

# Demography of the invasive woody perennial *Prosopis glandulosa* (honey mesquite)

JORDAN GOLUBOV\*, MARÍA DEL CARMEN MANDUJANO,  
MIGUEL FRANCO, CARLOS MONTAÑA†, LUIS E. EGUIARTE and  
JORGE LOPEZ-PORTILLO†

*Instituto de Ecología, Universidad Nacional Autónoma de México, Apartado Postal 70-275, 04510 DF, México;*  
and †*Instituto de Ecología, Apartado Postal 63, 91000 Xalapa, Veracruz, México*

## Summary

**1** To assess the effect of annual environmental variability on the long-term population dynamics of the invasive woody perennial *Prosopis glandulosa* var. *torreyana* (honey mesquite), we employed elasticity analyses of annual, mean and periodic matrix models. Growth, survival and reproduction were recorded for 1306 individuals in a 1-ha plot over a 4-year period. The volume of each individual was estimated, and transition matrices with nine size classes were constructed. Standard matrix analysis was performed, and the relative importance of individual life-cycle components to changes in the finite rate of population increase ( $\lambda$ ) was determined. **2** Periodic matrix analysis projected a 29% annual increase in population size ( $\lambda = 1.29$ ), while annual projection  $\lambda$ -values varied between 0.99 and 1.44. For both methods, elasticity of seedling recruitment was always very low in all 4 years, and the highest elasticities were generally associated with permanence in the same size class.

**3** Periodic and annual projections predicted similar elasticity patterns, with the relative contribution to a change in  $\lambda$  of different demographic processes changing between 'good' and 'bad' years. However, annual matrices identified two bad years, with fecundity and growth elasticity decreasing relative to survival, whereas periodic analysis identified only one such year, and elasticity changes were seen only in fecundity and survival.

*Key-words:* demographic parameters, demographic triangle, demography, elasticity, invasive species, life history, mesquite, periodic matrices, *Prosopis glandulosa*, sensitivity

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## Introduction

Projection of demographic data has provided a tool by which the dynamics of populations can be explored in detail (Piñero *et al.* 1984; van Groenendael & Slim 1988; Svensson *et al.* 1993; Horvitz & Schemske 1995; Caswell 1997). The benefits include allowing the estimation of extinction probabilities, the prediction of the invasiveness of both native and non-native species, and the study of life-history evolution. Sensitivity (Caswell 1978, 1989) and elasticity analyses (de Kroon *et al.* 1986) allow the contribution of different demographic pro-

cesses to be assessed, and this has improved our understanding of population dynamics as well as allowing comparisons to be made across taxa and populations (Silvertown *et al.* 1993, 1996; Franco & Silvertown 1996).

Projections of population growth must consider the temporal variation of demographic parameters (Tuljapurkar 1985; Nakaoka 1996). For long-lived perennials, the ways in which the effects of such variation over their lifetime influence their dynamics are not readily approximated by short-term demographic analyses (Cain & Damman 1997; Damman & Cain 1998). Environmental heterogeneity may interact with a sequence of intrinsic biological processes that only take place over long periods of time, and it is therefore necessary to assess popula-

tion dynamics of perennial species over long time periods. This is especially true for species inhabiting extreme environmental conditions where specific demographic processes, such as growth and reproduction, may be limited to occasional 'opportunity windows' (*sensu* Eriksson 1989). Several models have accounted for this variation by including a stochastic environmental component (Tuljapurkar 1985, 1989; Huenneke & Marks 1987; van Groenendael & Slim 1988; Nakaoka 1996; Damman & Cain 1998). We used periodic matrix models (a subset of stochastic models in which the assumption of time-invariance is relaxed; Skellam 1966) and their associated sensitivity and elasticity analyses (Caswell 1989; Caswell & Trevisan 1994). We assumed that the matrices reflect the range of environments encountered and that population growth can be described in a hypothetical habitat that cycles among the environments observed (Caswell & Trevisan 1994). We used a demographic study of *Prosopis glandulosa* var. *torreyana* over a period of 4 years to determine (i) how elasticity analysis of periodic matrix models provides information on the impact of different demographic processes at different stages of the environmental cycle; and (ii) how the use of this method in conjunction with annual and mean matrix models improves our understanding of the natural dynamics of populations.

### Materials and methods

*Prosopis glandulosa* var. *torreyana* (Benson) Johnston (honey mesquite), a woody perennial, has a wide distribution in the south-western United States and northern Mexico (Burkart 1976; Rzedowski 1988). Mesquites are a common, often dominant, species of arid and semi-arid ecosystems and typically bloom in spring before the main rainy season (Simpson & Solbrig 1977). They are considered to be aggressive invaders (Glendening 1952), although prior to livestock introductions they had been confined to mesic drainages and upland slopes and have only recently expanded into grasslands (Polley *et al.* 1994). A population of honey mesquite in a 1-ha plot of desert scrubland surrounding a water catchment in the southern Chihuahuan desert, Mexico (26°29' to 26°52' N and 103°32' to 103°58' W; 264 mm mean annual rainfall; 20.8 °C mean temperature; Montaña 1990), was censused annually from March 1994 to March 1998. Rainfall was below average throughout the study period (138.5 mm, 198.4 mm, 234.7 mm and 210.4 mm, in 1994–97, respectively; data from Mapimi Biosphere Reserve climatic station). In March 1994 the 1-ha plot contained 1306 individuals, of which 418 were reproductive adults. Because of its relatively round crown, the size of each mesquite can be estimated as the volume of a sphere the radius of which is half

the average of three plant measurements: height and two orthogonal horizontal widths. For each reproductive individual we calculated the yearly fruit set by averaging the number of pods recorded on three tagged branches of known volume per plant and extrapolating to the total volume of the plant. Fecundity per size class  $j$  at time  $t$  was calculated as the total number of seedlings recruited between times  $t$  and  $t + 1$ , weighted by the proportional contribution of an average individual in that size class to the total fruit set at time  $t$ .

Use of Moloney's (1986) algorithm suggested that the population should be divided into nine size classes. Seedlings and small plants (volume =  $vol \leq 0.8 \text{ m}^3$ ) were considered to be size 0, with size 1 representing volumes (in  $\text{m}^3$ )  $0.8 < vol \leq 1.7$ ; size 2,  $1.7 < vol \leq 2.2$ ; size 3,  $2.2 < vol \leq 3.7$ ; size 4,  $3.7 < vol \leq 4.7$ ; size 5,  $4.7 < vol \leq 5.4$ ; size 6,  $5.4 < vol \leq 6.5$ ; size 7,  $6.5 < vol \leq 8$ ; and size 8,  $vol > 8$ . With this classification we constructed four annual transition matrices to derive three kinds of models. First, the four annual matrices *per se*. These contained the transition probabilities and contributions of an average individual at each of the different stages of the life cycle for each of the four yearly intervals of study ( $\mathbf{A} = \{a_{ij}\}$ , where  $i, j = 0, 1, \dots, 8$ ; Caswell 1989) and were used to describe the population growth in individual years, which could be classed as 'favourable' ( $\lambda > 1$ ) or 'unfavourable' ( $\lambda < 1$ ). Secondly, the mean matrix was obtained by averaging each entry in the four annual transition matrices, and thirdly, a periodic matrix was produced by multiplying all four annual matrices sequentially (Caswell 1989; Caswell & Trevisan 1994).

In the deterministic analyses (for annual and mean matrices), population growth was projected by multiplying each annual matrix ( $\mathbf{A}$ ), or the mean matrix, by a column vector ( $\mathbf{n}$ ) that incorporated the number of individuals in each of the nine size classes. Thus  $\mathbf{n}_{t+1} = \mathbf{A}\mathbf{n}_t$  or, assuming matrix  $\mathbf{A}$  remains constant for a length of time  $t$ ,  $\mathbf{n}_t = \mathbf{A}^t\mathbf{n}_0$ , where  $\mathbf{n}_0$  is the initial population. The properties of this model are well known (Caswell 1989) and they include the facts that the dominant eigenvalue of the matrix is equivalent to the finite rate of population increase ( $\lambda$ ), i.e.  $\mathbf{n}_{t+1} = \lambda\mathbf{n}_t$ , and that there exist a right eigenvector and a left eigenvector associated with  $\lambda$ , which describe the stable size distribution ( $\mathbf{w}$ ) and the reproductive value distribution ( $\mathbf{v}$ ), respectively. We then calculated the sensitivity of  $\lambda$  to small changes in each matrix element,  $a_{ij}$  ( $s_{ij} = \partial\lambda/\partial a_{ij} = v_i w_j/\mathbf{v}\mathbf{w}$ , where  $v_i$  is the  $i$ th element in the reproductive value eigenvector  $\mathbf{v}$ ,  $w_j$  is the  $j$ th element in the stable size distribution vector  $\mathbf{w}$ , and  $\mathbf{v}\mathbf{w}$  is the product of the two vectors, a scalar; Caswell 1989). We also calculated the elasticity matrix ( $e_{ij} = s_{ij}(a_{ij}/\lambda)$ ; de Kroon *et al.* 1986) the elements of

which are the proportional change in  $\lambda$  that results from a proportional change in each  $a_{ij}$ .

In the periodic analysis, product transition matrices could be used to represent the effect of annual demographic variation assuming a cyclic environment. The dynamics of the population over a cycle can be described by the periodic matrix product (Caswell & Trevisan 1994):

$$\mathbf{n}_{(t+m)} = [\mathbf{B}^{(m)} \mathbf{B}^{(m-1)} \dots \mathbf{B}^{(h)}] \mathbf{n}_{(t)}$$

$$\mathbf{n}_{(t+m)} = \mathbf{A}^{(h)} \mathbf{n}_{(t)}$$

where each matrix  $\mathbf{B}$  corresponds to one phase of the cycle. The cycle has a duration of  $m$  time units and  $\mathbf{A}^{(h)}$  is the matrix product that projects the population through the whole cycle, starting at phase  $h$ . In our case, each phase lasted 1 year and we assumed the cycle had a duration of 4 years ( $m = 4$ ), the duration of the study. The product matrix that projects the population through the whole cycle, starting in phase 1 (1994–95), is therefore:

$$\mathbf{n}_{(t+4)} = [\mathbf{B}^{(4)} \mathbf{B}^{(3)} \mathbf{B}^{(2)} \mathbf{B}^{(1)}] \mathbf{n}_{(t)}$$

$$\mathbf{n}_{(t+4)} = \mathbf{A}^{(1)} \mathbf{n}_{(t)}$$

with  $\mathbf{A}^{(1)}$  indicating that the projection starts in phase 1, and  $\mathbf{B}^{(1)}$  to  $\mathbf{B}^{(4)}$  indicating the four annual projections (1 = 1994–95, 2 = 1995–96, 3 = 1996–97, and 4 = 1997–98). The long-term growth rate over the cycle is given by the dominant root of the product of the periodic matrices and can be written as  $\lambda^h$ . Due to the cyclic arrangement  $\lambda^h$  is the same for all  $h$ s and its value can be represented simply as  $\lambda$ . This value can be used to give an annual  $\lambda$  by either taking its  $m$ -root or by converting it first to  $r$  ( $r = \ln \lambda/m$ , where  $m$  scales it to the time step considered, in our case 1 year) and then taking its anti-logarithm.

Our study comprised 4 years (we had four annual  $\mathbf{B}^{(h)}$  transition matrices) and the elasticity values of each phase of the cycle could therefore be estimated by calculating four periodic  $\mathbf{A}^{(h)}$  matrices, and their corresponding four sensitivity matrices ( $\mathbf{S}_A^{(h)}$ ), for cycles ‘beginning’ in years 1994–97 (i.e.  $h = 1, 2, 3, 4$ ). The sensitivity of  $\lambda$  to changes in each entry of one of the matrices in the cycle ( $\mathbf{B}^{(h)}$ ) was calculated as (Caswell & Trevisan 1994):

$$\mathbf{S}_B^{(h)} = [\mathbf{B}^{(h-1)} \mathbf{B}^{(h-2)} \dots \mathbf{B}^{(1)} \mathbf{B}^{(m)} \mathbf{B}^{(m-1)} \dots \mathbf{B}^{(h+1)}]^T \mathbf{S}_A^{(h)}$$

(notice the formula excludes  $\mathbf{B}^{(h)}$ , and  $T$  is the transpose of the matrix product). For example, to calculate the sensitivity of  $\lambda$  to changes in each element of  $\mathbf{B}^{(3)}$ , cyclically permute the individual matrices  $\mathbf{B}^{(2)}$  to  $\mathbf{B}^{(1)}$ . When the latter appears at the right-hand end of the product matrix continue with  $\mathbf{B}^{(m)}$  (in this case  $m = 4$ ) and carry on until you

reach  $\mathbf{B}^{(h+1)}$  (i.e. in this case stop at  $\mathbf{B}^{(4)}$  because  $m = h + 1$ ). That is:

$$\mathbf{S}_B^{(3)} = \mathbf{B}^{(2)} \mathbf{B}^{(1)} \mathbf{B}^{(4)}]^T \mathbf{S}_A^{(3)}$$

The corresponding elasticity values were finally calculated as (Caswell & Trevisan 1994):

$$e_{ij}^{(h)} = (b_{ij}^{(h)} / \lambda) s_{ij}^{(h)}$$

where  $b_{ij}^{(h)}$  is each entry of matrix  $\mathbf{B}^{(h)}$ . All matrix analyses were performed with MATLAB<sup>®</sup> (The MathWorks 1995).

Because there was no reason to suspect our study period repeated itself indefinitely, we relaxed the assumption of a strict sequence of matrices and simulated all possible permutations of the four matrices in the cycle ( ${}_n P_n = n! / n = (n - 1)!$ ; Zar 1996). The projections that resulted from this process generated the distribution of possible outcomes given our 4-year data set and provided a confidence interval for the rate of population growth. The elasticities of different demographic processes for each product matrix were calculated and their confidence intervals were obtained with the percentile method (Meyer *et al.* 1986; Caswell 1989). To test the assumption of the first-order Markov process of the matrix models, we fitted a log-linear model (Bierzychudek 1982; Caswell 1989; Horvitz & Schemske 1995) using GLIM (Royal Statistical Society 1993). The models tested whether the transition probabilities during the time interval ( $t$  to  $t + 1$ ) depend only on the state at the beginning of the time interval and not on any other point in time ( $t - 1, t - 2$ , etc., i.e. serial correlation; Tuljapurkar 1997).

Matrix elements were classified into four demographic processes: (i) positive growth, or simply growth (lower diagonals); (ii) permanence in the same size class, or stasis (main diagonal); (iii) decrease in size, or retrogression (upper diagonals except elements on the first row); and (iv) fecundity (first row, except the first element, which belongs to the main diagonal). From the resulting elasticity matrices (annual, mean and periodic), we summed elasticities by size class and by each of these four demographic processes (Gotelli 1991; Silvertown *et al.* 1993). Finally, we investigated the variation in the relative contribution of different demographic processes to relative changes in  $\lambda$  according to the demographic interpretation of Grime’s triangle proposed by Silvertown *et al.* (1992). This was done by adding the elements of the main diagonal (stasis) to those of the upper diagonals (retrogression) to give a class called survival (L), and taking the values on the first row (but excluding stasis in the seedling category) into fecundity (F), and all subdiagonal elements into growth (G) (Silvertown *et al.* 1993; Franco & Silvertown 1996).

**Table 1** Values of the finite rate of increase ( $\lambda$ ) calculated for *Prosopis glandulosa* using three different methods of matrix projection. The demographic information was obtained from a 1-ha permanent plot of scrubland in the southern Chihuahuan desert

Year	$\lambda$	Total annual precipitation (mm)*
1994–95†	1.13	138.5
1995–96†	0.99	198.4
1996–97†	1.44	234.7
1997–98†	1.39	210.4
1994–98‡	1.29	195.5¶
1994–98§	1.29 ( $\pm 0.004$ )	

\*January–December of the year beginning the interval.

†Annual transition matrix.

‡Mean of four annual transition matrices.

§Periodic matrix product. Value in parentheses shows the 95% confidence interval.

¶Mean annual precipitation during the study period.

## Results

Each annual matrix provided an independent prediction of demographic fitness ( $\lambda$ ) for the population, with values for 3 out of 4 years indicating population increase ( $\lambda > 1$ ). Both mean and periodic matrices indicated a 29% annual population increase overall (Table 1). Elasticity values for all types of matrix projections showed that stasis (main diagonal) and growth (lower diagonals) contributed proportionately the most to population growth throughout the study (Table 2). Stasis was the most important demographic process in the mean matrix analysis (elasticity = 0.47), followed by growth, fecundity and retrogression (Table 2a). In the annual matrices for 1994–95 and 1995–96 (Table 2a), when  $\lambda$  was close to 1 (Table 1), stasis represented close to 60% of the total elasticity, and elasticities for fecundity were very low ( $\ll 0.01$ ). When  $\lambda$  predicted a significant yearly population increase ( $> 35\%$  in 1996–97 and 1997–98; Table 1), growth

contributed more than 40% to the total elasticities and the elasticity of fecundity was far more important than in the previous 2 years (Table 2a). When total elasticities were analysed for each size class, using annual projections, the 1995–96 interval gave very different results to all other annual time intervals (Fig. 1a). The class with the highest contribution to a change in  $\lambda$  in this period was class 7, while in the other years the highest contributions were given by seedlings and class 3, and class 7 made the lowest contribution to changes in  $\lambda$ .

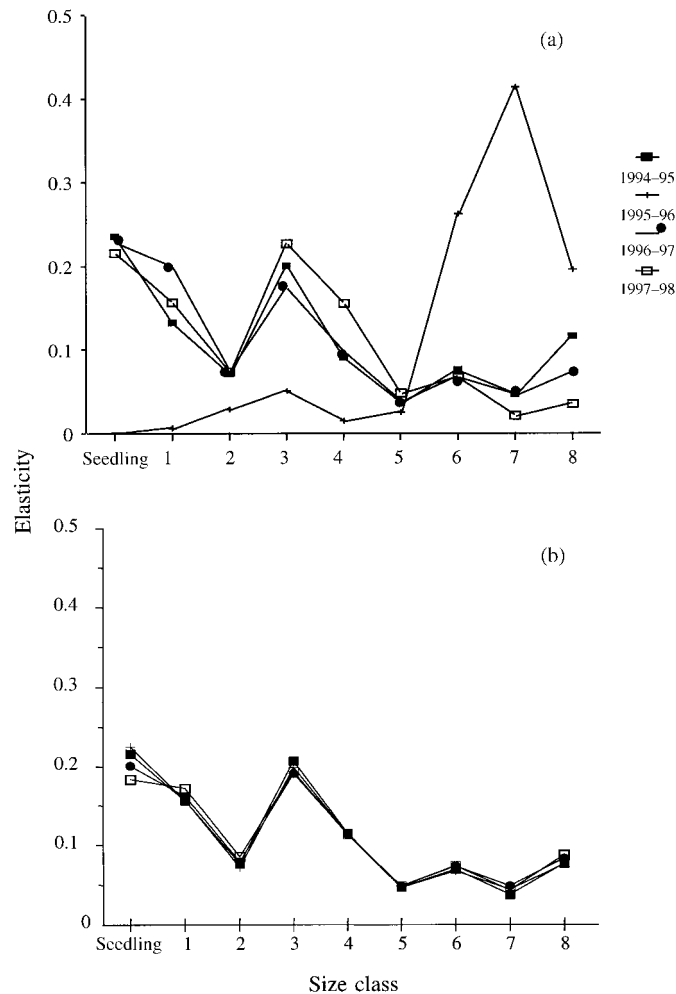
The periodic matrix analyses could be decomposed into four annual periods that each corresponded to one of the annual transition matrices. Elasticities of stasis were consistently higher than those for growth in all four years. Elasticity of fecundity was lower for 1995–96 than for any other year (Table 2b). The summed elasticity values per size class gave different results to those given by the annual projections. Periodic matrix analysis predicted relatively fixed elasticities in all years for all size classes, and the most important stage in all but one year was the seedling class (Fig. 1b). Finally, the log-linear analyses showed that successive matrices in the sequence were non-independent ( $\chi^2 = 1948$ , d.f. = 64).

## Discussion

By incorporating variation in demographic processes through several growing seasons, periodic matrix models provide a picture of mesquite population dynamics in changing environments that cannot readily be approximated by the average-year approach. This is because periodic matrix models allow investigation of the effect that differences in the order of occurrence of demographic events may have on the dynamics of the population. In the case of *Prosopis*, although the projected  $\lambda$  from individual annual matrices showed little variation (CV = 14%), such matrices could predict either

**Table 2** (a) Elasticity of annual and mean projection matrices of *Prosopis glandulosa*; and (b) elasticity ( $\pm 95\%$  confidence interval) of periodic projection matrices of *P. glandulosa* in the southern Chihuahuan Desert

Demographic process	1994–95	1995–96	1996–97	1997–98	Mean matrix 1994–98
(a) Elasticity of annual and mean projection matrices					
Fecundity	$9.22 \times 10^{-05}$	$1.01 \times 10^{-06}$	0.12	0.13	0.07
Stasis	0.62	0.58	0.41	0.40	0.47
Growth	0.26	0.25	0.44	0.43	0.39
Retrogression	0.12	0.17	0.03	0.04	0.07
(b) Elasticity ( $\pm 95\%$ confidence interval) of periodic projection matrices					
Fecundity	0.10 ( $\pm 0.02$ )	$1.5 \times 10^{-4}$ ( $\pm 4 \times 10^{-5}$ )	0.09 ( $\pm 0.03$ )	0.09 ( $\pm 0.03$ )	
Stasis	0.48 ( $\pm 0.04$ )	0.48 ( $\pm 0.04$ )	0.47 ( $\pm 0.04$ )	0.47 ( $\pm 0.03$ )	
Growth	0.37 ( $\pm 0.03$ )	0.37 ( $\pm 0.03$ )	0.39 ( $\pm 0.03$ )	0.39 ( $\pm 0.02$ )	
Retrogression	0.05 ( $\pm 0.01$ )	0.15 ( $\pm 0.03$ )	0.05 ( $\pm 0.01$ )	0.05 ( $\pm 0.01$ )	



**Fig. 1** Variation in elasticity among life-cycle stages of *Prosopis glandulosa* var. *torreyana* in the southern Chihuahuan desert, as calculated from (a) projection of annual matrices, and (b) projection of the periodic matrix model. The seedling class (class 0) includes seedlings and small plants (volume =  $vol \leq 0.8 \text{ m}^3$ ), and the remaining eight classes are defined by the following limits (in  $\text{m}^3$ ): (1)  $0.8 < vol \leq 1.7$ ; (2)  $1.7 < vol \leq 2.2$ ; (3)  $2.2 < vol \leq 3.7$ ; (4)  $3.7 < vol \leq 4.7$ ; (5)  $4.7 < vol \leq 5.4$ ; (6)  $5.4 < vol \leq 6.5$ ; (7)  $6.5 < vol \leq 8$ ; (8)  $vol > 8$ .

growth or decline depending on the year studied. Although the mean matrix, as well as the periodic matrix, can be used to estimate the annual population growth rate over the study period (Huenneke & Marks 1987; McFadden 1991), the average-year approach misses the correct estimation of the influence that different years and processes have on the population's long-term growth (Caswell & Trevisan 1994). This is especially important when specific demographic processes are sensitive to between-year environmental variation or when processes respond in opposite directions to environmental change (M. del C. Mandujano *et al.*, unpublished data). Thus, periodic elasticity analysis provides a means of evaluating the varying influence that different demographic processes have over time periods longer than 1 year. Furthermore, sensitivity and elasticity of periodic matrices can measure the influence of temporally correlated demographic events on popu-

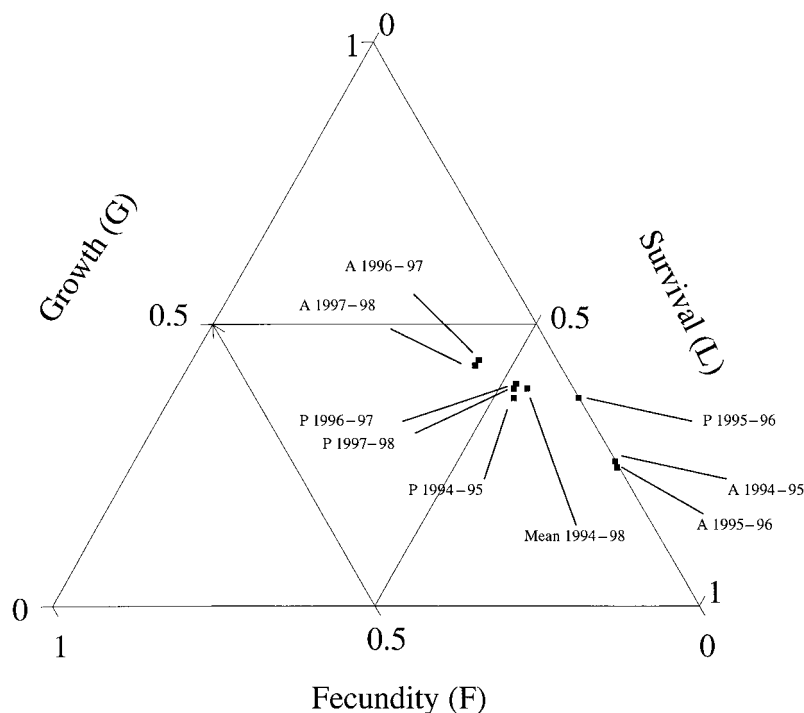
lation growth. Not surprisingly, such analyses give different results to those obtained with discrete, independent annual matrices. In *P. glandulosa*, although both annual and periodic analyses indicated that the different demographic processes switched in importance from year to year, the detailed patterns predicted were rather different.

The mean, periodic, and three out of four annual projections predicted positive population growth, even though all years had below-average rainfall (Table 1). For annual matrices, the highest  $\lambda$  corresponded to the year with the highest precipitation, in which growth was found to be the most important demographic process (Table 2a). In a study of mesquite clustering from aerial photographs in southern Texas, Archer *et al.* (1988) also found an apparent correlation between growth rate of clusters and precipitation over two time periods longer than 1 year (1941–60 and 1960–83). Because current year

growth in *P. glandulosa* depends to a large extent on the previous year's rain, the correlation with precipitation is in reality likely to be more complicated. Annual matrices project the population close to equilibrium ( $\lambda = 0.99$ ) in the period following the driest year (1995–96), but project population growth in all other time intervals, including the driest (1994–95). Our analyses suggest demographic factors that may enable woody species such as mesquites to be aggressive invaders of grasslands (as considered by Scholes & Archer 1997). First, annual matrices show that this mesquite population could grow even in drier-than-average years, and this characteristic will be especially important in variable habitats such as those found in arid environments. Secondly, elasticity analysis of both annual and periodic matrices shows that, overall, stasis is the predominant factor (contribution towards changes in  $\lambda > 40\%$ ) followed by growth ( $> 25\%$ ). This pattern is typically found in shrubs inhabiting frequently perturbed habitats (Silvertown *et al.* 1993; Franco & Silvertown 1996) and can be interpreted as a measure of adaptability to changing interannual environmental conditions in species where, once established, death of individuals is rare. Thirdly, however, while annual matrices indicate that growth and fecundity become increasingly important (with stasis and retrogression elasticities decreasing) as rainfall increases, the changes predicted by the elas-

ticity analysis of periodic matrices are more subtle. In these analyses, the elasticity values are rather constant in 3 out of 4 years and only in 1 year (1995–96, the one following the driest) do they show substantial differences (i.e. higher than the 95% confidence limits) in the elasticity values of fecundity (decreasing) and retrogression (increasing). This is in agreement with mesquites performing rather poorly after particularly bad years.

Although in annual projections there is an apparent correlation between fecundity and growth, this disappears in periodic analysis, as might be expected if several demographic processes are involved. While annual matrices assume independence among demographic events over time, periodic matrices take into account the sequence in which these events occur. Thus, while the elasticity of annual matrices segregates into two distinct groups (94–95 and 95–96, vs. 96–97 and 97–98; Table 2), which can be seen clearly when plotted on the demographic triangle (after Silvertown *et al.* 1992, 1993) (Fig. 2), values for periodic matrices are more clustered and all but one fall close to the position of the average matrix (Fig. 2). This difference may have important consequences for the way we perceive the life history of mesquites. Following the classification introduced by Silvertown *et al.* (1993), annual matrices would suggest that mesquites 'switch' strategies from one characteristic of shrubs in good years to one more



**Fig. 2** The position in the 'demographic triangle' of the elasticities of *Prosopis glandulosa* var. *torreyana* in the southern Chihuahuan desert, as calculated from the projection of four annual matrices (A), the average of these four matrices (Mean) and the projections of a periodic matrix model (P).

typical of longer-living trees in bad years (compare Fig. 2 with fig. 1d in Franco & Silvertown 1996). The periodic analyses, on the other hand, point out the response of mesquites to extremely poor environmental conditions within their invasive habit (Fig. 2).

In conclusion, while periodic elasticity analysis allows investigation of the way that different demographic parameters affect the long-term dynamics of the mesquite population, the analysis of annual matrices for perennial organisms can at best give a number of snapshots that are difficult to interpret in terms of the long-term dynamic picture. The use of annual and periodic matrix models for perennial species in changing environments can indeed produce contradicting results. For example, the size class that contributed most towards  $\lambda$  in our study changed between annual, but not between periodic, projections (for a similar pattern see Lesica & Shelly 1995). By incorporating at least some of the inter-annual demographic variation, periodic matrix models provide a more realistic and interpretable picture of population dynamics, thus adding to the explanatory power of the matrix method.

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