ecologist and the vegetation ecologist can profit from each other's work, or at least where the vegetation ecologist can very well use data and theories from the population ecologist:

1. Immigration-extinction.
2. Seed bank and rhizome bank.
3. Microassociation, micropatterns, and coexistence.
4. Dominance-diversity relations and structure of vegetation.
5. And last, but not least, population dynamics and succession.

Let us hope that vegetation scientists will realize the profits of cooperation with population ecologists, especially in the field of vegetation dynamics.

I should have ended with a synecological quotation from Darwin, but I did not really look for one because I expected not to find any. By the time of Darwin's death, the first textbook on community ecology had yet to be written. Instead I dared to change the two famous adages in a synecological way:

Striving for co-existence
Survival of the fitting

CHAPTER 4

THE ANALYSIS OF DEMOGRAPHIC VARIABILITY AT THE INDIVIDUAL LEVEL AND ITS POPULATION CONSEQUENCES

José Sarukhán, Miguel Martínez-Ramos, and Daniel Piñero

INTRODUCTION

Plants not only stay quietly in one place to be counted and measured by ecologists as they grow, reproduce, and die; they are also endowed with the ability to grow, reproduce, and die at rates that vary widely among individuals within the same population.

The display of this enormous variability has been a source of profound interest for man from the beginnings of civilization, when the earliest attempts at domesticating plants began. It has also been a source of puzzlement and study for biologists, the greatest of whom pointed out that:

> Selection acts only by the accumulation of slight or greater variation, caused by external conditions, or by the mere fact that in generation the child is not absolutely similar to its parents. Man, by this power of accumulating varia-

tions, adapts living beings to his wants . . . [and that] in nature we have some *slight* variation occasionally in all parts; and I think it can be shown that changed conditions of existence is the main cause of the child not exactly resembling its parents.

Letter from C. Darwin, Esq., to
Prof. Asa Gray, Boston, U.S.,
Down, September 5th, 1857.

Later, plant biologists delved deeper into this variability (e.g., Salisbury, 1942; Harper et al., 1970; Harper, 1977 and references therein; Bradshaw, 1965).

The seminal work by Kira et al. (1953) and Yoda et al. (1963) [reinterpreted and expanded later, principally by White and Harper (1970), Kays and Harper (1974), and White (1981)] has shown that variability in vegetative behavior has environmental constraints that enable the prediction of the average weight or size of individuals in even-aged, crowded populations. Size or weight distributions around the different mean values show a clear skewness. The work of Koyama and Kira (1956) with *Erigeron*; Obeid et al. (1967) with *Linum usitatissimum*; Ogden (1970) with several annual weed populations; Ford (1975) with *Tagetes patula*; Hiroi and Monsi (1966) with *Helianthus annuus*; Mohler et al. (1978) with *Abies balsamea* and other temperate arboreal species, and the many examples reviewed by White (1980) show that very marked size hierarchies are established among individuals of even-aged monocultures.

However, the occurrence of size hierarchies is not constricted to planted, even-aged monocultures. It has also been ubiquitously recorded for natural populations (mostly uneven-aged) of short- and long-lived species in both mono- and plurispecific communities (Leak, 1964; Day, 1972; references in Harper and White, 1974; Werner, 1975; Crisp and Lange, 1976; Hett and Loucks, 1976; Cook, 1980; Franco and Sarukhán, 1981; Kohyama, 1981; Knowles and Grant, 1983).

The generally spotty nature of studies on age or size structure in plant populations and the frequent inability to explain individual variance in vegetative and reproductive performance, made the demographic approach a very welcome contribution to the study of plant populations in the late 1960s and early 1970s (Tamm, 1956; Sagar, 1959; Harper, 1967; Sarukhán and Harper, 1973). This new approach triggered a cascade of actuarial studies with plant populations that had widely different habits and that grew in a multitude of environments (e.g., Baskin and Baskin, 1974; Sharitz and McCormick, 1975; Jefferies et al., 1981; Klemow and Raynal, 1981; Symonides, 1977; West et al., 1979; Van Valen, 1975; Hartshorn, 1975; Sarukhán, 1980; Piñero and Sarukhán, 1982; Bullock, 1980; Yadav and Tripathi, 1981; review by Silvertown, 1982b).

Although age was usually sought as a natural population vector, it was soon realized that age could be a poor predictor of vegetative, and especially reproductive, performance of individual plants; size or "stage growth" as an estimation of the vegetative status of an individual was found often to be better correlated with its demographic behavior (see Harper and White, 1974; Werner, 1975; Werner and Caswell, 1977; Kawano, 1975; Barkham, 1980; Bullock, 1982). However, when both relatively accurate age estimates and growth stages are used, the understanding of population dynamics and the responses of individuals to environmental factors becomes much greater. That vegetative status could vary rather independently from chronological age and could be a good indicator of a population's structure and dynamic stage was realized early by Soviet plant ecologists, who have produced an abundant literature on the demography of many herbaceous species (Rabotnov, 1960, 1969, 1978a; Uranov, 1960, 1975; Smirnova, 1967, 1968; Zhukova, 1961; references in the review by Gatsuk et al., 1980).

Demographic studies soon revealed certain general patterns of population behavior among plant species (namely, in the types of mortality patterns shown by species with different life-histories) and suggested the probable role played by physical or biotic factors of the environment. The average patterns of population behavior described different life-history traits.

Different life tables and population models have been derived for many of the species studied to date (e.g., Sarukhán and Gadgil, 1975; Hartshorn, 1975; Van Valen, 1975; Leverich and Levin, 1979; Callaghan, 1976; Bullock, 1980). All forms of representation of population flux correspond to average conditions of all individuals observed at different age or size classes, during the period of observation, from one or several localities. The vision conveyed by most actuarial studies of plants is that of the ideal plant for an age or size class, in an ideal year or period, and in an ideal site. The individual variance around the mean behavior either in the onthogenic, spatial, or temporal dimensions is virtually always absent from these studies.

It is the objective of this chapter to show the importance of individual variability in demographic parameters in explaining the components of individual fitness: survivorship, growth, and reproduction. We shall also attempt to explore the demographic consequences of individual variability and discuss some of the results of demographically interpretable studies dealing with the genetic or environmental explanation of such variability.

THE COMPONENTS OF FITNESS

Most modern population biology studies have concentrated on the question of defining, estimating, and explaining a measure of evolutionary advantage of individual organisms resulting from the basic demographic attributes of survivorship and reproduction. This evolutionary advantage is determined by the action of the whole environment and its fluctuations in time and space on the phenotypes in question (Figure 1), in relation to other phenotypes in the population. Within this context, it is vital to know (1) the effect of the environment on the survivorship, growth, and reproduction at different stages of the life cycle of each individual in a population; (2) the correlative changes between growth, reproduction, and survival resulting from compromises in the utilization of limited resources; and (3) the degree to which such individual responses to the environment are genetically determined and, therefore, potentially inheritable by the progeny left by each individual. Details of these three points are only very partially known, often based on data which only look at one of the corners of this triangle, details fundamental to the understanding of the evolutionary consequences of population dynamics.

Differential survivorship

The first indication of the presence of individual size-dependent mortality in plant populations came from studies of single-species, even-aged plantations growing under high-density stress. It is well known now that under these conditions a thinning process develops in

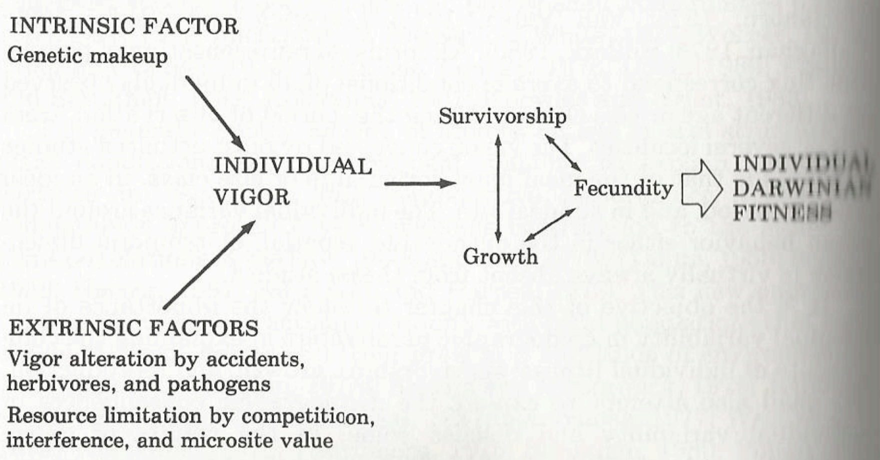

FIGURE 1. The factors intrinsic and extrinsic to an individual plant that determine its vigor and, consequently, its Darwinian fitness.

which, as plants increase their mean weight, mortality occurs, particularly among individuals in the lower end of the weight distribution. This density-dependent process in which mortality is differential and size-dependent has come to be known formally as the "self-thinning rule" or the "−3/2 power law" (Yoda et al., 1963; White and Harper, 1970). This rule, which is one of the few general rules in plant population biology, has been observed to apply in a large number of species from a wide spectrum of taxa, life forms, and environments (White, 1980).

In naturally occurring populations, size plays an important role in differential survivorship from very early in the life cycle of plants. A general hypothesis proposing that maternal expenditure on future progeny is adjusted to the predictability and availability of resources has been put forward by Lloyd (1980c). According to this hypothesis, plants control their maternal investment on the fruits (and eventually seeds) they will bear by determining sequentially the number of flowers produced, the development of the ovaries, the maturation of developed ovaries (or fruits), and finally the number of ovules that develop in each ovary as seeds. The on–off switching of energetic investment at each stage is determined by the level and predictability of resources available at that stage.

Genetic differences of the zygotes may lead to the production of size hierarchies in seeds through a differential allocation of maternal resources (Westoby and Rice, 1982). However, the seed vigor may be the result of factors extrinsic to the zygote's genotype, as is the case for *Lupinus texensis* (Schaal, 1980b), in which seed vigor is determined by the position of the ovule in the pod: those proximal to the peduncle of the fruit are the ones which will develop the larger seeds. Other examples of position-dependent seed size are presented by Janzen (1969) and Aker (1982).

The size (vigor) of seeds may have in some cases a definite influence in determining the performance of adult individuals (e.g., Salisbury, 1942; Harper and Obeid, 1967). Schaal (Chapter 9) observed a wide variation in individual weight within and between families of seeds produced by different mothers. The variation had a strong maternal effect, less than 10% of it being due to genetic causes. Larger seeds had significantly greater germination rates, germinated more, and produced more vigorous seedlings with a higher survival than smaller seeds.

Differential survivorship of seeds can also be influenced maternally through the amount of energy invested in the structures which protect the seeds in the fruit. Hare (1980) found that in *Xanthium strumarium*

(Compositae) predation of its seeds by insects decreased significantly with the size and thickness of the burr. Additionally, seed size has been shown to have a genetic component among different populations. Apparently in this case predators induce a selection toward increasing fruit size (and seed size?), attacking smaller burrs, which also have thinner walls and are therefore more susceptible to egg-laying. Seed size was found to be a better predictor of the susceptibility of being predated than either morphological or chemical traits (see Hare and Futuyma, 1978; and also Bridwell, 1918). However, Janzen (1969) has found the contrary for several legume species whose seeds are attacked by bruchids. In these species, small seed sizes are selected for because proper development and emergence of oviposited bruchids is not possible in small seeds.

Seed size is not, however, always correlated with differential germination (e.g., Cideciyan and Malloch, 1982, for *Rumex* spp.) or with seedling vigor (Solbrig, 1981, for *Viola* spp.). In other instances, shape rather than size is a source of differential survivorship. Dimorphic seeds are frequent in the family Compositae. Venable (Chapter 8) describes the occurrence of significant differences in the survival of seedlings originated from ray or disk achenes for two composites.

Seed size is clearly subjected to conflicting selective forces: from the compromise confronted by the mother on leaving an optimal number of progeny with maximum resources per seed (Westoby and Rice, 1982) to those which influence dispersal mechanisms, predator defense, germination ability, and vigor in a given temporal and spatial environment. Janzen (1969) has proposed in this context certain tradeoffs between seed size and number in the presence of predator pressure. Along the same line, a reduction in seed size could be the result of selective forces acting on traits favoring ample dispersal, as seems to be the case of pioneer tree species that colonize forest gaps in the tropics (Howe and Estabrook, 1977; Vázquez-Yanes, 1981; Brokaw, 1982). Howe and Richter (1982) studied the seeds of *Virola surinamensis* (a tropical forest canopy tree), and their results support the hypothesis that variation of seed size within and between crops of different parents could be caused by alternating pressures to (1) increase the probability of colonizing favorable sites with small seeds dispersed by endozoochory or (2), in the absence of dispersal agents, to increase the probability of survival of seedlings in conditions of environmental stress by bearing large seeds which produce robust seedlings.

The effect of environmental factors (especially biotic) on seed traits defined by maternal influence or otherwise, can be studied at the level of the plant–animal interface (e.g., Janzen, 1976; Dirzo, Chapter 7). In these studies, differential herbivory is simulated by removing different portions of the maternal capital in the seeds. In general, these studies show that the greater the amount of maternal resources re-

moved the greater the chances of future mortality at the seed and seedling stages. Also, the removal of seed capital produces a marked size hierarchy (both in height and number of leaves) among emerging seedlings. Patterns similar to those found in experimental studies have been observed under natural conditions for seedlings of *Nectandra ambigens*, an emergent species in neotropical rain forests, attacked by larvae of a fly (*Pteticus cyanifrons*) and beetles (*Pagiocerus frontalis* and a curculionid). Mortality is a function of how much seed capital is lost to the predator, the smaller seeds losing a greater proportion of it than larger seeds. Percentage germination and seedling vigor (height, number of leaves, and biomass) also show hierarchies (B. Córdova and J. Sarukhán, unpublished data).

Selection should act toward increasing maternal investment in seeds in environments where low levels of resource availability (i.e., light) affect seedling establishment. This has been found to be the case for shade-tolerant species in Malaysian forests (Ng, 1978); these species have large seeds that germinate rapidly and produce vigorous seedlings with high survivorship. In general, under suppressive forest-floor conditions, larger seedlings do have greater chances of survival and a greater ability to recover from accidental physical damage or defoliation by herbivores (see Dirzo, Chapter 7). We have found evidence of this in seedling cohorts of *Astrocaryum mexicanum*, a dominant understory palm of tropical rain forest in southeast Mexico (Piñero et al., 1977; Sarukhán, 1978). As shown in Figure 2, two-year-old individuals possessing three or more leaves had greater probabilities of surviving to their fifth year of life than individuals with fewer leaves. The same pattern was found for the category of infants (age classes between 1 to 8 years) and juveniles (age classes between 9 to 15 years) (cf. Figure 4); a larger standing leaf area means a greater survivorship chance for an individual, under light-limited conditions.

Intergenotypic differences have been shown for germination and seedling emergence (Eagles and Hardacre, 1979; Nelson, 1980) and seedling vigor (Voight and Brown, 1969; Fakorede and Ojo, 1981).

Differential mortality occurring among young individuals of temperate species and attributable to plant size or biomass has also been documented profusely (Werner, 1975; Cook, 1979b, 1980; Solbrig et al., 1980; Solbrig, 1981; Gross, 1981; Parker, 1982; Bazzaz, Chapter 16) (Figure 3).

The time required for germination and establishment seems to be crucial in determining the obtention of resources (Bazzaz et al., 1982), especially in environments open to colonization. Cook (1980) found that early recruitment in *Viola sororia* populations resulted in greater

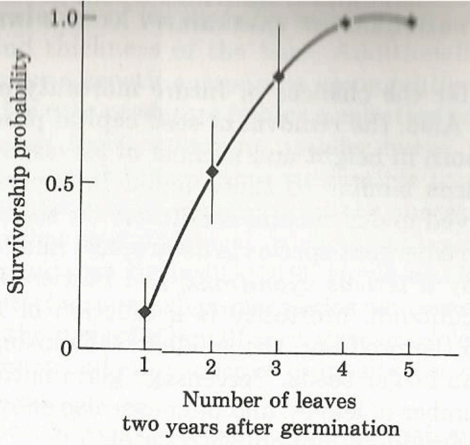

FIGURE 2. Survival probabilities to the fifth year for seedlings of the same cohort of *Astrocaryum mexicanum* as a function of the number of leaves that presented two years after germination. Data are means ± SD. The curve was eye-fitted.

vigor (i.e., individual weight) and consequently greater probabilities of survival than late recruitments of the same cohort (but see Venable, this volume). Experimental studies in *V. sororia* (Solbrig, 1981) showed that seed size is not correlated with either speed of germination or seedling growth rate. Field and laboratory studies indicated that the former factors as well as the probability of attaining a large size (and therefore greater expectations of survival and reproduction) depend to a greater extent on environmental factors rather than on genetic factors. Germination in favored microsites (nutrient rich; low density and predator-stress) may determine greater survival and reproductive success in phenotypes expressing larger individual size.

A similar situation was found by Fowler and Antonovics (1981a) and Antonovics and Primack (1982) in their studies on populations of *Salvia lyrata* and *Plantago lanceolata*; in these studies phytometers representing different groups of half-sibs were used. In *P. lanceolata*, however, there was evidence that some genotypes do better in some sites than in others, suggesting the existence of polymorphisms maintained by microspatial heterogeneity, much in the same way as those found earlier by Turkington and Harper (1979b) for *Trifolium repens*. At this scale, intraspecific density appeared as a factor defining the differences in individual performance and survival (Fowler and Antonovics, 1981a). Mortality was concentrated in individuals with lower leaf areas as a result of high growth rates in the summer.

It becomes clear that the "sifting" effect of the soil micro-

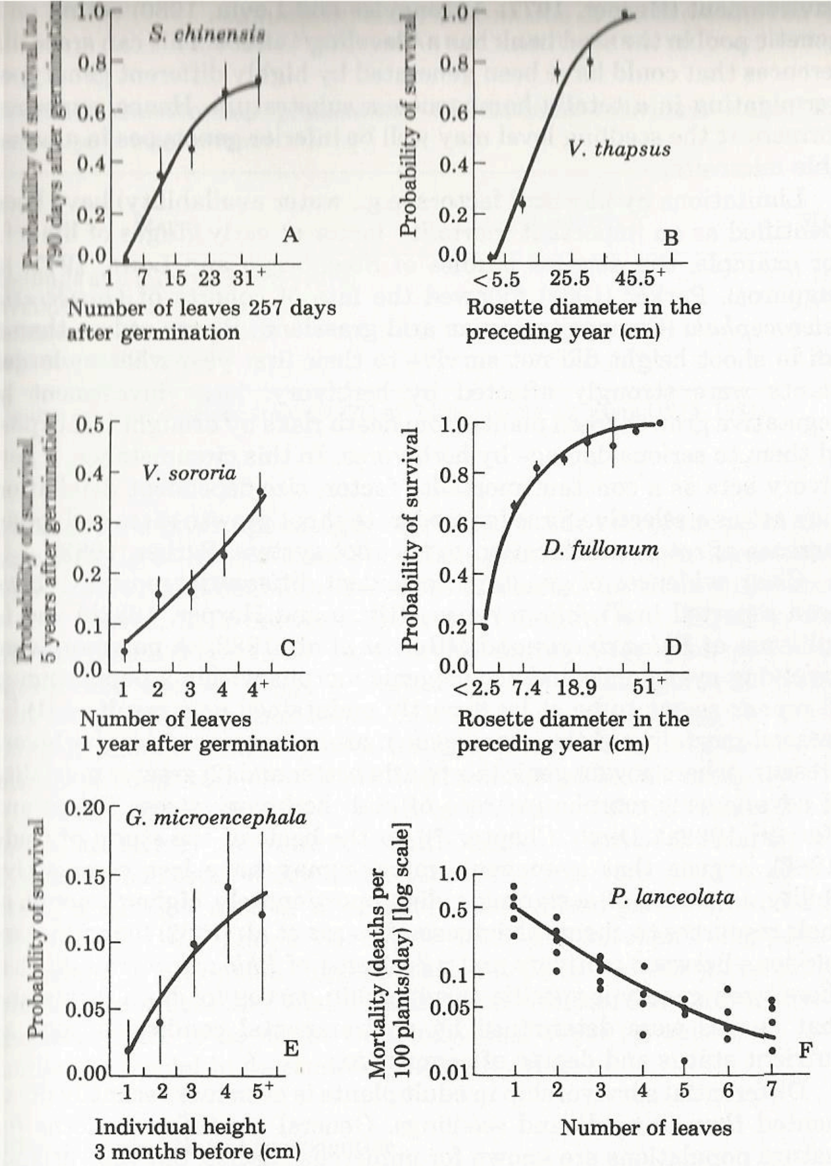

FIGURE 3. Survival probabilities as a function of individual size for seedlings. A. *Simmondsia chinensis*, a shrub of the Sonoran Desert (F. Molina and A. Castellanos, unpublished data). B. *Verbascum thapsus* (from Gross, 1981). C. *Viola sororia*, a herbaceous perennial (from Solbrig, 1981). D. *Dipsacus fullonum*, a biennial (from Werner, 1975). E. *Gutierrezia microcephala*, a desert shrub (from Parker, 1982). F. *Plantago lanceolata*, a herbaceous perennial (from Antonovics and Primack, 1982). Values for A through E are means ± SD. For F, points indicate different study sites. All curves were eye-fitted.

environment (Harper, 1977; Antonovics and Levin, 1980) acting on a genetic pool in the seed bank has a "leveling" effect. This can erase differences that could have been generated by highly different genotypes germinating in a totally homogeneous substratum. Hence, superperformers at the seedling level may well be inferior genotypes in a favorable microsite.

Limitations by physical factors (e.g., water availability) have been identified as an important mortality factor at early stages of life (cf., for example, the detailed studies of Steenbergh and Lowe, 1977, in saguaros). Parker (1982) followed the fate of cohorts of *Gutierrezia microcephala* (Compositae) in an arid grassland. Plants of less than 3 cm in shoot height did not survive to their first year whereas larger plants were strongly affected by herbivory: large investment in vegetative growth freed plants from death risks by drought but exposed them to serious damage by herbivores. In this circumstance, if herbivory acts as a constant mortality factor, size-dependent defoliation may act as a selective force for moderate shoot growth rates and for an increase of resource allocation to the root system (Parker, 1982).

Clear evidences of genotype-dependent differential mortality have been reported in *Trifolium repens* (Dirzo and Harper, 1982b) and in cultivars of *Phlox drummondii* (Bazzaz et al., 1982). A polymorphism involving cyanogenic and acyanogenic morphs within a population of *T. repens* seems to be at least partly maintained as a result of (1) increased mortality of the cyanogenic morphs in areas of low herbivore pressure where acyanogenic morphs do better and (2) greater mortality of acyanogenic morphs in areas of high herbivory stress (Dirzo and Harper, 1982a). Dirzo (Chapter 7), on the basis of the study of Cody (1966), argues that cyanogenic morphs may have less competitive ability as a cost of assigning a disproportionately higher amount of their resources to chemical defenses. Bazzaz et al. (1982) found in comparisons between cultivars and wild forms of *Phlox drummondii* that there were genotype-specific survivorship curves for both forms and that curves were determined by environmental conditions such as nutrient status and degree of competition.

Differential survivorship in adult plants is even more scantily documented than in seeds and seedlings. General mortality patterns for mature populations are known for numerous species, but the variance for each age or size class is mostly unknown. Data on age-specific mortality rates and their variability for populations of *Astrocaryum mexicanum* are shown in Table 1. The variance within each age class decreases with age, a finding suggesting, in addition to the existence of higher mortality risks, a much lower environmental predictability for seedlings and infant palms than for immature and mature stages (Piñero and Sarukhán, 1982).

Part of the interindividual variability in survival in infants and

TABLE 1. Survivorship probabilities for different individual stages in *Astrocaryum mexicanum*.[a]

Stages	Survivorship probabilities $\bar{X}$	SD
Seedlings and infants (1 to 8 years)	0.48	0.15
Juveniles (9 to 19 years)	0.86	0.09
Immatures (20 to 39 years)	0.95	0.04
Matures (≥ 40 years)	0.95	0.03

[a] Figures are data obtained from six 600-m² plots, during six years (1975–1981).

juveniles for a given age category is related to the size of the palm and more directly to its leaf area. For infant plants with eight leaves, the average survival probability is close to 1, whereas for those with three or four leaves, it is between 0.5 and 0.7 (Figure 4A). Equally, for juvenile palms (Figure 4B), survivorship during a four-year period is significantly greater ($D_{max} = 0.27$; $P < 0.01$; Kolmogorov-Smirnov test) for plants with four to six or more leaves, five being the most common number, and is poorer for individuals with three leaves or less; these constitute 45% of the deaths observed in this category.

The causes of mortality in adult individuals of *Astrocaryum mexicanum* are largely unknown to us, although one-third of the mature individuals (30 in total) which died after seven years were killed by direct hits by a falling branch or tree. Also, recently dead palms showed significantly ($P < 0.01$) fewer leaves ($\bar{x} = 10.20 \pm 3.30$) than living palms ($\bar{x} = 12.50 \pm 3.27$); this suggests that a depletion of resources could enhance the probability that an individual will die. Thus, for a given age-class, there is no doubt that individual vigor (in this case, leaf number) is crucial in determining mortality risks.

Differential growth and reproduction

Interactions between growth and reproduction are very complex and understood only at a rather superficial level. The mutual effects of growth and reproduction on each other have represented a fertile medium on which much of man's agronomic technology has been based. The empirical knowledge of the result of the interactions is ample, although it is only recently that systematic, experimental studies have started to disentangle growth and reproduction interactions and the effects of environmental constraints on them. For this

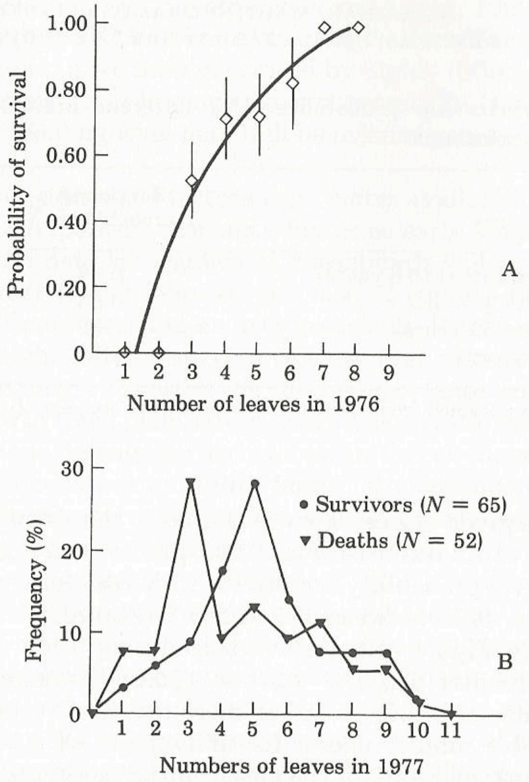

FIGURE 4. The relationship between number of leaves and survival in *Astrocaryum mexicanum.* A. Infants (1–8 years old) between 1976–1981. Means and SD are expressed. B. Juveniles (9–15 years old) between 1977 and 1980. Curves were eye-fitted.

reason, in this section we shall discuss variability in growth and reproduction simultaneously.

That individuals in even-aged populations under density stress develop size hierarchies implicitly indicates the existence of differential growth rates among them. Differential growth has been observed also in naturally occurring plant populations, but its demographic implications have been seldom documented. As a result of different growth rates, reproductive rates are necessarily affected and differentiated among individuals. Little information exists on individual reproductive variance in naturally occurring populations; moreover, the interaction of growth on reproduction and of this on further growth and survival have only fractionally been investigated in a demographic context.

Evidence for the genetic basis of differential growth rates and reproduction is slight. Burdon and Harper (1980) found that growth rate in *Trifolium repens* appeared to be yet another trait for which genetically based variation exists in naturally occurring populations; they point out that average growth rate estimates for a population obscure individual variability. Law (1979) and Law et al. (1977) found genetically based variation in the effects of reproduction on further growth, reproduction, and survival in *Poa annua.* Also, Primack and Antonovics (1981) found a genetic basis for variation in components of seed yield on *Plantago lanceolata.*

However, other causes have also been documented as determinants of individual variability in growth and reproduction. Gottlieb (1977) argues that for highly plastic annual plants such as *Stephanomeria exigua* ssp. *coronaria,* extreme variation in size and growth rates are not due to genetic differences and that these differences do not constitute the basis of evolutionary changes. Gibbs and Harrison (1976) have shown that viral diseases have an important impact on plant yield and growth form; often viral diseases are not self-evident, especially in highly variable natural populations, and their effects can be ignored or mistaken as caused by other factors.

Aker (1982), working with the desert plant *Yucca whiplei,* found a significant correlation between basal area of individual rosettes and the number of mature fruits produced by them, although other components of reproductive effort (ovules per capsule or seed weight) were not at all or only inconclusively correlated to plant size. Bentley and Whittaker (1979) and Bentley et al. (1980) reported that seed number per plant and seed weight are significantly affected by the effect of grazing on *Rumex crispus* and *R. obtusifolius* by a chrysomelid beetle. Milton et al. (1982) found that larger trees (based on diameter at breast height and crown diameter) of *Ficus yoponesis* and *F. insipida* produce larger fruit crops and at shorter intervals than smaller-sized trees and that these differences are sustained under differing environmental conditions.

Studies on the individual variability in both vegetative growth and reproduction in a demographic context have been carried out by Piñero and Sarukhán (1982) in populations of *Astrocaryum mexicanum.* Because of the strictly monopodic mode of growth of *A. mexicanum,* gains in size are achieved by virtue of new leaf production at the apical meristem, which in turn adds height to the trunk of the palm. Gains in height vary with the age of the individuals (Figure 5), an average of 1.5 to 6.5 cm per year from seedling to mature plants. This is equivalent to an average of 0.5 to 2.3 leaves per year, respectively. There are negligible differences in the mean number of leaves per individual produced once plants reach the mature stages.

A tenfold variation in the net height gains is shown by individuals

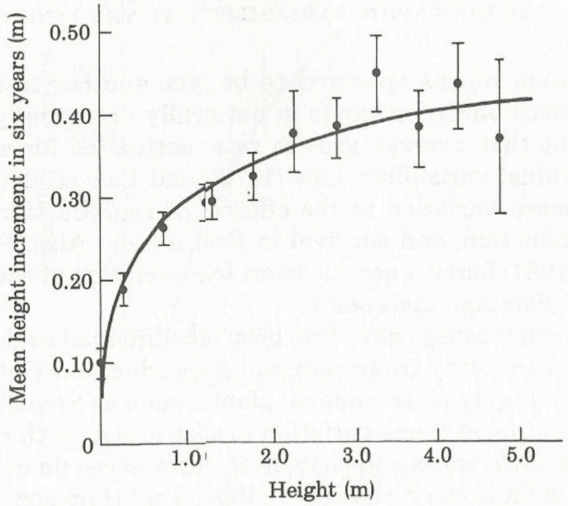

FIGURE 5. The general pattern of height gains for mature individuals of *Astrocaryum mexicanum* as a function of plant height. Data are means ± SE for each 0.5-m height class. Curve adjusted to a logarithmic model ($G = 0.30 + 0.08 \ln H$).

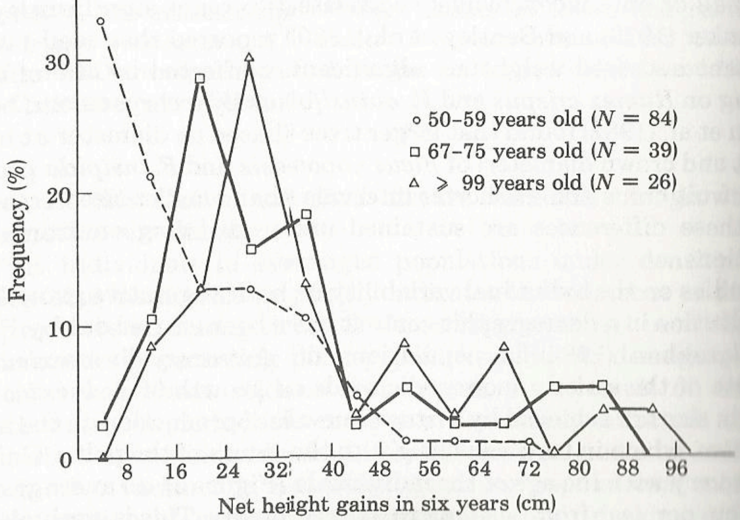

FIGURE 6. Height-growth differences within three groups of different ages of *Astrocaryum mexicanum*. Data are relative frequencies of individuals in different increment classes.

within three different age categories (matures of 1 to 1.5 m height; matures of 2 to 2.5 m; and matures taller than 4 m) during a six-year period of observations (Figure 6). Although about two-thirds of all individuals have a fairly similar (modal) net gain, some 30% in each category show gains two or three times greater than the modal gain. This difference, if maintained through long periods, would result in a continuously increasing advantage of certain individuals of older (taller) age categories over younger ones through the positioning of their crowns higher along the light gradient. The ever-changing nature of the forest canopies accounts for the great spatial dynamism that individuals experience many times during their life times.

Variability in reproduction in *A. mexicanum* arises from two sources: (1) the probability that a mature palm will reproduce; and (2) the number of fruits produced. Both vary amply with the age of the mature palms (Figure 7), with a clear tendency to increase as plants become older (or taller).

However, within each age category of mature plants (with an age interval equivalent to only 6-16% of the age class) there are markedly

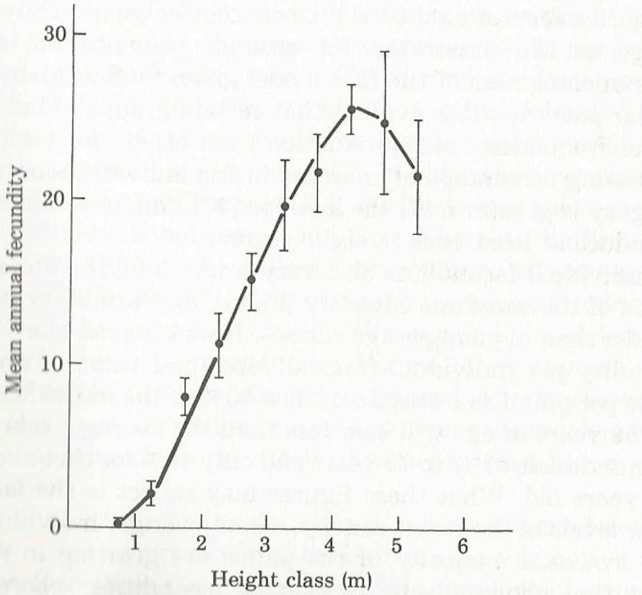

FIGURE 7. The pattern of yearly fecundity in *Astrocaryum mexicanum*. Data are means ± SE for height classes of 50 cm, based on seven years of observations. Curve was eye-fitted.

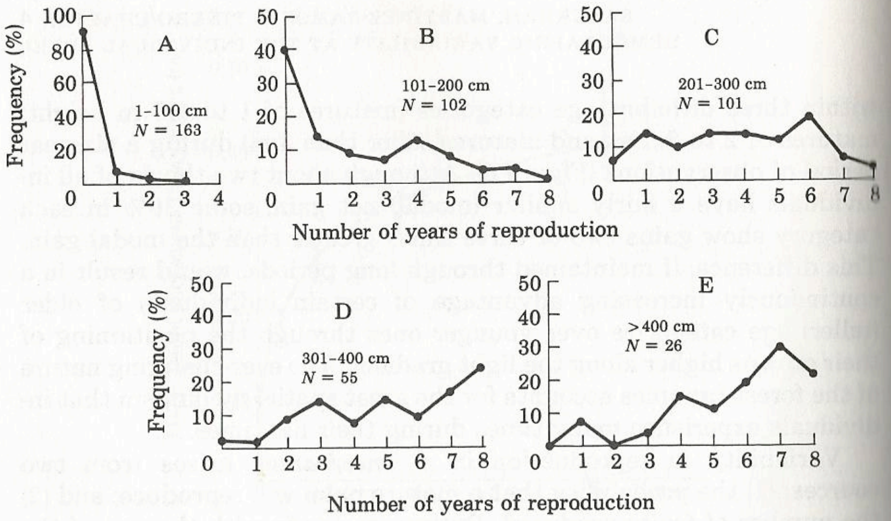

FIGURE 8. Relative frequencies of the number of reproductive years in five height classes (A–E) of *Astrocaryum mexicanum.*

different individual behaviors. Figure 8 shows the frequencies of number of years of reproduction for all individuals in different age categories for a period of eight consecutive years. Only five broader categories are illustrated for ease of presentation, although the original categories of the flux model given by Sarukhán (1978) follow similar patterns. It is evident that certain groups of individuals show higher frequencies of reproduction than others for each age class. A decreasing percentage of nonreproducing individuals occurs as the age category is greater until the last one (401 cm), in which all individuals reproduce at least once in eight years.

Individual fecundities also vary from 10-fold to almost 25-fold for palms of the same age category (Figure 9). Variability is much higher in older than in younger age classes. If we consider the overall average (31 fecundity per individual from all sites and years of observation (31 fruits per palm) as a standard, then 83% of the individuals between 50 and 59 years of age will bear less than the average; this figure is 59% for individuals of 67 to 75 years and only 43% for those between 99 and 106 years old. What these figures may reflect is the fact that at the lower levels of the forest canopy, where younger individuals have their leaf crowns, a majority of the palms are growing in environmental spots that allow only below-average fecundities, whereas more than one-half of the individuals between 99 and 106 years of age experience environments allowing above-average fecundities.

The rate at which an individual palm grows seems to affect in a dif-

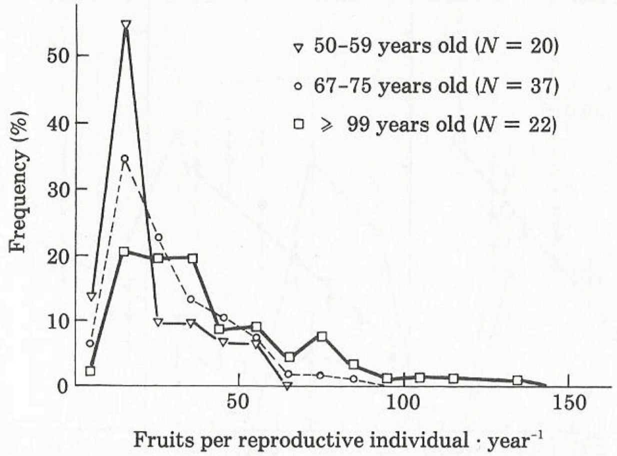

FIGURE 9. Relative frequencies of the annual production of fruits by reproductive individuals in three age classes of *Astrocaryum mexicanum.*

ferential way its fecundity. Figure 10 shows the correlation between the individual height and the number of infrutescences produced in seven years for three groups of palms: slow growers (3–20 cm height increase in six years), moderate growers (21–40 cm), and fast growers (more than 40 cm). In addition, recall that taller (older) palms reproduce more actively than shorter (younger) palms and that number of fruits per palm is more variable in older than younger individuals. The significant differences ($P < 0.05$) between these groups occur only for individuals between 1 and 2 m in height (the first two height categories in Figure 10). At least for younger, suppressed individuals, there may be a trade-off in vegetative versus reproductive investment. When the annual leaf production per individual is compared to their probability of reproducing (Figure 11), it appears that years of high leaf production are followed, in general, by years in which a relative decrease in reproduction occurred, whereas years when high probabilities of reproduction were attained were preceded by years of low leaf production.

A measure of plant vigor (or age, if age is closely correlated to vigor) is clearly a better predictor of an individual's vegetative and reproductive performance. Obviously, with this measure of vigor, a specific relation of the individual with its physical and biotic environment is normally implicated.

In an inductive way, the vegetative, and especially the reproduc-

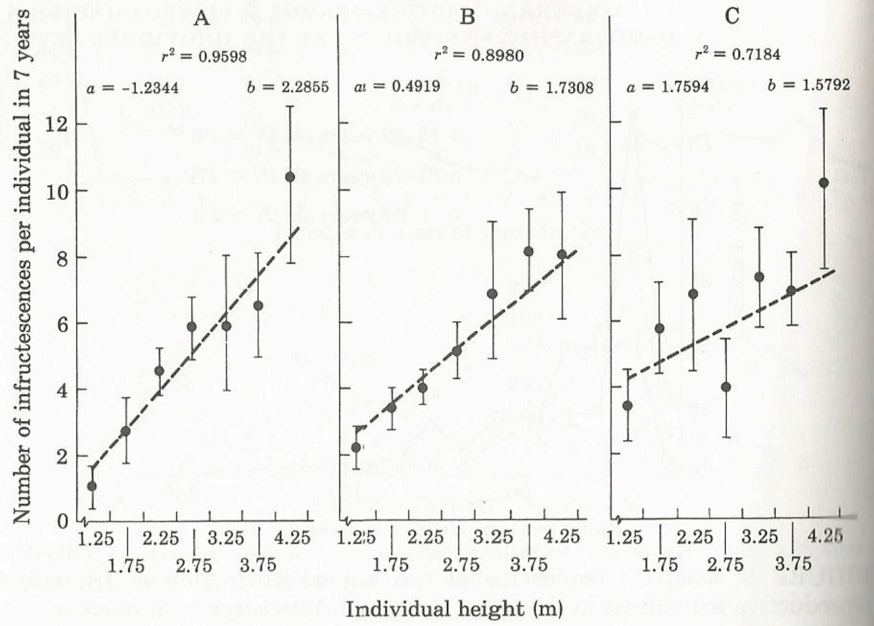

FIGURE 10. The relationship between height and number of infructescences produced per individual in seven years in *Astrocaryum mexicanum*. A. Individuals with low growth rate (<20 cm of net height gain in six years). B. Medium-growth-rate individuals (21 to 40 cm). C. High-growth-rate individuals (>40 cm). Data are means ± SE for eight classes of 50 cm each. The parameters of linear regressions are given as intercept (*a*) and slope (*b*).

tive behavior, may suggest aspects of the structure of the environment that may be relevant in determining such behaviors. The repetitivity with which an individual reproduces from one year to the next may be a good correlate of favorable environmental conditions. An analysis of reproductive frequencies for individuals of *A. mexicanum* of different size classes or ages and of different community stages suggests some of the ways in which favorable environments are distributed both within different community stages (Figure 12A) and in a vertical gradient for plants of different age (or size) (Figure 12B). The distribution of individuals among the different reproductive frequencies in the stable site is uniform (χ^2 = 7.3, P > 0.2) while in the nine-year-old forest gap there is a J-shaped distribution of frequencies, with the most repetitively reproducing trees being more abundant. Analyzing how reproductive palms of different ages (heights) perceive the environment, it becomes clear (Figure 12B) that younger individuals, placed lower down in the vertical gradient, show a distribution of frequencies skewed toward the low extreme, whereas the taller palms

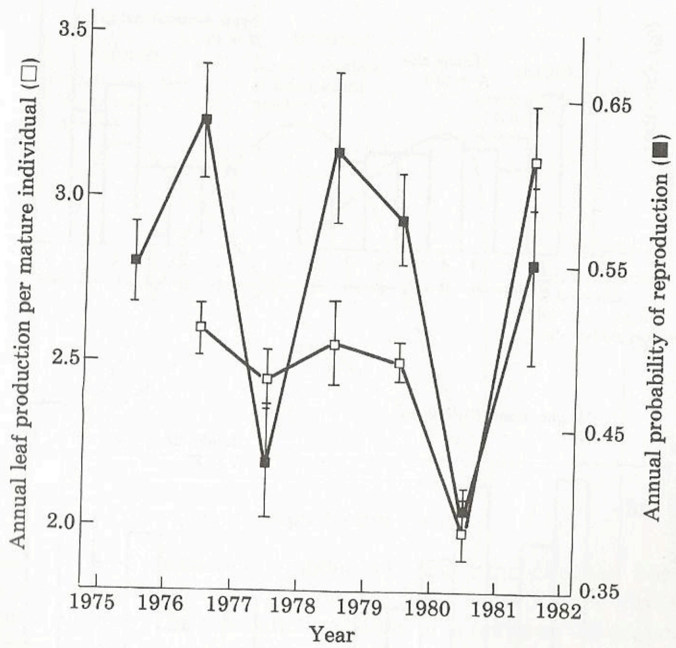

FIGURE 11. The temporal pattern of annual production of leaves and the annual probability of reproduction in mature plants of *Astrocaryum mexicanum*. Data are means ± SE.

show also a J-shaped distribution of frequencies, similar to that of the young-gap situation (Piñero and Sarukhán, 1982).

The former real distributions of the frequency with which reproductive individuals of *A. mexicanum* bear fruit suggest different model situations like those depicted in Figure 13. If environmental patches intermediate from the viewpoint of reproduction were more frequent, a normal distribution of reproductive frequency would be expected. This is not the case either for all individuals in stable or gap sites or for palms of different sizes and hence positions in the vertical gradient of the forest. A lower or higher proportion of favorable patches is therefore likely to be occurring. A high frequency of favorable patches would generate reproductive frequency distributions like that of Model 3, which would correspond to that observed for the taller palms. If the favorable patches are infrequent, a skewed distribution like that of Model 1 would be expected, with the distribution corresponding to that of the younger group of reproductive individuals (1–2 m tall).

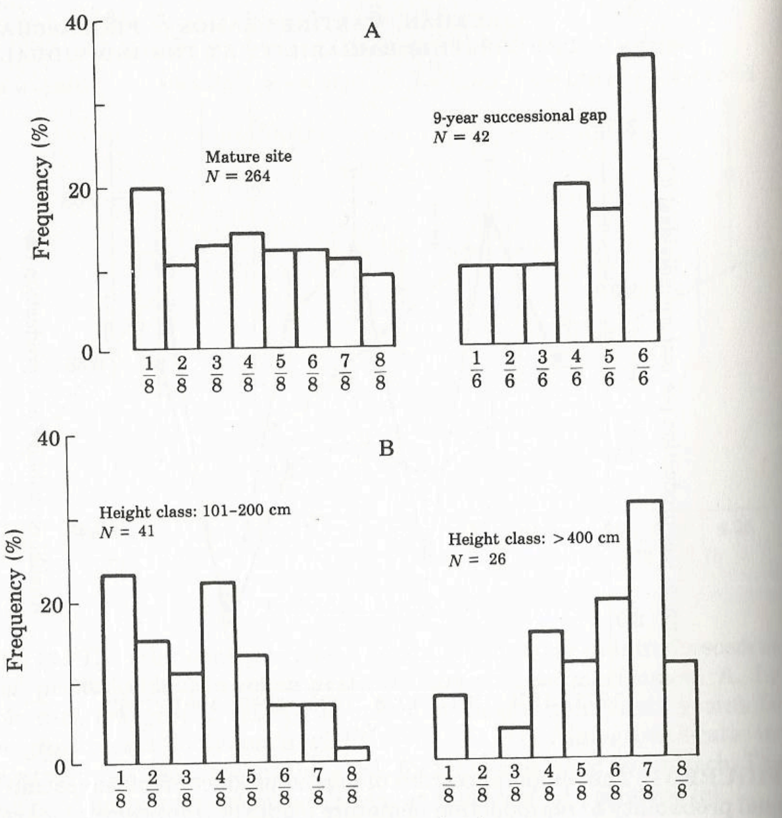

FIGURE 12. The relative frequencies of the number of years of reproduction of individuals of *Astrocaryum mexicanum* growing in (A) mature sites and a forest-gap, and in (B) two different height levels of the mature sites.

Finally, if the proportion of favorable, intermediate, and unfavorable patches is the same, then a distribution like that of Model 4 would be attained. This distribution occurs for all reproductive palms in the mature sites (Figure 12A), but it results from the combination of Models 1 and 3 for younger and older palms, respectively. It is difficult to think of one or a combination of several environmental factors that would have such even spatial distribution in a highly complex community like the tropical rain forest.

Of those physical environmental factors more likely to affect probabilities of reproduction of *A. mexicanum* from one year to the next, soil and light appear the most plausible. Because most soil characteristics, including nutrient levels, are not likely to change drastically from one year to the next, but particularly because of the

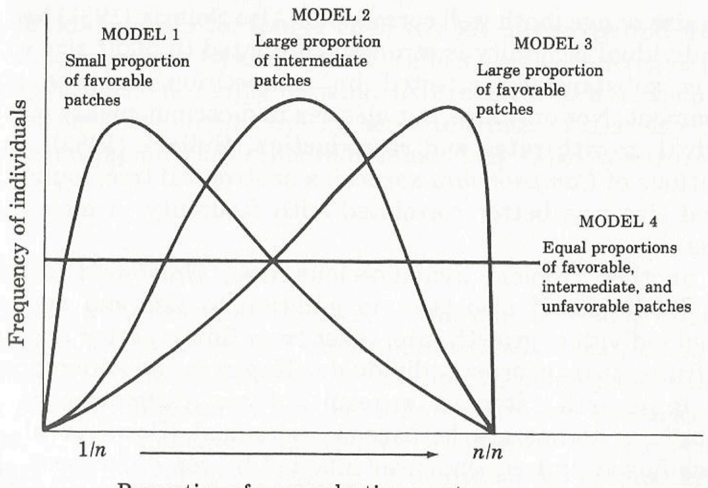

FIGURE 13. A hypothetical model of the reproductive behavior of *Astrocaryum mexicanum* in relation to the proportion of favorable environmental patches. The reproductive behavior is taken as the proportion of *n* reproductive events for a given plant. The assumptions of this model are that (1) the reproductive individuals are regularly distributed in the area, (2) the age structure of reproductive palms is uniform, and (3) the probability of reproduction is almost constant for the ages considered. For *Astrocaryum mexicanum* we have evidence to support all these assumptions.

different fruiting frequencies of young versus old palms within one piece of forest, light appears as a more likely factor influencing the probabilities of a palm reproducing in a given year. It also would adjust better to the assumptions of patchiness made for the models in Figure 13. Forest gaps with large openings would represent those large, aggregated patches of "favorable" environment for reproduction. This would be similar for those older palms which place their crowns in a higher place in the light-exhaustion gradient within the forest. (Imagine light as a stream of resource being sifted successively—in quantity and quality—by intervening tree canopies as it penetrates the forest from the top, until a few, separated trickles reach the forest floor.)

Individual variability in growth and reproduction in a demographic context has also been studied by Kohyama (1981) in *Abies veichtii*, Solbrig (1981) in *Viola* spp.; Bullock (1982) in *Compsoneura sprucei* and other neotropical trees, and Peters (1983) in *Brosimum alicastrum*.

Studying *Abies* forests, Kohyama (1981) found considerable individual variability in age at first reproduction and in reproductive patterns. His data show that age at first reproduction may be related to tree size or age (both well correlated). Also Solbrig (1981) has shown that individual fecundity is strongly correlated to plant size which, in turn, is substantially affected by competition and the physical environment. Not only size, but also sex in dioecious plants may affect individual growth rates and reproduction. Bullock (1982), studying populations of *Compsoneura sprucei*, a neotropical tree, found that individual size was better correlated with fecundity in males than in females.

In another tropical gynodioecious tree, *Brosimum alicastrum*, Peters (1983) found also that, in addition to size and age, sex influenced individual growth rate; taller trees flower earlier and produce more fruits than shorter individuals. However, no differences were found in growth rates as a result of sex differences in *Aralia nudicaulis*, a temperate herbaceous perennial (Bawa et al., 1982), whereas flowering frequency was affected by sex differences.

Lloyd and Webb (1977) proposed that these sex-induced differences reflect a cost which is associated with reproduction, so that a high energetic investment by females leads to a higher mortality risk and/or to a lower growth rate relative to males. Following these lines of reasoning, Bawa et al. (1982) think that the cost in reproduction may also be reflected in a more prolific flowering by males.

In studies of the population biology and population genetics of plants, it has been customary to try and establish the extent of the genetic determination of components of fitness, particularly those related to reproductive behavior (e.g., Primack and Antonovics, 1982). The converse (i.e., the effects of reproductive behavior on the genetic structure of the population) has been a lesser used approach. Bullock (1982) found for four dioecious tropical arboreal species a high dominance of the reproductive output for very few individuals, that is, only one tree accounted for more than 20% of all flowers produced. Because of the length of the study, it was not known for how long reproductively dominant trees would remain so. Analyzing data for *A. mexicanum*, we found that the same 58 individuals account for over 43% of the ca. 33,000 fruits produced during seven years of observation; the remaining 56% of the fruits were contributed by constantly different mixtures of some 130 other individuals every year. We have no data at the moment to establish any genetic basis for the continued reproductive behavior of these individuals. Also, we have reported elsewhere (Piñero and Sarukhán, 1982) that overreproductive palms are associated with overreproductive neighbors, that is, there seems to be a spatial factor that would clump highly reproductive individuals together. But it is clear that if such "reproductive dominance" by the

same individuals lasts for longer than the seven-year period we have observed, there might be an important effect on the genetic structure of the population. The highly dynamic nature of the forest canopy suggests that such dominance by the same few individuals may not be very long-lasting and that other individuals may take over as frequent reproducers.

GENERAL DISCUSSION

It is evident in the literature reviewed in this chapter and in other contributions to this book (e.g., Venable, Bradshaw, Schaal, Levin) that the ability to attribute individual variation in plant populations to genetic or environmental factors is still very limited. The discernible patterns, if any, indicate a greater environmental than genetic influence on the individual variability of demographic parameters. We believe that this difficulty arises partly from the highly dynamic nature of the environment (both physical and biotic) acting on a population on a life-time span, and partly from the dynamic response of plants (plasticity), which themselves are changing in size (height, crown size, root volume, etc.) and therefore modifying their response to that part of the environmental spectrum that they face at any given moment of their lives (see Jefferies, Chapter 17). The poorly known interrelationships between vegetative growth and reproduction and their demographic consequences in naturally occurring populations add to the difficulties of defining the genetic determination of individual variance.

The "genetic dominance" by a few individuals found in several plant populations provides an interesting way to explore the genetic determination of individual traits relevant to survival and reproduction, although here, too, environmental factors may obscure the situation by means of individual plasticity and the dynamic nature of such factors.

More rigorous studies of what constitutes the relevant environment for individuals of a population are needed to understand several key factors underlying individual variation in growth and reproduction. This is particularly complicated when a single arboreal individual in a forest may "sample" in its lifetime, not only differences in competitive interactions with its neighbors and the temporal fluctuations of the physical environment, but also different parts of it with the passage from seed to seedling, sapling, treelet, etc. Very probably not all "environmental stages" are equally relevant demographically speaking, but certainly it is necessary to determine how each of them shapes the final contribution of the individual to the dynamics of its population.

Much of the plant physiological literature available is concerned with phenomena observed either at the suborganismic level or in conditions with little direct relevance to that of a plant amidst its neighbors in the field. The exciting developments of new field methodologies enabled by the technological revolution in electronics makes it realistic, for the first time, to call for observational and experimental work with whole plants (see Mooney and Chiariello, Chapter 15) living under natural field conditions.

The real influence of the environment surrounding an individual will only be adequately understood when the demographic consequences of different physiological traits on survival, growth, and reproduction are known. This could only be done on a whole-plant level, under natural field conditions, and within a populational context.

On the other hand, a plethora of population genetics studies has mostly been concerned with the genetic characterization of populations. However, the very demographic expression of such changes in fitness (i.e., survival, growth, and reproductive rates) are seldom incorporated in those studies.

The study of an individual's variability in time and relative to that of its neighbors appears, to our view, as the source for understanding population-level dynamics. It is our contention that the studies of individual variability in demographic parameters within a demographic context provides not only a very sound basis for understanding patterns of population behavior, but also is the crossroads where plant population genetics, plant physiology, and plant demography may interact in the most fertile way.

CHAPTER 5

LOCAL-SCALE DIFFERENTIATION AS A RESULT OF COMPETITIVE INTERACTIONS

Roy Turkington and Lonnie W. Aarssen

INTRODUCTION

Population ecology is to a large extent a study of natural selection. Genetic variation within a population necessarily dictates that some individuals will leave more descendants than others. Consequently, all levels of biological organization are affected, and the relative frequencies of their components are in a state of continuous flux. Experimental ecology investigates the resultant patterns and the mechanisms and processes by which these patterns are generated. The scope of this chapter is defined by its title: the pattern we seek to describe is local-scale population differentiation and one of the mechanisms by which it is generated—competition. Topics of related interest are treated elsewhere in this volume (see Antonovics, Bradshaw, Jain), and also by Hamrick (1982).

The description of intraspecific adaptive differentiation in plants is not new, and various aspects of the literature have been reviewed by McMillan (1960), Bennett (1964), Heslop-Harrison (1964), Langlet (1971), and Hamrick (1982). Langlet (1971) cites 111 references to