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SPATIOTEMPORAL VARIATION IN DEMOGRAPHIC TRANSITIONS OF A TROPICAL UNDERSTORY HERB: PROJECTION MATRIX ANALYSIS[1]

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Abstract. Our goal was to elucidate the population dynamics of the perennial understory herb *Calathea ovandensis* in a rain forest in southern Mexico using matrix projection model analysis. We emphasize the magnitude and consequences of spatiotemporal variation in (1) basic demographic parameters (growth, survival, and reproduction) (2) asymptotic demographic properties of a given environment (the asymptotic population growth rate and the associated stable-stage distribution and reproductive values) and (3) demographic sensitivities associated with a given environment (sensitivity and elasticity).

We obtained 6 yr (1982–1987) of empirical data from four study plots (differing in substrate, light, and density) from which we used the first 5 yr (1982–1986) to construct 16 plot-year and 1 pooled population projection matrices. This stage-structured population was characterized by a long-lived seed bank, temporally variable seedling recruitment (10-fold variability among years), high mortality of seedlings (>90%), very low mortality of reproductives (usually <10%), fertility that increased markedly with plant size, and the ability of large plants to shrink rather than die under adversity. Within these broad outlines, the magnitudes of transitions representing demographic fates exhibited considerable variation through space and time, some parameters varying much more than others (CV from 22 to 400%). Growth and reproduction were positively correlated across environments. The least variable parameters were seed dormancy and stasis of small reproductives.

Observed stage distributions were reasonably close to the stable stage distributions (mean = 86.1% similar). In most plot-years, the stable-stage distribution was dominated by seeds, followed by seedlings, and then small reproductives and the reproductive values increased with size class.

Population growth rates, given by the dominant eigenvalue of the matrices, ranged from 0.73 to 1.25. Analysis of the mean dynamics gave $\lambda = 0.97$ (using a variety of analytical approaches) and our analysis of the overall pooled dynamics gave a $\lambda = 0.99$, indicating that the habitat at the study site favored the persistence of *Calathea ovandensis*. An el Niño event coincided with the year of the highest population growth rate.

Survival, growth, and reproduction varied significantly through space and time, and different plot-years were beneficial to different stages. Most interestingly, stage-specific sensitivity parameters (sensitivity and elasticity) also varied through space and time. Spatiotemporal variability of sensitivity structure has important implications. Determination of stages most "critical" to population dynamics will depend upon knowledge of this variation. Population growth rate was significantly positively correlated with elasticity of seed production, seed germination, and seedling growth. These results indicate that the opportunity for selection on plant characters affecting particular life history stages varies through space and time even if the effect on the single-stage transition probability does not vary. Selection on characters affecting juvenile stages may be stronger in populations of higher growth rates.

Key words: demography; elasticity; el Niño; perennial plant; population growth rate; reproductive value; sensitivity; stable-stage distribution; stage-specific transitions.

INTRODUCTION

Understanding the factors that determine population dynamics remains a central issue in ecology, both pure and applied. Population dynamics have consequences for the conservation of rare species (Menges 1986, 1990, Crouse et al. 1987, Fiedler 1987, Lande 1988, Boyce 1992, Schemske et al. 1994), the control of invasive species, the analysis of life history variation (Mertz 1971, Caswell and Werner 1978, Charlesworth 1980, Meagher 1982, Caswell 1982*a*, *b*, *c*, *d*, 1983, Caswell et al. 1984, Calvo and Horvitz 1990, Kalisz

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and McPeek 1992, Calvo 1993) and the evolutionary ecology of stage-specific selective factors (Charlesworth 1980), including species interactions (Horvitz and Schemske 1986*b*, Martinez and Alvarez-Bullya 1986, Hanzawa et al. 1988, Horvitz 1991).

Recently, there has been much interest in how spatiotemporal variation in demography affects plant populations; long-term predictions about population fates and insights about the evolution of life history may depend upon understanding how structured populations respond to such variation (e.g., Kalisz and McPeek 1993). Although the theory is developing rapidly (Tuljapurkar and Orzack 1980, Orzack and Tuljapurkar 1989, Tuljapurkar 1989, 1990), there are still relatively few complete sets of empirical data for all life history stages for multiple years (more than two) and multiple sites (more than two) for any species (Piñero et al. 1984, Huenneke and Marks 1987, Moloney 1988, van Groenendael and Slim 1988, Menges 1990). Thus, little is known about the magnitude of variation and correlation of demographic parameters. Also, there is considerable interest in sensitivity analysis for identifying critical or key life history stages that have the greatest impact on population dynamics (e.g., Crouse et al. 1987, Caswell 1989*a*, *b*, Aberg 1992*a*, *b*, Kalisz and McPeek 1992), but the extent to which the sensitivity structure itself varies has received little attention (van Groenendael and Slim 1988, Kalisz and McPeek 1992). Such variation would mean that a critical life history event in one environment might not be critical for the same species in a somewhat different environment.

Our goal was to elucidate the population dynamics of the long-lived neotropical forest herb *Calathea ovandensis* with emphasis on the magnitude and consequences of spatiotemporal variation in demographic parameters. Our results and conclusions are based on empirical measurements of demographic parameters, including seed production and seed fates, obtained at four sites over 5 yr within a secondary neotropical forest. We asked three questions: (1) What is the demographic pattern for this species and how does its demography differ through space and time? By demography, we mean the probabilities of survival, growth, and regression as well as the amount of reproduction for each life history stage. (2) How does the overall demographic character of the environment change through space and time? By overall demographic character of the environment, we mean the asymptotic population growth rate, stable stage distribution, and stage-specific reproductive values associated with a particular schedule of demographic transitions (Leslie 1945, Lefkovitch 1965, Caswell 1978). (3) How does the demographic sensitivity of the population change through space and time? By demographic sensitivity of the population, we mean both (a) the fitness response to perturbations of different life history transitions (analytical sensitivities) (sensu Caswell 1989*b*) and (b) the proportional contributions of different life history stages to the population growth rate (analytical elasticities) (sensu Caswell 1989*b*).

Because demographic analysis is becoming an important, perhaps essential, tool for conservation biologists and resource managers (Schemske et al. 1994), we also sought to make the protocols of demographic analysis accessible to a wide range of ecologists, not just to other demographers. To that end we present, in some detail, the many steps between the collection of empirical data and the results of the demographic analysis. We emphasize the biological interpretation of the mathematical properties of the projection matrix models used to represent population dynamics.

Study Site and Species

Our research was conducted in a secondary forest at Laguna Encantada, near San Andrés Tuxtla, Veracruz, Mexico. This patch of tropical evergreen rain forest is located at the periphery of a volcanic crater, covering an area of ≈ 0.75 km^2. The terrain is rugged, with narrow canyons and extensive areas of sharp, volcanic rock jutting from the forest floor. Pastures dominate the surrounding vegetation, laced with numerous "living fences" of *Bursera simaruba*, but patches of forest are common along the rivers and steep slopes.

Calathea ovandensis Matuda (Marantaceae) is an understory, perennial monocot of lowland secondary forests and successional patches within primary forests. The rainfall is seasonal (80% of the annual rainfall received from June to October) with a mean annual precipitation of 1996 mm and a peak (489 mm) in September (Soto 1976). Growth and reproduction of the study plant are seasonal. Plants shed all aboveground parts during the dry season, persisting as dormant underground rhizomes with energy stored in small round ($\approx 2.5 \times 1$ cm) starchy tubers. They reinitiate leaf production when rainfall increases in June. Shoots, each comprised of a whorl of leaves, are produced sequentially throughout the growing season from the underground rhizome. Individual plants (genets, sensu Harper 1977) are readily distinguished, as there is no vegetative propagation. Each shoot produces 4–6 leaves and, if reproductive, a single inflorescence. Individual reproductive plants produce one to several shoots and inflorescences.

Flowering peaks in August and fruit maturation and dehiscence coincide with peak rainfall in September (Horvitz 1980). Plant reproductive success is influenced positively by interactions with pollinators (Horvitz and Schemske 1984, 1988*a*, *b*, Schemske and Horvitz 1984, 1988) and ants at extrafloral nectaries (Horvitz and Schemske 1984, 1988*a*, *b*) and negatively by a specialist herbivore of reproductive tissues (Horvitz and Schemske 1984, 1988*a*, *b*), but the magnitude of these effects varies through space and time (Schemske and Horvitz 1988, Horvitz and Schemske 1990). When mature, the three-seeded fruits dehisce completely and the seeds, bearing oily white arils, are dis-

persed principally by ponerine ants (Horvitz 1980, 1981, Horvitz and Beattie 1980, Horvitz and Schemske 1986*a*, *b*, *c*). Ant transport of seeds is beneficial to seedling recruitment (Horvitz and Schemske 1994). Seeds do not germinate until the subsequent rainy season (Horvitz 1980). Peak seedling emergence occurs in July, about a month after the onset of the rainy season. Some seeds remain dormant beyond this period resulting in a long-lived (>1 yr) soil seed bank (Horvitz and Schemske 1994). Recruitment of seedlings from the seed bank is spatiotemporally heterogeneous, influenced by variation in the dispersers and enhanced in treefall gaps and in el Niño years (Horvitz and Schemske 1994).

Methods

Plots

To study spatiotemporal variation in demography and in plant–animal interactions, we set up four long-term plots, located from 80 to 250 m apart, within the Laguna Encantada forest in 1982. The plots were chosen to span the natural environmental variation, so that taken together they are representative of the range of habitats occupied by *C. ovandensis* in this forest, encompassing much variability in both biotic (Schemske and Horvitz 1988, Horvitz and Schemske 1990) and abiotic factors. The plots differed initially in substrate, density, and population stage structure. All the plots were in intermediately shady environments (not new gap and not entirely closed canopy), with plot 1 initially being the shadiest and plot 2 the least shady. The substrate at plot 1 was composed of large (up to ≈35 cm in height) volcanic rocks with intermittent patches of soil, while the substrate at the other plots was more uniform, with fewer large rocks and more gravel. Plot 1 had the lowest density and appeared to be composed of few seedlings and relatively more adults. We constructed a large plot for the extremely low density area and roughly equal-sized plots for the other three study areas. Upon detailed mapping of the plots, we found that the exact dimensions of the study plots, plot 1, 2, 3, and 4, respectively, were 8 × 8.4, 5.1 × 6, 5.2 × 5, and 5 × 5.2 m. The respective densities were 1.1, 8.4, 6.4 and 4.6 plants/m^2.

In August–September 1982, we marked all the individuals within each plot with a numbered tag attached to a small stake inserted into the ground at the base of each plant, for a total of 617 plants. Each individual was subsequently mapped to the nearest centimetre, using an x, y coordinate system for each plot. We censused these plots again in October 1982 and during the rainy seasons (July–October) of the next 5 yr (1983, 1984, 1985, 1986, and 1987) to obtain estimates of survival, growth, and reproduction in these populations, marking and mapping new seedlings as they appeared. Each year we conducted one complete census in early August, when vegetative development was nearly complete for a season, measuring the size and counting the reproduction of all individuals (all years), followed by censuses every 2 wk of reproduction through October (all years except 1987).

Plot 3 was vandalized in 1984, following the census, and we marked and censused an area adjacent to the plot as a replacement. For analyses of transitions to 1984 and earlier, the original plot was used; for analyses of transitions to 1985 and later, the replacement plot was used. For analyses of the patterns of variation overall, data sets including each of these were considered.

Although the calendar date of the 1987 census was comparable to the others, we later discovered that the phenological status of the population at that census was retarded, perhaps due to the extended dry season associated with that year's el Niño. Vegetative shoots were not fully developed and neither plant size estimates nor reproductive status of plants were comparable to those of other years. We therefore dropped the 1987 data from our analyses of demographic transitions. The count of new seedlings in 1987 was correct and we included these data in analyses of recruitment.

Plant sizes

Within a shoot, leaves are produced one at a time from a central meristem, as in other monocots. Leaf size increases sequentially both within a shoot and between shoots on a single plant. To estimate the sizes (total leaf area) of plants nondestructively, we measured the lengths of all the leaves of each individual. A study of leaf tracings had shown that leaf length was an excellent predictor of leaf area (the regression equation was: $\sqrt{\text{area}} = 0.62(\text{length}) - 0.55$; $N = 207$ leaves, spanning the range of natural leaf sizes with replication; $P < 0.0001$, $R^2 = 0.99$). Using this relationship, we calculated the total leaf area of each plant each year.

Stage classification

We devised a stage classification to characterize the population structure at the annual August census. Stages have been used rather than (or in combination with) ages for many organisms (e.g., Goodman 1969, Werner and Caswell 1977, Law 1983, Hughes 1984, Hughes and Connell 1987, Law and Edley 1990) to predict demographic behavior (Caswell 1989*b*). There have been basically two kinds of approaches to the definition of stage classes, numerical (Vandermeer 1978, Moloney 1986), based on maximizing within-class sample size while minimizing the errors in estimates of growth or survival, and biological (e.g., Lefkovitch 1965, Werner 1975, Usher 1976), based on size, sex, developmental, or other biological states. We chose a biological approach, combining reproductive criteria with size criteria (as in Menges 1990), because reproduction varied much more with size than did survival.

TABLE 1. Stage class criteria for eight stages. Abbreviations used throughout the paper are in boldface, set off by parentheses. (1) seeds—included both newly produced seeds as well as old seeds in the soil seed bank; (2) seedlings—newly germinated plants or plants of similar size; (3) juveniles—postestablishment (sensu Harper 1977) plants, usually at least in their 2nd yr, although a few seedlings attained this size the 1st yr; (4) "pre"reproductives—plants that were big enough to reproduce, but did not reproduce; (5) small reproductives; (6) medium-sized reproductives; (7) large reproductives; and (8) extra-large reproductives.

Stage	Characteristics		
	Leaf area (cm^2)	Leaf length (cm)	Reproductive?
I. Seed (**sd**)			
II. Vegetative: Nonreproductive			
A. Seedling (**sdlg**)	<1450	≤7	no
B. Larger than seedling			
1. Juvenile (**juv**)	<1450	>7 and <18	no
2. "Pre"reproductive (**pre**)	<1450	≥18	no
III. Vegetative: Reproductive			
A. Small (**sm**)	<1450	≥18	yes
B. Medium (**med**)	≥1450 and <2050	...	yes
C. Large (**lrg**)	≥2050 and <2950	...	yes
D. Extra-large (**xlrg**)	≥2950	...	yes

To develop classification criteria, we analyzed our data on (a) the size changes between years and (b) the relationship between size and reproduction. To classify the population consistently across plots and years, we utilized these developmental, size, and reproductive criteria to define eight stage classes (Table 1).

Two indices of plant size, total leaf area and length of the largest leaf, were useful for classifying plants into these classes (Table 1). The length of the largest leaf was a better classifier than leaf area for nonreproductives, while total leaf area was a better predictor of inflorescence production than the length of the largest leaf. Leaf length, which increased markedly between shoots for small plants, was especially diagnostic early in development. These plants mostly produced a single shoot per growing season. Larger plants produced multiple shoots in a single growing season and these shoots did not differ as much in leaf length, which approached its maximum. Also, leaf area accounted for 76, 88, 76, 73, 77, and 77% of the variance among all plants in inflorescence production in 1982, 1983, 1984 (includes initial plot), 1984 (includes replacement plot), 1985 and 1986, respectively. (Length of the largest leaf accounted for only ≈ 53, 58, 59, 59, 52, and 49%, respectively as above, of the variance in inflorescence production [PROC REG, SAS 1988].) For both size variables, we examined frequency distributions for discontinuities or multimodalities to find the cutoff points and the number of classes.

Reproduction

To estimate reproduction, we censused each inflorescence every 2 wk, counting the buds, flowers, immature fruits, and mature fruits present. We used more detailed censuses of fruit production from a sample of plants at/or near each plot to estimate seed production per inflorescence in 1984, 1985, and 1986 in each plot. In these censuses, individual fruits were marked with colored threads when initiated and fruits were censused every 3 d until mature (Horvitz and Schemske 1988*a*, 1990, Schemske and Horvitz 1988, 1989). To estimate seed production per inflorescence in other years, for each plot, we calculated the mean seed production per inflorescence over the 3 yr for which we had detailed data.

To quantify the effects of stage class on reproduction and to examine the spatiotemporal variation in inflorescence production, we analyzed the effects of plot, year, and stage, and their interactions, on inflorescence production with a three-way ANOVA (PROC GLM, SAS 1988). We also determined the mean number of inflorescences produced by a given stage in each plot and year, counting each plant-plot-year observation once. Plot, year, and stage were fixed effects in the ANOVA. The data on seed production per inflorescence for each plot and year were combined with data on the number of inflorescences per plant of a given stage class for each plot and year to estimate seed production per plant for each stage class for each plot and year (Appendix 1).

Seed fates

One can estimate seed fate probabilities only by experimental manipulation, since these fates may cryptically vary with seed age and with spatiotemporal heterogeneity in the habitat. Subsequent to fruit maturation each seed may germinate, remain dormant in the soil, or die. The seeds produced in a given time and place may contribute to several seedling cohorts, while a seedling cohort that emerges at a given time and place may well be composed of many different cohorts of seeds. Digging up soil samples to estimate the dormant seed pool is a destructive sampling method that cannot be carried out inside a plot that is under long-term demographic study. To fully quantify seed fate probabilities would require a massive experimental study in which marked seeds are dispersed by natural vectors into removable soil samples every year and

these are censused for germination and dormancy in subsequent years. There have been few large experimental studies on seed banks (Kalisz 1991), and none that also include natural dispersal.

We investigated seed fates of *C. ovandensis* in several field experiments, none of which was completely ideal, but each of which provided data helpful for quantitatively estimating seed fates in our demography plots. These experiments showed that seedling recruitment from the long-lived seed bank was significantly enhanced by ant transport of seeds, by treefall gaps, and by el Niño years (Horvitz and Schemske 1994). To estimate seed germination, seed dormancy, and seed survival in each year and plot of the present demography study, we combined data from the seed dispersal experiment and data on germination in el Niño years vs. non el Niño years (Horvitz and Schemske 1994) with data on spatial variation in seedling emergence in our demographic study plots (Appendix 2).

Fates of vegetative plants

The demographic fates of vegetative (nonseed) individuals were readily determined, as each plant retained its map location and identity tag between seasons. Plants were classified into stage classes each year and transition probabilities among stages and survival probabilities were determined by cross classifying, stage_t by stage_{t+1}, including "DEAD" as an extra class in the $t + 1$ year (using PROC FREQ, with a TABLES statement, SAS 1988).

To determine whether annual cohorts of seedlings showed variation in survivorship, survivorship curves were drawn for the 1982, 1983, 1984, 1985, and 1986 cohorts. These were statistically compared (Pyke and Thompson 1986, Hutchings et al. 1991). Plot 3, the vandalized plot, was excluded from analysis of 1982 and 1983 cohorts as the fates of seedlings in this plot could not be followed as long as those from other plots. To determine how plants changed stage as they aged, relative frequency distributions of stages were determined for each age class and compared across ages.

To determine whether transition probabilities varied through space and time, we performed log-linear analyses (as in Moloney 1988, Caswell 1989*b*, Harvell et al. 1990), considering state (stage_t) (seven stages, as above), year (four transition sequences: 1982–1983, 1983–1984, 1984–1985, and 1985–1986), plot (four plots, as above) and fate (stage_{t+1}) (seven stage classes + dead), as the categorical variables. In one set of analyses, we examined each state individually, considering, for that state, the effects of year and plot on fate. These analyses were based on a three-way contingency table for each state defined by the factors plot, *P*, year, *Y*, and fate, *F*. In a second analysis, we asked whether the entire state-by-fate transition probability table showed variability by plot and year; this analysis was based on the four-way contingency table defined by the factors state, *S*, plot, *P*, year, *Y*, and fate, *F*.

A log-linear model to explain the counts, m_{ijk}, in the three-way table may include various single-factor terms (*P*, *Y*, *F*) and interaction terms (*PY*, *YF*, *PF*, and *PYF*). We follow the conventional notation of hierarchical models to refer to different models (Caswell 1989*b*). For example, the fully saturated model (*PYF*), (Analysis 5, Appendix 4), is:

$$\log m_{ijk} = u + u_{P(i)} + u_{Y(j)} + u_{F(k)} + u_{PY(ij)} + u_{PF(ik)} + u_{YF(jk)} + u_{PYF(ijk)}. \quad (1)$$

This model states that one needs to know the values of each single-factor effect, all the two-way effects, and the three-way effect to predict the values in the three-way contingency table. Reduced models have similar equations, except that some terms are assumed not to be important for predicting cell frequencies; thus, these terms are set to zero. Of particular relevance to our analysis, the distribution of plants into plot and year categories, *P* and *Y*, was preset; thus, the model *PY,F* is the appropriate null model. This model asserts that fate, *F*, is independent of plot and year, given the preset plot × year interaction.

A distinct set of expected cell frequencies generated by each model is compared to the observed cell frequencies by means of the log-likelihood chi-square (G^2). A model "fits" the data, if the cell frequencies it predicts are close to the observed cell frequencies, that is, if the value of G^2 is small. The significance of an effect is always measured relative to another model that does not contain that effect; thus, there is more than one way to measure the significance of a particular effect (Fienberg 1980). For example, one can test the significance of the plot × fate interaction, *PF*, by comparing the G^2's of the models *PY,F* and *PY,PF* (marginal test) or by comparing the G^2's of the models *PY,YF* and *PY,YF,PF* (conditional test). Both of these comparisons involve addition of the *PF* term to a model without it. The marginal test asks whether simply adding plot (Analysis 2, Appendix 4) improves the fit, while the conditional test asks whether adding plot after year (Analysis 4, Appendix 4) improves the fit. More than one null model may "fit" a given data set (Bishop et al. 1975).

Similar theoretical development applies to the four-way contingency table, except that the saturated model has more terms and there are many more ways that a model may depart from complete independence. The null hypothesis for the four-way table was that fate, *F*, of an individual was independent of plot, *P*, and year, *Y*, conditional on its initial state, *S*. For this model the *YF* and the *PF* terms are set to zero (and any higher order terms with these interactions in them), resulting in *SPY,SF* (Caswell 1989*b*). To calculate the G^2 for this model and the related models, (1) *SPY,SYF*, (2) *SPY,SPF*, and (3) *SPY,SYF,SPF*, one can sum (over all stages) the stage-specific G^2's. These were calculated during analyses of the three-way contingency tables

for each stage (Caswell 1989*b*). To investigate how plot affected the state by fate transition structure within a year, and how year affected it for a given plot, we also analyzed the three-way tables for each year and for each plot in a similar fashion, the null hypotheses being *SP,SF* and *SY,SF*, respectively.

The log-likelihood statistics for each model were obtained with the CATMOD procedure, LOGLIN option (SAS 1988), adding 0.5 to all cells to avoid estimation problems for cells with zero observations (Fingleton 1984).

The Markovian nature of demographic fates

An important issue in population dynamics is whether the fate of an individual at time t depends only upon its state at time $t - 1$ or if it is additionally influenced by historical effects, its state at time $t - 2$, for example (Caswell 1989*b*). Independence from historical effects is termed "Markovian." The projection matrix model of population dynamics assumes that fates are "Markovian." We performed log-linear analyses to investigate this issue, three for each plot, asking whether the fates of plants in 1984, 1985, and 1986 were conditionally dependent upon their states in 1982, 1983, and 1984, respectively (except at plot 3, which was vandalized and then replaced in 1984, in which we were only able to perform two such analyses, that on fates in 1984 and that on fates in 1986). Three-way contingency tables, with the following effects were constructed: F_t, S_{t-1}, and S_{t-2}, respectively, the fate at time t, stage at time $t - 1$ and stage at time $t - 2$. Only plants with known states at all three censuses, t, $t - 1$, and $t - 2$, were used. Plants that died in the final year of each sequence were included, but plants that died in the 2nd yr could not be considered; neither could new recruits that appeared in the 2nd or 3rd yr. The null model we proposed for each test was $S_{t-2}S_{t-1}$, $S_{t-1}F_t$, asserting that fates in each year are dependent only upon states in the previous year. Against this null model, we tested the effects of adding the interaction $S_{t-2}F_t$, proposing the model with all the two-way interactions: $S_{t-2}S_{t-1}$, $S_{t-1}F_t$, $S_{t-2}F_t$. This test asks: given the effects of stage in any year on stage the next year, is any additional information obtained on the fate at time t by considering the stage at time $t - 2$?

Constructing the matrix model of population dynamics

Plot-year matrices.—To assemble a projection matrix model of population dynamics based on demographic probabilities, we used the estimates of reproduction, the estimates of seed fates, and the transition probabilities of the vegetative individuals for each transition year and plot, as described above, to develop 16 matrices, four years × four plots. The transition years were 1982–1983, 1983–1984, 1984–1985, and 1985–1986.

Summary matrix.—To summarize the pattern of dynamics over all years and plots, we also developed a single matrix by weighting the observed transitions by their frequency in the entire data set by pooling all the observations of particular transition events over the whole data set. Similarly, we determined the average reproduction of individuals of different stage classes from all years and plots, weighting the observations by the numbers of individuals in each stage class in each plot and year.

The pooled matrix is a better summary of the demography than a matrix of averages calculated over the 16 matrices because of the way rarely observed transitions affect the values. If the averages are taken, transition events that happen to many individuals in one year and plot are given equal weighting to transition events that happen to few individuals in one year and plot. Only for seed fates did we use the means of the 16 matrices, as these were proportional estimates only; they could not be assigned to particular weightings because the number of seeds in the soil seed bank in each year and plot was not known. We present the "mean" matrix (based on averages of the 16 matrices) in Appendix 5, although the summary matrix from the pooled observations was used in our analyses of the overall population dynamics.

Model.—The projection matrix model for all our analyses was:

$$\boldsymbol{n}(t + 1) = \mathbf{A} \times \boldsymbol{n}(t), \qquad (2)$$

where $\boldsymbol{n}(t)$ is a vector of all the individuals in the population at time t, classified by stage, $\boldsymbol{n}(t + 1)$ is the vector for the population at the next time interval, and $\mathbf{A}$ is the matrix that shows how individuals in each stage class at one time may become or contribute to each stage class by one time unit later, in which the columns refer to stage at time t and the rows refer to stage at time $t + 1$. For our population, $\mathbf{A}$ is an 8×8 matrix (Table 2), in which each entry, a_{ij}, refers to the contribution of individuals in the jth class at time t to the ith class one time unit later. Nonzero entries in Table 2 are for transitions observed at least once during the study.

The top left-hand corner, a_{11}, represents seed dormancy. The other entries in the top row represent the contribution of plants (counted at time t) to seeds (counted at time $t + 1$). The transition from seed to seedling (a complex transition involving dispersal, survival of seeds in the soil, and germination) is given principally in the second row, first column, a_{21}; other nonzero entries in the first column represent the probability that a seed becomes a seedling that grows very quickly.

The exact meanings of the other entries in the top row, a_{13} through a_{18} in our model, depend upon the timing of the census interval, as chosen by the investigator, with respect to the phenology of reproduction of a given organism (Caswell 1989*b*). These entries have often been poorly defined and incorrectly para-

TABLE 2. Structure for matrix model of population dynamics of *Calathea ovandensis*. Bold entries in the top row from the "Juv." to the "Xlrg." stage represent contribution to seeds. Entries along the diagonal represent survival without change of stage. Nonzero entries above the diagonal indicate regression, while those below the diagonal represent growth.

Stage at time $t + 1$	Stage at time t							
	Sd.	Sdlg.	Juv.	Pre.	Sm.	Med.	Lrg.	Xlrg.
Sd.	a_{11}	0	$\boldsymbol{a_{13}}$	$\boldsymbol{a_{14}}$	$\boldsymbol{a_{15}}$	$\boldsymbol{a_{16}}$	$\boldsymbol{a_{17}}$	$\boldsymbol{a_{18}}$
Sdlg.	a_{21}	a_{22}	a_{23}	0	0	0	0	0
Juv.	a_{31}	a_{32}	a_{33}	a_{34}	a_{35}	a_{36}	a_{37}	0
Pre.	0	a_{42}	a_{43}	a_{44}	a_{45}	a_{46}	a_{47}	a_{48}
Sm.	0	0	a_{53}	a_{54}	a_{55}	a_{56}	a_{57}	a_{58}
Med.	0	0	a_{63}	a_{64}	a_{65}	a_{66}	a_{67}	a_{68}
Lrg.	0	0	0	a_{74}	a_{75}	a_{76}	a_{77}	a_{78}
Xlrg.	0	0	0	a_{84}	a_{85}	a_{86}	a_{87}	a_{88}

meterized (discussed in Horvitz and Schemske 1986*a*, Caswell 1989*b*). In the current study, the population was censused in August and the total number of seeds at time t includes old seeds in the dormant seed pool and new seeds that have just been produced by plants. The entries for new seeds in the top row of the jth column are calculated by:

$$a_{1j} = \sum a_{ij} \times r_i, \tag{3}$$

summed over all reproductive stages (i goes from 5 to 8),

where a_{ij} = the probability that a plant of stage j will become a reproductive of stage i and r_i = the number of seeds produced per plant of stage i. This means that any stage that includes some plants that may become reproductives by time $t + 1$ may have a nonzero entry in the top row. For example, for the fourth stage class, the "pre reproductives," the probabilities that a plant in this class at time t will become a small, medium, large, or extra-large reproductive by $t + 1$ are a_{54}, a_{64}, a_{74}, and a_{84}, respectively (Table 2). Each of these is multiplied by the number of seeds contributed by each class at time $t + 1$ (Appendix 1). Summing these products gives a_{14}, the total seeds contributed to the population at time $t + 1$ by each prereproductive counted at time t.

Spatial and temporal variability in projection matrix parameters.—To examine the patterns and the spatial and temporal heterogeneity of the parameters in the projection matrices, we calculated the coefficients of variation CV (SD/mean; note that the CV is not defined when the mean = 0), overall and through space and time, as follows. This analysis only refers to those parameters corresponding to transitions that were observed at least once, yielding 46 matrix entries of the 64 possible ones (Table 2 shows the nonzero entries). For spatial variation, we calculated the CV's among plots in each year and then, to summarize, we calculated the mean of this statistic over the 4 yr (or fewer as in some cases the CV was not defined). For temporal variation, we calculated the CV's among years for a given plot and then, to summarize, we calculated the mean of this statistic over the four plots (or fewer as in some cases the CV was not defined). We then tested whether there was significantly more variation through space or through time by counting the number of entries for which spatial variability exceeded temporal variability and analyzing this pattern (sign test, Siegel 1956).

Environmental correlation among demographic parameters.—To reduce the dimensionality of the correlation matrix that would be used to determine whether environmental variation affected different demographic parameters similarly, we summarized the fates of plants into three categories: regression (becoming smaller), stasis (sensu Silvertown et al. 1993, survival without changing stage), growth (becoming larger) by summing the appropriate matrix entries. Also, for each plot and year, we used the number of seeds produced per individual by each of the four reproductive stages. Thus, there were four seed production parameters and eight parameters each for regression, stasis, and growth for each of the 16 plot-year matrices, resulting in a 28 × 28 correlation matrix (4 + (8 × 3)). In this context, environmental variation was represented by the 16 matrices. The signs of these correlations were analyzed by blocks to compare correlations of particular demographic features (regression, stasis, growth, and seed production) within and among stages. Within each block, to analyze whether there was a significantly positive or negative trend, a binomial test was applied (Siegel 1956).

Matrix analysis

Brief theoretical background.—A projection matrix representation is a useful way to summarize the overall demographic conditions of a given environment because the analytic parameters of the matrix, the eigenvalues and eigenvectors, have interesting biological interpretations. The matrix summarizes how the environment acts on a population through time to change the numbers and relative distribution of individuals in different stages. The dominant eigenvalue, when it exists (which it does for the kind of matrix structure, i.e., nonnegative, irreducible, and primitive, that corresponds to most life histories; Caswell 1989*b*) is of greatest biological interest. It corresponds to the asymptotic population growth rate, λ_1, a measure of

average fitness of the individuals living in a given environment; $\ln \lambda_1 = r$, the instantaneous growth rate (Fisher 1930, Charlesworth 1980, Caswell 1989*b*). The associated right (column) and left (row) eigenvectors correspond to the stable-stage distribution, $\boldsymbol{w}$ (scaled so that all the elements sum to 1), and stage-specific reproductive values, $\boldsymbol{v}$, respectively.

Further analyses based on these vectors yield a sensitivity value,

$$\delta\lambda_1/\delta a_{ij} = v_i w_j/\langle \boldsymbol{w},\boldsymbol{v}\rangle \quad (4)$$

(Caswell 1978) and elasticity value,

$$a_{ij}/\lambda_1 \times \delta\lambda_1/\delta a_{ij} \quad (5)$$

(Caswell et al. 1984, de Kroon et al. 1986) for each entry of the matrix, a_{ij}. In practice, one may scale the eigenvectors so that $\langle \boldsymbol{w},\boldsymbol{v}\rangle = 1$ (Caswell 1978) and then the expression for each sensitivity value is given by the product of the representation in the stable-stage distribution for the current stage, *j*, with the reproductive value of the future stage, *i*.

The full spectrum of eigenvalues and eigenvectors (there are as many as there are dimensions in the matrix) can also yield interesting biological information, elucidating the transient dynamics exhibited by populations that are not at the stable-stage distribution. Populations that are far from the stable-stage distribution will exhibit short-term behavior that may differ considerably from the asymptotic behavior. In this paper, we are concerned principally with the analysis of the asymptotic dynamics rather than the transient dynamics and we focus on the analyses of the dominant eigenvalue and its associated eigenvectors. Nevertheless, to indicate the relative importance of the dominant eigenvalue in the overall dynamics, we also present the

$$\text{"damping ratio"} = \lambda_1/\lambda_2, \quad (6)$$

where λ_2 is the subdominant eigenvalue, the one whose absolute magnitude is the largest among the remaining eigenvalues (Caswell 1989*b*). Its associated eigenvector is the other main "direction" in the trajectory of the population, next in importance to the stable-stage distribution.

Finding, scaling, and using the eigenvalues and eigenvectors.—For each of our matrices, we used the "eig" function of PC-MATLAB (MathWorks 1989) to obtain the eigenvalues and the eigenvectors. To obtain the right eigenvector we analyzed the matrix itself and for the left eigenvector we analyzed the transpose of the matrix. We then scaled the right and left eigenvectors such that all the elements of the right eigenvector summed to one and that $\langle \boldsymbol{w},\boldsymbol{v}\rangle = 1$ (Caswell 1978). We calculated sensitivity and elasticity using the scaled vectors.

Biological interpretations.—The biological interest in the asymptotic growth rate, λ_1, associated with a given matrix is not principally to predict future population size (which can only be done if the environment remains invariant with time, which it usually doesn't). Rather, it is most interesting as a synthetic measure of demographic success (and, thus, of average fitness) in a given environment. This single parameter is very useful for comparing the demography of different environments or for determining how small changes in single life history transitions will affect population fate. It puts into one currency changes affecting various kinds of vital rates.

The stable-stage distribution gives the steady-state proportion of individuals in each stage class, occurring as the asymptotic growth rate is realized. The relative frequencies of stages will converge on this distribution, no matter what the initial frequencies. The difference between an observed distribution and the stable distribution provides insight about the relevance of the asymptotic analyses to the near-term population dynamics.

To examine whether observed populations were significantly different from the stable-stage distributions, we did a *G* test comparing observed and expected distributions for each plot and year. We did these analyses for vegetative individuals only, not seeds, because we did not know how many seeds were in the soil seed bank. To determine how far the observed distribution was from the expected, we calculated the PS, the proportional similarity index,

$$\text{PS} = \sum_{n}^{i=1} \min(a_i, b_i) \times 100, \quad (7)$$

where there are *n* stages and a_i is the proportion of individuals in the ith stage of the stable-stage distribution and b_i is the proportion of individuals in the ith stage of the observed stage distribution.

The reproductive value of each stage class is a measure that reflects the expected relative "usefulness" of an individual of that stage as a parent in the current year and in the future (Fisher 1930, Mertz 1971, Caswell 1980, 1981, Yodzis 1981, Goodman 1982). To understand the meaning of reproductive value, imagine a new population is being founded in a particular environment in which the founders are composed entirely of one stage class. If the chosen stage is the stage of highest reproductive value, then the population will ultimately be bigger in absolute numbers at any time *t* than if any other stage had been chosen.

The sensitivity is one index that measures how changes in individual life history parameters influence population growth rate. The sensitivity is the slope of λ_1 with respect to a perturbation, defined as a small change in a particular demographic transition parameter in the neighborhood of the observed transition. High sensitivity for a given transition means that small changes in its value will have large effects on λ_1, which measures average fitness. Thus, sensitivity reflects the demographic potential for selection to act on characters that affect particular transitions; for selection to op-

erate, character variation must not only significantly affect particular fitness components but also these effects must translate into effects on overall fitness. The sensitivities are also the basis for calculating many other parameters, including the elasticities (Caswell et al. 1984, de Kroon et al. 1986) and the contributions of variance in demographic parameters to variance in population growth rate (Rao and Sarma 1986, Levin et al. 1987, Lande 1988, Caswell 1989*a*, *b*, Silva et al. 1991, Brault and Caswell 1993).

Some limitations to the insights gained from examining sensitivities should be considered, however. Sensitivities are affected by the scale of the demographic transitions themselves and are thus difficult to compare across stages of vastly different values, like seed production vs. survival probabilities. A "small change" (by a fixed amount, say ± 0.01) in survival is always proportionally greater than a "small change" (by the same fixed amount, ± 0.01) in seed production, simply due to scale differences. Also, they are only relevant in the neighborhood of the observed transitions. In general, λ_1 does not respond linearly to changes in transitions. For examining the effects of large perturbations, simulations may be the best technique. Lastly, sensitivities are defined even for transitions that have not been observed in a particular habitat so that they may unrealistically reflect the importance of these transitions (de Kroon et al. 1986, Moloney 1988).

Elasticity is a measure of proportional sensitivity. Each elasticity parameter is a product of the sensitivity with the actual transition value divided by the population growth rate (Eq. 5). Elasticity measures the effects of proportionally scaled perturbations; if all transition values are changed by $x\%$, what will be the proportionate contribution of each to changes in population growth? Unlike sensitivities they are only nonzero for transitions that are also nonzero. Elasticities are more readily comparable among stages than are the sensitivities because they are already scaled by the magnitudes of the transitions themselves. Also they are additive, summing to one for an entire matrix. They readily lend themselves to analyses of subsets of transitions summed together. For example, adding all the elasticities in a particular column gives that stage's total proportional contribution to population growth through several routes: making seeds, growing, shrinking, and remaining alive without growing.

Although older papers reported sensitivities and not elasticities (pre de Kroon et al. 1986), and many recent papers have done the opposite (post de Kroon et al. 1986), we prefer to report both indices, as they provide different information and different insights.

Spatial and temporal variability.—We examined the patterns of the spatial and temporal variability in the population growth rates, the stable-stage distributions, and the reproductive values graphically.

To examine the spatial and temporal heterogeneity of sensitivities and elasticities, we also present these data graphically. In addition, for the relevant subsets of the 64 entries in the sensitivity and elasticity matrices, we examined the mean value over the 16 matrices and the coefficients of variation CV (SD/mean, note that the CV is not defined when the mean = 0), overall and through space and time, as follows. We included sensitivity values for only transitions that were observed at least once, yielding 46 entries of the 64 possible ones (Table 2 shows the nonzero entries). We included elasticity values for nonzero entries in the elasticity matrix, yielding 44 of the 64 possible ones. For spatial variation, we calculated the CV's among plots in each year and then, to summarize, we calculated the mean of this statistic over the 4 yr (or fewer since in some cases the CV was not defined). For temporal variation, we calculated the CV's among years for a given plot and then, to summarize, we calculated the mean of this statistic over the four plots (of fewer since in some cases the CV was not defined). For both sensitivity and elasticity, we then tested whether there was significantly more variation through space or through time by counting the number of entries for which spatial variability exceeded temporal variability and analyzing this pattern (sign test, Siegel 1956).

Correlations of stage-specific elasticity with population growth rates

The importance of different life history events may vary according to how much populations are increasing or decreasing (or remaining stable) in size. We investigated this hypothesis by performing Spearman rank correlation analyses between λ_1 and the elasticity of each matrix entry, with $N = 16$ matrices for each correlation (as in Silvertown et al. 1993). We then adjusted the significance levels, calculating tablewise alphas by the Bonferroni sequential test (Rice 1989).

RESULTS

Overview of spatiotemporal variation

During the course of the study we had the opportunity to observe the demographic behavior of many individuals of our study organism facing several environments. Although we began this study by marking only 617 plants in 1982, by 1987, we had mapped, measured and observed 5944 plants. Not only was there initial variation among the study plots, but also there was environmental variation that occurred among years, including a treefall in 1 yr at one plot (in 1985 at plot 1) and el Niño events in 2 yr (1983 and 1987) affecting all plots. Both treefalls and el Niño events stimulate seedling recruitment from the seed bank, probably by causing an increase in soil temperature (experimental results in Horvitz and Schemske 1994). Also, the biotic interactions affecting seed production and seedling recruitment varied spatiotemporally, including dispersers (Horvitz and Schemske 1986*a*, *b*, *c*,

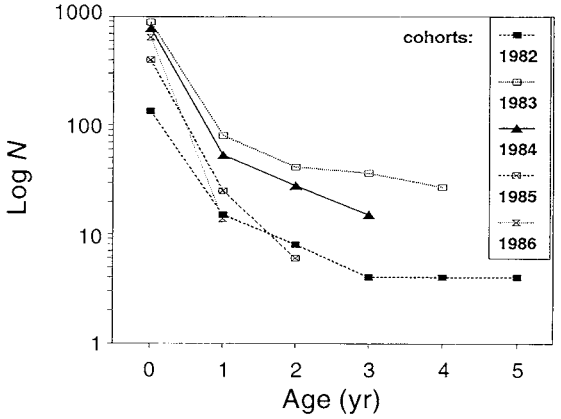

FIG. 1. Age-specific survivorship for five cohorts, in which age is defined as "time since germination." The age-specific mortality percentages for ages 0–1, 1–2, and 3–4 (not significantly different by cohorts) were 93.4, 52.0, and 22.5%, respectively (for year 1, $LR_0 = 2.22$ and df = 4, NS; for year 2, $LR_1 = 3.26$ and df = 3, NS; for year 4, $LR_3 = 1.00$ and df = 1, NS; Logrank Test [LR], Hutchings et al. 1991). For age 2–3, the 1983 cohort had 12.2% mortality, significantly less than the other cohorts with 50.0 and 46.4% ($LR_2 = 8.25$ and df = 2, $P < 0.025$).

1994), consumers of reproductive tissues (Horvitz and Schemske 1984, Schemske and Horvitz 1988), ant-guard defenders (Horvitz and Schemske 1984, 1990, Schemske and Horvitz 1988) and pollinators (Schemske and Horvitz 1984, 1989, Horvitz and Schemske 1990).

Spatiotemporal variability in seed production vs. seedling emergence.—The patterns of variability through space and time were different for seeds than for seedlings. Seed production varied more through space than seedling numbers (the mean CV among plots was 75 and 54%, for seeds and seedlings, respectively, $N = 5$ yr). Seedling numbers varied more through time than seed production (the mean CV among plots was 71 and 43%, for seedlings and seeds, respectively, $N = 4$ plots). These patterns underscore the fact that both spatial and temporal variability must be considered in estimating the production and the fates of seeds.

In the demographic study plots, the total number of seedlings emerging varied nearly 10-fold among years (from 195 to 1837 seedlings, during the years 1982–1987), while seed production varied only 2.4-fold among years (during the years 1982–1986). Seedling emergence in the years 1983–1987 was not correlated with the seed production in the previous year ($r = 0.34$, $N = 5$ yr, $P = 0.58$), but it was highly correlated with el Niño, scoring el Niño years as 1 and non el Niño years as 0 ($r = 0.91$, $N = 5$ yr, $P = 0.03$).

Age-specific survivorship and growth of seedling cohorts

To analyze the effects of age on survivorship and stage transitions, we defined "age" as "time since germination." New seedlings were considered age 0 (ages defined by "time since seed maturation" were unknown due to the long-lived seed bank). Age-specific survivorship curves were drawn for five seedling cohorts, 1982, 1983, 1984, 1985 and 1986 (Fig. 1). The slopes of these curves, indicating the risk of mortality, were remarkably similar; mortality dropped with age for most cohorts. There was no significant difference in mortality among the cohorts during the 1st, 2nd, or 4th yr of age. New seedlings suffered the highest mortality. Mortality the 2nd yr was about half as severe (Fig. 1). Third-year mortality differed significantly by cohort, dropping markedly for the 1983 cohort, while remaining higher for the 1982 and 1985 cohorts. Fourth-year mortality also dropped and 5th yr mortality was 0%.

Pooling observations during the 5-yr study of all the cohorts into age classes, we analyzed the size class distributions for the following ages: 1 yr olds ($N = 187$), 2 yr olds ($N = 83$), 3 yr olds ($N = 55$), 4 yr olds ($N = 31$), and 5 yr olds ($N = 4$). Seventy-five percent of 1 yr olds were in the juvenile size class. An increasing percentage of plants were of prereproductive size with each passing year (6, 22, 33, and 55% for ages 1, 2, 3, and 4, respectively). Similarly, the reproductives increased in relative numbers with age (0, 7, 16, and 16% for ages 1, 2, 3, and 4, respectively), with medium-sized reproductives found only among the 4-yr-old plants (3%). Of the very few plants that survived from germination to 5 yr of age during the 5-yr study, two were prereproductives and two were juveniles. These results indicate a general trend toward increasing size class with age, but they also indicate considerable developmental plasticity in growth.

Density of stage groups

To summarize variation in vegetative stage structure graphically for comparing among years and sites, we grouped stage classes into (a) seedlings, (b) nonreproductives (juveniles + prereproductives), and (c) all reproductives, and calculated the densities at each plot and year. The relative densities of these groups, as well as the total densities of vegetative individuals, varied among the four plots and among the 5 yr (Fig. 2). There was more variation among the plots than among the years for a given plot for all stage groups except seedlings. The density of reproductives varied nearly fourfold among the plots, and the density of seedlings varied even more (4.5-fold up to 10-fold) among years (Fig. 2). The years with the highest seedling densities were 1983 and 1987, both el Niño years (Fig. 2). Focusing on the nonseedling stage structure, we unexpectedly found that plot 2 was more similar to plot 4 in structure, while plot 3 was more similar to plot 1 (Fig. 2). Plots 2 and 4 had relatively more nonreproductives than reproductives in all years. In contrast, plots 1 and 3 had more reproductives or equal densities

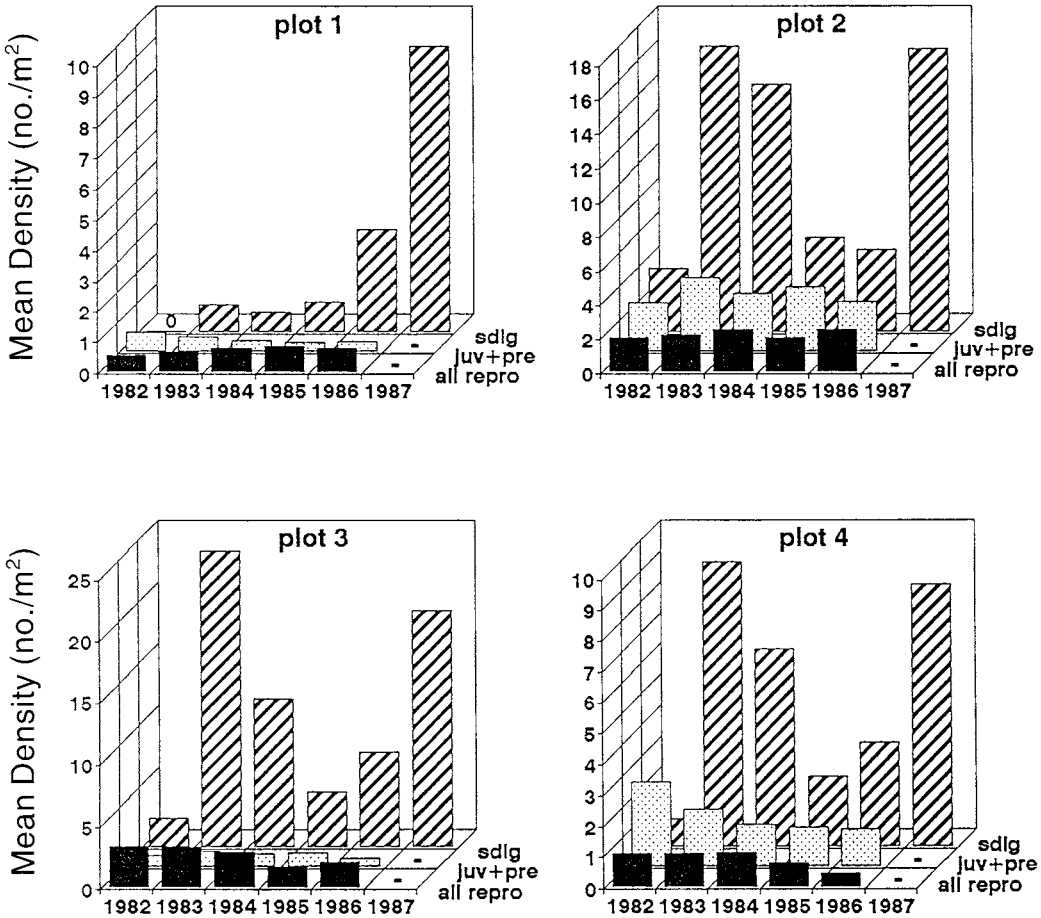

FIG. 2. Mean density of plants, the number of individuals per square metre, belonging to each stage group at each plot and year. Seedlings are represented by hatched bars. The juveniles and prereproductives were added together, represented by stippled bars, as were all the reproductives, represented by solid bars. The nonseedling plants in 1987 could not be appropriately classified and were not included. The density of reproductives, which varied more through space than time, ranged from a low of 0.68 individual/m^2 at plot 1 to a high of 2.53 individuals/m^2 at plot 3 (averaged over 5 yr for each plot). The density of seedlings, which varied more through time than space, showed over 10-fold variation among years at plots 1, 3, and 4, and 4.5-fold variation among years at plot 2. The two el Niño years, 1983 and 1987, had the highest seedling densities. Note that even plot 1, which had no seedlings at all in 1982, increased markedly (from 0 to 57) in numbers of seedlings between 1982 and 1983.

of reproductives and nonreproductives in most years (Fig. 2).

There was no a priori or apparent environmental factor responsible for the similarity of plots 2 and 4 vs. plots 1 and 3; in fact, plots 1 and 3 were farther apart from each other geographically and "looked" the most different from each other. Neither did plots 2 and 4 "resemble" each other in shadiness, substrate, or general aspect. Due to such unexpected patterns emerging from the data, we will continue to refer to the plots by their numbers rather than by some (unknown) descriptive phrase.

Effects of stage, plot, and year on inflorescence production

The number of inflorescences per plant varied significantly by stage class, plot, and year (Table 3). The F value for the effect of stage was 25–26 times larger than that of the effects of either year or plot (Table 3). The number of inflorescences per plant varied 3.5-fold among stages, 1.9-fold among plots, and 1.5-fold among years. The best plot for inflorescence production was plot 3 ($\bar{X} \pm$ SD $= 2.5 \pm 1.50$, $N = 234$ observations of reproductives in the original plot; 2.05 ± 1.4, $N = 135$ observations of reproductives in the replacement plot). The best year was 1983 (2.3 ± 1.5, $N = 211$). The number of inflorescences per plant increased with size class (1.27, 2.09, 2.87, and 4.42 inflorescences per plant for small, medium, large, and extra-large reproductives, respectively). Year and plot interacted significantly in their effects (Table 3). Most interestingly, there was a significant interaction between stage and year and a marginally significant interaction between stage and plot (Table 3), indicating

TABLE 3. Three-way ANOVA of the effects of plot, year, and stage (as fixed effects) on inflorescence production [$\sqrt{(\text{number of inflorescences} + 1)}$] of reproductive plants. In these analyses of the behaviors of stage classes, there were N's of 645, 202, 135, and 55 for observations of small, medium, large, and extra-large reproductives pooled over all years and plots, respectively. The model accounted for 59% of the variation in inflorescence production.

Source	df	F	P
Main effects			
Stage	3	153.6	0.0001
Year	4	6.6	0.0001
Plot	4	6.0	0.0001
Interaction effects			
Stage × Year	12	2.3	0.006
Stage × Plot	10	1.6	0.10
Year × Plot	12	4.3	0.0001
Stage × Plot × Year	18	1.2	NS
Model	63	22.42	0.0001
Error	973		

that even for a given stage, spatial and temporal effects were also important. Because of the interaction effects, separate two-way ANOVAs for each stage class were performed. These analyses confirmed the importance of temporal and spatial variation in inflorescence production for plants of each reproductive stage (Table 4).

Log-linear analyses of fates of vegetative individuals

In the analyses of each separate stage, we found that plot significantly affected transitions for three stages (seedlings, small reproductives, and juveniles) and that year significantly affected transitions for three stages (seedlings, small reproductives, and large reproductives) (Table 5). For year and plot effects, the marginal (Analyses 1 and 2, Appendix 4) and conditional (Analyses 3 and 4, Appendix 4) tests gave nearly the same results. We also found that historical effects were not significant, confirming the Markovian nature of the transitions (Table 6).

We describe how total survival of a stage class varied by plot and year (calculated by summing the appropriate column entries for each matrix in Table 7), emphasizing significant effects. The fates of seedlings and small reproductives were significantly affected by both plot and year (Table 5). The fates of large reproductives were affected by year, but not plot, and the fates of juveniles were affected by plot, but not year (Table 5).

TABLE 4. Results of two-way ANOVAs of the effects of plot and year on inflorescence production [$\sqrt{(\text{number of inflorescences} + 1)}$] for each stage class.

Stage	Model df_{model}	Model df_{error}	Model F	Plot	Year	Plot × year
Small	20	624	2.83***	NS	**	**
Medium	17	184	3.76***	*	NS	*
Large	15	119	3.27***	NS	**	*
Extra-large	8	46	2.98**	NS	†	NS

† $P < 0.08$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.0001$.

TABLE 5. Results of log-linear analyses of effects of plot and year on fates of *Calathea ovandensis*. Whether the null hypothesis fit and whether the incremental change in G^2 for the added effects of plot and of year were significant is indicated (see Appendix 4 for details).

Stage	Null fit?	Plot	Year
Seedlings	no	*	*
Juveniles	yes	*	NS
Prerep.	yes	NS	NS
Small rep.	no	*	*
Med. rep.	yes	NS	NS
Large rep.	yes	NS	*
Xlarge rep.	yes	NS	NS
All stages	yes	*	*

* $P < 0.05$ or less; both marginal and conditional tests of the effects.

Plots and/or years that were most beneficial to certain stages were not necessarily good for other stages. While plot 2 was the most favorable for the survival of seedlings, plot 1 was better for the survival of juveniles and small reproductives (Table 7). Similarly, 1982–1983 was the best year for seedlings, but the worst year for large reproductives, while 1985–1986 was the best year for small reproductives (Table 7). Not only was total survival of stages affected by plot and year, but similar variation was evident in the distribution of survivors among stage classes, how much they regressed, stayed the same, or grew (Table 7). For example, the stage fates of seedlings that survived the 1982–1983 year varied among plots. In plots 3 and 4 all the survivors advanced one stage, while in plot 2 some survivors advanced two stages (Table 7). Such spatiotemporal effects on the fates of individual life history stages provide motivation for analyzing the dynamics of the separate years and plots.

The analysis of the four-way contingency table of overall state by fate transitions showed that the null model *SPY,SF* fit the data (Table 5, Appendix 4, Analysis 1, four-way model), indicating that initial state was sufficient for predicting fate, given the distribution of states over plots and years. Nevertheless, the incremental changes in G^2 by adding the year and plot effects were significant (Table 5), underlining the importance of year and plot in refining the ability of the model to predict fates (H. Caswell 1989*b* and *personal communication*). That the null hypothesis fit the data indicates that state was so overwhelmingly predictive of fate that the variation among years and plots added

TABLE 6. Results of log-linear analyses of historical effects on demographic fates at each plot. The incremental G^2 and df for the conditional effects of stage at time $t - 2$ on fate at time t are given (none were significant).

	Plot 1		Plot 2		Plot 3		Plot 4	
Year, t	df	G^2	df	G^2	df	G^2	df	G^2
1984	3	0.7	8	4.2	9	3.9	3	0.5
1985	6	2.0	12	8.0	...	...	5	3.7
1986	5	4.0	9	10.1	4	1.6	4	1.0

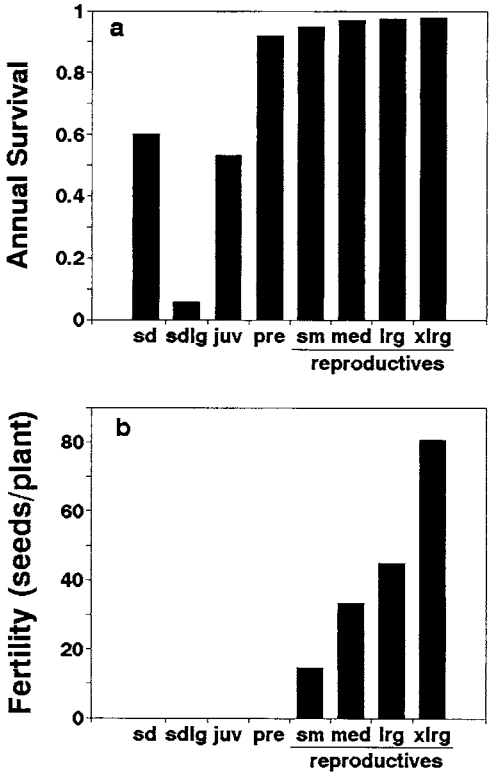

FIG. 3. (a) Annual survival for each stage class, sum of the appropriate entries in each column of the matrix for observations from all years and plots pooled. (b) Mean fertility, number of seeds produced per plant per year, for each stage class, averaged over observations of reproductive plants from all years and plots pooled.

little to explain the heterogeneity in the data. The analyses of three-way tables of the effects of plots in each year and of the effects of years in each plot also supported this conclusion. *SP,SF* fit the data for 4 yr (G^2's were 128.8, 133.7, 117.0, and 110.7, respectively, for 1982–1983, 1983–1984, 1984–1985 and 1985–1986, df = 147 in all years). Thus, given the distribution of states over years, state was a sufficient predictor of fate, while plot was not necessary. *SY,SF* fit the data in three of four plots (G^2's were 75.4, 117.7, 181.6, and 53.6, respectively, for plots 1, 2, 3, and 4, df = 147 in all plots, $P < 0.05$ for plot 3). Thus, given the distribution of states over plots, state was predictive of fate and year was not necessary, except at plot 3, where year was needed to predict fates.

These results emphasize that one overall set of state-by-fate transitions may reflect a meaningful synthetic view of the overall demographic patterns of this plant, even though, on a stage-specific basis, there was significant variation through space and time. In other words, there is motivation to consider the individual plot-year combinations as well as to analyze an overall pattern. This is the reason we present both the summary matrix and the 16 individual matrices.

The summary matrix: structure and analytical properties

The matrix surrounding the observations pooled over all plots and years shows the complexity of the life cycle for this understory herb. These plants could survive without a change in stage, or they could grow or shrink by one or several stages. Plants that were not reproductive in one year often contributed to the next year's seeds by becoming reproductive in the next year (Table 8). For five stages, including seeds, juveniles, prereproductives, small reproductives, and large reproductives, staying the same size was the most probable event for a survivor (Table 8). Only seedlings were more likely to advance a stage than to remain in the same size class (Table 8). Both medium and extra-large reproductives that survived were more likely to shrink to a smaller stage than to remain in the same stage or grow to a larger stage (columns 5 and 7, Table 8). All postseedling size classes had a nonzero probability of contributing to the next year's seed pool, due to advancement of at least some individuals to a reproductive size class by the following year (row 1, Table 8).

The stage-specific total survivals (calculated from the matrix in Table 8) varied considerably among the nonreproductive stages (Fig. 3a). Seedlings had the lowest survival. Juveniles' survival rate was 10 times

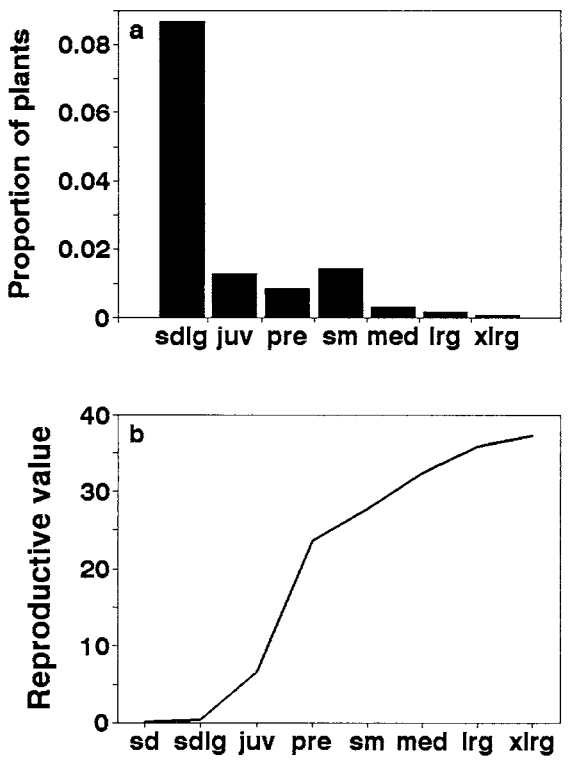

FIG. 4. (a) The stable-stage distribution for the vegetative (nonseed) portion of the population (0.87 of the stable population vector was seeds) and (b) the stage-specific reproductive values for the summary matrix based on observations pooled for all years and plots.

TABLE 7. Transition probability matrices. Table continues through p. 171.

Stage at time $t + 1$	Stage at time t							
	Sd.	Sdlg.	Juv.	Pre.	Sm.	Med.	Lrg.	Xlrg.
a) Plot 1								
				1982–1983				
Sd.	0.567	0	0.82	7.5	16.8	30.2	0	0
Sdlg.	0.0314	0	0	0	0	0	0	0
Juv.	0.0016	0	0.4737	0	0	0	0	0
Pre.	0	0	0.2632	0.4286	0.125	0	0	0
Sm.	0	0	0.0526	0.3333	0.5938	0	0	0
Med.	0	0	0	0.0952	0.2188	0.5	0	0
Lrg.	0	0	0	0	0.0625	0.5	0	0
Xlrg.	0	0	0	0	0	0	0	0
				1983–1984				
Sd.	0.585	0	0	10.8	19.4	25.8	35.7	0
Sdlg.	0.0146	0.0351	0	0	0	0	0	0
Juv.	0.0004	0.0702	0.4167	0	0	0	0	0
Pre.	0	0	0.25	0.3889	0.037	0	0	0
Sm.	0	0	0	0.5556	0.7407	0.5	0	0
Med.	0	0	0	0.0556	0.2222	0.2	0.3333	0
Lrg.	0	0	0	0	0	0.3	0.6667	0
Xlrg.	0	0	0	0	0	0	0	0
				1984–1985				
Sd.	0.558	0	1.8	14.3	20.7	28.6	25.9	0
Sdlg.	0.0408	0	0	0	0	0	0	0
Juv.	0.0012	0.0732	0.4	0	0.0286	0	0	0
Pre.	0	0	0.2	0.2737	0.0857	0	0	0
Sm.	0	0	0.1	0.6364	0.4571	0.2	0.4	0
Med.	0	0	0	0.0909	0.3143	0.3	0.2	0
Lrg.	0	0	0	0	0.0857	0.5	0.4	0
Xlrg.	0	0	0	0	0	0	0	0
				1985–1986				
Sd.	0.548	0	5	9.3	17.6	31.4	35.1	0
Sdlg.	0.0513	0	0	0	0	0	0	0
Juv.	0.0007	0.0156	0.4	0.25	0	0	0	0
Pre.	0	0	0	0.375	0.25	0	0	0
Sm.	0	0	0.2	0.375	0.6429	0.75	0.7	0
Med.	0	0	0	0	0.0357	0.1875	0.1	0
Lrg.	0	0	0	0	0	0.0625	0.2	0
Xlrg.	0	0	0	0	0	0	0	0

higher than seedlings, and the survival of seeds (Appendix 2) was 8 times higher than the survival of juveniles. The survival of all reproductives was quite high (over 90%), and varied little, increasing only slightly, with increasing stages (Fig. 3a). The stage-specific fertilities, the estimated number of seeds per plant (used as a component of the calculation of the top row of the matrix in Table 8), varied more than four-fold among the reproductive stages, increasing steadily from small to extra-large size classes (Fig. 3b). The λ_1 of this summary matrix was 0.9923, a value that is very close to one and indicates persistence of the population. The damping ratio for this matrix was 1.8, indicating the relatively large effect of the dominant eigenvalue, which suggests a rapid approach to the asymptotic dynamics.

The stable-stage distribution was composed of 87% seeds. Seedlings made up the highest proportion of the vegetative plants, accounting for 8.7% of the total vegetative population (Fig. 4a). Among the nonseedling vegetative plants, small reproductives and juveniles were nearly equally important (Fig. 4a). The smallest contributors to the stable-stage distribution were the other reproductives (Fig. 4a).

The reproductive values increased with increasing stage class, the steepest increase between the juvenile and prereproductive stage (Fig. 4b).

Sensitivity values varied over four orders of magnitude by stage class and type of transition. Population growth rate was most sensitive to rapid growth of seedlings (Fig. 5a) and least sensitive to alterations in the contributions to seeds made by each class (Fig. 5c), with intermediate sensitivity to the transitions among the other vegetative classes (Fig. 5b). Sensitivity analyses almost always reveal that rapid growth of early stages will have the biggest impact on population growth rate and that reproduction will have sensitivity values several orders of magnitude smaller (Caswell 1989*b*). Our results are consistent with these overall patterns. The behavior of small reproductives had the largest impact on population growth compared to the other nonseedling vegetative stages, both in terms of

TABLE 7. Continued.

Stage at time t							
Sd.	Sdlg.	Juv.	Pre.	Sm.	Med.	Lrg.	Xlrg.
b) Plot 2							
				1982–1983			
0.215	0	2.8	8.9	12.7	20.3	32.8	0
0.3407	0.0088	0	0	0	0	0	0
0.0392	0.115	0.3696	0.025	0.0541	0	0.1667	0
0	0	0.1739	0.4	0.1351	0.1333	0	1
0	0	0.1304	0.325	0.4865	0.4667	0	0
0	0	0.0217	0.05	0.1081	0.0667	0.1667	0
0	0	0	0.05	0	0.2667	0.5	0
0	0	0	0	0.027	0	0.1667	0
				1983–1984			
0.485	0	0.4	8.4	12.4	17.3	18.4	14.6
0.115	0.0098	0	0	0	0	0	0
0	0.0727	0.29	0.0313	0	0	0	0
0	0.0079	0.16	0.3438	0.1364	0	0	0
0	0	0.03	0.5	0.7045	0.7778	0.7778	1
0	0	0	0	0.0455	0.2222	0.1111	0
0	0	0	0.0313	0.0227	0	0.1111	0
0	0	0	0	0	0	0	0
				1984–1985			
0.512	0	0	1.4	3.6	5.2	7.1	0
0.087	0.0114	0	0	0	0	0	0
0.001	0.0727	0.4179	0.1351	0.0303	0	0	0
0	0	0.0896	0.5135	0.3182	0	0	0
0	0	0	0.2703	0.5606	1	0.3333	0
0	0	0	0	0.0606	0	0	0
0	0	0	0	0.0152	0	0.6667	0
0	0	0	0	0	0	0	0
				1985–1986			
0.504	0	0.6	9.8	17.6	35.8	77.4	0
0.0939	0.0417	0.058	0	0	0	0	0
0.002	0.0536	0.4638	0.087	0.0189	0	0	0
0	0	0.1594	0.413	0.1698	0	0	0
0	0	0.029	0.4783	0.7736	0.5	0	0
0	0	0	0	0.0377	0.25	0.3333	0
0	0	0	0	0	0.25	0.3333	0
0	0	0	0	0	0	0.3333	0

their moving to other stages (Fig. 5b) and their contributions to seeds (Fig. 5c). The juveniles were a close second to the small reproductives in their sensitivity values (Fig. 5b, c).

The elasticity, or proportional contribution to population growth, was greatest for the small reproductives (Fig. 6). Total elasticity for each stage class was calculated by summing its proportional contributions through seeds and through survival/growth/regression (Table 9). The relative importance of the different stages to population growth can be seen by examining the shape of the curve of total elasticity against stage (Fig. 6). The higher the peaks in these curves, the more proportional changes affecting a single stage dominate the proportional effects on population growth; the flatter the curve, the more even are the contributions of different stages to population growth rate response. The total elasticity of seed production was only 0.0523, an order of magnitude lower than the elasticity of the small reproductives by survival (Table 9). The single individual matrix parameter with the highest elasticity was the stasis of small reproductives (Table 9). The prereproductives were also important contributors to elasticity, with the next highest total contribution after small reproductives (Fig. 6), but for them advancement to the small reproductive stage was nearly as important as survival without changing stage (Table 9).

Matrices for each year and plot: variation and correlations

Structure of matrices.—Many kinds of transitions were observed. The occurrence of particular size classes and their fates varied among the 16 matrices. For example, only at plot 3 was the full size range of reproductives present in all 4 yr (Table 7c). Plot 2 had extra-large plants in only 1 yr (Table 7b), while plots 1 and 4 never had them (Table 7a, d). The survival and fate variation was presented above (*Results*: *Log-linear analyses of fates . . .*).

Spatial and temporal variability in projection matrix parameters.—The CV's for the matrix elements ranged from a low of 19% to a high of 400% (Table 10). The

TABLE 7. Continued.

Stage at time $t+1$	Stage at time t							
	Sd.	Sdlg.	Juv.	Pre.	Sm.	Med.	Lrg.	Xlrg.
c) Plot 3								
				1982–1983				
Sd.	0.458	0	0	28.6	30.4	45	57.2	72.4
Sdlg.	0.1378	0	0	0	0	0	0	0
Juv.	0.0041	0.0508	0.1875	0	0.0385	0	0	0
Pre.	0	0	0.25	0.1667	0.0385	0	0	0
Sm.	0	0	0	0.6667	0.3462	0.1429	0.0645	0
Med.	0	0	0	0	0.1923	0.1905	0	0
Lrg.	0	0	0	0	0.1923	0.3333	0.5161	0.1667
Xlrg.	0	0	0	0.1667	0.0769	0.2381	0.3871	0.8333
				1983–1984				
Sd.	0.571	0	0.7	2.9	16.5	13.5	26.2	39.3
Sdlg.	0.0287	0	0	0	0	0	0	0
Juv.	0.0003	0.0097	0.1154	0.3333	0	0	0	0
Pre.	0	0	0.0769	0.5	0.1111	0.3333	0.0345	0
Sm.	0	0	0.0385	0.1667	0.7222	0.5556	0.3793	0.12
Med.	0	0	0	0	0.1111	0.1111	0.3448	0.4
Lrg.	0	0	0	0	0	0	0.1724	0.28
Xlrg.	0	0	0	0	0	0	0	0.16
				1984–1985				
Sd.	0.55	0	0.9	5.3	11.3	15.7	16.4	27.5
Sdlg.	0.0478	0.0148	0.05	0	0	0	0	0
Juv.	0.0021	0.0148	0.1	0.1429	0.1111	0.0417	0	0
Pre.	0	0	0.05	0.1429	0.2222	0.2917	0.3636	0.0909
Sm.	0	0	0.05	0.2857	0.4444	0.25	0.3636	0.4545
Med.	0	0	0	0	0.1111	0.3333	0.0909	0.2727
Lrg.	0	0	0	0	0	0.0417	0.1818	0.0909
Xlrg.	0	0	0	0	0	0	0	0.0909
				1985–1986				
Sd.	0.556	0		18.8	36.6	60.2	83.8	116.6
Sdlg.	0.0438	0.0351	4.2	0	0	0	0	0
Juv.	0.0002	0.0351	0.25	0.0625	0	0	0	0
Pre.	0	0	0.0833	0.25	0.0455	0	0	0
Sm.	0	0	0.1667	0.5	0.5	0.0769	0	0
Med.	0	0	0	0.125	0.4091	0.6923	0.25	0
Lrg.	0	0	0	0	0.0455	0.0769	0.5	0
Xlrg.	0	0	0	0	0	0.1538	0.25	1

two least variable parameters were seed dormancy (a_{11}) and the stasis of small reproductives (a_{55}). The parameters that varied the most (CV = 400%) were the relatively rare transitions, including extremely rapid growth of seedlings, juveniles, and prereproductives (a_{32}, a_{63}, and a_{84}), and the shrinking of medium and large reproductives (a_{36} and a_{37}) (Table 10). In general, the projection matrix parameters varied more through space than through time, although the parameters representing seed fates (a_{11}, a_{21}, a_{31}) all varied more through time than through space. The average $CV_{\text{among plots}}$ exceeded the average $CV_{\text{among years}}$ for 24 of the parameters, while 9 were equally variable through space and time and 12 were more variable through time than through space (for the spatial analysis only 45 parameters were defined). This trend was marginally significant ($z = 1.833$, $P = 0.066$; sign test, Siegel 1956).

Environmental correlation among demographic parameters.—Matrix entries did not vary independently from one another across the environments. There were many negative and positive correlations of large magnitudes (Appendix 3). Because of the small sample sizes and large number of comparisons, it was not statistically meaningful to examine individual correlations. To present the main patterns in correlation structure, we examined the signs of the correlations (Table 11). Environments, represented by the 16 plot-year matrices, that were good for seed production by one stage class were also good for seed production of other stages (Table 11, e.g., 6 + and 0 −). Similarly, environments that favored growth of one stage also favored growth of other stages (Table 11). Growth and seed production were also positively correlated (Table 11). There were also 2.5 times more positive than negative correlations among the parameters that relate growth to stasis (Table 11). Not surprisingly, environments that favored growth or that favored stasis did not favor regression (Table 11). In the other blocks, the numbers of positive and negative correlations were not significantly different. For example, environments with high values of regression for certain stages did not also tend to have

TABLE 7. Continued.

Stage at time t							
Sd.	Sdlg.	Juv.	Pre.	Sm.	Med.	Lrg.	Xlrg.
d) Plot 4							
				1982–1983			
0.336	0	0	8.1	14.8	17	26.1	0
0.2533	0	0.0364	0	0	0	0	0
0.0103	0.0435	0.3273	0	0	0	0	0
0	0	0.0909	0.6	0.1818	0.1538	0	0
0	0	0	0.4	0.7273	0.6154	0.3333	0
0	0	0	0	0	0.1538	0.6667	0
0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
				1983–1984			
0.49	0	0	5.5	11	10.6	0	0
0.1087	0	0	0	0	0	0	0
0.0013	0.0167	0.3793	0.0556	0	0	0	0
0	0	0.0069	0.5556	0.1739	0.25	0	0
0	0	0	0.3889	0.7826	0.75	0	0
0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
				1984–1985			
0.513	0	0	3.2	7.2	0	0	0
0.087	0.0242	0	0	0	0	0	0
0	0.0303	0.2222	0.1765	0.1071	0	0	0
0	0	0.1667	0.4118	0.25	0	0	0
0	0	0	0.2353	0.5357	0	0	0
0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
				1985–1986			
0.524	0	0	1.2	10.5	0	0	0
0.0751	0.0172	0.1333	0	0	0	0	0
0.0009	0	0.3333	0.0588	0.0526	0	0	0
0	0	0.1333	0.7647	0.4211	0	0	0
0	0	0	0.0588	0.5263	0	0	0
0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0

high values for regression of other stages (Table 11, 8 + and 7 −).

Matrices for each year and plot: analytical properties

Lambdas.—The population growth rates varied from a low of 0.7356 to a high of 1.2477 (Fig. 7). Of the 16 matrices, five had λ_1 that were quite close to 1 (between 0.95 and 1.05). The arithmetic mean and geometric mean of the 16 matrices were 0.9695 and 0.9607, respectively. Temporal variation in λ_1 is often summarized by the geometric mean, while spatial variation is summarized by the arithmetic mean. To summarize the temporal variation at each plot, we report the geometric means for plots 1, 2, 3, and 4: 0.9677, 1.0368, 0.9595, and 0.8932, respectively. To summarize the

TABLE 8. Transition probability matrix for observations from all years and plots pooled (λ_1 = 0.9923; damping ratio = 1.80).

Stage at time t + 1	Stage at time t							
	Sd.	Sdlg.	Juv.	Pre.	Sm.	Med.	Lrg.	Xlrg.
Sd.	0.4983	0	0.5935	7.139	14.2715	24.6953	34.9027	40.5437
Sdlg.	0.0973	0.0110	0.0191	0	0	0	0	0
Juv.	0.0041	0.0442	0.3378	0.0698	0.0251	0.0065	0.0085	0
Pre.	0	0.0014	0.1355	0.4286	0.1736	0.0968	0.0427	0.0435
Sm.	0	0	0.0363	0.3841	0.6025	0.4258	0.2991	0.2174
Med.	0	0	0.0019	0.0254	0.113	0.2387	0.1709	0.2826
Lrg.	0	0	0	0.0095	0.0272	0.1548	0.3248	0.1957
Xlrg.	0	0	0	0.0032	0.0063	0.0452	0.1282	0.2391

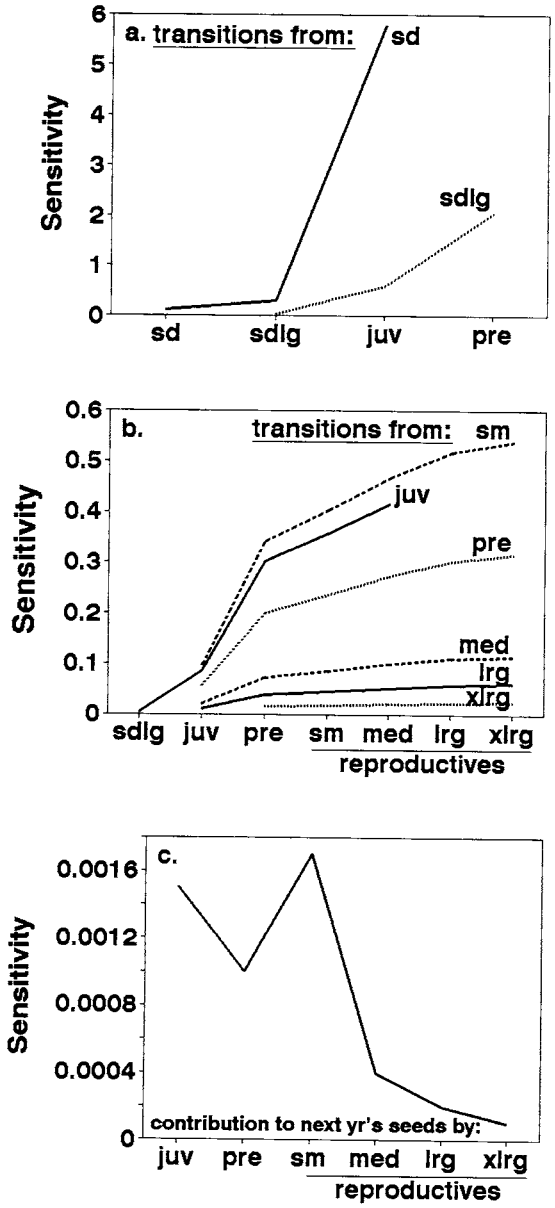

FIG. 5. Sensitivities for the summary matrix based on observations pooled for all years and plots of population growth rate to perturbations in (a) the transitions from seeds and seedlings to other classes, (b) the transitions *from* (the stages written on the lines) juveniles, prereproductives and all classes of reproductives *to* (stages indicated on the *x* axis) other classes, and (c) the contributions of each stage class to seeds. Stage class abbreviations are defined in Table 1.

spatial variation in each year, we report arithmetic means for 1982–1983, 1983–1984, 1984–1985, and 1985–1986: 1.0653, 0.9643, 0.8710, and 0.9772, respectively. By these calculations, the overall best plot was plot 2 and the overall best year was the 1982–1983 transition year. These results are also reflected in Fig. 7.

The population dynamics over the 4-yr sequence at each plot are given by matrix multiplication resulting in one 4-yr transition matrix, where the time interval of the matrix is 4 yr rather than 1 yr. The fourth root of this matrix may be considered a per-year "dynamic average" population growth rate. The dominant eigenvalues for the 4-yr matrix for plots 1, 2, 3, and 4 were 1.0201, 1.1382, 0.7832, and 0.6803, respectively. These analyses further support the conclusions that the population was declining most at plot 4 and increasing most at plot 2 (also seen in Fig. 7). The dynamic averages were 1.0050, 1.0329, 0.9407, and 0.9082. Although these were similar in relative magnitudes to the geometric means of the eigenvalues of the 4-yr matrices at each plot, they may not always be. The sequence of environments matters in the calculation of the 4-yr matrix (matrix multiplication is not commutative), but sequence does not matter in the calculation of the geometric mean. The arithmetic mean, averaging across the four plots, of these "dynamic" averages per plot was 0.9717.

Three of the four plots (plots 2, 3, and 4) shared a similar temporal trend, with the 1982–1983 year being the best and 1984–1985 being the worst year (Fig. 7). In contrast, at plot 1, which began with the lowest growth rate of any plot, 1984–1985 was the best year. A treefall occurred very near the plot during this year, resulting in a dramatic increase in light levels that offset the worsening of conditions in the general environment (Fig. 7).

Damping ratios.—These ranged from 1.38 to 2.29, 81% of them (N = 16 plot-year matrices) exceeding 1.5 (Table 12). This means that the dominant eigenvalue was >50% larger than the subdominant for most of the environments in our data set. This parameter reflects the relative importance of the asymptotic dynamics to the transient dynamics. A large number means that the approach to the stable-stage distribution will not be disrupted much by the transient dynamics. The damping ratio alone, however, cannot tell us exactly how long a given population will take to reach the stable-stage distribution (which depends addition-

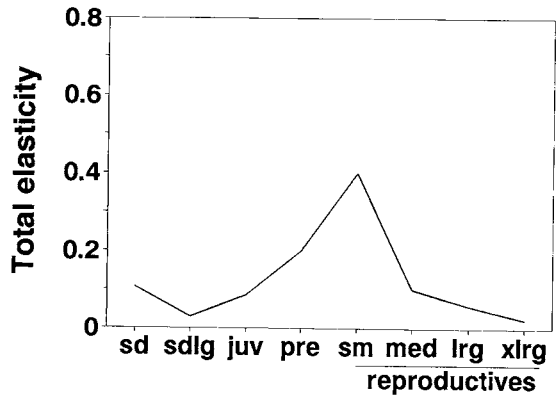

FIG. 6. The elasticities for the summary matrix based on observations for all years and plots pooled, summed for all contributions to and transitions of a stage class.

TABLE 9. Elasticities for matrix based on observations of all years and plots pooled. The single parameter of largest elasticity is in boldface.

Stage at time $t + 1$	Stage at time t								
	Sd.	Sdlg.	Juv.	Pre.	Sm.	Med.	Lrg.	Xlrg.	Sum cont. to seeds
Sd.	0.0528	0	0.0009	0.0073	0.0251	0.0092	0.0068	0.0030	0.0523
Sdlg.	0.0284	0.0003	0.0001	0	0	0	0	0	
Juv.	0.0239	0.0256	0.0290	0.0039	0.0024	0.0001	0.0001	0	
Pre.	0	0.0029	0.0413	0.0860	0.0596	0.0071	0.0016	0.0006	
Sm.	0	0	0.0131	0.0909	**0.2440**	0.0367	0.0134	0.0037	
Med.	0	0	0.0008	0.0070	0.0532	0.0239	0.0089	0.0057	
Lrg.	0	0	0	0.0029	0.0142	0.0172	0.0188	0.0043	
Xlrg.	0	0	0	0.0010	0.0034	0.0052	0.0077	0.0055	
Sums	0.1051	0.0288	0.0852	0.1990	0.4019	0.0994	0.0573	0.0288	

ally upon both the initial conditions and the difference between the dominant and subdominant eigenvectors). It can be used to answer the question: how many years before the dominant eigenvalue is x times more important? This is given by

$$t_x = \ln(x)/\ln(\text{damping ratio}), \quad (8)$$

where x is the number of relative importance (10, 20, or 30 . . .) and t is the number of years (Caswell 1989*b*). For example, for the environment with a damping ratio of 2.2906 (plot 2, 1982–1983), it would take 2.8 yr for the dominant eigenvalue to dominate by 10-fold. To compare, for the environment with the damping ratio of 1.3751 (plot 2, 1984–1985), it would take 7.2 yr.

Stable-stage distributions.—These were all dominated by the seed class (Fig. 8). More than 90% of the population belonged to the seed class for plots 1 and 3 for most years. In plots 2 and 4, a slightly lower percentage of the stable-stage population were seeds (Fig. 8). Among the nonseed stages, the stable-stage distribution was dominated by seedlings, exceeding 50% in most years and plots (Fig. 9). Even when seedlings made up <50%, they were always either the most frequent or the second most frequent class of the distribution. Among the nonseedling stages, small reproductives were the next most frequent class in 11 of the 16 matrices (Fig. 9). The four exceptions were: juveniles (both plots 2 and 3 in 1982–1983), extra-large reproductives (plot 3 in 1985–1986), and prereproductives (plot 4 in 1984–1985 and 1985–1986) (Fig. 9). Differences among the matrices in stable-stage distributions are important because they contribute to differences in sensitivity structure (Eq. 4).

All except one of the observed stage distributions differed significantly from the expected stable-stage distribution (Fig. 9). Nevertheless, the proportional similarities (Eq. 7) indicated that the observed distributions were not very far from the stable-stage distributions ($\bar{X}$ = 86.1%, SD = 7.9, N = 16).

Reproductive values.—These increased with increasing stage class for most years and plots (Fig. 10). This pattern results from a monotonic decrease in mortality and increase in fertility with size (Fig. 3), especially because plants increased stage classes, or at least they remained as reproductives, more than they regressed to nonreproductives (Tables 7 and 8). Exceptions to this pattern were found in the 1982–1983 transitions for plots 1 and 2 (Fig. 10). In both cases, even though the reproductive plants were observed to grow to a larger stage class, the fates of the class to which they were growing was a demographic dead end for that particular matrix (Tables 7a, b, 1982–1983). This "dead end" refers to the situation in which individuals belonging to a larger stage were not present in the year t, but were present in $t + 1$; since they were not present in t, the entries for their transitions or contributions to the population at $t + 1$ are zero.

Sensitivity.—Sensitivities are most comparable among parameters of similar order of magnitude in similar matrix positions and therefore comparisons

TABLE 10. Coefficient of variation (SD/mean × 100) of transition parameters. Values over 100 are shown in boldface. The two least variable parameters are underlined.

Stage at time $t + 1$	Stage at time t							
	Sd.	Sdlg.	Juv.	Pre.	Sm.	Med.	Lrg.	Xlrg.
Sd.	19	...	**147**	78	51	73	95	**198**
Sdlg.	89	**117**	**211**	...	...	...	...	...
Juv.	**238**	78	36	**117**	**135**	**400**	**400**	...
Pre.	...	**400**	61	39	62	**165**	**365**	**366**
Sm.	...	...	**131**	43	22	78	**127**	**271**
Med.	...	...	**400**	**165**	**106**	96	**115**	**279**
Lrg.	...	...	...	**281**	**194**	**126**	93	**239**
Xlrg.	...	...	...	**400**	**307**	**280**	**189**	**239**

TABLE 11. The signs of correlations analyzed by blocks to compare correlations of particular demographic features (regression, stasis, growth, and seed production) within and among stages (see Appendix 3 for magnitudes of the correlations). Within each block, to analyze whether there was a significantly positive or negative trend, a binomial test for small (S) or for large (L) samples was applied, depending on the number of correlations in the block (Siegel 1956) (z values are given only for L tests and probabilities and type of test are reported for significant analyses only).

Demographic feature	Regress	Stay the same	Grow	Make seeds
Regress	8+/7−			
Stay the same	14+/34− L* (z = −2.74)	16+/12−		
Grow	8+/34− L*** (z = −3.47)	30+/12− L* (z = −2.36)	19+/2− S**	
Make seeds	13+/11−	18+/14−	25+/3− L**** (z = −3.97)	6+/0− S*

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$.

across years and plots are more interesting than within-matrix comparisons. Following, we present both the general patterns and the spatiotemporal variations.

The sensitivity values for the parameters that represented the contribution to next year's seeds by each class were of the smallest order of magnitude (mostly <0.005) (Fig. 11, left) compared to other transitions (Fig. 11, center and right, and Fig. 12). Of these, there was a peak for reproduction by the small reproductives for most plots and years (Fig. 11, left). Exceptions were at plot 3 (1982–1983 and 1985–1986) and at plot 4 (1984–1985 and 1985–1986). The year that generally had the highest sensitivity for reproduction by each stage class was 1982–1983, and plot 2 had the highest of the plots in this year (Fig. 11, left). The plot that most consistently had low sensitivities for reproduction (<0.0015) was plot 1 (Fig. 11), while the most consistently high sensitivities for reproduction were found at plot 2 (Fig. 11).

The transitions from seeds include some of the sensitivities of largest order of magnitude (up to 40) (Fig. 11, center). Of these, the transition from seed to juveniles had the highest in most years and plots (Fig. 11, center, e.g., plot 1 in 1982–1983).

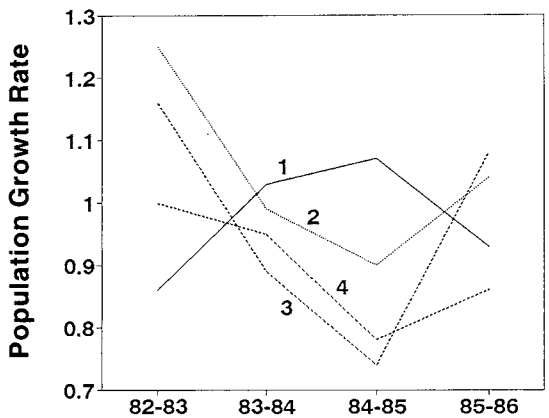

FIG. 7. Population growth rate for each year and plot, measured by λ_1, the dominant eigenvalue of the projection matrix for a given year and plot. Plots 1, 2, 3, and 4 are each represented by different lines.

Transitions from seedlings had the next highest sensitivities (up to 5.0) (Fig. 11, right), especially rapid growth of seedlings to juveniles and to prereproductives (Fig. 11, right). The 1982–1983 matrices generally had the highest sensitivities for the transitions from seedlings in all plots (Fig. 11, right). At two plots in some years [plot 3 (1982–1983 and 1985–1986) and plot 4 (1982–1983)], the sensitivity matrices exhibited notably higher values for seedling fates (from 3.7 to 4.8) than in the other matrices (always <2.0) (Fig. 11).

To summarize the patterns of sensitivities for contributions to seeds, seed fates, and seedling fates, we note that population growth rate was more readily influenced by certain demographic events at some plot-years and by different demographic events at other plot-years. For example, the population growth rate at plot 2 was more readily influenced by reproduction, while plot 1's growth rate was more sensitive to changes in seed fates. Both plots 3 and 4, in certain years, had growth rates that were most sensitive to changes in seedling fates than other plots (Fig. 11). This means that the fitness consequences of particular small changes in particular demographic probabilities differed through space and time.

Transitions from one size class to another for plants beyond the seedling stages had intermediate sensitivities (up to 1.0), lower than those for seeds and seedlings, but higher than those for contributions to seeds (Fig. 12). The transitions of small reproductives had

TABLE 12. Damping ratios (λ_1/λ_2) for projection matrices from each year and plot.

Year	Plot 1	Plot 2	Plot 3	Plot 4
1982–1983	1.4318	2.2906	1.8857	1.9735
1983–1984	1.5937	1.9769	1.5813	2.1032
1984–1985	1.8039	1.3751	1.4174	1.8799
1985–1986	1.8236	1.7378	1.6474	1.7039

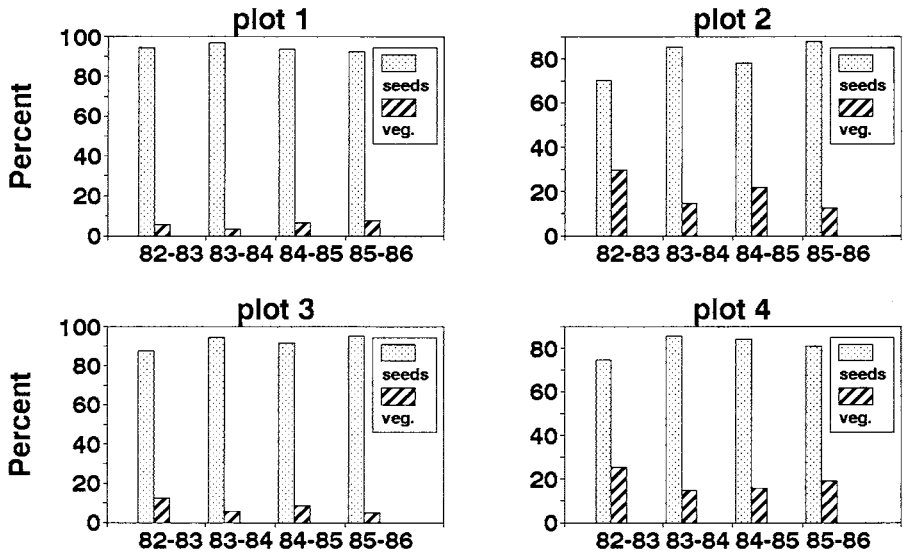

FIG. 8. The stable-stage distribution for each year and plot; the relative proportions of seeds and vegetative individuals.

higher sensitivities than transitions of other stage classes in 11 of the 16 matrices (Fig. 12), but their sensitivities varied among years and plots (Fig. 12). Similarly, so did the sensitivities of other nonseedling transitions (Fig. 12). Note that if sensitivities had monotonically decreased from left to right across the transition probability matrix (as they may do in age-classified populations), one would expect juveniles and prereproductives to have higher sensitivities than small reproductives. In 1982–1983, juveniles did show more sensitivity than in other years at plots 2, 3, and 4 (Fig. 12). The sensitivity of prereproductives exceeded that of small reproductives only at plot 4 in 1984–1985 and 1985–1986 (Fig. 12). The larger reproductives (medium, large, and extra-large) had low sensitivities (compare the curves for these stages to the curves for the others in each graph of Fig. 12), except in 1985–1986 at plot 3. Extra-large reproductive plants in that case had higher sensitivities than any other nonseedling stage.

Overall, there was significantly more spatial variability than temporal variability in sensitivity parameters ($z = 2.932$, $P = 0.0034$; sign test, Siegel 1956). In 31 out of 46 transition parameters the average $CV_{\text{among plots}}$ exceeded the average $CV_{\text{among years}}$; 4 parameters were tied and only 11 parameters had temporal variability exceeding spatial. The fates of juveniles had the largest number of exceptions to the general pattern; four of these parameters showed more variation through time than through space as did three parameters associated with the fates of small reproductives.

Elasticities.—The small reproductives were the stage class with the largest total elasticity for most plots and years (Fig. 13). Of all the life history paths involving small reproductives, their stasis was the single parameter of maximum elasticity out of the possible 64 in the matrix in most matrices (plot 1, all years; plot 2, 3 yr; plot 3, 2 yr; and plot 4, 3 yr). It ranged from 0.029 to 0.576 ($\bar{X} \pm \text{SD} = 0.282 \pm 0.169$). Exceptions to the pattern of the concentration of elasticity in small reproductives were also found. In 1982–1983, elasticity was more evenly spread out among the stages for all plots except plot 4 (Fig. 13), because the fates of seeds were relatively more important than in other years (Fig. 13). In plot 3 (1982–1983 and 1985–1986) elasticity was not dominated by small reproductives, but rather by extra-large reproductives (Fig. 13) who were also relatively more important in the stable-stage distributions for these two matrices than for any of the other matrices (Fig. 9). In plot 4, the elasticity in 1985–1986 was highly concentrated in the prereproductives (Fig. 13). Of all the plot-year matrices, the matrix for 1982–1983 at plot 2 was the one for which elasticity was most evenly distributed among the stages (Fig. 13).

To represent the elasticity for reproduction by a single parameter, we summed the elasticities across the top row for those classes contributing to new seeds for each plot and year (Fig. 14). The elasticities for reproduction were relatively small compared to the total elasticities (Figs. 13 and 14), except plot 2 in 1982–1983 (Fig. 14). At all plots, the year with the highest elasticity for reproduction was 1982–1983 (Fig. 14). At plots 1 and 4 reproduction was less important in 1983–1984 and 1985–1986 than in the other years.

Elasticities for each entry in the matrix varied significantly more through space than time ($z = 2.473$, $P = 0.0136$; sign test, Siegel 1956), similar to the sensitivities. Since elasticities are products of projection matrix entries with sensitivities and since both of these varied more through space than time, this result is not

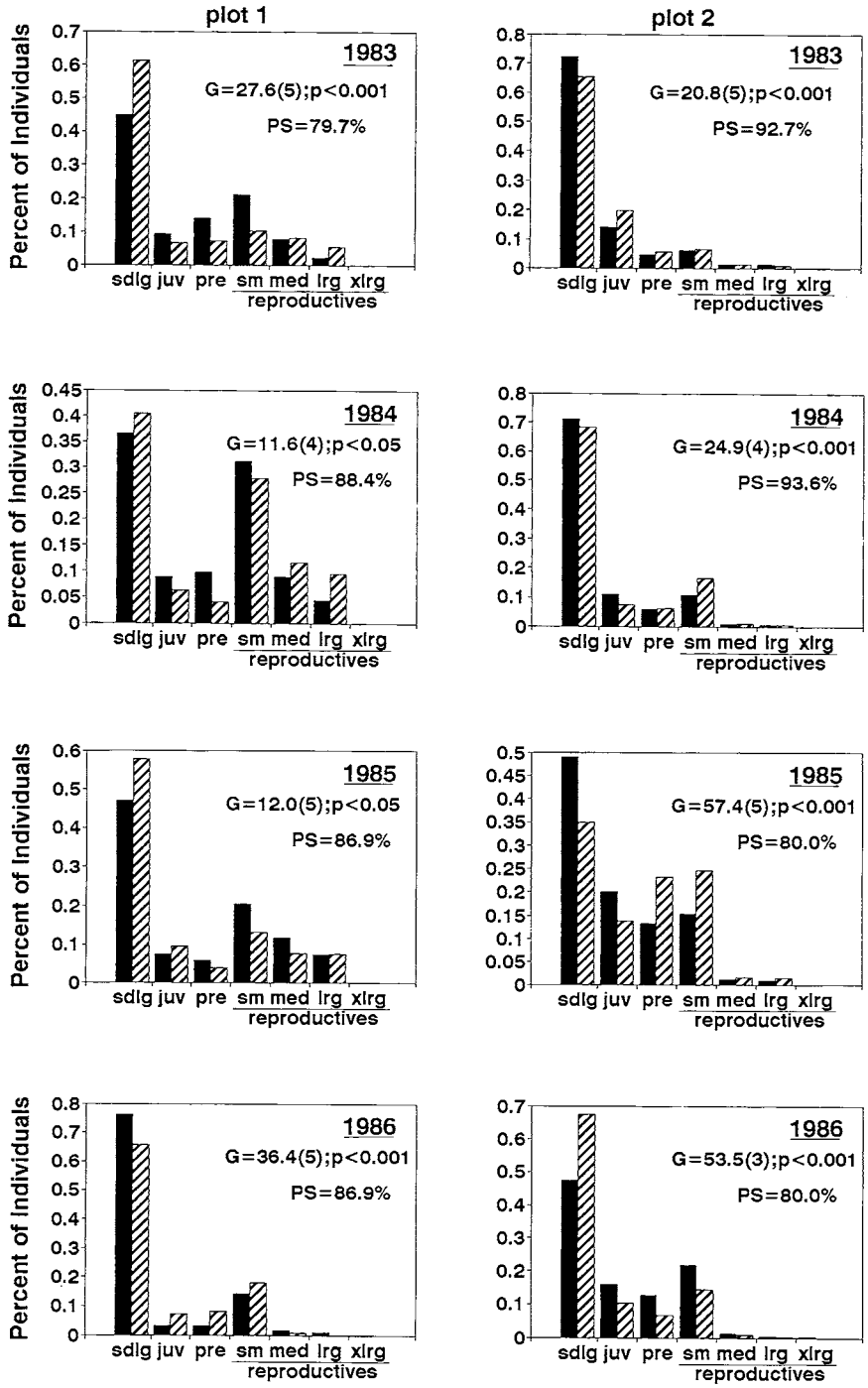

FIG. 9. The stable-stage distribution (hatched bars) for each year and plot; the structure for the vegetative individuals compared with the observed stage structure (solid bars) in the year being projected to (1983 in the 1982–1983 transition, for example). The G statistic, indicating whether there is a significant difference between the observed and the stable distribution, and PS, indicating the magnitude of the difference between the two distributions, are given.

surprising. In 24 out of 44 transition parameters the average $CV_{\text{among plots}}$ exceeded the average $CV_{\text{among years}}$; 12 parameters were tied and only 8 parameters had temporal variability exceeding spatial.

Correlations of stage-specific elasticity with population growth rates

Population growth rate was significantly positively correlated with elasticity of germination, seedling

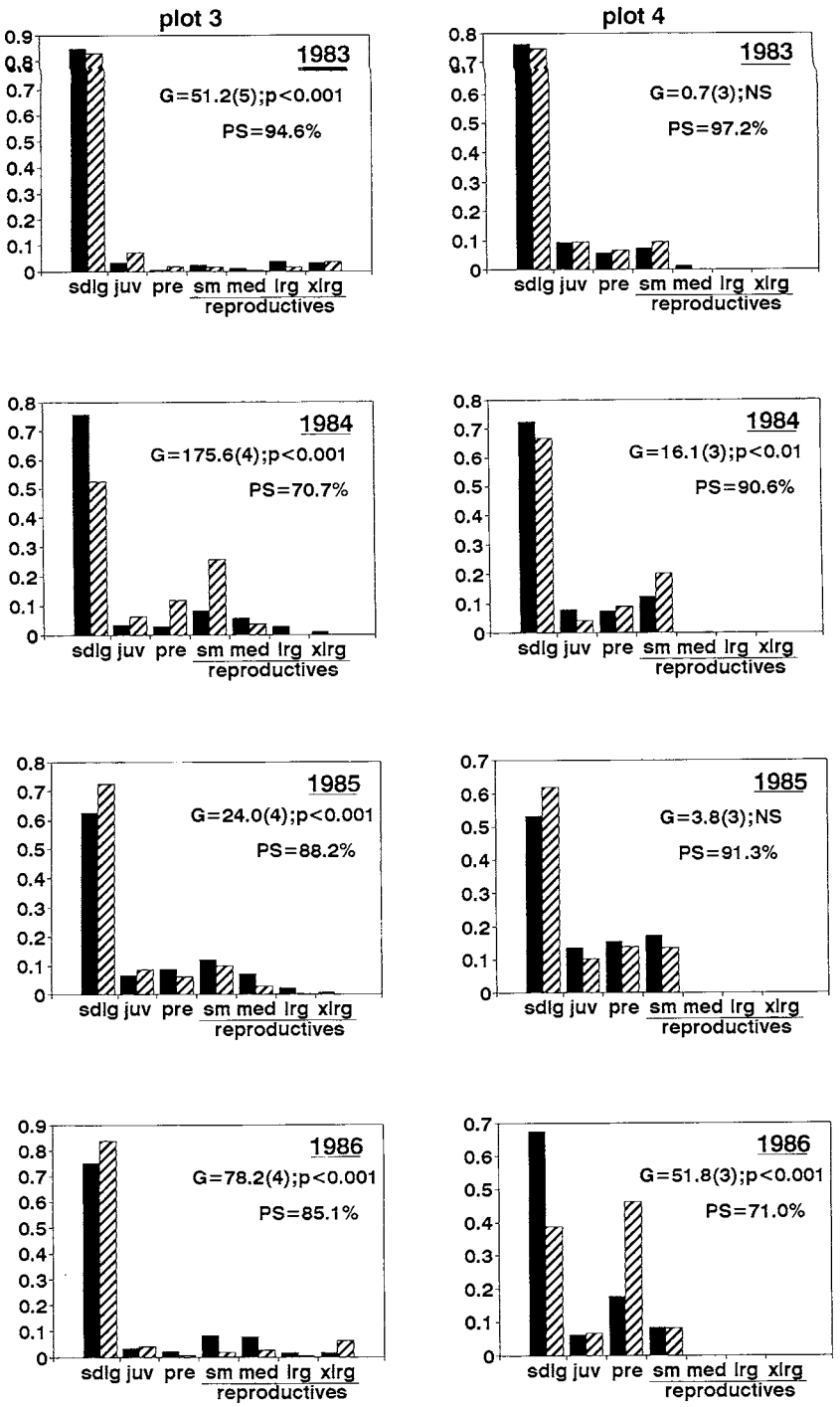

FIG. 9. Continued.

growth, and reproduction by large reproductives (Table 13).

DISCUSSION

This paper represents the demographic analysis that is the core of a long-term study of how animals interacting with plants affect plant fitness, where the average fitness of plants is measured by the population growth rate. Previous papers focused on the effects of plant–animal interactions on particular demographic transitions (Horvitz and Schemske 1984, 1986*a*, *b*, *c*, 1988*a*, 1990, 1994, Schemske and Horvitz 1984, 1988, 1989). The most relevant of the findings reported in the current paper is the spatiotemporal vari-

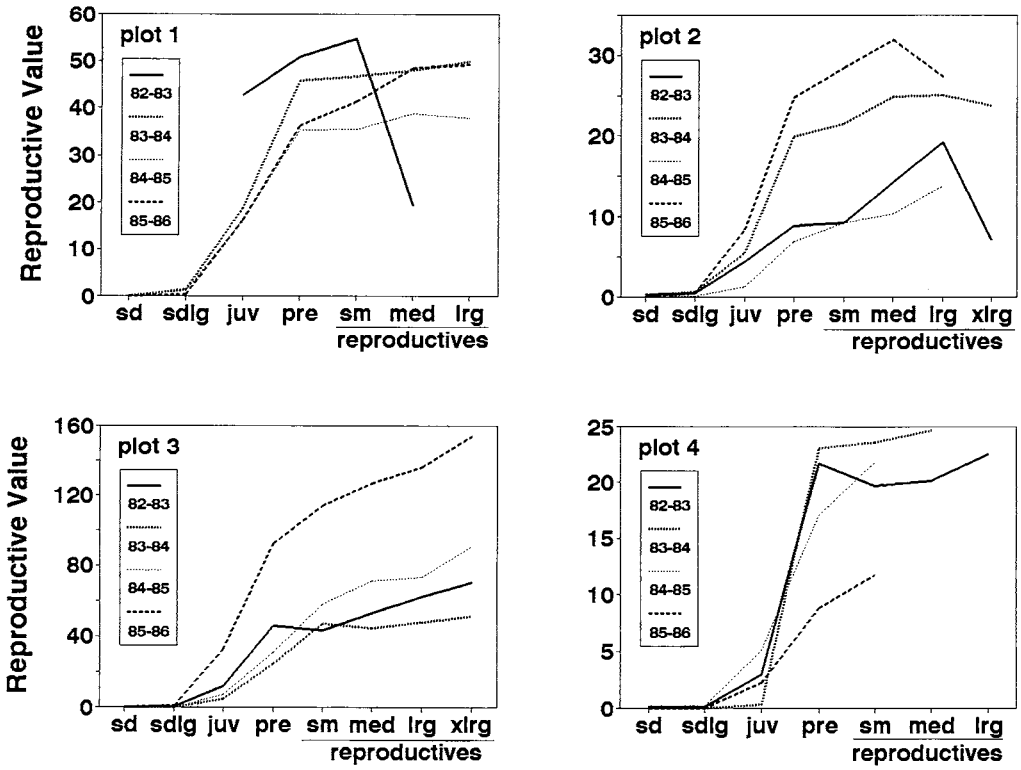

FIG. 10. The stage-specific reproductive values for each year and plot.

ability of sensitivity structure, which will limit the extent to which single-stage effects will be translated into effects on plant fitness. Thus, the potential for evolutionary responses of plant populations to the beneficial and detrimental animals that interact with them will also be heterogeneous in time and space.

Our goal in the discussion is (1) to synthesize the demographic analyses to present a picture of the overall demography of a rain forest understory herb and (2) to show how variations are important, particularly in our attempt to identify critical life history stages that are key to population fates or that represent greater or lesser opportunities for selection.

Synthesis: mortality and fertility

The first fundamental characteristic of the demographic pattern of our study species was high seedling mortality (93.4% of newly germinated plants died within the 1st yr) (Figs. 1 and 3a, Table 7) and low adult mortality (all reproductive stages had an annual survival >80% in all plots and years) (Fig. 3a, Table 7). The seed stage, which exhibited long-term facultative dormancy, also had lower mortality than the seedling stage. The vulnerability of the seedling stage and high survival of the adults is a pattern common to many perennial plants (Harper 1977, Piñero et al. 1984, Moloney 1988). In spite of the vulnerability at this stage, population growth was not highly sensitive to seedling fates in most plots and years by either sensitivity or elasticity parameters (Figs. 5, 11, 13). The low mortality for adults was coupled with an ability to change size in response to environmental changes; when the environment worsened, bigger plants tended to shrink rather than to die (Table 7). The second fundamental characteristic of the demographic pattern was that fertility increased with plant size (Fig. 3b).

Synthesis: stable-stage distributions and reproductive values

The mortality, fertility, and growth of the different life history stages (used to calculate the entries of the population projection matrix) determined the patterns of the stable-stage distribution and reproductive values. Observed stage distributions were reasonably close to the stable-stage distributions (mean = 86.1% similar), indicating that the analysis of the asymptotic dynamics was relevant to the characterization of the demographic environment at a given point and time. The stable-stage distribution was dominated by seeds; in most cases nearly 90% of the stable population vector was composed of seeds (Figs. 4a and 8). Seeds, however, had very low reproductive value (Figs. 4b and 10) because they still had to traverse the high mortality of the seedling stage and additionally survive through several prereproductive stages before reaching a reproductive size class. Seedlings were the second most abundant

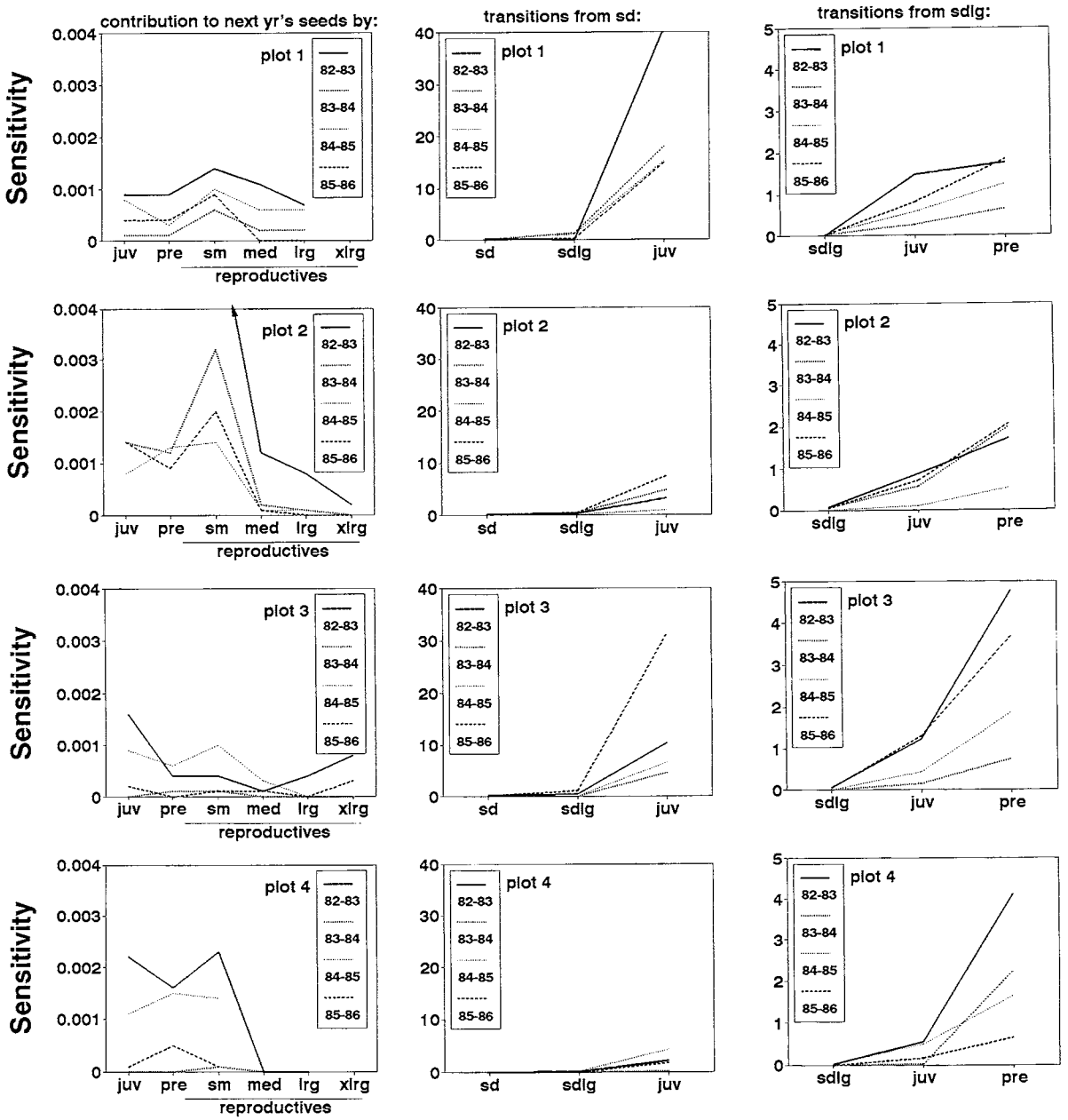

FIG. 11. The sensitivities for each year and plot of population growth rate to perturbations in: the contributions to seeds made by each stage class (left), transitions from seeds to other classes (center) and transitions from seedlings to other classes (right). For plot 2 in 1982–1983 the sensitivities for contributions of seeds by small reproductives, prereproductives, and juveniles were off the scale of the graph, with values of 0.006, 0.005, and 0.018, respectively.

class of the stable-stage distribution, usually representing from 4 to 8.5% of the stable population vector (Figs. 4a, 9). Seedlings were also low in reproductive value (Figs. 4b, 10), for the same reasons. The remaining stages varied in their relative importance, but small reproductives were frequently prominent among the nonseedling vegetative stages in the stable population vector. The reproductive value of the reproductive stages was high and increased with size class (Figs. 4b, 9), as these stages had low mortality and as fertility increased with size. The highest reproductive value was for extra-large reproductives, a stage class that was rarely present.

Synthesis: the transitions of highest elasticity in most years and plots

These patterns of the stable-stage distribution and of the stage-specific reproductive values resulted in population growth being particularly sensitive to the fates of small reproductive plants, which in turn resulted in

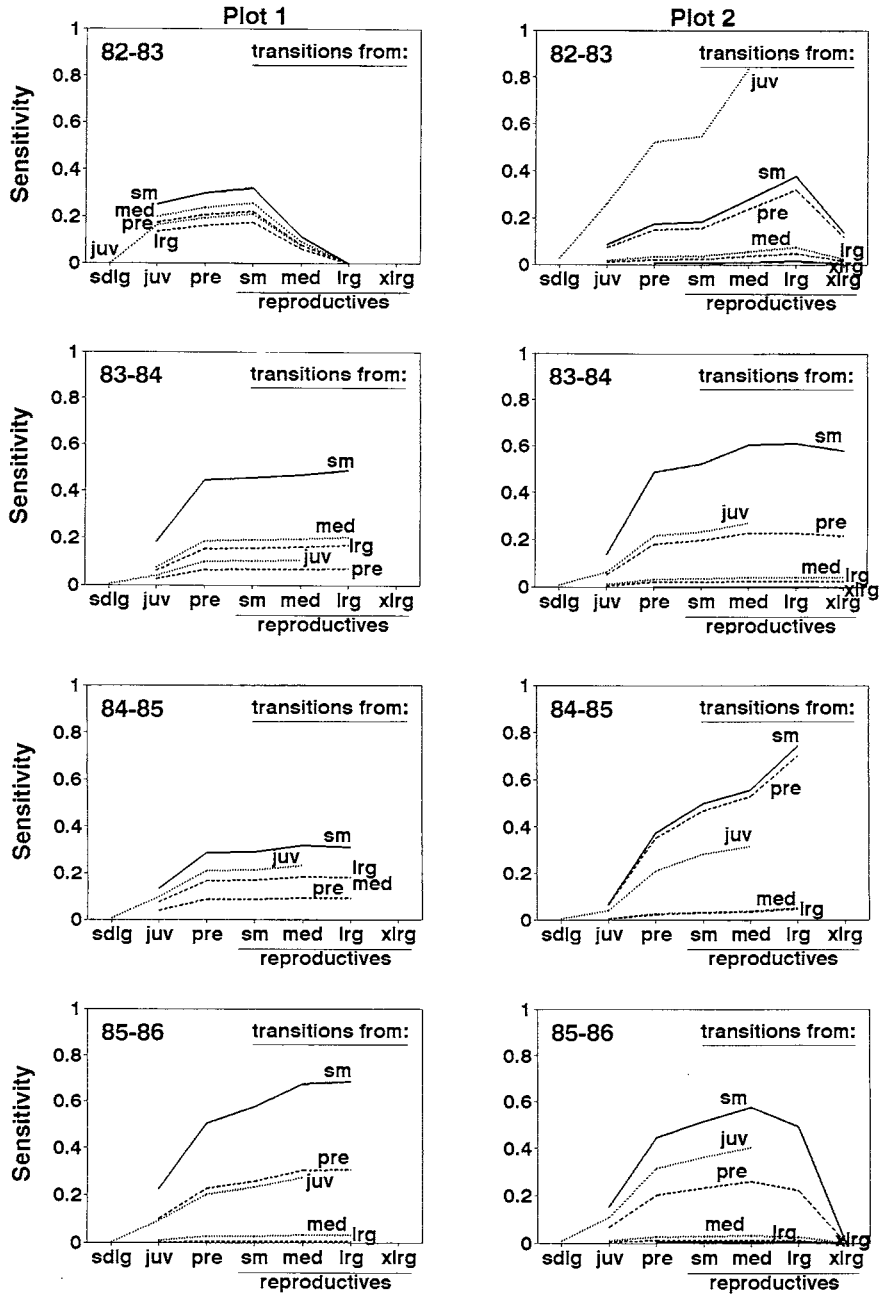

FIG. 12. The sensitivity for each year and plot of population growth rate to perturbations in the transitions *from* juveniles, prereproductives, and each class of reproductive *to* other classes, with each line in each figure corresponding to a given stage at time t and stages along the x axis corresponding to a stage at time $t + 1$; thus, transitions are *from* the stage associated with a given line and *to* the stage written on the x axis.

high elasticity for this life history stage in most plots and years (Fig. 13) and for the pooled population (Fig. 6). The sensitivity of population growth rate to the fates of young/small adults or the stage just previous to reproduction may be common in long-lived organisms in general, including mammals (Boyce 1988), birds (Meyer and Boyce 1993), and turtles (Crouse et al. 1987) as well as some trees (Piñero et al. 1984, and analyses therein of data from Enright and Ogden 1979). Examples of other plant studies have found high demographic sensitivities (measured by elasticity or by sensitivity) to be for other stages: the growth and survival of the next to largest sizes for a seaweed (Aberg 1992*a*); the transitions of the smallest stages for a savanna grass (Silva et al. 1991); the growth of young stages in a perennial temperate grass (Moloney 1988); and sprout production in both a clonal herb (Sarukhán and Gadgil 1974) and a clonal shrub (Huenneke and

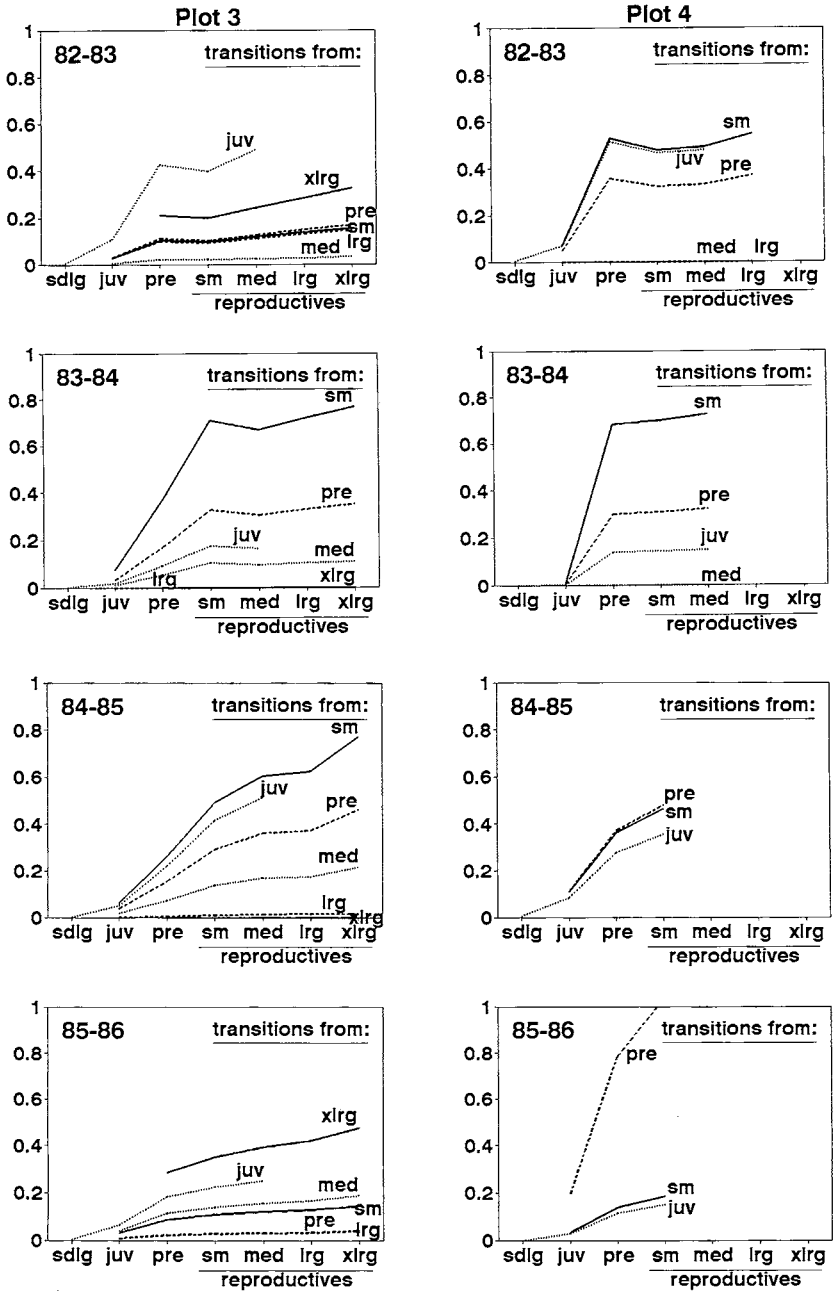

FIG. 12. Continued.

Marks 1987). Generally, survival has been found to be more important in trees while growth is more important in herbs (Caswell 1989*b*, Silva et al. 1991). Our study species, a long-lived perennial herb, behaved more like a tree in this respect in most years and plots, but more like other herbs in years/plots of highest population growth.

Spatiotemporal variability: stage structure, density, and recruitment

An important result of our study was significant spatial and temporal variability in demographic features of the population. The stage structure, expressed as the density of different stages, varied more across plots than across years with the notable exception of the seedlings (Fig. 2). Seedling recruitment from the seed bank was more variable among years: el Niño years were associated with large seedling numbers. The observed stage structure itself was not predictive of population dynamics; plots 2 and 4 had the most similar nonseedling stage structure (Fig. 2) but the least similar population dynamics. The observed variability among the plots in demographic features cannot be attributed

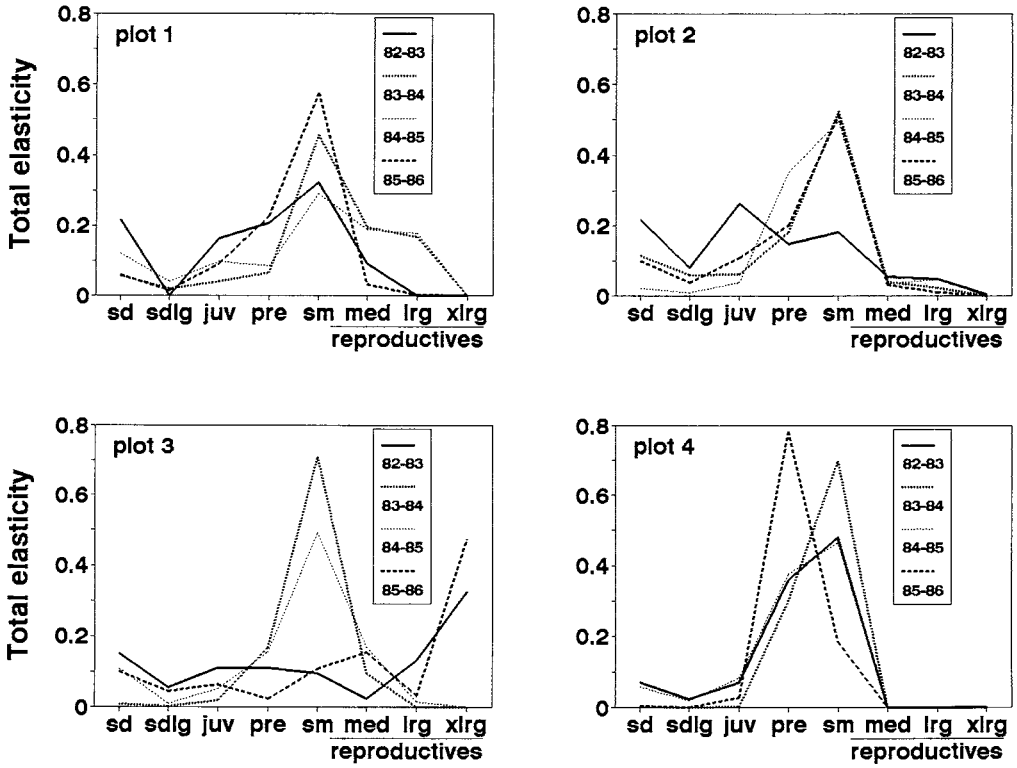

FIG. 13. The stage-specific elasticity, summed over the whole column to include the elasticities of contributions to seeds as well as those of transitions to future stages, for each stage class for each year and plot. Note that, within a figure for a given plot, each line describes the shape of the way elasticity is apportioned among the stage classes for a given year. The total elasticity of all the stage classes is constrained to sum to one.

to a single factor. The substrate, light environment, and biotic environment all varied over the spatial scale from which we drew our plots. The light environment, heat, moisture, and biotic environment also varied across the years of the study.

Spatiotemporal variability: fates of vegetative individuals

Not only did the stage structure and density vary, but also the demographic fates of several vegetative stages varied through space and time. In particular, the fates of seedlings and small reproductives, as well as inflorescence production per plant, were significantly affected by the environmental differences between years and plots. The fates of large reproductives varied among years but not plots, while the fates of juveniles varied among plots but not years. The magnitude of variation, given by the coefficient of variability for each parameter among the 16 plot-year matrices, ranged from 19 to 400%, indicating that some parameters showed very little variation, while others showed tremendous variation among the 16 environments (Table 10). The two least variable parameters were seed dormancy and stasis of small reproductives. We emphasize that variance was not predictive of how big a contribution to population growth is made by a particular event; these two life history transitions of very low variability differed greatly in their elasticities (in the pooled matrix, Table 9). The highest variabilities were observed for the rare transitions like rapid growth and shrinking by several stages (Table 10).

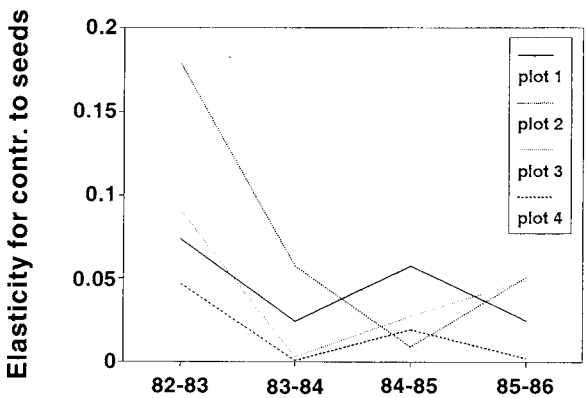

FIG. 14. The elasticity for the contributions made to seeds summed over all stage classes, for each year and plot.

We analyzed whether the demographic parameters in the population projection matrix varied more spatially than temporally and we found that there was a marginally significant trend for more spatial than temporal variation across the whole matrix structure. These

TABLE 13. Spearman rank correlations between λ and stage-specific elasticity (N = 16 matrices), arranged in the matrix locations of the elasticity parameters (e_{11}–e_{88}). Only matrix parameters that had more than two nonzero elasticities were analyzed (k = 31 correlations). Significance levels were determined by the Bonferroni sequential method for calculating tablewide probabilities, $\alpha/(1 + k - r)$, where r = the rank of the unadjusted probabilities (Rice 1989).

Stage at time $t + 1$	Stage at time t							
	Sd.	Sdlg.	Juv.	Pre.	Sm.	Med.	Lrg.	Xlrg.
Sd.	0.094	...	0.235	0.286	0.268	0.371	0.773*	...
Sdlg.	0.767*	0.246	−0.058	...	...	...	...	...
Juv.	0.369	0.799**	0.215	−0.534	−0.093	...	...	...
Pre.	...	...	0.321	−0.597	−0.585	−0.186	...	...
Sm.	...	...	0.197	−0.594	−0.326	0.051	0.052	...
Med.	...	...	...	0.406	0.041	0.107	0.545	...
Lrg.	...	...	...	...	0.440	0.611	0.604	...
Xlrg.	...	...	...	...	...	...	0.669†	...

† $P < 0.13$; * $P < 0.05$; ** $P < 0.01$.

kinds of data (CV's of demographic parameters across both space and time) have not been previously emphasized. Models of environmental variation often assume that all parameters vary equally (Menges 1992). Our data suggest that more realism could be introduced by using differing variances for different parameters.

Spatiotemporal variability: correlations of demographic parameters

Demographic features, including stage-specific regression, stasis, growth, and seed production, were frequently correlated across environments (Table 11). For example, if one stage found a particular environment good for reproduction, so did another. Also growth was positively correlated with reproduction; it was not negatively correlated (as a trade-off model of alternative investment strategies might suggest). Such positive correlations between growth and reproduction may be common for organisms with size-dependent fertilities. There are very few data on the correlated variation of demographic parameters in matrix models of plant populations (see Brault and Caswell 1993 for covariance of population projection matrix parameters among whale pods). Some models of environmental variation in demography have assumed that the parameters vary independently (Menges 1992). Our results suggest that correlations may be common and that the sign of the correlations may be related to the life history of the study organism.

Spatiotemporal variability: overall trends

Demographic transitions and sensitivities were more variable among patches of forest than among years for most stages, although for some stages the variation among years was greater. Notably, seed fates varied more through time than space. There were distinct temporal trends in the environment that affected the relative values of population growth rates among years for most plots similarly, except one plot in which a canopy gap opened up adjacent to the plot as the result of a treefall event. The best year for population increase, as reflected by population growth rates, was the 1982–1983 transition, which was also an el Niño year. The most favorable plot was plot 2, as reflected by population growth rates; it was also the least shady plot at the beginning of the study. Again, we emphasize that one cannot point to a single, particular transition parameter to explain these results.

Spatiotemporal variability and overall picture: population growth rates

The variability in demographic parameters resulted in variable population dynamics among our plots and years, with λ = 0.73 to 1.25. Nevertheless, our analyses of the mean dynamics gave λ = 0.97 (using a variety of analytical approaches) and our analysis of the overall pooled dynamics gave a λ = 0.99, indicating that the secondary forest at Laguna Encantada is a habitat that favors the persistence of *Calathea ovandensis,* even though there are some patches of the forest where the population was increasing and others where it was declining. The pooled sample weights the more successful plots and years more heavily, because it is weighted by individuals and there were higher numbers of individuals in the "better" years and plots. The variation in population growth rates among our study sites was relatively small, compared to other studies of herbs (Werner and Caswell 1977, 0.0–2.60; Bierzychudek 1982, 0.85–1.32; Fiedler 1987, 0.96–1.39; Moloney 1988, 0.60–1.43; van Groenendael and Slim 1988, 1.03–1.93; Menges 1990, 0.64–1.81; Silva et al. 1991, 0.27–1.25; Kalisz and McPeek 1992, 0.30–2.56). Our finding of λ close to 1 was more similar to reports of demography of trees and shrubs (Hartshorn 1975, Enright and Ogden 1979, Piñero et al. 1984, Huenneke and Marks 1987).

Other studies finding temporal variation for plant demography have tended to emphasize "good" vs. "bad" years. For example, "fire" vs. "nonfire" years for a fire-adapted savanna grass (Silva et al. 1991), "normal" vs. "ice" years for a seaweed (Aberg 1992*a*, *b*), and "good-" vs. "bad-for-vegetative-individuals" years for an annual with an age-structured seed bank (Kalisz and McPeek 1992, 1993). A few studies, in

contrast, have considered the combined effects of yearly sequences of matrices multiplied together (Huenneke and Marks 1987, Moloney 1988), to emphasize differences among plots even in the presence of temporal variation. For our study organism, it was less clear that the good vs. bad years could be as readily interpreted (e.g., "fire" vs. "no fire" is very distinct) as in some of these other studies. The finding that el Niño years are good years for understory plant populations in a Meso-American neotropical forest was surprising. The environmental factor(s) that may have caused the worst year for our study organism was unknown. In general, in moist tropical rain forests, year-to-year variation in plant population behavior has only recently been appreciated (Clark 1994). In a 6-yr demographic study of nine tropical forest trees in Costa Rica, Clark and Clark (1992) found striking between-year variation in growth rates that was expressed across species. The most surprising feature was that the best year for growth was the year of lowest rainfall at their site (Clark and Clark 1992), despite the general textbook notion that tropical rain forest stature is due to abundant rainfall. Our results together with their results emphasize that only long-term demographic studies can elucidate what kinds of environmental variability may be important to plant populations.

Spatiotemporal variability in sensitivity/elasticity: why it is interesting

The most interesting of our results was that not only did survival, growth, and reproduction vary through space and time, but also the degree to which population growth rate was sensitive to changes in these basic demographic features varied through space and time. This is interesting because it indicates that for a given change in a demographic transition, the fitness response is itself spatiotemporally variable. Thus, for characters that cause variation in stage-specific demographic transitions, selection on these characters would be variable through space and time, simply due to demographic characteristics of the population. A consequence for the study of plant–animal interactions is that the magnitude of selection by animals on plants may be variable simply due to variation in the plant's demographic sensitivity, even given the same animal with the same stage-specific effect. For sensitivity parameters, there was significantly more variation through space than through time.

The elasticity, the proportional contribution of life history paths to population growth, also varied spatiotemporally. The general trend in most plots and years was that small reproductives proportionately contributed the most to population growth compared to other stages. However, in the year with the highest growth rates (1982–1983, Fig. 7), elasticity was more evenly distributed and younger (smaller) stages were also important (Fig. 13). Also, in the same year, seed production was relatively more important than in other years (Fig. 14). Other reports of variation in elasticity structure for plants have emphasized the role of particular transitions in "good" vs. "poor" years. For an annual herb with a seed bank, the elasticity associated with the seed bank was much greater in years that had low population growth (Kalisz and McPeek 1992). For populations of *Plantago* living in variable habitats, seed production had higher elasticity compared to populations living in more stable habitats in which adult survival had relatively greater elasticity (van Groenendael and Slim 1988).

For *Calathea,* in the years and plots with the highest population growth rates, the sensitivity structure was not like that of the overall pooled matrix or like that of most years and plots. This finding is especially interesting in consideration of how the observed spatially and temporally varying patches may contribute to metapopulation dynamics. In a metapopulation sense, those environments with the highest λs could be more important in the long term than other environments, even if the others occur more often in the landscape (Horvitz and Schemske 1986*b*). The implication is that one cannot decide on the "critical" stages for population persistence based only on the sensitivity structure of the most common environments. Since the sensitivity structure of the rarer but most prolific environments may be quite different, the stage transitions of highest sensitivity in those particular environments may also be critical. This is the result of our study with widest implications for understanding population dynamics.

Correlations of stage-specific elasticity with population growth rates

The life history implication of the correlations that we found was that in environments favoring population growth, the proportional contribution to that growth by seeds and seedlings is larger than in environments less favorable to population growth. This result echoes some of the intuitive interpretations of r and K life history theory, but we note that it comes from a model that does not include density dependence. A significant positive correlation between seedling recruitment elasticity and population growth rate was also found by Silvertown et al. (1993) in their analysis of elasticity patterns across 21 plant species. When they broke the data into herbs and woody species, however, only the woody species had a strong correlation. Our understory herb behaved more like a woody species in this respect.

The implications for plant–animal interactions

The primary motivation for our study was the quantification of stage-specific plant–animal interactions on the fitness of plants. We were especially interested in the impacts of animals affecting seed production, seed fates, and seedling fates. One of our previous papers,

illustrating the demographic approach, investigated a model including seed dispersal, forest dynamics (gap-phase succession), and temporally variable demography (Horvitz and Schemske 1986*a*). There were no empirical data on the temporal variants so several potential patterns representing differing amounts of shade tolerance were investigated. The paper emphasized a simulation of the effects of dispersal and shade tolerance on the metapopulation dynamics. The main result from that model was that seed dispersal by ants (short distance dispersal) and shade tolerance should be strongly associated.

The main result of the present paper relevant to plant–animal interactions that influence single-stage demographic transitions is that the translation of single-stage effects into fitness effects will vary spatiotemporally. To illustrate the application of this result to the question of selection by animals on plants, we present an example. Our previous work has shown that seed production per inflorescence may vary nearly sixfold, from 6 to 33, depending upon the combinations of pollinators, antguards, and herbivores (Horvitz and Schemske 1984, 1988*a*, 1990, Schemske and Horvitz 1984, 1988, 1989). Yet, the present demographic analyses revealed that seed production contributed proportionately little to population growth, as indicated by low elasticity values for most plots and years. The demographic analyses presented here imply that even plots and years experiencing favorable combinations of animals (good pollinators, low herbivory, and good ant defense, for example) may still not exhibit much improvement in fitness unless the same plots and years have high sensitivities for contributions of seeds to population growth. Hence, the "windows" in time and space when animals affect particular components of the population projection matrix may not coincide with the time and space when those particular components have high contributions to population growth rates.

General conclusions

A final comment is that only through demographic analysis can we begin to identify the life history transitions that will be most critical for the ultimate persistence, increase, or decrease of populations. Reproduction is not the same as fitness; it is a component of fitness that is often not the most critical factor for population dynamics, particularly for long-lived organisms. Also, stages of high mortality (often referred to as "bottlenecks") are also not necessarily the stages that are the most critical for population dynamics; in fact higher elasticity is usually associated with higher survival or growth.

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APPENDIX 1

To estimate the mean number of seeds per plant for a stage in each plot and year, we: (a) calculated the mean number of inflorescences per plant of a particular stage in each plot and year and (b) then multiplied each of these by the number of seeds per inflorescence for each plot and year. To estimate the total number of new seeds made in each plot and year, we multiplied the stage–plot-year specific mean number of seeds per plant by the number of individuals in each stage class and summed over all the stage classes.

a)

		Stage											
		Small			Medium			Large			Extra-large		
Plot	Year	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N
1	1982	1.1	0.4	32	2.5	0.7	2	...	...	...	...	...	...
1	1983	1.2	0.4	27	1.8	1.0	10	2.7	0.6	3	...	...	...
1	1984	1.5	0.7	35	3.2	0.9	10	3.4	0.9	5	...	...	...
1	1985	1.5	0.7	28	2.6	1.2	16	2.6	1.6	10	...	...	...
1	1986	1.4	0.7	42	2.6	0.9	5	3.7	0.6	3	...	...	...
2	1982	1.0	0.3	36	1.2	0.4	15	2.0	0.9	6	4.0	...	1
2	1983	1.5	0.7	44	2.4	0.5	9	3.4	0.9	9	4.5	0.7	2
2	1984	1.3	0.7	65	2.4	1.1	5	3.3	1.2	3	...	...	...
2	1985	1.1	0.5	53	1.8	1.0	4	1.7	0.6	3	...	...	...
2	1986	1.1	0.4	67	2.5	1.3	4	3.0	1.4	2	7.0	...	1
3	1982	1.1	0.4	26	1.7	0.8	21	2.4	1.0	31	3.3	1.0	6
3	1983	1.5	0.7	17	2.2	0.8	9	3.2	0.8	29	4.9	1.7	25
3	1984	1.3	0.6	32	2.5	1.0	23	3.4	1.1	11	5.0	1.2	4
3	1984-rep	1.2	0.4	6	1.4	0.8	18	1.9	0.3	9	2.9	1.4	11
3	1985	1.5	0.7	22	2.3	0.8	13	3.2	0.5	4	7.0	...	1
3	1986	1.2	0.5	22	2.3	0.9	21	4.0	2.7	4	5.5	2.6	4
4	1982	1.1	0.3	11	1.5	0.7	13	1.7	0.6	3	...	...	...
4	1983	1.4	0.7	23	2.0	0.8	4	...	...	...	...	...	...
4	1984	1.1	0.4	28	...	...	...	...	...	...	...	...	...
4	1985	1.3	0.4	19	...	...	...	...	...	...	...	...	...
4	1986	1.1	0.3	10	...	...	...	...	...	...	...	...	...

b)

	Plot											
	1			2			3			4		
Year	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N	$\bar{X}$	SD	N
1984	10.7	5.6	25	11.2	9.5	42	13.5	10.9	30	13.1	8.4	17
1985	12.0	10.5	15	4.7	4.3	28	12.3	7.9	22	10.4	7.7	17
1986	17.7	13.4	25	18.6	11.4	24	21.2	11.9	22	20.0	11.2	30
Mean (over 3 yr) used for 1983	13.5	...	...	11.5	...	...	15.7	...	...	14.5	...	...

APPENDIX 2

Calculation of seed dormancy and seedling recruitment probabilities in each year and plot.—In 1985, 1080 marked seeds with intact rewards for dispersers were placed at 12 seed depots throughout the forest among naturally fruiting plants. Ants rapidly discovered and removed seeds. Seedlings arising from these naturally dispersed seeds were counted in each of three subsequent years. We were able to identify the seedlings because the seed coats remain attached to the seedlings. Neither 1986 nor 1988 were el Niño years, while 1987 was (Horvitz and Schemske 1994).

Since we knew that seedling emergence in the demography plots was much higher in el Niño years than in non el niño years, we were motivated to obtain estimates of germination percentage in these two kinds of years:

1) Germination percentage in a non el Niño

= 72 seedlings in 1986/1080 seeds dispersed in 1985
= 6.7% seedlings/seed,

where data from the depot experiments are used.

2) Germination percentage in an el Niño

$$= \frac{\text{seedlings}_{\text{el Niño}}}{\text{seedlings}_{\text{non el Niño}}} \times \frac{6.7\%\ \text{seedlings}_{\text{non el Niño}}}{\text{seed}}$$

$$= 3.07 \times 6.7\%$$

$$= 20.6\%\ \text{seedlings/seed},$$

where seedling emergence in the demographic plots was averaged for 1983, 1987 for the numerator and for 1982, 1984, 1985, 1986 for the denominator, giving the ratio of seedling emergence in an el Niño year to seedling emergence in other years.

We had other independent data on germination percentages from boxes that had known numbers of seeds sown in them, which corroborated these estimates. The intermediate light level treatment in an experiment on the effects of gaps on germination was comparable to the average conditions across plots and depots, and had 6.4% germination in a non el Niño year (compare to the estimate of 6.7% given above). The average germination across all boxes planted near the demography plots in a second experiment had 20.4% germination in an el Niño year (compare to the estimate of 20.6% given above).

To estimate survival of seeds we made two sets of calculations, one for 1986 and one for 1987, as follows. For 1986, the following calculations were made:

a) dormant seeds in 1986 in the seed depots

= 100 seedlings_{1987}/0.206 seedlings/seed
= 485 seeds;

b) dormancy percentage in 1986 in the seed depots

= dormant seeds in 1986/seeds dispersed in 1985
= 485/1080
= 44.9%; and

c) survival percentage in 1986 in the seed depots

= germination percentage + dormancy percentage
= 6.7% + 44.9%
= 51.6%.

For 1987, similar calculations were:

a) dormant seeds in 1987 in the seed depots

= 16 seedlings_{1988}/0.067 seedling/seed
= 239 seeds;

b) dormancy percentage in 1987 in the seed depots

= dormant seeds in 1987/dormant seeds in 1986
= 239/485
= 49.3%; and

c) survival percentage in 1987 in the seed depots

= germination percentage + dormancy percentage
= 20.6% + 49.3%
= 69.9%.

Then, a mean annual seed survival was determined,

(survival percentage in 1986 + survival percentage in 1987)/2

= (51.6% + 69.9%)/2 = 60%.

To incorporate differences among plots for the estimation of germination percentages in each year and plot, we used the data on annual seed production and seedling emergence in the demography plots. We calculated the parameter, s, seedling emergence to seed production ratio,

$$s = \frac{\text{seedlings}_t}{\text{seed production}_{t-1}},$$

where t denotes a given year. This is a black-box estimate of germination, not the true germination percentage, in that it ignores the dormant seed pool. We found the mean of all the plots in a given year and then expressed each plot's s relative to this mean. For each plot, p, and year, t, we then calculated an annual germination percentage as follows,

a) germination percentage (pt, el Niño year)

= (s_{pt}/mean s_t)·20.6%, and

b) germination percentage (pt, non el Niño year)

= (s_{pt}/mean s_t)·6.7%.

To incorporate plot differences in dormancy, we assumed that seed survival was constant among sites and years, at 60%. We then calculated an annual dormancy percentage for each plot, p, and year, t, as follows:

$$\text{dormancy percentage}_{pt} = 60\% - \text{germination percentage}_{pt}.$$

This approach assumes that most of the observed variation in germination is due to variation in dormancy behavior rather than in survival of seeds and that there is a negative correlation between dormancy and germination, an assumption justified by our previous experimental data (Horvitz and Schemske 1994).

APPENDIX 3

Correlations among stage-specific growth, survival, and reproduction parameters. The sum of the entries above the diagonal and the sum of the entries below the diagonal of the matrices give the regression and growth parameters for each stage. For

	Regress to smaller stages								Stay the same stage			
					Reproductives							
	Sds.	Sdlgs.	Juv.	Pre.	Small	Medium	Large	Xlarge	Sds.	Sdlgs.	Juv.	Pre.
Regress to smaller stages												
Sds.	...	...										
Sdlgs.	...	...										
Juv.	...	...	1.00									
Pre.	...	...	−0.06	1.00								
Small	...	...	0.62	0.30	1.00							
Medium	...	...	−0.24	0.34	−0.02	1.00						
Large	...	...	−0.08	0.27	−0.12	0.54	1.00					
Xlarge	...	...	−0.10	0.20	−0.04	0.33	0.46	1.00				
Stay the same stage												
Sds.	...	...	0.01	0.32	−0.04	−0.21	−0.09	−0.33	1.00			
Sdlgs.	...	...	0.25	−0.07	0.02	−0.28	−0.24	−0.18	0.21	1.00		
Juv.	...	...	−0.02	−0.42	−0.06	0.03	−0.24	−0.51	−0.07	0.10	1.00	
Pre.	...	...	0.47	0.07	0.44	0.19	−0.17	−0.28	−0.15	−0.09	0.35	1.00
Small	...	...	−0.03	0.16	−0.17	0.56	0.24	−0.10	0.09	0.13	0.36	0.50
Medium	...	...	−0.18	−0.23	−0.53	−0.41	0.09	−0.05	0.33	0.23	−0.02	−0.56
Large	...	...	−0.33	−0.17	−0.36	0.06	−0.05	−0.02	−0.03	0.34	0.14	−0.42
Xlarge	...	...	−0.18	−0.10	−0.43	−0.36	−0.21	−0.08	0.09	0.16	−0.43	−0.49
Grow to larger stages												
Sds.	...	...	−0.01	−0.32	0.04	0.21	0.09	0.33	−1.00	−0.21	0.07	0.15
Sdlgs.	...	...	−0.35	−0.41	−0.28	0.21	0.17	0.29	−0.55	0.15	0.25	−0.25
Juv.	...	...	−0.29	−0.39	−0.46	−0.57	−0.16	0.04	−0.09	0.11	0.27	−0.45
Pre.	...	...	−0.48	−0.59	−0.77	−0.21	−0.01	−0.13	−0.03	0.04	0.15	−0.66
Small	...	...	−0.37	−0.38	−0.64	−0.50	−0.19	−0.11	0.20	0.00	−0.09	−0.64
Medium	...	...	−0.27	−0.54	−0.57	−0.54	−0.32	0.20	0.04	−0.04	0.26	−0.50
Large	...	...	−0.01	−0.24	−0.35	−0.29	−0.29	−0.05	−0.24	0.34	−0.06	−0.41
Xlarge	...	...	...	...	...	...	...	...	...	...	...	...
Seed production												
Small	...	...	0.29	−0.03	−0.23	−0.39	0.11	−0.10	−0.00	0.08	−0.21	−0.22
Medium	...	...	−0.24	0.04	−0.63	0.00	0.46	0.11	0.07	0.19	−0.01	−0.56
Large	...	...	−0.29	0.13	−0.57	−0.15	0.21	0.17	0.23	0.23	−0.10	−0.66
Xlarge	...	...	0.10	0.14	−0.25	−0.12	0.00	0.23	−0.01	0.46	−0.37	−0.47

parameters with a mean and variance of zero across the 16 matrices, correlations are not defined (indicated by ellipses). For each correlation given, $N = 16$ plot-year matrices.

Stay the same stage				Grow to larger stages											
Reproductives								Reproductives				Seed production			
Small	Medium	Large	Xlarge	Sds.	Sdlgs.	Juv.	Pre.	Small	Medium	Large	Xlarge	Small	Medium	Large	Xlarge
1.00															
−0.20	1.00														
−0.29	0.15	1.00													
−0.48	0.54	0.36	1.00												
−0.09	−0.33	0.03	−0.09	1.00											
−0.10	−0.13	0.64	−0.05	0.55	1.00										
−0.41	0.49	0.40	0.23	0.09	0.40	1.00									
−0.23	0.49	0.52	0.50	0.03	0.48	0.57	1.00								
−0.57	0.67	0.53	0.72	−0.20	0.17	0.66	0.77	1.00							
−0.44	0.48	0.42	0.37	−0.04	0.24	0.79	0.76	0.82	1.00						
−0.30	0.29	0.44	0.68	0.24	0.25	0.35	0.54	0.47	0.51	1.00					
...	...	...	...	...	...	...	...	...	...	...	...				
−0.19	0.44	−0.09	0.52	0.00	−0.28	0.27	0.28	0.32	0.26	0.47	...	1.00			
0.03	0.65	0.40	0.41	−0.07	0.18	0.48	0.54	0.47	0.41	0.49	...	0.59	1.00		
−0.18	0.72	0.44	0.56	−0.23	0.09	0.55	0.51	0.60	0.45	0.53	...	0.57	0.89	1.00	
−0.19	0.45	0.31	0.59	0.01	0.01	0.12	0.21	0.33	0.21	0.77	...	0.45	0.58	0.65	1.00

APPENDIX 4

Log-linear analyses of the effects of plot, *P*, and year, *Y*, on fate, *F*, for each stage class (three-way models). Summing the effects of each stage class over all years gives, for all stages combined, the effects of plot and year on fate, conditional on the differences in states among plots and years (four-way model). Notation follows Caswell (1989*b*) and the convention denoting hierarchical models, such that all terms containing that interaction or lower order interactions are included (Fienberg 1980).

		G^2							
					Reproductives				
Three-way models	*df*	Seedlings	Juveniles	Pre-repro.	Small	Medium	Large	Extra-large	Sum (df) four-way model
Analysis 1: marginal test of the effect of year on fate									
PY, F‡	105	152.65***	95.76	78.39	136.92***	91.16	90.96	37.58	683.42 (735)^{NS}
PY, YF§	84	105.31	72.57	63.39	102.27	71.58	51.92	23.20	490.24 (588)^{NS}
YF	21	47.34****	23.19	15.00	34.65*	19.58	39.04**	14.38	193.18 (147)**
Analysis 2: marginal test of the effect of plot on fate									
PY, F‡	105	152.65***	95.76	78.39	136.92****	91.16	90.96	37.58	683.42 (735)^{NS}
PY, PF‖	84	81.81	54.09	53.89	77.81	62.71	75.89	22.10	428.30 (588)^{NS}
PF	21	70.84****	41.67***	24.50	59.11****	28.45	15.07	15.48	255.12 (147)****
Analysis 3: conditional test of the effect of year on fate									
PY, PF‖	84	81.81	54.09	53.89	77.81	62.71	75.89	22.10	428.30 (588)^{NS}
PY, PF, YF¶	63	41.20	30.02	38.75	45.63	42.51	38.01	10.34	246.46 (441)^{NS}
YF (given *P*)	21	40.61**	24.07	15.14	32.18**	20.2	37.88***	11.76	181.84 (147)*
Analysis 4: conditional test of the effect of plot on fate									
PY, YF§	84	105.31†	72.57	63.39	102.27†	71.58	51.92	23.20	490.24 (588)^{NS}
PY, PF, YF¶	63	41.20	30.02	38.75	45.63	42.51	38.01	10.34	246.46 (441)^{NS}
PF (given *Y*)	21	64.11****	42.55***	24.64	56.64****	29.07	13.91	12.86	243.78 (147)****
Analysis 5: test of the three-way interaction term *PYF*									
PY, PF, YF	63	41.20	30.02	38.75	45.63	42.51	38.01	10.34	
PYF	0	0	0	0	0	0	0	0	
PYF (given all two-ways)	63	41.20	30.02	38.75	45.63	42.51	38.01	10.34	

† $0.05 < P < 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$, **** $P < 0.001$.
‡ When summed over all stages gives the model for *SPY, SF*.
§ When summed over all stages gives the model for *SPY, SYF*.
‖ When summed over all stages gives the model for *SPY, SPF*.
¶ When summed over all stages gives the model for *SPY, SYF, SPF*.

APPENDIX 5

Mean transition probability matrix. Average of each matrix entry (for the 16 plot-year matrices).

	Stage at time *t*							
Stage at time *t* + 1	Sd.	Sdlg.	Juv.	Pre.	Sm.	Med.	Lrg.	Xlrg.
Seed	0.4983	0	1.08	9.00	16.19	22.29	27.63	16.90
Seedling	0.0973	0.0124	0.0174	0	0	0	0	0
Juvenile	0.0041	0.0421	0.3217	0.0849	0.0276	0.0026	0.0104	0
Prereproductive	0	0.0005	0.1346	0.4080	0.1688	0.0726	0.0249	0.0682
Small	0	0	0.0498	0.3860	0.5965	0.4116	0.2095	0.0984
Medium	0	0	0.0014	0.0260	0.1167	0.2005	0.1623	0.0420
Large	0	0	0	0.0051	0.0265	0.1457	0.2655	0.0336
Extra-large	0	0	0	0.0104	0.0065	0.0245	0.0711	0.1303