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A demographic model explains life-history variation in *Arabis fecunda*

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Summary

1. The distinction between semelparity and iteroparity is one of the most fundamental in life-history biology. Despite an abundance of theory proposed to explain the evolution of this dichotomy, few quantitative empirical tests exist.

2. We report here on life-history variation in the perennial herb *Arabis fecunda* (Brassicaceae), in which differences in the frequency of iteroparity and terminal flowering (facultative semelparity) are expressed among populations. These differences are consistent over time, and a common garden experiment suggested that they may be at least partly genetically based.

3. An analysis of demographic data over a 5-year period from three populations indicated that a simple demographic model of life-history evolution is consistent with life-history variation in this species. Individuals in populations with greater mean adult survival were more likely to express iteroparity than individuals in populations with lower adult survival.

Key-words: demography, environmental stress, iteroparity, life history, reproductive mode, semelparity, threshold trait

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Introduction

Semelparity is a life history characterized by a single massive reproductive episode followed by death. By contrast, iteroparity is characterized by repeated reproduction. The botanical terms monocarpy and polycarpy are synonymous with semelparity and iteroparity, respectively. Semelparity has evolved independently many times in plants and animals. The semelparity–iteroparity dichotomy can occur among species within a genus (Schaffer & Elton 1974; Schaffer & Schaffer 1979; Woolhead & Calow 1979; Young 1990); among populations within a species (Law, Bradshaw & Putwain 1977; Sano & Morishima 1982; van Groenendael & Slim 1988; Lesica & Shelly 1995); and among genotypes within a population (Grosberg 1988). Each of these provides opportunities to examine the selective forces that may be involved in the evolution of life histories. Intraspecific comparisons are particularly informative because there is less chance that observed life-history variation is a result of phylogenetic constraint. Although life-history variation remains a central topic in evolutionary biology (Stearns *et al*. 2000; Miller *et al*. 2002), comparative demographic tests of theory are rare because they require long-term monitoring of multiple populations (Reznick *et al*. 2004).

Natural selection favours those life histories that maximize lifetime reproductive success (Stearns 1992). Semelparity is therefore a superficially anomalous life history. Why would natural selection ever favour death after first reproduction? Theory provides several explanatory models (reviewed by Young & Augspurger 1991; Stearns 1992; Bulmer 1994; Charlesworth 1994). Underlying all theories is the well documented observation that semelparous individuals produce more offspring, or have greater reproductive effort in their single reproductive episode, than do iteroparous individuals in each of their reproductive episodes (Woolhead & Calow 1979; Grosberg 1988; Brenchley, Raven & Johnston 1996; Davies & Dratnal 1996; see reviews by Young 1981; Young & Augspurger 1991). Several qualitative interpretations of empirical patterns suggest that high adult mortality selects for semelparity (Silvertown 1996; Klinkhamer, Kubo & Iwasa 1997; Kohno 1997; Schneider & Lubin 1997). Young (1990) showed that a simple mathematical model accurately predicted the demographic conditions under which semelparity and iteroparity may have evolved in Mount Kenya lobelias. However, such quantitative tests of theory are rare (Schaffer & Schaffer 1979). Our understanding of this fundamental life-history dichotomy will remain tentative until we have multiple quantitative tests from a variety

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of natural systems. This paper builds on a previous qualitative analysis in a herbaceous perennial, *Arabis fecunda* Rollins (Lesica & Shelly 1995), by including life-history and fecundity data from nine additional populations over 2 years. We present a new quantitative analysis of demographic and life-history variation. We show that demographic differences can explain the observed variation in life histories among populations, and that these demographic differences appear to be associated with site-related stress, and present evidence that suggests partial genetic control of this variation.

Study species

Arabis fecunda (Brassicaceae) is a rosette-forming perennial, endemic to calcareous soils in south-west Montana, USA (Rollins 1993). *Arabis fecunda* appears to have a mixed mating system, with selfing predominating over outcrossing (Hamilton & Mitchell-Olds 1994). It has two reproductive modes: axillary flowering, in which one to many decumbent inflorescence stems develop from axillary buds among the tightly clustered leaves of the rosette; or terminal flowering, in which a single inflorescence stem is produced from the terminal bud at the centre of the rosette (Lesica & Shelly 1995). Terminal inflorescences are larger and leafier than axillary inflorescences, and terminal-flowering rosettes always die. An individual rosette can produce axillary inflorescences for many years (iteroparous). Other rosettes produce a terminal inflorescence once and are simply semelparous. A few plants exhibit a mixed life history, producing axillary inflorescences for one to many years before producing a large terminal inflorescence and then dying. Individuals occasionally branch at the root crown to form multirosette plants at any time during the life cycle. If an individual rosette in a multiple-rosette plant produces a terminal inflorescence, the whole plant usually, but not always, dies. These modes of reproduction allow intraspecific variation in life history in *A. fecunda* among populations and individuals (Lesica & Shelly 1995).

Table 1. Semelparous fecundity advantage (B_s/B_i, relative advantage of terminal flowering) for populations of *Arabis fecunda* and location information for 12 study sites in Montana

Site	B_s/B_i	Altitude (m)	Aspect (0° = N)	Latitude	Longitude
Charleys Gulch	2·7	1525	234°	46°15·31′	114°00·00′
Dewey	3·4	1760	100°	45°42·24′	112°54·21′
Fish Creek	3·0	2305	160°	45°48·14′	112°29·12′
Jerry Creek	3·0	1735	220°	45°47·18′	112°54·02′
Lime Gulch	3·0	1890	160°	45°23·52′	112°48·44′
Moosetown	2·0	2135	205°	45°47·56′	112°34·05′
Quartz Hill	2·1	2440	215°	45°42·24′	112°54·21′
Spring Gulch	2·2	1445	210°	46°14·52′	114°11·09′
Triangle Creek	2·0	1705	260°	45°46·43′	112°53·54′
Tucker Creek	2·6	2040	180°	45°47·24′	112°39·99′
Vipond Park	3·7	2195	195°	45°40·59′	112°52·13′
Wise River	2·7	1705	140°	45°47·09′	112°52·30′

Fecundity advantage was calculated as the ratio of mean number of seeds produced by terminal-flowering plants to that produced by axillary-flowering plants.

The traditional definition of semelparity is a life history characterized by a single reproductive episode per lifetime (Stearns 1992). Terminal-flowering *A. fecunda* plants have a life history characterized by a massive, fatal reproductive episode which is usually, but not always, the first. Many, but not all, terminal-flowering *A. fecunda* are truly semelparous. The fact that terminal flowering usually occurs at the first reproductive episode for most species (semelparity *sensu stricto*) is probably due to relatively fixed demographic conditions and constrained development (Young & Augspurger 1991). The critical question for life-history theory is: for a given reproductive episode, is it better to put all resources into current reproduction and die, or to save some resources for potential future reproduction? *Arabis fecunda* is ideal for testing life-history theory of the evolution of semelparity because it possesses sufficient developmental plasticity to 'choose' between a large fatal reproductive effort (semelparity) and survival with a smaller reproductive effort (iteroparity) at each reproductive episode in environments with spatial or temporal variation in survival probability.

Materials and methods

STUDY SITES

We sampled 12 of the 18 known sites for *A. fecunda* throughout its geographic range (Table 1) to obtain estimates of fecundity (seeds per plant) and mean terminal-flowering fecundity advantage. Charleys Gulch and Lime Gulch, the two most geographically divergent sites, are 140 km apart. Zonal vegetation at these sites included mountain Big Sagebrush (*Artemisia tridentata* Nutt.) steppe; Ponderosa Pine (*Pinus ponderosa* Laws) savannah; and Mountain Mahogany (*Cercocarpus ledifolius* Nutt.) woodland.

Five-year demographic studies were conducted at three of these sites: Charleys Gulch, Lime Gulch and Vipond Park. Charleys Gulch is in the foothills of the Sapphire Range. At Hamilton, ≈8 km south-west and 300 m lower, mean July temperature was 19·4 °C, and mean annual precipitation was 320 mm. The Lime Gulch and Vipond Park populations occur in the Pioneer Range. These two sites are separated from each other by ≈32 km and from Charleys Gulch by ≈130 km. For Divide, at 1675 m and north and east of Lime Gulch and Vipond Park, mean temperature for July was 17·2 °C, and mean annual precipitation was 310 mm. Vipond Park is appreciably higher than the recording station, and is probably cooler and wetter.

FECUNDITY AND REPRODUCTIVE MODE

We weighed the seed content of one mid-inflorescence fruit and counted the number of seeds from each of 12 plants with each reproductive mode at the Charleys Gulch and Vipond Park sites in 1996. These two sites span the range of elevation and vegetation cover among the 12 study sites (Table 1). We used ANOVA to examine the effect of site, reproductive mode and their interaction on the mean seed weight. Three fruits from axillary-flowering plants at Vipond Park had immature seeds and were not included in the analysis.

At each of 12 study sites we recorded the number of axillary- and terminal-flowering plants in 15 randomly selected plots located throughout each population in both 1994 and 1996. We recorded the number of fruits on each plant in 1996. Plot size varied among sites between 0·7 and 2·0 m^2 to ensure most plots had at least five *A. fecunda* plants. We collected one mid-inflorescence fruit from each of ≈10 randomly selected axillary- and terminal-flowering plants at each of the 12 sites in 1996, and counted the number of seeds per fruit. We used regression analysis to assess the relationship between mean fecundity (seeds per plant) and mean terminal-flowering fecundity advantage at the 12 sites and the mean proportion of terminal-flowering plants for 1994 and 1996. Percentage terminal flowering was log-transformed to improve the fit of regression equations with fecundity and fecundity advantage.

DEMOGRAPHY

A census of recruitment, mortality, size class, reproductive mode and fecundity of *A. fecunda* plants was taken annually from 1989 through 1993 at Charleys Gulch, Lime Gulch and Vipond Park (Lesica & Shelly 1995). Individual *A. fecunda* plants were mapped in two representative 10 m^2, permanently located belt transects at each site. Sample sizes were ≈100 individuals for Charleys Gulch, and 300–700 individuals for Lime Gulch and Vipond Park over the course of the study (Fig. 3 in Lesica & Shelly 1995). We recorded whether a plant was reproductive, and the mode of reproduction (axillary or terminal), for each reproductive plant. Fecundity for each plant was estimated using the recorded number of fruits and the mean number of seeds per fruit in each year sampled separately for axillary- and terminal-flowering individuals. The relative advantage of terminal flowering (fecundity advantage) was calculated as the ratio of mean number of seeds produced by terminal-flowering plants to that produced by axillary-flowering plants (B_s/B_i). Fecundity was measured as the estimated number of seeds per plant, calculated as the number of fruits multiplied by the mean seeds per fruit for each of the two reproductive modes.

BASIS OF INTERPOPULATION VARIATION IN REPRODUCTIVE MODE

Arabis fecunda seeds from 50 axillary-flowering Charleys Gulch plants and 50 terminal-flowering Vipond Park plants were planted into potting soil in September 1992 and grown in a glasshouse through April 1994. Mortality was high; the six surviving plants from Charleys Gulch and 15 plants from Vipond Park were transplanted into a common garden in Missoula, Montana. Mode of reproduction was recorded in spring of 1995 and 1996, by which time all but two plants from Charleys Gulch had flowered at least once. None of the plants survived into 1997. We used Fisher's exact test to assess the relationship in mode of reproduction between parents and offspring.

Results

FECUNDITY AND REPRODUCTIVE MODE

There was no evidence for a difference in seed weight between axillary- and terminal-flowering plants within sites ($F_{1,41} = 0{\cdot}03$, $P = 0{\cdot}86$), and the site–mode interaction was not significant ($P = 0{\cdot}14$). Seeds of *A. fecunda* from Charleys Gulch weighed 47% more than those from Vipond Park ($F_{1,41} = 45{\cdot}7$, $P < 0{\cdot}001$).

Weather was hot and dry during the 1994 growing season, while winter and spring moisture were above average before and during the 1996 growing season. Nonetheless, the proportion of flowering plants producing a terminal inflorescence at the 12 sites was significantly correlated between the two years ($r = 0{\cdot}61$, $P = 0{\cdot}035$), and there was little change in the rank order among sites (Spearman's $r_s = 0{\cdot}68$, $P < 0{\cdot}05$; see also Fig. 8 in Lesica & Shelly 1995).

The proportion of terminal-flowering plants decreased with increasing fecundity of axillary-flowering ($R^2 = 0{\cdot}58$, $P = 0{\cdot}004$) and terminal-flowering plants ($R^2 = 0{\cdot}37$, $P = 0{\cdot}035$) across the 12 populations (Fig. 1). The relative advantage of terminal flowering varied from 2·0 to 3·7 across the 12 sites, with a mean of 2·7 (Table 1).

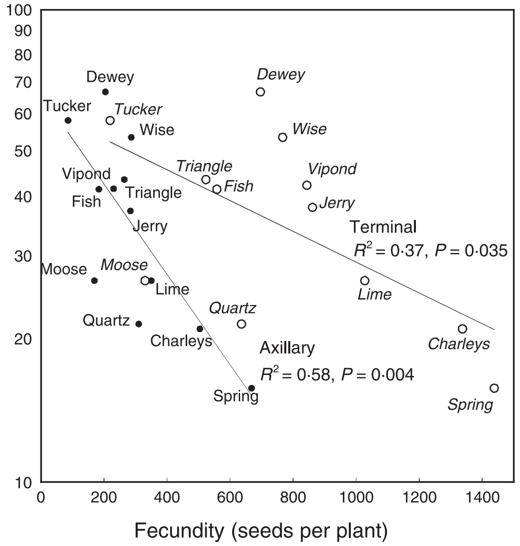

Fig. 1. Relationship between fecundity of axillary-flowering (closed symbols) and terminal-flowering (open symbols) *Arabis fecunda* plants in 1996, and percentage terminal flowering averaged over 1994 and 1996 for 12 populations (Table 1).

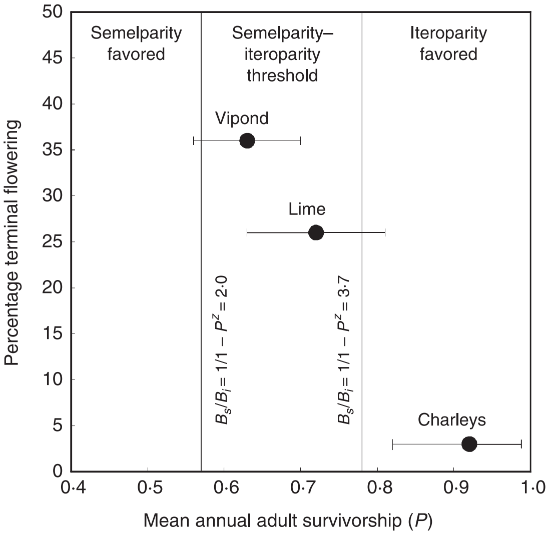

Fig. 2. Relationship between adult survival (with 95% confidence limits) and the proportion of individuals that are semelparous across three populations of *Arabis fecunda*, in the context of life-history theory. For a given value of adult survival, theory predicts how great the fecundity advantage of semelparity over iteroparity (B_s/B_i) must be in order for semelparity to be favoured (Young 1981). Semelparous *A. fecunda* plants produce between 2·0 and 3·7 times many seeds as iteroparous individuals (Table 1). The mathematical model (equation 5) predicts that the evolutionary threshold between semelparity and iteroparity should lie in the range of adult (iteroparous) survival, between 0·57 and 0·78 for this species. As populations with decreasing adult survival approach this threshold, the proportion of individuals that are semelparous increases.

There was a tendency for the proportion of terminal flowering to increase with the relative advantage of terminal flowering; however this trend was not statistically significant (R^2 = 0·23, P = 0·12). Nor was there a significant relationship between terminal-flowering fecundity advantage and fecundity of axillary-flowering plants (R^2 = 0·02, P = 0·45).

DEMOGRAPHY

The three *A. fecunda* populations at Charleys Gulch, Lime Gulch and Vipond Park differed in their demography and life history across the 5 years of the study (Figs 1 and 2), although population growth rates were all near unity during this same period (Lesica & Shelly 1995). The Charleys Gulch population had the highest annual survival of axillary-flowering individuals (0·92), and Vipond Park the lowest (0·63). Mean iteroparous flowering interval was similar among sites: 1·24, 1·12 and 1·19 years at Charleys Gulch, Lime Gulch and Vipond Park, respectively.

The proportion of individuals that produced a terminal inflorescence and died immediately afterward differed considerably among sites. Only 3% of adults at Charleys Gulch were terminal flowering, while 26% and 36% were terminal flowering at Lime Gulch and Vipond Park, respectively (Fig. 2). Many terminal-flowering individuals had previously produced axillary inflorescences at the latter two sites.

BASIS OF INTERPOPULATION VARIATION IN REPRODUCTIVE MODE

There was an association between parents and offspring for reproductive mode. Terminal flowering followed by death occurred in 11 of 15 progeny of Vipond Park terminal-flowering plants, but none of the four reproductive progeny of Charleys Gulch axillary-flowering parents in the common garden during 1995–96. These proportions of terminal flowering were statistically different despite the small sample size (Fisher's exact test, P = 0·018).

Discussion

The fecundity advantage of semelparity has been well documented in animals (Woolhead & Calow 1979; Grosberg 1988; Davies & Dratnal 1996) and plants (reviewed by Young 1990; Young & Augspurger 1991; see also Brenchley *et al.* 1996). Annual and biennial semelparous plants produce approximately twice as many seeds as close relatives that are iteroparous (Young 1990). Among long-lived perennials with life span measured in decades, the fecundity advantage of semelparous reproductive bouts averages about three to four times as many seeds as for iteroparous relatives (Young & Augspurger 1991). The mean fecundity advantage to terminal flowering for *A. fecunda* was estimated as 2·7 (range 2·0–3·7), an estimate unique in being derived from 12 different populations of the same species.

Theory (and intuition) suggest that semelparity should be favoured if the likelihood of future reproduction (adult survival) is low. If the population growth rate of iteroparous *A. fecunda* is less than that of a semelparous population, a switch to semelparity should be favoured. Semelparous (λ_s) and iteroparous (λ_i) population growth rates are given by:

$$\lambda_s = CB_s \quad \text{and} \quad \lambda_i = CB_i + P \qquad \text{eqn 1}$$

where C = juvenile survival (proportion surviving each year); P = adult survival (proportion surviving each year); B_s = semelparous birth rate (seeds per reproductive episode); and B_i = iteroparous birth rate (seeds per reproductive episode). Semelparous population growth will equal iteroparous population growth when:

$$CB_s = CB_i + P \qquad \text{eqn 2}$$

Dividing by C gives (Charnov & Schaffer 1973)

$$B_s = B_i + P/C \qquad \text{eqn 3}$$

substituting $C = \lambda_s/B_s$ (equation 1) and rearranging gives:

$$B_s/B_i = 1/(1 - P/\lambda_s) \qquad \text{eqn 4}$$

Assuming a stable population ($\lambda_s = 1$) and allowing for multiple years between reproductive episodes (z) gives:

$$B_s/B_i = 1/(1 - P^z) \qquad \text{eqn 5}$$

where z = mean number of years between reproductive episodes and P^z is percentage survival between reproductive episodes (Young 1981, 2002). We have estimates for all four variables for Charleys Gulch, Lime Gulch and Vipond Park.

The relationship between this model and our empirical data can be expressed graphically assuming 1·2 years between reproduction (mean of three sites). The central section of Fig. 2 represents the range of semelparity fecundity advantage estimates (B_s/B_i) for the 12 *A. fecunda* populations. Within this 'threshold range' the two reproductive modes should have approximately equal lifetime reproductive output. Populations with lower adult survival will have mean expected lifetime reproductive output to the right of this region, and should be iteroparous. Those with mean expectations of lifetime reproductive success, placed to the left of this region, should be semelparous.

The variation in life history among sites conforms to the predictions of the mathematical–demographic model expressed by equation 5. As the chance of survival and the advantage of repeated reproduction decline, more individuals display terminal-flowering life histories, in accordance with the predictions. Mean annual adult survival of axillary-flowering *A. fecunda* plants at Charleys Gulch was 92%. For this population, semelparity would be favoured only if semelparous individuals could produce >10 times more seeds than iteroparous individuals (equation 5). Terminal-flowering plants never attained an average fecundity advantage even half this great, so axillary flowering should be strongly favoured at Charleys Gulch; indeed, only 3% of the individuals at this site displayed terminal flowering. On the other hand, mean yearly adult survival of iteroparous *A. fecunda* individuals was 72 and 63% at Lime Gulch and Vipond Park, respectively. The fecundity advantage of semelparity needed to offset the loss of future reproduction was much less in these populations (3·25 and 2·36, respectively) and approaches that measured empirically (Table 1; Fig. 2).

The selective advantage of terminal flowering for an individual will depend on the quality of its microsite. Our estimates of demographic conditions are means based on a random sample of all individuals in a population, so we expect only about 50% of the individuals to express terminal flowering at the threshold postulated in Fig. 2. That this value approaches 40% represents a remarkable coherence of theory and empirical observation.

Heritability of semelparity is a necessary condition for the evolution of different life-history strategies among sites. Variation in proportion of terminal-flowering *A. fecunda* plants was much greater among sites than in years at the same site, although the weather was very different between the 2 years. This suggests that the propensity for terminal flowering was at least partly determined by a site-related factor: environmental, genetic or both. The results of our common garden study were consistent with the hypothesis that propensity for terminal flowering is partly under genetic control in *A. fecunda*. The progeny of terminal-flowering plants were more likely to flower terminally than were those of axillary-flowering plants. Caution should be exercised in interpreting these results: we did not control for maternal effects that could arise because terminal- and axillary-flowering parents came from different sites (Roach & Wulff 1987). Indeed, seeds from Charleys Gulch were larger than those from Vipond Park in 1996. However, flowering occurred in the plants' second or third year, and the influence of maternal effects tends to diminish later in the life cycle (Roach & Wulff 1987).

The fecundity advantage of semelparity (B_s/B_i) is often assumed to be essentially constant within a species (Young 1990). In *A. fecunda* our estimates varied by a factor of nearly two among the 12 sites. Terminal-flowering fecundity advantage explained 23% of the variation in the proportion of terminal-flowering plants. Demographic models that incorporate the fecundity advantage of semelparity as a variable rather than a parameter may have greater predictive power than those based on survivorship and reproductive frequency alone.

Previous studies have suggested that semelparity is associated with environmental stress. Likelihood of semelparity decreased with soil nutrient enhancement in *Picris*, *Scabiosa* (Verkaar & Schenkeveldt 1984) and bamboo (Janzen 1976). The results of our study are consistent with the hypothesis that environmental stress, acting to reduce adult survival, may be driving the evolution of semelparity. As ameliorating environmental stress with water or fertilizer generally results in increased fecundity (Lee 1988), we might assume that sites supporting plants with lower fecundity are more stressful. These sites had significantly higher frequencies of terminal flowering compared with sites with higher mean fecundity (Fig. 1), suggesting that terminal flowering increases with stress. This relationship could be explained by lower adult survival and/or increased terminal-flowering fecundity advantage at stressful sites. There was no relationship between axillary fecundity and fecundity advantage, so the relationship between stress and terminal flowering is best explained by lower adult survival (Fig. 2).

Arabis fecunda populations differ in adult survival, fecundity, fecundity advantage to terminal flowering, and expression of a life history similar to semelparity. The good quantitative fit between empirical observation and the demographic model's predictions suggest that the frequency of terminal flowering in *A. fecunda* can be explained demographically. This is only the second quantitative test of demographic life-history theory. A similar match of theory with site conditions, demography and life history was presented by Young (1990). Two species of giant rosette plants in the genus *Lobelia* occur in the alpine zone of Mount Kenya. The semelparous species is restricted to the driest sites. The iteroparous species occupies more mesic habitat. Populations of the iteroparous species displayed lower survival and frequency of reproduction as their habitats became more xeric. A mathematical model similar to equation 5, and based on empirically measured fecundity advantage of semelparity, predicted that semelparity would be favoured in the driest sites, and this closely matched the distribution of the two species in the field.

We view reproductive mode in *A. fecunda* as a threshold trait (Roff 1996). Differences in demography found among populations may also occur among microsites and among years within an individual population (Young 1985, 1994), and may explain much of the observed life-history variation in *A. fecunda*. Some plants become established in microsites characterized by lower adult survival, higher fecundity advantage, and/or longer intervals between reproductive episodes. In such microsites, soil moisture, nutrients or light below threshold may trigger terminal flowering, while plants in more benign microsites display axillary flowering. In addition, changing microsite conditions due to climatic variation could result in adaptive life-history switches from iteroparity to semelparity. Plasticity of response would interact with an evolved level of genetic propensity for terminal flowering determined by natural selection. We speculate that this interaction results in inter- and intrapopulation and within-individual variation for life history observed in *A. fecunda*. Models have also been developed that consider the role of environmental variation in the optimal timing of semelparous reproduction (Hirose & Kachi 1986; Metcalf *et al*. 2003). All predict a threshold size of age of reproduction, whereas empirical evidence shows more variable responses in real populations. Rees *et al*. (2004) suggest non-optimality reasons for this mismatch, to which we add the possibility that microsite variation could also contribute to these.

Although we examined a variety of edaphic and biotic factors at these sites, we have not identified specific environmental factors that drive the demographic differences among or within populations. Nonetheless, the close correspondence between a simple mathematical model and the demographic characteristics of these populations strongly suggests that life-history variation in this system is maintained by adaptive responses.

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