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A POPULATION MODEL OF *ASTROCARYUM MEXICANUM* AND A SENSITIVITY ANALYSIS OF ITS FINITE RATE OF INCREASE

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SUMMARY

(1) The demography of the palm *Astrocaryum mexicanum* is described from a study of six permanent plots in a tropical rain forest in Veracruz, Mexico, during 7 years.

(2) There are differences between the plots in transition probabilities, survival and fecundity estimates for some age classes.

(3) Yearly estimates of transition probabilities from one stage to the next are about 0·10 individual individual^{-1} year^{-1} for most stages.

(4) This palm has a survivorship pattern with high mortalities (0·69–0·95 individual individual^{-1} year^{-1}) during the first stages of the life cycle and almost no mortality (0–0·03) after its first reproduction.

(5) Individual fecundity shows an initial increase followed by constant values after the palms are about 70 years old.

(6) Estimates of the finite rate of increase (λ) vary between 0·9932 and 1·0399. The average for all plots, 1·0046, predicts a doubling time for a population of about 150 years.

(7) A sensitivity analysis of λ to various demographic parameters shows that fecundity and survival rates for older stages are between one and four orders of magnitude less important in changing λ than growth and survivorship estimates for intermediate stages.

INTRODUCTION

Detailed descriptions of the life-histories of tree populations have been used to understand their regulating mechanisms (Niering, Whittaker & Lowe 1963; Bannister 1970; Hartshorn 1975; Van Valen 1975; Melampy & Howe 1977; Enright & Ogden 1979; Lamont & Downes 1979; Bullock 1980; Hubbell 1980; Sarukhán 1980; Bullock & Bawa 1981) and to design managing criteria to harvest forest resources optimally (e.g. Usher 1972). What is needed for such studies is a transition matrix including data on transition probabilities, survival and reproduction for different life-history stages or age classes. Matrices like those developed by Leslie (1945) or Lefkovitch (1965) can be adapted for these needs. The largest positive root of either matrix is an estimate of a population's finite rate of increase whilst the right and left eigenvectors correspond, respectively, to the stable age structure and the reproductive value for each age class or stage. This information can then be used to know the effect that changes in any of the life-history parameters of the population will have on the finite rate of increase; this sensitivity analysis will help in understanding the aspects of a life table that play a key role in the regulation of numbers in a population (Caswell 1978). Other types of analyses (e.g. *K* factor analysis; Varley & Gradwell 1960) have been proposed to estimate the relative importance of mortality factors on the regulation of population size.

Estimates of the finite rate of increase have been obtained for annuals with discrete (Leverich & Levin 1979) and overlapping generations (Law, Bradshaw & Putwain 1977), biennials (Werner & Caswell 1977; Caswell & Werner 1978), perennial herbs (Sarukhán & Gadgil 1974; Fetcher & Shaver 1983), tropical (Hartshorn 1975; Bullock 1980) and temperate trees (Enright & Ogden 1979). A sensitivity analysis of different demographic parameters on the finite rate of increase has also been used to understand the regulation of population densities. This analysis has been applied in the case of the palm *Podococcus barteri* Man & Wendl., (Bullock 1980) and for the tropical tree *Pentaclethra macroloba* (Willd.) Ktze., and the biennial herb *Dipsacus sylvestris* Huds., (Caswell 1978).

For the period 1975–83 the tropical understorey palm *Astrocaryum mexicanum* Liebm. has been studied in Mexico. Data on population structure of this species in permanent plots and its reproductive schedules have been published (Piñero, Sarukhán & González 1977; Piñero & Sarukhán 1982). These studies have shown contrasting population and community structures for different plots and also that individual fecundity depends on the age of an individual, its position within the forest and also on the year. Survivorship estimates based on observed stage structure (assuming population stability) show a pattern with almost no mortality during the reproductive stages and low survivorship in early stages (Sarukhán 1978, 1980). Seven years of observations have provided survivorship data which realistically describe the demography of the population, and growth estimates for 6 years provide the means to estimate transition probabilities from one stage to the next. With that information we now address the following questions: (i) what are the dynamics of the population of *Astrocaryum mexicanum* in the forest plots?; (ii) are the populations in plots of different densities growing at the same rate? (iii) which characters of the life-history have a relatively greater effect on the finite rate of increase (λ) of the population?

THE SPECIES AND THE STUDY PLOTS

Long-term studies on the demography and population ecology of *Astrocaryum mexicanum* commenced in 1975 at the 'Los Tuxtlas' biological field station of the Instituto de Biología, Universidad Nacional Autónoma de México (18°36′N, 95°07′W) in the state of Veracruz. Andesitic and basaltic rocks are the most abundant parental material and the soils are mostly reddish to brown and slightly acidic latosols. Detailed descriptions of the geology, soils and climate of the area have been reported by Lot (1976). The mean annual rainfall at the station is about 4600 mm, and no month has less than 60 mm of rain.

Astrocaryum mexicanum is the most abundant species (in density as well as crown cover) in the lowest storey (up to 10 m tall) of the forest. The base of the oldest leaf of this palm is 5–7 m high. The palms grow fairly evenly throughout the year. The annual rate of leaf production (6-year average) is 1·34 leaves per individual for seedlings and 'infants' (1–8 year old individuals with bifid leaves), 1·60 for 'juveniles' (8–15 year old individuals with pinnatifid leaves), and 2·55 for immature individuals (non-reproductive, 16–25 year old individuals with a trunk) and for mature individuals (reproductive palms older than 25 years). These results and the fact that leaf scars remain permanently on the trunk allow for palms to be aged, assuming that the leaf production is constant for each age category over the years (Sarukhán 1978, 1980).

Astrocaryum mexicanum is monoecious; the inflorescences are protogynous and bear twenty–sixty female flowers and about 200 male flowers for each female flower. Preliminary studies on its reproductive biology suggest that cross-pollination is obligate (Pedroza 1982). Palms flower between late March and late April. The one-seeded fruits fall to the ground in October and start to germinate 5 months later. The general area of the field station represents the northern-most locality of *Astrocaryum mexicanum* in America; the southern limit is Honduras. It is restricted to tropical rain forests, usually on soils derived from limestone and often in karst topography; 'Los Tuxtlas' is the only part of its Mexican distribution with soils of igneous origin.

Six plots (each 20 × 30 m), representing three levels of density of mature individuals were selected in mature, stable sites with no signs of recent disturbance by natural gaps: plots A and AA had high, B and BB intermediate, and C and CC low density. A detailed description of the community structure, composition and other characteristics of the plots has been given by Piñero, Sarukhán & González (1977).

METHODS

All juvenile to mature individuals were labelled and located on a map in 1975; only one third of each 600 m^2 plot was censused for seedlings and infants. The number of live leaves on each individual was recorded and, for immature and mature individuals, the height of the trunk to the base of the petiole of the oldest living leaf.

Information on survivorship comes from censuses carried out every 6 months for infants (except during 1979 and 1980 in each of which only one census was done) and annually for mature individuals. Only two censuses were taken for juvenile and immature palms in May 1975 and July 1981.

Estimates of the proportion of individuals that grow onto the next stages of the life-cycle were obtained in one of two ways. (i) For 30% of the original juvenile to mature individuals ($n = 126$) and all the infants ($n = 142$), all the leaves were marked at the beginning of the study (in 1975) and the new leaves were recorded in July, every year. Each leaf produced represented an average increase in height of 2 cm. Thus after 6 years, the total increment in height could be estimated from the number of leaves produced. (ii) For the rest of the population, individual heights were measured in 1975 and in 1981 to yield a direct estimate of the transition probabilities. Every year, the number of infructescences and fruits per infructescence were recorded for each reproducing individual.

Data on predation of the fruits (particularly by the squirrels *Sciurus aureogaster aureogaster* Cuvier and *S. deppei deppei* Peters) while still attached to the infructescence were derived from an experiment carried out in 1975. Forty-one reproductive palms were selected, their number of infructescences and fruits per infructescence counted, and a light but sturdy net installed under the infructescences so that any mature fruit that dropped would be collected by it. A thick plastic sheet was wrapped around the trunk of these palms to discourage climbing vertebrates. The observations were continued until all the fruits had fallen naturally (by October). The fruits within each net were counted and compared with those originally on the infructescence. This quotient was used as the probability of surviving arboreal predation. A second experiment was carried out to determine fruit predation by ground mammals. On each of the six plots, five replicates of three fruit densities (4, 8 and 16 m^{-2}) were placed randomly on the ground on 1 October 1975. The plots were visited every 10–15 days and after 3 months the proportion of seeds taken was estimated as a mean of all conditions, assuming there was no fruit dispersion.

RESULTS

The life table

A demographic model for *Astrocaruym mexicanum* based on the average results for the six plots for 6 years of observations of individual growth and survivorship and observations from seven reproductive seasons is presented in Fig. 1.

The survivorship pattern shows that the highest mortalities are those for younger categories (0·92 for fruits and 0·31 for seedlings) whilst annual mortalities during the reproductive stages are very low (0–0·30).

The causes of mortality are largely unknown, but one third of the dead, mature individuals ($n = 26$) after 7 years showed evidence of having been killed by a falling branch or tree. Also, individuals which died showed significantly ($t = 2{\cdot}70$, $P < 0{\cdot}01$) fewer leaves (mean ± 1 S.D.; 10·20 ± 3·30) than living individuals (12·50 ± 3·27) which suggests that a reduction in the ability to capture resources could enhance the probability that an individual will die. This same phenomenon was observed for infant, juvenile and immature individuals (Sarukhán, Martínez-Ramos & Piñero 1984).

Transition probabilities vary during the life-cycle and are partly the result of differing lengths of the various categories. Usually 10% of the mature individuals move to the next category each year, whereas lower values, due to slower growth rates, are found in the early stages (e.g. 0·014 from infants to juveniles).

The probability of reproduction follows a logarithmic pattern since the last six categories are not statistically different in this respect (between 0·5 and 0·6 of the individuals bear flowers in any given year). Also, individual fecundity increases for the first part of the reproductive period while for older stages it is constant (about twenty-five fruits per palm). Finally, the total contribution of the reproductive stages follows a normal curve; individuals 65–75 years old make the largest contribution of fruits.

Factors that affect the transition probabilities are the same than those that affect reproduction (Piñero & Sarukhán 1982) and include age, microsites and individual year. Irradiance has been thought (Piñero & Sarukhán 1982) to limit individual growth and reproduction.

The transition matrices for individual plots

Transition matrices (Lefkovitch 1965) for a 6-year period were constructed. These include on the main diagonal the yearly probability that an individual stays in the i stage, in the subdiagonal the yearly probabilities of transition from the i stage to the $i + 1$ and on the first row the average individual fecundities per year (Table 1). The yearly transition probabilities from infants to juveniles were different ($P < 0{\cdot}05$) in plots C (0·0021) and CC (0·0034) from B (0·023) and AA (0·017). The other two plots, A (0·015) and BB (0·008) were not significantly different from all plots. All transition probabilities for other stages were not significantly different for all plots, as was the case for survival estimates except the juveniles. The highest survivorship for that stage occurred in plot CC (1·00) and was significantly different from that in both A and AA (0·95). Plots B, BB and C (0·97–0·98) did not differ from either group.

Fecundity is a composite estimate; the product of the probability of reproduction and the number of fruits per reproductive individual. Comparisons between plots show differences in only two stages (65–75 and 95–105 years old) using a Friedman two way analysis of variance. A multiple comparisons test showed that, for the first stage, only plots C (twelve fruits per individual) and B (33·5) were significantly different from each

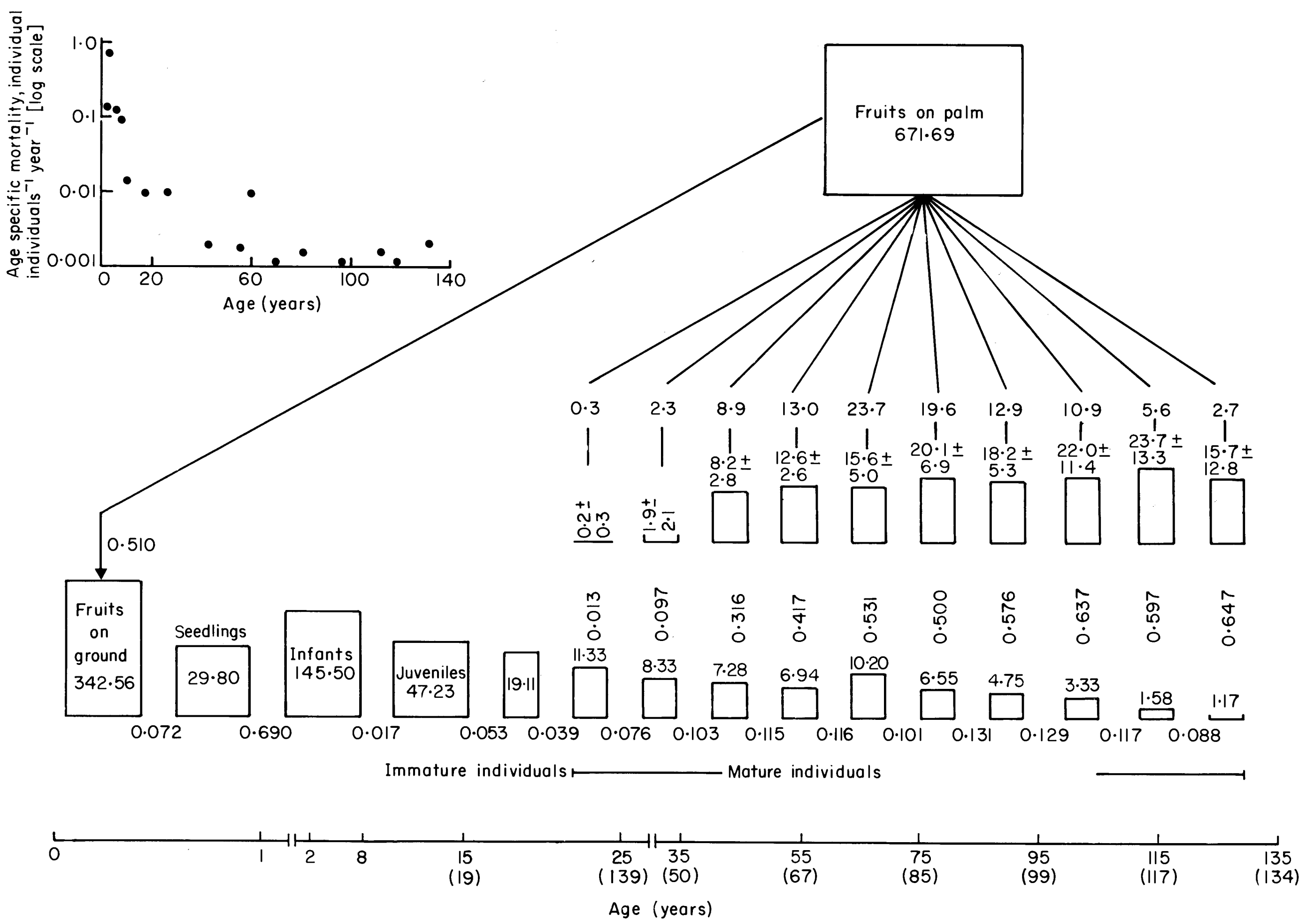

FIG 1. Population flux model for an average 600 m^2 plot of *Astrocaryum mexicanum* in 'Los Tuxtlas', Veracruz, Mexico. Box heights represent the density of individuals (on log scale). Numbers between boxes represent the annual probability of moving from one stage to the next. For the mature stages, the probability of reproduction, the mean individual fecundity (±1 S.D.) and the per cent contribution to the annual fruit production follow each box. Age was estimated from growth rates obtained by measuring directly individual heights in 1975 and 1981 (in parentheses) or from data on leaf production for 30% of the population between 1975 and 1979. The graph (inset) shows the relationship between age and stage mortality.

TABLE 1. Lefkovitch matrices for six *Astrocaryum mexicanum* plots in Veracruz, Mexico. (a)–(f) are data for plots A, AA, B, BB, C and CC, respectively. Stages are: (F), fruits; (I), infants; (J), juveniles; (IM), immature individuals and M1–M10 mature individuals. Average number of individuals per stage are to the left of each matrix (*n*). Values followed by an asterisk represent stages in which no individual died or moved to the next stage; In these cases we assigned a probability value of 0·001.

(a) Plot A

n		F	I	J	IM	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10
928	F						0·67	9·02	9·09	12·43	19·57	19·44	18·31	19·77	
264	I	0·039	0·823												
62	J		0·015	0·927											
20	IM			0·027	0·975										
17	M1				0·017	0·942									
8	M2					0·048	0·957								
7	M3						0·043	0·897							
11	M4							0·103	0·876						
19	M5								0·077	0·911					
13	M6									0·089	0·885				
7	M7										0·103	0·909			
2	M8											0·091	0·889		
1	M9												0·111	0·999*	
—	M10													0·001*	0·999*

(b) Plot AA

n		F	I	J	IM	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10
1136	F						1·86	7·40	12·32	21·21	21·75	26·40	31·59	30·43	19·23
208	I	0·036	0·841												
68	J		0·017	0·869											
25	IM			0·069	0·947										
10	M1				0·040	0·842									
17	M2					0·140	0·893								
8	M3						0·107	0·913							
4	M4							0·087	0·881						
5	M5								0·119	0·793					
7	M6									0·207	0·886				
8	M7										0·114	0·896			
9	M8											0·083	0·926		
4	M9												0·056	0·739	
3	M10													0·261	0·999*

TABLE 1. Continued.

(c) Plot B

n		F	I	J	IM	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10
784	F					0·13	5·85	12·68	12·48	19·71	26·16	13·00	40·35	45·64	4·50
190	I	0·033	0·848												
59	J		0·023	0·902											
34	IM			0·068	0·935										
16	M1				0·050	0·905									
9	M2					0·074	0·852								
11	M3						0·148	0·907							
4	M4							0·093	0·762						
9	M5								0·238	0·982					
3	M6									0·018	0·702				
4	M7										0·298	0·875			
2	M8											0·125	0·710		
1	M9												0·217	0·999*	
1	M10													0·001*	0·999*

(d) Plot BB

n		F	I	J	IM	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10
954	F					0·27	1·78	4·14	7·87	15·31	18·56	22·30	11·27	9·57	
243	I	0·039	0·836												
48	J		0·008	0·934											
12	IM			0·046	0·944										
10	M1				0·056	0·930									
6	M2					0·053	0·839								
11	M3						0·134	0·838							
15	M4							0·147	0·865						
20	M5								0·124	0·882					
14	M6									0·118	0·889				
6	M7										0·111	0·879			
2	M8											0·121	0·750		
2	M9												0·250	0·909	
—	M10													0·091	0·999*

TABLE 1. Continued.

(e) Plot C

n		F	I	J	IM	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10
327	F							7·48	16·00	7·64	7·77	16·00	15·00	20·00	27·81
64	I	0·023	0·888												
26	J		0·034	0·929											
7	IM			0·051	0·975										
8	M1				0·025	0·978									
1	M2					0·222	0·799								
5	M3						0·201	0·852							
3	M4							0·148	0·881						
4	M5								0·119	0·857					
3	M6									0·143	0·733				
3	M7										0·267	0·697			
5	M8											0·303	0·889		
1	M9												0·111	0·615	
2	M10													0·385	0·999*

(f) Plot CC

n		F	I	J	IM	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10
248	F					0·66	1·02	9·10	16·97	17·41	26·86	12·50	15·60		26·86
81	I	0·040	0·820												
21	J		0·021	0·952											
18	IM			0·048	0·934										
8	MI				0·057	0·859									
9	M2					0·141	0·946								
3	M3						0·054	0·883							
5	M4							0·117	0·931						
5	M5								0·069	0·896					
1	M6									0·104	0·999*				
1	M7										0·001*	0·500			
1	M8											0·500	0·999*		
—	M9												0·001*	0·999*	
1	M10													0·001*	0·999*

other, the rest were intermediate. For the second stage, the significant differences were between plot BB (13·5) and both AA and B (28·0).

Projected age structure and reproductive value

The Lefkovitch transition matrices were iterated for 256 years to obtain projected eigenvalues (estimates of the finite rate of natural increase, (λ) and the respective eigenvectors). The right eigenvector ($\bar{v}$) represents the stage structure after stability is reached, while the left eigenvector ($\bar{u}$) represents the projected reproductive value. There were significant differences between the observed and the projected stage structures after 256 iterations (Table 2; $\chi^2 = 181{\cdot}51$, d.f. $= 13$, $P < 0{\cdot}001$). This suggests that the stability assumption implicit throughout the analysis may be somewhat incorrect. An evaluation of the relative contribution of each stage to the χ^2 value shows that 70% of it is made up of juveniles and the last stage of mature individuals. Small sample sizes (0–3 individuals per plot) in the oldest stage could account for this, since the transition and survival estimates have large standard deviations. For the juveniles, where we do not have a small sample problem (the mean number of juveniles in each plot is about 283) the suggestion is that their survivorship is unstable. A similar analysis for the observed and projected reproductive values (Table 2) also yields significant differences ($\chi^2 = 57{\cdot}74$, d.f. $= 13$, $P < 0{\cdot}001$), where the contribution to the overall χ^2, although to a lesser degree, is not evenly distributed among the different stages in the life cycle. Mature individuals of the 55–65 year category and the juveniles and immatures have, respectively, smaller and larger reproductive values than the projected ones.

TABLE 2. Observed and projected age structure and reproductive values for *Astrocaryum mexicanum* in Veracruz, Mexico. The original Lefkovitch matrix was iterated 256 years.

	Age structure individuals on 3600 m² (equivalent ha⁻¹)		Reproductive value (fruits per individual)	
Stage	Observed	Projected	Observed	Projected
Fruits	4427·55 (12 300)	4514·91	1	0·06
Infants	1049·84 (2916)	975·64	1·96	1·91
Juveniles	283·40 (787)	177·28	3·96	18·99
Immature individuals	114·67 (319)	166·04	14·68	33·49
Mature individuals				
1	68·00 (189)	69·91	36·36	48·60
2	50·00 (139)	47·44	61·34	59·19
3	43·67 (121)	39·95	83·05	62·75
4	41·67 (116)	33·71	92·12	61·92
5	61·00 (169)	36·83	88·09	65·39
6	39·30 (109)	33·71	52·82	57·62
7	26·50 (74)	22·47	53·11	62·18
8	20·00 (56)	21·22	48·90	57·18
9	9·50 (26)	25·59	42·94	54·02
10	7·00 (19)	78·02	41·11	38·10

Finite rates of increase

The rates of increase after 256 years in the six plots fall near an expected value of unity (Table 3). The largest values were obtained for the low density plots C (1·0399) and CC (1·0228), whilst the lowest were obtained for plots A (1·0040) and BB (0·9932). The

TABLE 3. Estimates of the finite rate of increase (λ) for *Astrocaryum mexicanum* in the six plots after 256 years.

Plot	Finite rate of increase (λ)
A	1·0040
AA	1·0114
B	1·0194
BB	0·9932
C	1·0399
CC	1·0228
All plots	1·0046

combined value for the six plots based on the data in Fig. 1 is 1·0046 which represents an annual increase in the population of 0·46% and a doubling time of 151 years. These values might be significantly different between plots since we found differences in some stages for the demographic estimates, but to our knowledge there is no way we could assign standard errors to those estimates and thus we can not test the differences between plots and from the expected no growth value ($\lambda = 1$).

Sensitivity analysis

The product of the right (the stable age structure) and left (the stable reproductive value) eigenvectors is called the sensitivity matrix (Caswell 1978). Each element of this matrix is the reproductive value for each stage weighted by its relative abundance. Thus, the sensitivity matrix evaluates the relative importance that different stages have on the population's finite rate of increase.

For the population at 'Los Tuxtlas', λ is about three orders of magnitude less sensitive to changes in individual fecundity than it is to change in growth and survival (Table 4). Among transition estimates, the highest sensitivity occurs on the passage from infants to juveniles (0·56), from fruits to infants (0·26) and from immature individuals to the first reproductive stage (0·24); the smallest values (0·03) occur in the transition from reproductive stages 8 and 9 to the next ones (9 and 10).

Changes in the probability of remaining in the same stage affect λ in a similar way. The sensitivity of λ to the probability of remaining as an immature palm is relatively higher (0·17) than any other.

As already mentioned, the sensitivity of λ to changes in fecundity are by far the smallest of the matrix, and are fairly constant for most stages. The observed pattern, if any, is that individual fecundities of intermediate stages affect λ the least. These are also the stages that make the greatest contribution to the pool of fruits every year (Fig. 1). The sensitivity index (Caswell 1978), that evaluates the relative effects of changes in demographic parameters for different populations was 25·82.

DISCUSSION

Most of the life history studies on trees address questions about growth, survivorship and reproduction. Finite rates of increase or other estimates of the population growth rates are very scarce. In a still smaller proportion of the studies, a sensitivity analysis has been used to see which demographic parameters affect the most population growth rates. The survivorship pattern found for *Astrocaryum mexicanum* (Fig. 1), follows closely those reported for most of the other tree species studied (Hartshorn 1975; Van Valen 1975;

TABLE 4. Relative effect of changes of different life cycle parameters on the finite rate of increase (λ) for *Astrocaryum mexicanum* in Veracruz, Mexico. Stages are defined in Table 1.

	F	I	J	IM	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	
F					136	92	76	64	72	64	44	40	48	152	($\times 10^{-6}$)
I	0·26	0·06													
J		0·56	0·10												
IM			0·18	0·17											
M1				0·24	0·10										
M2					0·13	0·08									
M3						0·09	0·07								
M4							0·07	0·06							
M5								0·07	0·07						
M6									0·06	0·06					
M7										0·06	0·04				
M8											0·04	0·04			
M9												0·03	0·04		
M10													0·03	0·09	

Sarukhán 1978; Enright & Ogden 1979). This pattern is represented by a very high mortality in the early ages and a high survivorship during the reproductive period. A different pattern has been found in the vegetatively and sexually reproducing palm *Podococcus barteri* (Bullock 1980) where a high mortality was observed for seeds and seedlings, while stolons and adults had very low mortalities. This is similar to the situation for perennial herbs with vegetative reproduction (Sarukhán & Gadgil 1974).

At least three different fecundity patterns with age have been found in polycarpic tree species. (i) Individual fecundity increases linearly with age. This has been observed for *Pentaclethra macroloba* in Central America (Hartshorn 1975) and for *Podococcus barteri* in Africa (Bullock 1980). (ii) Individual fecundity has a peak for intermediate ages for *Araucaria cunninghami* D. Don ex. Ait (Enright & Ogden 1979). (iii) Fecundity first increases and then stays at constant values for most of the reproductive stages as in *Astrocaryum mexicanum* (Fig. 1). There is some evidence that for the last period it may decrease, but we have no statistical support for this.

These same patterns have been described when size is used instead of age (e.g. Downes & McQuilkin 1944), but a fourth pattern of an exponential increase of individual fecundity with size, which is also the most common one, emerges for several tree species (Niering, Whittaker & Lower 1963; Melampy & Howe 1977; Lamont & Downes 1979; Hubbell 1980; Bullock & Bawa 1981; Peters 1983).

While the stable age structure obtained for *Astrocaryum mexicanum* shows significant differences with the observed one (Table 2), the finite rates of increase were all very near an expected value of unity. This apparent contradiction is due to the fact that some stages of the life cycle are increasing, others are decreasing but the population as a whole is very near the equilibrium (Table 3).

The finite rates of increase reported for populations of tree species are very close to unity: they range from 1·002 for *Pentaclethra macroloba* (Hartshorn 1975) to 1·0399 for *Astrocaryum mexicanum* in plot C of this study. This suggests that most species studied are very close to a demographic equilibrium. This contrasts with the values found for herbs which show increasing or decreasing populations (e.g. Sarukhán & Gadgil 1974; Leverich & Levin 1979). The only sensitivity analysis published for trees was that of Caswell (1978) on data for *Pentaclethra macroloba* originally collected by Hartshorn (1975). We used Caswell's (1978) approach to obtain sensitivity matrices for *Podococcus barteri* based on the data published by Bullock (1980) and for *Araucaria cunninghamii* based on the study by Enright & Ogden (1979) (Table 5). Although the number of tree species is too small to reach a definite conclusion, some general patterns are apparent. The finite rate of increase (λ) is affected between 10 times (*Podococcus barteri*) and 10^6 times (*Araucaria cunninghamii*) less by sexual reproduction than it is by the probabilities of survival and transition in a given stage for the four species. *Pentaclethra macroloba* (10^3 times) and *Astrocaryum mexicanum* (10^4 times) are intermediate. Transition probabilities are 1–5 times more important in changing λ than survival probabilities in a given stage. This occurs more clearly in pre-reproductive stages (Tables 4 & 5).

Which stage is more critical in changing λ? For *Astrocaryum mexicanum* we showed (Table 4) that recruitment and survival during the pre-reproductive stages were more critical than the reproductive ones, whilst for fecundity intermediate stages are less important in changing λ that are the extreme stages. The published sensitivity matrix for *Pentaclethra macroloba* (Caswell 1978) shows peaks of importance for the early and the pre-reproductive stages for both recruitment and survival probabilities. Our analysis on data for *Podococcus barteri* shows that the transition from the asexually pre-reproductive

Table 5. Sensitivity analysis for (a) *Araucaria cunninghamii* and (b) *Podococcus barteri* based on data published by Enright & Ogden (1979) and Bullock (1980), respectively. In (a) the numbers 1–5 represent pre-reproductive individuals and 6–10 mature ones.

(a) *Araucaria cunninghamii*

	Seeds	1	2	3	4	5	6	7	8	9	10	
Seeds							324	144	54	8	3	($\times 10^{-9}$)
1	0·60	0·01										
2		0·82	0·10									
3			0·33	0·18								
4				0·55	0·09							
5					0·34	0·19						
6						0·72	0·23					
7							0·34	0·15				
8								0·10	0·04			
9									0·03	0·01		
10										0·003	0·001	

(b) *Podococcus barteri*

	Seeds	Stolons	Seedlings	Juveniles	Immatures	Matures 1	Matures 2
Seeds						0·01	0·01
Stolons		0·16			0·18	0·09	0·10
Seedlings	0·02		0·02				
Juveniles		0·20	0·09	0·23			
Immatures				0·32	0·34		
Matures 1					0·26	0·12	
Matures 2						0·11	0·13

stage to the next and the survival during the first asexually reproductive stage are the most important ones in changing λ. Also, the transition from the sexually pre-reproductive stage to the next is about double the other values (Table 5). For *Araucaria cunninghamii* the three most important values among the transition probabilities are those from seeds to the first juvenile stage, from the stage 5 to 6 (the last pre-reproductive stage), and from the first juvenile stage to the second. The smallest values were obtained for the transition from stages 8 and 9 to stages 9 and 10, respectively, while the values for survival are generally lower, the largest being the survival in the first reproductive stage. As observed for other species, the relative impact of changes in λ with fecundity decreases with age, but the phenomenon is most dramatic for *Araucaria cunninghamii.* It seems clear then, that the relative importance of the different life-history characters on the population growth of trees could be as follows: fecundity < survival < growth. The most critical stages are those near the age of first reproduction.

It is evident that the different environmental conditions in which populations grow determine the characteristic patterns of sensitivity found. In our case, we are dealing with a population in which nearly 90% of the individuals are suppressed, for they grow under conditions of severe resource limitation such as those near the forest floor, where only 2% or less of incident irradiance is available. It is interesting that the most critical stages influenced are those about to reach the reproductive stage which represent individuals that have invested the most energy before reaching the conditions of irradiance (at a height of about 1·5 m above the forest floor) which allow the plants to start growing faster and reproducing.

Sensitivity coefficients (Caswell 1978) for these four species vary from 1·07 (*Podococcus barteri*) to 15 711 (*Araucaria cunninghamii*); *Astrocaryum mexicanum* (25·81) and *Pentaclethra macroloba* (105·41) are intermediate. Except for the value for *Podococcus* *barteri* all others are among the largest found in natural populations (Caswell 1978). For comparison we have also calculated the sensitivity coefficients of λ for *Ranunculus repens* L. (2·94), *R. bulbosus* L. (5·68) and *R. acris* L. (1·65) for the 2 years reported by Sarukhán & Gadgil (1974). The value for *Dipsacus sylvestris* (65·79) was reported by Caswell (1978). Fetcher & Shaver (1983) reported values of 1·01–1·91 for different populations of the perennial sedge *Eriophorum vaginatum* L. It is difficult to draw any conclusions from this small amount of information; however, it appears that plants with vegetative reproduction and plants other than trees have less sensitive life-histories than trees with sexual reproduction only.

Lefkovitch matrices do not include aspects of density dependence or populations growing in heterogeneous environments. There is evidence in *Astrocaryum mexicanum* of density dependence (M. Martínez-Ramos & J. Sarukhán, unpublished) and of the populations living in heterogeneous environments (Martínez-Ramos 1980; Piñero & Sarukhán 1982). These aspects deserve more attention and we are studying how to incorporate them into the population flux model to make it more realistic.

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