



The demographic costs of nectar production in the desert perennial *Prosopis glandulosa* (Mimosoideae): a modular approach

Jordan Golubov^{1,*}, María C. Mandujano², Carlos Montaña³, Jorge López-Portillo³ and Luis E. Eguiarte²

¹Universidad Autónoma Metropolitana-Xochimilco, Departamento El Hombre y Su Ambiente, Lab. Sistemas de Información Geográfica, Calzada del Hueso 1100, Col. Villa Quietud, 04960, México D.F., México;

²Instituto de Ecología, Universidad Nacional Autónoma de México, Ciudad Universitaria, Apdo, Postal

70-275, México D. F. 04510, México; ³Instituto de Ecología A. C. Apdo. Postal 69, 91000, Xalapa Veracruz, México; *Author for correspondence (jgolubov@miranda.ecologia.unam.mx)

Received 8 October 2001; accepted in revised form 4 June 2003

Key words: Cost of nectar, Desert plants, Effects of nectar production, Matrix and log-linear models, Modular analysis of demographic parameters

Abstract

Nectar production in angiosperms is considered to represent a reproductive cost, and has been associated with a decrease in fruit set or an overall decrease in the energetic budget of the plant. Populations of *Prosopis glandulosa* var. *torreyana* (honey mesquite) are a suitable system to evaluate the demographic costs of nectar production, as populations are composed of a 1:1 proportion of nectarful to nectarless individuals. The study was carried out in a population of 404 individuals of *Prosopis glandulosa* var. *torreyana* found in an area with differing water availability in the Southern Chihuahuan Desert. The possible costs of nectar production were assessed on 1212 shoots of the honey mesquite that were tagged in 1994 and followed until 1998. We used two methods of analysis to describe the effect of nectar production on modular population dynamics: matrix analysis and log-linear models. Water availability and the varying environmental conditions affected plant growth, but nectar production did not have an effect on the demographic parameters we measured. The values of λ did not differ between nectar morphs and the only important effects we detected were the year to year variation in precipitation and microclimate differences at each site. Furthermore, the elasticity of each demographic process (growth, fecundity, retrogression and stasis) between nectar morphs did not differ. The log-linear models suggested a similar pattern but could discriminate the importance of each factor (nectar morph, year and site) on module fate. We were not able to detect a demographic cost of nectar production in the honey mesquite. The absence of a demographic response could be due to the negligible cost of producing nectar for this species or that the resources allocated for growth are different from those allocated for reproduction. Our results suggest that the modular fates of mesquites are mainly determined by environmental factors.

Introduction

Nectar production has been suggested to be a costly floral attribute (Southwick 1984) and under the principle of allocation, the energy and/or resources devoted to nectar production would not be available

for other functions, such as growth or other floral characters (Zimmerman 1988; Zimmerman and Pyke 1988). These costs would decrease growth and/or survival in the plants producing this floral resource, compared to plants not investing in its production. It is difficult to find systems in which the cost of nectar

production can be assessed under natural conditions. However, because populations of *Prosopis glandulosa* var. *torreyana* at the Mapimi Biosphere Reserve have a dimorphic system of nectar production (whereby half the individuals of any given population produce nectar while the other half never produce nectar, López-Portillo et al. 1993, Golubov et al. 1999a), this species is ideal to assess the cost of nectar production. Furthermore, flowering and growth occur simultaneously in *Prosopis* (Simpson et al. 1977; Golubov et al. 1999a), suggesting that common resources may be involved in the production of both reproductive and vegetative structures.

Incorporating reproductive attributes into the demographic behavior of plants is of importance because floral traits are related to plant reproductive fitness through male and female functions (Bell 1985). However, floral attributes, which are part of the cost of reproduction are quite often neglected (Zimmerman 1988), even though they may represent a high energetic cost (Southwick 1984; Pyke 1991). For example, a positive correlation between successive reproduction events coupled with an eventual decrease in plant size was demonstrated using matrix models on modular growth (McGraw and Antonovics 1983) and specifically, the cost of nectar production has been associated with a decrease in growth (Pyke 1991). However, there have been few studies that interpret the cost of a floral attribute in demographic terms (Calvo 1993; Ehrlén and Eriksson 1995; Lehtilä et al. 1994; Ashman and Shoen 1997), even though nectar is the most ubiquitous attractant among angiosperms and constitutes part of the rewards usually sought by the majority of pollinators (Kevan and Baker 1983).

Individual plants may be considered a population of repeated parts or modules (Bazzaz and Harper 1977), which can be defined as a countable, iterated unit of construction. The interpretation of the demographic behavior of modules (i.e., a node, an internode and its associated meristem, Harper 1977) can be considered equivalent to the demographic processes (growth, survival and reproduction) occurring within an individual. The modular approach to plant demography has been previously used to study intraspecific and interspecific competition (Jones 1985; Flores-Martínez et al. 1994), to determine the ecological effects on module demography of competition with nurse plants, to understand growth in extreme environments (Maillete 1987; López-Portillo et al. 1996), and to assess the effects of herbivory

(Whitham and Mopper 1985; Haukioja et al. 1990). However, only a few studies have implemented an explicit matrix population model (Maillete 1982; Flores-Martínez et al. 1994; Lehtilä and Syrjanen 1995) despite the benefits of being able to describe fine scale growth in terms of age or stage (Caswell 1989), especially as age is not a good predictor of plant performance and in many cases is difficult to determine (Mandujano et al. 2001). Furthermore, sensitivity and elasticity analyses can also be done at the modular level, increasing the potential of this tool to understand the processes involved in modular dynamics and to determine the causal factors behind the demographic behavior, both at the modular and at the individual level.

For the purpose of this paper, we studied the consequences of nectar production on the modular dynamics of mesquites over a 4-year period to assess the cost of nectar production in the dimorphic system, assuming that the allocation to plant reproduction (through nectar production) would have a demographic effect on growth. Additionally, we investigated the effect of environmental factors and nectar production on modular dynamics, employing log-linear models assuming that differences in resources and year to year variation would impact the fates of modules.

Methods

Field work was conducted within a 1-ha plot of desert scrubland in the Mapimí Biosphere Reserve MBR (26°N, 104°W, 1100 m altitude, 264 mm yearly average rainfall mainly in summer, 21 °C mean annual temperature), surrounding a temporal water-catchment area. Annual rainfall for the period 1994-1998 was 138.5 mm, 198.4 mm, 234.7 mm, 210.4 mm and 157 mm respectively. During the 1994 flowering season, we tagged three branches in each of 404 reproductive individuals in a N, SE and SW orientation (ca. 120° separation between branches). On each branch, we counted the number of modular units and the number of newly produced shoots (Figure 1), which are easily distinguished by the soft bright green tissue. This recording method was repeated yearly for the 1995-98 reproductive seasons. Nectar presence was determined by sampling 5 flowers of each of two inflorescences per tree using 2 µl micropipettes. Nectar sampling was done at dusk, in inflorescences bagged for at least 8 hr. In addition to demographic

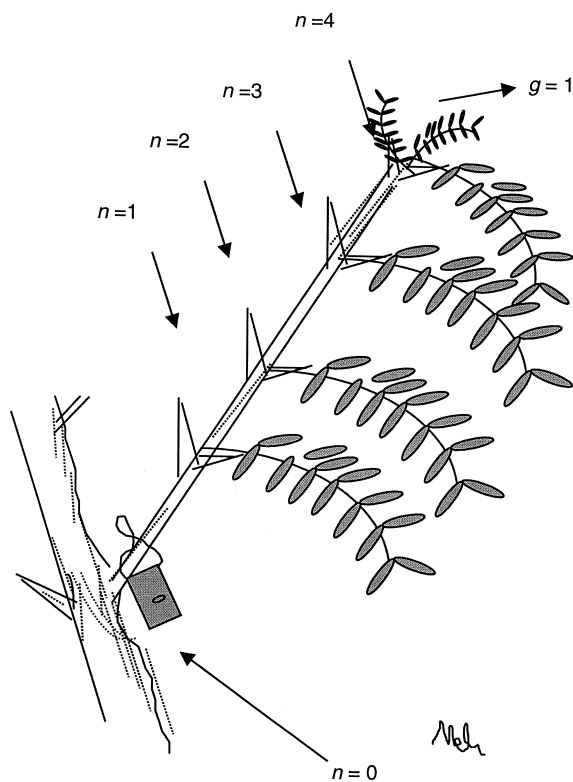


Figure 1. Honey mesquite shoot. n indicates nodes counted, and g indicates new growth in terms of number of shoots. In this case, $n = 4$ and $g = 1$.

data, our 1-ha study site was subdivided into three sub-plots according to water conditions (humid site HS, intermediate site IS, and dry site DS) inferred from the measurement of predawn water potentials (Golubov et al., 1999b). We tagged a total of 1212 shoots, 46% of which corresponded to the nectarful condition and 54% corresponded to the nectarless condition. Of all individuals, 62 were in site HS (humid site), 281 were in site IS (intermediate site) and 61 were found in site DS (dry site).

Matrix models

To compare modular growth of nectarful and nectarless individuals, we constructed size-structured transition matrices (\mathbf{M}) for each annual transition, using the following size-class limits in number of modular units (MU) for each branch: 1-20, 21-40, 41-60, and > 60 . Fecundity was defined as the number of new shoots produced per size-class at time t . Two demographic processes were considered in the first row of each matrix, fecundity (F_{1j} = sum of new shoots pro-

duced in a given year by a shoot in size class j / total number of shoots in size-class j), and the probability of retrogression to the smallest size class (R_{ij} = number of shoots of size i at time $t + 1$, which were in category j at time t / total number of shoots in size j at time t , when $i < j$). The main diagonal contains the probability of stasis or survival in the same class (S_{ij} = number of shoots in size-class i at time $t + 1$, which were already in this size-class at time t / total number of shoots in this same class at time t), the lower diagonals contained transition probabilities of growth to higher size classes (G_{ij} = number of shoots in size-class i at time $t + 1$ which were in size-class j at time t / total number of shoots in size class j at time t , when $i > j$), and the upper diagonals contained retrogression in size by death of MU's (R_{ij}). This yielded a matrix of the form:

$$\mathbf{M} = \begin{pmatrix} S_{11} + F_{11} & R_{12} + F_{12} & R_{13} + F_{13} & R_{14} + F_{14} \\ G_{21} & S_{22} & R_{23} & R_{24} \\ G_{31} & G_{32} & S_{33} & R_{34} \\ G_{41} & G_{42} & G_{43} & S_{44} \end{pmatrix}$$

The resulting transition matrices were constructed according to the three factors year, nectar conditions and water status: four study years (Y, 1994-98), two nectar conditions (N, nectarful and nectarless) and three water status sub-plots or sites (HS, IS and DS).

Thus, there were a total of 24 transition matrices. For each matrix, we calculated the dominant eigenvalue λ , and its associated right and left eigenvectors (\mathbf{w} , \mathbf{v}). We also conducted standard sensitivity and elasticity analyses (Caswell 1989; deKroon et al. 1986). As transition probabilities and fecundities are measured in different scales, the sensitivity analysis is difficult to interpret, so we used an analysis of elasticity that measures the proportional change in λ given a proportional change in each cell entry of \mathbf{M} (deKroon et al. 1986) which allows the interpretation of relative contribution of each demographic process to λ in each sub plot (Caswell 1989). This analysis was used to determine the routes and importance of demographic processes. We assigned confidence intervals on λ by performing 1000 bootstraps estimates and determining the 95% percentile limits (Meyer et al. 1986; Caswell 1989).

Log-linear models

To determine whether the fates of modules varied between years, sites and nectar conditions we conducted comparisons employing log-linear models (Caswell 2000). This method provided a means of testing specific hypotheses by comparing the results to a null model. In general, the method adjusts a log-linear model to the transition frequencies, after adding 0.5 to each cell (Fingleton 1984). The effect of initial module condition (I, the frequency of shoots in size-class i at time t) on the final state of modules (F, frequency of shoots in size-class j at time $t + 1$) was evaluated. In addition, we tested the effect of nectar condition (N), site (S) and year (Y) employing a 5-dimensional contingency table. The full model assumes that all terms and all higher order interactions contribute to predict cell frequencies. The null hypothesis is therefore a reduced model in which terms that are assumed not to be important for predicting cell frequencies are set to 0. In our specific case, this was done by setting the FN, FY and FS interaction terms to 0 as well as all higher order-interactions that involved these terms (Bishop et al. 1975). We then tested the effect of nectar condition, year and site on the fate of modules. This was done by assessing the goodness-of-fit of models that corresponded to each hypothesis, that resulted in the models that assessed the effect of nectar condition, site and year on module fates. In addition, we fitted models that included the interaction terms between FY and FS. A lack of fit of the model would suggest an important effect of one or more of the parameters tested (Bishop et al. 1975; Caswell 1989). The significant models were then collapsed by initial states in order to determine how each factor affected the fate of each module belonging to a specific initial state. All log-linear analyses were conducted with GLIM (Royal Statistical Society 1993).

Results

Matrix models and elasticity analyses

The finite rate of population increase (λ) was consistently lower in nectarless trees compared to their nectarful counterparts in the four yearly intervals (Figure 2, Table 1), but, confidence intervals obtained through 1000 bootstraps indicated that such differences were not significant (Table 1). Overall, the

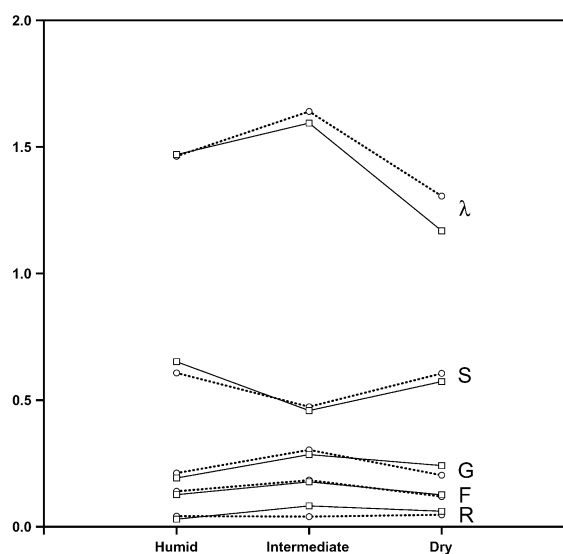


Figure 2. Mean values of elasticity for different demographic processes (growth, fecundity, retrogression and stasis) for the three sites. The symbols stand for S=stasis, R=retrogression, G=growth and F=fecundity. The top portion of the graph corresponds to the values of λ for the three sites. The solid lines correspond to the nectarless morph, and the dotted lines correspond to the nectarful morph.

Table 1. Values of λ (upper and lower 95% confidence intervals after 1000 bootstraps) for modules of nectarful and nectarless individuals over a four year study period.

Study period	Nectarful	Nectarless
1994-95	2.64 (2.10-3.39)	2.34 (2.08-2.64)
1995-96	2.36 (2.06-2.71)	1.90 (1.74-2.12)
1996-97	1.69 (1.56-1.84)	1.58 (1.43-1.80)
1997-98	2.14 (1.97-2.33)	2.01 (1.87-2.17)

population of mesquite modules is growing at a high rate, even though this growth rate may vary considerably between sites and nectar morphs ($\lambda = 1.69 - 2.64$, Table 1). Both nectar morphs had similar demographic behaviors between site and years (Figure 2, Figure 3), but the value of λ was highest in site IS, and lowest in site DS. Between years, the highest growth rate corresponded to the first year (1994-95, Table 1), probably because of the influence of higher rainfall during the previous season (293.4 mm, the highest during the study period).

There was no correspondence between water availability and the elasticity of demographic processes. Water availability was similar between sites HS and IS ($\bar{X} = -0.55 \pm 0.046$ MPa and $\bar{X} = -0.58 \pm$

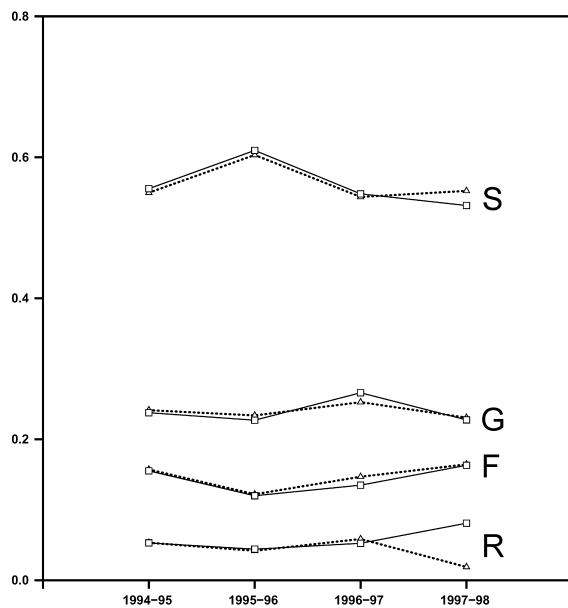


Figure 3. Mean values of elasticity for the different demographic processes (growth, stasis, fecundity and retrogression) during the 4 year study period (1994-98). The symbols stand for S=stasis, R=retrogression, G=growth and F=fecundity. The solid lines correspond to the nectarless morph while the broken lines correspond to the nectarful morph.

0.046 MPa) and both of these differed significantly from DS ($\bar{X} = -0.58 \pm 0.046 MPa$).

These water conditions were found to be consistent between years (C. Montaña unpublished data). Site HS had particularly low values for retrogression (shoot death) and the lowest values for growth causing the elasticity of stasis to be the highest (Figure 2). This behaviour, together with intermediate fecundity values suggest that these modules are growing at slow rates with decreased growth and death rates. On the contrary, the site IS had the highest fecundity and growth, but the highest mortality of modules (retrogression). The combination of high growth and retrogression caused the values of stasis to be the lowest. As expected, site DS had the lowest values of fecundity, but contrary to our expectations, had intermediate values of the other three demographic processes (growth, stasis and retrogression).

The year 1994-95 was characterized by intermediate values of fecundity, retrogression, stasis and growth (Figure 3). The lowest rainfall found during this period (138.5 mm) resulted in the low growth, fecundity and high stasis recorded during the 1995-96 season (Figure 3). Even though low fecundity was observed during this period, a higher rainfall was re-

corded which probably affected modular dynamics by increasing growth and retrogression and reflecting in a decrease in stasis. The highest rainfall recorded during the study period (234.7 mm, 1996-97 study period) also corresponded to an increase in fecundity during the following year (1997-98 season), with a consequent decrease in stasis, growth and retrogression. The values of λ for both nectar morphs were negatively and significantly correlated with retrogression (branch death $r = 0.36$, $P < 0.05$) and positively correlated with fecundity ($r = 0.37$, $P < 0.05$), suggesting that new shoot growth and death are important processes in our estimation of growth.

Growth was consistently lower in site DS. The nectarful population had slightly higher elasticity values for growth and fecundity, and lower mortality (retrogression) than those of the nectarless population for site IS; however, this pattern was inverted in site DS. Although these demographic processes were reversed, the importance of stasis affected the pattern of demographic processes buffering the possible effects of the other processes and maintaining the values of λ for the nectarless morph below those of the nectarful morph (Figure 2), even though these values were not significant. The largest difference in mortality rates occurred during the 1997-98 season when the nectarless morph was strongly affected by module mortality. The resulting decrease in retrogression for the nectarful morph was probably responsible for the increase in λ found during this period. Contrary to what would be expected if nectar production were costly, the nectarful subpopulation of modules had consistently higher values of λ in the driest site (DS). Our results indicate that the importance of different demographic processes vary between years and sites but are not significantly different between nectar morphs.

Log-linear models

The reduction in deviance from the first log-linear analysis involving the effect of initial state (I) on the final condition (F) suggested that modular behavior is strongly determined by initial modular size ($X^2 = 3522$, $df=12$, $P < 0.01$). The appropriate null model of conditional independence was therefore NSYF, IF (N=nectar morph, S=site, Y=year, F=fate and I=initial state). To determine the effect of nectar condition (N) on module fate, we fitted the model NSYF, YSFI (Table 2). In addition, to test the effect of year (FY) and site (FS) we fitted the models NSYF, NSFI

Table 2. Log-linear analysis of nectarful and nectarless mesquite module transition frequencies for a four-year period at 3 sites. Parameters in the models stand for N = nectar morph, I = initial module state, F = final module state, Y = year and S = site

Model	Deviance	df	p
NSYI, IF (null model)	611.49	368	< 0.01
NSYI, FISY (nectar)	162.40	192	0.9408
NSYI, FINS (year)	434.27	288	< 0.01
NSYI, FINS (site)	246.34	256	< 0.01
NSYI, FINS, FIYN (year × site)	186.53	192	0.597

Table 3. Deviance of the collapsed models that take into account the effect of site (S) and year (Y) on modular fate depending on initial modular states (I). * significant at $\alpha < 0.05$, ** significant at $\alpha < 0.01$

Stage (I)	Site (FS)	Year (FY)
1	89.916*	115.24**
2	102.12**	131.63**
3	97.026**	109.2 **
4	60.278	78.206

and NSYF, NYFI respectively. The test that involved nectar condition fit the data, suggesting that nectar condition is not important in determining modular fate. The lack of fit of the models that had either year or site suggested that one or both of these factors were responsible for the lack of fit. In order to determine if these factors interacted, we fitted models that contained the interaction term $FY \times FS$. These models, containing the site and year interaction fit the data, suggesting that both year and site contribute significantly and independently to the fate of modules (NSYF,YSFI Table 2).

The most important effects on modular fate were both site and year (Table 2). When we decomposed the significant models to determine the relative importance of each of these factors on the initial states, these models suggested that the smaller size classes were affected by both the site (S) and the year (Y) (Table 3), and the largest size-class (> 60 modules) were unaffected. Significance of the site was given by size-class 2 (21-40 modules) during 1995-96, by size-classes 2 and 4 during 1996-97, and by size-classes 1 to 3 during the 1997-98 season. The only consistent effect of site was for stage 2 that affected modular fate in three out of four transitions. With respect to year, fate of modules in size-classes 1 (1-20 modules) and 2 were consistently affected throughout the study period, with a decreasing effect for larger modules (Table 4). Year to year variation

Table 4. Significance of the effect of site on fate for each initial module state (FS) for each of four initial states (I) and in each sampling year (Y). Numbers in bold we significant at $\alpha=0.05$

Initial Module State (I)	Year (Y)			
	1994-95	1995-96	1996-97	1997-98
1	0.813	0.854	0.337	0.001
2	0.616	0.052	0.007	0.001
3	0.549	0.339	0.708	0.001
4	0.943	0.292	0.034	0.11

Table 5. Significance of the effect of year (Y) on modular fate (F) for each initial state (I) and each site (S). Numbers in bold are significant at $\alpha = 0.05$

Initial Module State (I)	Site(S)		
	1 (Humid)	2(Intermediate)	3(Dry)
1	0.017	0.001	0.002
2	0.015	0.001	0.027
3	0.661	0.001	0.093
4	0.918	0.001	0.765

affected modules in size classes 1 and 2, by means of modular death (Table 5), suggesting that these branches are affected to a larger extent by lack of resources. This model is consistent with the results provided by the matrix models, a significant effect of site and year-to-year variation on module fates.

Discussion

Nectar has been thought to represent a significant cost to reproduction in plants (Pleasants and Chaplin 1983; Southwick 1984; Pyke 1991; Ashman and Shoen 1997), but evidence suggests small energetic costs of nectar production (Harder and Barrett 1992). Our results employing both matrix and log-linear analyses also suggest that nectar production does not conflict with plant growth (modular dynamics). Both matrix and log-linear analyses showed similar patterns: an important effect of year to year variation, due to the varying rainfall regimes, as well as an important effect of the microclimatic conditions within each site. The effects of environmental heterogeneity are similar to those found when measuring complete individuals of mesquite (Golubov et al. 1999b). However, the values of λ (always above equilibrium) when studying modules were consistently higher than

those for the demography of individual plants of adults for both nectar morphs. When comparing their demographic processes, however both modular and individual tree elasticity analyses show that mesquites behave as perennial trees (Silvertown et al. 1992; Golubov et al. 1999b) in terms of the sensitivity of λ to the different matrix elements, and this contribution is dominated by stasis (Golubov et al. 1999b). The results presented here suggest that nectar production in honey mesquites does not represent a cost in terms of vegetative growth. If this were not the case, we would expect a negative relationship between the presence of nectar and modular growth which would be reflected in lower values of λ for nectarful, as compared to nectarless individuals. Surprisingly, however, λ was consistently lower in the nectarless population, and in DS (assuming water-resource limitation). This was remarkable, particularly because the study period experienced below average rainfall.

The lack of evidence to support a significant cost of nectar production could be due to several characteristics of mesquites. The production of foliage in *Prosopis* coincides with the reproductive season, and they both rely on resources (mainly rainfall) that were most likely obtained the previous season (Golubov et al. 1999b). This makes the energetic expenditure on nectar and growth to be in part supported by resources, generated by foliage, that are being produced during the current reproductive season. This was demonstrated in part by the differences between sites, by the important site specific effects that contributed to differences in modular fates. The effects of different site specific conditions has been previously documented for different factors such as the importance of large environmental conditions (Horvitz and Schemske 1995; Mandujano et al. 2001), interspecific competition (Flores-Martinez et al. 1994), year to year variation (Golubov et al. 1999b; Mandujano et al. 2001) and density effects (Harvell et al. 1990).

Nectar production does not pose a significant drain on plant resources as suggested by the results or does not have the same limiting factor underlying the activities of growth and reproduction. Unfortunately it is difficult to discriminate between these two possible explanations. Mesquites are well known to be adapted to arid environments (Simpson et al. 1977; DeSoyza et al. 1996), being facultative phreatophytes that exploit water resources from areas that are 0.3 m deep, regardless of individual size (Ansley et al. 1990; DeSoyza et al. 1996). In addition shoot growth, the production of foliage, and reproductive events

(where nectar is involved) are all temporally coupled, suggesting that resources such as water can be considered to be coming from a common pool. The effect of water availability was in part responsible for the significant effect on canopy growth, probably due to the extreme arid conditions found during the study period that clearly affected modular dynamics. The environmental effect was especially true for branches in the smallest size classes (branches having < 40 modules), that were usually affected more often in varying environmental conditions. Contrary to what López-Portillo et al. (1996) reported, we found a significant effect of site on the demographic behavior of modules. However, this difference could be due to higher water availability in our study because the site is surrounded by a water catchment that accumulates water after heavy rainy seasons. However, water availability did not entirely explain the demographic processes involved in the population as λ was consistently lower in HS than in IS. Further studies regarding other aspects of modular growth (such as the investment of modules to sexual reproduction, by the production of flowers) would be important.

Arid environments pose important constraints on resources, because of the unpredictable rainfall periods and extreme temperatures (Noy-Meir 1973). Heterogeneity of resources can be due to abiotic factors such as temporal and spatial variability and to biotic factors such as the creation of islands of fertility by the effect of certain species (e.g., mesquite). The unpredictable nature of arid environments can result in demographic processes that are dependent on environmental cues and therefore unpredictable too (Golubov et al. 1999b). Studies that use matrix models that span several years or habitats have now tried to incorporate environmental heterogeneity into the models (Bierzychudek 1982; Oostermeijer et al. 1996; Mandujano et al. 2001). In the case of mesquites, year to year environmental variation was an important component of modular dynamics. We have previously shown that mesquites are particularly able to change demographic behaviors between years (Golubov et al. 1999b). In addition to year to year variation, ecological conditions specific to certain sites also play an important role in modular dynamics. These can be due not only to different water availability but also to other factors such as competition and herbivory. We can therefore conclude that modular fates in mesquites are determined by factors other than nectar condition, and that prevailing envi-

ronmental conditions are the prime determinants of modular fate in *P. glandulosa*.

Aknowledgements

The authors would like to thank S. Herrera, A. Herrera, Y. Verhulst, E. Vega, A. Martínez and F. Herrera for field assistance, and A. Valera and R. Pérez-Ishiwara for help in matrix analysis. We also thank A. Flores-Martínez, M. Franco, R. Wesselingh and two anonymous reviewers for helpful comments on previous versions of this manuscript. The Department of Biology at NMSU gave us additional computer and logistic support. Support was given by CONACyT and DGAPA sabbatical scholarship to LEE at UC Irvine. Fundación UNAM, DGAPA-UNAM and CONACyT also supported this research which is part of the Ph.D. dissertation of JG at the Facultad de Ciencias, Universidad Nacional Autónoma de Mexico.

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