

Empirical Models of Pollen Limitation, Resource Acquisition, and Mast Seeding by a Bee-Pollinated Wildflower

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ABSTRACT: Synchronous mast seeding is increasingly recognized as common in plant populations. Recent theoretical models show that synchronous mast seeding could be a consequence of resource allocation and storage within individual plants, coupled by pollen limitation in low-flowering years. We used long-term population and weather data to parameterize models of flowering based on stored resources and pollen limitation in *Astragalus scaphoides*, a bee-pollinated plant that flowers in alternate years. We used these models to test whether internal resource dynamics could explain mast seeding in *A. scaphoides* and, if so, whether synchrony was caused by pollen limitation and/or fluctuations in precipitation. We compared predictions of models that included all combinations of three factors: constant versus precipitation-dependent resource gain, uniform versus heterogeneous resource gain (among individual plants), and resource-dependent versus resource- and pollen-limited fruit set. Pollen limitation and heterogeneous resource gain were necessary and sufficient to explain alternate-year flowering, but precipitation increased the quantitative match between model predictions and flowering dynamics. Together, our results support the importance of density-dependent pollen limitation as an ultimate and proximate cause of mast seeding in *A. scaphoides*. Precipitation does not act as a direct cue for synchrony in this species but might affect long-term resource gain and fruiting dynamics.

Keywords: *Astragalus scaphoides*, pollen limitation, mast seeding, precipitation, Allee effect.

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Synchronous, episodic reproduction, often known as mast seeding, has long been of interest to plant ecologists (Janzen 1976; Silvertown 1980). Recent reviews (Kelly 1994; Herrera et al. 1998; Kelly and Sork 2002) suggest that synchronous flowering and/or seed set are common in plant populations (e.g., Waller 1979; Brockie 1986; Kelly et al. 1992, 2001; Donaldson 1993; Sork et al. 1993; Koenig et al. 1994; Tapper 1996; Selås 2000). Synchronous bearing in alternate years is also widely reported in fruit and nut crops (Davis 1957; Sparks 1974; Monselise and Goldschmidt 1982). Across a broad group of woody plants, reproductive output is bimodally distributed in time (Herrera et al. 1998; but see Koenig and Knops 2000; Greene and Johnson 2004). In other words, many—possibly most—plant populations fluctuate between high and low years of flowering, with few average years. Mast seeding causes a diverse array of phenomena at higher trophic levels, including outbreaks of rodents and rodent-borne diseases (Ostfeld et al. 1996; Gallardo and Mercado 1999) and increased wildlife-human contacts (Mattson et al. 1992; Norman 2003). Nonetheless, although mast seeding is a widespread and ecologically important phenomenon, predictive models of mast seeding remain elusive. Here, we investigate the possible importance of pollen coupling, a recently proposed mechanism of mast seeding, for a perennial wildflower, *Astragalus scaphoides*.

Ecologists have traditionally explained mast seeding at two levels, which are not mutually exclusive. First, researchers have long believed that mast seeding increases plant fitness through increased seed output or survival when many seeds are produced, often called economies of scale (reviewed by Janzen 1976; Silvertown 1980; Kelly 1994; Kelly and Sork 2002). Numerous possible economies of scale have been proposed, but only two have been widely tested and supported: predator satiation, meaning more seeds are produced than can be consumed by predators in mast years, and pollination efficiency, meaning plants are more pollen limited in low- than in high-flowering years. Kelly and Sork (2002) review numerous examples of reduced seed predation in mast years and of increased pollination efficiency for wind-pollinated species in high-

flowering years (e.g., Smith et al. 1990; Kelly et al. 2001). Surprisingly, Kelly and Sork (2002) could not find convincing examples of pollination efficiency as an advantage of mast seeding in animal-pollinated plants. Nonetheless, a number of studies of insect-pollinated plants report lower pollinator visitation and/or fruit set in smaller or more isolated populations (Jennersten 1988; Kunin 1993, 1997; Groom 1998; Steffan-Dewenter and Tscharrntke 1999; Hackney and McGraw 2001; Wolf and Harrison 2001; Knight 2003; Vázquez and Simberloff 2004), including one recent example in a mast-seeding species (Forsyth 2003).

The second category of explanation for mast seeding involves resource, climate, or weather cues that trigger flowering or fruiting in plants (Janzen 1976; Silvertown 1980; Kelly 1994; Kelly and Sork 2002). In some cases, these resource cues directly relate to a plant's ability to gain resources or produce reproductive structures (Lesica 1999; Kaye et al. 2001; Inouye et al. 2002; Schaubert et al. 2002; Post 2003). In others (Ashton et al. 1998; Crawley and Long 1995; Tapper 1996; Hamann 2004), resource cues appear to be far removed from mechanisms of seed production, possibly indicating that such cues have evolved to facilitate economies of scale (Kelly and Sork 2002). The apparent lack of correspondence between environmental conditions and mast seeding could be partly explained by reproduction based on stored resources. At least some plant species show significant reductions of stored mobile carbon pools during mast years (Kozłowski 1992; Miyazaki et al. 2002; but see Hoch et al. 2003).

Recent pollen coupling models that combine resource allocation and pollen limitation have the potential to change the way ecologists think about mast seeding. Rather than reflecting direct climate cues, mast seeding could reflect temporal patterns of individual resource allocation and costs of reproduction. In two related models, Isagi et al. (1997) and Satake and Iwasa (2000) assumed that an individual plant requires more resources to flower and set seed than it gains in a year and therefore flowers only above some threshold amount of stored resources. These rules cause plants to have alternate-year or chaotic patterns of reproduction over time if seed production depletes stored resources (Isagi et al. 1997). Given alternate-year reproduction by individuals, only small amounts of environmental variation are needed to synchronize individuals within plant populations (Rees et al. 2002; Satake and Iwasa 2002). Furthermore, if plants are pollen limited in low-flowering years, synchronous mast seeding could occur in the absence of any environmental variation (Satake and Iwasa 2000). If they are pollen limited, plants that flower out of synchrony with their population would not make as many fruits. If resource costs of flowering are less than the additional costs of seed production, these plants would have enough stored

resources to flower the next year, entraining them with other plants (Satake and Iwasa 2000).

Pollen coupling models are based on the dynamics of internal resource stores, as a function of past flowering, current conditions, and pollen availability. The term "pollen coupling" refers specifically to the idea that coupling via density-dependent pollen limitation could cause synchronous flower and seed production even in the absence of external environmental variation (Satake and Iwasa 2000). However, the models actually include two innovations for understanding mast seeding. The first is that density-dependent pollen limitation is actually better at synchronizing reproduction than fluctuations in climate variables (Satake and Iwasa 2002). The second—and arguably more fundamental—is that mast seeding should be interpreted in light of the dynamics of internal resource reserves within plants as opposed to relating weather or climate variables to current reproduction.

Changes in mobile resource reserves over time are difficult to measure in individual plants, particularly in herbaceous plants that do not produce permanent, above-ground storage organs. Rees et al. (2002) developed a method for estimating the dynamics of stored resources over time from time series individual reproduction and estimated resource gain. They fitted these models to time series of flowering by *Chionochloa pallens*, a strongly mast-seeding, wind-pollinated tussock grass that does not experience pollen limitation in low-flowering years (Kelly and Sullivan 1997). Models including internal resource dynamics and fluctuations in growing-degree days among years were strikingly good at matching patterns of flowering by *C. pallens* over time, in contrast to simple regressions of reproduction versus climate variables (Rees et al. 2002). Thus, explicitly considering internal resource dynamics may be central to understanding mast seeding in plants even in the absence of pollen limitation.

To test whether pollen coupling might cause synchronous flowering, we adapted techniques developed by Rees et al. (2002) to fit a series of related models to monitoring data for *Astragalus scaphoides*, an herbaceous perennial, bee-pollinated plant endemic to sagebrush steppe in a small area of southwest Montana and adjacent Idaho. Three populations of *A. scaphoides* were monitored from 1986 to 1999 (Lesica 1995; Crone and Lesica 2004; see fig. 1). During this study, fruit set increased with flowering plant density, indicating density-dependent pollen limitation (Crone and Lesica 2004). In addition, precipitation was the strongest positive correlate of fruit set (Crone and Lesica 2004). We therefore developed a set of models to ask whether dynamics of stored resources could explain mast seeding in *A. scaphoides* and, if so, whether synchrony could be caused by precipitation or pollen limitation. In addition, we ask whether density-dependent pollen limi-

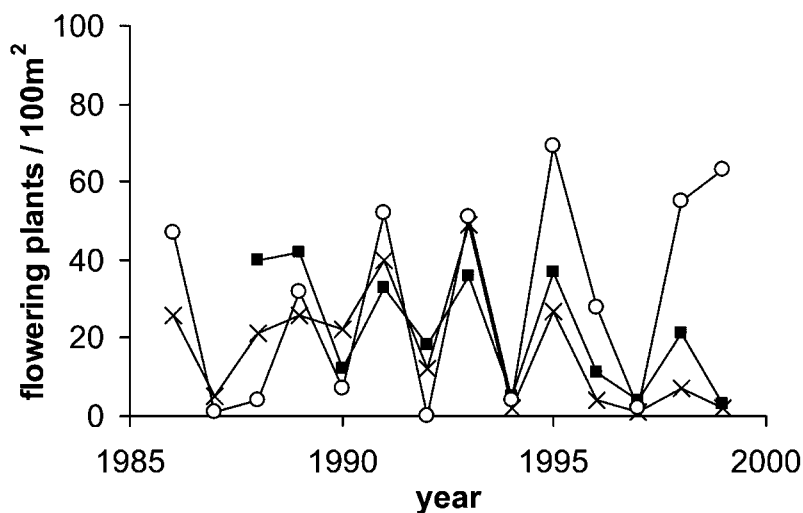


Figure 1: Synchronous flowering by *Astragalus scaphoides* at two sites in Idaho (squares = McDevitt Creek, crosses = Haynes Creek) and one in Montana (circles = Sheep Corral Gulch). From Crone and Lesica (2004).

tation and precipitation-dependent resource gain are either necessary or sufficient to cause synchrony in this species.

Methods

We used a model selection approach to evaluate the ability of models of internal resource dynamics, synchronized by precipitation and/or pollen limitation, to explain mast seeding in *Astragalus scaphoides*. Specifically, we developed a series of models adapted from Satake and Iwasa's (2000) pollen coupling model and Rees et al.'s (2002) model of internal resource dynamics. These models included all eight possible combinations of three factors: fruit set limited by stored resources versus resource and pollen limitation, precipitation-dependent versus constant resource acquisition, and uniform versus heterogeneous rates of resource gain among individual plants. We used methods directly analogous to those of Rees et al. (2002) to fit each of these eight models to monitoring data from *A. scaphoides*. We evaluated whether each set of factors could potentially explain mast seeding in *A. scaphoides* by testing whether model parameters indicated alternate-year flowering, similar to our observations in natural populations, as well as by comparing statistics of overall model fit. Below, we describe each step in detail: monitoring, model development, parameter estimation, and model evaluation.

Study System and Field Monitoring

Astragalus scaphoides (Fabaceae) is an iteroparous legume endemic to high-elevation sagebrush steppe in a small area

of Beaverhead County in southwestern Montana and adjacent Lemhi County in east-central Idaho (Barneby 1964). Local populations are scattered on south-facing slopes with relatively deep soils. *Astragalus scaphoides* is an herbaceous plant that produces one to many 15–40-cm inflorescences and has long, narrow, woody roots (Lesica 1995). *Astragalus scaphoides* does not reproduce vegetatively and, like many *Astragalus* species (Karron 1987; Geer et al. 1995), is visited by a number of generalist bumblebees (*Bombus* spp.) and solitary bees (probably including *Anthophora* spp. and *Osmia* spp.; E. E. Crone, unpublished data). Flowering occurs from late May to mid-June. In most years, plants dehisce seeds by mid-July. Lesica (1995) reported average survival of flowering plants of 0.88 and an average of 3.3 new seedlings per reproductive plant. Using data from Lesica (1995), Ehrlén and Lehtilä (2002) calculated *A. scaphoides* longevity at 21 years, conditional on reaching the flowering stage. Patterns of flower and seed production over time are highly concordant in *A. scaphoides* (Crone and Lesica 2004), making “mast seeding” an appropriate term for flower and fruit production, as well as “seeding” per se.

This study is based on monitoring of marked individual plants at two sites (Sheep Corral Gulch, MT, and Haynes Creek, ID) established in 1986 and a third site in Idaho (McDevitt Creek) established in 1988. In this analysis, we use data from plants observed during more than 5 years because Rees et al.'s method is biased when plants flower fewer than three times (Rees et al. 2002); 371 plants met this criterion. Monitoring methods and life history are described in greater detail by Lesica (1995) and Crone and

Lesica (2004). We compiled precipitation data for our analyses from weather stations in Dillon, Montana, and Salmon, Idaho (NOAA 2003). To estimate precipitation for the Montana site in year t , we summed monthly precipitation over the 12 months before fruiting (July $t - 1$ through June t). For the two Idaho sites, we performed the same calculation using precipitation data from Salmon, Idaho.

Model Development

We began with a general model of internal resource dynamics including pollen limitation, slightly modified from Satake and Iwasa (2000):

$$D_{i,t+1} = \begin{cases} D_t + P_{i,t} - b & \text{if } D_{i,t} \leq C \\ D_{i,t} + P_{i,t} - Af_t^\beta(D_{i,t} - C) - b & \text{if } D_{i,t} > C \end{cases} \quad (1)$$

where $D_{i,t} \leq C$ is for nonflowering plants, $D_{i,t} > C$ is for flowering plants, f_t is the proportion of flowering plants in a population in year t (a surrogate of pollen availability; discussed in app. A), $D_{i,t}$ is an estimate of the internal resources of plant i in year t , C is the minimum resource level needed for flowering, $P_{i,t}$ is resource acquisition for plant i in year t , b is reproductive effort of plants below the threshold, A is the resource cost of reproduction, and β scales the strength of pollen coupling. This model predicts constant flowering effort when the cost of reproduction (A) is less than 2 and alternate-year or desynchronized chaotic flowering when the cost is above 2, depending on the strength of pollen coupling (β) and environmental fluctuations (see apps. A, B). This model is similar to Satake and Iwasa's (2000) pollen coupling model, rather than the model used by Rees et al. (2002), in that we allowed for density-dependent (pollen-limited) fruit set and assumed that the costs of reproduction were proportional to the costs of fruit set. Equation (1) differs from both Satake and Iwasa (2000) and Rees et al. (2002) in that we allowed individuals to have different rates of resource gain.

The eight specific models we fitted to data are all special cases of this general model, with $P_{i,t}$ constant over i and/or t and/or $\beta = 0$. We compared two hypotheses for resource expenditure and fruiting effort: fruit set dependent on estimated stored resources only ($\beta = 0$) and fruit set dependent on the both stored resources and the number of flowering plants in that year, as would be expected with pollen limitation ($\beta > 0$). We considered two a priori hypotheses for resource acquisition: constant acquisition over time (P_i constant over t) and resource acquisition dependent on precipitation ($P_{i,t}$ proportional to precipitation in year t). During the initial stages of model fitting, we often had difficulty obtaining model convergence be-

cause of substantial among-plant variance in the number of years between flowering events. Thus, we added two a posteriori hypotheses about resource acquisition: constant resource gain over time but with a different average rate for each plant and precipitation-dependent resource gain with a different conversion factor from water to stored resources for each plant. In this article, we will refer to these models as "uniform" versus "heterogeneous" resource acquisition. We fitted all eight combinations of these three factors (pollen-limited fruit set, precipitation-dependent resource acquisition, and heterogeneous resource acquisition) to monitoring data for 371 individual plants at three sites in Idaho and Montana from 1986 to 1999.

Parameter Estimation

Following logic directly analogous to that of Rees et al. (2002), these models can be fitted to monitoring data using two sequential regressions. Full derivation of our method is presented in appendix A. In brief, the similarity is evident by comparing our equations (2) and (3) to Rees et al.'s equations (6) and (8), respectively. First, linear regressions of cumulative reproduction versus cumulative resource availability over time estimate an individual's rate of resource gain. Using the same notation as equation (1) and $F_{i,y}$ to represent fruit set by plant i in year y , the first regression becomes

$$\sum_{y=0}^t F_{i,y} = D_{i,0} + m \sum_{y=0}^t P_{i,y} - D_{i,t} \quad (2)$$

Here, the slope parameter m converts energy units into flower units. This relationship describes linear regressions with cumulative fruit set over the course of the study as the dependent variable and surrogates of cumulative resource availability as the independent variable. Cumulative reproduction was assessed using two surrogates: number of fruit set and the sum of the number of inflorescences and fruits, weighted by their average mass. Nearly identical results were obtained with both reproductive surrogates, so we report only results using the number of fruits. Following Rees et al. (2002), we fitted a unique intercept ($D_{i,0}$) for each plant, which estimates the stored resources of a plant at the beginning of the study. To test whether resource gain was constant or precipitation dependent, we fitted models using cumulative years versus cumulative precipitation as the surrogate of cumulative resource availability. To test whether resource gain was uniform or heterogeneous across individual plants, we fitted models with a single, constant slope parameter (m) versus a different slope for each individual plant (i.e., an individual \times time interaction).

Residuals of these regressions ($D_{i,t}$) are an estimate of the stored resources each individual plant has in each year (Rees et al. 2002). These residuals become an independent variable for models of annual reproduction versus stored resources and pollen availability, as inferred from the proportion of flowering plants:

$$F_{i,t+1} = \begin{cases} b & \text{if } D_{i,t} \leq C \\ Af_t^\beta(D_{i,t} - C) + b & \text{if } D_{i,t} > C \end{cases} \quad (3)$$

For the assumption that fruit set is limited only by stored resources ($\beta = 0$), this model reduces to a piecewise linear regression, with some constant, low level of fruit production (b) up to a threshold level of stored resources (C) and a linear increase in fruit production with stored resources above the threshold. If fruit set is both resource and pollen limited, this model is a piecewise nonlinear regression, with fruit set above the threshold dependent on both stored resources and the proportion of flowering plants at each site in each year. We estimated parameters for each model using the SAS NLIN procedure (SAS Institute 2002).

Model Evaluation

To evaluate support for each model, we considered two measures of fit, both of which test whether a model can potentially generate features of the data to which it was fitted: first, whether maximum likelihood parameters from the model predicted alternate-year flowering in a constant environment and, second, whether simulations using the fitted parameters from each model and precipitation data recovered qualitatively similar patterns to monitoring data. Kendall et al. (1999) discuss why these criteria are not circular even though model predictions are compared to the data set used to estimate model parameters. As a third criterion for model evaluation, we compared AICc (Akaike's Information Criterion, corrected for low sample size) statistics for each model. AICc is a measure of the statistical support for a model, adjusted for the number of parameters, described in detail by Burnham and Anderson (2002). We selected this statistic in part because it is suitable for comparing nonnested models, and we discuss its strengths and limitations more extensively in "Discussion." In brief, the model with the lowest AICc is best supported, models within two of the lowest AICc are essentially equivalent to the best model, and models with AICc more than 10 above the best have significantly less support. Note that AICc differs from our first two criteria in assessing which models are best supported by the data rather than which are able to re-create observed dynamics.

To evaluate whether fitted models predicted alternate-year flowering (our first criterion), we calculated the max-

imum Lyapunov exponent for the cost (A) and pollen coupling (β) parameters estimated for each model (see app. B). Lyapunov exponents are a measure of the extent to which trajectories predicted by a model diverge over time from similar initial conditions (Ruelle 1989; see also Satake and Iwasa 2000). Negative exponents mean trajectories tend to converge; positive exponents mean they tend to diverge. Because the alternate-year flowering predicted by these models is technically coherent periodic chaos (Satake and Iwasa 2000), negative (or 0) Lyapunov exponents identify parameter conditions that do not predict alternate-year flowering.

To compare observations to stochastic simulations (our second criterion), we used maximum likelihood parameters from each model and precipitation data (NOAA 2003). We also quantified individual survival using logistic regressions of survival versus estimated stored resources for the 371 plants used in internal resource reconstruction analysis. Survival increased with estimated stored resources (precipitation-dependent acquisition: $\chi^2 = 10.2$, $P = .0014$; constant acquisition: $\chi^2 = 2.2$, $P = .1414$). We used numerical simulations to estimate the relationship between fruits in year t and new recruits in year $t + 1$ that led to approximately constant population sizes over time. Preliminary exploration of alternative models of reproduction (e.g., a constant number of recruits in each year) did not substantially affect the autocorrelation or coefficient of variation (CV). Because precipitation was not significantly autocorrelated over time (Dillon, MT: $r = 0.11$, $P = .73$, $n = 14$ years of data; Salmon, ID: $r = -0.12$, $P = .69$, $n = 14$ years of data), we simulated annual variation in precipitation by drawing independent random numbers from a lognormal distribution with the empirically estimated mean of 28.26 cm and SD of 14.74 cm (NOAA 2003). We compared the CV (ratio of variance to mean number of flowering plants) and temporal lag-one autocorrelation from stochastic simulations based on each model to statistics estimated for each of the three monitoring sites.

We calculated AICc's (our third criterion) using likelihoods calculated from models of fruit set versus estimated stored resources, equation (3) (see Burnham and Anderson 2002, p. 63). It was not entirely clear whether we should use the number of parameters from both regressions or only from the regression used to calculate likelihood (i.e., the second of the two regressions). We calculated both and obtained essentially congruent results. We present statistics calculated using the full number of parameters from both regressions because that statistic is a more conservative test of the hypothesis that resource gain differs among individual plants.

Results

Of eight mechanistic models fitted to the monitoring data, six predicted constant flowering effort, and two—the only two with both pollen limitation and heterogeneous resource acquisition—predicted alternate-year flowering (fig. 2). Both Satake and Iwasa’s (2000) phase plane and our Lyapunov exponent calculations indicate that the latter two models lead to “coherent periodic” flowering dynamics (Lyapunov exponents > 0), while all others predict constant, stable flowering effort (exponents ≤ 0). In spite of the slight modifications we made to their model, Lyapunov estimates matched predicted dynamics based on the phase planes presented by Satake and Iwasa (2000). Thus, by our first criterion—the ability of a model to generate alternate-year flowering—pollen-limited fruit set and heterogeneous resource acquisition are both necessary and sufficient to generate alternate-year flowering in *Astragalus scaphoides*, and precipitation-dependent resource gain is unimportant.

However, both stochastic simulations and AICc statistics indicate that all three factors we considered, precipitation-dependent resource gain, pollen-limited fruit set, and heterogeneous resource acquisition, contribute to alternate-

year flowering in *A. scaphoides*. Autocorrelations of fruiting in natural populations fell within 95% limits of stochastic autocorrelations of three models: heterogeneous resource acquisition with pollen-limited fruit set, heterogeneous resource acquisition with precipitation-dependent resource gain, and the model with all three factors. Across all eight models, CVs were lower than observed in natural populations, and only the model with all three factors generated a stochastic CV near the values of natural populations. Similarly, the AICc of the model with all three factors was vastly better supported than that of any other model (table 1; see fig. 3 for visual comparison of model fits).

Estimated differences in resource gain among individual plants were large (fig. 4) and, although likely in retrospect, somewhat unanticipated. Among-plant differences in cumulative fruit set over time were statistically supported by the first regression of the internal resource analysis, independent of the second regression used to evaluate models (precipitation: $F = 18.7$, $df = 370, 2,566$, $P < .0001$; constant: $F = 17.2$, $df = 370, 2,566$, $P < .0001$), and remained statistically significant even after plants that never

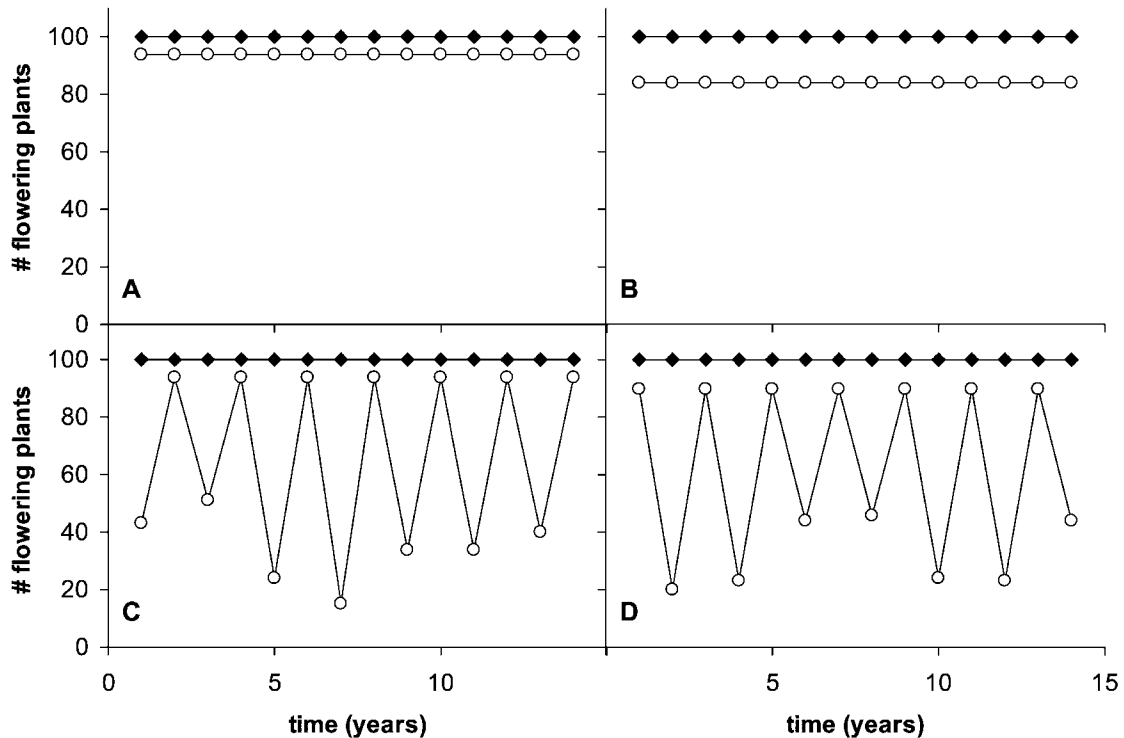


Figure 2: Predicted *Astragalus scaphoides* flowering dynamics based on estimated parameters for (A) resource-dependent fruiting and constant resource acquisition, (B) resource-dependent fruiting and precipitation-dependent resource acquisition, (C) pollen-limited fruiting and constant resource acquisition, and (D) pollen-limited fruiting and precipitation-dependent resource acquisition. Diamonds = uniform resource acquisition among individuals, circles = heterogeneous resource gain.

Table 1: Results of parameter estimation and stochastic simulations

Pollen limitation?	Resource surrogate, $P_{i,t}$	Resource acquisition, $P_{i,t}$	Fruiting cost, k	Pollen coupling, β	Deterministic dynamics	Stochastic autocorrelation	Stochastic CV	Δ AICc
Yes	Precipitation (variable over t)	Heterogeneous (variable over i)	1.62 (1.49, 1.76)	.59 (.53, .66)	Coherent periodic ($\lambda = .29$)	-.33 ^a (-.71, .16)	.51 ^a (.28, .77)	0
Yes	Constant (constant over t)	Heterogeneous (variable over i)	1.62 (1.48, 1.76)	.60 (.53, .67)	Coherent periodic ($\lambda = .30$)	-.46 ^a (-.97, .89)	.37 (.04, .68)	566
Yes	Precipitation (variable over t)	Uniform (constant over i)	.17 (.09, .25)	.59 (.52, .67)	Constant ($\lambda = .00$)	.62 (.01, .93)	.04 (.02, .08)	12,418
Yes	Constant (constant over t)	Uniform (constant over i)	.22 (.14, .30)	.60 (.52, .67)	Constant ($\lambda = .00$)	.63 (.06, .94)	.04 (.02, .09)	12,810
No	Precipitation (variable over t)	Heterogeneous (variable over i)	.66 (.59, .73)	0	Constant ($\lambda = -.42$)	-.07 ^a (-.42, .65)	.30 (.04, .55)	31,369
No	Constant (constant over t)	Heterogeneous (variable over i)	.71 (.64, .78)	0	Constant ($\lambda = -.35$)	.69 (.13, .95)	.06 (.03, .10)	32,006
No	Precipitation (variable over t)	Uniform (constant over i)	-.42 (-.46, -.38)	0	Constant ($\lambda = -.88$)	.68 (.09, .94)	.04 (.02, .08)	47,600
No	Constant (constant over t)	Uniform (constant over i)	-.39 (-.43, -.35)	0	Constant ($\lambda = -.95$)	.67 (.16, .95)	.04 (.02, .09)	48,265

Note: Parameter estimates include 95% confidence limits, and simulation results include upper and lower bounds for 95% of values. Lyapunov exponents (λ) for deterministic dynamics are included in parentheses. Simulation results are based on 1,000 stochastic simulations over 100 years. Autocorrelation and coefficient of variation (CV) are compared to the range of values observed in natural populations. Autocorrelations: Haynes: -0.17; McDevitt: -0.21; Sheep Corral Gulch: -0.39. CV: Haynes: 0.87; McDevitt: 0.68; Sheep Corral Gulch: 0.88.

^a Confidence limits include statistics from natural populations.

flowered were removed from analysis (precipitation: $F = 16.7$, $df = 177, 1,351$, $P < .0001$; constant: $F = 15.0$, $df = 177, 1,351$, $P < .0001$). Plants that never flowered did not affect model parameters estimated during the second part of the regression (E. E. Crone, unpublished analysis) because they simply led to a large number of data points with estimates of no stored resources and no fruit set. These data points also would not affect interpretation of likelihoods from this second regression; the large number of well-predicted zeros adds a constant to the log likelihoods for all models.

Qualitative predictions of deterministic and stochastic simulations were similar when recruitment exactly matched mortality. In models with individual heterogeneity, the primary differences were decreased magnitude of negative autocorrelations and increased CV in the presence of stochasticity (e.g., cf. CVs and autocorrelations of constant resource gain models, which include only demographic stochasticity, and precipitation-dependent models, which include both environmental and demographic stochasticity; table 1). However, when births did not exactly match deaths, density-dependent pollen limitation led to a strongly destabilizing Allee effect (L. Polansky and E. E. Crone, unpublished simulations). If reproduction was too high, per capita seed production increased as plant density increased (and pollen limitation decreased), and populations grew faster than exponentially. If reproduction was too low, population size de-

creased faster than exponentially until populations became extinct. In a few of our simulations, demographic stochasticity led to these kinds of highly unstable dynamics even when average recruitment exactly matched average survival, accounting for the positive autocorrelations under many of the models in which plants flowered every year in deterministic models (table 1).

Discussion

Our results indicate that pollen limitation and heterogeneous resource acquisition are necessary and sufficient to cause alternate-year flowering in *Astragalus scaphoides*. Although we have not experimentally tested the importance of pollen coupling in *A. scaphoides*, two anecdotal observations further support the importance of internal resource dynamics as the mechanism of alternate-year flowering. First, in 2004, March and April were very dry, conditions predicted to cause low flowering (E. E. Crone and P. Lesica, unpublished manuscript). At most sites, few plants flowered, but at one—the only site with high flowering in 2002 and low flowering in 2003—many plants flowered in spite of dry spring conditions (E. E. Crone, personal observation). Second, near Haynes Creek, Idaho, we have observed a large proportion of plants flowering in a pack trail that runs through the site even in low-flowering years. Because of trail use by horses and cattle, these plants are usually browsed before fruit set (E. E.

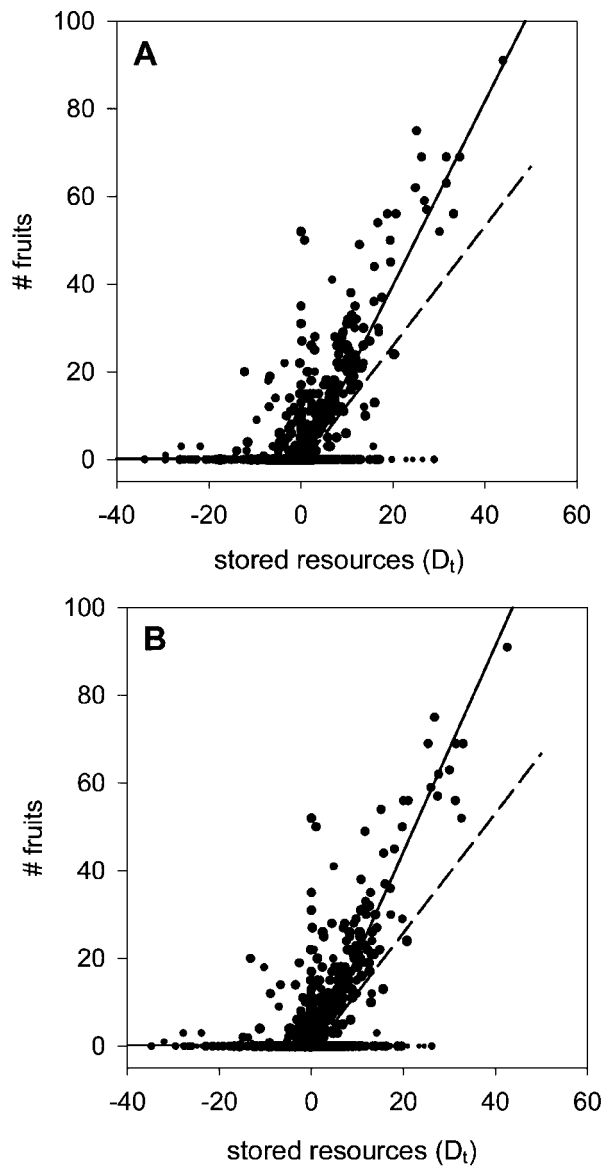


Figure 3: Fruit set versus estimated stored resources (D_t) from models with pollen-limited fruit set, individual heterogeneity, and (A) precipitation-dependent resource gain versus (B) constant resource gain. Diameter of circles indicates the number of flowering plants in at each site in each year. Because fruit set depends on the number of flowering plants, solid lines indicate expected fruiting averaged over the number of flowering plants for all plants that fruited, and the dashed lines indicate expected fruit set averaged over all years.

Crone, personal observation) and therefore seldom set fruit. Pollen coupling models predict that plants that do not set fruit would flower every year.

The importance of precipitation for alternate-year flowering in *A. scaphoides* is less clear because its importance depends on our criteria for model evaluation. Each cri-

terion we used evaluates models in different ways, which we will discuss in turn. Our first criterion was whether parameters estimated for each of the eight models predicted one key feature of *A. scaphoides*, alternate-year flowering, in the absence of external environmental forcing. All eight models are capable of generating alternate-year flowering, at least for some parameter values (Satake and Iwasa 2000, 2002; Rees et al. 2002). Given that we estimated parameters from time series with alternate-year flowering, it is perhaps more surprising that maximum likelihood parameters for six models did not predict alternate-year flowering than it is that those of two models did. It is also not surprising that adding precipitation-dependent resource gain did not improve model fit by this criterion because we explicitly evaluated dynamics under constant environmental conditions. It is, however, striking that large fluctuations in reproductive output of *A. scaphoides* (fig. 1) could occur in a perfectly constant environment (fig. 2).

Our second group of criteria, stochastic autocorrelations and CVs, compare the ability of different mechanisms to reproduce fruiting dynamics in the presence of demographic and environmental stochasticity. Autocorrelations are a measure of the tendency for low-flowering years to follow high-flowering years, and CVs are a measure of the overall variability of fruit set over time. All else being equal, increasing the inherent instability of flowering (our first criterion) would increase both the negative autocorrelation and CV, and increasing the magnitude of negative autocorrelation would increase a population's CV. However,

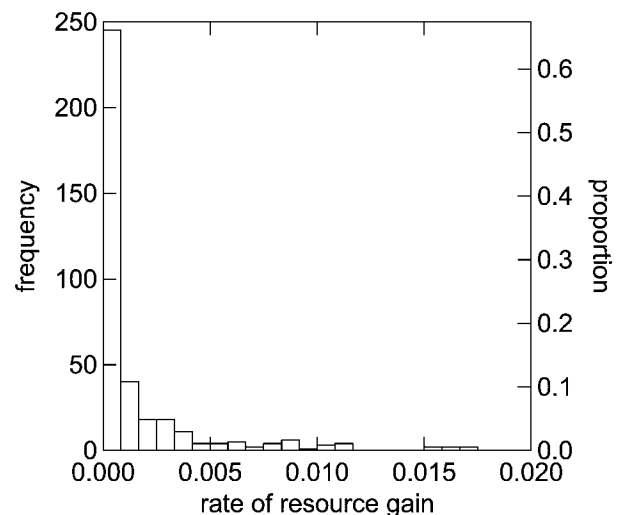


Figure 4: Histogram of estimated resource gain coefficients for individual plants based on slopes of cumulative fruit set versus cumulative precipitation. Out of 371 plants, 190 never flowered and had estimated coefficients of 0.

these three measures can vary independently in principle and do not consistently co-vary in concert across species (Koenig et al. 2003). For *A. scaphoides*, only predictions from the most complex model, which included pollen limitation, heterogeneous resource acquisition, and precipitation-dependent resource gain, did not differ significantly from the estimated autocorrelation or CV in natural populations. Even this best model does not perfectly re-create the noise of observed flowering; the autocorrelation is too strong (an average of -0.33 in simulations vs. -0.26 in natural populations) and the CV too low (an average of 0.51 in simulations vs. 0.81 in natural populations).

In contrast, Rees et al. (2002) were able to nearly perfectly reproduce qualitative and quantitative features of tussock grass (*Chionochloa pallens*) flowering by using models of internal resource dynamics synchronized by fluctuations in growing degree days. Several reasons may explain this discrepancy between the results of the two studies. *Chionochloa pallens* is one of the most striking mast seeding plants known, with more dramatic fluctuations between high- and low-flowering years than *A. scaphoides* (Kelly and Sork 2002; Rees et al. 2002). Less predictable flowering by *A. scaphoides* may indicate that a more complex suite of processes contributes to flowering in this species. Another difference is that *C. pallens* is a very long-lived grass, and Rees et al. therefore did not have to consider complicating effects of births and deaths. *Astragalus scaphoides* individuals live ~ 20 – 25 years (Ehrlén and Lehtilä 2002), long enough to experience pollen coupling but short enough that births and deaths may add a substantial amount of noise to flowering dynamics. The simple models we used for survival and fecundity may not adequately describe population dynamics. Finally, less is known about limiting resources in *A. scaphoides* than in *C. pallens*. Relationships between growing-degree days and photosynthesis are well documented in *C. pallens*, whereas we have never directly measured resource gain in *A. scaphoides*. Unlike Rees et al., if we were looking for a simple explanation of exact dynamics of *A. scaphoides* flowering over time, the stochastic simulations indicate that none of our eight models is adequate, in spite of similar qualitative predictions and convincing AICc's. However, ecologists may not often expect an exact match between simple models and natural populations (but for examples of notably good matches, see Rees and Rose 2002; Metcalf et al. 2003).

Our final criterion for model evaluation is AICc, an information-theoretic measure of statistical support of different models, adjusted for the number of parameters relative to sample size (Hilborn and Mangel 1997; Burnham and Anderson 2002). Unlike our first two criteria, AICc is a measure of the goodness of fit of each model rather than a test based on model predictions that are independent of parameter estimation. Specifically, AICc statistics

quantify the relative ability of different models to predict specific fruit set of each plant in each year, given knowledge of past precipitation, past reproduction, and the number of flowering plants. Because they evaluate the ability of models to explain as much of the variation in data as possible rather than key qualitative features, AICc and related statistics tend to select highly descriptive, parameter-rich models for large data sets (Beissinger and Snyder 2002). For *A. scaphoides*, the slight improvement in model fit led to large differences in AICc; the difference between figure 3A and 3B represents an AICc difference of more than 500. Together, our three criteria imply that, although precipitation-dependent resource gain may not be necessary to cause alternate-year flowering in *A. scaphoides*, knowledge of precipitation, possibly in combination with more detailed understanding of resource gain and demography, would be needed to make quantitative predictions about flowering over time.

In contrast with the somewhat ambiguous relationships among precipitation, resource gain, and flowering, our empirical models strongly support the importance of heterogeneous resource acquisition among individual plants. Although individual heterogeneity was not considered in our initial set of a priori models, plant ecologists have long known that plant growth and reproduction depend on a variety of factors that can differ among microsites at very fine scales and that genetic differences among individuals can lead to differences in resource gain and resource allocation (Harper 1977; Gurevitch et al. 2002). We did not initially include individual heterogeneity in our analyses because we did not expect that the predictions of average models fitted to all plants together would differ radically from the average predictions of models that allowed different rates of resource gain for different plants. Our results add to a growing number of situations in which average parameters do not predict aggregate features of populations and/or communities (e.g., Palmer et al. 1997; Ruel and Ayres 1999; Fox and Kendall 2002; Kendall and Fox 2002; Pfister and Peacor 2003; Irvine et al. 2004). Because our analysis estimated resource gain coefficients for individual mapped plants, we could return to these individuals and test how they differ in terms of surrounding biotic and abiotic environment, as well as physiological status (carbon assimilation, leaf nitrogen, leaf water potential). These measurements might help identify other resources that regulate flowering in *A. scaphoides*.

Predicting fluctuations in the reproductive output of mast seeding plants remains a difficult question in plant ecology. Our study is the second to assess internal resource dynamics as a potential mechanism of mast seeding in iteroparous perennial plants. Our results for *A. scaphoides* provide an interesting contrast with Rees et al.'s (2002) analysis of *C. pallens*. Masting by *C. pallens*, a wind-

pollinated tussock grass, was driven by external resource availability, but, in order to explain dynamics of seed production over time, Rees et al. had to explicitly account for internal resource dynamics. Masting by *A. scaphoides*, a bee-pollinated wildflower, is not clearly related to external resource availability but is apparently caused by internal resource dynamics, coupled by pollen limitation. Although two species of plants do not provide a very broad comparison, both contradict the general expectation that pollen limitation is more likely to cause mast seeding in wind-pollinated than in animal-pollinated plants (Kelly 1994). Nonetheless, in both cases, internal resource models were able to explain patterns of seed set, whereas simpler relationships with weather variables were not (Rees et al. 2002; Crone and Lesica 2004). Although some exceptions exist, resource cues for mast seeding have been hard to identify for a wide number of plant species and remain highly difficult to test experimentally. Internal resource and pollen coupling models are a promising method for understanding and predicting mast seeding in plants.

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APPENDIX A

Complete Model Derivation

In this appendix, we outline the procedure used to convert the equations of Satake and Iwasa (2000) to regression models, directly analogous to those of Rees et al. (2002). Here, we derive our most general model. Other models may be obtained by holding terms constant over individuals and/or time; the model fitted by Rees et al. (2002) is a special case of this more general model, as are all the variants we fitted to the *Astragalus scaphoides* monitoring data.

Our analysis is based on models very similar to those proposed by Satake and Iwasa (2000) for reproductive effort of individual plants:

$$S_{i,t+1} = \begin{cases} S_{i,t} + P_{i,t} & \text{if } S_{i,t} + P_{i,t} - L_T \leq 0 \\ S_{i,t} + P_{i,t} - (Af_t^\beta)(S_{i,t} + P_{i,t} - L_T) & \text{if } S_{i,t} + P_{i,t} - L_T > 0 \end{cases} \quad (\text{A1})$$

where $S_{i,t}$ is the stored resources of plant i at time t , $P_{i,t}$ is the acquired resources for plant i at time t , L_T is a threshold amount of resources needed for flowering, A is the resource cost of reproduction, β is a parameter that controls the dependence of plant i on pollen availability, and f_i is the proportion of plants flowering in each population, a surrogate of pollen availability. Use of f_i as a proportion, rather than a sum of a measure of flowering effort, preserves congruence of the parameter β between our equation (A1) and the phase plane presented by Satake and Iwasa (2000). This approximation may be suitable only for species such as *A. scaphoides*, for which the number of flowering plants is highly correlated with total inflorescence production (Crone and Lesica 2004).

For each plant, fruit production, $F_{i,p}$ is described by

$$F_{i,t} = \begin{cases} (Af_t^\beta)(S_{i,t} + P_{i,t} - L_T) & \text{if } S_{i,t} + P_{i,t} - L_T > 0 \\ 0 & \text{if } S_{i,t} + P_{i,t} - L_T \leq 0 \end{cases} \quad (\text{A2})$$

In order to fit this model to time series for *A. scaphoides*, we repeated the procedure used by Rees et al. (2002). Rees et al.'s insight was to express the above equations in terms of deviations from an equilibrium energy budget, \tilde{S} , which ultimately allows internal resource dynamics to be estimated from time series of flowering effort and resource gain without directly measuring a plant's energy stores. At equilibrium, $S_{i,t+1} = S_{i,t}$ for all plants i , and therefore $f_{t+1} = f_t$ for all i , so the pollen limitation factor is constant for all plants; that is, $f \equiv f_t^\beta$ is constant, given some pollen coupling parameter, β . Following Rees et al. (2002), equilibrium calculations assumed $P_{i,t} = P_i$ constant over time, analogous to P_s in Rees et al.'s formulation. Substituting these relationships into equation (A1), we solved equation (A1) for equilibrium resource stores, $\tilde{S} = (P_i/Af) - P_i + L_T$, and deviations from equilibrium resources, $D_{i,t} = S_{i,t} - \tilde{S}$. Directly following equation (5) of Rees et al. (2002), we rewrote our recursive equation (A1) as a function of cumulative energy gain and fruit set:

$$S_{i,t} = \tilde{S} + D_{i,0} + m \sum_{y=0}^t P_{i,y} - \sum_{y=0}^t F_{i,y}, \quad (\text{A3})$$

for which $D_{i,0}$ is the initial deviation of a plant's energy stores at the beginning of a study (year 0), y indexes years from year 0 to year t , m converts resource availability to a plant's stored resources, and all other variables are as defined above. This equation can be rearranged as a relationship between cumulative fruiting and cumulative energy gain, directly analogous to Rees et al.'s equation (6):

$$\sum_{y=0}^t F_{i,y} = D_{i,0} + m \sum_{y=0}^t P_{i,y} - D_{i,t}. \quad (\text{A4})$$

As noted by Rees et al., this relationship indicates that $D_{i,t}$ are residuals from the regression of cumulative reproduction versus cumulative energy gain. As noted by Rees et al., the conversion factor m allows surrogates of cumulative energy gain (in our case, cumulative precipitation or cumulative time) to be used in empirical models.

Using estimates of $D_{i,t}$, we estimated coefficients for equation (A1). To do this, we rearranged equation (A1) in terms of deviations from energy equilibrium ($D_{i,t}$):

$$D_{i,t+1} = \begin{cases} D_{i,t} + P_{i,t} - b & \text{if } D_{i,t} + \frac{P_{i,t} - b}{Af} \leq 0 \\ D_{i,t} + P_{i,t} - Af^\beta \left(D_{i,t} + \frac{P_{i,t} - b}{Af} \right) - b & \text{if } D_{i,t} + \frac{P_{i,t} - b}{Af} > 0 \end{cases}. \quad (\text{A5})$$

Note that this equation reduces to Rees et al.'s equation (7) with $\beta = 0$ and the shifts $P_{i,t} \rightarrow P_{i,t} + b$ and $Af_t^\beta \rightarrow 1 + Af_t^\beta$. Setting $\beta = 0$ simply means reproduction was not pollen limited in the system studied by Rees et al. The parameter b describes a low level of reproduction below the threshold, which was not included in Rees et al.'s equation (7) but was used in their analyses (Rees et al. 2002, p. 48). Converting $1 + Af_t^\beta$ to Af_t^β is equivalent to assuming the total cost of reproduction is proportional to the cost of fruit production. We tested this assumption by comparing model fits of this simplified model with one that assumed separate costs of inflorescence and fruit production. The more complicated model was less efficient for parameter estimation but produced identical results in terms of dynamical stability and model selection, so we chose to present the simpler model. These modifications did not appear to affect predicted stability of flowering dynamics (see app. B).

The critical parameters determining flowering dynamics are the resource cost of reproduction and the pollen coupling parameter β (Satake and Iwasa 2000). Therefore, equation (A5) can be simplified to

$$D_{i,t+1} = \begin{cases} D_{i,t} + P_{i,t} - b & \text{if } D_{i,t} \leq C \\ D_{i,t} + P_{i,t} - Af_t^\beta (D_{i,t} - C) - b & \text{if } D_{i,t} > C \end{cases} \quad (\text{A6})$$

where $C = (P_i - b/Af)$ is the threshold level of stored resources above which plants produce flowers. Using equation (A6), reproductive output in year $t + 1$ is given by

$$F_{i,t+1} = \begin{cases} b & \text{if } D_{i,t} \leq C \\ Af_t^\beta (D_{i,t} - C) + b & \text{if } D_{i,t} > C \end{cases} \quad (\text{A7})$$

We used this relationship to estimate parameters A , β , b , and C from piecewise nonlinear regressions of fruit production by individual plants ($F_{i,t}$ as recorded in monitoring data) versus estimated resource residuals ($D_{i,t}$) and flowering effort (f_t , estimated as proportion of flowering plants in each population in each year; see eq. [A2]). Note that in this parameterization, our cost estimate, A , is equal to $k + 1$ in Satake and Iwasa's phase plane (fig. 5 in Satake and Iwasa 2000). In other words, we subtracted 1 from A to estimate k for comparison with Satake and Iwasa's stability results.

APPENDIX B

Lyapunov Exponent Calculations

The model structure and definition of the variables and functions used to derive the Lyapunov exponent may be found in Satake and Iwasa's (2000) equations (8a) and (8b). Let y_i be the dimensionless resources of plant i , k be the cost parameter, and β be the pollen coupling parameter. The difference from Satake and Iwasa (2000, their app. B) is that we include the possibility of self-pollination, so $P_i(t) = \{(1/N) \sum_{j=1}^N [y_j(t)]_+\}^\beta$. Then,

$$\frac{\partial y_i}{\partial y_j} = \frac{\partial}{\partial y_j} [y_i + 1 - (kP_i + 1)[y_i]_+]. \quad (\text{B1})$$

If $i = j$, then equation (B1) is

$$\frac{\partial y_i}{\partial y_i} = 1 - \frac{\partial}{\partial y_i} [(kP_i + 1)[y_i]_+] = 1 - (kP_i + 1)\theta(y_i) - k \frac{\partial}{\partial y_i} (P_i)\theta(y_i)y_i$$

and

$$\frac{\partial P_i}{\partial y_i} = \frac{\partial}{\partial y_i} \left(\frac{1}{N} \sum_{l=1}^N [y_l]_+ \right)^\beta = \frac{\beta}{N} \left(\frac{1}{N} \sum_{l=1}^N [y_l]_+ \right)^{\beta-1} \theta(y_i).$$

If $i \neq j$, then equation (B1) is

$$\frac{\partial y_i}{\partial y_j} = - \frac{\partial}{\partial y_j} [(kP_i + 1)[y_i]_+] = -k \frac{\partial P_i}{\partial y_j} y_i \theta(y_i)$$

and

$$\frac{\partial P_i}{\partial y_j} = \frac{\partial}{\partial y_j} \left(\frac{1}{N} \sum_{l=1}^N [y_l]_+ \right)^\beta = \frac{\beta}{N} P_i^{(\beta-1)/\beta} \theta(y_j).$$

Combining the above terms gives

$$\frac{\partial y_i}{\partial y_j} = [1 - (kP_i + 1)\theta(y_i)]\delta_{ij} - \frac{k\beta}{N} P_i^{(\beta-1)/\beta} \theta(y_i)\theta(y_j)y_i. \quad (\text{B2})$$

Let $\mathbf{J}(k)$ be the matrix of partials at time $t = k$ as defined in equation (B2). To evaluate the dynamics of the system, we looked at the maximum Lyapunov exponent, where the i th Lyapunov exponent is defined by $\lambda_i = \lim_{t \rightarrow \infty} \ln |$ the i th eigenvalue of $\prod_{k=0}^{t-1} \mathbf{J}(k)|$, as described by Ruelle (1989).

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