included these new leaves plus all other live leaves and all the old, dead leaves.

Year-to-year variation in leaf production rate was assayed by marking ten tillers in each of four tussocks in 1978, and observing leaf production of the surviving vegetative tillers through the summers of 1978, 1979 and 1980. Mean production ( $\pm$  S.E.) of new leaves by these marked tillers was  $2.56 \pm 0.10$  ( $n = 40$ ),  $2.75 \pm 0.11$  ( $n = 39$ ), and  $2.74 \pm 0.11$

( $n = 35$ ) leaves tiller<sup>-1</sup> year<sup>-1</sup>. There was no significant difference in leaf production rate over the 3 years ( $P > 0.05$ ), and thus tiller age was estimated using long-term averages for leaf production rate (Table 1).

Variation in leaf production rate with total leaf number was determined from counts of new leaf number and total leaf number on individual tillers from each site. In four of the five sites, there was no significant correlation between the two counts ( $P > 0.05$ ) because new leaf number remained essentially constant as total leaf number increased. In tillers from the vehicle track at Eagle Creek there was a slight but significant tendency for leaf production rate,  $y$  (leaves tiller<sup>-1</sup> year<sup>-1</sup>) to increase with total leaf number,  $x$  (leaves tiller<sup>-1</sup>) ( $r^2 = 0.052$ ,  $n = 222$ ,  $P < 0.001$ ). The regression equation describing this relationship was  $y = 2.39 + 0.48x$ . However, in estimating tiller age, leaf production rate was assumed to be constant with total leaf number for all five sites. Because tillers from the vehicle track were the shortest-lived of all sites (Fig. 1), the maximum error in age associated with this assumption was about one half year for the oldest tillers from the track.

Except in the fertilized area at Toolik Lake, the rates of leaf production used to estimate tiller age were those listed in Table 1. In the fertilized area, the leaf production rate for undisturbed tundra was used because it was a better estimator of leaf production rate prior to fertilization. The fertilizer had been applied in July 1978, only one year before sampling in August 1979. Because leaf production rate in fertilized tussocks was 3.1 leaves tiller<sup>-1</sup> year<sup>-1</sup> in 1979 v. 2.2 leaves tiller<sup>-1</sup> year<sup>-1</sup> in the undisturbed area, we subtracted one leaf from the total leaf number for each tiller on fertilized tussocks, and divided that number by the long-term mean leaf production rate from undisturbed tundra to estimate tiller age in the fertilized area.

#### Demography of tillers

In August 1979, five tussocks of *E. vaginatum* were collected from each of the five sites (undisturbed tundra at Eagle Creek and Toolik Lake, the scraped and vehicle track areas at Eagle Creek, and the fertilized area at Toolik Lake). The diameter of the tussocks ranged from 15 to 33 cm except in the scraped and vehicle track areas, where the tussock diameters were 11–22 cm. Although the tussocks from the disturbed areas were smaller, the number of tillers per tussock was similar to that found in undisturbed tundra because the density of tillers was higher (Fetcher & Shaver 1982). Larger diameter tussocks were not available on these two disturbed areas. On all five sites, only tussocks relatively free of invasion by moss and other vascular plants were selected (class 2 or class 3 tussocks in the classification of Fletcher & Shaver 1982). The tillers from each of the sample tussocks were then treated as a population in subsequent demographic analyses.

Tiller populations were sampled by breaking apart each tussock, classifying each tiller of a random subsample of fifty live tillers into one of the categories of Table 2, and counting the number of new live leaves, old live (green) leaves, and dead leaves on each tiller. Tiller age was determined as described above.

To determine the age distribution of tiller mortality, the total number of leaves was counted on all the dying tillers encountered in a tussock. Dying tillers were distinguished by the absence of a new leaf or by a single, yellowed, necrotic new leaf. Observations on marked tillers showed that tillers with these characteristics did not produce new leaves in the following year. In preliminary studies in 1977 and 1978 an alternative method was used: dead tillers were selected at random. The results were similar to those in the substantive work. Dying rather than dead tillers were preferred because it was impossible to determine how long ago the dead tillers had died. Because dead tillers remain intact for an

TABLE 1. Rate of leaf production (leaves tiller<sup>-1</sup> year<sup>-1</sup>) for tillers of *Eriophorum vaginatum* from three sites in Alaska in various conditions.

	Year(s) of measurements	Mean	S.E.	n
Eagle Creek				
Undisturbed	1977-81	2.52	0.02	1028
Disturbed				
Scraped	1977-80	3.04	0.05	361
Vehicle track	1977-79	3.02	0.04	359
Toolik Lake				
Undisturbed	1979-81	2.23	0.03	479
Fertilized	1979	3.05	0.05	252

TABLE 2. Categories of live *Eriophorum vaginatum* used for demographic analysis.

Category	Criterion
Adult tiller	One or more old leaves (as indicated by a brown senescence band); if no old leaves, then more than two green leaves
Mother tiller	Tiller with current-year daughter tiller
Inflorescence bud	Tiller that has developed an inflorescence but the inflorescence is not exerted
Inflorescence bud and mother	Inflorescence bud with current-year daughter
Flowering tiller	Tiller with exerted inflorescence
Inflorescence and mother	Flowering tiller with current-year daughter
Current-year daughter tiller	(i) No dead or old leaves and fewer than three new leaves and (ii) More than 2 mm long

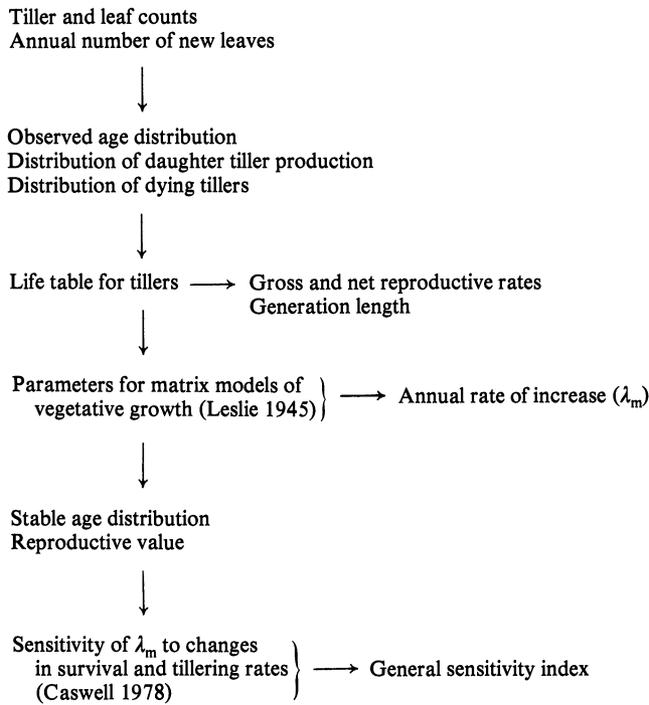
unknown but very long time, it was possible that the age distribution of randomly selected dead tillers did not accurately represent the age-specific mortality patterns of the mid to late 1970s.

The age-specific rates of daughter tiller production were determined by calculating the age of tillers that had produced current-year daughters (Table 2). These 'mother' tillers usually produced only one current-year daughter, but occasionally two or three. For a given age  $x$ , then, the age-specific rate of new tiller production ( $m'_x$ ) was the total number of current-year daughters on mothers in age class  $x$  divided by the total number of tillers in that age class.

Steps in the data analysis are summarized in Table 3. Data from each set of five replicate tussocks were pooled to estimate demographic parameters. The age-specific probability of survival from age 0 to age  $x$  ( $l_x$ ) was determined by assuming that the age distribution of dying tillers represented survival v. age in a single cohort (Deevey 1947). Under this assumption,  $l_x = S_x/N_d$ , where  $S_x$  was the number of dying tillers that survived to age  $x$  and  $N_d$  was the total number of dying tillers. Watson (1979) used a similar approach to determine survival of moss ramets growing along an altitudinal gradient in New Hampshire. Life expectancy ( $e_0$ ) was calculated from  $l_x$  as the number of years from birth at age 0 to death of an average tiller (Keyfitz 1968, p. 14 f).

Gross reproductive rate and net reproductive rate were calculated as  $\Sigma m'_x$  and  $\Sigma l_x m'_x$ , where  $m'_x$  was the age-specific rate of daughter tiller production defined above. Gross reproductive rate (GRR) was the expected number of daughters produced by a tiller that lived as long as the oldest tiller in the population. Net reproductive rate (NRR) was the average number of daughter tillers produced by a tiller that lived to the average tiller age. Generation time ( $T_c$ ) was calculated as  $\Sigma x l_x m'_x / \Sigma l_x m'_x$  (Caughley 1967). It represents the mean interval between the production of a tiller and production of its daughter tiller.

TABLE 3. Flow chart for analysis of results of counts of leaves and tillers of *Eriophorum vaginatum*.



The age-specific tillering rates ( $m'_x$ ) and probabilities of survival from age 0 to age  $x$  ( $l_x$ ) were used to construct constant coefficient models of population growth (Leslie 1945). The models have the form:

$$\mathbf{M} = \begin{matrix} & f_0 & f_1 & f_2 & \cdot & \cdot & \cdot & f_x \\ \begin{matrix} p_0 \\ 0 \\ 0 \\ \cdot \\ 0 \end{matrix} & \begin{matrix} 0 \\ p_1 \\ 0 \\ \cdot \\ 0 \end{matrix} & \begin{matrix} 0 \\ 0 \\ p_2 \\ \cdot \\ 0 \end{matrix} & \begin{matrix} \cdot \\ \cdot \\ \cdot \\ \cdot \\ \cdot \end{matrix} & \begin{matrix} \cdot \\ \cdot \\ \cdot \\ \cdot \\ \cdot \end{matrix} & \begin{matrix} \cdot \\ \cdot \\ \cdot \\ \cdot \\ p_{x-1} \end{matrix} & \begin{matrix} 0 \\ 0 \\ 0 \\ \cdot \\ 0 \end{matrix} \end{matrix}$$

where  $p_x$  is the probability of survival from age  $x$  to age  $x + 1$  and  $f_x$  is the number of daughters that are produced in the interval  $t$  to  $t + 1$  per female age  $x$  to  $x + 1$  at time  $t$  and who will be alive in the age group 0 to 1 at time  $t + 1$  (Leslie 1945). The value of  $p_x$  was calculated as  $l_{x+1}/l_x$ , and that of  $f_x$  was calculated from the age-specific tillering rates adjusted for juvenile and maternal mortality as recommended by Leslie (1945). We used a 1-year time step. To simplify the models, we assumed that they described tiller populations at mid-winter. This formulation was used because *E. vaginatum* produces tillers continuously during June and July, with some production continuing into August. An alternative formulation, the discrete model proposed by Schaffer & Rosenzweig (1977), was also analysed with nearly identical results.

Once the coefficients in the matrices were determined we calculated the stable age distribution and the vector of reproductive values according to

$$\mathbf{M}\bar{u} = \lambda_m \bar{u}$$

and

$$\bar{v}^T \mathbf{M} = \bar{v}^T \lambda_m$$

where  $\lambda_m$ , the dominant eigenvalue of the matrix  $\mathbf{M}$ , represents the annual rate of increase when the population is in the stable age distribution (Leslie 1945);  $\bar{u}$  is the vector of frequencies of individuals in each age class when the population achieves a stable age distribution; and  $\bar{v}^T$  is the transposed vector of reproductive values for tillers in each age class (Leslie 1948; Keyfitz 1968; Caswell 1978). Reproductive value was originally defined (Fisher 1958) as the expected number of offspring that remain to be born to an individual of age  $x$  relative to the number that remain to be born to a new-born individual (of age 0). Leslie (1948) found that the left eigenvector,  $v$ , of the matrix  $\mathbf{M}$  associated with the dominant eigenvalue was equivalent to Fisher's formula for reproductive value.

To determine the effect of changes in the age-specific rates on the annual rate of increase, we made a sensitivity analysis (Caswell 1978) on the matrices for the five populations. The sensitivity of the annual rate of increase ( $\lambda_m$ ) to small perturbations in age-specific tillering rate ( $m'_m$ ) was calculated as

$$d\lambda_m/dm'_x = v_0 u_x / [\bar{u}^T, \bar{v}]$$

where  $v_0$  is the reproductive value of the age class 0,  $u_x$  is the frequency of the population in the age class  $x$ , and  $[\bar{u}^T, \bar{v}]$  is the inner product of the vectors ( $\bar{u}$ ,  $\bar{v}$ ). We calculated the sensitivity of  $\lambda_m$  to small changes in age-specific mortality ( $p_x$ ) using

$$d\lambda_m/dp_x = v_{x+1} u_x / [\bar{u}^T, \bar{v}]$$

where  $u_{x+1}$  is the reproductive value of age class  $+1$ . We also calculated the general sensitivity index proposed by Caswell (1978), namely,  $S = |\bar{u}| |\bar{v}| / [\bar{u}, \bar{v}]$ . This index can take values greater than or equal to 1.0. According to Caswell (1978), high values for  $S$  indicate potentially greater sensitivity of  $\lambda_m$  to changes in population parameters.

The effect of variation in leaf production rate on population summary statistics was studied by setting leaf production rate to the upper and lower bounds of the 95% confidence interval (Table 2) and recalculating age-specific tillering and mortality rate ( $f_x$  and  $p_x$ ) and the associated values for annual rate of increase, gross reproductive rate, net reproductive rate, and generation time.

## RESULTS

### *Survival of tillers*

At Eagle Creek the survival of tillers from undisturbed tundra was significantly greater ( $P < 0.01$ ; Smirnov test, Conover 1971) than that of tillers from the scraped area and the vehicle track (Fig. 1(a)). By greater survival we mean that the probability of survival,  $l_x$ , from age 0 to age  $x$ , for the undisturbed tundra was greater than for the disturbed areas at all ages. Survival at the vehicle track was similar to survival at the scraped site. At Toolik Lake, survival of tillers from fertilized tussocks was not significantly different from that of tillers from undisturbed tundra (Fig. 1(b)). Therefore, the survival results from fertilized and undisturbed tundra were pooled for subsequent analyses. Tillers from tussocks in

*Life histories of Eriophorum vaginatum tillers*

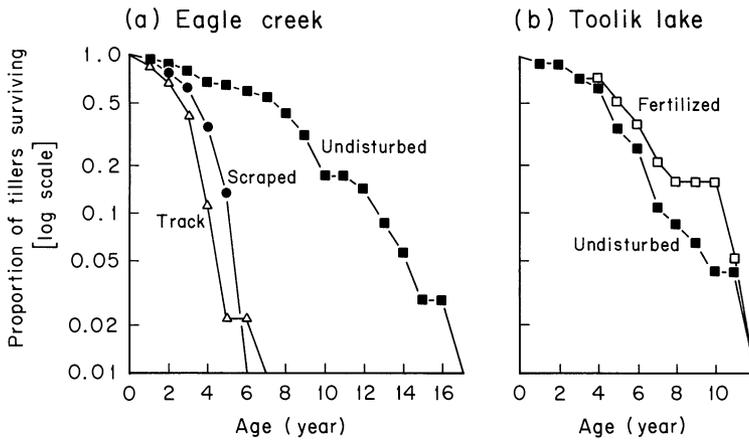


FIG. 1. Survival curves for vegetative tillers of *Eriophorum vaginatum* at two sites in Alaska. Symbols: ■, undisturbed tundra; ●, scraped areas; △, vehicle track; □, fertilized tundra.

undisturbed tundra at the southern site (Eagle Creek) had significantly greater survival ( $P < 0.01$ ) than tillers from the northern site (Toolik Lake).

A log-linear plot of survival for *E. vaginatum* tillers shows a pronounced departure from a straight line (Fig. 1), indicating that the probability of death is not the same at all ages. Instead, mortality is less for 0, 1, and 2-year old tillers than it is for older ones.

*Production of daughter tillers*

The distribution of age-specific tillering rates,  $m'_x$ , shifted in response to disturbance (Table 4). Tillering was less at earlier ages and greater at older ages in undisturbed tundra

TABLE 4. Age-specific tillering rates,  $m'_x$ , (leaves tiller<sup>-1</sup> year<sup>-1</sup>) for flowering and non-flowering tillers of *Eriophorum vaginatum* from tussocks at two sites in Alaska.

Age class (year)	Site and treatment				
	Vehicle track	Eagle Creek Scraped area	Undisturbed	Toolik Lake Undisturbed	Toolik Lake Fertilized
0					
1	0.115	0.261	0.044	0.028	0.420
2	0.279	0.440	0.263	0.158	1.040
3	0.360	0.642	0.379	0.375	1.171
4	0.4	0.649	0.063	0.408	1.571
5	0.67	0.640	0.200	0.484	2.524
6		0	0.786	0.150	2.563
7		1.33	0.412	1.0	2.077
8			0.33	0.889	1.556
9			0.133	0.100	0.500
10			0.286	1.0	1.4
11			0.0		1.0
12			0.0		1.0
13			0.5		4.0
14			0.5		0.5
15					0.5
Number of tillers	251	256	246	279	256

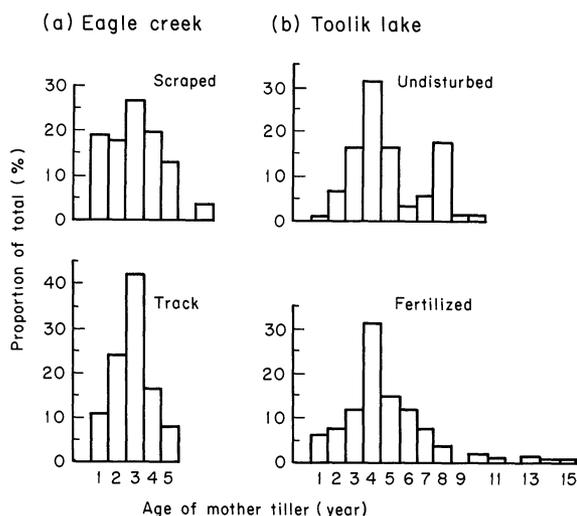


FIG. 2. Distribution of daughter tillers of *Eriophorum vaginatum* by age of mother tiller at two sites in Alaska: (a) Eagle Creek, scraped with a bulldozer (upper) and vehicle track (lower); (b) Toolik Lake, undisturbed (upper) and fertilized (lower).

compared to disturbed tundra at Eagle Creek. At Toolik Lake, fertilization of undisturbed tundra greatly increased tillering rates for all age classes of tillers.

The effect of physical disturbance on the distribution of age-specific tillering rate was similar whether the disturbance occurred once as for the scraped area or repeatedly as for the vehicle track. The distribution of age-specific tillering rate depends on two distributions: the distribution of adult tillers by age, and the distribution of daughter tiller production by age class of mother. To test for differences in the age-specific tillering rate it was first necessary to test for differences in the observed age distribution of tillers one year old and older. The observed age distributions of adult tillers from the vehicle track and the scraped area were not significantly different ( $P > 0.05$ ; Smirnov test). The distributions of daughter tiller production at the two sites were tested, therefore, and were found to be not significantly different (Fig. 2).

The main effect of adding nutrients at Toolik Lake was to increase daughter tiller production greatly, not to shift the ages at which daughter tillers were produced. The age distribution of adult tillers in undisturbed tundra was not significantly different from that of tillers in fertilized tundra. The age distributions of daughter tiller production also were not different (Fig. 2).

#### Summary statistics

*Eriophorum vaginatum* apparently has the ability to undergo shifts in the distribution of age-specific mortality and tillering rate without changing the annual rate of increase of tiller populations ( $\lambda_m$ ). There was no consistent effect of disturbance on net reproductive rate (NRR) and the annual rate of increase (Table 5). Thus, the annual rate of increase in the scraped area of Eagle Creek in 1979 was 1.08 whereas it was 1.11 in undisturbed tundra. On the other hand, generation time ( $T_G$ ) was almost twice as long in undisturbed tundra as in disturbed areas (Table 5). Tiller life expectancy from age 0 was more than

TABLE 5. Gross reproductive rate (GRR), net reproductive rate (NRR), generation time ( $T_c$ ), annual rate of increase ( $\lambda_m$ ), general sensitivity of the matrix ( $S$ ), and life expectancy ( $e_0$ ) (see text for explanation) for *Eriophorum vaginatum* tillers from two sites in Alaska in various conditions. Values in parentheses are the values obtained when leaf production rate was set to the lower and upper limits of the 95% confidence interval of the leaf production rate used for each site. The units of GRR, NRR and  $\lambda_m$  are tiller tiller<sup>-1</sup> year<sup>-1</sup>;  $S$  is dimensionless.

Site	Eagle Creek			Toolik Lake	
	Undisturbed	Vehicle track	Scraped area	Undisturbed	Fertilized
GRR	3.40 (3.24, 3.50)	1.83 (2.39, 1.83)	2.63 (3.41, 2.63)	4.59 (4.28, 4.14)	15.82 (15.71, 15.66)
NRR	1.74 (1.59, 1.18)	0.53 (0.60, 0.53)	1.34 (1.39, 1.34)	1.27 (1.24, 1.18)	5.63 (5.60, 5.35)
$T_c$ (year)	5.33 (5.34, 5.36)	2.32 (2.69, 2.32)	2.70 (2.88, 2.70)	4.75 (4.70, 4.59)	4.24 (4.29, 4.10)
$\lambda_m$	1.11 (1.09, 1.11)	0.77 (0.83, 0.77)	1.08 (1.10, 1.08)	1.05 (1.05, 1.03)	1.65 (1.64, 1.64)
$S$	1.07	1.05	1.01	1.25	1.91
$e_0$ (year)	7.06	2.68	3.32	4.61	5.37

twice as long in undisturbed as it was in disturbed tundra (Table 5). Gross reproductive rate (GRR) was slightly greater in undisturbed environments as well (Table 5). These results indicate that *E. vaginatum* has extremely plastic tillering rates and tiller mortality.

The response to fertilization was quite different from the changes produced by physical disturbance. Production of new tillers was increased greatly in the first season following fertilization while the age distribution of mortality was unaffected. The result was a large increase in gross reproductive rate, net reproductive rate, and the annual rate of increase compared to the values obtained in undisturbed tundra (Table 5).

#### Effect of variation in leaf production rate

The effect of changing leaf production rate on the summary statistics was small in most instances (Table 5). Gross reproductive rate was the most sensitive to variation, while the annual rate of increase was almost unchanged. Sometimes, the values obtained at the upper and lower boundaries of the 95% confidence interval of the leaf production rate did not overlap with the values obtained at mean leaf production rate. For example, when gross reproductive rate was calculated for undisturbed tundra at Toolik Lake, the values obtained at the upper and lower boundaries were 90% and 93% of the value obtained at the mean leaf production rate. This occurred because changing the leaf production rate changed the assignment of mother and adult tillers to age classes and altered both the numerator in the formula for age-specific tillering rate, namely, the number of daughter tillers on mothers in a given age class, and the denominator, the total number of tillers in that age class. The net effect was that age-specific tillering rate and the parameters that incorporate age-specific tillering rate did not always change in a consistent fashion. Because some tillers in the older age classes were reassigned, the statistics that incorporated survival (NRR,  $T_c$  and  $\lambda_m$ ) as well as age-specific tillering rate were less affected than was gross reproductive rate, which incorporated only age-specific tillering rate.

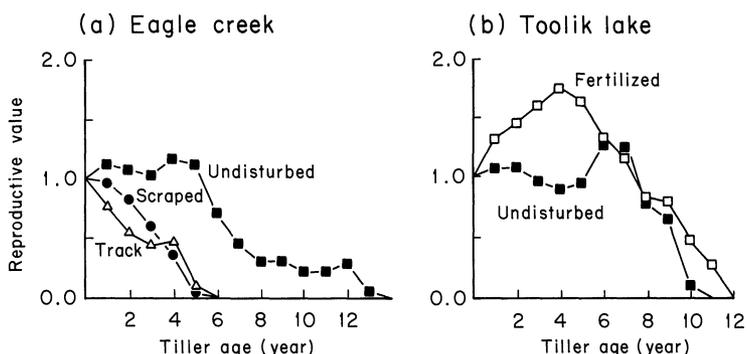


FIG. 3. Reproductive value (see text) for tillering v. tiller age in tussocks of *Eriophorum vaginatum* at two sites in Alaska. Symbols: ■, undisturbed tundra; ●, scraped area; △, vehicle track; □, fertilized tundra.

*Reproductive values*

Reproductive values exhibited one of three patterns. In the first pattern, reproductive value declined from a maximum at age 0; this type of curve was found in the short-lived populations from the vehicle track and the scraped area (Fig. 3). The second pattern was found for tillers growing in fertilized tundra and had a single hump followed by a monotonic decline in reproductive value (Fig. 3). The third pattern consisted of an initial plateau followed by a gradual, irregular decline and a plateau or a peak in the older age classes (Fig. 3).

*Comparison of stable and observed age distributions*

Stable age distributions for tillers were compared to the observed distributions (Fig. 4). Because the predicted stable age distribution corresponds to a midwinter population and the harvests were performed in late summer, the observed distribution was corrected using

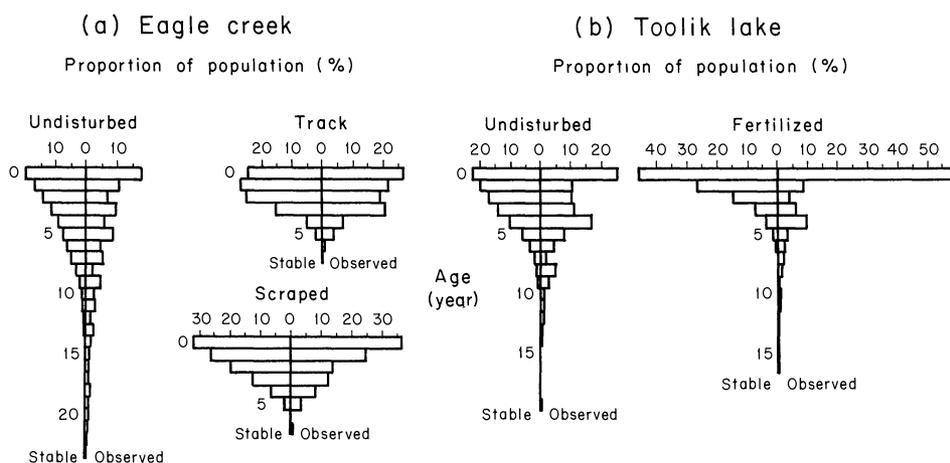


FIG. 4. Calculated stable (to left) and observed (to right) age distributions for vegetative tillers of *Eriophorum vaginatum* at two sites in Alaska.

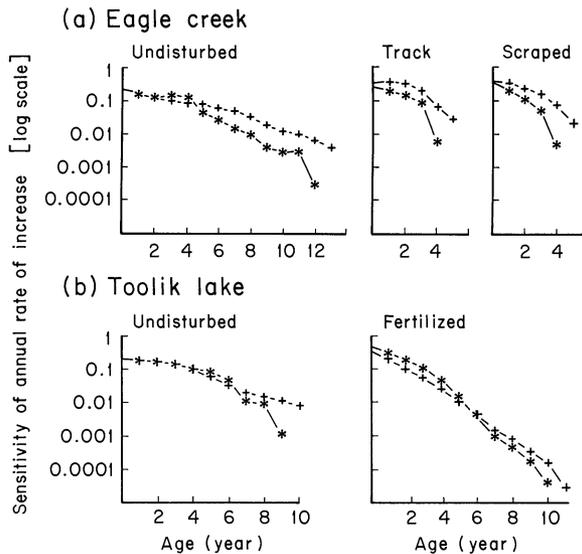


FIG. 5. Sensitivity (see text) of the rate of increase  $\lambda_m$  (tiller tiller<sup>-1</sup> year<sup>-1</sup>) to changes in age-specific tillering rate (†) and survival (\*) of tillers of *Eriophorum vaginatum* at two sites in Alaska.

half-year survival probabilities. When tested by the Kolmogorov test (Conover 1971), only the scraped site was not significantly different ( $P > 0.05$ ) from the stable age distribution.

The deviations of the other tiller populations from the stable age distribution suggest that either the populations have had insufficient time to achieve a stable age distribution or that the coefficients of the model are changing. According to Charlesworth (1980) five generations are sufficient for most natural populations to converge to the stable state. In undisturbed tundra, five generations of tillers corresponds to about 25 years. Since the undisturbed tundra has been untouched for much longer than 25 years, we conclude that the failure of the stable age distribution to agree with the observed age distribution stems from changes in the coefficients of the model.

The coefficients that are most likely to vary are those relating to tillering rate rather than those relating to mortality. Recruitment of daughter tillers in undisturbed tundra at Eagle Creek and Toolik Lake was higher in 1979 than in other years (G. R. Shaver, unpublished). A higher rate of recruitment generated a stable age distribution that was skewed towards the younger age classes. This distribution was more skewed than the observed distribution, which had its origin in previous years when recruitment of daughter tillers was lower.

#### Sensitivity analyses

The sensitivity analysis revealed rather similar patterns in the sensitivity of the annual rate of increase ( $\lambda_m$ ) to small changes in age-specific mortality of tillering rate (Fig. 5). Sensitivity in the oldest age classes to changes in new tiller production or mortality was only 1% of that in the youngest age classes. An exception was the rapidly growing population of tillers from fertilized tussocks at Toolik Lake, where sensitivity declined by three orders of magnitude (Fig. 5). Sensitivity to changes in tillering rate appeared to be greater than sensitivity to changes in mortality, particularly after the shoots were 3 years

old. The general sensitivity ( $S$ ) of the matrix models from disturbed and undisturbed tundra at Eagle Creek was the same (Table 5).

## DISCUSSION

### *Tiller life histories*

We have shown that physical disturbance in tussock tundra is associated with a change in the distribution of age-specific tiller mortality and tillering rate of *Eriophorum vaginatum* so that both tiller mortality and tillering take place at earlier ages. The change amounts to a shift in the life history of tillers and appears to depend little on the type of disturbance. Both a single scraping with a bulldozer and continual disturbance by vehicles over about 15 years produced similar decreases in tiller survival at Eagle Creek. These results contrast sharply with those of Noble, Bell & Harper (1979), who studied survivorship of tillers of *Carex arenaria* at an undisturbed site in sand dunes and at a similar site that had been grazed and subject to trampling. They found little difference in survival between the two sites. The differences between our results and those of Noble, Bell & Harper (1979) may reflect differences in the degree of disturbance normally experienced by the plants. If *Carex arenaria* is adapted to the changing sand dune environment, additional disturbance would not be expected to produce marked changes in survival. On the other hand, Noble, Bell & Harper (1979) found that addition of nutrients increased the rates of tillering and mortality, whereas our results show only an increase in rate of tillering. Perhaps the growing season at Toolik Lake was not long enough for the effect of fertilization to be observed. Further investigation will be required to establish the long-term effect of fertilization on tiller survival.

Apart from the work of Noble, Bell & Harper (1979), previous comparisons of clonal plants in disturbed and undisturbed environments have focused on the balance between sexual reproduction and vegetative growth (Gadgil & Solbrig 1972; Sarukhán 1974; Silander & Antonovics 1979; Grace & Wetzel 1981). However, for species that rely extensively on vegetative propagation, changes in age-specific rates of ramet production and mortality may be as important in maintaining the plants in a particular locality as the allocation of greater or lesser amounts of biomass to sexual reproduction (Tamm 1972; Noble, Bell & Harper 1979; Barkham 1980). Ramet dynamics are important for *Eriophorum vaginatum* because in undisturbed tundra seedling recruitment is rare (Lachenbruch, Chapin & Shaver 1981; McGraw & Shaver 1982).

### *Shapes of tiller survival curves*

Survival curves for *E. vaginatum* tiller populations in both disturbed and undisturbed areas had shapes intermediate between Type I and Type II (Deevey 1947). Most of the published survival curves for ramets are of Type I (Noble, Bell & Harper 1979; Bernard 1976) or intermediate between Type I and Type II (Langer 1956; Watson 1979). Exceptions are the curves found by Lovett Doust (1981a). Type I curves have also been reported for leaves (Bazzaz & Harper 1977; Solbrig, Newell & Kincaid 1980; Shaver 1981; Lovett Doust 1981b; Maillette 1982). This shape of survival curve may come about because of the energetic relationship of the vegetative shoot to the originating unit. The shoot gradually becomes independent and exposed to a greater risk of dying after an initial period during which it depends on the originating unit for nutrients (Marshall & Sagar

1965, 1968; Mattheis, Tieszen & Lewis 1976). This pattern of development is similar to that of animals with extended parental care. It is therefore not surprising that survival curves for ramets and leaves and for animals with extended parental care should have similar shapes.

#### *Reproductive value and vegetative demography*

For humans and other warm-blooded vertebrates the reproductive value function peaks soon after the onset of reproduction (Fisher 1958; Charlesworth 1980). An early peak occurs because fecundity in warm-blooded vertebrates does not increase markedly after the onset of reproduction. Hence the component of reproductive value that is derived from fecundity remains constant or declines soon after the onset of reproduction. For the longer-lived populations of *Eriophorum vaginatum* in the present study, namely, those from undisturbed and fertilized tundra, peak reproductive value occurred 2–4 years after the onset of reproduction at 1 or 2 years of age (Fig. 3). The delayed peak in reproductive value for longer-lived populations can be attributed to the increase in age-specific tillering rate with age (Table 4). The increase was apparently sufficient to offset the decline in the component of reproductive value derived from survival, and hence reproductive value increased. The increase in age-specific tillering rate with tiller age could result from the need to accumulate the carbohydrates and inorganic nutrients necessary to produce daughter tillers. Several growing seasons may be required to accumulate sufficient reserves to produce daughter tillers.

#### *Sensitivity analysis and tiller life histories*

Sensitivity analyses were performed to identify the component of the life history that had the greatest influence on the rate of increase ( $\lambda_m$ ). Our initial hypothesis was that  $\lambda_m$  in disturbed tundra would show the greatest sensitivity to survival in 3–6-year old tillers because survival decreased markedly in disturbed tundra. This idea was not supported, however. Instead, it appears that  $\lambda_m$  could be increased most effectively by increasing either tillering or survival in the youngest ages, because  $\lambda_m$  was most sensitive to changes early in the life history (Fig. 5). Furthermore, because  $\lambda_m$  was equally sensitive to change in either tillering or survival, an increase in either one of these parameters as a result of selection for increased annual rates of increase would have the same effect on  $\lambda_m$ .

Although the sensitivity graphs are suggestive, they reflect the sensitivity of  $\lambda_m$  to only one element of the matrix  $\mathbf{M}$  at a time. As any changes in life history are likely to involve more than one element of  $\mathbf{M}$  (Templeton 1980), the graphs can do no more than indicate likely areas for the increase of  $\lambda_m$ .

The interpretation of sensitivity values may be enhanced with an understanding of how different life history parameters interact. Bell (1980) and Caswell (1982) suggest that there may be a cost attached to increased fecundity (production of new tillers) in the form of decreased survival. The survival cost of producing a daughter tiller is the decrease in survival from one year to the next ( $p_x$ ) with each increase in tillering rate ( $m'_x$ ). Mathematically,

$$c_x = -dp_x/dm'_x$$

where  $c_x$  is the survival cost of producing a daughter tiller at age  $x$ . If the cost of tillering is assumed to equal 1.0 for all ages, each increase in tillering rate could be countered by an equal decrease in survival ( $p_x$ ). When the sensitivity values are equal,  $\lambda_m$  would not change. When the sensitivities are not equal, as in the older age classes, then we would

expect selection for a high  $\lambda_m$  to increase the most sensitive parameter, either tillering or survival. The parameter that had the greatest sensitivity would become greater, while the other would decrease by an equal amount because the cost of tillering is assumed to be 1.0. The result would be a net gain in the annual rate of increase. Changes should take place at the ages where there is the greatest difference between sensitivity to age-specific tillering rate ( $d\lambda_m/dm'_x$ ) and sensitivity to survival from one year to the next ( $d\lambda_m/dp_x$ ).

However, the costs of tillering apparently increase from less than one adult tiller per daughter at age 1 year to greater than one adult tiller per daughter at later ages (N. Fetcher, unpublished). When the costs of tillering are taken into account, it appears that the greatest increase in the annual rate of increase would be effected either by increasing tillering rate at younger ages or by increasing survival at older ages. These two possibilities may lead to divergent distributions of age-specific mortality and tillering rate, such as we observed at Eagle Creek.

#### *Life history shifts and recovery from disturbance*

The shifts in tiller life histories may have an important effect on the rate of change of species composition after disturbance. In undisturbed tundra, the survival of *E. vaginatum* tillers is increased, and this contributes to tussock longevity and thereby decreases the rate at which *E. vaginatum* is replaced by invading shrubs and mosses. Furthermore, increased tiller survival allows litter production to continue, as each tiller produces two to three leaves per year. Grime (1979) pointed out that litter accumulation is an important component of dominance in plant communities; litter can restrict the growth of less common species by shading or by physically impairing their establishment and growth. The combination of tussock longevity and continued litter production may explain why *E. vaginatum* is not often replaced.

Our results also support indirectly the hypothesis that species replacement occurs during succession because later successional plants are able to tolerate lower fluxes of light, water, or nutrients than pioneer species can (Connell & Slatyer 1977; Grime 1977, 1979). In tussock tundra, the later stages of succession are associated with low availability of nutrients. Shaver & Chapin (1980) found that nitrogen and, to a lesser extent, phosphorus limited above-ground production of several plant species including *E. vaginatum*. Wein & Bliss (1974) found higher concentrations of foliar nitrogen and phosphorus in *E. vaginatum* from vehicle tracks than from undisturbed tundra. *Eriophorum vaginatum* apparently adjusts to lowered nutrient concentrations by switching from high tillering rate and low survival to low tillering rate and high survival. This pragmatic strategy may increase the ability of *E. vaginatum* to persist in undisturbed tundra for long periods and allow it to exploit both open, disturbed environments and to tolerate conditions in the closed community.

#### ACKNOWLEDGMENTS

We thank F. S. Chapin III and P. C. Miller for support and encouragement, and R. M. Andrews, F. S. Chapin III, J. Fox, and J. McGraw for commenting on the manuscript. This work was supported by grants from the Department of Energy and U.S. Army Research Office. Computer funds were provided by the Biology Department of Virginia Polytechnic Institute and State University.

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(Received 17 May 1982)