

Plant Demography: A Community-level Interpretation

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I. INTRODUCTION

As with many other approaches which focus only on parts of the population biology of organisms, demography has been sometimes considered as an end in itself in the study of plant populations. Besides describing and explaining populational behaviour of plants, demographic studies must constitute a dual avenue to study phenomena at two levels of organization: at the individual (or sub-populational) and at the community (or supra-populational) levels. Long-term demographic studies may be used to spot and interpret individual-level variability concerning those components of individual Darwinian fitness such as differential survivorship, growth and fecundity (Sarukhán, Martínez-Ramos & Piñero 1984). Typically plant size (especially when it estimates closely the amount of photosynthetic or reserve tissue) is positively correlated with survivorship, growth and fecundity, rather independently of age. When individuals of the same age encounter a patchier environment, the variance of individual behaviour increases correspondingly (Sarukhán, Martínez-Ramos & Piñero

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1984). The studies that render themselves suitable to such analyses show that individual-level variability has important implications, through genetic hierarchy, on the genetic structure of the population, at least in the short term (Sarukhán, Martínez-Ramos & Piñero 1984; Bullock 1982; Piñero & Sarukhán 1982). It is impossible at the moment, with the available information on individual-level variability of demographic parameters, to find any discernible patterns by which such variation in plant populations may be attributed to genetic or environmental factors. A better understanding of what constitutes the relevant environment for individuals of a population is needed to help determine the causes of individual variation. This is particularly complicated when individuals may sample differences in competitive interactions with neighbours and when as a result of growth they also sample different parts of the environment of the community they live in.

The aim of this essay is to discuss some of the community-level consequences that may be derived from demographic information about one component of the community and so gain insight into some of its synecological processes (in the sense of Anglo-American ecologists such as Whittaker 1978). This second avenue of application of actuarial information about a plant population has been seldom explored, and few examples exist that give to synecological studies a dimension of populations and individuals.

II. PLANT DEMOGRAPHY AND THE STUDY OF MOSAIC REGENERATION IN TROPICAL FORESTS

Forest regeneration in the tropics occurs in gaps formed by tree-falls, by the filling or 'healing' of the gaps through succession of different communities of species, both pioneer, colonizing taxa and light-demanding, suppressed, late secondary or primary forest species. Many authors (Sarukhán 1968; Whitmore 1974, 1975; Hartshorn 1978, 1980; Denslow 1980; Brokaw 1982) have described the importance which secondary succession and the gap-forming processes in the tropical forests have on the composition and dynamics of the forest as well as on its diversity. Gap-forming tree-falls are caused usually during storms (cyclones, hurricanes) when combined conditions of water saturation of the soil and very strong winds bring down the most exposed trees in the forest canopy, forming cleared areas of up to 600–700 m². Gaps can of course be smaller, if only a small tree or the large limbs of a tree fall.

A mosaic of different regenerative phases thus comprises what is often colloquially spoken of as 'virgin' or untouched tropical forest. Various descriptive studies of such patchwork of vegetation have been carried out (e.g. Oldeman 1978).

Lang and Knight (1983) have summarized the problems that beset the study of the dynamics of tropical forests, specifically of the late successional stages; there are generally poor records on the history of forest disturbance, there is a

widespread lack of time-recording structures in tropical plants, such as annual growth rings, and there is a paucity of long-term observations of forest dynamics. Of these, the first two may be solved, at least partially, by information and knowledge coming from studies at the population level. Our research on the detailed population dynamics of *Astrocaryum mexicanum* has allowed us to bridge the levels of population and community studies. The capacity to record the passage of time rather accurately, by means of the scars left by successive leaf cohorts on the trunk of the palm, has been discussed in detail (Sarukhán 1978, 1980; Piñero, Martínez-Ramos & Sarukhán 1984) and provides a vital time axis not only for demographic purposes, but also to date environmental events that affect the community in which the palm lives.

In addition to recording the passage of time, a special feature of the behaviour of the palm has proved to be an asset in allowing the understanding of forest dynamics. *Astrocaryum mexicanum* palms possess a single erect trunk which never produces suckers since it has one, terminal leaf bud. Severe damage to this will result in the death of the individual. The main source of mortality of mature palms (over 1.5 m tall) is an accidental hit by large, falling branches and entire trees blown over in the process of gap formation in the forest. However, when the hits by large falling objects are not direct or do not kill the terminal bud, palms are very often bent downwards, and frequently all the way to the forest floor without becoming uprooted, since they have an excellent anchoring root system. On average, over a quarter of all the adult individuals in the forests we have studied (corresponding to c. 360 palms per hectare) have been hit and bent at least once during their lifetime.

If the palm survives the hit and the bending, it will do two interesting things (see Fig. 1). First, the terminal meristem will start growing upwards, producing a well-defined kink that remains permanently in the trunk. Second, if the palm has been totally bent, it will normally change the morphology of its adult leaves to that of an immature individual and cease reproduction if it already was a reproductive adult. Very often surviving palms lose much of their leaf crown; this affects for some years their growth and reproduction. Mendoza (1981) has experimentally produced defoliation and observed the resulting effects on survivorship, growth and reproduction in palms of all ages.

Of these two behaviours, the one relevant for the present discussion is the turning upwards of the bent trunk within a year or two of the accidental event. By counting the leaf scars below the kink (l_1 in Fig. 1) we can estimate the age at which an individual was hit and brought downwards, and by estimating the age above the kink (l_2 in Fig. 1), we know how long ago was the palm brought down. The presence, in one spot of the forest, of several palms bent at the same time is considered as a strong suggestion that a disturbing event, severe enough as to have formed a gap in the above canopy, has occurred.

Besides the permanent observation plots, where most of the studies on the demography of *A. mexicanum* have been carried out at Los Tuxtlas (Piñero,

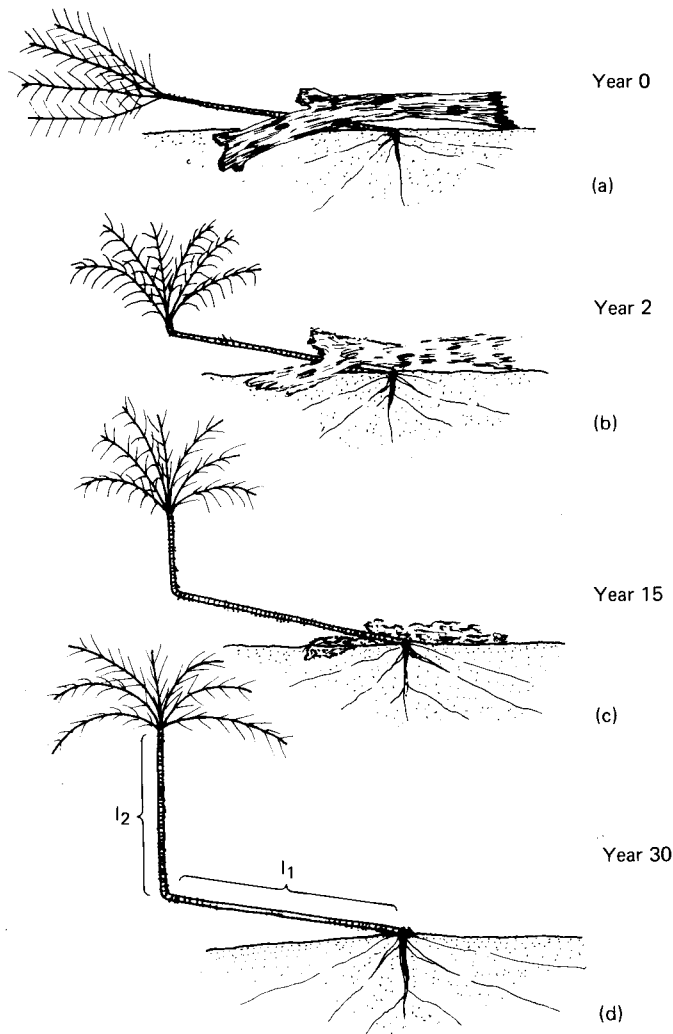


Fig. 1. A schematic sequence showing a, knocked-down individual; b, up-turn of the trunk 1–2 years afterwards; c, growth of the up-turned portion of the trunk; and d, the usual form in which bent-down palms are found in the forest. See text for explanation of l_1 and l_2 .

Sarukhán & González 1977; Sarukhán 1978; Pínero, Martínez-Ramos & Sarukhán 1984), a 5-hectare permanent forest plot has been set up where all trees 1 cm diameter at breast height (dbh) and larger have been recorded in a detailed map of the site, measuring their girth, height, crown cover and crown depth. These include all *A. mexicanum* adult individuals, whether they are erect or bent. A total of approximately 3482 adult individuals (≥ 1 m in trunk height) of the palm have been recorded and measured in the 5-ha plot, of which c. 1800 show a

distinctively bent trunk. Several important pieces of information are derived from these observations.

The first is that sizable disruptions of the forest canopy, sufficient to produce light gaps of differing sizes, occur regularly in time and space. Because of the frequency with which *A. mexicanum* palms occur in the forest and their longevity, we can estimate for each spot of the forest where several individuals have been bent, how long ago it was last subjected to a gap-forming event. The 5-ha site has been divided in a 5×5 -m grid; for each 25-m^2 subsite all the palms showing a bent trunk have been selected, counting how many years back each individual was brought down. The modal frequency of the ages of all the up-turned trunks represent the age after disturbance for that subsite. A map of the mosaics of gap stages of different age, from recently opened gaps to very old successional sites, is then made (M. Martínez-Ramos, J. Sarukhán & E. Alvarez-Buylla, unpublished). A considerable degree of heterogeneity at a very small scale (25 m^2) is apparent in the mosaic of the forest (Fig. 2). We have also observed at the site a gradient of younger to older stages from an exposed forest edge to the central, more protected part of it. This is also true for the steepest slopes within the forest, which support a more disturbance-prone mosaic of younger, successional gap phases.

A second aspect is that we can detect periods at which the forest as a whole

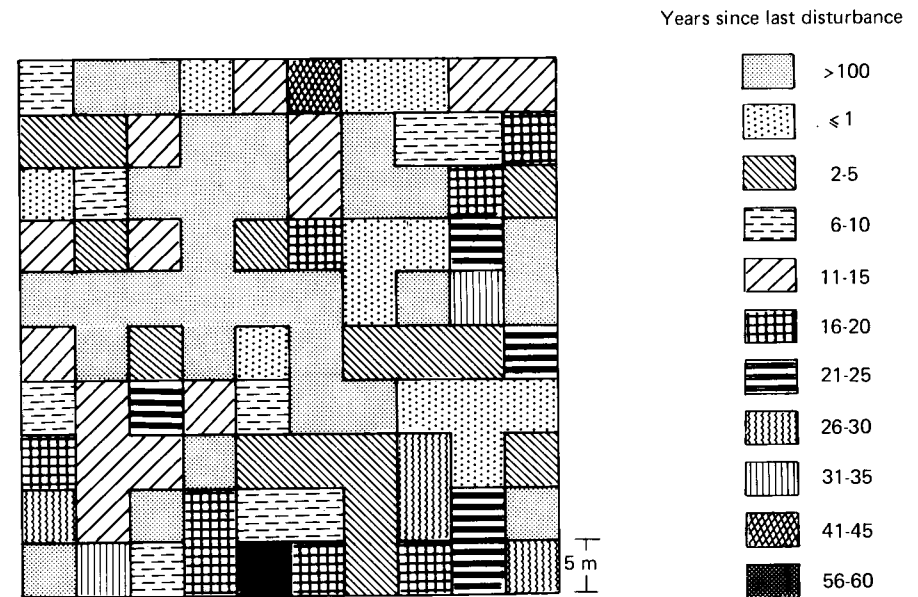


Fig. 2. A portion of 2500 m^2 (50×50 m) of the 5-ha permanent plot of observation at the tropical rain forest in Los Tuxtlas, Veracruz, Mexico. Each 5×5 -m subsite shows the age of that particular spot of the forest. The most frequent forest ages are over 100 years, 29%; 2–5 years, 15%; and 11–15 years, 14%.

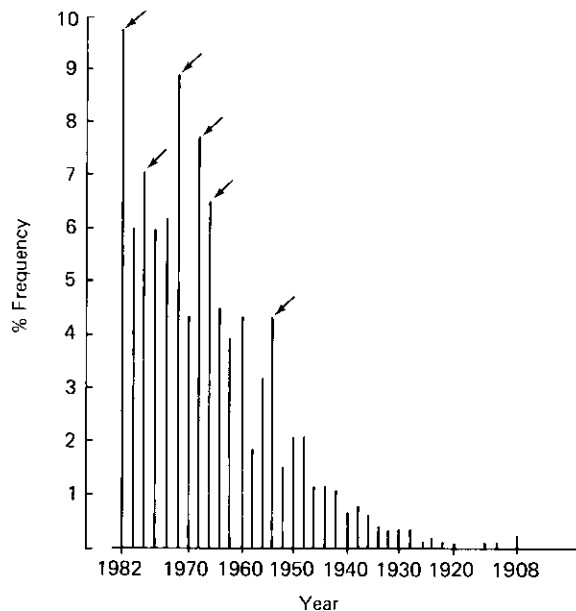


Fig. 3. Frequencies of *A. mexicanum* palms bent at different years in the 5-ha permanent plot at the tropical rain forest at Los Tuxtlas, Veracruz, Mexico. Arrows point at years of extensive perturbation by tree falls. $N = 1800$ individuals ≥ 1 m tall.

was subjected to unusually high rates of gap formation. In Fig. 3, periods of severe perturbation can be spotted at 2, 12, 16–18 and maybe 24 and 30 years prior to the recording date in 1982. Because of the dwindling numbers of older categories of palms, it is difficult to detect clearly generalized events of perturbation for all the forest earlier than 1950.

Besides using *A. mexicanum* palms as 'recording devices' of important environmental events in the regenerative processes of the tropical rain forest, it has been possible to relate the structure and floristic composition of every spot of the forest by means of correlating these to the age of each gap phase in the forest, down to a scale of some 100 m². In consequence, we are able to assemble together isolated 'frames' of successive ages of spatially and temporally isolated events of gap formation and regeneration for the same forest.

III. DETERMINATION OF FOREST TURNOVER RATES

The possibility of using the detailed understanding of a species' population dynamics to interpret events at the synecological level has proved to be of importance. The use of *A. mexicanum* palms as indicators of time of disturbance has allowed us to assess with great precision the turnover rates for different parts of the forest; thus, we calculate for the tropical rain forest at Los Tuxtlas a

turnover rate of 144 years for the more stable portions and of only 24 years for the forest edges. The rates for the stable portions differ very little from the values found for forests in Barro Colorado, Panama (137 years, Lang & Knight 1983), and La Selva, Costa Rica (135 years, Hartshorn 1978). Reviews on the subject by Martínez-Ramos (1985) and Brokaw (1985) coincide fairly closely with the former estimates. The rates for the forest edges bear importance from the conservation point of view, since long edges in forest reserves will mean large areas which are very susceptible to being naturally disturbed with greater frequency. Whether this high rate of turnover can be buffered and contained within a certain width of the forest, or whether it has a considerable domino effect, is unknown. Floristic composition in gap phases at the forest edge could be considerably changed by the replacement of many long-lived upper and mid-storey species by shorter-lived, high-turnover, pioneer species.

IV. THE STUDY OF THE DYNAMICS OF FOREST STRUCTURE AND COMPOSITION

A logical consequence of being able to age the patches composing a forest mosaic is to achieve a fairly rapid understanding of many aspects of the structural dynamics and floristic composition of the forest. So far, most descriptions of the dynamics have been based on somewhat vague estimations of age of forest phases or on information from distinct forest plots, distant in either space or time, or both.

The distributions of diameter classes for two different sets of species (pioneers and upper-canopy 'nomads') in three different gap phases, aged by means of upturned trunks, of *A. mexicanum* are shown in Fig. 4. The first group of species require light gaps for their seeds to germinate and include *Cecropia obtusifolia*, *Heliocarpus appendiculatus*, *Bellotia campbellii*, *Trema micrantha*, *Carica papaya* and *Cnidocolus multilobus*. They show a transition from a reverse J-shaped distribution of diameter classes (gaps 1–10 years old) to one in which small-diameter classes are almost absent (20- to 30-year-old gaps). Of course, a given gap may experience one or more subsequent disturbances which renew parts of the gap; this results in the presence of pioneers of a size (or age) that would not be expected had the gap undergone only one successional sequence; this, in fact, is the case for Fig. 4c. The second group of species are those which will not germinate in light gaps, but their seedlings and saplings will be 'released' from a state of light suppression and will grow very actively, sometimes dominating a portion of the gap with saplings and small trees. The data in Fig. 4d, e and f show a clear tendency for greater representation of larger-diameter classes of this group of species as the succession proceeds.

An immediate consequence of the preceding is the generation of tree growth curves for each species as a function of age. A schematic representation for such

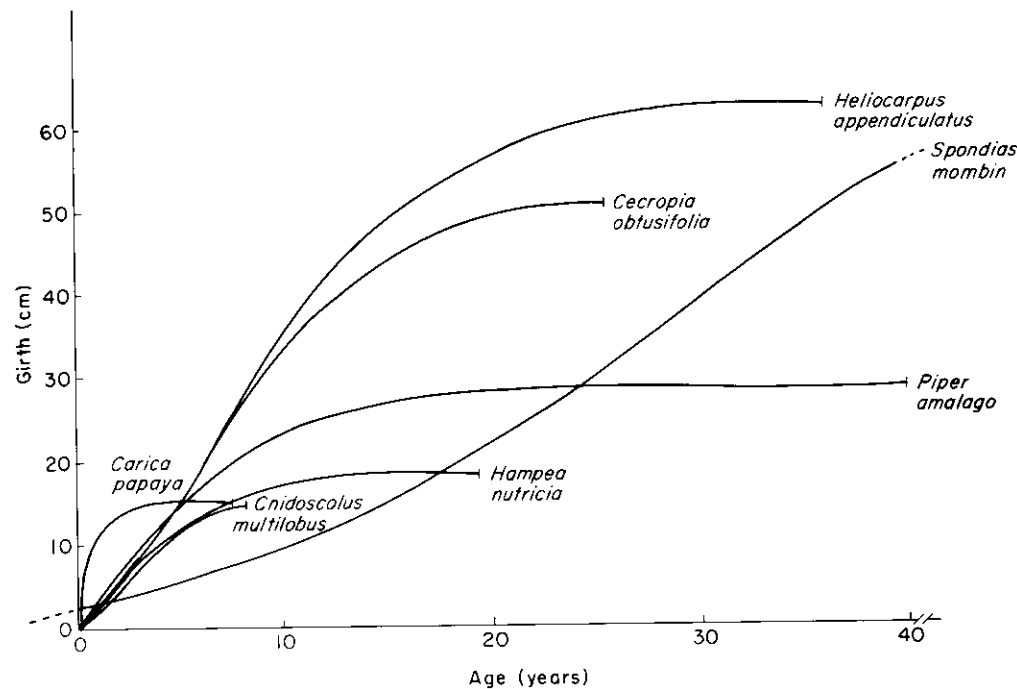
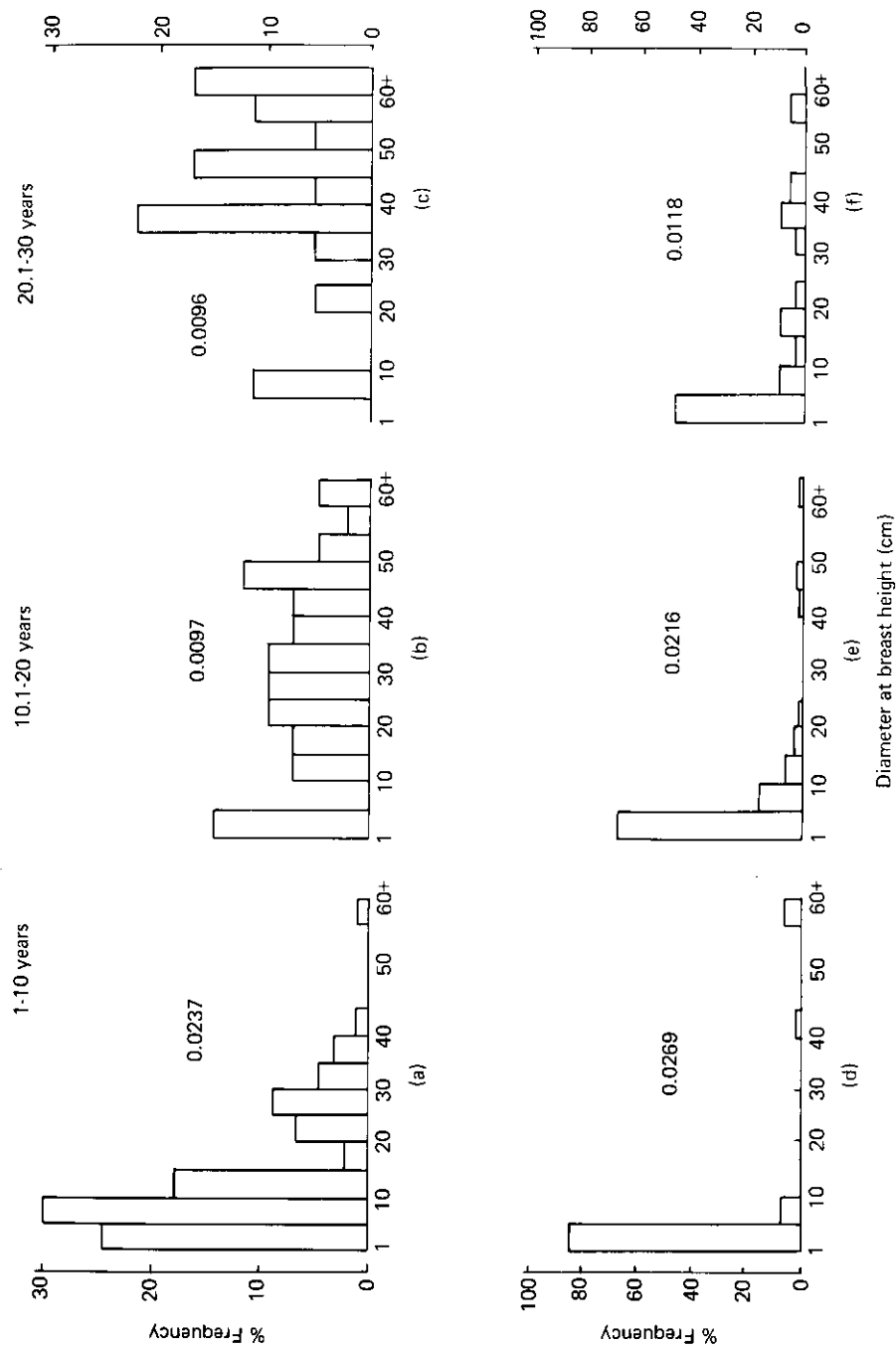


Fig. 5. Schematic growth curves for selected secondary species growing in gap phases in the tropical rain forest at Los Tuxtlas, Veracruz, Mexico. *Spondias mombin* was recorded with already established individuals in the newly opened gap.

curves obtained by M. Martínez-Ramos (unpublished) is shown in Fig. 5 for some of the light-demanding pioneer and nomad species at Los Tuxtlas, based on measurements of individuals present in gaps of different ages, using *A. mexicanum* individuals as estimators of gap age. *Spondias mombin* (a nomad), which started with already established individuals, *Heliocarpus appendiculatus* and *Piper amalago*, appear as the longest-lived, whereas *Carica papaya* and *Cnidoscolus multilobus* have maximum life span of 9 years and *Hampea nutricia* extends its life to nearly 16 years. This method provides very detailed information of growth rates and life spans for many of the important species participating

Fig. 4. Distributions of diameter classes for groups of pioneer (top row) and upper-canopy nomad (lower row) species in three different gap phases (1-10, 10.1-20 and 20.1-30 years) present in the tropical rain forest at Los Tuxtlas, Veracruz, Mexico. Pioneer species: *Cecropia obtusifolia* (a, b, c), *Heliocarpus appendiculatus* (a,b,c), *Bellotia campbellii* (a,b,c), *Trema micrantha* (a,b,c), *Carica papaya* (a) and *Cnidoscolus multilobus* (a). Nomad species: *Spondias mombin* (d,e,f), *Omphalea oleifera* (d,e,f), *Sapium lateriflorum* (d,e,f), *Bernoullia flammea* (f), *Bursera simaruba* (d,e,f) and *Robinsonella mirandae* (d,e,f). Letters in brackets indicate which species are involved in each histogram. Population density (m^{-2}) is indicated above each histogram.

in the regeneration of light gaps, without having to follow regenerative processes for long periods of time.

V. THE INFLUENCE OF *ASTROCARYUM MEXICANUM* ON FOREST DIVERSITY

The high diversity of tropical rain forests is probably one of the main biological features of this type of vegetation; woody (particularly arboreal) species are usually represented by only a few individuals per hectare, many of them by even lower densities. In certain forests, however, where this situation holds true for arboreal species, some species, not normally counted as trees either because of their form or their relatively small girths, may be exceedingly abundant and may play an important role in influencing the structure and composition of their communities. They may do this by exerting great influence on the environmental conditions of the forest floor, where all future recruitments for all the species of the forest are established. One of the most obvious influences is through the modification of light regimes, which in turn determine the germination behaviour (Vázquez-Yanes 1976; Valio & Joly 1979; Vázquez-Yanes & Orozco-Segovia 1982; Vázquez-Yanes & Smith 1982; Aminuddin and Ng 1982). Such is the case for *A. mexicanum* in the tropical rain forest of Los Tuxtlas, and indeed in much of its area of distribution in tropical Mexico. There is a marked negative relationship between the abundance of *A. mexicanum* palms and the diversity of the specific patch of forest in which it may be found. Figure 6 shows such a relationship, in which total leaf cover of the palm is compared to the number of the other species present in the forest. This dominating role of a species such as *A. mexicanum* is confirmed by the fact that in certain areas of the forest where *A. mexicanum* is not abundant, another species of very similar size (*Faramea occidentalis*, Rubiaceae) fills the niche left by the palm and attains similar values of importance (in terms of number of individuals, basal area and crown cover). If one combines values of these two species to the diversity of forest patches, the negative correlation becomes even stronger (Martínez-Ramos 1980). Palms and other small trees typical of and restricted to the understory (up to 7–9 m tall) may be playing a controlling role in certain tropical rain forests. This is not fully realized, since normally the attention of plant ecologists and foresters is caught by the large canopy and emergent trees.

An additional evidence of the important role played by *Astrocaryum mexicanum* in the community it lives in is its effect on both the pattern of distribution of its own recruitments in the forest and the probability of survivorship of seedlings and juvenile palms. The permanent plots, where demographic observations on populations of this tropical palm are being carried out, represent different densities of palms (Piñero and Sarukhán 1982), an equivalent of 1100–2800 individuals per hectare.

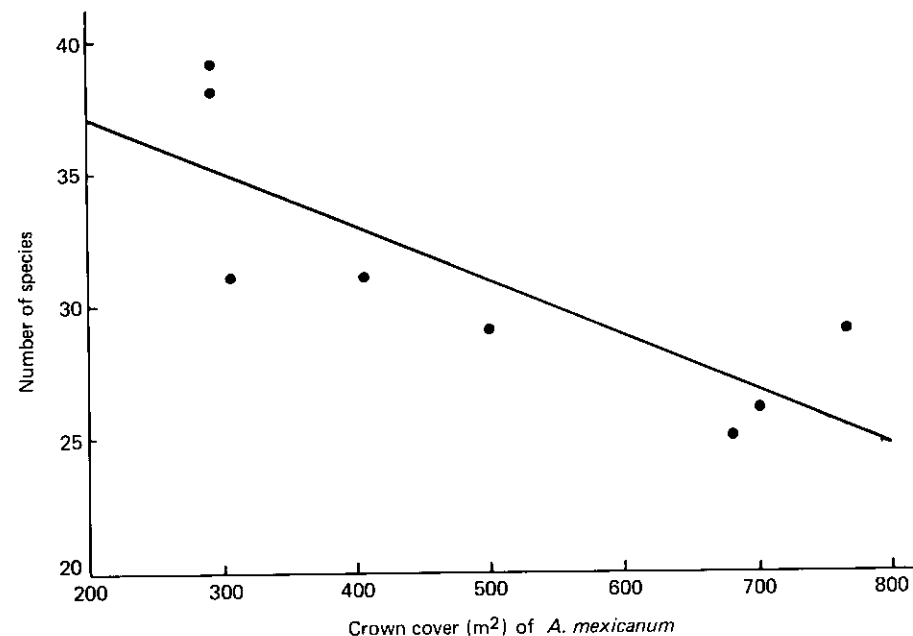


Fig. 6. The relationship between the importance (estimated as crown cover) of *Astrocaryum mexicanum* in a site and the number of species with individuals ≥ 1 cm dbh present at the same site in the tropical rain forest at Los Tuxtlas, Veracruz, Mexico ($p < .005$, $r = .8147$).

One of the first interesting observations about distribution patterns is that they change markedly with age from a highly aggregated one at the seedling stage in high-density sites to a far less aggregated and almost regular distribution for the reproducing matures in low-density sites (D. Piñero, unpublished data). But of greater relevance is the detailed analysis of how the density of *A. mexicanum* plays an important role in defining not only pattern, but also, and very precisely, spatial fixation of individual leaf crowns and of new recruitment to the population. As described elsewhere (Piñero, Sarukhán & González 1977), exact distribution maps of every palm individual in each of six 600-m² permanent sites have allowed us to make detailed analyses of individual distributions. Populations of *A. mexicanum* establish a strict hierarchical distribution, more easily detectable in high-density sites. If the leaf-crown sizes of all the mature individuals are projected into the forest floor, two features become obvious. Crown projections of the mature individuals very seldom superimpose, so that in very high densities, one obtains a crowding of circles of different sizes, touching the neighbouring ones only tangentially, but never overlapping, despite the fact that crowns of palms of different age may be placed at different heights above the forest floor (see Fig. 7), sometimes up to 6–7 m in difference. It is as if each mature palm cast an invisible, untraversable vertical cylinder, producing together something like the tubing of an enormous pipe organ.

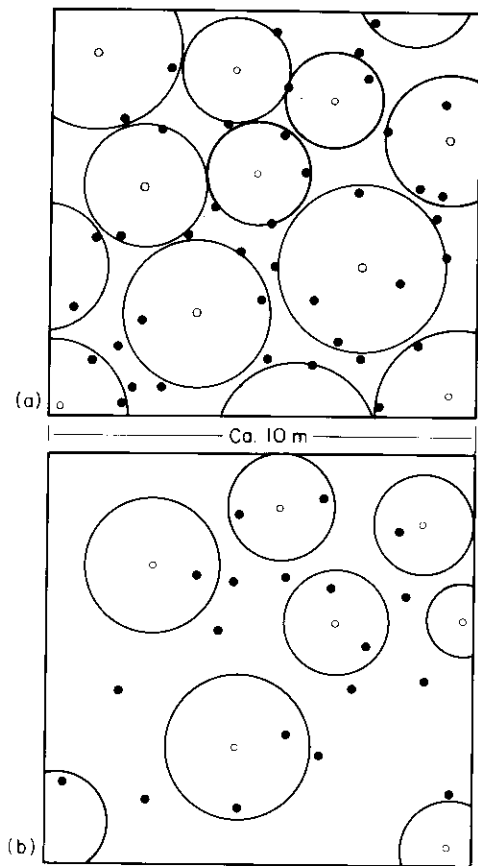


Fig. 7. Portions of the schematic maps of sites with a, high density ($= 2,800 \text{ ind. ha}^{-1}$); b, low density ($= 1,100 \text{ ind. ha}^{-1}$) of *A. mexicanum* in the tropical rain forest at Los Tuxtlas, Veracruz, Mexico. Large circles represent the projection on the ground of the leaf crown of mature individuals (over 1.5 m tall) of *A. mexicanum*; small circles mark the position of the trunk. Black dots mark the position of each seedling and juvenile individual of the palm.

The positions and consequently the chances of survivorship of seedlings and juveniles, are strictly determined by the crown projections of their mature conspecifics. An analysis of the location of these two younger categories of plants in sites of high density (Fig. 7a) shows that there is a probability of .85 that a seedling or juvenile of *A. mexicanum* will occur within a band 0.5 m at each side of the circular projection of the crown of mature individuals. This constriction in the location of seedlings and juveniles is loosened or even lost in sites of lower density of mature palms (Fig. 7b), where the probabilities for an individual of these two categories of appearing within or outside the 1-m band around the crown projection are no more than those expected by chance.

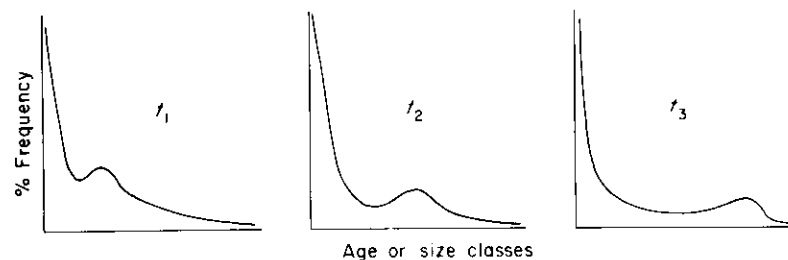


Fig. 8. The progression of a single demic wave caused by a gap formation influencing demographic components such as fruit production, seed and seedling survivorship and growth rate of seedlings and juvenile palms. There may be more than one hump simultaneously in a given population of *A. mexicanum*.

Quite clearly, it is not only the density of mature individuals of *A. mexicanum* that may affect the distribution of its own recruitment, and indeed of seedlings and saplings of many other species, but also the age structure of its mature individuals. Sequences of different age structures have been observed for *A. mexicanum*, having originated mostly as a result of the opening of large gaps in the forest; these gaps usually affect groups in the vicinity of 100 mature palm individuals and their seedling and juvenile phases, creating, by virtue of differential survivorship and transition probabilities, a so-called demic wave that displaces itself along time in the population until it disappears by the death of the last individuals belonging to it. Figure 8 is a schematic representation of one such 'demic wave' sequence, based on data obtained at our stable forest and gap-phase sites at Los Tuxtlas, Veracruz. The increased relative densities of varying age classes determine the greater abundance of individuals with leaf crowns placed at certain heights, and therefore exerting different spatial influences from one spot of the forest to the next and also along time for the same area.

VI. CONCLUDING REMARKS

John L. Harper started his Presidential Address to the British Ecological Society by pointing out the contrast between the approach of the 'vegetationalists', with their concern to describe and interpret areas of land, and Darwin's preoccupation with numbers, when he asked questions about the plants and vegetation in his back garden (Harper 1967). This depicted the neglect by many plant ecologists of dynamic, short-term changes in populations, and of plant demography, which by that time had not gained its present momentum. Now, 18 years later, we may ask ourselves if we can make an effort to link population ecology (and plant demography) with the vegetational approach that (in the words of Harper) had been brought to adulthood by Schimper and Warming. This would indeed be one very fruitful closing of a generation gap!

ACKNOWLEDGMENTS

There are events in the academic life which influence permanently much of what one achieves as a scientist; sometimes, this influence transcends the individual and affects a whole group. The stay of one of us (J. S.) at the School of Plant Biology, University College of North Wales, under John L. Harper's guidance had such an effect. We, and much of Mexican plant ecology, are in great and permanent debt to him.

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