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EXPERIMENTAL ECOLOGY OF *DRYAS OCTOPETALA* ECOTYPES

II. A DEMOGRAPHIC MODEL OF GROWTH, BRANCHING AND FECUNDITY

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SUMMARY

(1) A general model of plant growth, branching, and seed production is described. The model simulates plant growth by considering the plant to be an assemblage of repeated units (modules). A shoot module, defined as a meristem and associated live leaves, passes through growth, branching, and flowering stages governed by size-dependent transition probabilities. Lefkovich matrices formed from these transition probabilities are used to project shoot-module population size, and therefore, plant growth.

(2) Model parameters were calculated for two ecotypes of *Dryas octopetala*, a perennial dwarf shrub of circumpolar arctic-alpine distribution. Shoot-module size categories were defined by leaf area. Censuses of tagged shoots in 1979 and 1980 revealed size-dependent growth, branching, and flowering patterns for both ecotypes.

(3) Rates of new shoot production increased with shoot size as did the proportion of flowering versus branching shoots. Contrasting patterns of allocation of materials for the two ecotypes maintained positive and comparable rates of vegetative growth for natural populations found in different habitats in the field.

(4) A sensitivity analysis showed shoot population growth to be most sensitive to annual growth increments, especially of small shoots, and less sensitive to the rate at which shoots produced 'offspring' shoots.

(5) Growth was relatively insensitive to the proportion of shoots which flowered (rather than branched), the number of offspring shoots produced per branching shoot and the number of offspring shoots produced per flowering shoot.

INTRODUCTION

Plant size and changes in it have become focal points of study for many aspects of plant ecology. Environmental factors which are ecologically important will often affect not only physiological functioning, but plant growth (McGraw & Wulff 1983). Fecundity and mortality in many plants depend on the sizes of individuals in the population. Production and cycling of biomass are based on growth and turnover of plant parts. Formal analysis of plant growth arose from economic theory (Blackman 1919). Relative growth rate and net assimilation rate, for example, have become useful tools for comparison of plant performance under controlled conditions (Hunt 1978).

Individual plants, unlike most animals, may be considered populations of repeated parts, or modules (Bazzaz & Harper 1977). These modules (e.g. leaves, shoots, or meristems) each have a characteristic life history analogous to the life history of whole individuals (Bazzaz & Harper 1977; Harper 1980). Module population size, and hence the size of an individual plant, depends on the timing of growth, reproduction, and death of individual

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modules. Studies of module dynamics have furthered analysis of growth form (Harper & Bell 1979) and plant architecture (Halle & Oldeman 1970; Bell 1974, 1976, 1979) as well as growth rates (Yokoi 1967a, b; Bazzaz & Harper 1977; Noble, Bell & Harper 1979; Abul-Fatih & Bazzaz 1980). The development and recent rejuvenation of the concept of the plant as a population of parts has been reviewed by White (1979).

Life histories of individuals, or of modules, may be described in several ways. While age-dependent models of population growth are most commonly employed for animals, life-history parameters frequently vary predictably with body size (Blueweiss *et al.* 1978). In plants, numerous studies have shown that fecundity and mortality are largely size- or stage-dependent (Sarukhan & Gadgil 1974; Hartshorn 1975; Werner 1975; Sohn & Policansky 1977; Weaver & Cavers 1980; Rausher & Feeny 1980; Meagher 1982). In the present paper, we extend size-dependent demography to shoot module populations and thereby develop a general, predictive model of plant growth.

The model was developed for three principal reasons. In a previous paper, we demonstrated, with reciprocal transplant studies, the present functioning of viability selection in maintaining genetic differences between ecotypes of *Dryas octopetala* L. over short distances (McGraw & Antonovics 1983). However, in the reciprocal transplant of adult plants, short-term growth rate was not clearly higher for plants transplanted to 'home' sites (McGraw 1982). One purpose of the model was to allow prediction of long-term growth from short-term measurements, making the interpretation of growth effects on the long-lived *Dryas octopetala* plants more realistic. A second purpose was to relate plant growth to seed production to provide a means of evaluating fecundity as well as viability components of selection. A third purpose was to identify the components of yearly growth and allocation of materials which are critical to long-term plant growth.

In this paper, we apply the model to a random sample of natural shoot populations of two *Dryas octopetala* ecotypes in the field to obtain estimates of growth parameters. An extension of established sensitivity analysis procedures was used to identify features of growth and allocation which have the greatest potential effect on the long-term plant growth.

METHODS

Model

The fate of a population of individuals grouped into equal size classes may be modelled by determining the probabilities of making a transition from one class to each possible class in a given time. With data on the current population state (the distribution of individuals among size classes), the set of transition probabilities for all size classes may then be used to project a future population state. The general equation for projection of population size (Lefkovitch 1965) may be written:

$$\begin{pmatrix} a_{11} & a_{12} & \cdot & \cdot & a_{1j} \\ a_{21} & a_{22} & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ a_{i1} & \cdot & \cdot & \cdot & a_{ij} \end{pmatrix} \times \begin{pmatrix} M_1(t) \\ M_2(t) \\ \cdot \\ \cdot \\ M_j(t) \end{pmatrix} = \begin{pmatrix} M_1(t+1) \\ M_2(t+1) \\ \cdot \\ \cdot \\ M_j(t+1) \end{pmatrix} \quad (1)$$

To predict growth of an individual plant, eqn (1) may be applied to shoot modules, defined here as a meristem and the live leaves produced by that meristem, where a_{ij}

represents the probability that a shoot module of size i will be derived from a shoot module of size j during one time interval. $M_j(t)$ is the number of shoots of size j at time t . The set of values for M constitutes the state vector for the shoot module population. Shoot population size, and therefore individual plant size, is the sum of the elements of the state vector. Where plant growth follows a seasonal pattern, as in the present study, one iteration of eqn (1) represents the passage of 1 year. A different interval would be required for plants which show flushes of growth more than once annually.

A shoot module follows one of four possible paths annually (Fig. 1). It may remain a single shoot, or it may branch, or flower, or die. (See Table 1 for definition of terms.) Branching and flowering are similar in that both processes constitute investment in structures not directly supporting the parent shoot. However, branching and flowering shoots may differ in the rates of production of lateral shoots which may be of different sizes. To allow for these possible differences, separate model parameters were specified for each type of shoot, as described below.

The probability associated with a particular size transition, a_{ij} , is made up of contributions from growing shoots, branching shoots, and flowering shoots. The contribution of growing shoots to a_{ij} is g_{ij} , the probability that a shoot will grow from size j to size i . As used here (Table 1), 'growing' does not necessarily imply an increase in size; the model permits shoot size to increase, decrease, or remain the same, so long as the shoot remains alive. The contribution of branching shoots to a_{ij} is determined by several parameters including: (i) r_j , the probability that a shoot of size j will produce new lateral shoots while vegetative or while flowering; (ii) $1 - \alpha_j$, the fraction of such shoots of size j which will branch; (iii) MB_j , the mean number of live shoots (including parent and offspring shoots) which will be produced per branching parent shoot of size j ; and (iv) b_{ij} , the probability that a shoot of size i will result from the branching of a shoot of size j . In an analogous way, the contribution of flowering shoots to a_{ij} is determined by: (i) r_j , (same as above); (ii) α_j , the fraction of reproducing shoots of size j which will flower;

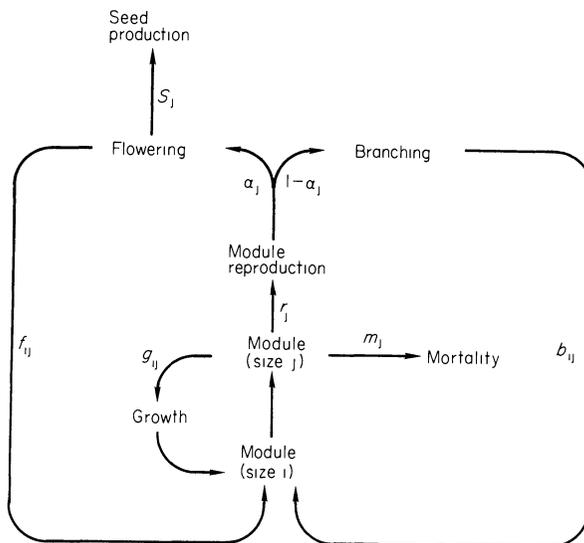


FIG. 1. Possible fates of a shoot module in 1 year. Variables governing probabilities of following given paths are explained in the text and in Table 1.

TABLE 1. Definitions of model parameters and terms for a general model of plant growth. All are based on shoot behaviour over 1 year.

Parameter	Definition
g_{ij}	proportion of size j shoots which grew to size i
r_j	proportion of size j shoots which reproduced, i.e. either branched or flowered
α_j	fraction of reproducing shoots of size j which flowered
$1 - \alpha_j$	fraction of reproducing shoots of size j which branched
MB_j	mean number of shoots derived from a branching shoot of size j , including parent shoot, if alive
MF_j	mean number of shoots derived from a flowering shoot of size j , including parent shoot, if alive
b_{ij}	proportion of shoots derived from size j branching shoots which grew to size i
f_{ij}	proportion of shoots derived from size j flowering shoots which grew to size i
s_j	mean number of full seeds produced per flower
m_j	proportion of size j shoots which died
M_j	number of shoots of size j
Term	
Shoot or shoot module	a dead, dormant, or live meristem and all live leaves directly adnate to the axis of that meristem
Flowering shoot	a shoot in which the meristem becomes converted to a flower during the census interval; lateral meristems may or may not grow during the interval
Branching shoot	a vegetative shoot in which lateral meristems grow during the census interval
Growing shoot	a shoot which remains alive (possesses live green leaves during the growing season), but does not branch or flower during the census interval

(iii) MF_j , the mean number of live shoots (including parent and offspring shoots) which will be produced per parent shoot of size j ; and (iv) f_{ij} , the probability that a shoot of size i will result from a flowering shoot of size j . The overall probability that a shoot of size j will complete a given size transition may now be expressed as:

$$\alpha_{ij} = g_{ij} + r_j(1 - \alpha_j)(MB_j)(b_{ij}) + r_j(\alpha_j)(MF_j)(f_{ij}) \quad (2)$$

The three summed terms are the contributions of growing, branching, and flowering shoots, respectively.

When eqn (1) is iterated, using matrix elements specified by eqn (2), the shoot population eventually reaches a stable distribution of shoots among size classes. When this occurs, eqn (1) may be rewritten:

$$\gamma \times \begin{pmatrix} M_1(t) \\ M_2(t) \\ \cdot \\ \cdot \\ M_j(t) \end{pmatrix} = \begin{pmatrix} M_1(t+1) \\ M_2(t+1) \\ \cdot \\ \cdot \\ M_j(t+1) \end{pmatrix} \quad (3)$$

At the stable size distribution, γ is a measure of the rate of increase of the shoot population, and therefore it is a long-term prediction of whole plant growth rate. γ is analogous to λ in the description of populations of individuals, and is derived analytically as the largest positive eigenvalue of the transition matrix.

A subroutine of the model computes annual seed production using another parameter,

s_i , the mean number of seeds produced by a flowering shoot of class i . Yearly seed production is then calculated for each iteration of eqn (1) as:

$$\text{Annual seed production} = \sum_{i=1}^j s_i r_i a_i M_i(t-1) \quad (4)$$

Cumulative seed production is also calculated as a measure of long-term fecundity.

Transition probabilities and other parameters governing growth behaviour in the model are estimated by observing the actual growth transitions in the field.

Field studies

The study site was located above timberline in east-central Alaska, 153 km north-east of Fairbanks on the Steese Highway (65°26'N, 145°30'W; altitude 1050 m). The site comprised an environmental and vegetational gradient including an exposed ridgetop, an area of late-lying snow, and wet tundra below the snowbed (McGraw and Antonovics 1983). Two extreme ecotypes of *Dryas octopetala* reach peak abundances in the snowbed and on the ridgetop. These forms are referred to as snowbed and fellfield ecotypes, respectively (see McGraw & Antonovics (1983) for detailed description of vegetation zones and ecotypes). While intermediate phenotypes may be found at the site, they are rare; model parameters were estimated only for the two common forms.

Genetic individuals of *D. octopetala* could not be identified due to spread and mixing of clones as well as the occasional separation of branches by the disintegration of connecting stems. Growth parameters derived from field measures therefore represented growth patterns of each ecotype as a whole. In mid-August 1979, when growth had ended, five 5-m transects were placed at random in each of fellfield and snowbed sites. A random sample of 100 shoots was tagged along each transect to give a total sample of 500 shoots per ecotype. Shoot module size was estimated by counting the number of leaves and measuring the leaf lengths of all live leaves on every tagged shoot. The number of offspring shoots was also noted. In mid-August 1980, the same measurements were made on all tagged shoots and on offspring shoots produced during the preceding year. The seed production by flowering shoots was also recorded. The sample of flowering shoots was too small to detect size-dependent seed production, therefore s_j was taken to be the mean seed production of the flowering shoots. Model parameters (Table 1) were estimated from the behaviour of the shoots between the two censuses.

Two complete sets of model parameters were calculated for natural populations of each of fellfield and snowbed *D. octopetala*. One set was based on leaf number as the size category, the other using leaf area size classes. The total leaf area of a shoot module was determined by deriving first an allometric relationship between leaf length and leaf area (Fig. 2). With this relationship, the leaf area was determined for each leaf and the areas were summed to give the shoot module leaf area. In this paper, data using leaf area are used; qualitatively, the results of simulations using leaf number were similar. Shoot population dynamics were projected for a 10-year period beginning in August 1980. The model calculated shoot and leaf population size, growth rates, seed production, and mean shoot size for each subsequent year.

Sensitivity analysis

The sensitivity of plant growth (γ) to changes in the life history of shoot modules may be analysed with the following formula developed by Caswell (1978):

$$\delta\gamma/\delta a_{ij} = u(i) \cdot v(j) \quad (5)$$

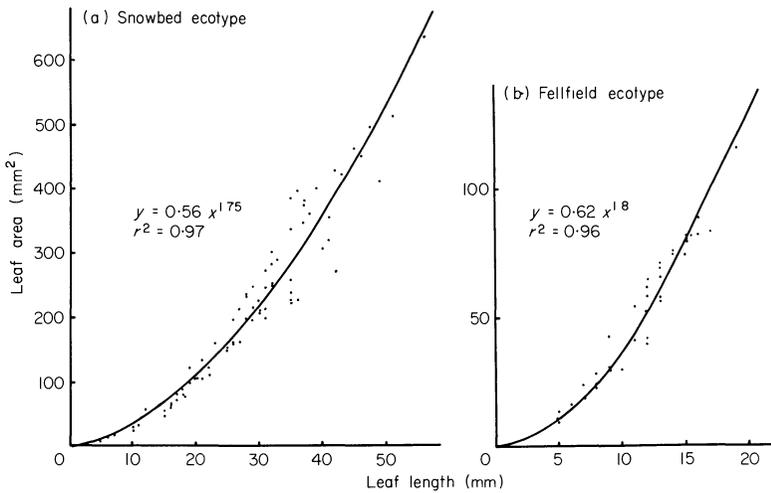


FIG. 2. Relationship between measured leaf lengths and leaf area (calculated by tracing leaves and weighing the paper image) for (a) snowbed and (b) fellfield ecotypes of *Dryas octopetala* at Eagle Summit, Alaska. The logarithms of length and area for each leaf were used to estimate a linear regression equation for each ecotype.

where $u(i)$ is the reproductive value of the i th size class (the i th element of the left eigenvector of the transition matrix), and $v(j)$, the j th element of the stable-stage distribution vector (the j th element of the right eigenvector of the transition matrix). This general formula describes how responsive plant growth is to shifts in a given size transition, when other transitions are held constant. Where a_{ij} is itself a function of several growth parameters, the sensitivity of γ to each parameter (here arbitrarily designated p_i) is:

$$\delta\gamma/\delta p_i = (\delta\gamma/\delta a_{ij})(\delta a_{ij}/\delta p_i). \quad (6)$$

Equation 6 was used to provide an index of the sensitivity of whole plant growth to each growth parameter measured in the field.

RESULTS

Model parameters

For ecotypes of *Dryas octopetala* the leaf area of a shoot showed a high correlation with future leaf area (Table 2). Between-year size correlations were greater in the snowbed than in the fellfield plants. In both ecotypes a better correlation was found in the growing shoots than in the branching or flowering shoots. The number of leaves was not as closely correlated between years as was the leaf area of shoots.

The production of side shoots and flowers increased with greater shoot size (Table 3). The proportion of shoots which reproduced (r_j) was greater in the fellfield ecotype than in the snowbed ecotype for shoots of comparable size. However, snowbed *D. octopetala* shoots had up to ten times more leaf area than shoots of the fellfield ecotype. The probability of branching or flowering was much greater in the large snowbed *D. octopetala* shoot size classes than in any size class of fellfield shoots. Despite the large differences in size-dependent values of r_j , fellfield and snowbed plants had overall rates of shoot reproduction ($\Sigma r_i M_i / \Sigma M_i$) of 13.7% and 14.2%, respectively.

TABLE 2. Coefficients of determination (r^2) for the relationship between shoot sizes, as leaf numbers per shoot, or leaf area per shoot of two ecotypes of *Dryas octopetala* at Eagle Summit, Alaska, between 1979 and 1980 in growing (G), branching (B) and flowering (F) shoots. Significance levels refer to the probability that the correlation coefficient is greater than 0. NS, not significant.

Ecotype	Leaf number			Leaf area		
	G	B	F	G	B	F
Fellfield	0.02 (NS)	0.002 (NS)	—	0.66 ($P < 0.01$)	0.54 ($P < 0.01$)	—
Snowbed	0.48 ($P < 0.01$)	0.40 ($P < 0.01$)	0.27 (NS)	0.77 ($P < 0.01$)	0.70 ($P < 0.01$)	0.40 (NS)

TABLE 3. Size-specific model parameters governing the contribution of branching and flowering shoots to shoot population growth and seed production in two ecotypes of *Dryas octopetala* at Eagle Summit, Alaska. Key to symbols is given in Table 1.

Fellfield	Size class as shoot leaf area (cm ²)										
	0-0.49	0.5-0.99	1-1.49	1.5-1.99	2-2.49	>2.5					
r_j	0.08	0.11	0.16	0.29	0.25	0					
$1 - \alpha_j$	1.00	1.00	0.94	0.93	1.00	1.00					
α_j	0	0	0.06	0.07	0	0					
MB_j	2.40	2.50	2.71	2.77	2.33	0					
MF_j	0	0	3.00	4.00	0	0					
s_j	25	25	25	25	25	25					
m_j	0.11	0.01	0.01	0.02	0.04	0					
Snowbed	0-1.99	2-3.99	4-5.99	6-7.99	8-9.99	10-11.99	12-13.99	14-15.99	16-17.99	18-19.99	>20
r_j	0.01	0.04	0.07	0.13	0.20	0.30	0.57	0.69	0.43	0.50	0.75
$1 - \alpha_j$	1.00	1.00	1.00	0.70	1.00	0.70	0.63	0.55	0.83	0.67	0.33
α_j	0	0	0	0.30	0	0.30	0.37	0.45	0.17	0.33	0.67
MB_j	3.00	2.25	2.00	3.00	2.50	2.71	2.50	3.17	3.60	2.50	2.00
MF_j	0	0	0	2.33	0	3.33	4.50	4.60	2.00	4.00	4.00
s_j	24	24	24	24	24	24	24	24	24	24	24
m_j	0.08	0.05	0.02	0.05	0.05	0.12	0.04	0.06	0.07	0.50	0

The fellfield and snowbed plants differed greatly in the probabilities of flowering compared with branching (α_j and $1 - \alpha_j$, Table 3). All the fellfield shoot size classes had a low flowering frequency, while up to 67% of the shoots of snowbed plants in large size classes flowered. Overall flowering frequencies ($\Sigma r_j \alpha_j M_j / \Sigma M_j$) were 0.4% and 3.4% for fellfield and snowbed plants, respectively. The number of new shoots produced (MB_j and MF_j) may have been greater for large shoots. However, due to the low replication in some size classes, these parameters did not consistently increase with shoot size.

The mortality of shoots (m_j) decreased with size in fellfield *D. octopetala*, but showed no consistent pattern in the snowbed plants. Overall mortality of shoots ($\Sigma m_j M_j / \Sigma M_j$) was 6.2% and 4.9% in snowbed and fellfield populations, respectively.

Simulations

The model projections for natural shoot populations forecasted annual rates of whole plant growth of more than one for fellfield and snowbed ecotypes (Fig. 3). After ten iterations (years), shoots of the fellfield ecotype reached a stable rate of increase (γ) of 1.17 per year. In the snowbed ecotype, after ten iterations, the stable shoot population growth rate was 1.13 per year. The growth rates in population leaf area for both ecotypes approached the same stable rates as those for shoot numbers after 5-10 years. The approach to stable growth rates was usually monotonic; however, it was possible to

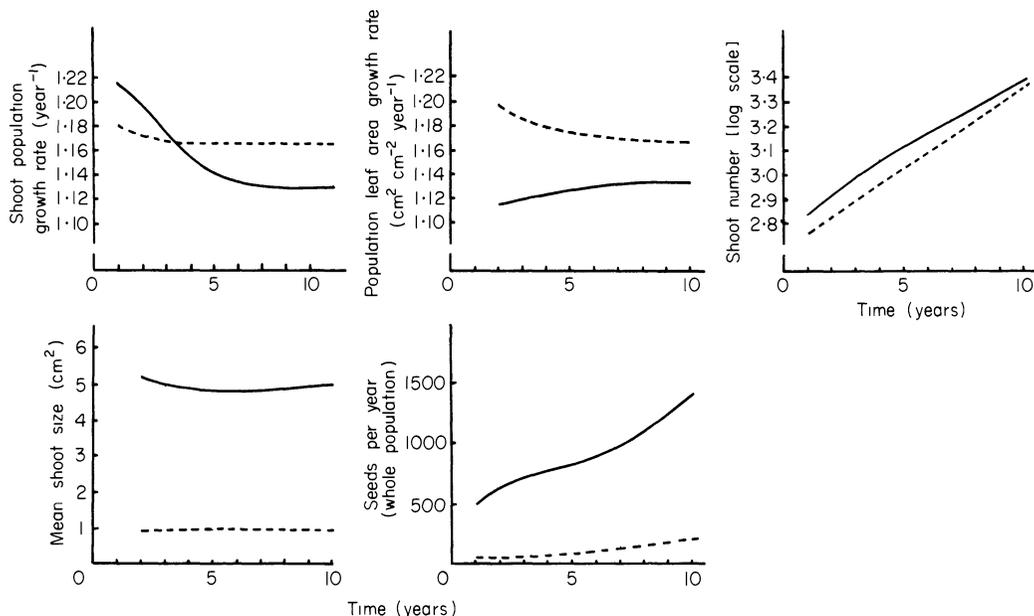


FIG. 3. Model predictions of several shoot population parameters for two ecotypes of *Dryas octopetala* at Eagle Summit, Alaska. Solid lines represent the predicted course of change for the snowbed ecotype and hatched lines that for the fellfield ecotype over 10 years.

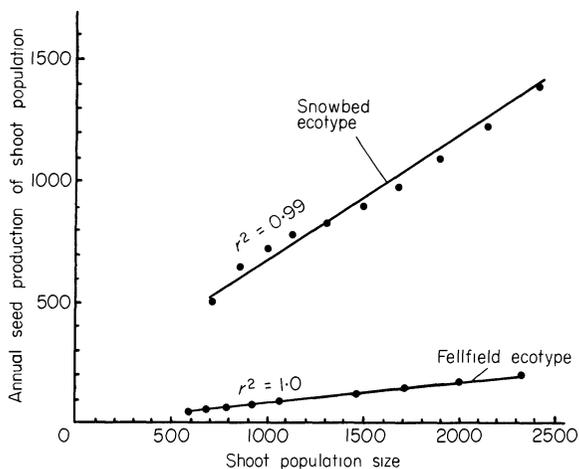


FIG. 4. Relationship between total number of shoots in a population of *Dryas octopetala* and number of seeds produced by the entire population during 1 year as predicted by model simulations.

overshoot stable values (Fig. 3, mean shoot size). The simulations predicted a simultaneous increase in total seed production for the population and in shoot number. Therefore, for the 10-year simulation period there was a high correlation between shoot population size and seed production (Fig. 4). The leaf area per shoot increased slightly in the fellfield ecotype during the simulation before reaching stability. Leaf area per shoot fell sharply in the first 6 years in the snowbed ecotype, but rose slightly to a stable value over the next 4 years.

Model sensitivity

Reproductive values ($u(i)$) and stable size distributions ($v(j)$) of the shoots were similar in form for the two ecotypes (Table 4). The proportion of shoots in a size class decreased with size. The reproductive value of a shoot was the expected contribution of shoots to future population growth (Caswell 1978), and this value increased with size, reaching a peak in medium-large shoots in both ecotypes. The reproductive value was less than 1 for only two size classes in both ecotypes. In the snowbed ecotype however, these classes comprised 62% of the shoot population.

The sensitivity ($\delta\gamma/\delta a_{ij}$) of growth (γ) to changes in individual elements of the transition matrix was greatest for transitions in the lower left portion of the matrix (Table 5), i.e. for the probabilities of small shoots giving rise to large shoots in one time increment. If values for transitions which were never observed ($a_{ij} = 0$) are eliminated, the most important elements of the matrix for shoot population growth were a_{41} and a_{31} , for fellfield and snowbed plants, respectively. These elements governed the probability that shoots in the smallest size class would increase in size by two or three size classes during 1 year.

Extension of the sensitivity analysis to components of a_{ij} clearly illustrated which parameters were critical to overall shoot population growth. Shoot size transitions of growing, branching, and, in the snowbed ecotype, flowering shoots had the largest mean sensitivity values (Table 6). Sensitivity to the probability of shoot reproduction (r_j) was somewhat lower, while sensitivities to the proportion of branching or flowering shoots which flower (α_j) and offspring shoot numbers (MB_j and MF_j) were at least an order of magnitude lower than the sensitivity to size transitions. The effect of r_j , the proportion of shoots either branching or flowering (Table 1), was potentially high on a few elements of the transition matrix, as indicated by the high maximum sensitivities in both ecotypes. Sensitivity to the proportion of flowering shoots (α_j) was negative, indicating that an increase in α_j would depress plant growth.

TABLE 4. Stable size distribution (proportion of shoots in each size class) and size-specific reproductive values (expected contribution to shoot population growth of a shoot of a particular size) as predicted by a model of two *Dryas octopetala* ecotypes with data obtained at Eagle Summit, Alaska.

Ecotype	Size class (cm ²)	Stable size distribution	Reproductive value
Fellfield	0-0.49	0.34	0.77
	0.50-0.99	0.24	1.00
	1-1.49	0.17	1.20
	1.5-1.99	0.14	1.34
	2-2.49	0.04	1.12
	>2.5	0.07	0.90
Snowbed	0-1.99	0.43	0.52
	2-3.99	0.19	0.78
	4-5.99	0.13	1.11
	6-7.99	0.07	1.32
	8-9.99	0.06	1.61
	10-11.99	0.03	2.06
	12-13.99	0.04	2.60
	14-15.99	0.02	3.01
	16-17.99	0.01	2.53
	18-19.99	0.01	1.79
	>20	0.01	3.01

TABLE 5. Table of values for the sensitivity ($\delta\gamma/a_{ij}$) of shoot population growth rate to small changes in elements of transition matrices estimated for two *Dryas octopetala* shoot populations at Eagle Summit, Alaska. The position of each sensitivity value in the table corresponds to the position of each non-zero element (a_{ij}) of the transition matrix.

Snowbed ecotype										
0.22	0.10	0.07	0.04	0.03	0.01	0.02	0.01	0.003	0.004	0.006
0.33	0.15	0.10	0.06	0.05	—	0.03	0.02	0.01	—	—
0.48	0.21	0.15	0.08	—	—	—	—	—	—	—
—	0.25	0.17	0.10	0.08	0.04	0.05	—	—	—	—
—	0.31	0.21	0.12	0.10	0.05	0.06	0.03	0.01	—	—
—	—	0.27	0.15	0.13	0.06	0.08	0.04	—	—	—
—	—	0.34	0.19	0.16	0.07	0.10	0.05	—	—	0.03
—	—	—	—	0.19	0.09	0.11	0.06	0.02	0.02	—
—	—	—	—	0.16	0.07	0.09	0.05	0.02	—	—
—	—	—	—	—	—	0.07	0.04	0.01	—	0.02
—	—	—	—	—	0.09	0.11	0.06	0.02	0.02	0.03
Fellfield ecotype										
0.26	0.19	0.13	0.11	0.03	—	—	—	—	—	—
0.34	0.25	0.17	0.14	—	—	—	—	—	—	—
0.41	0.29	0.20	0.17	0.04	—	—	—	—	—	—
0.46	0.33	0.22	0.19	0.06	0.09	—	—	—	—	—
—	0.27	0.19	0.16	0.05	—	—	—	—	—	—
—	—	—	0.12	0.04	0.06	—	—	—	—	—

TABLE 6. Sensitivity of growth as shoot numbers in ecotypes of *Dryas octopetala* to changes in individual growth parameters. Rank order in parentheses. Values are derived from a model based on field data obtained at Eagle Summit, Alaska.

	Parameter	Mean sensitivity	Maximum sensitivity	Minimum sensitivity
Fellfield	r_j	0.0570 (3)	0.5240	0
	α_j	-0.0030 (5)	0.0373	-0.0435
	MB_j	0.0031 (4)	0.0181	0
	MF_j	0.0001 (7)	0.0016	0
	g_{ij}	0.1759 (1)	0.4595	0.0316
	b_{ij}	0.0576 (2)	0.1366	0
	f_{ij}	0.0028 (6)	0.0061	0
Snowbed	r_j	0.0160 (4)	0.6688	0
	α_j	-0.0003 (6)	0.0227	-0.0262
	MB_j	0.0007 (7)	0.0048	0
	MF_j	0.0002 (5)	0.0037	0
	g_{ij}	0.1682 (1)	1.2913	0.0035
	b_{ij}	0.0320 (2)	0.0994	0.0030
	f_{ij}	0.0185 (3)	0.1073	0

DISCUSSION

In *Dryas octopetala*, life-history traits of shoot modules varied greatly with shoot size as measured by leaf area. Growth transitions, probabilities of flowering or branching, offspring shoot production, and mortality all showed size-specificity to varying degrees. The demographic model allowed a prediction of several important plant features: shoot population growth rates, growth rate as leaf area, shoot number, leaf number, leaf area, mean shoot size, and seed production.

Non-destructive field measurements permitted sampling of the same shoot population in successive years, as required for estimation of model parameters. The measurement and recording of shoot size required little time in the field (2–4 days for 1000 shoots); this allowed a large sample size, including the wide variation in shoot growth behaviour observed under natural conditions, to be obtained. Different ways of measuring shoot size represent compromises between the speed of making measurements and the accuracy in estimating shoot size. For plants of uniform leaf size, leaf number would adequately characterize shoot size. For species where leaf size and shape are variable, two or more leaf dimensions would need to be measured to assess accurately leaf area, and hence shoot size. In *D. octopetala*, leaf size varied widely, even within populations, and therefore an estimation of leaf area per shoot improved the correlation between sizes in 1979 and 1980. However, leaf shape was relatively constant, and therefore leaf area could be derived from length alone.

Size alone explained a large part of the observed variability in future shoot size (Table 2). Several factors could account for the remaining variance, including variable environment, proximity to other shoots or plants of other species, chance historical events, and shoot or whole plant age. These other factors appeared to be more important in fellfield than in snowbed *D. octopetala* and lead to a poorer correlation of shoot sizes between 1979 and 1980. Leaf area was nevertheless a dominant factor in determining shoot growth.

The reduced predictability of 1980 shoot size from 1979 shoot size in the branching and flowering shoots relative to the growing shoots may be attributed to the increased production of plant parts for which the net carbon balance is negative. Growing shoots funnel resources primarily into new leaves, while branching and flowering shoots may devote resources to offspring shoots in varying numbers and sizes. In addition, flowering shoots may variously abort flower buds, produce male flowers or perfect flowers, or fill few to many seeds. These increased possibilities for resource allocation compared with growing shoots may account for the decrease in predictability of allocation to new leaf area.

Several studies have suggested that flowering represents a 'cost' to growth or branching (Sohn & Policansky 1977; Law 1979; Calow 1979). In *D. octopetala*, a large size was necessary before the flowering of a shoot became probable, and fewer new leaves were produced by flowering shoots. Conversion of the meristem to a flower killed the parent shoot in the following year, although live leaves often persisted for a year in the evergreen snowbed *D. octopetala*. Flowering did not reduce the current-year production of lateral shoots, but parent shoot death, caused by conversion of the apical shoot meristem to a flower, obviated future branching. Another indication that flowering represented a 'cost' was the negative sensitivity of plant growth, γ , to increases in the proportion of shoots flowering (α). This meant that plant growth would decrease if the flowering:branching ratio increased (with a constant total number of shoots which either branch or flower). More data on flowering shoots are needed to investigate further the balance between growth, branching, and production of seeds in *D. octopetala*. Nevertheless, the demographic model is useful for investigating possible conflicts between long-term shoot population growth (vegetative spread) and seed production.

The model assumes that parameters do not vary significantly between years. This possibility has not been tested here, but the model predictions themselves suggest that values of parameters estimated for 1979–80 could not indefinitely remain the same. Shoot population growth rates of 1.13 and 1.17 would soon result in very high shoot densities in which interactions between shoots would depress growth. A second assumption of the

model is that within the size classes used, the shoots have a stable size distribution. The probability that this assumption will be violated can be reduced by specifying small size classes, but errors of parameter estimation are then introduced (Vandermeer 1978).

When model assumptions are valid for several consecutive seasons, simulations will be useful in predicting the course of plant growth. Such predictions are useful even if parameters vary in response to environmental change for they characterize the potential long-term effect of that shift. For example, several successive years of growth as in 1979–80 for *D. octopetala* would result in a significant increase in abundance (number of shoots) and cover (leaf area) of both ecotypes studied. Moreover, the effects of successive favourable years would not be additive. Shoot and seed production would increase in an approximately exponential manner as modified by the size structure and size-specific behaviour of the shoot population.

Perhaps more important than its predictive value is the structure provided by the model for the study of perennial plant growth and its relationship to fecundity. Most plant growth analysis relies on destructive harvesting amenable to short-lived plants growing under controlled conditions, but not to long-lived plants in the field (Harper 1980). A non-destructive, predictive model is most appropriate for perennial plants, in which growth over several years is more critical to fitness than short-term growth. The model is not intended to ascertain a mean growth rate of an organism as in classical growth analysis, but to include variation in growth at the suborganismal (module) level and to predict the consequences of this variation in terms of whole plant growth and whole plant seed production. The two approaches are complementary.

The great sensitivity of shoot population growth to changes in size transitions of shoots was an unexpected result of the sensitivity analysis. A priori, the probability of branching or flowering (r_j) and the number of offspring shoots produced (MB_j and MF_j) might be expected to be critical to shoot population growth. However, because r , MB , and MF increased greatly with size, the rate at which large sizes were attained was most critical to shoot population growth.

To achieve generality, Caswell's (1978) sensitivity analysis, and our extension of it, assumes that one element of the transition matrix can be shifted independently of the other elements. This means that an increase in a particular element occurs by a decrease in mortality of members of a particular size class. This assumption resulted in the sensitivity of γ to individual elements always being positive. Even for matrix elements governing the probability that shoots would get smaller, the sensitivity index ($\delta\gamma/\delta a_{ij}$) was positive. This is counter-intuitive since small shoots tended to have high mortality rates and low reproductive values; increases in the probability of large-to-small transitions should have decreased population growth rates. An improved sensitivity index for demographic analysis involving size-class transitions would account for interdependence of transition matrix elements, particularly of those in a given column of the matrix. However, generality would be lost as assumptions would need to be made concerning the precise functional relationship between elements for the population under study. Caswell's (1978) index, and our extension of it, probably gave reasonable *relative* sensitivities (Tables 5 and 6) in the present study despite the assumption of parameter independence.

The significance of shoot or module demography may extend beyond providing a framework for study of plant growth (White 1979; Harper 1980). The present model suggests that seed production of a collection of shoots depends on: (i), shoot population size; (ii), the distribution of shoots among size classes; (iii), the rate at which shoots reach flowering size; and (iv), the rate of seed production by shoots of flowering size. If an

individual plant is then viewed as a collection of shoots, the fecundity schedule of that collection clearly depends not only on shoot population size, but on the entire set of parameters comprising a shoot life history.

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