

LIFE HISTORY OF THE LONG-LIVED GYNODIOECIOUS CUSHION PLANT *SILENE ACAULIS* (CARYOPHYLLACEAE), INFERRED FROM SIZE-BASED POPULATION PROJECTION MATRICES¹

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Alpine plants often appear to have long life-spans as an adaptation to harsh and unpredictable environmental conditions, yet many lack reliable indicators of age that would make it possible to determine their true longevity. Their extended life-spans also pose problems for measuring lifetime reproductive success, a key component of breeding system evolution in species such as the gynodioecious cushion plant *Silene acaulis*. For a population of *S. acaulis* in south-central Alaska, we applied a recently derived analytical approach using size-based population projection matrices that allowed us to estimate: (1) the relationship between cushion diameter and age; and (2) lifetime reproductive success through seed production by females relative to hermaphrodites. Because of a combination of slow growth, frequent shrinkage, and extremely high adult survival, we estimate that the largest cushions in our study population exceed 300 yr in age, and some may live substantially longer, despite the seemingly inhospitable alpine environment they inhabit. Females are estimated to produce 4.4 times as many offspring via seed production over the course of their lives as do hermaphrodites, a difference that is more than sufficient to assure the persistence of females despite their inability to transmit genes through pollen. These results highlight the utility of size-based projection matrices for studying the life histories of herbaceous perennials whose life-span and lifetime reproductive success cannot be determined easily by any other means.

Key words: alpine perennial plant; Caryophyllaceae; gynodioecy; life history; moss campion; net reproductive rate; *Silene acaulis*; survivorship.

Life history theory predicts that perenniality and polycarpic reproduction will be favored where offspring survival is low (Charnov and Schaffer, 1973) or unpredictable (Murphy, 1968), two features that typify arctic and alpine environments. While high-altitude and high-latitude plants are often claimed to exhibit a high degree of perenniality (Billings and Mooney, 1968; Bliss, 1971; Walter, 1979), we presently have a poor understanding of the true life-spans of many species, preventing a full quantitative comparison of plant life history strategies in tundra vs. other biomes. This ignorance reflects the fact that for arctic and alpine plants, as for the dominant plants in many other biomes (e.g., grasslands and deserts), it can be exceedingly difficult to obtain direct estimates of plant life-spans. Because of their longevity, it is impractical to follow cohorts of tundra plants from birth until death. In addition, many characteristic tundra species have herbaceous growth forms, so that standard methods for determining an individual's age (such as counting annual growth increments as is often done with woody plants) are usually either inappropriate (because many species lack clearly delineated growth increments) or require disturbance or destruction of sampled individ-

uals (Svensson and Callaghan, 1988) that is incompatible with ongoing population studies. A second but related challenge posed by the longevity of tundra perennials is that of measuring lifetime reproductive success. While it is possible to infer lifetime life history components of nonwoody plants using size-based population projection matrices, which can be parameterized easily with short-term data, few life history studies have actually taken this approach. In this paper, we develop a projection matrix for the long-lived arctic and alpine cushion plant, moss campion (*Silene acaulis* L.; Caryophyllaceae). We then apply recently developed analytical methods (Cochran and Ellner, 1992) to our estimated projection matrix to address two questions concerning the life history of moss campion.

The first question we address is: what is the relationship between size and age in moss campion? Moss campion plants often inhabit early-successional sites created in recent centuries, such as disturbed tundra (Griggs, 1956) and glacial moraines created during the Little Ice Age (Benedict, 1989). Because of its longevity, some authors have suggested that moss campion plants be used to date disturbances in the not-too-distant past, but doing so requires an estimate of the relationship between plant size and age. Previous studies have correlated maximum cushion size with the age of known glacial substrates to calibrate an age-size relationship (Benedict, 1989; McCarthy, 1992), but such a calibration requires a detailed knowledge of local geology, relies upon maximum rather than typical growth rates, and is unlikely to be accurate throughout the circumboreal range of moss campion due to regional variation in vital rates. In contrast, the methods of Cochran and Ellner (1992) allow the relationship

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between size and age to be estimated for a particular site knowing only the rates of survival and growth for plants at that site.

Our second question is: to what extent do females and hermaphrodites of moss campion differ in their lifetime reproductive success as seed parents? *S. acaulis* has a gynodioecious breeding system, with both females and hermaphrodites present in most populations (Hermanutz and Innes, 1994; Shykoff, 1988, 1992). In fact, Desfeux et al. (1996) have argued that gynodioecy may be the ancestral breeding system in the genus *Silene*. Ecologists and evolutionary biologists have long been interested in reproductive differences between the genders in gynodioecious plants (Darwin, 1877; Lewis, 1941; Lloyd, 1974, 1975, 1976; Charlesworth and Charlesworth, 1978; Ross, 1978; Kohn, 1988; Frank, 1989; Schultz, 1994), and population genetic models point to three important consequences of such reproductive differences. First, and most importantly, the maintenance of females in gynodioecious populations will be facilitated if they have a fitness advantage in reproduction through seeds relative to hermaphrodites, which can transmit genes through both seeds and pollen (Lewis, 1941; Lloyd, 1974, 1975; Charlesworth and Charlesworth, 1978; Charlesworth, 1981; Delanney, Gouyon, and Valdeyron, 1981; Gouyon, Vichot, and Van Damme, 1991). Second, relative fitness through seeds may influence the average frequency of females in gynodioecious populations under several genetic mechanisms of gender determination (Lloyd, 1974; Charlesworth and Charlesworth, 1978; Frank, 1989). Third, when gender is determined by both nuclear and cytoplasmic factors (as appears to be the case in other *Silene* species (Taylor, 1994) and seems likely in *S. acaulis* as well (Hermanutz and Innes, 1994; Desfeux et al., 1996; L. Delph, personal communication, Indiana University), relative seed fitness of females may influence the degree of temporal fluctuation in gender frequencies (Gouyon, Vichot, and Van Damme, 1991). Because of these important consequences, many studies have measured differences in seed production by females and hermaphrodites in gynodioecious plants (see reviews in Lloyd, 1976; Van Damme, 1984; and Richards, 1986). Indeed, for moss campion, females usually produce more seeds than do hermaphrodites (Shykoff, 1988; Hermanutz and Innes, 1994; L. Delph, personal communication). However, these studies have only measured gender differences in the average number of seeds produced within single growing seasons, while population genetic models of breeding system evolution consider lifetime differences in seed production. For perennial plants, gender differences in annual vs. lifetime seed reproduction may not be perfectly correlated, due to differences in the pattern of survival, growth, or reproduction as a function of size. Thus ideally, we should assess how much more seed reproduction females achieve relative to hermaphrodites over the course of their entire lives. Lifetime reproduction of long-lived plants is difficult or impossible to measure directly. However, we used the methods of Cochran and Ellner (1992) to estimate three age-based parameters (age at maturity, net reproductive rate, and generation time) that allow us to assess gender differences in lifetime fitness achieved through seed production.

MATERIALS AND METHODS

The study species—*Silene acaulis* is an herbaceous perennial characteristic of alpine and arctic tundra throughout the circumboreal zone (Hultén, 1974). Individual plants are composed of tight, elliptical aggregations of short-leaved branch tips (termed “rosettes”); because of this compact, cushion-like morphology, plant size is easy to measure, and individuals are usually easy to distinguish from one another. Each cushion has a single taproot, and branches do not root adventitiously; thus there is no clonal reproduction.

Some individuals in our census were infected with the anther-smut fungus *Microbotryum violaceum*. The infection rate among flowering individuals varied from 0 to 35% among sites. Smut infection causes both females and hermaphrodites in this and other *Silene* species to produce spore-filled anthers (Baker, 1947; Alexander and Antonovics, 1988; Hermanutz and Innes, 1994). Moreover, anther smut causes sterility in individuals of both genders. For these reasons, we omitted smutted plants from all analyses involving reproduction. Smutted and non-smutted plants did not differ in the fraction of individuals changing vs. not changing size from year to year (G test: $G = 0.01$, $df = 1$, $P = 0.908$), and thus we use both for our estimates of growth and survival rates.

Population censuses—In 1995, we established permanent 1-m wide transects at haphazard locations in each of five nearby sites along an elevational gradient in the Wrangell Mountains near the town of Kennicott, AK (61°30'N, 142°50'W). All sites were above tree line (elevations varied from 900 to 1800 m). The background community varied from vegetated fell-field (Ridge site), to tundra meadow (Pass and Crest sites), to a relatively unvegetated scree gully (Gulch site), to a rock glacier community dominated by fruticose lichens (principally *Cladonia*, *Cladonia*, *Cetraria* and *Stereocaulon* spp., Rock Glacier site). Every moss campion individual encountered along the transects (a total of 1236 individuals with ≥ 1 rosette across the five sites) was marked with either an aluminum wire tag threaded through the cushion or, for the smallest plants, with wooden toothpicks inserted in the substrate. The position of each plant was also recorded to facilitate relocation in subsequent years. We also recorded the gender of all flowering individuals; because many hermaphrodites produce pistillate as well as perfect flowers, we scored any plant that produced perfect flowers as hermaphrodite. In late August (after fruit production and growth had largely ceased for the current growing season, but before fruits had dehisced), we recorded plant size, the total number of fruits produced that year and, in 1996, whether the plants had survived the previous year. To measure plant size, we counted the number of rosettes for plants with ≤ 20 rosettes. For larger plants, we used forestry calipers to measure to the nearest millimetre the length of the major axis of the cushion. Rather than measuring to the tips of leaves (which, because of leaf dieback, might lead to greater interannual variation in estimates of plant size), we defined the major axis as the distance between the centers of the two most distant rosettes in the cushion. We inserted wooden toothpicks into each cushion to insure that we measured along the same axis each year.

Statistical analysis of demographic data—To determine whether construction of a size-based projection matrix for *S. acaulis* was warranted, we tested for effects of plant size on survival and fruit production. We also tested whether the two genders differed in survival, growth, and reproduction. Effects of size on survival were assessed using a G test. Because *S. acaulis* is so long lived, we did not detect any mortality among the large plants in our sample (see Results). Consequently, for this test we classified plants into only three size classes (one rosette, 2–20 rosettes, and >20 rosettes per plant) to avoid an excess of zero cells in our log-linear model (Sokal and Rohlf, 1995). Because only the larger (flowering) plants could be assigned genders, we could not test directly for differences in survival between the two genders. However, we did perform a G test to ascertain whether the two

TABLE 1. Definition of size classes and measures of survival, growth, and fecundity (size class 1 is newborns).

Size class	No. of rosettes	Major axis (mm)	Census plants, 1995					Mean annual fruit production						
			N	Diameter (mean \pm 1 SD)	Percent surviving to 1996	Percent of survivors growing	Percent of survivors shrinking	Females			Hermaphrodites			
								1995	1996	Average	1995	1996	Average	
2	1	—	207	—	86.275	3.297	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
3	2–10	—	229	11.61 (6.98)	89.216	4.167	0.521	0.0	0.0	0.0	0.0	0.0	0.0	0.0
4	11–20	—	119	27.73 (9.60)	97.96	9.783	5.435	1.917	0.6	1.259	0	0	0	0
5	>20	0–50	134	39.3 (7.45)	95.83	23.684	0.877	3.061	1.964	2.513	0.625	0.429	0.527	
6	>20	50–75	153	62.1 (7.59)	99.14	14.286	3.361	2.674	2.650	2.662	0.882	1.385	1.134	
7	>20	75–100	99	86.62 (7.29)	99.17	11.539	1.282	6.091	6.172	6.132	2.276	2.324	2.300	
8	>20	100–125	89	112.00 (6.94)	100.0	20.000	0.0	7.59	7.800	7.695	2.621	1.731	2.176	
9	>20	125–150	58	137.15 (7.84)	100.0	2.564	2.564	11.577	6.652	9.115	1.125	1.789	1.457	
10	>20	150–175	34	160.59 (6.21)	100.0	6.897	3.448	21.000	13.714	17.357	6.000	3.923	4.962	
11	>20	175–200	27	187.33 (7.54)	100.0	13.333	6.667	18.571	24.600	21.586	3.222	1.000	2.111	
12	>20	>200	87	277.06 (74.22)	100.0	0.0	2.500	29.324	19.722	24.523	4.688	7.667	6.178	
Total			1236											

genders differed in the proportion of individuals growing, shrinking, or remaining in the same size class from year to year. In addition, we tested indirectly whether the genders differed in survival and growth by performing a *G* test to compare the observed distributions of females and hermaphrodites among diameter classes, combining data from all sites in 1995.

Differences between genders in fruit production were tested using analysis of covariance with cushion diameter as the covariate. A significant gender \times cushion diameter interaction term in the ANCOVA indicates that fruit production increases more steeply with size for one gender than for the other. When the interaction term was nonsignificant, we tested for a main effect of gender on fruit production in a model lacking the interaction term. Because fruit production must approach zero as plant size declines, we forced the regressions to pass through the origin (analyses with nonzero intercept gave similar results).

Construction of size-based population projection matrices—We combined plants from all sites to build size-based projection matrices for the entire moss campion population in the Kennicott region (while it would have been preferable to build separate matrices for each site, sample sizes were not adequate to do so). We first divided the population into 12 size classes based upon the number of rosettes and maximum cushion diameter (Table 1). Using a large number of classes allowed us to incorporate both sharp changes in survival with size among small plants and a continual increase in fruit production with size among large plants (see Results), and it reduced the potential for artificially low estimates of age-related parameters that can plague matrices with too few stages (Enright, Franco, and Silvertown, 1995).

Construction of the projection matrix requires estimates of four demographic parameters for each size class *i*: $B_{1,i}$, the average number of “newborns” (size class 1) produced each year by individuals in size class *i*; $P_{i,i}$, the fraction of class *i* individuals that survive between censuses but remain in class *i*; $P_{i+1,i}$, the fraction that survive and grow to size class *i* + 1; and $P_{i-1,i}$, the fraction that survive but shrink into size class *i* – 1 (throughout the paper, we follow the terminology and matrix notation of Cochran and Ellner, [1992]). Only one out of 1236 plants in our sample changed by more than one size class, so for simplicity we allowed plants to change by at most one size class per year. The estimated values of $P_{i,i}$, $P_{i+1,i}$, and $P_{i-1,i}$ provide the diagonal, subdiagonal, and supradiagonal elements, respectively, of the “survival” matrix **P** (Cochran and Ellner, 1992), and the $B_{1,i}$ values provide the first row of the “birth” matrix **B** (all other entries in these matrices are zero). Adding the matrices **P** and **B** yields the size-based population projection matrix **A** (Cochran and Ellner, 1992).

Calculating the elements of the **P** matrix was straightforward—we simply multiplied the fraction of surviving plants in each size class by the proportion that shrank, remained the same size, or grew, to estimate

the $P_{i-1,i}$'s, $P_{i,i}$'s, and $P_{i+1,i}$'s, respectively. As noted above, all of the large plants in our census population survived for the duration of our study. Because it is unrealistic to assume that large plants never die, we assigned the six largest size classes survival probabilities of 0.995, which exceeds the survival of the largest class in which we had observed mortality (Table 1). Also, because our data provided no evidence that females and hermaphrodites differed in survival or growth (see Results), we used our single estimate of **P** for both genders. Estimation of the elements in the birth matrix (i.e., the number of new plants produced by adults in each size class) was more complex. Due to difficulties in obtaining accurate demographic data for seedlings, which are difficult to locate in the field, we assumed that newborn plants have the same annual survival probability as do single-rosette plants (stage 2, Table 1), which are readily distinguished from seedlings but whose demography we believe is more reliably reflected in our census data. Details of the procedure we used to estimate separate birth matrices for females and hermaphrodites, \mathbf{B}_f and \mathbf{B}_h , are described in the Appendix. We discuss the minor effects of our assumed newborn survival on each of the estimated life history parameters below.

We used the estimated survival and birth matrices to create three population projection matrices: one for females ($\mathbf{A}_f = \mathbf{P} + \mathbf{B}_f$), one for hermaphrodites ($\mathbf{A}_h = \mathbf{P} + \mathbf{B}_h$), and one for the total study population, \mathbf{A}_t (the average \mathbf{A}_f and \mathbf{A}_h , weighted by the fraction of each gender in the population). Because the matrices \mathbf{A}_f and \mathbf{A}_h summarize fruit production by a single maternal gender, yet allow for offspring of both genders in the newborn class, these are exactly the matrices we need to estimate the lifetime number of offspring (regardless of gender) produced through seed production by females or hermaphrodites (see below). They also serve as concise summaries of the size-specific life histories of the two genders. We used the matrix \mathbf{A}_t to address the dynamics of the entire study population and to compute gender-independent life history parameters.

Calculation of life history parameters—Although one could estimate age-based life history parameters from the \mathbf{A}_f , \mathbf{A}_h , and \mathbf{A}_t matrices by means of computer iteration (e.g., Rausher and Feeny, 1980), these methods are cumbersome and time-consuming, and they require the researcher to decide arbitrarily when to stop the iteration process. Fortunately, Cochran and Ellner (1992) have derived exact, analytical formulae that allow one to calculate lifetime life history parameters using matrix operations that are quickly and easily implemented. All calculations reported in this paper were performed using Mathematica version 2.2.3 (Wolfram, 1991; the Mathematica code we used to perform the calculations is available from the first author).

We used the formulae of Cochran and Ellner (1992) to calculate seven life history parameters (below, “C&E” refers to equation numbers in their paper; where Cochran and Ellner provide formulae for SDs

as well as means of age-based parameters, we report both). Four gender-independent parameters were calculated using the \mathbf{P} and \mathbf{A}_i matrices: the survivorship function (C&E Eq. 2) and the conditional total life-span (C&E Eq. 6) for newborn plants, the average age in each size class at the stable stage distribution (C&E Eq. 23), and the mean age of residence in each size class (C&E Eq. 29). The survivorship function l_x gives the probability that a newborn will survive to age x . Because our assumed survival rate for newborns likely overestimates the true survival of 1st-yr plants (seedlings), the l_x function derived from our estimated \mathbf{P} matrix probably overestimates survivorship to older ages as well (although the shape of the survivorship curve beyond the first year of life would be unaffected). Consequently, we also calculated, for those size classes that we were able to census in the field ($i = 2$ to 12), the mean age at death for newborns given that they survive long enough to enter size class i at least once, $\Lambda_{i,1}$, which Cochran and Ellner have named the "conditional total life-span." Because in our matrix survivors never return to size class 1, the conditional total life-spans we calculate for the larger size classes are independent of our assumption of the newborn survival rate. We use $\Lambda_{12,1}$, the mean age at death of newborns given that they survive long enough to enter the largest size class at least once, as a measure of potential longevity.

The parameters above are useful descriptors of longevity, but they do not tell us how old a plant of a given size encountered in the field is likely to be. Thus we calculated two additional parameters that relate size and age in different ways. The parameter y_i is the average age of all plants found in stage i once the population has reached the stable stage distribution. Thus y_i is affected by the rate of population growth, because skewing of the population toward younger ages in a growing population will reduce the average age of individuals in all size classes (Cochran and Ellner, 1992). Our study population does not currently fit the stable stage distribution predicted by the matrix \mathbf{A}_i (calculations not shown), and thus y_i is an imperfect measure of the size-age relationship in the field population. One of several plausible reasons for the observed deviation from the stable stage distribution is that insufficient time has elapsed since the population was founded for convergence to have occurred. Thus we also calculated the mean age of residence $S_i(1)$, defined as the mean age at which a cohort of newborns will be in stage i . Because $S_i(1)$ may be a more appropriate indicator of the size-age relationship for a relatively young population that is far from the stable stage distribution (Cochran and Ellner, 1992), it provides a useful complement to y_i . Note that $S_i(1)$ accounts for all possible paths by which an individual might have arrived at stage i , including those that involve repeated rounds of growth and shrinkage. Because $S_i(1)$ describes the fate of a single cohort given the transition probabilities among size classes in the \mathbf{P} matrix, it is unaffected by population growth, unlike y_i (Cochran and Ellner, 1992).

We also calculated three life history parameters that are potentially influenced by reproductive differences between females and hermaphrodites: the mean age at maturity (C&E Eq. 15), the net reproductive rate (C&E Eq. 17), and the generation time (C&E Eq. 27). Each of these parameters was calculated for both the \mathbf{A}_f and \mathbf{A}_h matrices. Mean age at maturity $E(\alpha_i)$ is the average number of years required for a newborn to reach a size at which reproduction commences, given that it survives to reproduce. $E(\alpha_i)$ is a more appropriate measure of age at maturity than is the minimum number of years it would take a newborn to reach a reproductive size class (which in our matrix is equal to the index of the smallest reproductive size class), because only a very small proportion of individuals grow year after year, as would be required to reach maturity in the minimum number of years (Cochran and Ellner, 1992). The net reproductive rate R_0 is the average number of offspring (both female and hermaphrodite) that an individual plant produces through seed production over the course of its life, weighing potential offspring produced at each age by the probability that the parent plant survives to attain that age. As such, R_0 is affected by gender differences in total fruit production, survivorship, and the reproductive schedule. As an aside, we note that if our goal is to ask whether relative lifetime

seed production by females exceeds the critical level for their persistence specified by existing population genetic models of breeding system evolution (which portray populations with nonoverlapping generations), the net reproductive rate R_0 is a more appropriate metric than is the dominant eigenvalue of the \mathbf{A}_f or \mathbf{A}_h matrices (given that the generation times of the two genders are comparable). Due to the extremely long generation time of moss campion (see Results), generations overlap extensively. Thus the eigenvalue reflects reproduction by offspring that mature while the parent remains alive, and is not a measure of lifetime fitness of individuals, as is R_0 . The timing of reproduction also influences the generation time $\mu_1(1)$, defined as the average number of years that elapse between the entry of a newborn plant into the census population and the appearance of one of its offspring, weighted by parental survival. Our assumed survival of newborns has no effect on the estimated mean age at maturity or generation time, and while it does influence the absolute estimates of R_0 , it does not alter the relative number of offspring females and hermaphrodites are expected to produce, provided that the survival rates of female and hermaphrodite seedlings are truly equal (see Discussion).

Finally, we used the total population matrix to calculate standard stage-based population parameters such as the asymptotic rate of population growth λ and the stable size distribution (i.e., the dominant eigenvalue and right eigenvector of \mathbf{A}_t , Caswell, 1989). We also evaluated the possible impact on our estimated λ of the approximation technique we used to calculate 1st-yr survival (see Appendix). For each of the entries in our \mathbf{A}_t matrix that could have been influenced by our estimated newborn survival rate (i.e., $P_{2,1}$ and the fecundities $B_{1,4}$ through $B_{1,12}$, Table 3), we computed its proportional contribution to λ (i.e., the elasticity; Caswell, 1989). The sum of the elasticities of these matrix elements (a conservative measure of the potential bias introduced by our assumptions, because additional factors such as fruit production also played a role in estimating fecundities) was only 0.0158. Thus our assumptions concerning newborns could have had only a minor impact on the predicted λ . Note that the relatively low fecundity elasticities of the long-lived moss campion render it more similar in overall life history to woody plants than to most other herbaceous perennials (Silvertown et al., 1993; Franco and Silvertown, 1996).

RESULTS

Year-to-year survival, growth, and shrinkage of cushions—Annual survival was extremely high, even for single-rosette plants (Table 1). None of the 295 marked plants greater than 100 mm in diameter died during the study. Despite the overall high values, survival increased with plant size (Table 1). Even after collapsing the number of size categories to only three, there was a highly significant lack of independence between plant size and the fraction surviving from 1995 to 1996 ($G = 56.77$, $df = 2$, $P < 0.001$). Thus the construction of a size-based projection matrix for moss campion is justified. During the 1995–1996 winter, the Gulch Site experienced a rock avalanche that buried many of the plants. Nevertheless, none of the marked plants at this site actually died; they simply grew out from under the rocks. However, because many plants were sharply reduced in size due to what appeared to be an infrequent catastrophic event, we omitted plants from this site in our estimates of growth, shrinkage, and reproduction.

For most size classes, individuals both grew and shrank over a 1-yr interval from 1995 to 1996, but the fraction growing exceeded the fraction shrinking in all but one size class (Table 1). The differential between growth and shrinkage was greatest for the intermediate size classes. Some portion of both the growth and shrink-

age rates may represent measurement error for plants whose sizes lie near the boundary between two size classes, but at least part of the observed shrinkage represents plants that experienced notable dieback of portions of the cushion (W.F. Morris and D.F. Doak, personal observations). As a result, we included both growth and shrinkage in our size-based matrix.

A G test indicated that females and hermaphrodites did not differ in their propensity to grow, shrink, or remain the same size ($G = 0.42$, $df = 2$, $P = 0.81$). Moreover, the distributions of females and hermaphrodites among diameter classes did not differ ($G = 10.25$, $df = 9$, $P = 0.33$). Thus there was no evidence that survivorship or growth differed between the genders. However, there was a significantly greater number of females ($N = 237$) than hermaphrodites ($N = 170$) among the flowering individuals ($\chi^2 = 11.34$, $df = 1$, $P < 0.001$). Female-biased sex ratios are also found in high-latitude sites in Canada (Hermanutz and Innes, 1994).

Fruit production—A preliminary analysis of covariance of fruit production vs. gender and site using cushion diameter as the covariate uncovered a significant gender by site interaction (1995: $F_{4,392} = 5.93$, $P < 0.001$; 1996: $F_{3,343} = 3.72$, $P = 0.012$), indicating that the degree to which the two genders differed in fruit production varied among sites after accounting for the effect of plant size. Consequently, we performed separate analyses of fruit production for each site. In eight of nine site-year combinations, the regression line for fruit production vs. cushion diameter had a lower slope for hermaphrodites than for females (Fig. 1), indicating that for plants of equivalent size, females tended to produce more fruits than hermaphrodites. Analyses of covariance indicated that the slopes were significantly different in seven of nine cases (Table 2). At the Pass site in 1996, the regression line for fruit number vs. cushion diameter was actually steeper for hermaphrodites than females (Fig. 1, Table 2). However, this result must be viewed with caution, because the slopes do not differ significantly if the two largest hermaphrodites (Fig. 1) are omitted from the analysis. In both site-year combinations in which the regression slopes do not differ (the Pass site in 1995 and the Crest site in 1996), there is a significant main effect of gender on fruit production in a model lacking a gender \times diameter interaction term (Table 2), indicating that females produce more fruits than hermaphrodites across the range of cushion diameters (Fig. 1). Thus despite variation among sites and years, females generally produce more fruits than hermaphrodites of comparable size.

Table 1 also shows the average annual fruit production of plants in each size class. As is apparent in Fig. 1, fruit production increases with size, but is always higher for females than for hermaphrodites. In addition, a proportion of the females in size class 4 produced fruits both in 1995 and in 1996, while no hermaphrodites in this size class fruited in either year (Table 1).

A stage-based population projection matrix for *S. acaulis*—We used the measured rates of survival, growth, and shrinkage (Table 1) to calculate elements in the "survival" matrix \mathbf{P} (Table 3). An exhaustive search for single-rosette plants in all the transects in 1996 yielded 558

individuals. By substituting this estimate, along with the estimate for size class 2 of the probability of surviving without growing ($P_{2,2} = 0.86275$, Table 1), into the equation given in the Appendix, we arrived at an average annual input of 88.8 newborns into the census population. Apportioning these among the reproductive size classes in proportion to the number of plants in the census times the mean fruit production per plant (Table 1) yielded estimates of fecundity for plants of each gender in each size class (Table 3).

The projection matrix for the total population, \mathbf{A}_t , has a dominant eigenvalue of 1.0095, suggesting that if present conditions hold, our study population will eventually grow at the slow rate of 0.95%/yr.

Longevity—The estimated survivorship function for newborn plants (Fig. 2) indicates that, following a characteristic type III decline in the number of survivors during the early years of life, longevity may be extremely high in the study population. Survivorship to age 50 is 8.0%, while 4.9, 2.9, and 1.8% of newborns are predicted to reach 100, 200, and 300 yr of age. Because the magnitude of the initial decline in the survivorship function is influenced by our assumption of equal survival probabilities of newborns and single-rosette plants, it is instructive to examine the conditional total life-spans for plants in size classes 2–12 (Fig. 3). Because survival is lower in the smaller size classes (Table 1), average total life-span conditional on reaching these size classes at least once is relatively short. However, if plants survive to reach the largest size class, they can expect to live for centuries. For example, plants that reach the largest size class enjoy an average life-span of 338.2 yr (Fig. 3). High variance in total life-span (see large standard deviations in Fig. 3) means that many plants will not reach this expectation; conversely, some plants are predicted to live substantially longer than the average.

The relationship between size and age—The mean age at which a cohort of new plants resides in each size class, $S_i(1)$, provides the most direct way to examine the size-age relationship (Fig. 3). The method of calculating age-based parameters assigns an age of 1 yr to newborns when they first appear in the census (Cochran and Ellner, 1992). Subsequently, mean age of residence increases steadily with size class, culminating in a predicted value of 322.1 yr for plants in size class 12. Once again, high variance in age of residence means that some survivors of a cohort will be quite older than 300 yr while they are in size class 12.

The mean age of individuals in size class i in a population that has reached the stable stage distribution, y_i , gives an indication of the eventual age distribution among size classes we would expect to see in the field if current demographic rates hold. Because the fraction of plants in a given size class that are members of more recent (younger) cohorts increases as the rate of population growth increases (Cochran and Ellner, 1992), and because the overall projection matrix for moss campion has a dominant eigenvalue exceeding 1, the calculated values for y_i are lower than those for the mean age of residence, $S_i(1)$ (Fig. 3). These estimates indicate that population growth will have little influence on the age-size relationship for

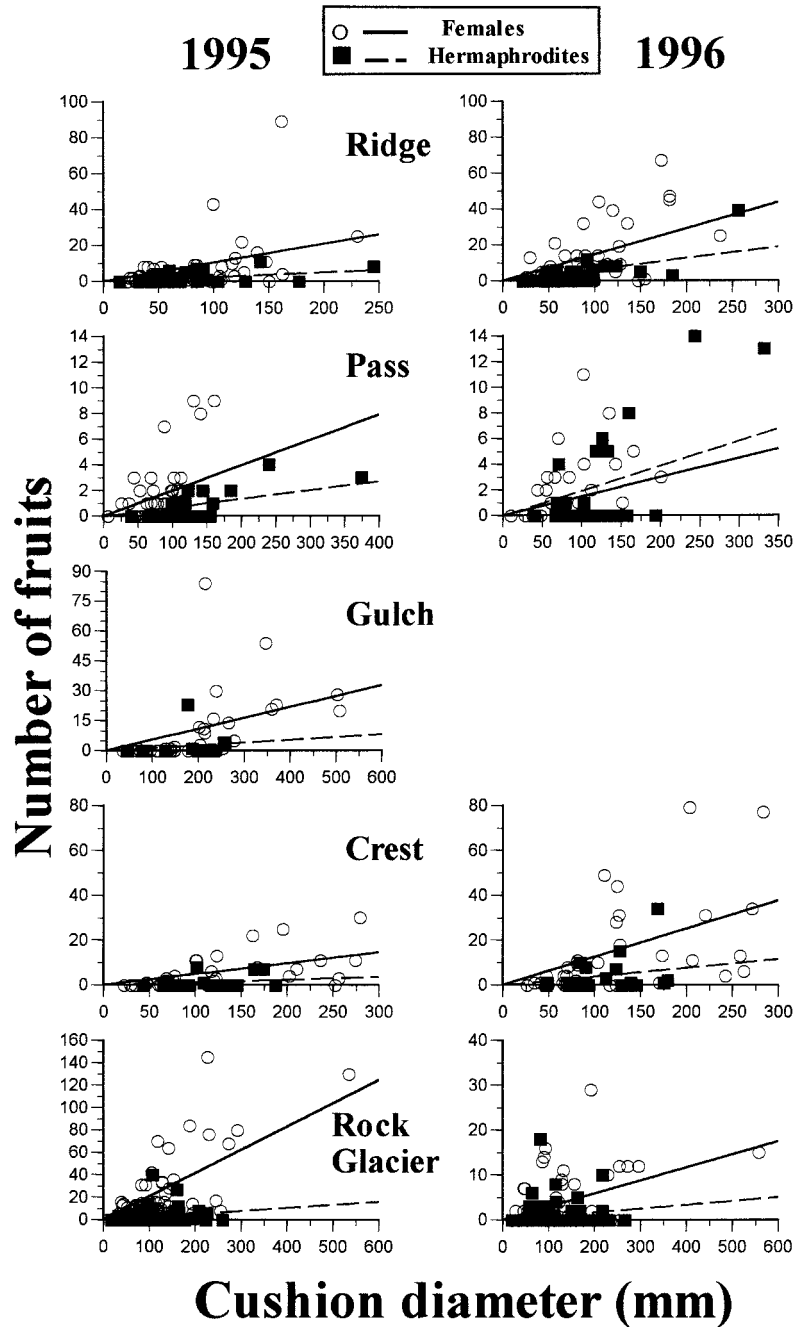


Fig. 1. The relationship between maximum cushion diameter and annual fruit production for females and hermaphrodites at five sites in two years. Plants at the Gulch site did not produce fruits in 1996 following a rock avalanche in the winter of 1995–1996.

smaller plants, but that $S_i(1)$ and y_i will differ substantially for larger plants in the field (Fig. 3). Once the stable size distribution has been reached the average plant in the largest size class will exceed a century and a half in age, about one-half the mean age of residence.

Gender differences in lifetime reproduction through seeds—Some females began reproducing in size class 4, while hermaphrodites did not fruit until size class 5. Because plants in the smaller size classes grow slowly (Table 3), this difference in size at first reproduction trans-

lates into a ~10 yr difference in mean age at reproductive maturity (Table 4). On average, plants require 2–3 decades to attain a size at which fruit production commences, a relatively lengthy delay for an herbaceous plant.

The separate projection matrices for females and hermaphrodites, A_f and A_h , predict very different values of the net reproductive rate, R_0 (Table 4). Females are expected to produce 4.4 times as many seed offspring over the course of their lives as do hermaphrodites. The generation time is similar for the two genders (Table 4), al-

TABLE 2. F statistics and significance levels for the gender \times cushion diameter term in an analysis of covariance with fruit production as the dependent variable. When the slope of a regression of fruit production on diameter did not differ between the two genders (indicated by a nonsignificant P value), test results for the gender term in a model lacking a gender \times diameter interaction are given; * $P < 0.05$.

Site	Year	N	Gender \times cushion diameter interaction in full model	Gender main effect in model with no interaction	
Ridge	1995	86	$F_{1,83} = 7.24, P = 0.009^*$	$F_{1,73} = 11.70, P = 0.001^*$	
	1996	86	$F_{1,83} = 5.74, P = 0.019^*$		
Pass	1995	75	$F_{1,72} = 1.01, P = 0.318$		
	1996	75	$F_{1,72} = 7.29, P = 0.009^*$		
Gulch	1995	51	$F_{1,48} = 4.47, P = 0.040^*$		$F_{1,55} = 4.91, P = 0.031^*$
Crest	1995	57	$F_{1,54} = 4.23, P = 0.045^*$		
	1996	57	$F_{1,54} = 2.32, P = 0.134$		
Rock Glacier	1995	133	$F_{1,130} = 43.99, P < 0.001^*$		
	1996	133	$F_{1,130} = 4.48, P = 0.036^*$		

though it is slightly shorter for females, probably because they begin reproducing earlier (Table 3). Due to the longevity of individuals in the reproductive size classes (Fig. 3), the reproductive period may last for many years, causing the estimated generation times to be greater than two centuries.

DISCUSSION

Moss campion longevity—Taken together, the age-related life history parameters we have estimated here paint a rosy picture for moss campion plants, which appear to enjoy extremely high longevity in the Wrangell Mountains of Alaska, despite the fact that they inhabit a seemingly harsh, high-latitude alpine environment. High rates of survival combined with slow growth and frequent regression in size due to dieback mean that the largest cushions may have taken centuries to reach their present size, and may yet continue to live for a long period of time. For example, the average total life-span, conditional on reaching the largest size class in our matrix, is 338.2 yr. Moreover, because the SD of the age at death for plants reaching the largest size class is 210.9 yr (Fig. 3), life-spans in excess of 500 yr are well within the realm of feasibility. Thus the upper end of the longevity estimates for *S. acaulis* is comparable to the maximum observed longevity for clonal herbaceous species compiled by Cook (1983) and Noodén (1988), which range from 400

to 1400 yr. This comparison makes the longevity of moss campion even more striking, because its genets do not rely upon clonal reproduction to attain such venerable ages.

The relationship between size and age—We obtained an approximation to the size-age relationship for moss campion (Fig. 4) by comparing the mean diameter of plants in each size class in our census (Table 1) to our two estimates of mean age (Fig. 3). Neither of these curves is a true growth curve for moss campion, because the mean age of residence applies to a single cohort of plants, which the plants in our census are unlikely to represent, and our population is not at the stable-stage distribution, as was assumed in the calculation of y_i . Nevertheless, these two estimates of age give an idea of the general range in which the true growth curve may lie. Dividing the mean diameter of plants in size class 12 by the two estimates of age yields estimated average growth rates of 0.86 and 1.63 mm/yr. We reiterate that these estimates of average growth rates are crude, not the least because they gloss over the fact that the growth rate appears to vary with size or age (Table 1). Nonetheless, these rates lie at the low end of those estimated for moss campion in the Alps and Greenland (7.4 and 7.1 mm/yr, results of R.E. Beschel reported in Benedict, 1989), in Colorado (0–20 mm/yr, depending on size; Benedict, 1989), and in the Canadian Rocky Mountains (0.6–18.2 mm/yr; McCarthy, 1992). If true, these slower growth rates may explain why the largest plants in our study population are estimated to be older than the largest plants in Colorado, where Benedict estimated longevity of moss campion to be 100 yr or less. (Benedict arrived at his estimate by noting that diameter appeared to reach

TABLE 3. Entries in the stage-based projection matrices for *S. acaulis*. All other entries in the **P** and **B** matrices are zero.

Size class, i	Shrinkage ($P_{i-1,i}$)	No size change ($P_{i,i}$)	Growth ($P_{i+1,i}$)	Fecundities, $B_{i,j}$		
				Females	Hermaphrodites	Both genders ^a
1	0.0	0.0	0.86275	0.0	0.0	0.0
2	0.0	0.86275	0.02941	0.0	0.0	0.0
3	0.00510	0.93368	0.04082	0.0	0.0	0.0
4	0.05208	0.81247	0.09375	0.04545	0.0	0.02645
5	0.00870	0.74790	0.23481	0.09074	0.01903	0.06077
6	0.03333	0.81669	0.14167	0.09614	0.04094	0.07307
7	0.01276	0.86744	0.11481	0.22143	0.08306	0.16359
8	0.0	0.79600	0.19900	0.27790	0.07858	0.19458
9	0.02551	0.94397	0.02551	0.32916	0.05262	0.21357
10	0.03431	0.89207	0.06862	0.62683	0.17918	0.43971
11	0.06633	0.79600	0.13267	0.77954	0.07624	0.48556
12	0.02488	0.97013	0.0	0.88562	0.22309	0.60868

^a Average of female and hermaphrodite fecundities, weighted by the population sex ratio (58.2% female).

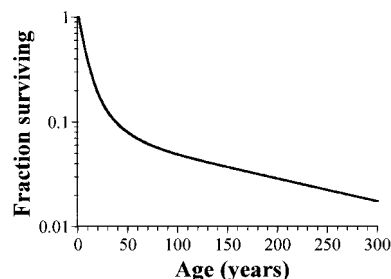


Fig. 2. The survivorship function for newly germinated plants predicted by the **P** matrix in Table 3.

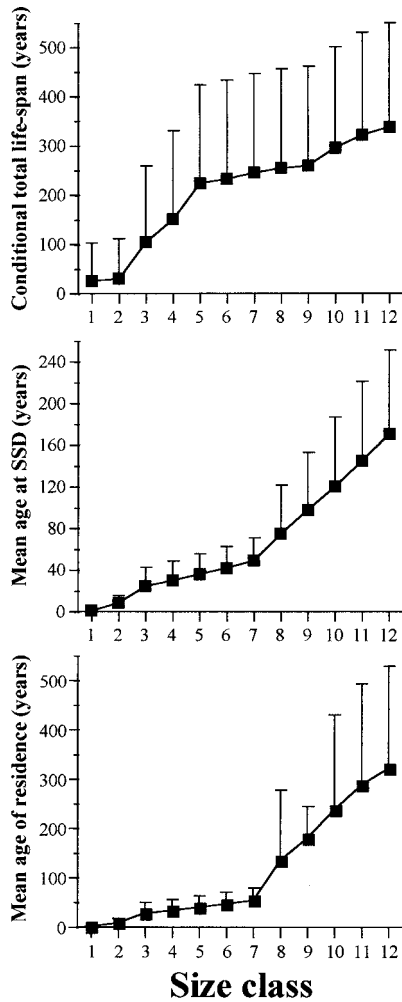


Fig. 3. Four age-related life history parameters for moss campion, inferred from the **P** matrix in Table 3. SDs calculated using formulae of Cochran and Ellner (1992) are shown above each parameter estimate. SSD is the stable size distribution.

an asymptote at ~100 yr of age, a pattern that could be due not to the death of plants after 100 yr but to a decline in growth.) Despite the crudity of our measures, they have three advantages over the method of comparing maximum diameter and known substrate age. First, they can be calculated for any site without knowledge of its geological history—one need only perform population censuses to measure the demographic rates used to construct the matrix. Second, the projection matrix approach compares estimated age to mean size rather than maximum size, which may be more variable due to stochastic events affecting the relatively few large plants in any population, and which is likely to be more dependent upon sample size. Finally, we found the size–age relationship to be nonlinear, with a downturn in growth at ~40 yr of age (Fig. 4). Thus, diameter growth does not appear to be constant with age. Quantitative methods such as those of Cochran and Ellner, which allow the entire size–age relationship to be estimated, promise to be a substantially more accurate way to judge the age of plants in the field than does the use of a single, average growth rate.

TABLE 4. Life history parameters describing reproduction of females and hermaphrodites via seed production (SD in parentheses).

Parameter	Females	Hermaphrodites	Ratio of females to hermaphrodites	Entire population
Age at maturity, $E(\alpha_1)$ (years)	24.7 (16.4)	34.4 (21.4)	0.72	24.7 (16.4)
Net reproductive rate, R_0 (number of offspring)	7.80	1.78	4.38	5.28
Generation time, $\mu_1(1)$ (years)	274.12	276.13	0.99	274.4

Gender differences in lifetime reproduction through seeds—To our knowledge, this study is the first to estimate differences between genders in lifetime reproduction via seeds in a long-lived gynodioecious plant. Our results underscore the utility of a lifetime measure to compare the female fitness of the different genders. Depending upon the size class examined, the ratio of females to hermaphrodites in mean annual fruit production ranged from 2.3 to 10.2 (Table 1). Using formulae of Cochran and Ellner (1992) to integrate these fitness differentials over the life-span, we calculated that females produce 4.4 times as many offspring through seed production over the course of their lives. Greater relative seed fitness of females parallels results of Shykoff (1988), Hermanutz and Innes (1994), and L. Delph (unpublished data, Indiana University), who found two- to threefold greater annual seed or fruit production by females in their study populations. Thus, female moss campion plants in our Wrangell Mountain sites appear to have an even higher relative reproductive success than those that have been measured at other locales. Some of the difference between genders may be due to the earlier onset of reproduction in females (Table 4). However, our estimates indicate that fruit production by size class 4 females is slight (Table 1), and thus the difference in age at maturity, if real, is not expected to contribute much to the excess in net seed reproduction by females. Rather, the bulk of the difference is due to the greater magnitude of annual seed production by females at all sizes (Fig. 1), with dif-

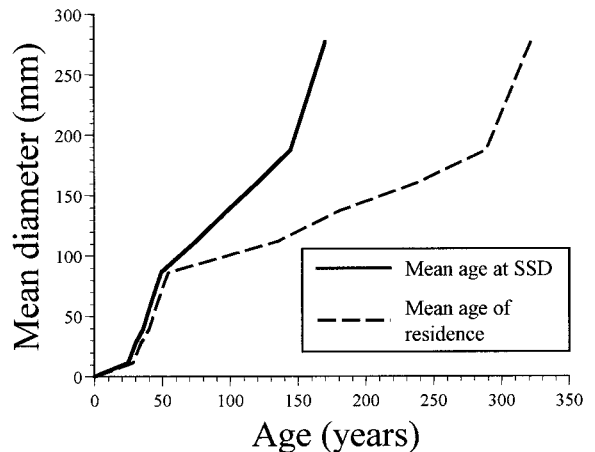


Fig. 4. Two estimates of the relationship between cushion diameter and age. SSD is the stable size distribution.

ferences in the pattern of fruit production as a function of size (Table 1) also playing a small role.

The higher lifetime reproductive success of females as seed producers (Table 4) is more than sufficient to assure the maintenance of females in our study population under any genetic model of gender determination that has yet been examined theoretically (Lewis, 1941; Lloyd, 1974, 1975; Charlesworth and Charlesworth, 1978; Charlesworth, 1981; Delannay, Gouyon, and Valdeyron, 1981; Gouyon, Vichot, and Van Damme, 1991). High seed fitness of females, combined with a cytoplasmic component in the gender determination mechanism, could also contribute to the significant excess of females we observed in our study population (Lloyd, 1974; Frank, 1989; also see Hermanutz and Innes, 1994).

In fact, our results may represent a conservative estimate of relative lifetime seed production by females, which would render their persistence despite the absence of male function even less problematic. Shykoff (1988) found that seedlings emerging from both selfed and outcrossed seeds produced by hermaphrodites had lower survival in the greenhouse than did seedlings produced by females (also see Jolls and Chenier, 1989). If hermaphrodite adults are more likely than females to produce hermaphrodite offspring (as would be expected under a nucleocytoplasmic sex determination mechanism), then Shykoff's results suggest that hermaphrodites may suffer higher rates of mortality early in life. Because we had no way to evaluate whether seedling survival in our study population would show the same degree of gender difference that Shykoff found in the greenhouse, and because we observed no survival differences among flowering individuals whose genders we could determine, we used the same survival matrix \mathbf{P} for both genders. However, because the net reproductive rate weighs offspring produced at each age by the probability that the parent survives to that age, lower early survival of hermaphrodites, if any, would render their net reproductive rate even smaller than we have estimated. Thus the functional gender of hermaphrodites may be even more male-like than our R_0 estimates indicate, shifting the breeding system of *S. acaulis* more towards effective dioecy than gynodioecy. Once again, the use of age-based life history parameters as we have advocated here means that differences in survival at any stage, if supported by additional data collected from our study populations, could easily be incorporated into an integrated measure of lifetime reproductive differences.

Caveats and conclusions—In considering our results, a few caveats about the way we constructed the projection matrices should be kept in mind. First, we could only indirectly estimate production and survival of newborns (see Appendix); we are currently improving our estimates by means of field plots to which we have added known numbers of seeds, whose fates we will follow through time. Second, there may be subtle variation in survival among the largest size classes that we could not detect with our sample sizes. It is not unlikely that the survival rates for large plants in our matrix are too low, which would cause the estimates of longevity and net reproduction, although high, to be underestimates. Finally, our estimated rates of growth and survival are based on only a

single annual census interval, although demographic rates of moss campion do not appear to vary much from year to year in other, longer term studies (L. Delph, personal communication, Indiana University). As a result, we have assumed (as do many studies that apply projection matrices to plant populations; see the review by Silvertown et al. [1993]) that entries in the matrix do not vary from year to year. Environmental variability is likely to change the means of the life history parameters reported above. Environmental variation, as well as estimation error involved in calculating mean vital rates, will also elevate the variances in life history parameters above the values we have calculated here (which are based only upon stochasticity in the life-cycle paths realized by different individuals following the fixed projection matrix). Increased sample sizes and ongoing censuses will allow us to address these questions in the future.

In conclusion, our results demonstrate that extracting age-based parameters from size-based projection matrices is a promising tool for better understanding the life histories and breeding systems of long-lived, nonwoody alpine plant species such as *Silene acaulis*. Since the publication of Cochran and Ellner's paper, only three other papers have actually used their methodology (Lehtilä, Tuomi, and Sulkinoja, 1994; Enright, Franco, and Silvertown, 1995; Franco and Silvertown, 1996). We hope that future studies will make greater use of this approach to convert information gained from short-term studies into insights about lifetime patterns in plant performance, thus helping to link field studies of long-lived species with predictions from life history and population genetic theory.

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APPENDIX

This appendix outlines the procedure we used to estimate fecundities in our projection matrix. We chose not to use the seedlings in our census to represent the newborn class, both because seedlings are difficult to find reliably in the field (where they are often located beneath other plants or in crevices between rocks) and because seedling emergence is likely to be among the most variable events in the moss campion life cycle, thus complicating the task of inferring lifetime components of life history from short-term census data. A second alternative (using single rosette plants to represent newborns) is incorrect, both because it omits the 1-yr delay between seedling emergence and entry into the single-rosette stage (no individual in our census remained a seedling for >1 yr) and because many individuals remain in the single-rosette stage for several years (note high survival and low growth in Table 1). Thus as a compromise, we adopted the following procedure to obtain a more time-averaged measure of reproduction using the observed number, survival, and growth of single-rosette plants. First, we assumed that the number of individuals entering and leaving the single-rosette stage (size class 2) each year is constant, as would be true for a population at a stationary stage distribution and is approximately so for our slowly growing study population. If X_1 and X_2 are the numbers of newborns and single-rosette plants, respectively, then in a stationary population $P_{2,1} X_1 = (1 - P_{2,2}) X_2$ (here we have ignored the low rate of shrinkage of plants in size class 3, Table 3). Second, we assumed that newborns had the same annual survival rate as single-rosette plants, which we could obtain from our census data. That is, we assumed that $P_{2,1} = P_{2,2}$, so that we could estimate the number of newborns entering the census population each year as $X_1 = (1 - P_{2,2}) X_2 / P_{2,2}$. To apportion this total number among reproductive size classes, we first summed the fruits produced by all census plants (both genders in all reproductive size classes) and then divided the number of newborns by the total number of fruits to obtain a proportionality constant relating fruits produced in one year to the number of newborns in the following year. Multiplying the average fruit production by females or hermaphrodites in size class i by this constant yields the estimate of $B_{1,i}$. We used fruit number rather than seed number because we did not have separate estimates of the number of seeds per fruit for the two genders, although both Shykoff (1988) and L. Delph (personal communication, Indiana University) reported no differences in seed number per fruit at their study sites in Colorado.