



**Direct and Indirect Estimates of Neighborhood and Effective Population Size
in a Tropical Palm, *Astrocaryum mexicanum***

Luis E. Eguiarte, Alberto Burquez, Jorge Rodriguez, Miguel Martinez-Ramos, Jose Sarukhan, Daniel Pinero

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DIRECT AND INDIRECT ESTIMATES OF NEIGHBORHOOD AND
EFFECTIVE POPULATION SIZE IN A TROPICAL PALM,
ASTROCARYUM MEXICANUM

LUIS E. EGUIARTE, ALBERTO BÚRQUEZ¹, JORGE RODRÍGUEZ,
MIGUEL MARTÍNEZ-RAMOS, JOSÉ SARUKHÁN, AND DANIEL PIÑERO
*Centro de Ecología, Universidad Nacional Autónoma de México,
Apartado Postal 70-275, México 04510, D.F., MÉXICO*

Abstract.—To estimate the relative importance of genetic drift, the effective population size (N_e) can be used. Here we present estimates of the effective population size and related measures in *Astrocaryum mexicanum*, a tropical palm from Los Tuxtlas rain forest, Veracruz, Mexico. Seed and pollen dispersal were measured. Seeds are primarily dispersed by gravity and secondarily dispersed by small mammals. Mean primary and secondary dispersal distances for seeds were found to be small (0.78 m and 2.35 m, respectively). *A. mexicanum* is beetle pollinated and pollen movements were measured by different methods: a) using fluorescent dyes, b) as the minimum distance between active female and male inflorescences, and c) using rare allozyme alleles as genetic markers. All three estimates of pollen dispersal were similar, with a mean of approximately 20 m. Using the seed and pollen dispersal data, the genetic neighborhood area (A) was estimated to be 2,551 m². To obtain the effective population size, three different overlapping generation methods were used to estimate an effective density with demographic data from six permanent plots. The effective density ranged from 0.040 to 0.351 individuals per m². The product of effective density and neighborhood area yields a direct estimate of the neighborhood effective population size (N_b). N_b ranged from 102 to 895 individuals. Indirect estimates of population size and migration rate (Nm) were obtained using F_{st} for five different allozymic loci for both adults and seeds. We obtained a range of Nm from 1.2 to 19.7 in adults and a range of Nm from 4.0 to 82.6 for seeds. We discuss possible causes of the smaller indirect estimates of Nm relative to the direct and compare our estimates with values from other plant populations. Gene dispersal distances, neighborhood size, and effective population size in *A. mexicanum* are relatively high, suggesting that natural selection, rather than genetic drift, may play a dominant role in patterning the genetic variation in this tropical palm.

Key words.—*Astrocaryum mexicanum*, effective population size, gene flow, neighborhood, palm, pollen dispersal, seed dispersal, tropical rain forest.

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One of the most important processes affecting genetic variation in natural populations is genetic drift. To estimate the relative importance of genetic drift, the effective population size (N_e) can be used. This is the number of individuals in an ideal population that would experience the same genetic change due to genetic drift as a real population with a specific census number (Wright, 1931; Crow and Denniston, 1988; Hartl and Clark, 1989). Most of the formulas to estimate N_e have been developed for discrete, isolated populations (Crow and Denniston, 1988). For continuously distributed populations, Wright (Dobzhansky and Wright, 1943; Wright, 1943a, 1943b, 1946)

proposed the isolation by distance model: large populations are not panmictic over their entire distribution range, but are genetically structured due to limited progeny dispersion.

Main determinants of genetic movement in plants are the outcrossing rate, pollen dispersal, and seed dispersal (Levin and Kerster, 1974; Turner et al., 1982; Loveless and Hamrick, 1984). These three variables, if small, can generate genetic differentiation among sites in a continuous population (Rohlf and Schnell, 1971; Turner et al., 1982). To obtain an estimate of this spatial structure, Wright (1943a, 1943b) proposed the concept of the neighborhood area (A), later expanded to include haploid gene movement as pollen and diploid gene movement as seeds in plants (Levin and Kerster, 1968; Crawford, 1984a, 1984b). Within the neighborhood a high proportion

¹ Present address: Estación Regional Noroeste, Centro de Ecología, Universidad Nacional Autónoma de México, Apartado Postal 1354, Hermosillo 8300, Sonora, México.

of the parents of the individuals from the center of the area are found [if pollen moves very short distances compared to the seeds 86.5% of the parents are inside the neighborhood, while if pollen moves considerably more than seeds 81.6% of the parents are inside the neighborhood (Crawford, 1984b)]. Thus the neighborhood area can be considered a "panmictic" area. Neighborhood area estimates for plant species (reviewed by Crawford, 1984a; Nic Lughadha and Parnell, 1989; Eguiarte, 1990) are usually small. Once the neighborhood area is obtained, an appropriate method for isolated populations may be applied to estimate the effective population size inside this area [N_b (Begon, 1977)].

All the above estimates correspond to direct estimates [sensu Slatkin (1987)] of the effective population size. Indirect estimates of gene flow can be obtained from the distribution of the genetic variation in the populations (Slatkin, 1987). One of the most robust and reliable methods for indirect estimation of gene flow (Slatkin and Barton, 1989), is to obtain a joint estimate of the effective population size (N_e) and the migration rate, Nm , from F_{st} (which is a measure of population differentiation using allelic frequencies; Wright, 1951, 1965; Nei, 1987). Neighborhood effective population size N_b , should be of the same order of magnitude as Nm , depending on the characteristics of the population (Slatkin and Barton, 1989). For instance, if the population structure conforms to a stepping stone model, $N_b = 2\pi Nm$ (Slatkin and Barton, 1989). For some other population structure models, N_b is approximately equal to Nm (Slatkin and Barton, 1989).

There are few comprehensive estimates of the effective population size for long lived perennial plants (see Crawford, 1984a). In this paper we present various estimates of seed and pollen dispersal in the tropical palm *Astrocaryum mexicanum*. Using seed and pollen dispersal data we calculate the neighborhood area (A). We obtain the effective population density of *A. mexicanum* using demographic data from six permanent plots (Piñero et al., 1984) using overlapping generation methods. This is the first application of these methods in a plant species. The product of effective population density and

the neighborhood area gives a direct estimate of the effective population size in the neighborhood (N_b). Finally we compare direct estimates of N_b with an indirect estimation of gene dispersal (Nm) obtained using F_{st} for five allozymic loci for both adults and progeny genotypes in four plots at Los Tuxtlas rain forest.

MATERIALS AND METHODS

Study Organism

Astrocaryum mexicanum is a monocious understory palm of the tropical rain forest. It ranges from Veracruz, Mexico, to the Atlantic coast of Honduras (Vite, 1985). *A. mexicanum* is the most abundant vascular plant in the Los Tuxtlas Rain Forest, with an average density of 0.5 individuals per m^2 and an almost regular (uniform) spatial distribution (Piñero et al., 1977; Piñero and Sarukhán, 1982; Martínez-Ramos et al., 1988a), growing well in both light gaps and in the mature rain forest (Martínez-Ramos, 1985). Detailed studies on its demography (Piñero et al., 1984; Sarukhán et al., 1984; Martínez-Ramos et al., 1988b), reproductive biology (Piñero and Sarukhán, 1982; Búrquez et al., 1987), role in community dynamics (Martínez-Ramos et al., 1988a, 1988b, 1989), and population genetics (Eguiarte, 1990; Eguiarte et al., 1992) have been reported.

Astrocaryum mexicanum is pollinated by several species of beetles (Búrquez et al., 1987). Female and male flowers are present in common inflorescences. Female flowers in an inflorescence open synchronously in the first day, lasting one day (mean number of female flowers per inflorescence = 27.8). The next morning the male flowers start to produce pollen (mean number of male flowers per inflorescence = 4,885) (Búrquez et al., 1987). Individuals are self-compatible, but self-pollinations produce lower fruit-set than out-crossed pollinations [23% fruits/flowers, relative to cross-pollinations (Búrquez et al., 1987)]. Outcrossing rates were estimated using both single and multilocus methods, for five allozymic loci, for four sites and three years, and in most cases were not statistically different from 1.0 (Eguiarte et al., 1992). The temporal and spatial separation of the female and male flowers in a

given inflorescence and the low probability that a single individual palm presents more than one active inflorescence (0.1 to 0.5%) (Piñero and Sarukhán, 1982; Búrquez et al., 1987) probably contribute to this high outcrossing rate. Although adult *A. mexicanum* densities are relatively high (0.14 individuals per m² on average), the densities of open inflorescences can be very low, as one adult produces only from 0 to 5 (median 1) inflorescences during a long reproductive season of three months (March to May) and as one open inflorescence lasts only three days, generating quite large distances between male- and female-phased inflorescences (Piñero and Sarukhán, 1982; Búrquez et al., 1987).

Infructescences average 23.2 fruits (Búrquez et al., 1987) and each fruit represents a single large seed (3 × 4 cm), covered with spines (Búrquez et al., 1987). Fruits are dispersed primarily by gravity and secondarily by small mammals (especially by squirrels *Sciurus aureogaster* and *S. deppei*), which destroy ca. 95% of the total seed crop (Sarukhán, 1980; Coates-Estrada and Estrada, 1986; Eguiarte, 1990). Seeds survive no more than three years in the soil before germination (Eguiarte, 1990).

The Los Tuxtlas *A. mexicanum* population presents relatively high levels of variation in phenotypic characters, demographic behavior (Piñero and Sarukhán, 1982; Sarukhán et al., 1984), and allozymes ($P = 31.8$ and $H = 0.153$) (Eguiarte et al., 1992). Mortality is high in younger individuals but very low in adult plants (Sarukhán et al., 1984). The average finite rate of increase of the population (λ) for six permanent plots is 1.0046, indicating that the population is not changing in size (Piñero et al., 1984, 1986). Demographic analysis indicates that the population is very near the stable age distribution (Piñero et al., 1984; Caswell, 1989). An excess of heterozygotes both for adult and seed stages was found [mean F : -0.41 for adults, -0.19 for seeds (Eguiarte et al., 1992)]. Low but significant levels of genetic differentiation between sites in Los Tuxtlas were found, especially for adults [mean F_{ST} : 0.040 for adults, 0.009 for seeds (Eguiarte et al., 1992)]. There was a positive relationship between trunk growth and individual heterozygosity, but no sig-

nificant correlation was found between heterozygosity and fecundity (Eguiarte et al., 1992). The genetic structure of *A. mexicanum* appears to be the result of relatively long distance cross-pollination by beetles, reducing genetic differentiation among plots. Natural selection may act over the long life span (mean age of reproductive individuals is ca. 72 years) to increase the genetic differentiation among sites and the proportion of heterozygotes (Eguiarte, 1990; Eguiarte et al., 1992).

Study Site

The Los Tuxtlas Tropical Station of the National Autonomous University of Mexico (UNAM) is located on about 700 ha of coastal slope of Los Tuxtlas range, Veracruz, Mexico (longitude between 95°04' and 95°09'N, latitude between 18°34' and 18°36'W). Vegetation and climate have been described by Piñero et al. (1977) and Bongers et al. (1988). Compared to other tropical rain forests, Los Tuxtlas has low tree diversity and density (Bongers et al., 1988). Plots used in this study are 20 × 30 m permanent plots of virgin rain forest mapped and tagged in 1975, and are the same described in Piñero et al. (1977, 1984) and Eguiarte et al. (1992).

Seed and Pollen dispersal

Primary seed dispersal distance, defined as the distance from a naturally dispersed seed (= fruit) to the trunk of the nearest palm was measured for 658 seeds from 45 different isolated palms in September 1987. [These measurements were relatively easily done, given the large size of the seeds (3 cm in diameter) and the low and constant number of seeds per infructescence (ca. 23)]. To avoid possible confusion over the identity of the mother due to overlapping seed shadows, we measured primary dispersal for palms isolated by 20 m or more from any other reproducing *A. mexicanum* individual.

Secondary seed dispersal data were obtained in November 1990. In 157 randomly chosen seeds, a small hole (2.0 mm diameter) was made and a thin nylon string (0.25 mm diameter) was firmly attached to the seed. The string, 30 m long, was curled up into a small reel that was then inserted in

the soil by means of a metallic hook. Treated seeds were placed 20 cm away from the reel and mixed with other normal seeds. When an animal moved a treated seed, it left a track of string. The distance reported here is that of a straight line from the original seed position to the final seed position.

Three approaches were used to estimate pollen dispersal:

1) *Fluorescent dyes*. In March and April of 1983 and 1988 we applied fluorescent dyes to male-phased inflorescences (day 2 of flowering). The next day, all the active inflorescences in a radius of at least 80 m were collected (29 inflorescences in 1983, 7 in 1988). Distances from the source inflorescence to the female inflorescences were recorded. The presence/absence of fluorescent dyes was determined in the laboratory under UV light.

2) *Minimum distance from male- to female-phased inflorescences*. As the inflorescences of *A. mexicanum* present a clear temporal separation in male and female functions (Búrquez et al., 1987) and as there is no appreciable self-pollination (Eguiarte et al., 1992), a minimum distance of pollen movement can be estimated as the minimum distance between a male-phased and a female-phased inflorescence. This distance is considerably larger than the average minimum distance between two reproductive adults [mean = 2.4 m (Piñero and Sarukhán, 1982)] because of the very low density of active inflorescences in a given day. This distance was measured during the 1983 reproductive season for 70 different male/female inflorescence pairs.

3) *Progeny analysis*. In 1987 and 1988 all the seeds produced by all the adults in 20 × 30 m permanent plots (Piñero et al. 1977, 1984) were genotyped for five different allozymic loci [*Mdh-1*, *6-Pgd-1*, *Pgi-1*, *Adh-1*, and *Lap-2* (Eguiarte et al., 1992)]. Also, the genotypes for these five loci of all the adults that reproduced in a given year within each plot, and those within a strip of 10 m around the plot (producing a site of 40 × 50 m) were obtained (Eguiarte, 1990; Eguiarte et al., 1992). For the present analysis the seeds that had the *Lap-2* allele 3 (*Lap-2₃*) were used because it has a low allelic frequency (0.03), and is present in very few adults. For each seed bearing the allele

Lap-2₃, it was determined whether a possible pollen donor (an adult with *Lap-2₃*) was inside the extended plot using all five loci as exclusion criteria. All adults bearing *Lap-2₃* inside the extended plot were considered possible pollen donors. For some seeds only one possible pollen donor was found and the "donor distance" could be specified. Alternatively, a "least distance" was estimated as the smaller of the distance: (1) to the border of the extended plot, if there were no possible fathers within the plot or if this distance was shorter than the distance to a possible pollen donor; and (2) the shorter distance for two or more possible pollen donors.

Neighborhood Area

From dispersal distances of seeds and pollen, we obtained the axial variance [V_0 = half the variance in dispersal distance in all directions considering a mean distance of zero for each measurement (Wright, 1969; Crawford, 1984a, 1984b)]. We also corrected for deviations from normality (Wright, 1969) by estimating the kurtosis parameter K_0 and with it we obtained the factor a ($K_0 = 0$ and $a = 0.5$ for a normal distribution, $K_0 < 0$ and $a < 0.5$ for platykurtosis, $K_0 > 0$ and $a > 0.5$ for leptokurtosis). From a , we approximated an area correction factor (AF) (Wright, 1969), which is equal to 4 if the distribution is normal. Neighborhood area (A) was estimated for seeds as $A_s = \pi \cdot \text{Area correction factor} \cdot (\text{Axial variance for the seeds})$, and for pollen as $A_p = \pi \cdot \text{Area correction factor} \cdot (\text{Axial variance for the pollen})/2$ (Crawford, 1984a). Modifications to the formulas to include the effects of the outcrossing rate are also presented by Crawford (1984a).

Total neighborhood area is the sum of the different neighborhood areas (Beattie and Culver, 1979). Here we obtained it as the sum of the neighborhood areas produced by the primary dispersal of seeds + the secondary dispersal of the seeds + the pollen dispersal.

Effective Population Size: Direct Estimation

The standard methods for isolated populations (Crow and Denniston, 1988) may be applied to estimate the effective popu-

lation size within a neighborhood area (N_b) (Begon, 1977; Daly, 1981; Chepko-Sade et al., 1987). For the case of organisms with overlapping generations some formulas (Nei and Imaizumi, 1966; Crow and Kimura, 1972) for isolated populations consider the genetic drift generated by random survival differences. Other formulas (e.g., Hill, 1972, 1979), consider only variance in fecundity, which implicitly includes variance in survival. All these formulas could be used to estimate the variance effective population size (Kimura and Crow, 1963). Variance N_e is related to the amount of change in allelic frequencies among different subpopulations due to genetic drift. Kimura and Crow (1963) also recognized the inbreeding effective population size. Inbreeding N_e is related to the fixation index (F), which increases with genetic drift. If population size remains constant, both effective population sizes (by variance and by inbreeding) reach the same values (Kimura and Crow, 1963; Crawford, 1984a).

To estimate effective population size we used the formulas for populations with overlapping generations of Nei and Imaizumi (1966), Crow and Kimura (1972), and Hill (1972, 1979). Demographic parameters presented by Piñero et al. (1984) for six permanent plots of 20 × 30 m were used to estimate the generation time (L ; Krebs, 1978), Nr (the number of individuals born in a given year that will reach reproduction), N_0 (the number of individuals born in a given year) and i (the sum for all the ages of the squared specific age survival*the specific age fecundity) (Nei and Imaizumi, 1966; Crow and Kimura, 1972). Data on reproduction for 13 years (Piñero and Sarukhán, 1982, and unpubl.) were used to estimate fecundity variance (Hill, 1972, 1979; Wood, 1987). The Nei and Imaizumi (1966) formula is $N_e = Nr * L$ (assuming little variation in the number of individuals born every year, low mortality among reproductive individuals and a stable age structure). Crow and Kimura (1972) state that $N_e = N_0 * L * i$ (assuming that the population is not growing and has a stable age structure). Assumptions for both of these formulas appear to hold for *A. mexicanum* (Piñero et al., 1984; Caswell, 1989). The Hill (1972, 1979) formula is $N_e = [4(N_0 - 2)L]/(\text{Variance in}$

the families sizes + 2), and requires only that the population has stable age structure. This has been considered as the most reliable method for estimating the effective population size (Kimura, 1983; Wood, 1987).

Effective population density was estimated as the effective number of individuals per square meter by dividing the estimated N_e within the plot by its area (600 m²). The effective population density, when multiplied by the neighborhood area (A) gives N_b , which is an estimate of the effective population size in a continuous population with some degree of isolation by distance.

Effective Population Size: Indirect Estimation

In this paper we used the F_{st} estimates for both adults and seeds of *A. mexicanum* at Los Tuxtlas for five loci (*Mdh-1*, *6Pgd-1*, *Pgi-1*, *Adh-1*, and *Lap-2*) and four permanent plots (20 × 30 m; A, B, C, and CC; Piñero et al., 1977, 1984) with Nei (1987) formulas, presented in Eguiarte et al. (1992). The average distance between the plots is 365 m (range 200–560 m). Here we additionally calculated the 95% confidence intervals for each F_{st} with a jackknife procedure (Weir, 1990).

Nm was estimated by a method that considers the effects of having few subpopulations (Crow and Aoki, 1984): $F_{st} = 1/(4aNm + 1)$ where $a = [n/(n - 1)]^2$ and n is the number of subpopulations. Slatkin and Barton (1989) show that Nei's (1973, 1987) formulas for estimating the F_{st} are usually less biased than Weir and Cockerham's (1984) methods for obtaining F_{st} when estimating Nm . Other indirect estimates of gene flow, such as the ones based on rare and/or unique alleles (Slatkin, 1981, 1985a) could not be applied in *A. mexicanum*, because we found no unique alleles or alleles that were common in some plots and very rare in others, probably due to high gene flow among plots.

RESULTS

Seed and Pollen Dispersal

The mean primary seed dispersal distance and axial variance (V_0) were 0.78 m and 0.489 m² respectively (Table 1). Secondary seed dispersal distance was significantly

TABLE 1. Primary and secondary seed dispersal estimates and different estimates of pollen dispersal (see text) in *Astrocarum mexicanum* in Los Tuxtlas, Veracruz, Mexico. Data were obtained in 1987 for primary seed dispersal and in 1990 for secondary seed dispersal. For data on pollen dispersal see text.

	N	Mean (m)	Median (m)	V_r (m ²)	V_0 (m ²)	K_0 (t, P)	a	AF	A^1 (m ²)
Primary	658	0.78	0.62	0.36	0.489	1.32 (6.9, P < 0.001)	0.77	4.07	6.25
Secondary	157	2.35	1.50	4.74	5.125	3.85 (9.8, P < 0.001)	1.09	3.95	63.3
Dyes 1983	29	22.98	16.8	296.02	406.9	-0.24 (0.23, NS)	0.44	3.97	2,537
Dyes 1988	7	22.34	18.1	282.83	370.8	-0.38 (0.20, NS)	0.40	3.92	2,283
Dyes '83 + '88	36	22.85	17.4	285.36	399.9	-0.26 (0.32, NS)	0.43	3.95	2,481
Female/Male	70	17.14	15.0	167.80	229.6	1.37 (2.34, P < 0.05)	0.77	4.06	1,465
<i>Lap23</i> donor	36	16.68	17.0	55.49	166.0	-1.44 (1.76, P < 0.01)	0.00	3.00	782
<i>Lap23</i> least	41	12.74	13.0	16.70	89.0	-1.69 (12.21, P < 0.05)	0.00	3.00	421

¹ V_r is the real variance of the data; V_0 is the axial variance considering a mean of 0 (see text); K_0 is the kurtosis of the distribution; t-test for significance of the departures from normality (Sokal and Rohlf, 1969); a is a factor calculated to obtain the area correction factor; AF is the area correction factor (see text); A is the neighborhood area.

greater than primary seed dispersal and its axial variance was larger (Table 1; mean = 2.35 m; t-test = 10.76; $P < 0.001$; axial variance = 5.125 m²). Both dispersal distance distributions were significantly leptokurtic (Table 1).

Fluorescent dye movement was not significantly different between years (Table 1; 1983, mean = 23.0 m; median = 16.8 m; 1988, mean = 22.3 m, median = 18.1 m; ANOVA on means, $F_{1,34} = 0.25$, $P = 0.61$; Bartlett test for differences in axial variances between years $\chi^2_1 = 0.020$, $P > 0.75$). Therefore both were pooled for further calculations (Table 1). Pooled axial variance for pollen is 399.9 m². The mean minimum distance between active male and female inflorescences was 17.1 m (Table 1). This is an estimate of the minimum distance the pollen needs to travel to find a receptive female stigma. Direct estimates of pollen movement using progeny analysis of the *Lap-23* give a mean "donor" distance of 16.7 m and a mean "least" distance of 12.7 m (Table 1). Given the relatively small size of the plots (40 × 50 m), maximum detectable distances in these progeny analyses were in general smaller than 50 m; thus these estimates may be biased towards small distances. Comparing the five different estimates of pollen dispersal (Table 1), the least distance for the *Lap-23* is smaller than the other values. The remaining four estimates present similar mean distance ($F_{3,138} = 1.62$; $P = 0.182$), and axial variances (Bartlett test, $\chi^2_3 = 7.087$, $P = 0.069$). We use the pooled fluorescent dye estimates for further calculations because we considered them the more reliable measures of pollen dispersal given that the sampled areas were larger. However calculations using the other estimates are also presented in Table 1.

Neighborhood Area

Corrections for deviations from normality (K_0 , a, and AF) needed for the pollen and seed dispersal estimates are shown in Table 1. With the exception of the estimates from *Lap-23*, all other corrections of the area factor (AF) are very small (from 3.92 to 4.07).

Outcrossing rate was not considered in the neighborhood area calculations because it is 1 in *A. mexicanum* (Eguiarte et al.,

TABLE 2. Demographic parameter estimates in *A. mexicanum* for six different plots (20 × 30 m) at Los Tuxtlas, originally described in Piñero et al. (1977 and 1984).

Plot	Numbers of				Lambda per plot ¹	SD (<i>P</i>) ²
	Seedlings	Juveniles	Adults	Total		
A	264	62	105	431	1.004	0.042 (NS)
AA	208	68	100	376	1.0144	0.059 (NS)
B	190	59	94	343	1.0194	0.048 (NS)
BB	243	48	98	389	0.9932	0.063 (NS)
C	64	26	42	132	1.0399	0.057 (<i>P</i> < 0.05)
CC	81	21	52	154	1.0228	0.045 (NS)

¹ Finite rates of increase, lambda, from Piñero et al. (1984 and 1986).

² Standard deviation of the lambdas and significance departures from a lambda = 1 (that corresponds to a constant population size) from Piñero et al. (1986).

1992) and thus pollen dispersal does not need to be discounted to account for selfing (Crawford, 1984a). Using the pooled data from fluorescent dyes and both primary and secondary seed dispersal distances (Table 1), we obtained a total neighborhood area $A = 2,551 \text{ m}^2$. The other estimates of pollen movement produce smaller areas (see Table 1), for example, using the donor distance of the progeny analysis, the total neighborhood area $A = 852 \text{ m}^2$.

Effective Population Size: Direct Estimates

The numbers of individuals and demographic characteristics of the six permanent plots are presented in Table 2. The generation time (L) for *A. mexicanum* for each of the six permanent plots ranged from 62.8 to 85.8 years, with a mean of 72.4 years (Table 3). Other parameters used to estimate N_e are also presented in Table 3. According to Nei and Imaizumi (1966) formula, N_e ranged from 23.7 to 100.53 individuals in the six 20 × 30 m plots (Table 3), generating a mean effective density of 0.09 individuals/m². The Crow and Kimura (1972) formula gave a similar range

of N_e (from 26.9 to 91.7, Table 3), with a mean effective density of 0.10 individuals/m² (Table 3). The Hill (1972, 1979) formula generated a range of N_e from 59.65 to 210.4 individuals and a mean effective density of 0.22 individuals/m² (Table 3).

In Table 4 we present the estimated neighborhood effective population sizes (N_b) obtained by multiplying the effective densities by two estimates of the total neighborhood area (A , using the pooled fluorescent dye pollen dispersal data plus both seed dispersal distances, and using the *Lap-2*₃ donor distance plus both seed dispersal distances) obtained previously. Thus the direct estimates of the N_b in *A. mexicanum* range from 34 to 895 individuals (Table 4).

Effective Population Size: Indirect Estimates

The F_{st} and their 95% confidence intervals of the five different loci are presented in Table 5 for both adults and seeds. The associated Nm estimated by the method of Crow and Aoki (1984) ranged (considering the 95% confidence intervals) for adults from 1.2 to 19.7 and for seeds from 4.0 to 82.6 (Table 5). Using Slatkin and Barton (1989)

TABLE 3. Estimates of parameters used in obtaining the equivalent to the isolated populations effective population size (N_e) for *A. mexicanum* by three methods for overlapping generations in six different permanent plots (see text, Materials and Methods).

Plot	Gen. time L	N_0	Nei & Imaizumi $N_e = Nr \times L$		Crow & Kimura $N_e = N_0 \times L \times t$		Hill $N_e = (4N_0 - 2)L/[\text{Var}(f) + 2]$	
			Nr	" N_e "	t	" N_e "	Var (f)	" N_e "
A	64.86	928	1.299	84.3	0.00154	91.7	1,261.0	190.5
AA	85.81	1136	0.700	60.0	0.00066	64.2	2,634.4	147.8
B	68.45	784	0.431	29.5	0.00088	47.2	1,817.9	117.9
BB	71.70	954	1.402	100.5	0.00137	93.6	1,297.8	210.4
C	80.60	327	0.294	23.7	0.00102	26.9	1,762.2	59.7
CC	62.77	248	0.501	31.4	0.00278	43.3	955.7	64.9

TABLE 4. Neighborhood effective population numbers (N_b) of *A. mexicanum* estimated as the product of the effective densities (obtained by different overlapping generations methods) and the neighborhood areas (A) (see text). The effective density per m^2 , was obtained by dividing the " N_e " (Table 3) by the area used in its estimation ($600 m^2$). N_b was calculated using two different methods for estimating pollen movement: 1) Fluorescent dye + both seed distances ($A = 2,551$), and 2) *Lap-23* "donor" distance + both seed distances ($A = 852$) (see text).

Plot	Fluorescent dyes N_b			<i>Lap-23</i> donor distance N_b		
	N. & I.	C. & K.	Hill	N. & I.	C. & K.	Hill
A	357	390	811	119	130	271
AA	255	273	628	85	91	210
B	125	202	500	42	67	167
BB	429	398	895	143	133	299
C	102	115	253	34	38	84
CC	133	184	276	44	61	92
Mean	234	260	560	78	87	187

stepping stone formula to obtain N_b from Nm , N_b ranged (considering the confidence intervals) for adults from 7.8 to 123.6, and for seeds from 25.4 to 518.9 (Table 5). The better indirect approximation of N_b for *A. mexicanum* lies between the values of Nm and the stepping stone N_b , probably nearer and latter, as the simulations by Slatkin and Barton (1989) indicate.

DISCUSSION

Despite its clear importance for evolutionary and conservation biology, effective population size remains one of the least un-

derstood and least studied parameters in natural populations (Crawford, 1984a; Simberloff, 1988). In this paper we report the first application of overlapping generation methods to estimate effective population sizes for a plant.

Seed and Pollen Dispersal

Dispersal distances for seeds in *A. mexicanum* are substantially smaller than pollen dispersal distances. Our estimates of the primary seed dispersal distances may be biased downwards, given that we may have overlooked seeds that moved relatively far. The secondary seed dispersal estimates may also be biased downwards, considering that the string may limit or discourage seed movement by dispersers or limit it to 30 m. In addition, long distance seed dispersal could be rarer than one in 157 (our sample size), and thus would not be detected in our study. Home ranges for some of the animals that disperse *A. mexicanum* seeds in Los Tuxtlas can be larger than 75 m in radius (Coates-Estrada and Estrada, 1986) suggesting that longer distance dispersal of *A. mexicanum* seeds may not be uncommon.

Pollen could also move farther than the estimated distances. Fluorescent dye estimates were made during the peak of the flowering of *A. mexicanum*. Pollen movement may be greater before and after this peak, because the minimum distance that a pollinator must travel increases when the

TABLE 5. F_{st} statistics for five polymorphic loci and four plots for *A. mexicanum* adults and seeds from Eguiarte et al. (1992), 95% confidence intervals (in parentheses) obtained by a jackknife procedure (Weir, 1990), associated Nm [estimated with Crow and Aoki (1984) formula], and indirect estimate of N_b for a stepping stone population structure model [obtained with Barton formula, (unpubl., in Slatkin and Barton, 1989)]. $N = 240$ adults; $N = 963$ seeds.

Locus	F_{st} (95% C.I.)	Nm (95% C.I.)	N_b (95% C.I.)
Adults			
<i>Mdh-1</i>	0.0318 (0.0071–0.0575)	4.3 (2.3–19.7)	26.9 (14.5–123.6)
<i>6Pgd-1</i>	0.0563 (0.0110–0.1016)	2.4 (1.2–2.6)	14.8 (7.8–79.2)
<i>Pgi-1</i>	0.0141 (0.0098–0.0184)	9.8 (7.5–14.2)	61.8 (47.1–89.3)
<i>Adh-1</i>	0.0537 (0.0277–0.0797)	2.5 (1.6–4.9)	15.6 (10.2–31.0)
<i>Lap-2</i>	0.0422 (0.0148–0.0696)	3.2 (1.9–9.4)	20.1 (11.8–58.8)
Seeds			
<i>Mdh-1</i>	0.0258 (0.0180–0.0336)	5.3 (4.0–7.7)	33.4 (25.4–48.2)
<i>6Pgd-1</i>	0.0048 (0.0029–0.0067)	29.2 (20.8–48.4)	183.2 (131.0–303.8)
<i>Pgi-1</i>	0.0046 (0.0026–0.0066)	30.4 (21.2–53.9)	192.0 (133.0–338.9)
<i>Adh-1</i>	0.0058 (0.0017–0.0099)	24.1 (14.0–82.6)	151.5 (88.4–518.9)
<i>Lap-2</i>	0.0044 (0.0021–0.0067)	31.8 (20.8–66.8)	200.0 (131.0–420.0)

density of flowering individuals is lower (Schmitt, 1983; Fenster, 1991). In the analysis of the *Lap-2_s*, given the size of the plots used, we were not able to measure distances larger than 50 m. Despite various possible sources of bias towards short distances in the measurements of pollen dispersal, the different methods used gave similar means, medians, and axial variances. These results suggest that most pollinators of *A. mexicanum* (several species of beetles with a wide range of sizes, see Búrquez et al., 1987) move mainly between nearest receptive inflorescences. Nevertheless, the distance that pollen moves is larger than the average distance between nearest neighbor in adults [2.41 m (Piñero and Sarukhán, 1982)] because of the low densities of open inflorescences in a given day. We consider the fluorescent dye data the more reliable data, as the area and sampled numbers were larger than for the progeny analysis and because the minimum distance between complementary inflorescences is the least possible distance the pollen should travel.

Comparing the data on pollen movement in *A. mexicanum* with other tropical species (Linhart, 1973; Webb and Bawa, 1983; Linhart et al., 1987; Adams, 1989; Hamrick and Loveless, 1989) we can say that in this palm pollen movement is intermediate, given that sometimes we detected pollen dispersal distances of more than 50 m, but most of distances were around 20 m. In a similar beetle-pollinated species, *Dieffenbachia longispatha* (Araceae) the average mean dispersal distance is 80 m, which corresponds to the nearest female inflorescence, generating a N_b of between 750 to 8,900 plants (Young, 1986). Our genetic analysis of pollen movement was related to methods that use genetic markers (Levin and Kerster, 1974; Schaal, 1980; Handel, 1983; Smyth and Hamrick, 1987). To carry out a paternity analysis in *A. mexicanum*, given what is known about its pollen movement, very large plots would be needed, but still very long distance movements would be extremely difficult to detect.

Direct Estimates

In our estimations of effective density we used three different models developed for populations with overlapping generations.

The first two (Nei and Imaizumi, 1966; Crow and Kimura, 1972) consider that the important component for the random changes in genetic variation is survival variance, while differences in fecundity among surviving organisms are less important and are Poisson distributed. Other assumptions of the Nei and Imaizumi (1966) formula (little variation in the number of individuals born every year, low mortality among reproductive individuals, and a stable age structure) are reasonable for *A. mexicanum* (Piñero et al., 1984; Caswell, 1989), as are the other assumptions of the Crow and Kimura (1972) formula [that the population is not growing and has a stable age structure (Piñero et al., 1984; Caswell, 1989)]. The Hill (1972, 1979) formula considers that the fecundity variance includes survival variance and only requires that the population has stable age structure. This method has been considered as more complete and less restrictive than other methods (Kimura, 1983; Wood, 1987; Crow and Denniston, 1988). These overlapping generations methods have been used mainly for human populations (Crawford, 1984a; Wood, 1987) and this is the first application to plant populations.

The effective densities estimated using Nei and Imaizumi (1966) and Crow and Kimura (1972) formulas are very similar and lower than the effective densities estimated from Hill (1972, 1979), suggesting a relatively low variance in fecundity in this palm. However, a good approximation of the effective density in *A. mexicanum* appears to be the number of adults at a given moment [e.g., the range of densities of adults in the six permanent plots was 0.07 to 0.175 per m² (Table 2), while the range of the effective population sizes ranged from 0.040 to 0.351 per m² (Table 3)]. All effective population size estimates are smaller than the total number of living palms (Tables 2 and 3). Thus, the effective population size averages between 18% to 43% of the total population. This yields a neighborhood effective population size N_b for *A. mexicanum* in Los Tuxtlas between 102 and 810 individuals within a genetic neighborhood (considering the neighborhood derived using the fluorescent dye data plus the primary and secondary seed dispersal distances as the more reliable estimate of the neighborhood area).

The neighborhood area and N_b in *A. mexicanum* can be compared with estimates in other species obtained using similar methods (see reviews in Crawford, 1984a; Nic Lughadha and Parnell, 1989; Eguiarte, 1990). However, most of these studies do not consider variation in survivorship or fecundity among individuals. *A. mexicanum* presents one of the largest neighborhood areas (2,551 m²), surpassed only by a few insect and wind pollinated plants (Crawford, 1984a; Smyth and Hamrick, 1987; Young, 1986; Adams, 1989; Eguiarte, 1990). Associated estimates of the neighborhood effective population size (N_b) span a wide range, but a mean value for herbs (364 ± 606 SD, $N = 22$ species) and for trees [292 ± 460 SD, $N = 10$ species (Eguiarte, 1990)] indicate that the values estimated here for *A. mexicanum* are within the range of these means. We can conclude that the N_b of *A. mexicanum* is comparatively large.

Indirect Estimates

The indirect estimates of the gene dispersal as Nm obtained from the F_{st} statistics in *A. mexicanum*, are always greater than one (mean Nm seeds = 34; mean Nm adults = 8). According to Wright (1931), this observation indicates very little genetic differentiation by genetic drift among different plots. Seed genetic data may better reflect the extent of pollen movement, because F_{st} for adults is also affected by other microevolutionary forces, especially natural selection, which seems to increase the differentiation among plots in *A. mexicanum* (Eguiarte et al., 1992). F_{st} was estimated using Nei's (1973, 1987) methods which, as shown by Slatkin and Barton (1989), tend to slightly underestimate Nm . Thus our values are conservative gene dispersal estimates.

We can compare our indirect estimates of Nm to others also obtained by using F_{st} (Crow and Aoki, 1984; Govindaraju, 1989). The mean Nm for 34 mainly self-pollinated species was 0.82 ± 1.86 SD, and mean Nm for 20 mostly outcrossed species was 2.11 ± 2.39 SD (Govindaraju, 1989). Most of our confidence intervals of Nm for the different loci for both adults and seeds in *A. mexicanum* are larger than both these

means, further supporting that *A. mexicanum* has relatively extensive gene dispersal.

Nm should be in the order of magnitude of the neighborhood effective population size N_b (Slatkin and Barton, 1989; see also Govindaraju and Cullis, 1991). The actual relationship depends on the population structure of a given population and on the relevance of other evolutionary forces (Slatkin and Barton, 1989). For instance, in the case of the stepping stone model, $N_b = 2\pi Nm$ (Slatkin and Barton, 1989). The stepping stone structure model has been considered as the most adequate model for species like conifers, which are continuously distributed over an area, but show some degree of subdivision in local subpopulations (Govindaraju and Cullis, 1991), as appears to be the case for *A. mexicanum* (Eguiarte et al., 1992). Using this model we obtained a mean neighborhood (N_b) of 47.3 individuals for adults and 214 for seeds.

Although our indirect estimates of Nm are high relative to other plant species, even the values for the seeds (that are higher than for adults) are about one order of magnitude lower than the direct estimates of N_b . One reason for expecting differences in the direct and indirect estimates of gene movement may be that the formulas of Nei (1973, 1987) give conservative estimates of Nm that are slightly biased towards small values (Slatkin and Barton, 1989). Nevertheless, as stated by Slatkin and Barton (1989), indirect estimates should be considered as rough indicators of gene flow that can have errors depending on the departures of data from the models used (Slatkin and Barton, 1989). On the other hand, our indirect estimates of N_b for the case of the stepping stone model for the seeds (mean = 214) are very similar to the direct estimates using fluorescent dyes by the Nei and Imaizumi (mean = 234) and the Crow and Kimura (mean = 260) methods. A possible scenario is that, despite strong gene flow via pollen, differentiation is increased each generation by subsequent selection, and thus the allele frequencies never reach an equilibrium due to gene flow (Eguiarte, 1990; Eguiarte et al., 1992). For these reasons we consider that the seed genotypes better reflect the extent of gene flow. Another possibility is that the *A. mexicanum* population is behaving in a way that

is very different from assumptions of the migration models, making the indirect estimate of Nm different from the direct estimation of N_b . Differences between direct and indirect estimates of gene flow are commonly found, and have been discussed by Slatkin (1985*b*, 1987, 1989), although, at least in animals, the pattern found is usually the opposite from what we found and less gene flow is suggested by the direct method than by the indirect ones.

Conclusions

In general our estimates of gene movement in *A. mexicanum* are in accordance with the patterns expected from its genetic structure (Eguiarte et al., 1992). Genetic structure provides no evidence for inbreeding, as most fixation indices are negative both in seed and adults. There is low genetic differentiation among plots for seeds, and genetic differentiation is higher in adult individuals. Negative fixation index values could be explained in part by natural selection (see Eguiarte et al., 1992) and/or by a process described by Prout (1981), where he found that if there is extensive pollen movement and seeds move very little (as in the case of *A. mexicanum*) local excess of heterozygotes (negative fixation indices) could be obtained.

Despite differences in the values of the direct and indirect estimates of the effective population size in *A. mexicanum*, comparisons with other plant species indicate that all measures of gene dispersal for *A. mexicanum* are large. The values found in *A. mexicanum* are large enough to allow gene flow and/or natural selection to be the dominant forces, but not so large as to preclude some geographic genetic structure (Wright, 1931, 1932; Crawford, 1984*a*; Slatkin, 1989). Characteristics of the genetic structure and of gene flow for *A. mexicanum* are similar to the patterns described in other tree species (*Eucalyptus*, tropical trees and conifers; Eguiarte, 1990; Eguiarte et al., 1992). Effective population estimates not only have implications for the understanding of the population genetics and evolution of tree species in general and tropical trees in particular, but also for conservation strategies in forest ecosystems (Eguiarte, 1990; Eguiarte et al., 1992).

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