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Aspects of the population biology of the gregarious tree *Cordia elaeagnoides* in Mexican tropical deciduous forest

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ABSTRACT. *Cordia elaeagnoides* is locally important within a large area of southern México as a highly gregarious canopy tree of dry forest and as a timber species. Its recruitment is problematic so studies of its reproduction and population dynamics were undertaken. The distylous flowers are apparently self-compatible, and pollination and seed dispersal are by wind. Pre-dispersal mortality is largely from embryo abortion, and post-dispersal predation is mostly by generalist rodents. Some seeds may survive in enforced dormancy for two or more years. Recruitment was apparently absent for more than a decade, but had previously occurred within established stands, where size classes were interspersed at random. Population size structure suggests that recruitment over the last century occurred in several pulses. Growth rates determined from ring counts and remeasurement of marked trees support a size–age relationship. The youngest reproductive trees are estimated to be about 18 years old, and about 5% of the present population is over 95 years old.

RESUMEN. *Cordia elaeagnoides* es una especie gregaria del dosel muy importante localmente en la selva tropical caducifolia del sur de México; además es maderable. Ya que su reclutamiento no es regular se llevaron a cabo estudios sobre su reproducción y dinámica poblacional. Las flores diestílicas aparentemente son autocompatibles y la polinización y dispersión de semillas son por el viento. La mortalidad predispersión es principalmente por aborción de embriones y la posterior a la dispersión por roedores generalistas. Aparentemente no hubo reclutamiento durante más de una década, pero sucedió anteriormente dentro de los parajes, donde árboles de diferentes clases de tamaño se encuentran entremezclados al azar. La estructura poblacional por tamaños sugiere que el reclutamiento durante el último siglo occurió en varios pulsos. Tasas de crecimiento determinados por conteo de anillos y por remedición de árboles marcados sostienen una relación tamaño-edad. La edad de los árboles reproductivos más jóvenes se estima en 18 años y un 5% de la población actual tiene más de 95 años.

KEY WORDS: demography, growth, México, population structure, recruitment, reproduction, seed biology, size–age relationship, spatial distribution, tropical deciduous forest.

INTRODUCTION

The management of tropical forests for exploitation or conservation depends on our understanding of the population dynamics of the dominant plant life forms.

The continuing scarcity of studies on the population dynamics of tropical trees (Sarukhán 1978, Swaine 1989) is particularly acute for dominant species in low-diversity stands (Hart *et al.* 1989, Martijena & Bullock 1994) and for species of dry or deciduous tropical forests in general. Regeneration in moist or wet forests is often related to frequent small-scale disturbance due to the falling of branches or trees (Platt & Strong 1989). There is no evidence that this is important in dry forest, where larger-scale disturbance may predominate, particularly via drought-related, widespread branch and tree mortality, fire and human intervention. Virtually nothing is known of the scales of time and space relevant to the dynamics of tree populations disturbed by drought. Even for moist/wet forests the understanding of spatial distributions and temporal processes suffers from the difficulty of incorporating reasonable age estimates (Lieberman *et al.* 1985). Recently, some progress has been reported in dating trees via annual rings in various regions where growth seasonality is marked (Baas & Vetter 1989). There is, on the other hand, a relative multitude of studies of the processes involved in mortality between flower and seedling stages, as well as studies of dispersal and germination, which have contributed to characterizing regeneration strategies. However, there is a need for studies incorporating both the annual cycle of regeneration processes and the resulting population structure and history.

The present study focuses on *Cordia elaeagnoides* DC. (Boraginaceae), a species which often achieves dominance of deciduous forest and is remarkable for its combination of life history features. Dense wood suggests that it is not a pioneer, but reproductive features (self-compatibility, dispersal of pollen and seeds by wind) do suggest a colonizing life strategy. *C. elaeagnoides* is a canopy tree endemic to deciduous and semi-deciduous forest on the Pacific slopes of México; it is also of interest as a valuable timber tree. In this paper we examine the size and spatial distributions of trees within distinct patches and estimate both growth rates and ages, as indications of the flux of population structure in space and time. We also detail some of the processes underlying recruitment, particularly seed production, survival and germination.

STUDY SPECIES AND SITE

Species

The geographic range of *C. elaeagnoides* extends from Jalisco to Chiapas at elevations up to 500 m, or occasionally to 800 m as in the Río Balsas basin (Pennington & Sarukhán 1968). It grows to 20 m height on shallow soils derived from igneous or metamorphic rocks, or in the deeper soils of arroyos. *C. elaeagnoides* is highly gregarious and dominates areas of many hectares. However, these patches do not dominate the landscape in our study area: In random samples, *C. elaeagnoides* comprised only 2.5% of the stems (Bullock & Solís-Magallanes 1990, Lott *et al.* 1987). In this area seedling and sapling populations are rare,

and germination in the field attained only 1.4% as a maximum after experimental introduction of fruits (Guevara-Fefer 1977). The wood specific gravity is rather high (0.88), which exceeds 68% of the tree species at the site (Barajas-Morales & León 1989). *C. elaeagnoides* also regenerates rapidly from stumps after injury. 'Barcino' is of some economic importance for its attractive, strong and decay-resistant wood.

The flowers are distylous, and probably wind-pollinated; compatibility exists within individuals and style morphs, but is lower than between morphs (Bullock 1985). These features contrast with the strong tendency for out-crossing and zoophily in *Cordia*, but the genus is known for its morphological and functional diversity (Opler *et al.* 1975). The flowers are 2.0–2.5 cm across, actinomorphic, cream-coloured and borne in paniculate cymes. Anthesis is just before sunrise and receptivity is lost about six hours later. The ovary has four loculi, each with one ovule. The fruits are dark brown, woody nutlets with one to four seeds. Each seed is about 6 mm long with an embryo of about 1 mm and reserves in the cotyledon. The corolla persists as a wind-dispersal device, and the calyx persists for some time in the soil.

Study site

Our studies were done in the area around the Estación de Biología Chamela (19° 30′ N, 105° 03′ W), Jalisco; the deciduous and semi-deciduous forests of the area were described by Lott *et al.* (1987). Annual precipitation averaged 707 mm (1977–1991), with about 80% falling between mid-June and September (Bullock 1986). At Chamela, *C. elaeagnoides* flowers abundantly in October, which is usually after the end of the wet season, and the fruits ripen at least a month later. Dispersal continues until February (Bullock & Solís-Magallanes 1990).

METHODS

Spatial and age distributions

Seven plots of various sizes were surveyed, in as many disjunct stands ranging in size from one to four hectares (September to November 1985; Table 1). In each plot, all *C. elaeagnoides* trees were mapped on a scale of 1:500 and their girths measured at breast height (gbh at 150 cm); also, it was noted if the tree had more than one stem and if reproductive structures were present. Plots 1–6 were situated on hillsides in deciduous forest, and plot 7 was in a small canyon along a dry stream in semi-deciduous forest. In plots 5–7 the girth of 33 marked trees had been measured in 1979 (by LAP-J), so the new measurements allowed a six-year increment to be calculated. Increment data for eight years (1986–1993) were obtained for 32 trees in plot 1.

To examine the size–age relationship, girth was measured and the conspicuously marked rings in the xylem were counted in 32 fence posts made of *C. elaeagnoides* of about 8–70 cm girth. We make the assumption that these rings

are annual. This often has been doubted for tropical species (Bormann & Berlyn 1981) but recent information supports the idea of annual rings, especially when there is some seasonality in the climate (e.g. Bhattacharyya *et al.* 1992, *Cordia trichotoma* in Boninsegna *et al.* 1989, *C. goeldiana* in Vetter & Botosso 1989, Worbes 1989). Given the extremely seasonal rainfall at Chamela, the assumption of annual rings seems warranted (see also Tschinkel (1966) on *C. alliodora* in Costa Rica). Further size–age projections were made on the basis of 1979–1985 growth increments using the procedure of Lieberman & Lieberman (1985). This simulates growth trajectories by random selection of actual increments from the sample population near the appropriate size. The ignoring of autocorrelation by this method is probably not a major concern given the long period between measurements.

The maps of each population were used to test for clumping of regeneration with respect to older trees. The test of relative dispersion of young and old trees compares observed and expected nearest neighbour distances (procedure of Hamill & Wright 1986).

Seed biology

Soil samples were taken in October, before dispersal of the 1985 fruit crop but after 1985 germination, to inspect for old fruits. The samples were *c.* 20 cm × 20 cm and 5 cm deep; one sample was taken from each of plots 4, 5 and 7, and seven were taken from plot 1. These fruits were sectioned to count the number of seeds. This was also done for fresh fruits collected by late November from 10 trees distributed along 60 km of highway south-east of Chamela. The style morph of each was determined to detect any effect of style morph on seed set. Fruits also were collected in January 1987 (1986 crop), after a wetter period of fruit maturation, for similar counts. Anatomical preparations were made of rudimentary structures present in the many empty loculi. These preparations were stained with toluidine, inspected for the presence of embryos and compared with the literature (Corner 1976, Netolitsky 1926) to determine if the frequency of fertilization was low. Total and percentage fruit production was estimated for one tree from counts of empty pedicels and of fruits per panicle, and an estimate of total number of panicles.

The fruits were inspected for signs of insect attack. Fresh and old fruits were also used in feeding tests with *Liomys pictus pictus* (Rodentia: Heteromyidae), the most abundant rodent in the area (Ceballos & Miranda 1986).

Germination tests were performed with the fruits from the 1985 and 1986 fruit crops, in 1987 and 1988, respectively, with the fruits buried in compost mixture and incubated at 30°C. Some of the seeds were leached before incubation (four replicates with and without washing, 25 fruits each). Possible inhibitory effects of the leachate from the fruits was tested on seeds of commercial lettuce (*Lactuca sativa*), incubated on moist filter paper at 20°C.
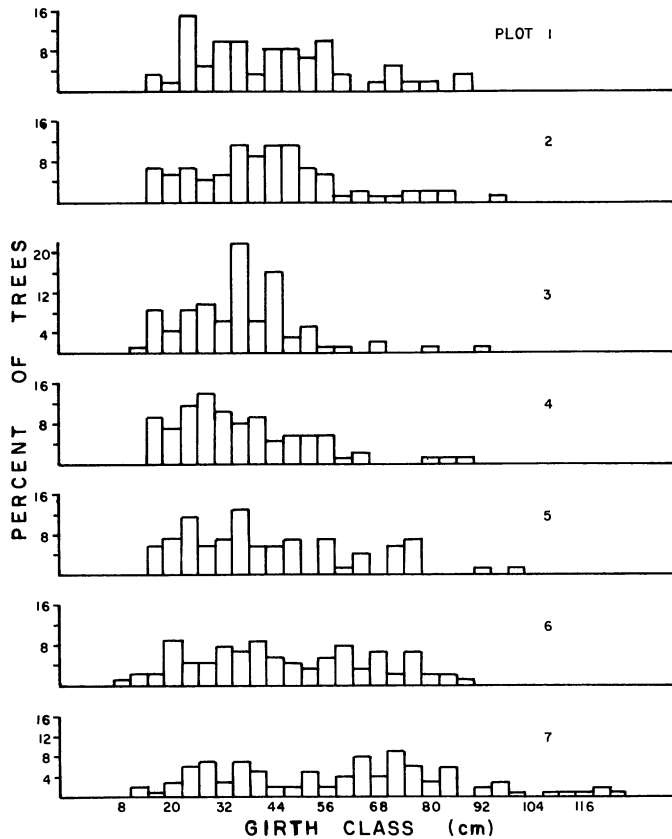
Figure 1. Size distributions for plots in seven stands of *C. elaeagnoides* at Chamela, southern Mexico.

RESULTS

Population structure

The size distributions of *C. elaeagnoides* trunks in the seven plots were diverse but shared several important features (Figure 1): (i) all the distributions were multi-modal; (ii) none were dominated by small trees; (iii) trunks smaller than 10 cm gbh were virtually absent; and (iv) the majority of trunks in all stands were larger than 28 cm gbh. Plot 7, the only plot situated in a valley, was notable as the only stand with a majority of trees larger than 60 cm gbh.

Another similarity was the minimum size for flowering. Above 30 cm gbh the percentage of trees flowering in 1985 stabilized at $80 \pm 10\%$ over all plots (Figure 2; Table 1). Multi-stem trees were common, but more abundant in plots 5–7 (Table 1). This might reflect incidental felling by man because these plots bordered an old track between Chamela and interior towns. Regarding mortality, the percentage of genets with at least the largest stem dead (but standing) ranged from 0 to 3.4% in plots 1–4, and was 5% or greater in plots 5–7; plot 6 was notable with 14.5% standing dead.
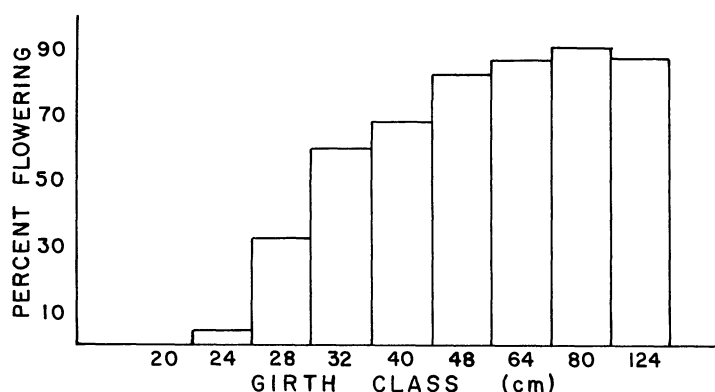
Figure 2. Percentage of individuals flowering in 1985 by girth class.

Table 1. Description of *C. elaeagnoides* plots at Chamela. Percentage flowering refers to trees with gbh > 30 cm. Clumping refers to the Hamill–Wright test of relative dispersion of smaller (gbh <30 cm) and larger (gbh >60 cm) trees (KS = Kolmogorov–Smirnov statistic; * P ≤ 0.05).

Plot	Number of trees	Area ha	Percentage of trees				Clumping	
			gbh <30	gbh >60	Multi-stem	Flowering	KS	P
1	59	1.20	29	14	12	95	31	ns
2	87	0.24	28	13	21	73	35	ns
3	90	0.28	35	4	11	86	46	ns
4	85	0.54	46	6	11	84	44	ns
5	68	1.17	38	21	32	65	262	*
6	88	1.27	30	25	51	76	98	ns
7	97	1.20	21	50	28	84	−186	ns

The density of *C. elaeagnoides* varied among plots by a factor of eight (Table 1). The relative dispersion of younger trees in relation to older trees in general was random (Kolmogorov–Smirnov statistic; Table 1). One case of significant positive association was found when younger trees were defined by gbh <30 cm. With a broader definition of younger (gbh <40 cm) there were three cases of positive and one negative association among the seven plots.

Growth

The six-year increase in girth ranged from almost 9 cm to less than 1 cm, decreasing rapidly as a function of initial size (Figure 3a). The data were best fitted by the relation

$$\text{increment} = 15.64 - 3.05 \ln \text{gbh} \ (r = -0.586, N = 32, P < 0.001).$$

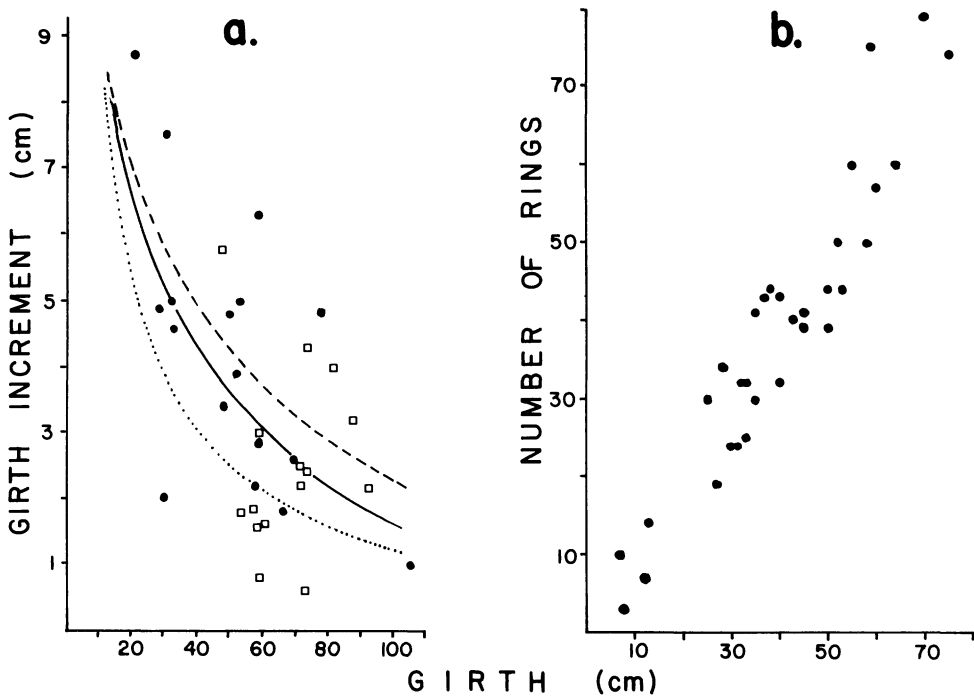The best fit for single-stem trees was given by

Figure 3.   (a) Increase in girth of *C. elaeagnoides* over the growth periods of 1980–1985, plotted against initial girth. Closed symbols are for single-stem trees and open symbols are for multi-stem trees. The dashed line is for single-stem trees and the solid line is for all trees. A hypothetical growth curve, for a constant volume independent of size, is shown by the dotted line. (b) Number of growth rings plotted against girth for fence post sample.

$$\text{increment} = 15.73 - 2.93 \ln \text{gbh} \quad (r = -0.605, N = 17, P < 0.05).$$

Age–size estimates were obtained directly from the regression of ring counts on girth (Figure 3b). The best fit was given by

$$\text{number of rings} = 0.67 \, \text{gbh}^{1.09} \quad (r = 0.954, N = 32, P < 0.001).$$

This yielded an estimate of 90 years for 90 cm gbh. Similarly, the age at first reproduction, at about 30 cm gbh on average, was estimated to be *c.* 27 years. However, this method probably underestimated age because the smaller annual rings are easily overlooked in the dark wood.

The six-year increment data of single-stem trees were used to estimate the age–size relation using the simulation algorithm proposed by Lieberman & Lieberman (1985). These simulations suggested a linear age–size relation up to about age 130 (Figure 4). Assuming a girth of about 30 cm at the age of 24 years, trees of 90 cm girth would have an age of about 112 years, with 95% confidence limits at 99 and 131 years. The difference between single-stem and multi-stem trees was conspicuous in these simulations, with estimated growth
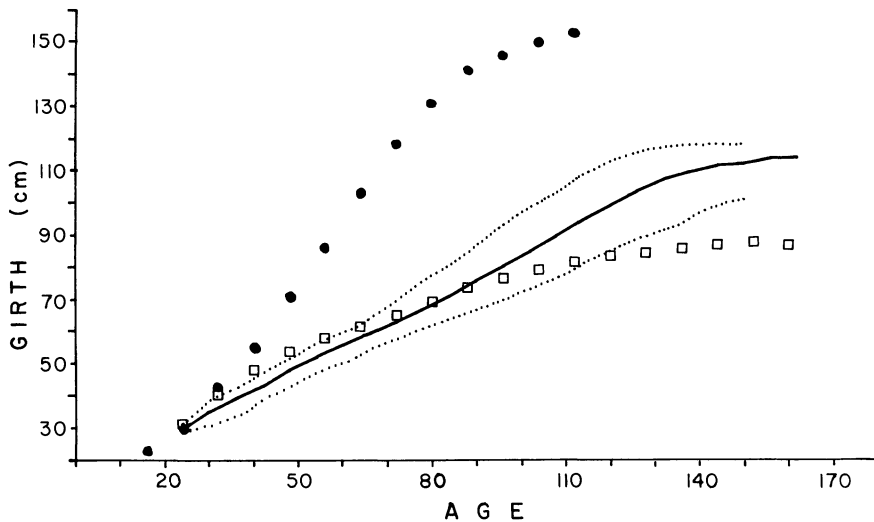
Figure 4. Simulated diameter growth curves (median; initial N = 1000) from periodic increment data for *C. elaeagnoides* based on single-stem trees: solid line, 1980–1985, N = 18, with 95% confidence limits (dotted); open symbols, 1986–1993, N = 32. For comparison, a simulated growth curve (closed symbols) is shown for the early successional tree *Cochlospermum vitifolium* from the same study area (1986–1993, N = 61, based on data from Bullock, unpublished).

rates of adults of 0.657 and 0.342 cm gbh y^{-1}, respectively. Because there were no multi-stem trees smaller than 48 cm gbh, growth at smaller sizes was not projected and no age estimates were attempted. The eight-year increments from plot 1 produced a curvilinear age–size relation, with higher growth rates for ages 20–80 years, and an asymptotic size slightly below 95 cm gbh (Figure 4).

Reproduction: seed production

Cordia elaeagnoides is distinctly distylous with an almost perfect separation between short style (SS) and long style (LS) morphs (Figure 5). Variation existed between years and/or sites but this did not affect the degree of separation. In general there were very few differences between morphs in seed set (Table 2). In both an average of three out of four loculi developed, around 18% showed signs of having developed some seed material, and fully grown seeds were found in 9% of the fruits from the 1985 crop. However, the 1986 crop, which matured under wetter conditions, had a considerably better seed set of around 16%, independent of style morph. Moreover, per fruit more ovules developed into seeds in the 1986 crop (1.14 ±0.34 SD, N = 73; compared with 1.00 ±0.00, N = 43 in the 1985 crop). In general, there were also very few signs of insect attack (Table 2). The main difference between morphs was the greater abortion rate of SS morphs. This could have been enhanced by the fact that flowers had been collected from relatively isolated trees. However, even when the fruits seemed empty, anatomical study showed that tiny structures of <0.5 mm were present in the loculi; dissection of about 20 of these structures showed that each contained a rudimentary embryo.
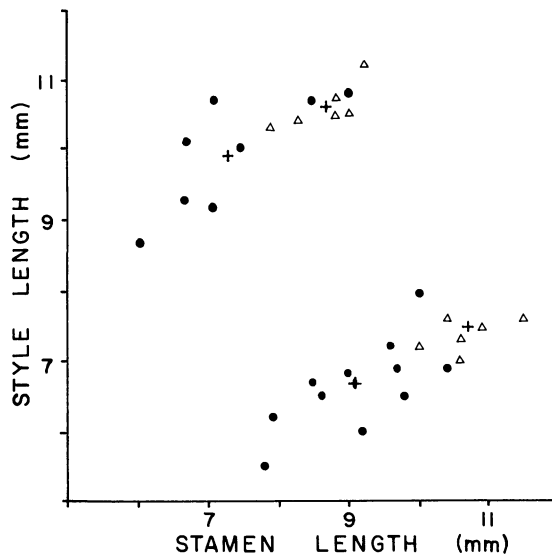
Figure 5. Distyly in *C. elaeagnoides* as shown by length of style *vs* length of stamens. Standard errors varied between 0.2 and 0.5 mm. Closed circles refer to 1985, open triangles to 1983; crosses are means for each data set.

Table 2. Mortality and survivorship (%) between flowering and seed dispersal in long- and short-styled individuals of *C. elaeagnoides*. Means and standard deviations for the 1985–1986 crop were calculated from five individuals per style morph (50 fruits each), except for the percentage flower abortion, which was based on three individuals per morph and 10 panicles per individual. Means and standard deviations for the 1986–1987 crop were calculated for four samples of 100 fruits each without taking the style morph into account.

Sample source	Aborted flowers	Developed loculi	Fruits with seeds	Fruits maturing	Fruits with bruchids
1985–1986 LS	57.0 ±2.4	75.3 ±13.0	17.6 ±16.6	8.8 ±12.2	2.4 ±5.4
1985–1986 LS	72.2 ±2.0	77.0 ±7.9	17.6 ±13.2	8.4 ±6.2	1.6 ±3.6
1986–1987 LS + SS	—	81.6 ±6.8	17.0 ±4.0	16.3 ±3.9	1.3 ±2.5

Estimates of reproduction at several stages were combined to give an approximate maximum figure for total fruit production. One free-standing tree, with a deep crown and covered on all sides by flowers, possessed about 10^3 panicles. The panicles each contained about 130 ($\pm$112 SD) flowers (N = 13), and on average 35% of these flowers matured into fruits (Table 2). These figures suggested about $45 \cdot 10^3$ fruits per tree as a rough maximum. For a canopy of 12 m^2, this suggests a seed rain of 3750 m^{-2}.

Fate of seeds

The soil seed bank in October, after the wet season and before shedding of the 1985 crop, amounted to an average of 4083 ($\pm$1430) fruits m^{-2} (N = 10). However, 29 $\pm$13% of these fruits were rotten (N = 3, 100 fruits in each count) and 8 $\pm$3% showed signs of being gnawed by rodents. Apparently, viable seeds were present in only 2 $\pm$2%, or about 82 fruits m^{-2}.
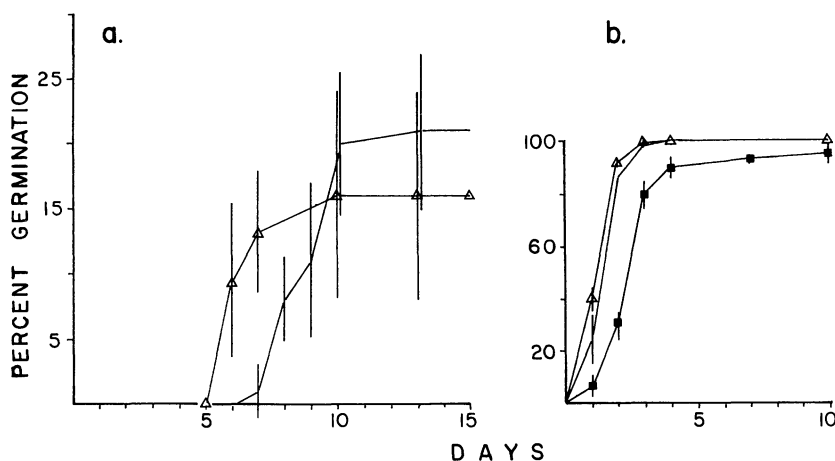
Figure 6.   (a) Percentage germination of fruits of *C. elaeagnoides* from the 1986–1987 crop with (open triangles) and without prior washing of fruits. (b) Percentage germination of lettuce seeds wetted with distilled water (open triangles); wetted with distilled water that contained old fruits for one day (no symbol) and wetted with distilled water that contained fresh fruits (1986–1987 crop) for one day (closed squares).

Given the low frequency of filled seeds, *C. elaeagnoides* is a poor-quality resource for animals, but the seeds seem to be eaten because *Liomys pictus pictus* eats *C. elaeagnoides* seeds in captivity (A. Miranda García, personal communication). However, two animals that were put on an exclusive diet of *C. elaeagnoides* died after 1 and 1.5 days. Other tests showed that *L. pictus* is able to select filled seeds: filled seeds were reduced from 19% of the offering of fresh seeds to 2% after one day; old fruits showed a change from 27% to 14%.

Germination of seeds from intact *C. elaeagnoides* fruits was generally poor. No germination was observed in the greenhouse from fruits from the 1985 crop. However, fruits from the 1986 crop did germinte (Figure 6a), producing 1.1 seedlings per fruit. Germination percentage was enhanced by washing (Figure 6a), and 1.2 seedlings per fruit were produced. Similarly, speed of germination of lettuce seeds was reduced by the leachate from the perianth (Figure 6b). Note that percentage of fruits with germination was similar to the percentage containing full-grown seeds (Table 2). This suggests the lack of any innate dormancy mechanism.

DISCUSSION

The life histories of dry forest trees, and the dynamics of dry forests themselves, are poorly known. As a useful, common and often highly dominant species, *Cordia elaeagnoides* merits particular attention, although its characteristics may appear peculiar from the conceptual perspective of other ecosystems. It is a rather slow-growing canopy tree but coppices vigorously and may rarely exceed 150 years of age; it is distylous but apparently self-compatible and wind-pollinated; its wind-dispersed seeds are mostly destroyed by generalist rather

than specialist predators, and form a multi-age seed bank (due to enforced dormancy) from which recruitment is both scant and sporadic.

The yearly increment of *Cordia elaeagnoides* is not high compared to other tropical trees (in terms of diameter, 2.3 mm y^{-1} for single-stem trees and 1.8 mm y^{-1} averaged over all trees). No data are available for other species from Chamela with comparably dense wood. In Costa Rican plantations, medium-sized *Cordia alliodora* trees increase by 10 mm dbh per year (Tschinkel 1966). For moist and wet forest trees, there is considerable information on growth rate (Lieberman *et al.* 1985) that shows a wide range of median rates and their utility in comparative studies of population dynamics. For example, Worbes (1989) found differences according to the successional position: a wet forest pioneer like *Pseudobombax munguba* (Bombacaceae) had a yearly diameter increment of 16 mm, while a typical understorey tree like *Psidium acutangulum* (Myrtaceae) grew less than 2 mm. A contrast between dry forest canopy species is illustrated here by *Cochlospermum vitifolium*, an early successional species, and *Cordia elaeagnoides* (Figure 4).

Another interesting aspect of growth is the decrease in increment with increasing size. Negative curvilinear relationships also are found for mangrove trees (Shiokura 1989) and for *Cordia alliodora* (Tschinkel 1966). This is not a generally necessary relationship, as shown by contrary data (e.g. Boninsegna *et al.* 1989, Rai 1978, Shiokura 1989), although at some point a decreasing relation must result from constraints of physiology and mechanics. Compared to the curve of equal annual volume increment, our data show a consistent bias to higher rates at intermediate sizes (Figure 3a). Also, curves of this form cannot be extrapolated to the smallest size classes, because impossibly high growth rates would be implied. Moreover, the curve is less than ideal because the vast majority of the variation is not explained.

The age at first reproduction in tropical trees, despite its practical and theoretical importance, has not received much attention. Reproduction in *C. elaeagnoides* starts at estimated ages of 20–30 years. This is late compared to early secondary trees in the same area, such as *Cnidoscolus spinosus* (Euphorbiaceae), *Cochlospermum vitifolium* (Cochlospermaceae) and *Ipomoea wolcottiana* (Convolvulaceae), all at less than five years (Bullock, personal observation). Some estimates based on demographic study of natural populations are 3.5–5.5 years for *Scalesia pedunculata* (Compositae, Hamann 1979) and 2–3 years for *Cecropia obtusifolia* (Moraceae, Alvarez-Buylla & Martínez-Ramos 1992). This age may vary greatly with micro-environmental conditions: cultivated trees of *Penthacletra macroloba* (Mimosoideae) reproduced at 15 years, but forest trees may not mature until the age of 150 years (Hartshorn 1972, p. 66). 'Fully insolated saplings' of *Ateleia herbert-smithii* (Papilionoidae) are estimated to initiate reproduction at age 5–6 years (Janzen 1989). The maturation of *C. elaeagnoides* in closed forest is also relatively late when compared with temperate forest trees (Rohmeder 1967). The relative importance of age, size and other conditions is yet to be studied.

The age of *C. elaeagnoides* individuals of 100 cm girth was estimated to be more than 100 years. Recently, it has become clear that many tropical trees form distinct annual rings (Baas & Vetter 1989) and data have started to accumulate about ages, mostly from moist/wet forests. Worbes (1989) gives estimates based on the diameter of the thickest tree and annual increment data for *Piranhea trifoliata* (Euphorbiaceae) of 350–400 years and for *Tabebuia barbata* (Bignoniaceae) of 100–120 years (in this latter case the stand itself might have been in an early stage of succession). Boninsegna *et al.* (1989) report a maximum age for *Cedrela fissilis* (Meliaceae) of 220 years. Projections of increment data for wet forest trees suggest longevities of about 100 years for shade-intolerant trees, and several hundred years for other canopy trees. In this context the estimated age of a large *C. elaeagnoides* tree is not exceptionally old.

A distinctive feature of *C. elaeagnoides* is the monodominant patches if often forms in an otherwise highly diverse forest (Lott *et al.* 1987), although even in the most dense stands it is by no means the only tree in the canopy layer. Within existing stands, the spatial pattern of recruits is typically clumped, but is not negatively associated with adult trees. Hubbell (1979) found more dry forest tree species showed aggregated rather than random distributions, and also showed that juveniles are even more commonly aggregated. Hubbell and others have emphasized that the spatial scale of clumping and of thinning processes among juveniles varies tremendously among species and among different dispersal and mortality processes. Aggregation may be promoted by dispersal processes, coppicing or limitation by soil type. On the other hand, patches may tend to disintegrate due to localized mortality from predation, pathogens or physical stresses. Information to weigh these effects is nearly absent for monodominant tropical forests (Boucher 1981, Clark & Clark 1984, Martijena, unpublished). However, unlike *Celaenodendron mexicanum* (Euphorbiaceae) in the same region (Martijena & Bullock 1994), *C. elaeagnoides* is not virtually restricted to its own monodominant stands.

Recruitment is not from long-lived cohorts of suppressed saplings, but from a substantial seed bank. The effectiveness of the seed bank is reduced because of the 90% loss of viability of the seeds present within the fruits (by tetrazolium tests) after eight months in the field (Guevara-Fefer 1977). Further study is needed of the seasonality and causes of seed mortality. Despite these losses, the result of enforced dormancy of the seeds (due to remains of the perianth and compounds it contains) and of large annual inputs of fruits should be the build-up of a substantial seed bank, roughly 700 viable seeds m^{-2} in January. These reserves are substantial compared to temperate hardwood canopy species (Kellman 1974). In *Acacia* species, large seed banks appear to be typical, due to great longevity, and non-annual recruitment is more often attributed to non-germination than to high seedling mortality (Skoglund 1992).

Recruitment of *C. elaeagnoides* might be a function of mast fruiting, which would satiate predators and surpass stress-related mortality. The major factor controlling mast fruiting must be variation in embryo abortion rate, because

flowering is annual and abundant, and the pollination vector non-limiting. Because seeds are filled after the usual end of the wet season, abortion may be strongly influenced by soil moisture in this period. This idea is supported by the lower seed maturation in 1985 (9%) than in 1986 (18%) with rainfall relative to average in the relevant period (October–December) of 32% and 98%, respectively. Considerable variation in rainfall between years is characteristic of the early dry season (67% coefficient of variation, compared to 24% in the wet season). Sporadic recruitment on a time scale of decades is demonstrated by the estimated age structure of *C. elaegnoides*.

Forest openings or gaps favourable to establishment may be related to two known sources of mass mortality of trees: hurricanes, and prolonged or severe drought. With few decades of data, multi-year fluctuations in rainfall were shown in the region of distribution of *C. elaeagnoides* (Bullock 1986). Patches of mass mortality of trees were observed following the extremely dry years of 1985 and 1986 (with 64% and 77% of normal rainfall). This drought also affected *C. elaeagnoides*: one stand surveyed in 1994 had 31.4% mortality; many genets (16.7%) had produced new shoots from the base. Massive damage from hurricanes also may be important for long-lived trees: landfall frequency varies along the coast but was estimated at 0.12 per 100 km coast per 10 years for a region including Chamela (Bullock 1986). Sometime after such disturbances, seasons of substantial rainfall might favour recruitment within established stands and their expansion, or founding of new populations.

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