

The effects of dataset length and mast seeding on the demography of *Frasera speciosa*, a long-lived monocarpic plant

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Abstract. *Frasera speciosa* (Gentianaceae) is a long-lived monocarpic plant with mast seeding, a type of plant whose demography is rarely studied. Using a 35-year dataset from an ongoing study, we described the population dynamics of *F. speciosa* using matrix projection models, addressed how many years of data are needed to estimate population growth and elasticity values consistently, and examined the effects of mast seeding on demographic parameter estimates. Our results indicated that our population is likely stable, with the annual population growth rate near one ($\lambda = 0.969$, $\lambda_s = 0.967$ with 95% CI = 0.923–1.013). Mean generation time was 40 years and the mean estimated lifespan was 6.86 years with a high variance of 181.8 years for individuals starting in the seedling stage, consistent with observations of very long-lived individuals in the field. Elasticity values were highest for the transitions representing stasis and lowest for reproduction. For dataset length, 15 years of data yielded lambda estimates that were within 1% of the long-term estimate, but 20 years of data were needed to yield lambdas with confidence intervals that consistently overlap one. Although mast seeding is generally defined using the inter-annual variation in seed production per unit area, stochastic lambdas were not correlated with this measure of reproduction but instead correlated with per capita dormant seed production and per capita recruit production. Mean survival rate was also positively correlated with stochastic lambda estimates, despite the necessary increase in mortality in years with high reproduction. Our results indicated that the demography of *F. speciosa* is similar to that of other long-lived monocarps without mast seeding, that long datasets may be needed to capture the variation in demographic rates even for stable populations, and that life history stages with low elasticity values can still be very important to population growth.

Key words: alpine habitat; data availability; Gentianaceae; long-lived monocarpic perennial; long-term study; mast flowering; population dynamics; population matrix modeling.

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INTRODUCTION

The reproductive strategies of monocarpy (flowering once followed by death) and mast seeding (synchronous, episodic flowering) in long-lived plants have long been of interest to evolutionary biologists (Cole 1954, Charnov and

Schaffer 1973, Janzen 1976, Silvertown 1980). Specifically, researchers have focused on how delayed reproduction within an individual and reproductive synchrony among individuals would optimize individual fitness despite risking higher mortality and missing opportunities for reproduction. For monocarpic perennials, de-

layed reproduction is compensated by having a single, larger reproductive effort that leads to higher reproductive success than separate reproductive episodes in polycarpic plants (Young 1990, Young and Augspurger 1991, Klinkhamer et al. 1997). Monocarpy is often associated with a minimum size threshold for flowering, which may be a physical threshold related to the accumulation of sufficient resources for reproduction (Tissue and Nobel 1990, Metcalf et al. 2003, Kuss et al. 2008). In unproductive habitats, reproduction may be further delayed because it takes longer to reach this threshold (Metcalf et al. 2003). The advantages of mast seeding for perennial plants are due to economies of scale, meaning that a large, synchronized population-level reproductive event increases individual success via pollinator attraction, predator satiation, or other mechanisms (Norton and Kelly 1988, Kelly 1994, Kelly and Sork 2002, Visser et al. 2011). Plants in less productive habitats may be more likely to exhibit mast seeding, because they could be unable to reproduce at a sufficiently large scale to attract pollinators or satiate predators every year (Kelly and Sork 2002).

Thus both monocarpy and mast seeding in long-lived perennials are related to maximizing reproductive effort in a resource-limited environment to ensure reproductive success. Although these strategies may have evolved independently in species that exhibit both traits (Young and Augspurger 1991), several studies suggest they may be driven by the same evolutionary mechanisms. For woody bamboos and the tropical canopy tree *Tachigali(a) versicolor*, high seed production at the individual- and population-levels helps to satiate predators and allow some offspring to escape predation (Janzen 1976, Foster 1977, Klinkhamer et al. 1997, Forget et al. 1999). For the canopy tree *Cerberiopsis candelabra*, flowering at a larger size and in synchrony with more individuals would create a larger canopy gap after tree death to enhance seedling establishment (Read et al. 2006, 2008). In the herbaceous perennial *Isoglossa woodii*, the evolution of mast seeding and monocarpy may have been driven by both predator satiation and seedling facilitation (Tsvuura et al. 2011).

Regardless of the mechanism, if these reproductive strategies optimize individual fitness, then they should also be sufficient to prevent

population decline. Indeed, demographic studies of monocarpic perennials generally find population growth rates to be stable, with the finite rate of increase, or lambda (λ), close to one (Poorter et al. 2005, Kuss et al. 2008, Ramula 2008). In a study of the monocarpic thistle, *Cirsium palustre*, when the proportion of reproductive individuals with delayed flowering was simulated to increase from the observed 10% to 50%, the population growth rate was not significantly affected because the higher reproductive output by the larger plants compensated for later flowering (Ramula 2008). Another study simulated polycarpy in the monocarpic tree *Tachigali vasquezii* using demographic data from other tree species in the community (Poorter et al. 2005). In this case mortality after flowering of the monocarpic individuals was compensated by faster growth and a shorter generation time compared to the polycarpic population (49 compared to 79 years) so that population growth rates did not differ (Poorter et al. 2005). These results suggest that long-lived monocarps exhibit the stable population growth that is characteristic of plants with long life spans in general (García et al. 2008). Long-lived herbaceous plants also tend to have low elasticity values for the transitions representing reproduction and high elasticity values for survival transitions, indicating a greater importance of survival than fecundity to the rate of population growth (García et al. 2008), and this has also been observed in long-lived monocarpic perennials (Poorter et al. 2005, Kuss et al. 2008).

In contrast, the population dynamics of mast seeding species are not well-studied and may not follow the same pattern. Whereas populations of long-lived herbs tend to have lower among-year variation in fecundity than short-lived plants (García et al. 2008), mast seeding species are defined by having high inter-annual variation in seed production (Silvertown 1980, Kelly 1994, Herrera et al. 1998). A recent study examined the demographic costs of mast seeding in the polycarpic dipterocarp tree *Shorea leprosula*, and found that infrequent flowering increases the rate of population growth when there is high seed predation (Visser et al. 2011). The demographic pattern of this population is similar to that of other long-lived plants, with the observed rate of population growth slightly above one and high

elasticity values for stasis and survival (Visser et al. 2011). However, the effects of mast seeding on demography may be different for herbaceous species because trees and herbs tend to have different population dynamics (Silvertown et al. 1993), and also for monocarpic species because they exhibit not only high temporal variation in reproduction but also in adult mortality (death occurs after flowering).

When vital rates such as fecundity and survival vary greatly between years, long datasets are needed to obtain an accurate description of the long-term population dynamics and the relative importance of various life history stages (Horvitz and Schemske 1995, Benton and Grant 1996). Although data availability is a well-recognized limitation to demographic studies, few studies have examined how many years of data would be sufficient (Fieberg and Ellner 2001, Doak et al. 2005), especially for long-lived species (but see Fox et al. 2006). Encouragingly, a demographic model based on a three-year dataset accurately predicted the observed population growth, generation time, and net reproductive rate for the long-lived monocarp *Campanula thyrsooides* (Kuss et al. 2008). Using a 35-year dataset, which is among the longest datasets used in published meta-analyses of mast seeding species (Kelly and Sork 2002, LaMontagne and Boutin 2009), we describe the population dynamics of the long-lived, mast seeding monocarp *Frasera speciosa* (monument plant, green gentian; Gentianaceae). We also examine whether short datasets can accurately estimate demographic parameters for this population, by subdividing the dataset into shorter subsets and using these to construct population models.

Frasera speciosa occurs in the Colorado Rocky Mountains and other western states in the USA, and its pollination (Beattie et al. 1973), life history (Taylor and Inouye 1985), and temporal pattern of flowering (Inouye and Taylor 1980) have been described previously. We have monitored an alpine population of *F. speciosa* in the Elk Mountains of southwestern Colorado annually from 1973 to the present. Using this dataset, we build stage-based population matrix models and perform elasticity analyses to examine: (1) whether its population dynamics are similar to monocarpic perennials without mast seeding, (2) how many years of data are needed to estimate

consistently the asymptotic population growth rate and elasticity values, and (3) the importance of mast seeding and fecundity to population growth. Because dataset length has also been shown to affect whether deterministic or environmentally stochastic demographic models yield more accurate results (Doak et al. 2005), we apply both types of models to our data. The deterministic model uses mean transition probabilities that are averaged over the entire dataset, whereas the stochastic model incorporates the variance and correlation of the transition probabilities across years (Tuljapurkar 1990, Caswell 2001, Boyce et al. 2006).

MATERIALS AND METHODS

Study site and study species

Beginning in 1973, ramets of *Frasera speciosa* were individually tagged in a study plot (now 18 × 29 m) in a south-facing alpine bowl at an elevation of 3,740 m near Cumberland Pass (Gunnison County), Colorado (38°41.632, 106°28.549). The plants grow in a matrix of tundra plants, at about the upper elevational limit of the distribution of the species in the Rocky Mountains. An aluminum tag with an embossed number was placed next to each plant using a 16d nail; in cases where plants were too close to tag individually, distances and directions from a nail to each adjacent plant were recorded and used to identify individuals.

An annual census in July was made of all *Frasera* plants in the plot; newly discovered plants were tagged, the number of leaves in the basal rosette of tagged plants was counted, length and width of leaves of some rosettes were recorded, and the height and number of flowers were recorded for flowering plants. To facilitate relocation of tagged plants, the plot was marked into 1m squares with a grid of string, and plant locations were recorded to the nearest quarter square meter. Typically over 98% of plants were refound each year (pocket gophers sometimes bury them, and there is some tag damage from grazing cattle, elk, or deer). A careful search was made for seedlings around each of the dead flower stalks for the next few years following flowering. When untagged 2-leaf plants are found near old stalks, indicating that they were missed for their first few years (during which

their two leaves may only be a few mm long), we recorded them as offspring of the nearest old stalk. This method slightly underestimates recruitment, because while seeds are generally deposited within a meter or two of the parent stalk, strong winds may move a few seeds significant distances through the air or across the snowpack, and recruitment from those seeds would be missed. Mean height of the 109 undamaged inflorescences in the plot measured from 1975–2010 is 47.4 cm (range 23–76 cm).

The basal rosettes of *Frasera* plants typically have a fixed number of leaves each growing season, with on average 86% of each year's rosettes having exactly 2, 4, 6, 9, 12, 16, 20, 25, 30, 36, 42, or 49 leaves at Cumberland Pass. Plants at lower altitudes sometimes have 56, 64, 72, 80, or 90 leaves (Taylor and Inouye 1985). Leaves expanded in a particular season are preformed 2–3 years prior to appearing above ground, as are inflorescences (Inouye 1986). Thus, plants may be flowering in response to an environmental cue that occurred years previously.

Matrix construction

This study used the *F. speciosa* data from 1974 to 2010 (2009–2010 data were used only for seed dormancy data, see below), during which period the average number of individuals with two leaves or more observed per year was 823, ranging from 228 to 1687 individuals (see Appendix A for population sizes across the study period). The demography of this population was described by: $\mathbf{n}_{t+1} = \mathbf{A}_t \mathbf{n}_t$, where the matrix \mathbf{A}_t projects the population vector (\mathbf{n}) from the current year (t) to the next year ($t+1$). The stage-classified model distinguished stages based on the observed pattern of rosette sizes described above. We placed plants into the following leaf number categories: 2 (1–2 leaves), 4 (3–4 leaves), 6 (5–6 leaves), 9 (7–10 leaves), 12 (11–14 leaves), 16 (15–17 leaves), 20 (18–22 leaves), 25 (23–27 leaves), 30 (28–32 leaves), 36 (33–38 leaves), 42 (39–45 leaves), or 49 (46–64 leaves, but only 7 plants had more than 54 leaves). Plants can remain in the same category, regress one or more categories, or advance one or more categories between years. We have observed plants flowering after reaching the 12-leaf stage, but the most common size before flowering was 25–36 leaves.

We built matrices following the methods of Horvitz and Schemske (1995). We calculated transition rates (a_{ji}) as the percentage of the individuals starting at stage i that were in stage j the next year.

Reproduction.—We constructed the matrix models based on post-breeding censuses so that the measure of reproductive output is the mean number of seedlings (we refer to these as 'recruits') or dormant seeds per individual. We have observed that seeds germinate up to three years after flowering (new seedlings appearing around the base of an old flower stalk), and therefore two dormant seed categories were included (first year dormant and second year dormant). Because no experimental data were available, we estimated seed dormancy and germination rates from observational data. We assumed a constant germination rate for a cohort of seeds, which we calculated by dividing the total number of recruits from a flowering event by the total number of seeds produced (see Appendix B for details on how seed production was calculated). We calculated the fecundity values for production of recruits (f_{3i}) as the total number of recruits observed the next year produced by all individuals starting in stage i , divided by the total number of individuals starting in stage i . We calculated the fecundity values for production of first year dormant seeds (f_{1i}) as the total number of recruits observed in the second and third years produced by all individuals starting in stage i , divided by the germination rate (this provides an estimated number of seeds that go dormant in order to yield the observed number of seedlings), and then divided by the total number of individuals starting in stage i . We calculated the transition from first-year dormant seeds to second-year dormant seeds in next year's matrix (f_{21}) as the total number of recruits observed in the third year divided by the germination rate, then divided by total number of dormant seeds produced this year. We used the same germination rate as the transition probability from first-year dormant seeds to recruits in next year's matrix (f_{31}), and as the transition probability from second-year dormant to recruits in the third year's matrix after flowering (f_{32}). We used data from 2009–2010 to determine the seed dormancy rates for the final matrix representing transitions

from 2007 to 2008.

Deterministic models

For each starting year from 1974 to 2007, we divided the number of individuals that made a particular transition from stage i to stage j in the next year by the number of individuals that started at stage i , to obtain the transition probability (a_{ji}). To obtain datasets of different lengths, we retained these transition probabilities for different lengths of consecutive years (from 2 to 35 years). For each subset of data, we constructed one matrix from the average transition probabilities across those years. In other words, for the dataset length of 35 years, this produced one matrix with the average of the 34 annual probabilities for each transition. For the dataset length of 34 years, this produced two matrices, one averaging over the years 1974–2007 and the other over the years 1975–2008. There were 34 matrices for the dataset length of 2 years (these 2-year matrices are archived online in the Digital Repository at the University of Maryland, DRUM and can be found at <http://hdl.handle.net/1903/10050>).

To describe population dynamics, we calculated the annual population growth rate (λ) for each matrix produced following procedures from Caswell (2001, section 5.3.4). We calculated the stage-specific generation time, or mean age at reproduction, because our population has two types of offspring (dormant seeds and recruits). This yielded a vector of generation times for individuals born in stage j , which is calculated as $\mu^{(j)} = \text{diag}(\mathbf{FNe}_j)^{-1} \mathbf{FNUn}_j$, where \mathbf{U} is the transient matrix, \mathbf{F} is the fertility matrix, \mathbf{N} is the fundamental matrix, and \mathbf{e} is a vector of ones (Caswell 2009, section 4.5). We calculated the stage-specific lifespan, or the expected time to death for an individual starting at each stage, and the variance in lifespan due to individual stochasticity, following the methods in Caswell (2009, sections 4.2–4.3). For μ and lifespan estimates, we present only the values calculated for an individual starting life as a dormant seed and as a recruit.

We also estimated elasticity values, which quantify the proportional changes in the population growth rate resulting from small changes in each of the matrix elements, or each deterministic matrix following procedures from Caswell

(2001, sections 9.1, 9.2). Because the elasticity values for a matrix sum to one, these values can be used to compare the relative importance of each transition to changes in the population growth rate (de Kroon et al. 1986, Caswell 2001). To facilitate the comparison of elasticity values between biologically meaningful categories, we summed elasticities in two ways. First, we calculated summed elasticities for these transition categories: reproduction (contributing to seeds and recruits in the following year), growth (growing to any larger stage), shrinkage (reverting to any smaller stage), and stasis (staying in the same stage). Second, we calculated summed elasticities for the fates of these reproductive categories: seeds, recruits, non-reproductive rosettes (between stages 2–12 leaves), and reproductive rosettes (greater than 12 leaves).

Stochastic models

To build environmentally stochastic models, we constructed one matrix for every two consecutive years of data, resulting in the same set of 34 matrices yielded from the deterministic analysis with dataset length of two years. We estimated the stochastic rates of population growth (λ_s), and their 95% confidence intervals, for different lengths of this dataset (from 3 to 35 years, because at least 2 matrices are required) by simulation (Caswell 2001, section 14.3.6.1). For this, we used R code modified from the *popbio* package version 2.2 (Stubben and Milligan 2007), with 10,000 iterations and equal probability of drawing each matrix within a sub-dataset. The elasticity of λ_s to changes in both the mean and standard deviation of the matrix elements (E^S ; Tuljapurkar et al. 2003) were calculated following the methods of Haridas et al. (2009) using the full dataset, and were compared to the deterministic elasticities (E^{det}).

To examine the dataset length needed to yield consistent estimates of population growth rates, we calculated the deviation of individual lambda estimates from the population growth rate based on our full 35-year dataset (called the “long-term estimate”) for the deterministic and stochastic models. For this accuracy parameter, we took the absolute difference between each lambda estimate for the sub-datasets and the long-term estimate and divided it by the long-term estimate, and then averaged across the values for

each dataset length. For the stochastic models, we also examined the length of the dataset that would consistently yield confidence intervals overlapping one, to match that of the long-term estimate (see *Results*). To determine the dataset length needed to yield consistent rankings of life history stages by their contribution to population growth, we ranked the elasticities summed by transition and by reproductive categories from highest to lowest for each subset of data. Each ranking was compared with the ranking produced by the full 35-year dataset. For each dataset length, the proportion of sub-datasets that yielded matching rankings was calculated. Because deterministic and stochastic elasticity values were very similar (see *Results*), we used only the deterministic elasticities for this analysis.

To examine specifically the effects of mast years on population dynamics, we compared stochastic population growth rates from mast years and non-mast years. Mast years may be best defined as years in which reproduction is more than one standard deviate above the long-term mean (LaMontagne and Boutin 2009). Although this metric is often calculated using reproductive output per unit area (e.g., seeds per m^2), fecundity rates in a matrix model are measured as per capita seed production and/or per capita recruit production. Therefore we defined mast years using three measures of reproduction: years in which the seed density (total seed production divided by plot area, 522 m^2), per capita recruit production, or per capita dormant seed production was one standard deviate above the 35-year average (the total number of inflorescences was also examined, but the pattern was identical to that for seed density). Per capita reproduction measures were averaged across all reproductive stages (12 leaves or larger), so that it represents the mean expected reproduction per adult per year. We compared λ_s from three-year subsets of data containing a mast year defined in these ways, with estimates from subsets that do not contain mast years using a two-sample *t*-test. We also analyzed the relationship between λ_s from three-year subsets of data and the mean values of the reproductive measures across the same three years, as well as the mean survival of all individuals with two leaves or more, using a linear regression.

All described analyses were performed in R

version 2.12.1 (R Development Core Team 2010).

RESULTS

Population dynamics

Based on the full 35-year dataset, the deterministic estimate of the population growth rate (λ) is 0.969 and the environmentally stochastic growth rate (λ_s) is 0.967 (95% CI = 0.923–1.013; Fig. 1). The mean matrix, consisting of the average transition rates across all 35 years, is presented in Appendix C. The stage-specific generation time, μ , is 40.98 and 39.97 years for individuals starting as a dormant seed and as a recruit, respectively. The stage-specific lifespan estimate for a seed is 1.02 years with a variance of 0.31 years, whereas the lifespan estimate for a recruit is 6.86 years with a variance of 181.81 years.

We summed and ranked the elasticity values by transition and reproductive categories to examine which type of vital rates (stasis, growth, shrinkage, or reproduction of seeds and recruits), and which type of life history stages (non-reproductive rosettes, reproductive rosettes, recruits, and seeds), contributes the most to the rate of population growth. Based on the transition categories, the summed deterministic elasticity values (E^{det}) are highest for the transitions representing stasis (0.598), followed by those for growth (0.257), shrinkage (0.129), and reproduction (0.016). Summed by reproductive categories, elasticity values are highest for the fates of non-reproductive rosettes (0.611), followed by those for reproductive rosettes (0.384), recruits (0.016), and seeds (0.004). We obtain the same rankings from summing stochastic elasticities (E^S): 0.601, 0.252, 0.133, and 0.014 for stasis, growth, shrinkage, and reproduction; and 0.604, 0.378, 0.015, and 0.004 for non-reproductive, reproductive, recruit, and seed stages, respectively.

Effects of dataset length

To examine how many years of data are needed to obtain consistent estimates, we calculated population growth rates and elasticity values from subsets of data of different lengths. For population growth, 15 years or more of data would yield lambda estimates that are within 1% of the long-term estimate based on the full dataset, for both deterministic and environmen-

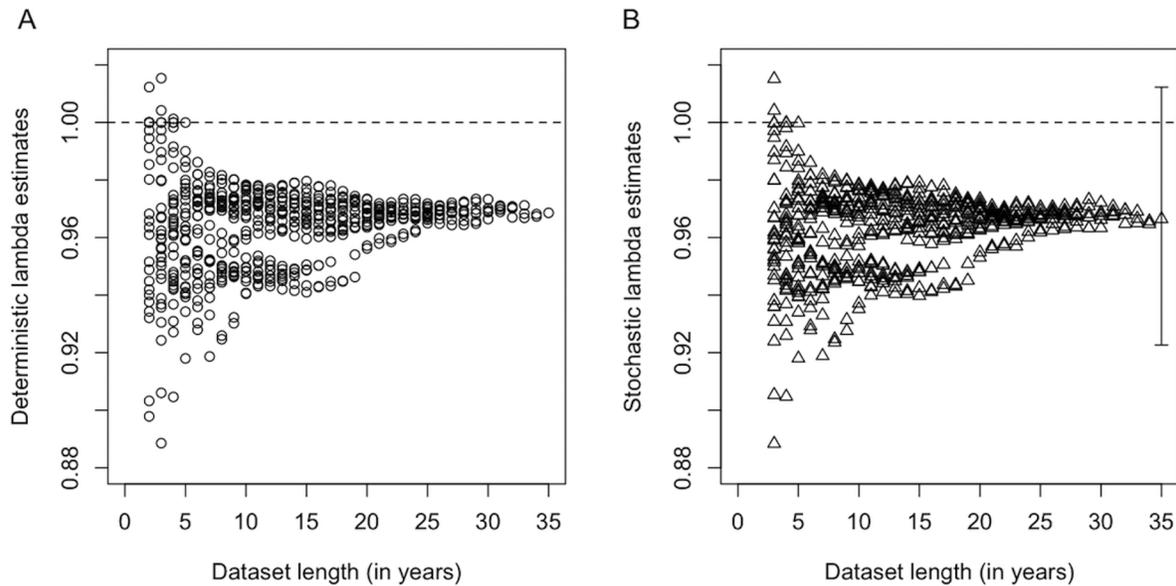


Fig. 1. Deterministic (A, as circles) and environmentally stochastic (B, as triangles) population growth rate estimates calculated from all possible subsets of consecutive years of data, from 2-year subsets to the full 35-year dataset. The 95% confidence interval of the stochastic lambda estimates is shown for the estimate based on the full dataset only.

tally stochastic models (Fig. 2A). However, the data length requirement differs between deterministic and stochastic models when we qualitatively compare lambda estimates to the long-term estimate. The deterministic model always yields lambda estimates less than one when the dataset is six years or longer (Fig. 1A), whereas the stochastic model requires datasets that are 20 years or longer to yield confidence intervals that consistently overlap one (Fig. 3). For elasticity values, nine and ten years of data would yield consistently the same rankings as the full dataset when deterministic elasticities are summed by transition and reproductive categories, respectively (Fig. 2B). The transition category of stasis has the highest elasticity values for all dataset lengths. Nine or more years of data would consistently rank growth transitions higher than shrinkage transitions (not shown). When elasticities are summed by reproductive categories, seeds have the lowest elasticities for all dataset lengths, and the fates of non-reproductive rosettes are consistently ranked as more important than reproductive rosettes when 10 or more years of data are used (not shown).

Effects of mast years

All three measures of reproduction exhibit the high variability that is characteristic of mast seeding species, with CVs of 1.33, 2.89, and 2.22 for total seed production per unit area, per capita recruit production, and per capita dormant seed production, respectively. However, the different measures of reproduction identified different years as mast years, which are defined as those in which reproduction is at least one standard deviate above the mean (Fig. 4). When measured as seed density, 1981, 1985, 1992, and 2003 are mast years in which seed production is greater than 189 seeds/m² (Fig. 4A). Only three years qualify when measured as the per capita number of dormant seeds produced, and two years qualify as mast years when reproduction is measured as the per capita number of recruits produced, with thresholds at 384 dormant seeds and 1.62 recruits per adult per year (Fig. 4B, C). Only 1992 qualifies as a mast year under all three measures of reproduction. Examining the effects of mast years on population growth, three-year subsets of data that include the two mast years defined by per capita recruit production yield higher lambda estimates ($\lambda_s = 0.99 \pm 0.005$) than

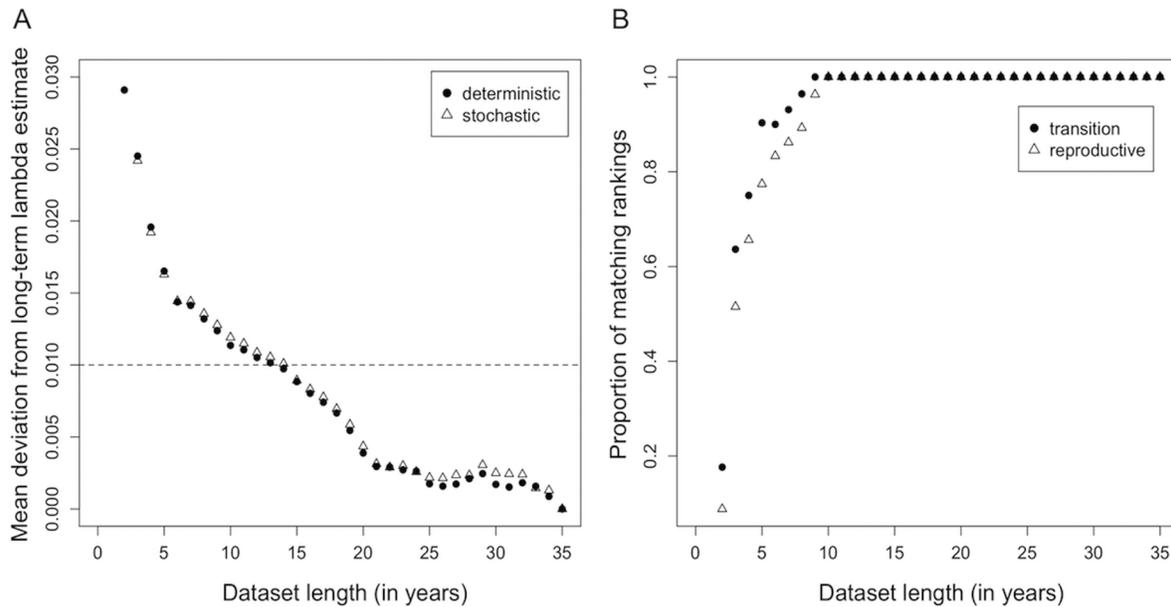


Fig. 2. The effects of dataset length on the consistency of population growth estimates and elasticity values. (A) Mean deviation of the environmentally stochastic (open triangles) and the deterministic (solid circles) population growth estimates from the long-term estimates, shown by the length of the dataset used. (B) Proportion of datasets that yielded a ranking of the elasticities, summed by transition categories (filled circles) or reproductive categories (open triangles), that matched the ranking based on the full dataset.

subsets that do not include those mast years ($\lambda_s = 0.96 \pm 0.029$; $t_{30} = 5.78$, $p < 0.001$). There is no difference in the stochastic lambdas between mast years and non-mast years for the other two measures of reproduction. Further, three-year lambdas are significantly related to the mean per capita recruit production and mean per capita dormant seed production across the same three years (coefficient = 0.015 and 0.00006, $t = 3.66$ and 3.25 , $p = 0.001$ and 0.003 , respectively), but not to the mean seed density (coefficient = 0.00007, $t = 1.07$, $p = 0.29$). Stochastic lambdas are also significantly related to the mean survival of all individuals with two leaves or more (coefficient = 0.534, $t = 5.38$, $p < 0.001$).

DISCUSSION

Population dynamics

Our population of *Frasera speciosa* has a near-stable rate of population growth, with long-term deterministic and environmentally stochastic estimates of lambda close to one and the confidence interval of the stochastic lambda overlapping one. Stable population growth is

characteristic of other monocarpic perennials that do not exhibit mast seeding (Poorter et al. 2005, Kuss et al. 2008, Ramula 2008; but see Jongejans et al. 2006), and of long-lived herbaceous plants in general (García et al. 2008). The deterministic and stochastic models yield similar lambda estimates, which indicates that vital rates do not exhibit high temporal variation (Benton and Grant 1996, Doak et al. 2005). Thus, the fluctuations in reproductive rates due to mast seeding are not sufficient to reduce stochastic lambda estimates significantly. This is likely because of the low importance of the reproductive transitions as indicated by their elasticity values. Stochastic elasticity values were also similar to deterministic elasticities calculated from the average matrix, again indicating low temporal variation in the important vital rates (Caswell 2001, Haridas and Tuljapurkar 2005, Haridas et al. 2009).

Generation time for our population is estimated at ~ 40 years, which is slightly higher than an earlier estimate of 36 years for the mean age at flowering in this population (Inouye and Taylor 1980). Therefore, our 35-year dataset may still be

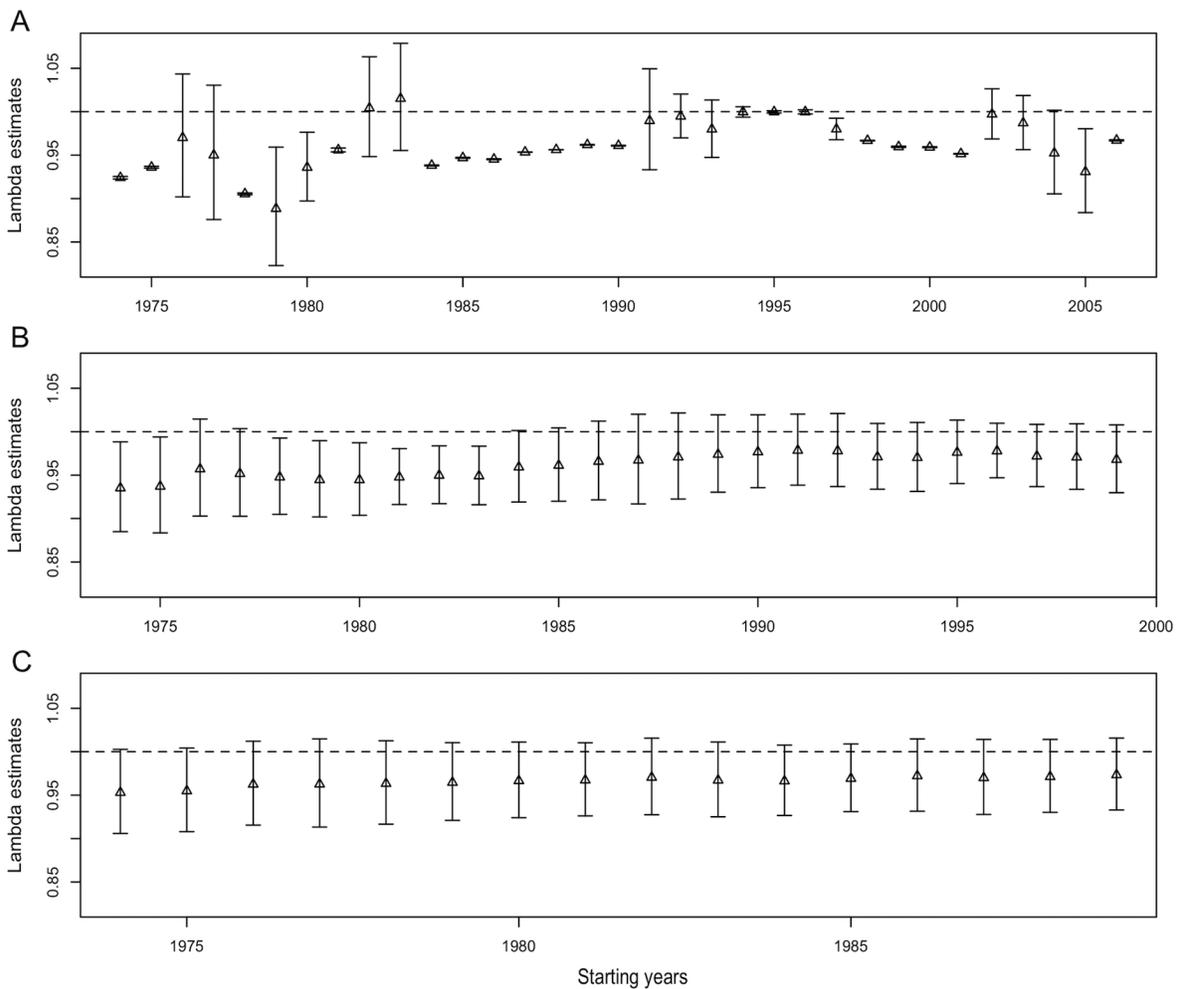


Fig. 3. Stochastic population growth rate estimates (with 95% confidence intervals) calculated from subsets of data that are three years in length (A), ten years in length (B), and 20 years in length (C), shown by the starting year of the dataset.

a few years short of capturing one generation of the *E. speciosa* population. The mean expected lifespan for individuals starting at the seedling stage is 6.86 years, which is lower than our generation time estimate because of the high mortality of juveniles. The very high variance in this lifespan estimate also indicates that some individuals of this population may live for many decades. These results are consistent with observations in the field, where 498 individuals have been observed for at least 20 years, and 31 plants that have been observed for the entire length of the study, from 1974–2010, have not yet flowered.

Elasticity analysis indicates that stasis and survival contribute the most to changes in long-term population growth, and reproduction contributes the least, which is similar to other long-lived monocarps (Poorter et al. 2005, Kuss et al. 2008). While it is possible that the relatively large number of stages that we chose for our models inflated the elasticity values for stasis (Enright et al. 1995), we believe that the relative importance of stasis, growth, shrinkage, and reproduction to population growth is likely robust. When grouped into reproductive categories, elasticities are highest for the fates of non-reproductive rosettes, which was also found in a short-lived

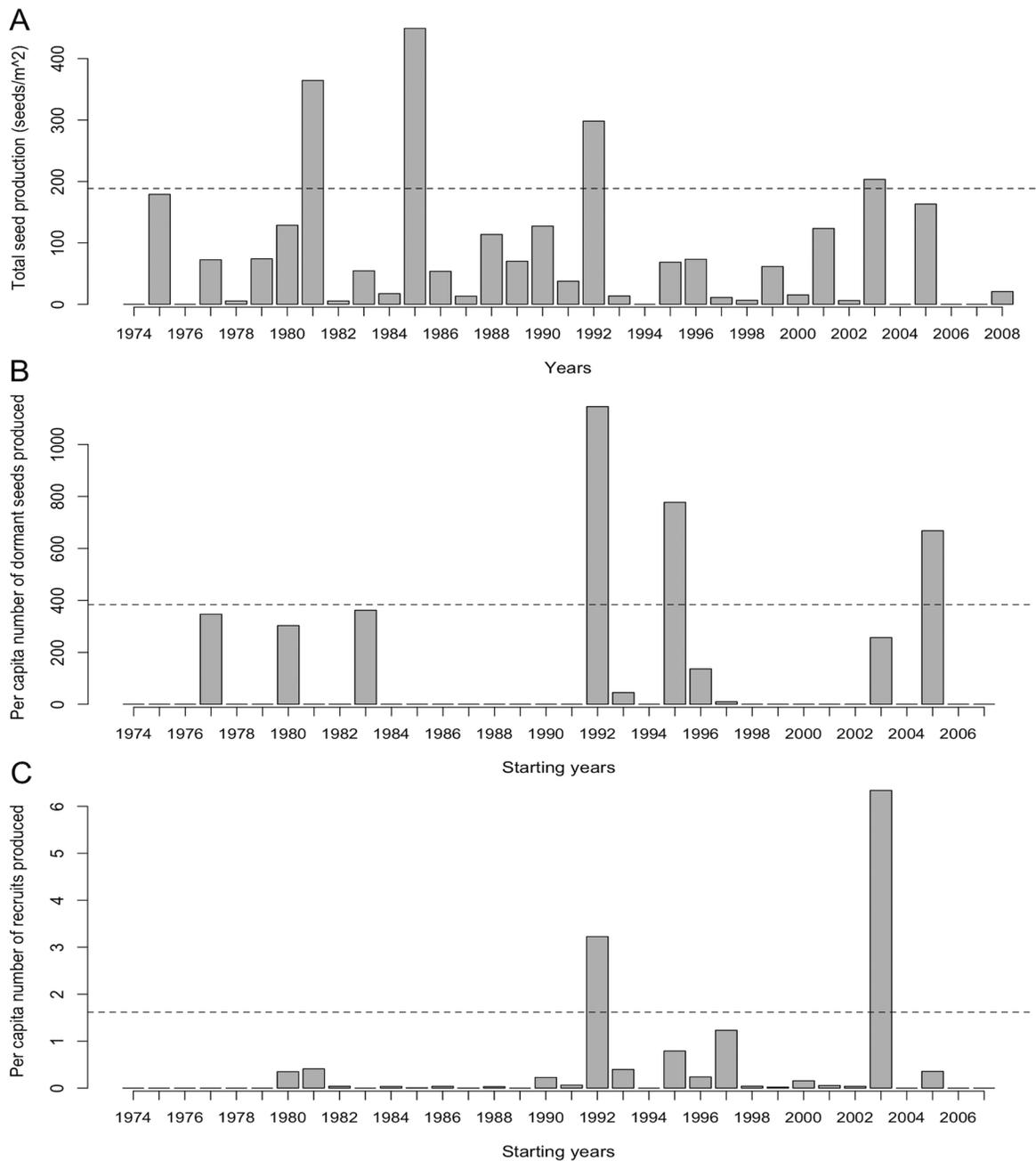


Fig. 4. Three measures of reproduction over the study period: seed density (number of seeds per m²; A), per capita dormant seed production (B), and per capita recruit production (C). Dashed line indicates one standard deviate above the mean across all years, and years in which reproduction exceeded this threshold are mast years.

monocarpic perennial (Lesica and Shelly 1995). However, these patterns in elasticity values may not be solely related to the monocarpic perennial life history. Some perennial monocarps have high elasticity values for reproduction (Rees and Rose

2002, Jongejans et al. 2006), and long-lived, polycarpic alpine plants in the Colorado Rocky Mountains exhibit similarly low values of elasticities for reproduction (~ 0.01 ; Forbis and Doak 2004). Further, populations with stable or declin-

ing growth rates tend to have low elasticity values for reproduction and high elasticities for survival (de Kroon et al. 2000). Thus, these patterns may be attributed to the suite of traits exhibited by *Frasera speciosa*, including monocarpy, longevity, and stable population growth, and mast seeding does not appear to alter the pattern significantly.

Effects of dataset length

Using our *Frasera* dataset, both the deterministic and environmentally stochastic models require 15 years of data to converge to within 1% of the long-term population growth estimates. Deviation from the long-term estimates is similar between the two models for all dataset lengths, because lambda estimates are similar between the models even for short datasets. Both models yield lambda estimates that are consistently less than one when more than six years of data are used, but 20 years of data are needed to consistently yield stochastic lambda confidence intervals that overlap one. Thus, we did find that the simpler (deterministic) model can yield consistent results with fewer years of data than the stochastic model, as previously shown in a simulation study (Doak et al. 2005), but in our case the result may be misleading as it suggests a slightly declining population rather than a stable one. For the stochastic model, the data length requirement of twenty years is also the length at which a dataset starting in 1974 would include the flowering event in 1992 (i.e., 1992–1993 is the last matrix, making a 20-year dataset from 1974 to 1993), the first year in our study in which there were both high per capita recruit production and per capita dormant seed production (Fig. 4). Thus, the inclusion of at least one mast year as defined by the per capita reproduction was needed to estimate consistent lambda confidence intervals, and that may be as short as three years or as long as 20 years. For elasticity values, datasets of 10 years or longer would consistently rank the transition and reproductive categories by their relative importance to population growth. This suggests that a decade of data is needed to sufficiently capture the range of transition probabilities observed for our population, so that the mean probabilities (from which elasticities are calculated) are similar to those from the full dataset.

A previous study found that a three-year dataset provided accurate demographic parameter estimates for a long-lived monocarp (Kuss et al. 2008), but our results indicate that longer datasets are required for our population. Although some of the stochastic lambda estimates from three-year datasets have confidence intervals that overlap one, both the lambda estimates and the size of the confidence intervals varied greatly among years compared to those from 10-year or 20-year datasets (Fig. 3). The difference between our study and theirs may be due to the different modeling approaches: the flexibility of their individual-based integral projection model may be better able to describe population dynamics using smaller datasets than our stage-based matrix population model. However, a more important difference is likely to be the episodic flowering in our population, which requires a longer study period to capture the long-term reproductive rates and population dynamics. Although it did not focus on demographic rates, a study of the mast-seeding grass *Chionochloa pallens* showed that inclusion of at least 4 mast seeding events and about 12 years of data are needed to model accurately the energy reserves for that species (Rees et al. 2002).

Other studies have examined dataset length requirements for demographic studies using a broad range of study organisms and modeling methods, and estimating various demographic parameters. With 35 years of data on the survival rates of a Florida scrub-jay population, one study found that at least 10 years of data were needed to estimate the parameters representing how family and age affect survival (Fox et al. 2006). A simulation study found that stochastic population growth rates remained imprecise even with 11 years of data (Fieberg and Ellner 2001). A third study showed that 10 years of data yielded a narrow confidence interval for population growth estimates in a desert tortoise population, while the confidence interval for a winter annual plant with highly varying demographic rates continued to narrow with increasing dataset length beyond 20 years, with no clear dataset length limit (Doak et al. 2005). Examining extinction probabilities as a function of a population's intrinsic rate of increase (r), one study showed that populations with high r values required 15 years of data to estimate extinction

probability with 80% accuracy, whereas populations with low r values required more than 50 years of data to achieve the same accuracy (Fagan et al. 1999). Another study estimating extinction risk found that 10 years of data were not sufficient, and recommended that at least 20 years of data would be needed to produce precise extinction estimates (Holmes et al. 2007). With the variety of parameters estimated and organisms studied, it is somewhat surprising that these studies and ours tend to agree that at least 10–15, and preferably 20, years of data would provide reliable demographic parameter estimates in most cases. Further, dataset requirements can be large even for short-lived species such as the winter annual, and species with stable population growth such as *F. speciosa*. These results suggest that more than a decade of observation is needed to capture the variability in vital rates, the correlations among vital rates, and/or the range of environmental conditions that affect those vital rates for different populations. Unfortunately, demographic datasets of this length are extremely rare. Only 3% of studies modeling the extinction risk of plant populations obtained more than 10 years of data (Menges 2000), and the mean dataset length of studies on long-lived, mast seeding species was 11.1 years (Kelly and Sork 2002).

Effects of mast years

Mast years have generally been defined as years with high total seed production per unit area (Kelly 1994, Kelly and Sork 2002, LaMontagne and Boutin 2009), and this is a relevant measure when examining the evolutionary advantages of mast seeding, such as predator satiation. However, we find that per capita measures of reproduction are more correlated with population growth rates than seed density. Additionally, few measures of mast seeding take into account the success of the produced seeds, whereas the probability of germination greatly affects how seed production contributes to the maintenance of the population. Our two measures of per capita reproduction essentially reflect the success of the produced seeds because they are calculated from the observed number of recruits produced by our population. The per capita recruit production is based on the number of recruits observed the following year, and the

per capita dormant seed production is based on the number of recruits observed in the subsequent second and third years. These measures of reproduction also indicate a stronger tendency toward mast seeding in our population (i.e., they have higher CVs) than seed density, perhaps because some of the years with high seed density, which may have been sufficient to satiate predators, had environmental conditions that were not favorable for seed germination or viability. Both per capita measures of reproduction are significantly correlated to stochastic lambda estimates, indicating that reproduction is important to the growth rate of this population, despite low elasticity values. Those elasticities reflect the low probability that a seed or recruit will survive to reproduce compared to that for larger stages (Forbis and Doak 2004; the reproductive value, or the expected number of recruits produced by an individual in a given stage, is 0.004 for a seed and 3.13 for a recruit, compared to 17.7 for 30-leaf and 20.2 for 36-leaf stages), rather than the actual importance of reproduction. Therefore, as previously suggested, elasticity values must be combined with biological knowledge when determining the relative importance of various life history stages to population dynamics (de Kroon et al. 2000).

In addition to reproduction, stochastic lambda estimates are significantly correlated with mean survival rates. This correlation is positive despite the necessary increase in mortality in years with high reproduction, meaning that the survival of the remaining, non-flowering plants is also important to the maintenance of the *Frasera* population. In fact, the highest lambda estimates are calculated from the datasets that included 1983 (Fig. 3), a year in which there was high mean survival (0.94) and moderate per capita dormant seed production (362). On the other hand, including 2005 reduced the lambda values and confidence intervals because it had the lowest mean survival rate (0.68), despite having high per capita dormant seed production that year (668).

Because previous studies of mast seeding, long-lived monocarps have focused on the evolutionary advantages of the reproductive strategy rather than demography, there are few studies with which we can compare our results and discuss the generality of these findings. The

mast seeding, polycarpic tree *Shorea leprosula* has a similar pattern of elasticity values but a higher rate of population growth, with the 95% confidence interval for stochastic population growth above one (Visser et al. 2011). This is likely due to their polycarpic life history (multiple reproductive episodes per individual and lower mortality rates for adults), as well as higher mean survival rates for seedlings (~68% compared to ~34% for *F. speciosa*, Appendix C). *Isoglossa woodii* is an herbaceous monocarpic perennial with mast seeding, but its flowering strategy is more highly synchronized than that of *F. speciosa*. For example, >90% of the plants in one population of *I. woodii* flowered in the same year (Tsvuura et al. 2011), whereas only about 10% of our population would flower in a given year. Because of the extremely high mortality associated with reproduction, the correlation between survival rates and population growth for *I. woodii* may not be positive as we find for our population.

Further, there are differences in the flowering pattern between this and other populations of *F. speciosa* that may affect population dynamics. Our Cumberland Pass population is in an alpine area, at the top of the altitudinal range of the species, whereas most of the populations in Colorado and Utah are sub-alpine. One potential difference between populations is that plants at lower altitudes may have faster individual growth rates and may flower at younger ages than those in the alpine populations. For example, in a lower elevation experimental plot (9,500 feet) started from seed in 1982, the first plant flowered in 2003, which is only half of the 40-year generation time estimated for the alpine population (D. W. Inouye, *personal observation*). Another difference is that years with flowering in the alpine population are more frequent, but with a smaller proportion of adults flowering, than at lower elevations (Taylor and Inouye 1985). In fact, the correlation between numbers of flowering plants in the alpine plot and a montane study site is both weak ($r^2 = 0.021$) and non-significant ($p = 0.43$). Because of their larger size at flowering, lower-altitude plants likely also have higher per capita reproductive rates. These factors would lead to even greater temporal variation in reproduction at the lower altitude populations, which may affect their population growth rates. However, the contribution of

reproduction to population growth should be similarly low at the lower altitude populations because of their longevity and monocarpic life history, and thus any effects would likely be small. Overall, we expect that the same pattern of stable population growth and high relative importance of stasis and survival would be found across all populations of *F. speciosa*.

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APPENDIX A

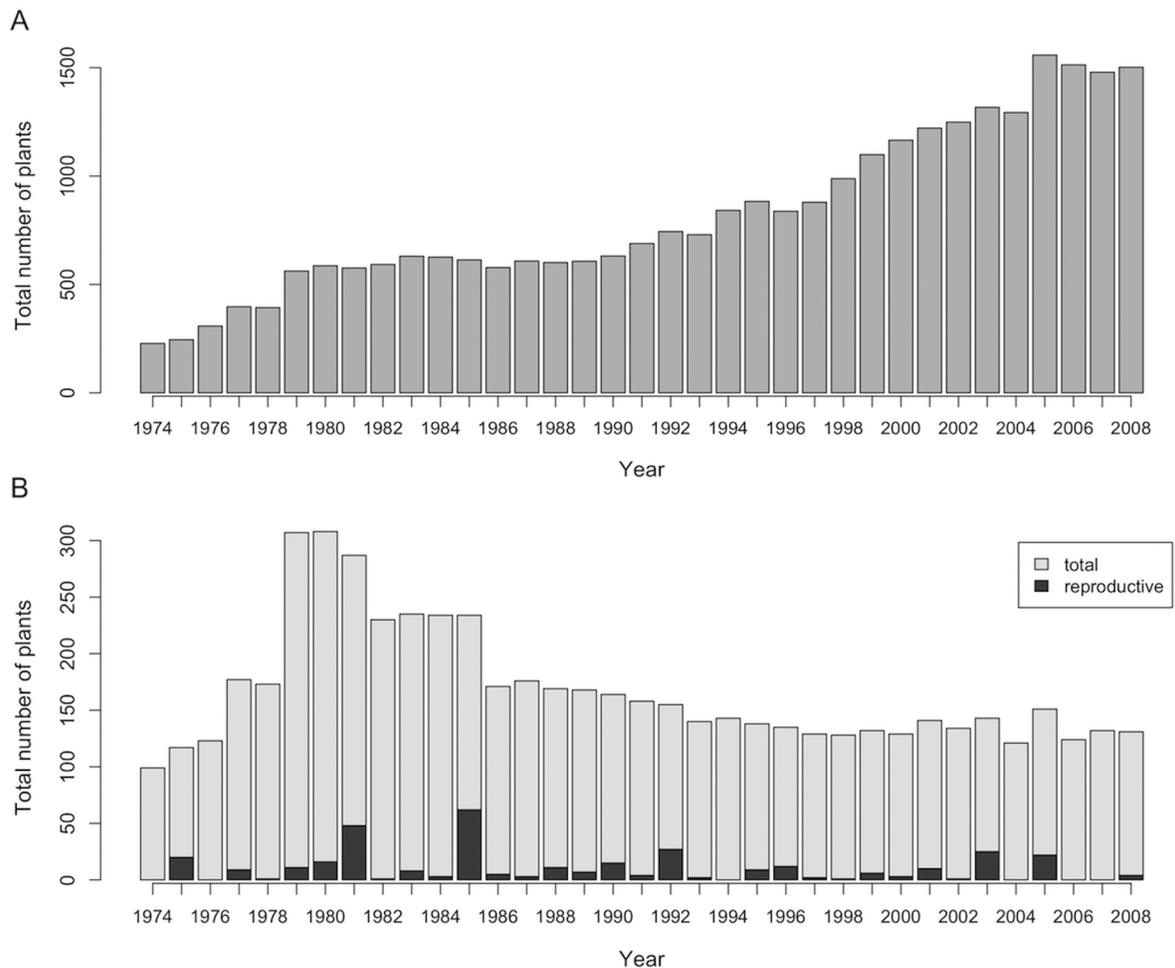


Fig. A1. The number of *Frasera speciosa* individuals with two leaves or more observed in 1974–2008 (A), which were the focal years of the study, and the number of plants in reproductive stages (≥ 12 leaves) over the same period (B). The subset of plants in potentially reproductive stages that actually flowered is shown in darker portions of the bars in (B). The increasing number of plants shown in (A) reflects in part an increased effort over the years at finding very small plants in the plot and an increase in the size of the plot from 504 to 522 m² in the 1980s.

APPENDIX B

Table B1. The average number of seeds produced per flowering plant in each stage in 1992. These data were used as the estimated seed production per plant when neither the seed number nor flower number was recorded for a reproductive individual (209 plants).

Stage	$N_{\text{seed}}/\text{individual}$
12	1121
16	1121
20	651
25	2898
30	4035
36	6007
42	11431
49	8677

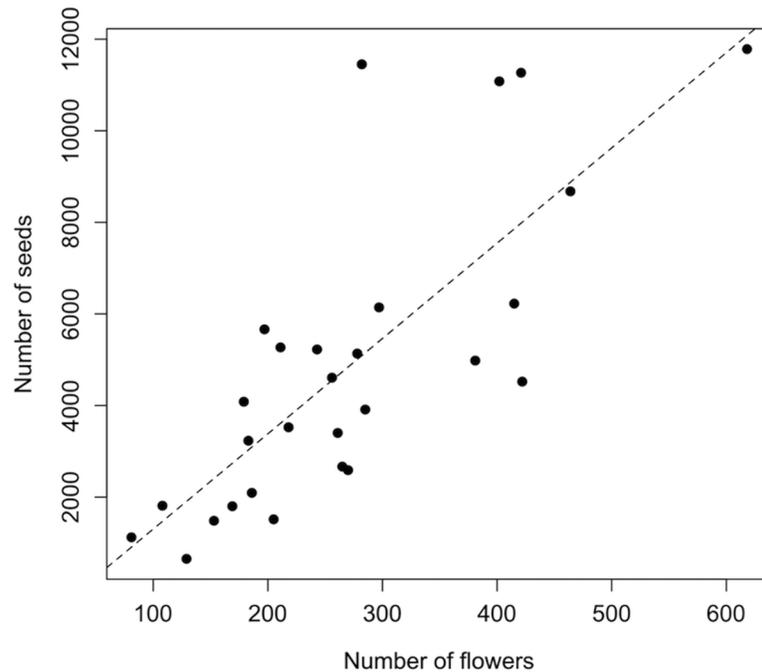


Fig. B1. Relationship between the number of flowers and number of seeds for all reproductive individuals in 1992 ($N_{\text{seed}} = 20.81 \times N_{\text{flr}} - 778.8$, $r^2 = 0.602$, $N = 28$). This regression equation was used to estimate the number of seeds produced for individuals that reproduced but only had flower numbers recorded (135 plants).

APPENDIX C

Table C1. Mean matrix from the 35-year dataset: transitions from the first nine stages (dormant seeds 1, dormant seeds 2, recruits, and 2-leaves to 16-leaves).

Stage	dorm1	dorm2	recruit	2	4	6	9	12	16
dorm1	0	0	0	0	0	0	0	1.65	6.84
dorm2	0.011	0	0	0	0	0	0	0	0
recruit	0.001	0.001	0	0	0	0	0	0.004	0.007
2	0	0	0.289	0.581	0.184	0.008	0.001	0.001	0.001
4	0	0	0.054	0.282	0.679	0.132	0.007	0.001	0
6	0	0	0.000	0.006	0.094	0.551	0.172	0.002	0.002
9	0	0	0.000	0.001	0.012	0.281	0.643	0.151	0.009
12	0	0	0	0	0.000	0.004	0.149	0.549	0.157
16	0	0	0	0	0	0.001	0.013	0.238	0.534
20	0	0	0	0	0	0.000	0.002	0.039	0.234
25	0	0	0	0	0	0	0.000	0.002	0.028
30	0	0	0	0	0	0	0	0.001	0.001
36	0	0	0	0	0	0	0	0	0.001
42	0	0	0	0	0	0	0	0.000	0
49	0	0	0	0	0	0	0	0	0

Table C2. Mean matrix from the 35-year dataset: transitions from the remaining six stages (20-leaves to 49-leaves).

Stage	20	25	30	36	42	49
dorm1	19.41	51.55	93.32	246.96	235.24	298.68
dorm2	0	0	0	0	0	0
recruit	0.08	0.15	0.37	1.09	0.53	1.09
2	0	0	0	0	0	0
4	0	0	0	0	0	0
6	0	0	0	0	0	0
9	0	0	0	0	0	0
12	0.013	0.001	0.001	0	0	0
16	0.111	0.005	0	0	0	0
20	0.563	0.130	0.010	0.002	0	0
25	0.217	0.525	0.161	0.016	0.006	0
30	0.034	0.206	0.528	0.123	0.026	0.007
36	0.001	0.031	0.155	0.546	0.151	0.044
42	0	0.009	0.015	0.082	0.500	0.115
49	0	0	0.004	0.024	0.095	0.355