THE ROLE OF DENSITY DEPENDENCE IN THE POPULATION DYNAMICS OF A TROPICAL PALM

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Abstract. The role of density dependence in the population dynamics of tropical trees has been a subject of considerable debate. Here, we present data on the demography of the edible palm *Euterpe edulis,* classified into seven size categories and monitored over three years. On average, each adult palm contributed 98 seedling recruits per year into the population. The pattern of mortality was similar to that of other palms, with mortality being highest among the smallest plants. Those plants with a diameter at soil level >20 mm had an annual mortality <7%. Density dependence was found to act only on the seedling stage of the life cycle. The probability of survival and transition of seedlings to the next size class were affected both by the density of seedlings and the presence of conspecific adults. Matrix modeling indicated that the true finite rate of population increase (λ) was 1.28 and that the observed reverse ''J''-shaped size distribution of plants was a consequence of the density dependence operating in the population. Elasticity analysis showed that the survival elements in the matrix contributed most to the value of λ, and that the position of the transition matrix in growth–survival–fecundity (G–L–F) space was influenced by density. The matrix model incorporating density dependence predicted size distributions and densities approximating the maximum observed in the field. Spatial simulations indicated that the predictions from the matrix model relating to the size structure of plants are robust, but that the predictions of densities are sensitive to the precise spatial dynamics of the population.

Key words: Atlantic Forest, Brazil; density dependence in tropical trees; edible palm; elasticity analysis; Euterpe edulis; *matrix analysis; palmito; plant population dynamics; population regulation; size structure; spatial dynamics; transition matrix in* G–L–F *space.*

INTRODUCTION

While the role of density dependence in the population dynamics of plants has been clearly demonstrated for a range of annuals and herbaceous perennials (e.g., Barkham and Hance 1982, Watkinson et al. 1989, Gillman et al. 1993, Rees et al. 1996), the role of density dependence in the population dynamics of trees, and especially tropical trees, is much less clear. That density dependence occurs in tropical trees is not in dispute (Alvarez-Buylla et al. 1996). A range of studies has shown that density may have a negative impact on seed and seedling survival (Augspurger and Kelly 1984, Clark and Clark 1984), juvenile growth and survival (Hubbell et al. 1990, Condit et al. 1992), and adult growth, survival and fecundity (Hubbell et al. 1990, Alvarez-Buylla 1994, Gilbert et al. 1994). What is unclear is the significance of density dependence for the dynamics of tropical trees. On the one hand it has been argued that there is virtually no role for density dependence and that abundance of different species can be explained by a multinomial random walk (Hubbell

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1979, Hubbell and Foster 1986), known as the community drift model. In contrast to this nonequilibrium model, it has been argued at the other extreme that density-dependent and distance-related recruitment may be responsible for the low mean densities of many tropical trees and the consequent high species diversity (Janzen 1970, Connell 1971). In this latter case, specialist herbivores, seed predators, and pathogens are envisaged as maintaining populations around low densities and high species diversity. Critics of the Janzen–Connell model have suggested that the strength of density dependence is insufficient to remove the clumped distributions of seedlings beneath parents (Hubbell 1980).

The community drift model of tropical forest dynamics, on the other hand, has also been criticized on the basis that it fails to take into account high levels of compositional similarity in disjunct samples of forest (Terborgh et al. 1996). Moreover, Wills et al. (1997) have found that intraspecific density-dependent effects are far stronger and more common than was previously thought. Significant effects on recruitment were found in 67 of the 84 most common species in the Barro Colorado Island study area in Panama, and significant effects on the intrinsic rate of increase were seen in 54 of the 84 species. The mechanisms underlying the density dependence were not evaluated, but Wills et al.

argue for an important role for host–pathogen interactions.

A critical question remaining is whether the degree of density dependence is sufficient to regulate populations at observed densities (Condit et al. 1994). Population models that include population regulation have, however, only been developed for a few species for which complete life cycle information is available (Alvarez-Buylla et al. 1996). Evidence for the role of density dependence in the population dynamics of tropical trees comes from studies of three species in the neotropics: *Astrocaryum mexicanum* (Palmae), *Cecropia obtusifolia* (Cecropiaceae), and *Trichilia tuberculata* (Meliaceae). In the case of *A. mexicanum,* higher estimates of population growth were obtained for populations growing at low densities (Piñero et al. 1984). Details of the conspecific responses to density have been reported by Sarukhán et al. (1985) and Martínez-Ramos et al. (1988); the pattern of recruitment is related to the density of adult palms, and mortality amongst both seedlings and juveniles increases with the total density of plants, but not amongst immature and mature palms. Unpublished work of J. Sarukhán et al. and M. Martínez-Ramos (cited in Alvarez-Buylla et al. [1996]) also indicates that the probability of seed removal increases with density. It is reported, although details are not provided, that when density-dependent seed predation and transition of seeds to seedlings are incorporated into a Lefkovitch matrix, the model predictions are population densities six times higher than those observed in the field. While the predicted densities are high, they are in line with observations that current populations are increasing.

In the case of *Trichilia tuberculata,* Hubbell et al. (1990) reported that population growth rates decreased monotonically from low- to high-density stands as a result of density effects on the survivorship of mature plants. Moreover, the model developed for *T. tuberculata* predicted population densities at equilibrium and size class distributions similar to those found in the field. Unfortunately, no details of the model are provided. It is the study of Alvarez-Buylla (1994) on *C. obtusifolia* that presents the most detailed study to date of the role of density dependence in the population dynamics of a tropical tree; the model incorporates both a Lefkovitch matrix with density dependence and patch dynamics. Negative effects of density on fecundity and survival were documented; fecundity was negatively related to the density of neighbors >4 cm in diameter, and mortality was highest among trees >10 cm in diameter, as a result of density effects from neighbors >10 cm. There was also a positive density-dependent relationship in survival amongst plants <10 cm, but this was attributed to site quality rather than resource availability.

One of the most important results to emerge from the study of Alvarez-Buylla (1994) was that the nature of patch and spatial dynamics interacted with density-dependent processes in determining population size. In particular, the models showed that the strength of density dependence would have been underestimated by a factor of 13 if patch dynamics had been ignored. In this example, patch dynamics were included by considering how trees were packed into suitable patches within a forest matrix. The models do not, therefore, include the consequences of the form of dispersal and the development of spatial structure within populations for population dynamics. While a range of studies have explored the consequences of spatial structure for the dynamics of forest species (see Clark and Ji 1995), no study has examined in detail how such processes affect predictions of population structure and population numbers under field conditions.

In this paper, the effects of density on the population dynamics of the tropical palm *Euterpe edulis* Mart. are investigated using a matrix and patch-modeling approach. The models summarize demographic data collected over a three-year period from the Atlantic Forest in southeastern Brazil. In particular, we address the following questions: (1) What are the effects of density on the survival, growth, and fecundity of *E. edulis*? (2) What impact does density dependence have on population structure? (3) What effect does density have on the position of the transition matrix for *E. edulis* in growth–survival–fecundity (*G–L–F*) space (Silvertown et al. 1993, Silvertown and Franco 1993)? Finally, (4) how do patch dynamics interact with density dependence to determine the abundance of *E. edulis*?

MATERIALS AND METHODS

Species and study site

Euterpe edulis is a subcanopy palm (5–12 m) with a single straight stem and pinnate leaves (Henderson et al. 1995). It occurs in forests primarily along the Atlantic coast of Brazil, reaching inland at least to Brasília and just reaching Argentina and Paraguay. Typically, the plant is found on wetter soils, often in swampy areas, where it was previously locally abundant. Intensive harvesting, however, has led to the decline of the palm over much of the region, and many of the surviving populations are small and fragmented. *E. edulis* (commonly known as juçara or jiçara palmito) is intensively exploited, due to the quality of the heart of palm that it yields (Pollak et al. 1995). The heart of palm, or palmito, corresponds to the apical meristem of the plant, together with the developing new leaves, and is harvested by cutting stems. *E. edulis* has a single apical meristem, and removal of the heart of palm results in the death of the plant.

Previous studies of *Euterpe edulis* indicate that flower production may begin when the plants are 6–8 years old (Bovi et al. 1988); the peak of flowering occurs at the beginning of the wet season (Silva Matos and Watkinson 1998). Reproductive plants in natural forests typically produce a mean of one to two inflorescences

TABLE 1. The size classification of *Euterpe edulis,* as defined by the morphology of plants, diameter of plants at soil level (DAS), and reproductive state, together with the maximum, minimum, mean, and coefficient of variation (CV) in densities across the plots over the three years of study.

	DAS (mm)		Density (no. plants/25-m² plot)			
Size class	Minimum	Maximum	Maximum	Minimum	Mean	CV
1†	0	(3 leaves)	1300	0	74.50	2.49
2	(>3 leaves)	10	76	0	7.17	1.49
3	10.1	20	14	0	1.03	2.10
4	20.1	30	8	0	0.31	3.01
5	30.1	60	11	0	0.61	2.54
6	60.1	120	7	0	0.38	2.32
7‡	120.1	...	8	0	0.71	2.13

† Seedlings.
‡ Reproductive adults.

(range 1–10) and 1500–4800 fruits/plant (Reis 1995, Silva Matos and Watkinson 1998); the fruits usually contain a single seed. Many of the fruits fall directly to the ground, but they are also eaten and dispersed by several bird species (Zimmermann 1991, Silva Matos and Watkinson 1998). The seeds are able to germinate immediately, if the pericarp is removed (Bovi and Cardoso 1975); otherwise most seeds die within three months of shedding (Silva Matos and Watkinson 1998).

The study was carried out in a swampy area of mesophyll semideciduous forest at the Municipal Reserve of Santa Genebra in the state of São Paulo, Brazil (22°49′45″ S; 47°06′33″ W). The reserve has an area of 252 ha and is at an altitude of 580–610 m. Its floristic composition is typical of semideciduous forests in the region; the vegetation belongs to the Atlantic Forest Region and is classified as a Subtropical Moist Forest (Tosi and Vélez-Rodrigues 1983) and as Montane Seasonal Semideciduous Forest (Rizzini et al. 1991) according to the Brazilian Vegetation Classification (Veloso et al. 1991). The climate has two distinct periods: the rainy season extends October–March, when there is a mean temperature of 23°C and 74% of the rainfall occurs; while the dry season, with a mean temperature of 17°C, extends April–September. The mean annual rainfall is ~1365 mm.

Harvesting of palms occurred until the area was designated as a nature reserve in 1979. *E. edulis* is found predominantly in the reserve in a ~2-ha area of swampy forest, which extends ~10 ha in total. The most common species in this region are *Alchornea triplinervia* (Euphorbiaceae), *Erythrina falcata* (Leguminosae), *Inga* spp. (Leguminosae), *Palicourea marcgravii* (Rubiaceae), *Rollinia silvatica* (Annonaceae), *Talauma ovata* (Magnoliaceae), and a number of species belonging to the Myrtaceae. There are two other species of palms: *Geonoma brevispatha* and *Syagrus romanzoffiana.*

Population monitoring

Within the swampy area of the forest, where *Euterpe edulis* is abundant, an area of 100 × 100 m was marked out and then divided into a 5-m grid. One hundred randomly located 5 × 5 m plots were then set up within the grid, and within each of these plots a 1 × 1 m area was demarcated at one of the plot corners. All plants with ≤3 leaves were tagged inside the 1-m² plots with a numbered label, while all of the plants with >3 leaves were tagged in the 25-m² plots; plants with ≤3 leaves were counted only in the 1-m² plots because of their abundance. The distance to the nearest reproductive plant was also measured for each 1-m² plot.

The plots were initially set up in January 1991, when the size of each tagged plant was determined by measuring its diameter at soil level (DAS) above the cone of the roots. The diameter at soil level, rather than the dbh, was used because it is the single common measure that could be collected for individuals from all size classes. The reproductive status of plants was also recorded. The fates of the plants were subsequently monitored in January 1992, April 1993, and January 1994, when all new plants were also tagged within the sampling subplots, so that their subsequent fate could be monitored.

Transition matrix analysis

Population dynamics were analyzed using a Lefkovitch, size-based matrix model with seven size classes (Table 1). This approach relies on using information on the survival of individuals, the growth of individuals from one size class to the next, as well as the reproductive output of mature plants, in order to describe and project population dynamics (Caswell 1989). The probability of survival and remaining in the same size class (P_i) is defined as the product of the probability of an individual in class i surviving for a year and the probability of remaining in the same size class; the probability of survival and growth to the next size class (G_i) was obtained by multiplying the survival probability by the probability of surviving individuals making the transition to class $i + 1$. Reproduction only occurred amongst plants in size class 7. The number of offspring produced per reproductive palm per year (F_7) was expressed in terms of the mean number of plants in size class 1 (≤3 leaves) produced per plant of size class 7 (>120 mm diameter). This rate was

obtained by dividing the density of new recruits alive at the end of a year by the density of adults observed at the beginning of the year.

The annual estimates of P_i, G_i, and F_7 were calculated separately for each plot, and then the mean was computed across all of the plots to yield annual estimates of P_i, G_i, and F_7. These annual estimates were further averaged to give an overall mean estimate. These elements were then incorporated into a transition matrix, **A**, of the following form:

$$\mathbf{A} = \begin{bmatrix} P_1 & 0 & 0 & 0 & 0 & 0 & F_7 \\ G_1 & P_2 & 0 & 0 & 0 & 0 & 0 \\ 0 & G_2 & P_3 & 0 & 0 & 0 & 0 \\ 0 & 0 & G_3 & P_4 & 0 & 0 & 0 \\ 0 & 0 & 0 & G_4 & P_5 & 0 & 0 \\ 0 & 0 & 0 & 0 & G_5 & P_6 & 0 \\ 0 & 0 & 0 & 0 & 0 & G_6 & P_7 \end{bmatrix}. \quad (1)$$

In order to examine the effects of density on the various transition probabilities, the probability of surviving and remaining in the same size class (stasis) and the probability of surviving and growing to the next one (growth), were plotted for each size class against (1) the density of palms in each size class separately, (2) the total number of plants excluding seedlings, and (3) the total number of palms per plot. This analysis indicated a strong effect of the density of size class 1 on G_1, with no evidence of density dependence or competitive effects in the other transition rates (results not presented). The best fit models obtained for G_1 as a function of density were then incorporated into the transition matrix **A** of the population.

The finite rate of population increase was calculated from the dominant eigenvalue (λ) of each of the transition matrices; two values were calculated, one with G_1 estimated from the mean observed values, and one with G_1 set at its maximum, as estimated from the calculated density-dependent function. Confidence intervals were calculated using a Taylor's series expansion, following Alvarez-Buylla and Slatkin (1993), and using the standard errors of the transition rates across the 100 plots for each year. These standard errors therefore measure the uncertainty in λ owing to sampling variations in the transition rates.

We also calculated elasticity values, which provide important information on the extent to which population growth depends on survival, growth, and reproduction at different stages in the life cycle (de Kroon et al. 1986, Caswell 1989, Silvertown et al. 1993). An estimate of the elasticity of each element of the transition matrix for the population of *E. edulis* was calculated, based on the values in the transition matrix over a range of different densities. Following Silvertown et al. (1993), the elasticities in the transition matrix were divided into three groups to allow comparison of the relative importance of growth G (the G values

of **A**), survival L (the P values of **A**), and fecundity F (F_7 in **A**). All of the elasticities sum to unity, and the standardized nature of this procedure means that comparison can be made between species by triangular ordination. In particular, we wished to measure the degree to which the position of a population within G–L–F space may be affected by density dependence and hence determine the degree to which density dependence affects life history characteristics.

Description of density-dependent processes

For each of the plots, for each year subsequent to the initial count, we have counts of the number of individuals moving from one size class to the next. These data are by their nature discrete. If individuals move from one size class to the next with a constant probability, then the frequency distribution of the number of individuals changing size class will be a binomially distributed random variable.

Initial analysis indicated that the effects of density dependence could only be detected on G_1, the probability of individuals moving from size class 1 to size class 2. The procedure for fitting a model to describe the effects of density on G_1 was formulated by assuming a binomial distribution of recruits around the mean predicted value. The maximum likelihood estimators of the elements of the density-dependent function were found by numerically using a Rosenbrock pattern search (Rosenbrock 1960).

The density-dependent function used to describe the effect of increasing the density of seedlings of class 1 on the value of G_1 was

$$G_1 = G_m(1 + aN_1)^{-1}. \quad (2)$$

The function has two parameters, G_m, which is the maximal mean transition rate at low densities, and a which is a parameter that measures the strength of the reduction in G_1 with increasing density. Standard errors for the parameters of Eq. 2 were estimated by a jackknife procedure in which each individual value was successively excluded and then the model refitted; the distribution of the estimates of G_m and a was then used to generate standard errors.

In addition to exploring the effect of increasing the density of seedlings on the probability of seedling growth, we also explored the effect of the adult canopy. In particular, the residuals from the regression of G_1 on N_1, where residual value r is defined as G_1(observed)/G_1(predicted), were plotted against the distance from the nearest adult (class 7) plant. This showed that few seedlings could grow from class 1 to class 2 underneath the canopy of an adult plant.

Simulated population dynamics

Using an initial population vector $\mathbf{n}_0$, the trajectory of a population can be calculated from the density-independent transition matrix (Eq. 1) using the following equation:

$$\mathbf{n}_t = \mathbf{A}^t \mathbf{n}_0. \tag{3}$$

Population trajectories were explored using the density-independent transition matrix (Eq. 1) with G_1 set at its maximum value, and also with a density-dependent form of the transition matrix, including the density-dependent reduction in G_1 (Eq. 2) and the effect of adult plants on recruitment of seedlings to class 2. The effect of adult plants on the recruitment of seedlings to the next size class was modeled by assuming that no seedlings could grow from class 1 to class 2 underneath the canopy of an adult plant. If z is the crown area of an adult (we assume a value of $\sim$7 m^2) then, assuming a Poisson distribution of adult plants, the reduction in G_1 occurring as a consequence of the presence of adults, r_G, is given by

$$r_G = \exp\left(-\frac{z}{\rho} N_7\right) \tag{4}$$

where ρ is the area of a plot (i.e., 25 m^2). This is also a form of density dependence and we use this simplistic formulation to analyze the general consequences of density dependence before exploring a spatially realistic model. Note that all population projections based on the transition matrix relate to a patch size of 25 m^2 and are derived from an initial population vector with a size structure equivalent to that found in the field. This density-dependent version of the model was solved iteratively by updating the value of the density-dependent function in each generation, as well as calculating densities, asymptotic rate of population increase, and elasticities in each generation.

It is very difficult to obtain reliable estimates of adult plant survival from short-term studies. In this case, as the estimated value of P_7 (probability of stasis $\equiv$ probability of survival for class 7) was very high (0.9954), producing plants with absurd longevities, we explored the consequences for the population trajectories of two alternative values of P_7 that produced plants with more realistic longevities. These were a value of 0.99 (corresponding to a mean longevity of 100 yr within the adult class) and a value of 0.95 (corresponding to a mean longevity of 20 yr within the adult class). These values are also more in line with those produced in other studies (see *Discussion*). Only the consequence for the results of one of the P values is shown, unless they produce different predictions of population behavior.

Spatial dynamics

The form of density dependence modeled using Eq. 4 is inherently spatial, depending as it does on the distance between adult plants, and hence their spatial distribution, and depends critically on whether adult plants are present or not. In patches containing adults, recruitment of seedlings to the larger size classes will be nil or negligible (see also the formulation adopted by Alvarez-Buylla [1994]). However, in patches where adults are absent, recruitment will depend on (1) the density of seedlings present, and (2) the number of seedlings arriving through dispersal. Here we outline a spatially realistic model for the particular purpose of determining the degree to which our conclusions from the simplistic nonspatial formulation in Eq. 4 are affected by including more realistic spatial dynamics.

The spatially explicit version of the model was formulated by assuming a grid of 50 $\times$ 50 hexagonal patches, each of 7 m^2 (approximately the area of an adult crown) in size. The model made the following assumptions: (1) in patches where no adults were present, the full matrix (Table 2) including the density-dependent recruitment of seedlings (Eq. 2) was used to model changes in numbers; (2) in patches where adults (class 7 individuals) were present, the value of G_1 was set to zero; (3) a fraction f of seeds disperse from their natal cell to the six first-order neighboring cells, i.e., a number $fF_7/6$ recruit into class 1 within each of the surrounding cells. This restricted form of dispersal is in line with levels of dispersion reported by Silva Matos and Watkinson (1998), where dispersal distances of only a few meters are recorded. Only whole numbers of individuals were used in the simulations, with noninteger values stochastically rounded, according to the method of Perry and Gonzalez-Andujar (1993). The results presented are arithmetic mean population sizes that are recorded from the final 100 generations of a 1000 generation simulation and replicated 10 times for each parameter combination.

Specifically, we use the model to explore the impacts of varying levels of dispersal within a spatially structured habitat on the predictions of the nonspatial model. Also, although density dependence in the survival and fecundity of adult plants was not observed, the final set of simulations explores the potential importance of density dependence in the adult stage of the life cycle, through its effect on fecundity relative to the observed impact of density dependence at the seedling stage of the life cycle. To do this, we simply modified the outlined model to set the number of new seedlings produced per patch as a constant, irrespective of the number of adult plants present. This is equivalent to the number of seeds produced per plant declining with density.

RESULTS

Transition rates and density dependence

The mean density of adult palms was 0.71 trees/m^2 (i.e., 284 trees/ha), while that of seedlings was two orders of magnitude higher (Table 1). Table 3 shows the annual survival, growth, and transition rates for plants during each of the three years of the study. The survival of plants increased with size; that of plants in the larger size classes (classes 4–7) was particularly high, ranging 0.94–1. Mortality of adult plants in the largest size class (class 7) was rare; during the period

TABLE 2. Transition matrices for the population of *Euterpe edulis* based on the demographic data from Table 3 for the years 1991, 1992, and 1993, and the combined data from all three years. The final matrix is the estimated density-dependent transition matrix using the combined data with the density-dependent element G_1.

State at time $t + 1$	State at time t						
	n_1	n_2	n_3	n_4	n_5	n_6	n_7
1991 ($\lambda = 1.186 \pm 0.05$)							
n_1	0.5180						35
n_2	*0.2297*	0.7542					
n_3		0.0832	0.6096				
n_4			0.2731	0.5629			
n_5				0.4371	0.8450		
n_6					0.1150	0.7900	
n_7						0.2100	1.0000
1992 ($\lambda = 1.281 \pm 0.06$)							
n_1	0.4316						90
n_2	*0.2788*	0.7133					
n_3		0.1594	0.6733				
n_4			0.2510	0.6500			
n_5				0.3440	0.8443		
n_6					0.1504	0.7604	
n_7						0.2396	0.9850
1993 ($\lambda = 1.253 \pm 0.06$)							
n_1	0.5851						170
n_2	*0.2580*	0.8242					
n_3		0.0841	0.8507				
n_4			0.1232	0.6053			
n_5				0.3947	0.7212		
n_6					0.2267	0.7496	
n_7						0.1136	1.0000
Overall ($\lambda = 1.240 \pm 0.06$)							
n_1	0.5116						98
n_2	*0.2555*	0.7639					
n_3		0.1089	0.7366				
n_4			0.1995	0.6110			
n_5				0.3867	0.8010		
n_6					0.1790	0.7800	
n_7						0.1900	0.9954
Density-dependent matrix† ($\lambda = 1.284 \pm 0.06$)							
n_1	0.5116						98
n_2	G_1	0.7639					
n_3		0.1089	0.7366				
n_4			0.1995	0.6110			
n_5				0.3867	0.8010		
n_6					0.1790	0.7800	
n_7						0.1900	0.9954

Notes: The values for G_1, which are in italics, have been averaged across all the plots and densities of class 1. The corresponding value of λ for each matrix is also given (mean $\pm$ 1 SE). Missing matrix elements all have value of zero.

† This matrix, when multiplied by a population vector, provides estimates of the number of plants in a patch 25 m^2 in area. The value of G_1 can be calculated (see Eqs. 10 and 12) from the function $G_1 = 0.486(1 + 0.01228N_1)^{-1} \exp[(-7/25)N_7]$. The value of λ for the density-dependent matrix is calculated with G_1 set at its maximum (0.486). Note also that the simulations are based on this matrix with P_7 set at either 0.95 or 0.99 (see text for further details).

of study, only one adult of *E. edulis* died. The levels of transition from one size class to the next were appreciable, ranging 0.09–0.42. These rates varied considerably with the size category of plant, but were typically relatively high for plants in classes 1 and 4 and low for plants in classes 2, 5, and 6. The number of recruits per adult palm was lowest in 1991 (35) and highest in 1993 (170).

The transition matrices in Table 2 correspond to the data in Table 3. While there is some evidence of slight year-to-year variations in the estimates of the transition probabilities, estimates are generally consistent from one year to the next, and with the overall mean values (Table 2). The only exception is the estimate of fecundity, which appeared to increase over the course of the study.

The mean values shown for G_1 in Table 2, which are indicated in italics and have been computed across all of the plots and densities of class 1. There is, however, strong evidence of a decline in the rate of transition from class 1 to class 2 with increasing density of class 1 (Fig. 1a); there was no evidence of density dependence in the other transition rates. Eq. 2 gave a good fit to these data (combined over the three years of the

TABLE 3. The density of individuals within each size class (January 1991, January 1992, and April 1993) and the respective survival rates, transition rates to the next size class, and the number of new recruits per adult in 1991, 1992, and 1993.

Measure	Size class						
	1	2	3	4	5	6	7
1991							
No. palms/ha	22 000	2172	260	124	204	164	260
Survival rate	0.63	0.73	0.94	1.00	1.00	1.00	1.00
Transition rate	0.27	0.09	0.28	0.42	0.12	0.17	...
No. recruits/palm	...	...	...	...	...	...	35
1992							
No. palms/ha	24 400	2624	320	140	244	148	288
Survival rate	0.57	0.84	0.92	0.97	0.98	1.00	0.99
Transition rate	0.36	0.18	0.19	0.41	0.14	0.19	...
No. recruits/palm	...	...	...	...	...	...	90
1993							
No. palms/ha	35 600	3808	652	108	288	144	300
Survival rate	0.81	0.90	0.95	1.00	0.94	0.94	1.00
Transition rate	0.28	0.09	0.12	0.41	0.16	0.09	...
No. recruits/palm	...	...	...	...	...	...	170

Note: The size classes of the plants are defined in Table 1.

experiment) yielding parameter estimates (means ± 1 SE) of $G_m = 0.486 ± 0.024$, $P < 0.001$; and $a = 0.307 ± 0.029$ m², $P < 0.001$. As the value of a was estimated from data taken from 1-m² plots, it has to be divided by 25 to give a value of $a = 0.01228$ in Eq. 2, so that the density-dependent matrix (Table 2) can be applied to 25-m² plots.

There was also clear evidence of the presence of adult trees on the growth of seedlings from class 1 to class 2. As shown in Fig. 1b, transition rates were reduced by >80% within 1 m of an adult tree, compared with the level of recruitment predicted by the fit of Eq. 2. Following exclusion of the plots that were within 1 m of an adult tree, there was still a highly significant fit of Eq. 2 to the relationship between G_1 and density of seedlings. The parameters of Eq. 2 were affected only a little, presumably because most (mean of 90% over the three years) plots were >1 m from an adult palm. The revised parameter estimates were $G_m = 0.492 ± 0.022$, $P < 0.001$; and $a = 0.275 ± 0.030$ m², $P < 0.001$.

Analysis of the transition matrix and simulated population dynamics

The current average rate of population growth estimated from the linear Lefkovitch matrix (Table 2) is 24% annually ($\lambda = 1.24$), whereas the estimate of λ based on the density-dependent matrix with G_1 set at its maximum value (0.486) is 1.28, indicating a maximum population growth rate of 28% annually (Table 2).

Fig. 2 compares the observed size structure of the population of *E. edulis* with those predicted by the matrix model (Table 2) at low densities (i.e., density-independent population growth; only the distribution for $P_7 = 0.95$ is shown for this population, as the stable-stage distribution was unaffected to three significant

figures by changing P_7) and at the equilibrium density (i.e., density-dependent population growth), with P_7 set at either 0.99 or 0.95. It is clear from Fig. 2 that the populations showed a reverse ''J'' pattern of population structure, and that this arises as a consequence of the density dependence in the population; at low densities, when density dependence is effectively absent, the population structure is approximately log-linear. At high densities, when competitive effects are strong, the inhibition of the growth of seedlings resulting from the presence of adults and the density of seedlings leads to a decline in the proportion of intermediate size classes. The impact of increasing P_7 for the stable-stage distributions is to decrease the proportion of individuals in the intermediate size classes, with the proportions of individuals in the seedling and adult classes being proportionately unaffected.

The importance of this difference for the dynamics of populations is illustrated in Fig. 3, where the proportion of adults is plotted against the proportion of seedlings for 200 generations of population growth in the density-independent and density-dependent cases; P_7 is set at 0.95. It is clear, in cases where the initial relative proportions of adults and seedlings were the same, that the effects of density dependence lead to a rapid divergence in the size structures of the populations after only a few generations.

Figs. 4 and 5 analyze the impact of density dependence on the elasticity of the net rate of population increase, λ. There are clear differences between the elasticities for the matrices depending on whether the populations are in the density-dependent or density-independent phase of population growth (Fig. 4). In both cases, the largest elasticity is that of P_7, the probability of survival of adults. However, this is larger in the density-dependent phase than in the density-independent phase. The elasticities of the probabilities of
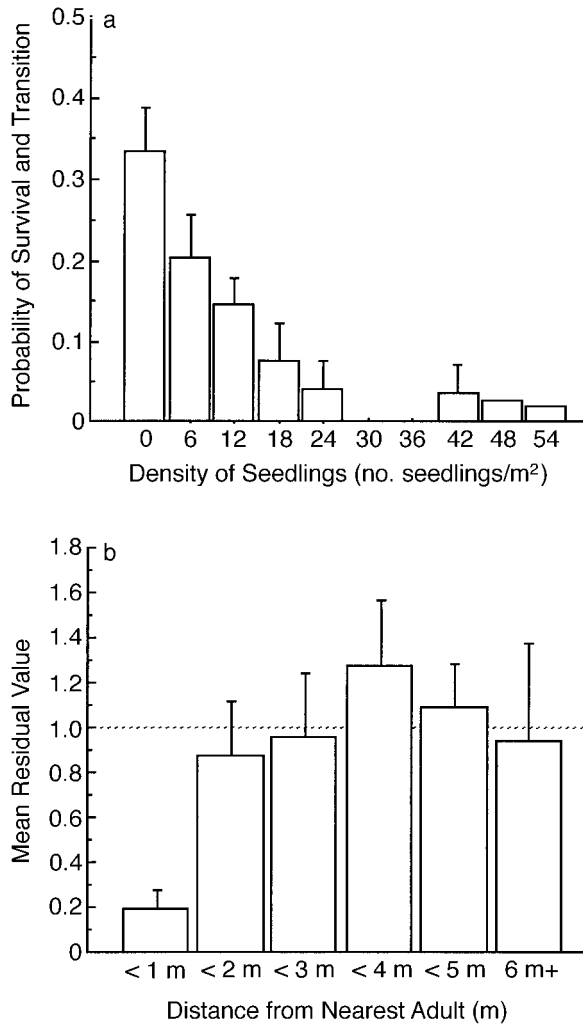
FIG. 1. Density effects in populations of *Euterpe edulis*. (a) The effects of increasing the density of seedlings within size class 1 on the rate of transition from class 1 to class 2. The mean transition rate within each group is shown, with the errors bars indicating +1 SE. (b) The effects of the presence of adults on the transition rate of seedlings from class 1 to class 2. The mean residual value is estimated for each plot as the observed rate of transition, divided by the rate predicted by the density-dependent function (Eq. 10). A value of unity (········) indicates no difference between the observed and predicted rates. Only the mean residual value for the transition rates in plots <1 m from the nearest adult is significantly different from unity ($t = 8.53$; df = 11; $P < 0.0001$).

survival and growth, *G,* are the same for all size classes as expected (de Matos and Silva Matos 1998) in both the density-dependent and density-independent cases, but very much reduced in the density-dependent case (Fig. 4b). The ordination of elasticities in Fig. 5 places *E. edulis* in the lower right hand portion of the *L–G–F* triangle (i.e., growth and survival have the greatest elasticities), in line with the position of a number of other tree populations. The position of *E. edulis* de-

pends, however, on density. The points in Fig. 5 represent a time series, with the population originating at the middle of the *L*-axis, moving in a transient phase towards the apex with the *F*-axis, and eventually settling in between these extreme values.

Analysis of the impact of spatial processes

The spatial model is a spatially explicit realization of the population processes that are assumed in the nonspatial model (Eq. 4). Differences between the predictions of the two models therefore highlight the importance of spatial processes. The effect of changing the fraction of seeds dispersing to neighboring patches on the size structures of simulated populations, compared with the size structure predicted by the mean-density model, is shown in Fig. 6. There is relatively little impact of changing the fraction of seeds dispersing on the general pattern of the distribution of individuals among the size classes. The main difference between the different levels of dispersal, or between the spatial and nonspatial models concerns size class 2, where the proportion of individuals in this class is higher under low levels of dispersal, or in the nonspatial model.

Fig. 7 shows the effect of changing the dispersal fraction, *f,* on the mean densities per patch of seedlings (Fig. 7a) and adults (Fig. 7b), compared for two levels of P_7, the probability of stasis within the adult class. The dashed horizontal lines in Fig. 7 give the prediction of the mean-density model, based on the assumption of a random distribution of adults, whilst the solid lines give the maximum density observed in plots during the period of study. Under either level of adult mortality, the density of seedlings and adults is higher in the spatial simulation than in the nonspatial model. This effect is due to the increased local densities of seedlings that arise from local dispersal, which then, through growth, lead to higher adult densities. The maximum density of plants recorded in the field is a little lower than that predicted by any of the models.

Fig. 8a compares the stable-stage distributions of populations with high ($f = 0.01$) and low ($f = 0.15$) levels of dispersal, with or without density-dependent fecundity, and with P_7 set at 0.95. There is clearly very little impact of density-dependent fecundity on the stable stage distribution, indicating that the density-dependent growth of seedlings plays the dominant role in determining population structures in these populations. However, density-dependent fecundity may play some role in determining numbers (Fig. 8b), with the numbers of seedlings being lower where there is density-dependent fecundity.

DISCUSSION

Density dependence

The search for density dependence and its impact on the abundance of tropical forest trees has proved par-

FIG. 2. Observed and simulated size class distributions. Bars indicate the size distributions predicted from the mean transition matrix with $P_7 = 0.95$ or 0.99 (see Table 2), when population growth is density independent (i.e., with G_1 set at its maximum, density-independent value), as compared with the patterns predicted when population growth is density dependent. The points indicate the mean size distribution across the three years of study.
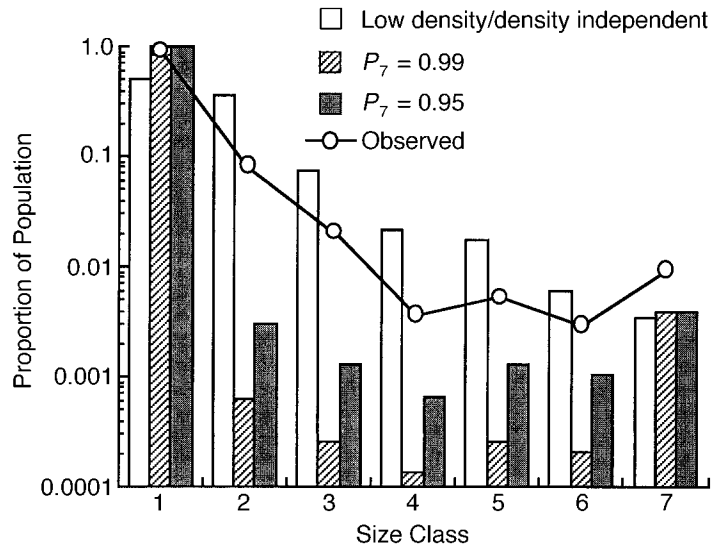
ticularly elusive. This study has clearly quantified the impact of density on the growth and survival of *Euterpe edulis* and shown that it has a major impact on dynamics. It would appear, however, that density affects only the survival and growth of the smallest size class. While it is evident that the effects of density dependence on the finite rate of increase of populations is relatively slight (mean population growth rate was reduced by only 5%), the impacts on population structure are profound. This is clear from Figs. 2 and 3, where observed population structures differ markedly from those predicted at low densities, or where low levels of density dependence during the initial stages of pop-

ulation growth lead to large deviations from density-independent patterns of size structure development.

A number of other studies have also demonstrated effects of density on the growth and survival of tropical trees, particularly during the early stages of the life
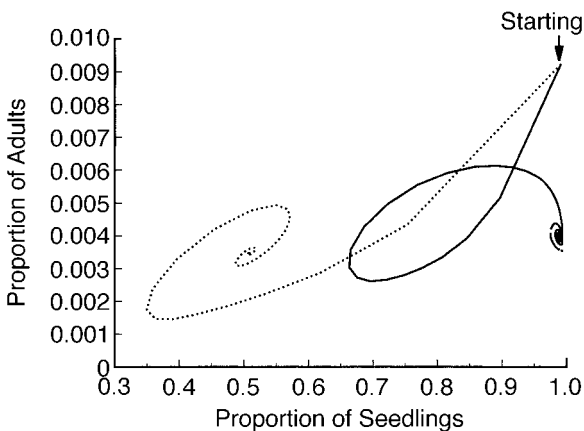
FIG. 3. Size-structure trajectories predicted from the mean transition matrix with $P_7 = 0.95$ (see Table 2) in populations of *Euterpe edulis*. The trajectories of size-structure change (shown as the proportion of adults plotted against the proportion of seedlings) are described for both the density-independent model (i.e., with G_1 set at its maximum, density-independent value; ········) and the density-dependent model (———).
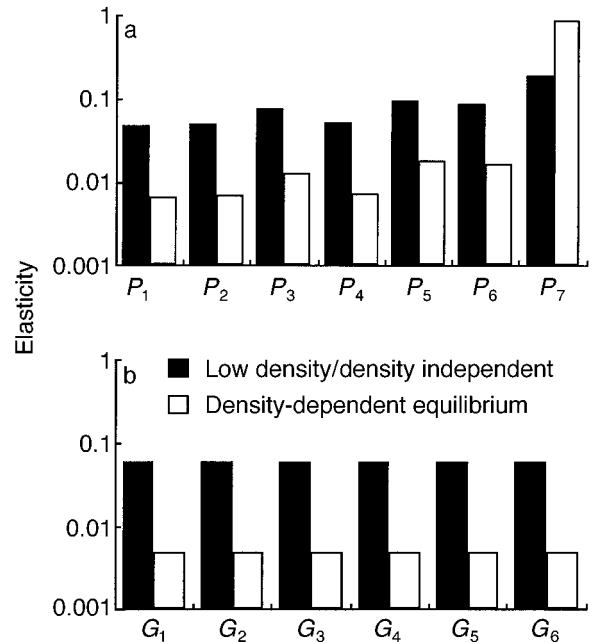
FIG. 4. Elasticity analysis of the contribution of stasis and growth to the population finite rate of increase. (a) The elasticities for the probabilities of stasis (P_i); (b) the elasticities for the probabilities of survival and growth (G_i). The elasticities, derived from the mean transition matrix with $P_7 = 0.95$ (see Table 2), are shown for models in which population growth is density independent (i.e., with G_1 set at its maximum, density-independent value) and for the equilibrium population in the density-dependent model.
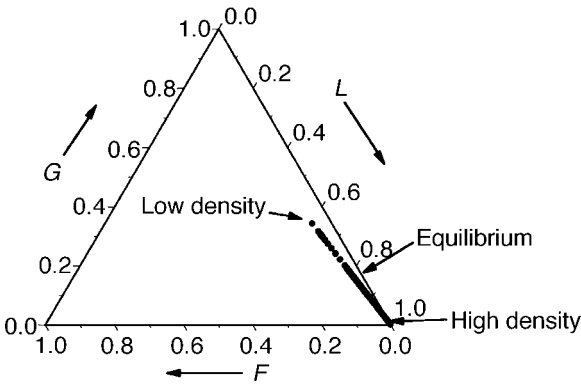
FIG. 5. *G–L–F* triangular ordination of the population growth elasticities, derived from the density-dependent transition matrix (see Table 2) with $P_7 = 0.95$, when populations were allowed to grow from low densities to an equilibrium. G = growth, L = survival, F = fecundity.

cycle. Seed predation (Janzen 1970, Sarukhán 1978), seedling mortality (Augspurger 1984, Clark and Clark 1984, Martínez-Ramos et al. 1988, Hubbell et al. 1990, Condit et al. 1994), and recruitment (Sarukhán et al. 1985, Condit et al. 1994) have all been shown to be affected by density. The only study to date that has demonstrated an effect of density on fecundity is that of Alvarez-Buylla (1994) on *Cecropia obtusifolia.* Effects of density on fecundity are perhaps expected to be uncommon amongst tropical tree species where adult individuals are frequently scarce, and Wills et al. (1997) have speculated that host–pathogen interactions are likely to be particularly important in determining the numerous density-dependent effects that they observed on recruitment. Positive effects of density on survival during early stages near adult trees have also been documented (e.g., Schupp 1992). We would argue

that the overall regulating role of density dependence in such circumstances depends on the differential between maximal survival near adult trees and survival further away. If such a differential exists, then density dependence may still be stabilizing at the level of the population, even if positive at the local level. Owing to the relatively small number of studies that have analyzed sources of density dependence in detail, it is hard to generalize about what kinds of species (e.g., understory and canopy) show density dependence at which stage of the life cycle. Few studies to date have examined sufficient stages of the life cycle for evidence of density dependence.

The mechanism(s) of density dependence are unclear for *E. edulis,* but it results from both the presence of high densities of seedlings and the presence of adults. A number of factors result in seedlings being suppressed in the immediate vicinity of adult plants (Hutchings 1997), including shade cast by the adult plant, root competition, specialist insect herbivores and pathogens associated with the canopy overhead, and intraspecific competition from high densities of seedlings. In this analysis, we have disentangled the effects of high densities of seedlings on survival and growth from the other factors associated with the presence of the adult plants. Previous studies have shown that the mortality of small plants of *E. edulis* may be related to the availability of resources (Bovi et al. 1990) and herbivory (Leão and Cardoso 1974, Carvalho and Martins 1993, 1994). Intraspecific competition amongst seedlings for soil water might be expected to be particularly acute, as more than half (by mass) of the root system is concentrated in the top 20 cm of the soil surface (Bovi et al. 1978), and soils dry out during the dry season. The effects of adults on the recruitment of seedlings can occur through falling fronds creating
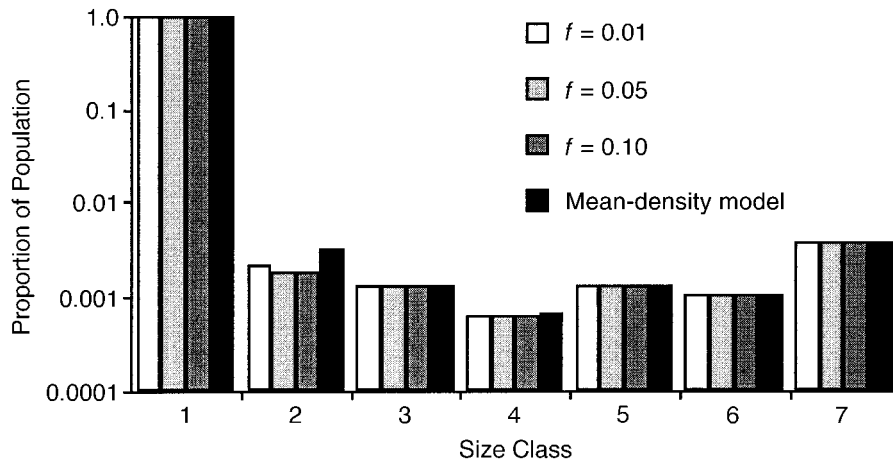

FIG. 6. Effects of changing the dispersal fraction on the stable size distribution in the spatial simulation model, and a comparison with that predicted by the mean-density model. The equilibrium stable size distributions are shown for populations in which *f,* the fraction of seeds dispersing from the natal patch, was set at 0.01, 0.05, or 0.10. These are compared with the stable size distribution predicted by the density-dependent form of the nonspatial transition matrix with $P_7 = 0.95$ (see Table 2).
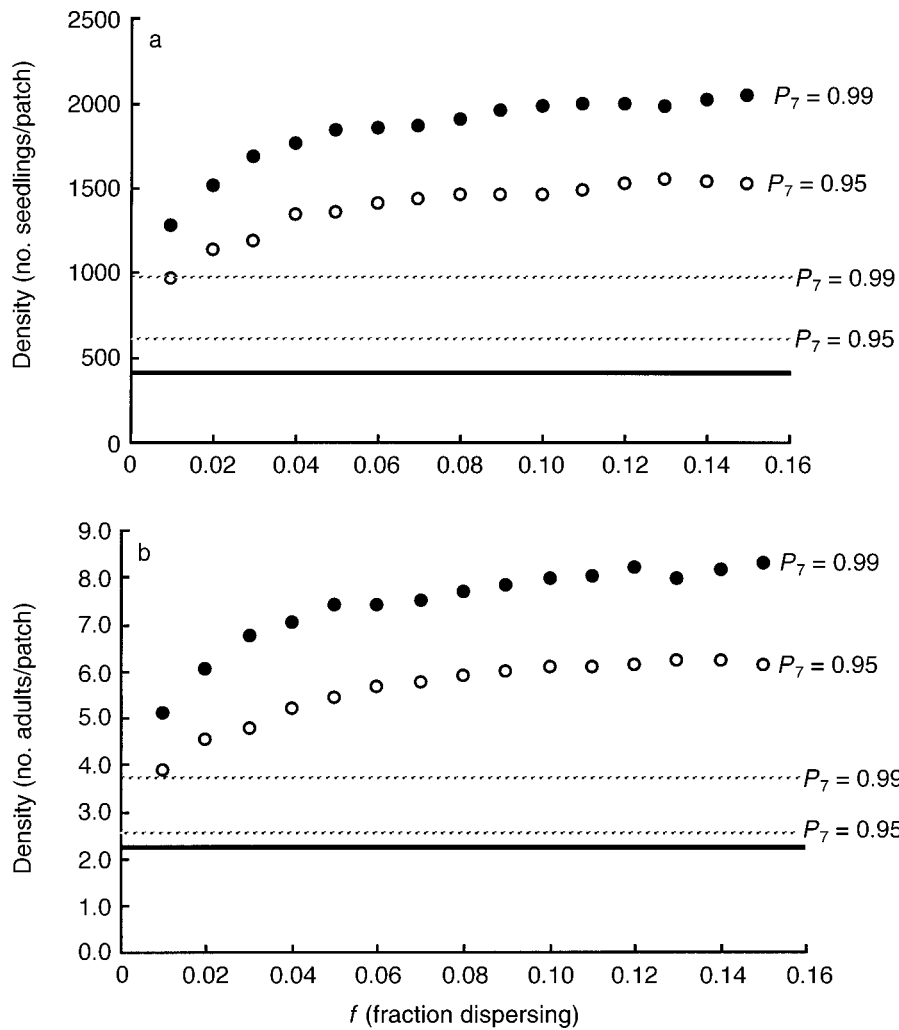
FIG. 7. Effects of changing the dispersal fraction on the equilibrium mean density in a 7-m² patch of (a) seedlings and (b) adults in the spatial simulation model, and a comparison with equilibrium densities predicted by the density-dependent form of the mean-density model. The equilibrium densities predicted by the spatial simulation with P_7 set at 0.99 (●) and 0.95 (○) are shown. The horizontal dotted lines show the corresponding predictions of the nonspatial density-dependent model with P_7 set at 0.95 or 0.99 (see Table 2). The solid horizontal lines show the maximum densities recorded in plots during the period of study.

"zones of death" around the base of the maternal palm (e.g., Denslow et al. 1991). This would generate density dependence, since as the density of adult plants becomes high, the overall per capita rate of population change declines. While, at the level of the individual plant, this mechanism would not appear to be density dependent, at the larger scale of a population, the process would generate density dependence.

We found no evidence for a density-dependent reduction in the fecundity or survival of individuals in the larger size classes of the population, although this may have been owing to insufficient data. Such processes, however, might be expected to play a secondary role in regulating population dynamics (Clark and Ji 1995). This is particularly evident when we consider

the dynamics of mortality within patches, as in the spatial simulation. What happens in the spatial model is that, while more than one plant may initially recruit within a patch, the patch will eventually become dominated by just a single adult, as others die off. The density of adults, therefore, plays little role in determining patterns of demography within patches; rather the presence or absence of adults is more important. The simulation results also indicate that density-dependent fecundity may play only a weak role in determining the size structure of populations or in determining densities (Fig. 8). Rather, the observed patterns of density dependence, namely, the effects of density on the growth of seedlings, would appear sufficiently strong to provide population regulation.
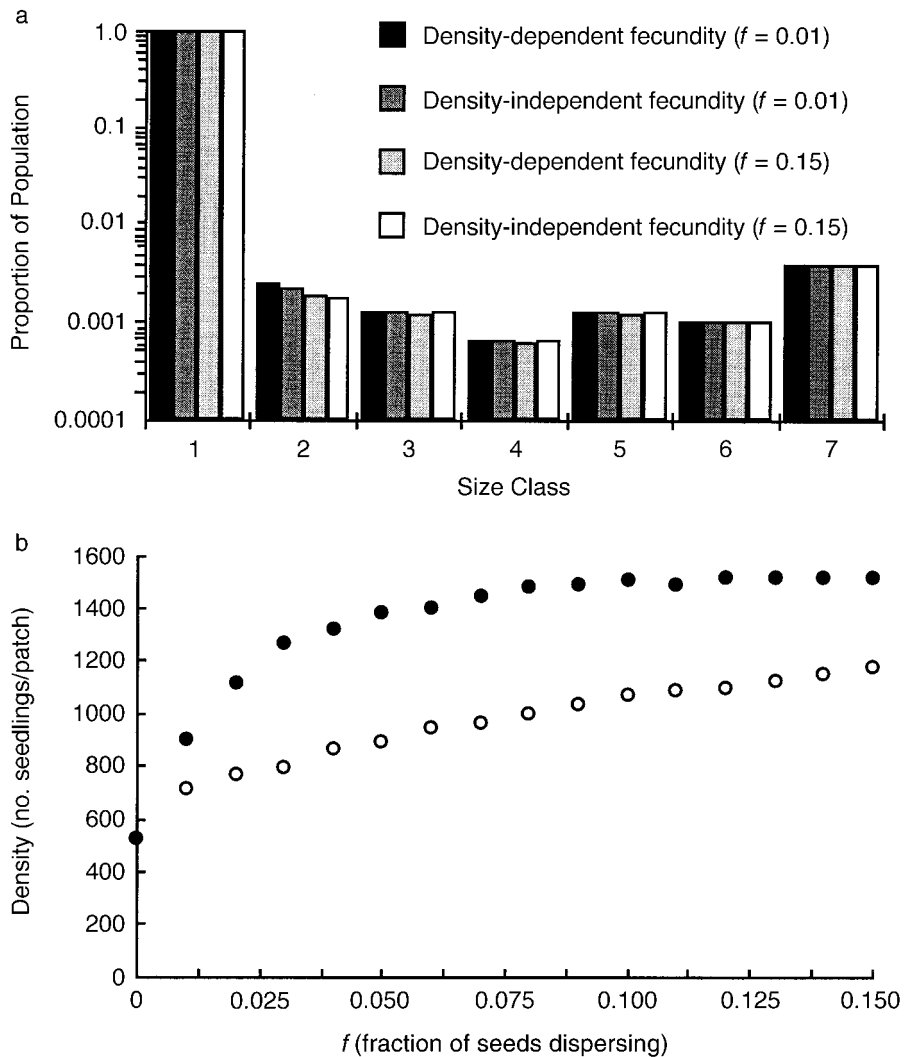
FIG. 8. Effects of density-dependent fecundity on predictions of stable size distributions and equilibrium densities. (a) The equilibrium stable size distributions when seedling production (n_7F_7) is set at a constant (i.e., is density dependent), compared with those predicted when seedling production is a function of adult density (i.e., is density independent). The fraction of seeds dispersing from the natal patch (f), was set at a low value ($f = 0.01$) or a high value ($f = 0.15$). (b) The equilibrium densities in a 7-m² patch when seedling production (F_7) is set at a constant (○) (i.e., is density dependent), compared with those predicted when seedling production is a function of adult density (●) (i.e., is density independent), shown as a function of f, the fraction of seeds dispersing from the natal patch.

Size structures and patterns of mortality

The size structure of the population of *Euterpe edulis* in the swampy area of the Municipal Reserve at Santa Genebra, Brazil is typical of climax species, with continuous recruitment and both juveniles and adults occurring together (Whitmore 1988). A number of authors (Solbrig and Solbrig 1984, Whitmore 1990, Felfili 1995) have commented on the reverse "J" shape of size structures that occur in tree populations. Clearly, the exact shape of the size distribution depends on the class intervals that are used to define the population structure. However, the analysis here indicates that, when density dependence is weak, the population structure is approximately log-linear; whereas, when density-dependent effects are strong, the size structure has the characteristic reverse "J" shape. This is because the inhibition of the growth of seedlings, resulting from the presence of adults and the density of seedlings, leads to a decline in the proportion of intermediate size classes. The current size distribution of the population at Santa Genebra (Fig. 2) is between that which might be expected when a population is not affected at all by density and that which might be expected at equilibrium when density dependence is strong.

The pattern of mortality in relation to plant size was similar to that found in other palm species (Van Valen 1975, Sarukhán 1978, Enright and Watson 1992), with mortality being highest among the smallest plants. Dur-

ing the period of study, annual mortality amongst plants in the four largest size classes was <7%. Such estimates of mortality are in line with those from other studies. In a review of the dynamics of tropical tree populations, Swaine et al. (1987) found that the annual mortality of trees (≥10 cm dbh) ranged 1–2%. De Steven and Putz (1985), however, reported slightly higher estimates of mortality (≤9.3% annually) for immature and adult individuals of some palm species. Mortality as a result of leaf or tree falls has been shown to be common amongst other palm species (Vandermeer 1977, Piñero et al. 1984, Martínez-Ramos et al. 1988), although these factors may not be significant in determining the mortality of clonal palms (see De Steven 1989). Tree fall was, however, the cause of mortality of the only adult plant in size class 7 that was observed to die in this study.

Mortality of plants in the largest size class plays a critical role in determining population size and population structure through modulating the flux of individuals from the seedling stage through the intermediate size classes. This is clearly evidenced by the strong elasticity of the finite rate of population increase to changes in P_7, the probability of survival in class 7. This mortality rate is, unfortunately, the hardest to estimate. Data from long-term surveys have shown that the mortality of tropical trees is best estimated from such extended surveys, since extreme events such as droughts may play a significant role in determining patterns of mortality, particularly amongst larger plants (Condit et al. 1995). Future studies need to analyze tree mortality in this way in order to obtain estimates of both mean levels of mortality as well as to quantify patterns of mortality in extreme years.

The highest probability of plants surviving and growing to the next size class was observed for plants growing from class 4 to class 5. This transition, from <30 mm diameter at soil level (DAS) to 30–60 mm DAS corresponds to the stage at which the palms become caulescent and at which growth rates are relatively rapid. In general, the transition rates observed in *E. edulis* are higher than those obtained for other palm species. Piñero et al. (1984) found lower transition rates in early stages than mature ones (e.g., 0.014 from infants to juveniles and 0.10 to mature plants). They argued that the higher transition rates of larger plants might reflect the light conditions; it was argued that plants of ~1.5 m in height (mature plants) were in better light conditions and consequently able to grow faster and reproduce. In contrast, and as found to a certain extent in *E. edulis,* Enright and Watson (1992) found that the lowest transition rates for *Rhopalostylis sapida* occurred in the progression of seedlings to juveniles and amongst the tallest palms. They argued that this pattern resulted from variations in size, age, light conditions, and interference from lianas.

In considering variation in transition rates between classes however, it is also important to take account of the size classification system, as the length of the var-

ious categories will undoubtedly influence transition rates (Piñero et al. 1984). Inevitably, the total number of size classes used to describe the population, as well as their boundaries, is arbitrary. Too many classes reduces sample sizes upon which vital rates (e.g., survival and fecundity) are estimated, and too few categories may increase the skewing in the within-category distribution of individuals (Vandermeer 1978). Enright and Watson (1992) have verified that the presence of a large number of individuals within a class, but close to the class boundary, can overestimate transition rates. Furthermore, the number of stages used in a model can influence the analysis of transition matrices (Enright et al. 1995).

Finite rate of population increase

Published estimates of the finite rate of population increase λ for tree species are derived from linear Lefkovitch matrix models. Thus, estimates reflect the actual rate of population growth for a population characterized by the set of survival and fecundity schedules measured during the period of study. Undoubtedly, many of these estimates are influenced by density, therefore failing to represent the true finite rate of population increase, which is the rate of population growth at low densities. Our estimates of the true finite rate of population increase (λ = 1.28) indicate that the population will increase at low densities at ~28% annually, if the population is in its stable size distribution. The only other estimate of the true finite rate of population increase comes from the study of Alvarez-Buylla (1994). Analysis of the transition matrices provided by Alvarez-Buylla (1994) indicates that the finite rate of increase of populations of *Cecropia obtusifolia* is much lower, 1.06, when intraspecific densities are set to zero (compared with the value of 1.01, calculated by computing the mean across densities).

Estimates of the current rate of population increase for *E. edulis* at the Municipal Reserve of Santa Genebra, derived for the linear Lefkovitch matrix, indicate that the population is increasing at the rate of about 24% annually (λ = 1.24). This rate is considerably higher than the expected rate for a population at equilibrium (λ = 1) and indicates that the population is still undergoing a period of growth. The rate of population increase is higher than that of many other tropical palm species that have been studied. Across a number of studies, values of λ range 0.97–1.20 (Bullock 1980, Piñero et al. 1984, Enright and Watson 1992, Pinard 1993, Olmsted and Alvarez-Buylla 1995, Alvarez-Buylla et al. 1996). Many other trees and shrubs have also been found to have finite rates of increase close to unity (Silvertown et al. 1993), including a number of long-lived tropical forest canopy trees (Alvarez-Buylla et al. 1996). Given the short duration of many studies, and the fact that many populations are undoubtedly affected by density (Wills et al. 1997), it is not surprising that many of the estimates of λ in the studies cited here are close to one. However, compar-

isons between the finite rates of increase of different populations are difficult, due to the general lack of confidence intervals on estimates of λ. It should also be noted that the durations of the studies vary considerably, and this will undoubtedly have consequences for the robustness of estimates of survival, growth, and reproduction, as will the longevity of the species and the size classification scheme used (Enright et al. 1992).

The factors responsible for the high rate of population increase in *E. edulis* are not altogether clear. It could be that the population is responding to a changed environment that has resulted from forest fragmentation and isolation, or that the population is recovering from past exploitation in the community. This latter explanation is perhaps the most likely. Before the designation of the area as a nature reserve in 1979, people living around the forest used to exploit *E. edulis* for the heart of palm that it produces, as well as exploiting a number of other tree species. That the population of *E. edulis* is recovering from past exploitation is suggested by the fact that the mean number of adult plants per hectare (284 plants/ha) at Santa Genebra is ~10% lower than that found by Bovi et al. (1987) (310 plants/ha) and 27% lower than that reported in the Florestar Estatístico (1994) (~360 plants/ha) in the Atlantic Forest.

Elasticity analysis

Elasticity analysis of the transition matrix showed that the position of the basic matrix for *E. edulis* in G–L–F space was similar to that of other trees (including four palm species) from forest habitats (Silvertown et al. 1993); woody plants from forest habitats lie near the *L*-apex of the triangle. This position indicates that the probability of surviving and remaining in the same size class contributes most to λ. However, the inclusion of density effects within the transition matrix had a significant impact on the position of *E. edulis* in the triangular ordination, with the population moving toward the *L*-apex as density increases. This indicates that the relative importance of fecundity and growth declines as the rate of population increase declines and population densities approach equilibrium. Silvertown et al. (1993) similarly concluded from their comparative review that the relative importance of fecundity decreased as λ decreased. Other studies on palms and canopy tree species from tropical forests (Alvarez-Buylla et al. 1996) have found that the largest elasticity values are for survival during the preadult and adult stages of the life cycle. The elasticity analysis for *E. edulis* confirms this result, with the largest elasticity value being for the survival of adults (P_7). However, the relative importance of this elasticity value was larger during the density-dependent phase of population growth than in the density-independent phase. This is because the mortality of adults determines the rate at which gaps occur into which seedlings may recruit.

Silvertown and Franco (1993) used the demographic triangle to demonstrate how the demographic characteristics of populations change with a variety of environmental factors such as grazing, fire, and habitat succession. A large range of biotic and abiotic factors change during succession, including, for example, plant density, interspecific competition, and herbivory. The study reported here shows that density, in itself, can have a large impact on the position of a species in G–L–F space, with populations moving toward the *L*-apex as density increases.

Population dynamics and abundance

Inclusion of density-dependent processes in the model for population dynamics indicated that there are clear effects of density dependence on the structure of populations, with the population structure at low densities differing markedly from that at high densities (Fig. 2). Additionally, the analysis of the models indicated that the inclusion of density dependence markedly affects the time trajectory of size structure dynamics. The analyses of the effects of changing the survival rates of adults, as well as comparisons with the predictions of the spatial simulation, indicated that the predictions of stable size distributions are relatively robust (Figs. 2, 6, and 8a). This contrasts with the predictions of densities of plants, which are sensitive both to changing the level of adult mortality and the level of seed dispersion (Fig. 7). In general, it is difficult to judge the success of this kind of model in predicting the densities of plants, since adequate data on equilibrium (or long-term mean) population numbers are typically unavailable. The results of the spatial simulation model indicate that population numbers may double or treble above present maximum densities, depending on the nature of dispersal. On the other hand, the nonspatial model indicates that maximum population densities at present may be close to the equilibrium density predicted by the density-dependent matrix model.

The considerably higher densities of both adults and seedlings, as predicted by the spatial model, may be attributed to the increase in local densities of seedlings occurring as a consequence of restricted dispersal. The increase in the densities of plants that occurs as a consequence of increasing the level of dispersal results from the increasing ability of plants to colonize empty patches. The mathematical basis for this type of phenomenon has been discussed by Chesson (1996). In particular, numerical changes in the nonspatial model are estimated on the basis of a density-dependent function taken at the mean density *across* patches; the spatial model operates on the basis of the mean strength of density dependence *within* patches. Owing to the nonlinear nature of the density-dependent functions, these two forms of averaging do not yield the same mean population change.

Alvarez-Buylla (1994) also stressed the importance of considering the nature of patch dynamics in param-

eterizing models for the dynamics of tropical trees, but found, in contrast to this study, that densities were depressed by explicitly including patch dynamics. This difference results from the more complex spatial nature of the habitat in the the patch dynamics model of *C. obtusifolia,* in which plants tend to be concentrated into small areas of favorable habitat within a matrix of unfavorable patches.

In this study, we have shown that although the current mean densities of *E. edulis* are still increasing, the observed density-dependent and density-independent processes are sufficient to explain the maximum densities observed in patches in the field. Since few studies have attempted to determine the detailed nature of regulatory processes that operate within populations of tropical trees, it is impossible to determine the generality of the results presented here. The most important general results to emerge are that the simple linear models of population growth, based on stage-structured matrices, are adequate to describe population structures and the qualitative nature of population growth. They are inadequate, however, when more detailed predictions of densities are required. The spatial simulations that we have presented indicate that such predictions are very sensitive to the nature of spatial dynamics within populations. It seems likely that these general results will hold for most tropical trees.

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