OPTIMAL LIFE-HISTORY CHARACTERISTICS AND VEGETATIVE DEMOGRAPHY IN *ERIOPHORUM VAGINATUM*

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SUMMARY

(1) Two independent models for optimal life histories were used to predict attributes of the demography of tillering of *Eriophorum vaginatum* growing at two sites in Alaska.

(2) The first model predicted the optimal age of first production of daughter tillers, where the optimum is defined as the age of first tillering that maximizes the rate of population growth when the population acquires a stable age distribution. The predicted age was 4·5 years. The observed distribution of ages at which daughter tillers were produced had a peak at 4 years. Because most tillers of *E. vaginatum* less than 5 years old are producing daughters for the first time, the results appear to support the model.

(3) Survival costs of tillering were estimated by dividing the change in age-specific survival rate by the change in age-specific tillering rate. The second model predicted that such costs would increase with age. This prediction was supported also.

(4) Tillers of *E. vaginatum* may have optimal life histories, where the optimum is reached when the rate of growth of the tiller population in the stable age distribution is maximized.

INTRODUCTION

Theoretical models of life histories have been used to predict several attributes of life histories of living organisms. Such attributes include reproductive effort as a function of age (Gadgil & Bossert 1970; Schaffer 1974; Charlesworth & Leon 1976; Michod 1979), and optimal age of first reproduction (Gadgil & Bossert 1970; Bell 1976, 1980; Charlesworth 1980). In plant population biology, life-history models have been used to analyse the balance between monocarpic and repeated reproduction (Caswell & Werner 1978; Schaffer & Schaffer 1979).

Life-history models may also be useful in analysing patterns of vegetative growth, for they assume an asexual, clonally reproducing population (Stearns 1976). This paper explores the use of theoretical models for optimal life histories as a means of predicting the characteristics of a population of ramets. If the model's predictions are supported, it implies that the age distribution of vegetative growth is subject to the same selective pressures as the life histories of genetically distinct organisms.

Two models were chosen. The first was proposed by Bell (1980). It predicts the optimal age of first reproduction for iteroparous organisms whose fecundity increases with age. The second model was that of Caswell (1982). It predicts a different attribute of an optimal life history, namely, the age distribution of survival costs of reproduction. Survival costs of reproduction are defined as the change in age-specific survival associated with a change in age-specific fecundity. Age-specific survival rate (p_x) is the probability of

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surviving from one age to the next; age-specific fecundity is the average rate of production of offspring by a parent. Because energy and nutrients that are allocated to the production of offspring are not available for growth and maintenance, age-specific survival is expected to decrease as age-specific fecundity increases. For example, if age-specific survival declines from 0·9 to 0·8 as age-specific fecundity increases from 1 to 2 offspring, then the survival costs of reproduction could be calculated as $(0·9 - 0·8)/(1 - 2) = -0·1$. The existence of survival costs of reproduction has been confirmed for some organisms (Snell & King 1977; Law 1979).

The models were chosen because their parameters could be estimated using results from a study of the vegetative demography of *Eriophorum vaginatum* L. (Fetcher & Shaver 1983). *E. vaginatum* is a sedge with a circumboreal distribution. It grows in tussock tundra and in bogs (Wein 1973). Adult plants form tussocks consisting of 300–600 tillers (Fetcher & Shaver 1982). Parameters for the life history of vegetative tillers were used in the models of Bell (1980) and Caswell (1982) to predict the optimal age of first tillering and the survival costs of tillering, respectively. The predicted values were then compared with observed values.

Model predictions

In Bell's (1980) model the optimal age of first reproduction is that age that maximizes the rate of increase (λ_m) of a population with a stable age distribution. The model assumes an organism in which fecundity increases with age. For graminoid plants, the vegetative equivalent of age-specific fecundity is age-specific tillering rate (m'_x), which is the average number of daughter tillers produced by a mother tiller of age x. In the case of *E. vaginatum*, age-specific tillering rate increases up to a certain age and then starts to level off or to decline (Fetcher & Shaver 1983).

Bell's model requires estimates of two parameters, i.e. potential fecundity and adolescent survival. Potential fecundity is defined as the fecundity of an organism reproducing for the first time. The fecundity of such an organism is supposedly greater than the fecundity of a similar organism of the same age which has already reproduced. Potential fecundity is also assumed to increase with age, at least up to a point. Since this paper deals with vegetative growth, potential age-specific tillering rate will be used as the equivalent of potential fecundity.

Bell (1980) defines adolescent survival as the average rate of survival from the age when an organism is first capable of reproducing to the age when it actually reproduces. Adolescent survival is assumed to be constant. For tillers of *E. vaginatum* the vegetative equivalent of adolescent survival is survival from age 1, when tillers first become capable of producing daughter tillers up to the age at which they actually do produce daughters. I shall call this parameter 'pre-tillering survival rate'. According to the results of Bell (1980) the optimal age of first tillering is the age at which the natural logarithm of the slope of the curve of potential age-specific tillering rate equals the negative of the logarithm of pre-tillering survival rate. If the curve of potential age-specific tillering rate is a parabola, then the optimal age of first tillering is expected to occur between the age at which tillering reproduction is first possible and the age of greatest potential tillering rate. If pre-tillering survival is low, then the optimal age of first tillering is expected to occur at an earlier age than it would if pre-tillering survival rate were higher.

Caswell's (1982) model predicts the age distribution of the survival costs of reproduction. Caswell showed that, if a life history is optimal, where the optimum is defined as in Bell's model (maximization of λ_m), then the survival costs of reproduction (tillering)

should vary as the inverse of reproductive value. Reproductive value is the number of future offspring expected from an individual of a given age relative to the number expected from an individual of age 0 (Fisher 1958). In the present case, reproductive value (v_x) is defined as the number of daughter tillers expected from a tiller of age x relative to the number expected from a tiller of age 0.

Mathematically,

$$c_x = -\mathrm{d}p_x/\mathrm{d}m'_x = \frac{v_0}{v_{x+1}} \tag{1}$$

where c_x is the cost of tillering at age x, p_x is the age-specific survival rate, and m'_x is age-specific tillering rate. Survival costs of tillering are inversely related to reproductive value. Because reproductive value generally decreases with age after the age of first tillering, survival costs of tillering are expected to increase with age.

MATERIALS AND METHODS

Parameters for the two models were estimated from data on the vegetative demography of *Eriophorum vaginatum* growing at two sites in Alaska: Eagle Creek (Lat. 65°N, Long. 149°W) and Toolik Lake (Lat. 69°N, Long. 149°W). The sites are described in Fetcher & Shaver (1983). Life tables for vegetative tillers were constructed according to methods described in Fetcher & Shaver (1983). The tables consisted of age-specific tillering rates (m'_x) and the probability of tiller survival from age 0 to age x (l_x). Values for l_x were used to calculate age-specific survival rates.

Flowering characteristics were not considered in estimating the parameters for the models. Data were not available to evaluate the production of seed by various ages of inflorescences, for flowering occurs much less frequently than tillering. Only 4% of the adult tillers examined by Fetcher & Shaver (1983) produced inflorescence buds compared with 31% that produced daughter tillers. To see whether the age of flowering was different from the age of tillering, the distribution of inflorescence buds by age was calculated by the same methods used for estimating the age distribution of other types of tillers.

Bell's model

Bell's model requires an estimate of potential fecundity as a function of age. However, the absolute values of potential fecundity are not necessary, because only the shape and location of the curve on the age-axis need to be determined.

An area of undisturbed tundra at Toolik Lake was fertilized in July 1978 with NH_4NO_3 (25 g m^{-2}), superphosphate (25 g m^{-2}), and potassium fertilizer (26·2 g m^{-2} as K). Age-specific tillering rate for fertilized plants from this area was used to estimate the shape and location of the potential fecundity curve. Although the distribution of mother tillers by age was not significantly different between fertilized and undisturbed tundra (Fetcher & Shaver 1983), greater production of daughter tillers per mother tiller at ages 3–6 caused the age-specific tillering rate to rise earlier to a peak (Fig. 1). The curve from the fertilized tundra was used, because the circumstances under which it was produced more nearly matched the assumptions of Bell (1980).

Inorganic nutrients, particularly nitrogen and phosphorus, are an important limitation on the growth of *E. vaginatum* in undisturbed tundra, whereas carbohydrates are in ample supply (Shaver & Chapin 1980). Addition of nutrients in the form of fertilizer produces great increases in tillering (Shaver & Chapin 1980). It seems reasonable to presume that
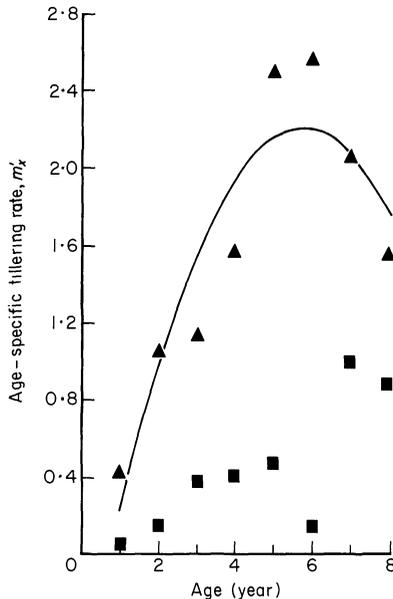
FIG. 1. Age-specific tillering rate (m'_x) for tillers of *Eriophorum vaginatum* from fertilized (▲) and undisturbed (■) tundra at Toolik Lake, Alaska. The equation for the curve is $m'_x = -0.68 + 1.01x - 0.09 \, x^2 \; (R^2 = 0.84, F = 13.2, P < 0.02)$.

fertilization supplies nutrients that would normally be accumulated over several years. Such reserves would be necessary for the production of daughter tillers. Bell's (1980) concept of potential fecundity is based on the assumption that individuals that are reproducing for the first time have more reserves and hence higher fecundity rates than individuals that have already reproduced. Therefore, tillering rates for fertilized tundra were used to estimate the potential fecundity curve.

Pre-tillering survival rate, the other parameter required by Bell's model, was calculated from the survival curve for tillers in undisturbed tundra at Toolik Lake. The survival curve for undisturbed tundra was used because the genetic control of tiller life history probably developed under the conditions prevailing in undisturbed tundra as opposed to conditions in the fertilized area. Tillers at ages 1 and 2 are capable of producing daughter tillers at low rates in undisturbed tundra (Fig. 1). No tillers of age 0 and only 3% of the tillers of age 1 produced daughter tillers. Hence, no tillers of age 1 and only 3% of the 2-year old tillers would have produced daughter tillers previously. Of the 3-year old tillers, 13% may have produced daughters previously. Thus, the tillers in age classes 1 and 2 appeared to fit Bell's definition of adolescent organisms. Pre-tillering survival was calculated using the average annual rate of survival from age 1 up to, but not including, age 3.

Caswell's model

For Caswell's model, the parameters were estimated using data from Eagle Creek. Age-specific tillering rates (m'_x) and age-specific rates of tiller survival (p_x) were calculated for both undisturbed tundra and for a site that had been scraped with a bulldozer 9 years previously and had since been recolonized by *E. vaginatum*. The scraped site was surrounded by undisturbed tundra (Chapin & Chapin 1980). Constant-coefficient matrix models for growth of tiller populations were constructed for both populations (Fetcher &
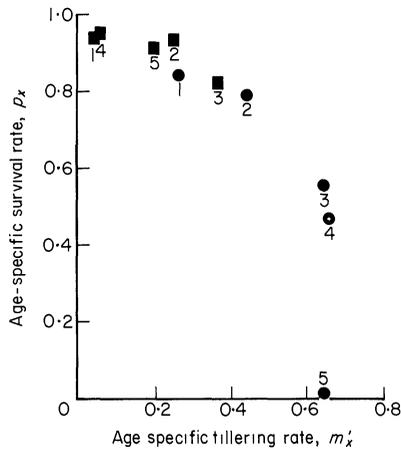
FIG. 2. Relationship between age-specific survival rate (p_x) and age-specific tillering rate (m'_x) for tillers of *Eriophorum vaginatum* from scraped (●) and undisturbed (■) tundra at Eagle Creek, Alaska. The numbers next to each point represent the age (years) associated with each value.

Shaver 1983). Analysis of the models showed that the annual rate of tiller population increase (λ_m) was nearly the same for the two sites, being 1·11 for undisturbed area and 1·08 for the scraped area (Fetcher & Shaver 1983). On the other hand, generation time was 5·3 years in undisturbed tundra—almost twice as long as for the scraped tundra. These results were obtained because tillers from undisturbed tundra lived significantly longer than tillers from the scraped area and produced daughter tillers at a later age (Fetcher & Shaver 1983). Age-specific tillering rate was negatively correlated with age-specific survival rate (Spearman rank correlation, $P < 0.05$), suggesting that there was a cost of tillering that was expressed in reduced survival (Fig. 2).

It was assumed, therefore, that the decreased survival observed in the scraped area could be attributed directly or indirectly to the effects of increased tiller production (i.e. to a 'cost' associated with tiller production). Although no experimental information is available for the survival costs of tillering for *E. vaginatum*, this assumption appears correct for at least two reasons. First, increased mortality has been found when tillering rates of *Carex arenaria* were increased by fertilization with mineral nutrients (Noble, Bell & Harper 1979). Secondly, most production of new tillers takes place in the centre of tussocks, while most mortality occurs near the edge (N. Fetcher, personal observation). Nutrients and light may be less available near the edge of tussocks (Chapin, Van Cleve & Chapin 1979). If tiller production were to increase, then the rate at which tillers are forced towards the edge would also increase. Thus, mortality may increase as an indirect result of new tiller production.

Tillers did not live longer than 5 years in the scraped area, so no values for cost of tillering could be calculated for greater ages. For ages 1–5, the survival costs of tillering were estimated by finding the difference in age-specific survival rate between scraped and undisturbed tundra for each age class from 1 to 5 and dividing by the difference in age-specific tillering rate for that age class.

Predicted values for the survival costs of tillering were calculated according to eqn (1) using reproductive values determined by Fetcher & Shaver (1983). Two sets of predicted values were calculated, corresponding to reproductive values from undisturbed tundra and from the scraped area, because *E. vaginatum* appears to be well-adapted to both

undisturbed and disturbed habitats (Fetcher & Shaver 1983). Ideally, it would be desirable to measure survival costs of tillering in both habitats because Caswell's model is strictly valid only for instantaneous changes in tillering and survival rates. Such data were not available, so the approach described above was used as an approximate measure of the survival cost of tillering.

RESULTS

Bell's model

To determine potential tillering rate, a quadratic curve was fitted to the age-specific tillering values of the fertilized tillers (m'_x) by least squares regression (Fig. 1). Adolescent survival was 0·9 for tillers from undisturbed tundra at Toolik Lake (Fetcher & Shaver 1983).

Figure 3 shows the age-specific tillering rate on a logarithmic scale and the straight line corresponding to the pre-tillering survival rate. The optimal age of first tillering is predicted to occur at the age where the slopes of the two lines are equal. The mean age of mother tillers in undisturbed tundra was considered as an estimate of the age of first reproduction, because most mother tillers less than 5 years old are generally tillering for the first time. The predicted value (4·5 years) was close to the mean age of mother tillers (4·8 years).

Because some tillers in the greater age classes may have produced daughter tillers previously, the mean age of mother tillers may be an overestimate of the mean age of first tillering. Therefore, the distribution of mother tillers was adjusted under the assumption that a certain proportion had produced daughters in the previous year. Because the proportion of tillers that produced daughters in each age class was known, it was possible to estimate the probability that a tiller had previously produced a daughter. By reducing the representation of mother tillers in each age class accordingly, an estimate could be made of the age distribution of tillers that were producing daughters for the first time. Thus, the number of mother tillers in year 2 was reduced by the fraction of all tillers that
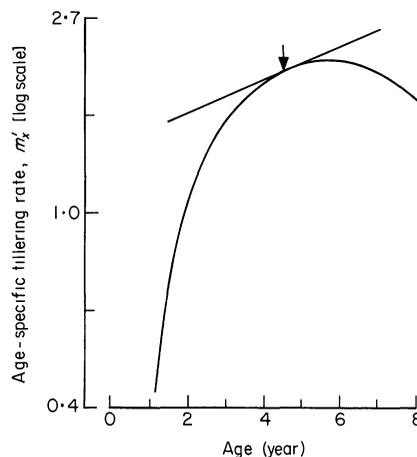

FIG. 3. The optimal age of tillering for *Eriophorum vaginatum* at Toolik Lake, Alaska. The tangent to the curve has a slope of 0·11. This value is the absolute value of the natural log of the estimated average annual survival rate of tillers that are capable of producing daughter tillers but have not yet done so. Where the curve has a slope of 0·11 (arrowed) is the optimal age of tillering (4·5 years).
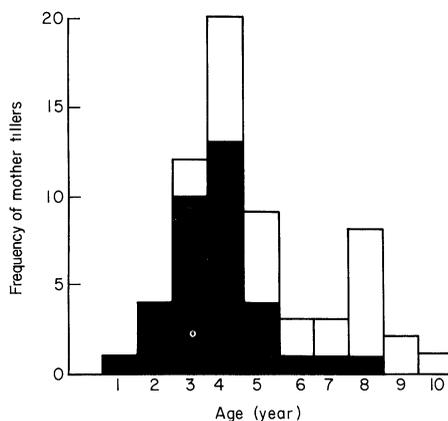
FIG. 4. Age distribution of mother tillers of *Eriophorum vaginatum* in undisturbed tundra at Toolik Lake, Alaska. The solid portion of each bar represents the age distribution of mother tillers adjusted for the probability of previous production of daughters (see text for detailed explanation).

produced daughters in year 1. Similarly, the number of mother tillers in age class 3 was reduced by the probability that a tiller had produced a daughter at age 1 or age 2 or both. The adjusted distribution of mother tillers represents a worst case in which all of the tillers are presumably those which have not previously produced daughters.

Bell's model, like most deterministic models, predicts a single point and does not make any statement about the distribution of values around that point. On the other hand, the observed age of mother tillers in undisturbed tundra was a distribution with peak at age 4 (Fig. 4). The distribution of mother tillers adjusted for previous tillering also had a peak at age 4 (Fig. 4). Because Bell's model does not predict the shape of the distribution of ages of first tillering, the Kolmogorov statistic was used to test whether either distribution was significantly different from a Poisson distribution with a mean of 4·5 years. It was not ($T_1 = 0·114$ for the observed distribution, $T_1 = 0·271$ for the adjusted distribution, $P >$ 0·05), which suggests that Bell's model was able to predict the mean age of first tillering of *E. vaginatum* tillers at Toolik Lake.

Distribution of flowering tillers

The age of flowering may be closely tied to the age of daughter tiller production. Examination of the distribution of inflorescence bud production by age of tillers showed that it was not significantly ($P < 0·05$) different from the age distribution of mother tillers in three out of four populations studied by Fetcher & Shaver (1983). Only in the tillers from the fertilized tundra at Toolik Lake was there a difference. A fifth population, from undisturbed tundra at Eagle Creek, had no inflorescence buds. Furthermore, the capacity to produce flowers seems to be related to the production of vegetative daughters. Three-quarters of the tillers that produced inflorescence buds also produced daughter tillers.

Caswell's model

Survival costs of tillering calculated from $-\Delta p_x / \Delta m'_x$ increased with age (Fig. 5(a)). Predicted survival costs also increased with age (Fig. 5(b)). The agreement between prediction and observation is less satisfactory than for Bell's model; nevertheless, the results indicate qualitative support for Caswell's model.
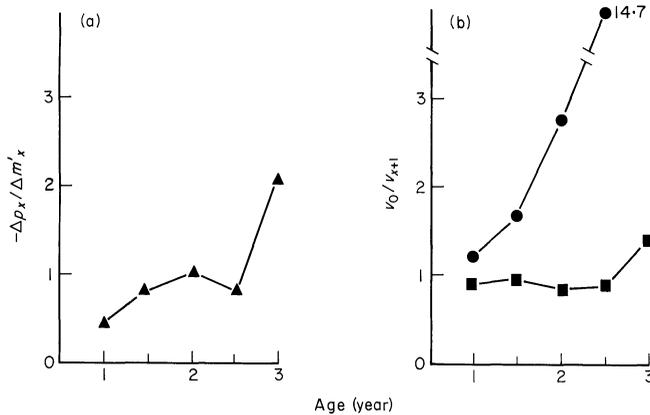
FIG. 5. (a) Observed survival costs of producing daughter tillers of *Eriophorum vaginatum* $(-\Delta p_x/\Delta m'_x)$ at Eagle Creek, Alaska. (b) Predicted survival costs (v_0/v_{x+1}) for (■) undisturbed tundra and (●) the scraped area.

DISCUSSION

Despite the apparent success of the models of Bell (1980) and Caswell (1982) in predicting characteristics of the life history of tillers of *E. vaginatum*, some questions remain about the general assumptions of the models, such as a stable age distribution and density independent population growth. The optimization criterion for both models is the maximization of the rate of population increase when the population is in the stable age distribution. Of the tiller populations used in the present analysis, only the population from the scraped area was not significantly different from the predicted stable age distribution (Fetcher & Shaver 1983). It is quite likely that tillering rates change from one year to the next (Fetcher & Shaver 1983) and, therefore, the tiller populations may never achieve a stable age distribution. Hence, there is some doubt about the validity of predictions made by models that use the maximum value of the rate of increase when the population is in the stable age distribution as their optimization criterion. This criticism can be applied to most models for optimal life histories. Models need to be developed that utilize transient properties of populations for their optimizing criteria, as was done by Caswell & Werner (1978); they found great similarity between the predictions made by a life-history analysis based on stable age distributions and one based on transient properties. Such results are encouraging, but, as Caswell & Werner (1978) point out, such agreement may not be the general case. Until models for optimal life histories are developed for populations with unstable age distributions and changing parameters, the best course seems to be a cautious application of the existing models.

Both Bell's and Caswell's models assume a density-independent environment in which fecundity and survival rates are unchanged as population density increases. The opposite situation, density dependence, is difficult to model for plant populations, because plants are not uniformly distributed (Schaffer & Leigh 1976). According to Fetcher & Shaver (1982), average rates of daughter tiller production in larger tussocks were lower than in smaller ones. The decrease was apparently negatively correlated with tiller density, for tiller density decreased with increased tussock size (Fetcher & Shaver 1982). Density dependence in the usual sense may not affect the behaviour of tiller populations.

The preceding analyses suggests that the patterns of tillering and tiller mortality in *Eriophorum vaginatum* conform to an optimal life history as predicted by two independent models. Because the optimum is defined as a maximum value for the rate of increase, these results imply that there is selection for maximizing the number of tillers of *E. vaginatum*. Support for this hypothesis comes from the observation that the response of *E. vaginatum* to fertilization with mineral nutrients is to increase greatly the number of tillers while tiller size increases less dramatically (Shaver & Chapin 1980). It may be possible to construct other models for allocation of carbon and nutrients in plants based on the idea that the number of tillers, leaves, or other modules is to be maximized subject to various constraints. Such models could provide new insight into patterns of carbon and nutrient allocation and enhance the applicability of demographic techniques to problems of plant growth.

ACKNOWLEDGMENTS

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