Demographic Studies in Astrocaryum mexicanum and Their Use in Understanding Community Dynamics

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Demographic studies in plants have been shown to be useful in understanding the regulation of population numbers (Silvertown 1982) as well as in designing management techniques for use with wild populations (Soulé and Wilcox 1980). Demographic techniques are also used to ascertain the aspects of the life history that may be under intense selective pressure (Law et al. 1977, Dirzo and Sarukhán 1984). These techniques started being used in studies of tropical trees more than ten years ago (Bannister 1970, Hartshorn 1975, Sarukhán 1978). The basic demographic data usually estimated are: a) the age or stage of the individual, b) the survival probabilities in each age or stage category and, c) the fecundity during the reproductive phase. If the time scale used to estimate these vital statistics is shorter than the time interval considered in each age or stage category, then transition probabilities from one stage or age category to the next should also be calculated. With these data a matrix (usually a Lefkovitch matrix in which the categories do not have the same duration) is constructed and an estimate of the finite rate of population increases (λ) can be obtained. With this basic information, the aspects of the life cycle that most affect the finite rate of increase can also be determined (Caswell 1978, de Kroon et al. 1986). The reliability of the estimates usually depends on the population's sample size and the duration of the study. Unfortunately, detailed demographic studies spanning over many years are rare. Palms have been shown to be a very cooperative life form in demographic analyses because growth often can be directly recorded as the number of leaves produced, especially in the tropics, where palms are frequently abundant and trees generally lack growth rings (Bannister 1970, Sarukhán 1978, Vandermeer et al. 1974, Bullock 1980, Piñero et al. 1984, Oyama 1984).

We have been carrying out field studies on the demography of the tropical understory palm *Astrocaryum mexicanum* Liebm. since 1975. These studies have been useful not only in helping us to understand the population dynamics of this species but also in learning about the ways in which the number of leaves in an individual crown is regulated, as well as in describing the dynamics of canopy gap formation within the forest. Even though the demography of a population may be the main objective of a given study, detailed understanding of a population can in time yield information about the whole community. In this paper we describe how our studies are scaled from the individual to the community levels as well as some of the restrictions to this type of approach.

One of the aspects that we have started

to study is the demography of leaves within individuals. The construction of life tables for leaves has been used to predict the life expectancy of an individual leaf and the relative contributions of individual leaves to future leaf production (Abul-Fatih and Bazzaz 1980), as well to assess the effects of defoliation on leaf demography (Hartnett and Bazzaz 1984). This information coupled with physiological data on photosynthetic rates and nutrient concentrations in leaves can be used to better understand the adaptations of plants to their environment (Chabot and Hicks 1982).

Our study plots are located at the Los Tuxtlas field station (Universidad Nacional Autónoma de México) at Veracruz, México. The site includes a Tropical Rain Forest with trees up to 40–50 m. Rainfall is usually over 4,000 mm per year and average temperatures vary around 24–25° C. Soils are shallow, acidic, rich in nitrogen, and of volcanic origin. The total number of tree species within the 700 ha field station is approximately 210 (Ibarra 1985).

Demographic data have been obtained from 8 permanent plots (600 m² each) that include different *A. mexicanum* densities (from 500 mature individuals per ha to 1,200/ha), as well as sites in which large gaps were produced by treefalls in 1970 and 1974 (for details see Piñero et al. 1977, Martínez-Ramos 1980). Ages of palms were estimated using data on leaf production and transition data from one height category to the next over a six year period; survival probabilities and fecundity estimates were obtained from data on individual palms censused each year (Piñero et al. 1984). Data to construct leaf life expectancy tables came from the census of the cohorts of leaves starting in 1975 and ending in 1982. Fecundity of leaves (the photosynthetic contribution of a leaf to the production of new leaves) was assumed to be a function of the concentration of nitrogen in individual leaves.

When a tree or a large branch falls and bends over an *A. mexicanum*, the palm usually survives and starts growing upwards again. By knowing the rate at which palms produce new leaves under such conditions we can estimate the time that has elapsed since the treefall during which the palm was bent over. These data were obtained from censusing all *A. mexicanum* individuals in a 5 ha permanent plot. Besides the usual data (height, the number of leaves on the crown, and localization), measurements were also obtained on the length of the trunk between angles in the stem that were produced in response to the fall of a tree or a large branch.

One way to understand the dynamics of gap formation and closure is to use *A. mexicanum* to age gaps up to eighty years old. This information is translated into a frequency distribution of gap formation, a kind of age structure for gaps of the past. To our knowledge, this is the first demographic study of palms or any other plant that has been utilized in understanding the regeneration mosaic of a tropical forest and also in aging the different parts that form it.

Leaf Demography

Understanding the dynamics of populations has sometimes been followed by an analysis of its possible causes. One way to approach this problem at the individual level in plant populations has been to describe the dynamics of plant parts (e.g., Sydes 1984). While leaf survival is relatively easy to estimate, leaf fecundity estimates are difficult to obtain because we would need to know the proportion of a leaf's photosynthates that is allocated to the production of new leaves. In studies of this kind, it is generally assumed that for leaves of different ages, the same proportion of photosynthates is allocated to the production of new leaves. Leaf fecundity is then assumed to be proportional to photosynthetic activity (e.g., Hartnett and
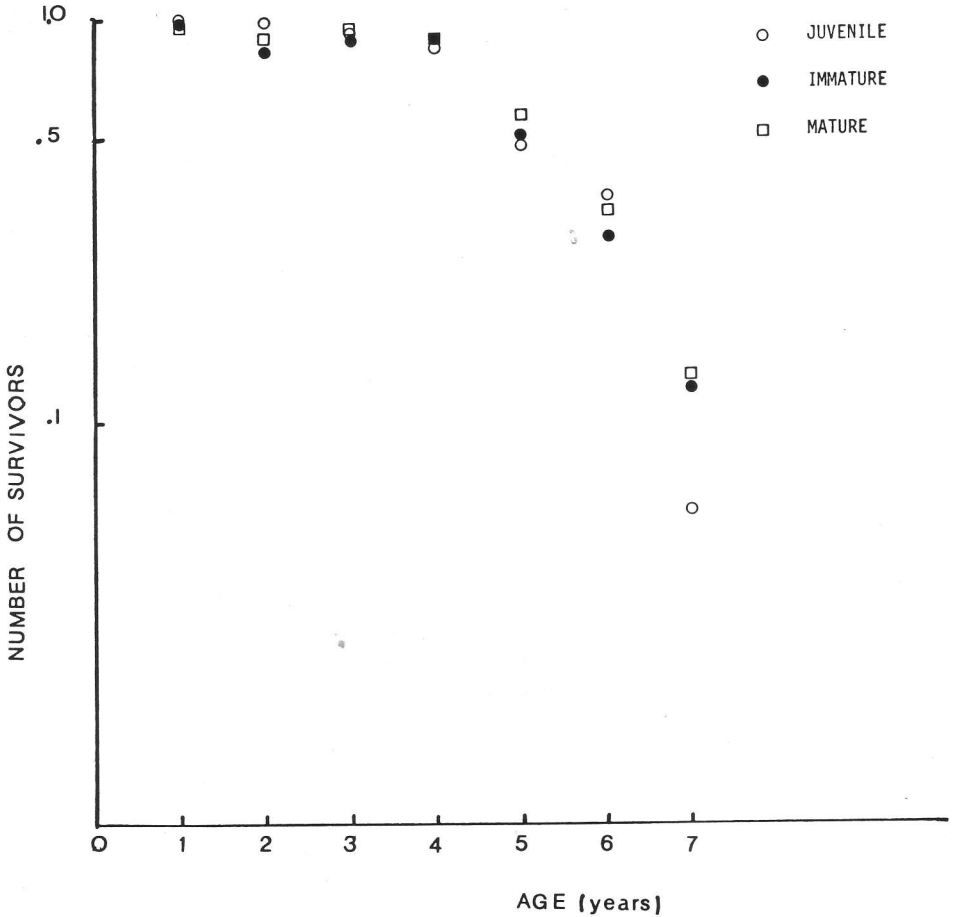
1.   Survivorship curves for leaves of juvenile, immature, and mature individuals of *Astrocaryum mexicanum* in Veracruz, México. Each point is the proportion of living leaves in 1982 of those originally marked in the 600 m² plots (with no gap disturbance) between 1975 and 1981.

Bazzaz 1984), which is in turn assumed to be proportional to the relative concentration of nitrogen in a leaf (Gulmon and Chu 1981). We estimated leaf fecundity as the proportion of the contribution of leaves of different ages towards the leaves produced in a year, using the relative content of nitrogen as an indicator of photosynthetic rates. Leaf survival estimates were obtained by marking annual cohorts of leaves (a cohort is defined as those leaves produced in a year) between 1975 and 1981 and counting those still alive in

1982. In other words we estimated survival for independent cohorts of leaves.

Survival data for leaves from other plants generally fit a convex curve with high survivorship during early age (Bazzaz and Harper 1977, Abul-Fatih and Bazzaz 1980, Hartnett and Bazzas 1984, Sydes 1984). *A. mexicanum* is no exception to this (Fig. 1). For the first three years survivorship probability is close to one for leaves of individuals between 12 and 150 years old. After an individual is approximately 12 years old, the same proportion

Table 1.   Life expectancy table for leaves of mature individuals of Astrocaryum mex-icanum *at the 600 m² permanent plots (with no recent gap formation) in Veracruz, México.*

Age Category (years)	Probability of Survival (leaf × leaf^{-1} × year^{-1})	Fecundity (leaf × leaf^{-1} × year^{-1})	Mean Leaf Life Expectancy (years)	Age Structure (leaves)
0	1.00	0.24	5.16	3.10
1	0.94	0.21	4.46	2.79
2	0.89	0.13	3.67	1.82
3	0.92	0.16	2.57	2.35
4	0.87	0.16	1.69	2.23
5	0.57	0.14	1.32	1.42
6	0.33	0.15	0.91	0.87
7	0.13	0.15	0.54	0.35

of remnant leaves die each year. These estimates are based on data from all six 600 m² plots in which there are large tree-falls. Leaf mortality patterns may change when a gap is produced in the forest.

Life expectancy for leaves varies from 6 months for 7 year old leaves, to 5 years for newborn leaves (Table 1). Fecundity estimates show that leaves during their first two years (usually there are about six leaves younger than two years in a crown with 15 leaves) contribute approximately half of the photosynthate used by the newly produced leaves while the rest of the leaves in the crown (9) contribute the other half. There is then a hierarchy of leaves, with the younger ones more pro-ductive. We are now working to obtain similar data for palms growing in treefall gaps because we think that a comparative approach using a demographic technique to understand crown dynamics in palms will help us determine which are the fac-tors that limit growth, survivorship, and reproduction in *A. mexicanum*.

Population Dynamics

Six years of survivorship and transition data and 8 years of fecundity estimates (Piñero et al. 1984) are available for *A. mexicanum*. The general pattern shows

that individuals can live up to 150 years at which time the palms are approxi-mately 6.5 m in height if they have not been knocked over. The population has a Deevey type III survivorship curve with the highest mortalities in the first stage of the life cycle and little mortality during the reproductive stages which start when individuals are 25–30 years old (1.0–1.5 m in height). Leaf production is highest and constant once the individuals start flowering (Table 2). We have found very little temporal variation during the six years for which we have observed leaf production. This contrasts with the high annual variability found for reproductive characteristics (Piñero and Sarukhán 1982). Fecundity increases with age until it reaches a plateau when individuals are approximately 50 years old.

Elucidating the causes of variation in growth and reproduction appears to be a very interesting avenue for future research. This variation has also been observed in other plant species and thus it is a phenomenon that has to be consid-ered in demographic analyses of all plant populations (Silvertown 1982). Due to the variation, conclusions from demographic studies are not definitive unless many years of data are available on a large number of individuals. It will be extremely difficult

Table 2. *Average annual leaf production per year for* Astrocaryum mexicanum *individuals between 1975 and 1981 in Veracruz, México. Means are followed by one standard deviation.*

	Number of Leaves Produced per Year
Juveniles	1.64 ± 0.48
Immatures	2.08 ± 0.77
Matures	2.42 ± 0.55

to obtain reasonable estimates for demographic parameters for some species that live in frequently disturbed environments. When mortality is so high that very few of several hundred individuals are left after two or three years, it is also difficult to have good estimates of variation in growth, survival, and reproduction. Ways around this problem consist of marking many plants but not doing any observations on them until they reach an age with a smaller mortality.

We have described the variation in demographic parameters for *A. mexicanum* and proposed some possible causes for it, such as the heterogeneity of the light environments within the forest (Piñero and Sarukhán 1982). Without demographic data from different forest plots we would not have been able to identify the causes for such high variation. Whether aspects such as light and forest dynamics affect other palms in the tropics in the same way is not known, but it is clear that both have been recognized as key factors in the establishment and growth of other tree species (e.g., Vázquez-Yanes and Orozco-Segovia 1984, Brokaw 1985*a*, Martínez-Ramos 1985, Hubell and Foster in press).

The growth rate of a population can be expressed as the dominant latent root of the demographic matrix, a parameter known as the finite rate of increase (lambda). Values larger than one mean that the population is growing, while values

Table 3. *Finite rate of increase and its statistics for the 600 m² permanent plots (with no recent gap disturbance) of* Astrocaryum mexicanum *in Veracruz, México. Estimates followed by the same letter are not significantly different at the 5% level (t-test).*

Plot	Finite Rate of Increase (λ)	Variance (λ)	Different from $\lambda = 1.00$
A	1.0040 ab	0.00178	no
AA	1.0114 ab	0.00346	no
B	1.0194 ab	0.00232	no
BB	0.9932 a	0.00397	no
C	1.0399 b	0.00326	yes
CC	1.0228 ab	0.00205	no
All plots	1.0046	0.00121	no

between zero and one show that the population is decreasing in numbers. Although we have estimated the finite rate of increase for the plots with no gaps (Piñero et al. 1984) we have not been able to incorporate a variance term in the estimates of lambda. The analysis of variability in the demographic parameters appears to be particularly relevant in species like *A. mexicanum* in which finite rates of increase are very close to one (Table 3). To determine the way in which demographic variation affects the estimates of the finite rate of increase, we obtained an estimate of the variance in lambda.

To estimate the variance of lambda we simulated for each plot 50 transition matrices similar to those published by Piñero et al. (1984). Each value of these matrices was obtained from a randomly generated function. If it was a fecundity value, a normal distribution function with the mean and variance obtained from field observations was used. If it was a transition or a survival estimate, then a binomial distribution was assumed with the parameters being the observed probabilities and

the sample sizes used. Another assumption was that the values of the demographic matrices are independent, an assumption that would not be necessary if we knew how the parameters influence one another. We need to know more about the causes of "good" and "bad" demographic years. The variances associated with the estimation of the finite rates of increase are small and range from 0.00121 (all plots) to 0.00397 (plot BB). Only the finite rate of increase for plot C (1.0399) is different (using a t-test) from a non-growth expectation and among plots, only plot BB (0.99320) is significantly different from plot C.

One final point that needs to be considered is that estimates of age also have an associated variance because they assume that leaf production is constant. We have estimates of the variation in leaf productions (Table 2), and a technique similar to the one described for the finite rate of increase could be used to estimate the variance associated with age estimation.

Gap Dynamics

Gap-phase regeneration has been shown to be very important in forest dynamics in the tropics (Brokaw 1985b, Martínez-Ramos 1985). The rain forest at Los Tuxtlas is no exception to that rule (Sarukhán et al. 1985). The main responses that $A.$ $mexicanum$ individuals have to gaps are: a) an increase in leaf production, b) an increase in fecundity through increasing both the probability of flowering and the number of fruits produced, and c) an increased probability of transition from prereproductive to reproductive stages which produces a demographic "wave" that modifies a normally J-shaped age structure. These "gap cohorts" in $A.$ $mexicanum$ appear to limit the recruitment of other species. There is an inverse relationship between the density of adult $A.$ $mexicanum$ individuals and the number of tree species in the 600 m^2 plots. Other

Table 4. *Parameters of gap dynamics in a 5 ha linear transect in the Los Tuxtlas rain forest, (hectare 1 is near the forest edge and hectare 5 is in the inner part of the forest). Turnover rate is defined as the average time elapsed between the formation of two gaps at the same site. Estimations are based on four years of gap monitoring. Minimum gap size considered was 5 m^2.*

Ha	Turnover Rate (years)	Mean Number of Treefall Recurrency per 25 m^2 Square	Aggregation Index (Variance/Mean)
1	38	0.74	1.70**
2	50	0.64	1.53**
3	258	0.31	1.53**
4	52	0.32	1.65**
5	53	0.41	1.56**

** Significantly different (t-test) from an aggregation index of 1.00 at a 0.01% level.

data which support this idea have been obtained from monitoring a 5 ha permanent plot that runs across a slope gradient from the edge to the inner part of the forest. We censused all trees more than 1 m tall. For four years (1982–1985) we also recorded and measured each gap formed according to the criteria given by Brokaw (1982). Finally, using 2000 25 m^2 plots we calculated the approximate time when the last gap was formed in each quadrat (see also Sarukhán et al. 1985). We have found that the turnover rates of this forest are significantly higher towards the edges. The central part of the forest with the smallest slope, had the lowest gap disturbance rate (Table 4). Other workers have suggested that gap opening favors the regeneration of most tree species (Hartshorn 1980, Denslow 1980, Brokaw 1985a, Martínez-Ramos 1985). One would expect a higher regeneration (e.g., more abundant saplings) at the sites with a larger proportion of area with gaps and
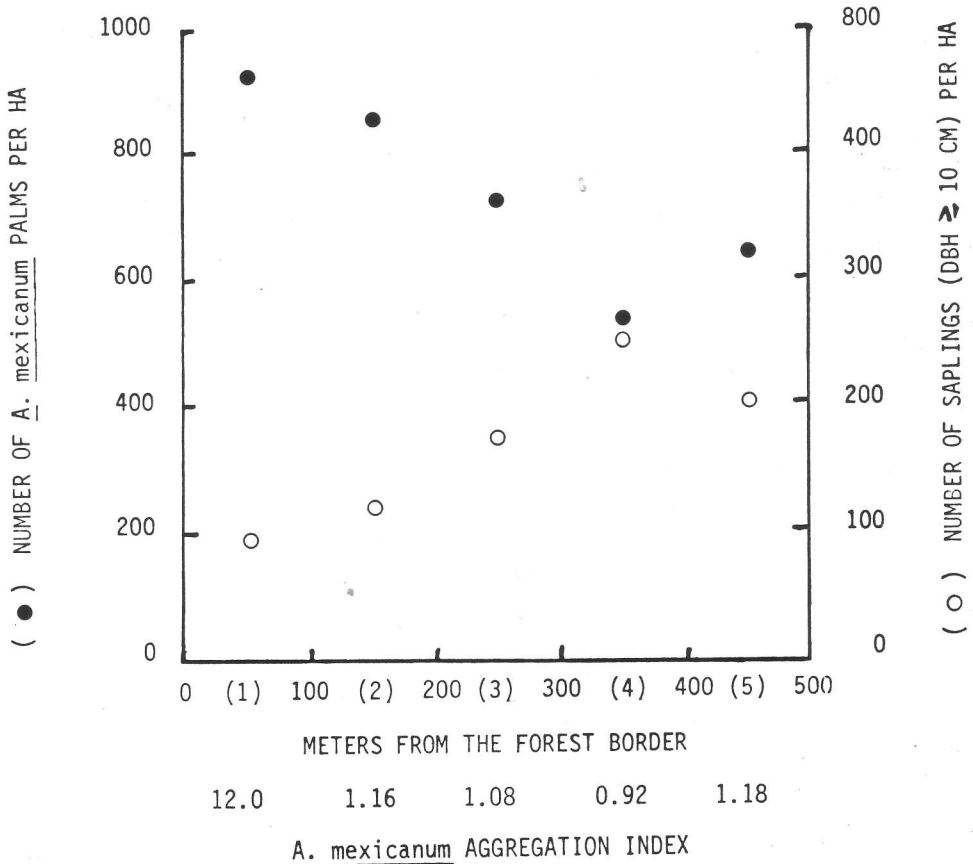
2. Number of *Astrocaryum mexicanum* individuals (●— — —●) and number of tree saplings (O— — —O) in a 5 ha permanent plot in Veracruz, México.

regenerating forest but we found the opposite. The plots near the edge have a lower number of saplings than was observed in the more centrally located plots with lower turnover rates (Fig. 2). One hypothesis we propose to explain this difference is that an increase in *A. mexicanum* density lowers the sapling density of other tree species. The highest density of the palm occurs precisely in the part of the 5 ha plot with greatest disturbance while the lowest density occurs in areas with lower disturbance. We also predicted

that a higher disturbance will produce a greater aggregation of these palms. The aggregation at the edge of the forest is the greatest ($s^2/\bar{x} = 12.0$) while in areas with lower disturbance palms are randomly distributed ($s^2/\bar{x} = 1.0$; Table 4). A high palm aggregation appears to produce a closed subcanopy which limits regeneration of light demanding species. Surely, *A. mexicanum* does not affect all tree species in the same manner. And we are now analyzing relationships with 60 different tree species. Will it be possible to predict the

forest structure by changing the degree of disturbance and/or the density of *A. mexicanum*? There is evidence that suggests that, for temperate forests, structure can be predicted using the relative abundance of tree guilds (Runkle 1985). By experimentally manipulating densities of *A. mexicanum* this question may be answered. Possibly new ideas about the mechanisms that operate in tropical rain forests at the community level will emerge from such experiments.

Conclusions and Perspectives

The ecology of palms has been one of the most active areas in tropical plant ecology. Palms have proven to be a very amenable group for both demographic and ecophysiological studies. We have shown that detailed long-term demographic studies can broaden our understanding of both population and community dynamics. We also showed that there are limitations in these studies mainly related to the high variability at the individual level in growth, survival, and reproduction. One way of dealing with this problem is to develop the relevant statistics for age and population growth estimates. Another method of research would be to understand the relative importance of different factors on the variation described. We think that ecophysiological studies are needed to complement the approach presented here. At the population level, on the other hand, analysis of the genetic structure of the population appears to be the most rewarding approach. The analysis of pollination biology that we started some years ago may help us make predictions about the way in which the genetic variation is maintained in these populations. Finally, an experimental analysis at the community level on the effect that *A. mexicanum* has on the establishment of other tree species appears to be very promising. We have started working in these three directions to further understand the biology of *A. mexicanum*.

Acknowledgments

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