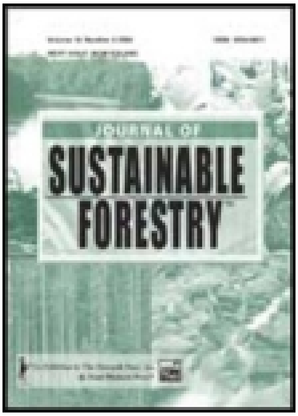

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Tree Life History Patterns and Forest Dynamics

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TREE LIFE HISTORY

Tree Life History Patterns and Forest Dynamics: A Conceptual Model for the Study of Plant Demography in Patchy Environments

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The demographic information presented in this paper was compiled over many years of study at Los Tuxtlas following the leading work on tropical plant population ecology carried out by José Sarukhán. Much of the later work was done in conjunction with Daniel Piñero, Elena Alvarez-Buylla, Rodolfo Dirzo and a large number of students, among them, we specially thank George Dyer, Araceli Enriquez, Tere Hernández and Jorge Rodríguez. Many of the ideas presented were discussed with David Ackerly, Elena Alvarez-Buylla, Peter Ashton, Fahkri Bazzaz, Bill Bossert, Gary Carlton, Peter Feinsinger, Ned Fetcher, Francis Putz, Otto Solbrig, Virgilio Viana, and Peter Wayne. Comments of three anonymous reviewers improved the manuscript. Funding was provided by a grant from the Consejo Nacional de Ciencia y Tecnologia (Mexico) and a Bullard Fellowship from Harvard University to Miguel Martínez-Ramos.

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ABSTRACT. Forest trees are usually classified into broad ecological groups (e.g., pioneers vs. mature-phase species) based on the importance of natural disturbance for their regeneration. These classifications only tie into account a small component of the plant's life-cycle, usually seeds and seedlings, and therefore may over-simplify the role of natural disturbance in the evolution of life-history traits. We present a conceptual model for the study of plant demography within heterogeneous environments, and illustrate its use by reviewing how natural disturbance influences the demography of several lowland tropical tree species at Los Tuxtlas, Mexico. Our model assumes that habitat patches such as treefall gaps in tropical forests can affect a plant at all stages of its life-cycle, and reveals many potential life history patterns in relation to forest dynamics. We propose that only detailed demographic studies of whole life histories and genetics of tree populations, as well as forest disturbance regimes, will allow us to elucidate convergent life histories and the existence of discrete ecological groups among tropical forest trees. *[Article copies available for a fee from The Haworth Document Delivery Service: 1-800-342-9678. E-mail address: getinfo@haworth.com]*

INTRODUCTION

Tropical rain forest trees exhibit a great deal of inter-specific variation in fruit, seed and leaf morphology (e.g., Longman and Jenik 1982, Janson 1983, Givnish 1984, Foster and Janson 1985, Foster 1986), architecture (e.g., Hallé et al. 1978, Tomlinson 1987, King 1990), phenology (e.g., Frankie et al. 1974, Opler et al. 1980, Yap and Chan 1990), seed dispersal (e.g., Janson 1983, Augspurger 1986), germination behavior (e.g., Vázquez-Yanes and Orozco-Segovia 1984, Garwood 1983), leaf secondary chemistry (e.g., Coley 1983, Coley et al. 1985, Coley and Aide 1991), photosynthetic rates (e.g., Bazzaz 1984, 1991), and water regulation capacity (e.g., Becker and Castillo 1990). Differences in these characteristics may be the result of evolutionary responses to heterogeneity in the plants' abiotic and biotic environment. This heterogeneity, in turn, can affect different components of a plant's life-cycle, such as establishment, survival, growth and fecundity. We can therefore expect to find inter-specific differences in the structure and dynamics of plant populations in response to environmental heterogeneity.

In tropical forests, a major source of environmental heterogeneity is the patch dynamics promoted by limb and treefall disturbances that create gaps in the forest canopy (Denslow 1987). Gaps and subsequent regeneration create a resource patchwork (e.g., of light environments) in the understory (e.g., Chazdon and Fetcher 1984) and phylogenetically unrelated species exhibit similar life histories in response to this resource heterogeneity. For example, species in the genus *Cecropia* (Moraceae) in the neotropics and most species in the genus *Macaranga* (Euphorbiaceae) in Asia produce large crops of seeds that are widely dispersed through the forest. Both taxa have rapid growth rates, an early age of first reproduction, and short life-spans (Whitmore 1982). These traits allow *Cecropia* and many *Macaranga* species to establish and complete their life-cycles in large but relatively ephemeral patches where the forest canopy has been disrupted. In contrast, long-lived species belonging to distantly related families such as Dipterocarpaceae, Lauraceae, and Myristicaceae generally have small crops of large seeds, slower growth rates, a later age of first reproduction, and the ability to regenerate successfully beneath the closed forest canopy.

These two extreme life histories correspond to the pioneer and climax species groups commonly described by ecologists and foresters, based on correlations between seed germination and light conditions (e.g., Swaine and Whitmore 1988, Whitmore 1989). Such a classification, however, ignores other stages of the tree's life-cycle and over-simplifies the impact of spatial and temporal environmental heterogeneity on the demography of tropical forest trees. Since trees are sessile, they complete their life-cycle in a single location following dispersal; differential survival, growth, and reproduction may occur as individual trees grow through successive life-cycle stages, encountering the environmental heterogeneity found along the forest profile. Demographic variability may also arise as a result of the drastic environmental changes that individuals may experience at any point in their life-cycle as neighboring tree falls create gaps in the forest canopy (Martínez-Ramos et al. 1988 1989). Therefore, to understand population. dynamics and life history strategies in forest trees we need to employ a single conceptual framework that incorporates both demography and forest patch dynamics. Although an increasing number of studies describe the disturbance regime of tropical forests (see review in Clark 1990), there is a conspicuous lack of information on demography of tropical trees. Furthermore, most studies focus either on transitions for a single life stage in two or more habitats (e.g., Sork 1985, Dirzo 1987, Howe et al. 1985, Howe 1990a,b) or present average life tables and reproductive schedules that do not permit the analysis of the demographic intra-population variability associated with the forest regeneration mosaic (Bullock 1980, Hartshorn 1975, Oyama 1990, Palomeque 1988, Peters 1991).

In this paper we present a demographic model that helps to describe plant life-histories within patchy environments. The model illustrates the many tree life-history patterns that can emerge even when just four life-cycle stages (seed, juvenile, pre-mature and mature stages) and two forest patch types ("young" and "mature" forest sites) are considered. With the appropriate data, the model can be used to simulate population dynamics and to carry out sensitivity analyses on population responses to changes in both demographic rates and forest patch dynamics (see also Horvitz and Schemske 1986, Martínez-Ramos et al. 1988, Alvarez-Buylla and García-Barrios 1991, Alvarez-Buylla 1994). Using demographic information gathered for several species at the Los Tuxtlas rain forest, Mexico, we demonstrate the use of the model, discuss some evolutionary and ecological issues regarding tree life histories and forest gap dynamics, and propose how this model can be used to explore the existence of species guilds in tropical rain forest tree communities.

TROPICAL FORESTS AS PATCHY ENVIRONMENTS

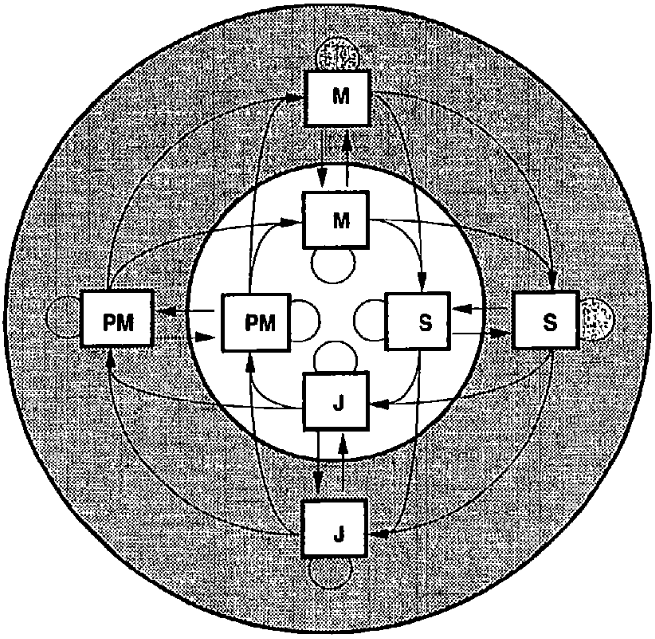
Tropical forests are shifting mosaics of patches at different successional stages (e.g., Hubbell and Foster 1986, Brokaw and Scheiner 1989). The forest canopy is commonly disrupted by branches snapping or trees falling (e.g., Brokaw 1985a, Martínez-Ramos et al. 1988, Clark 1990). The resulting understory patches receive more light (e.g., Chazdon and Fetcher 1984, Canham et al. 1990, Lawton 1990) and light reaching the forest floor is enriched at the red end of the electromagnetic spectrum (e.g., Endler 1991). Where the canopy has been disrupted, patches may also have more soil water available (Becker et al. 1988), and soils may have more nutrients compared to those of the surrounding understory (Vitousek and Denslow 1986, Uhl et al. 1988). The extent to which the microclimate under a canopy gap differs from the surrounding forest understory depends on the magnitude of the disturbance (Chazdon and Fetcher 1984, Barton et al. 1989) and the origin of the gap (Putz et al. 1983). Canopy gaps can range from small openings that enable direct sunlight to reach the understory only at certain times of day, to large scale clearings caused by multiple treefalls and landslides. Trees that die standing or are snapped off create patches that receive increased light levels, but there is no soil disturbance; uprooted trees create large canopy gaps and mineral soil is exposed near the root of the tree. Following disturbance canopy gaps are closed by lateral crown expansion of neighboring trees, sprouting, growth of seedlings and saplings present when the gap was formed, and newly established seedlings (Bazzaz, 1984).

Gaps of different sizes, origins and ages will differ in the microclimates associated with them, which will in turn affect physical conditions, resource availability and the nature and strength of biotic interactions that affect plants at different life-cycle stages. The number of seedlings present in a given patch is determined by the number of propagules arriving at the site, the number of dormant seeds in the soil, the probabilities of germination and the survival of seeds and seedlings (Schupp et al. 1989). There is evidence that some wind and mammal dispersed seeds tend to be deposited at higher densities in recently created gaps than in the forest understory (Augspurger and Franson 1988, Brokaw 1986, Denslow and Gómez-Díaz 1990). Seed predation also seems to be different among different patches in the forest: some studies indicate that predation of large seeds may be higher within gaps (Schupp 1988a, b, Schupp and Frost 1989), while others have found higher predation in the gap edges (Dirzo and Dominguez 1986) or in mature forest sites (Martínez-Ramos et al. 1988, Samper 1992). Seedlings grow larger in gaps in response to increased light resource levels (e.g., Denslow et al. 1990, Popma and Bongers 1988), although survival will be limited by competition with other seedlings (e.g., Brokaw 1985b), attack from pathogens (Augspurger 1984, Augspurger and Kelly 1984), and mechanical damage from falling litter and branches (Aide 1987, Clark and Clark 1989,1991). Less is known about differences in the distribution of animal pollinators, herbivores and dispersers over the mosaic of habitats in a forest, although we might expect to find less patch specificity in these animals than in plants due to their mobility. The activity of herbivorous insects may be related to patch types (Braker 1991), although these patterns are not as clear for larger and more mobile vertebrate pollinators such as hummingbirds (Feinsinger et al. 1988).

THE MODEL

Considering the heterogeneous and changing environmental scenario within which life-cycles of forest trees take place, a better understanding of population dynamics and life history strategies of forest tree species requires a conceptual tool that explicitly relates tree demography and forest patch dynamics in a unified framework. Figure 1 illustrates a conceptual model that can be used to understand plant demography within patchy environments. The model encompasses all major stages in a tree's life-cycle and includes the dynamic distribution of disturbed canopy patches in space and time. For simplicity, we have divided the life-cycle into seed, juvenile, premature, and mature (reproductive) stages, and assume that populations grow in a forest mosaic composed by two environ-

FIGURE 1. Schematic representation of forest tree demography in a patchy environment. A plant may complete its life-cycle in any one of two environments, in this case young (inner circle) and/or mature (stippled circle) patches. The life-cycle if divided into four stages for simplicity: seed (S), juvenile (J), pre-mature (PM) and mature (M). On a unit time basis, arrows and loops represent transition probabilities between life-cycle stages and/or forest patches. Those arrows connecting the M and S stages indicate the *per capita* contribution of mature trees to seeds falling in the same patch type (arrows within the same circle) or in other patch type (arrows crossing circles). Arrows between life-cycle stages within the same circle indicate transition probabilities between stages for those individuals remaining in the same forest patch. Arrows between life-cycle stages and crossing circles indicate transition probabilities between stages and patches. Arrows between the same life-cycle and crossing circles indicate probabilities to change from one forest patch to other for those individuals remaining in the same life-cycle stage. Loops indicate probabilities of remaining in the same life-cycle stage and patch type. See text for further details.



mental patch types ("young" and "mature"). Mature patches are defined as those sites with closed canopies while young patches are those forest sites which have suffered recent treefall disturbances. We define patch type from the population's perspective. Thus, the time that individuals remain in young patches depends on the rate to which survival, growth and/or reproduction values return to those observed in mature patches.

Arrows in the model indicate demographic transitions between life stages and/or patches and they show the multiple pathways that a single individual tree can follow during its life-cycle (Figure 1). Evaluation of the hypothetical life-history patterns requires the study of relationships between forest patch dynamics and demographic traits of populations, including seed dispersal, germination, age (size) at first reproduction, longevity, survivorship, growth and fecundity rates. Some of the factors that are likely to play an important role in the evolution of life-history traits for tropical forest trees include: (i) the total area covered by each patch, which affects the proportion of the population affected by a patch; (ii) the rate at which patches are created (e.g., the number of gaps opening per unit area, per unit time) and the rate at which they change to the other patch type; (iii) the probability that a given patch size will affect individuals in one or more life-cycle stages; (iv) the rates of survival, growth and reproduction for plants within each patch; (v) the rates of change in demographic parameters as one patch type changes into another patch; and (vi) the amount of genetic variability in life-history traits that is available for selection to operate on.

Studies in plant demography often rely on the use of matrix models to project population changes over time. These models display the transition probabilities between different ages or sizes as a matrix, which is multiplied by a vector representing the age or stage structure of the population. This product is the population structure in the subsequent generation (e.g., Lefkovitch 1965, Hartshorn 1975, Solbrig et al. 1988, Caswell 1989). To study populations in heterogeneous environments we must obtain estimates of transition probabilities for each patch type, as well as the transitions between habitats in any stage. Plants are able to move between patch types as seeds, but at other times of their life-cycle are fixed at one location and depend on environmental changes such as the opening of a gap overhead. The population stage structure, usually represented as a vector in demographic studies, would then correspond to the number of seeds, juveniles, premature and mature individuals in each patch type.

To analyze population dynamics, our graphic model may be transformed into a matrix model that combines a stage-based Lefkovitch population model with a Markov model of forest dynamics (Figure 2). The demographic parameters in the model include population structure (the number of plants in each stage and patch type at a given time) and the following probabilities: (i) transition probabilities between stages within the same patch ($T_{ij}W$); (ii) transition probabilities between stages and patches ($T_{ij}B$); (iii) probability of remaining in the same stage within the same patch ($R_{ii}W$); and (iv) probability of remaining in the same stage for individuals experiencing a change in patch type ($R_{ii}B$). All transition probabilities (T_{ij}) are obtained by multiplying the proportion of the individuals in stage i that move to stage j and the survivorship probability (S_i) of individuals in stage i. The probability of remaining within a patch or a stage (R_{ii}) can be calculated as $S_i - T_{ij}$. To obtain population estimates for the whole forest, Ts and Rs must be multiplied by the proportion of forest area in each patch type (W) and by the proportion of forest area that changes from one type to the other (B). The transition between mature and seed stages is expressed as fecundity rates (F = number of seeds produced per individual per unit time). The number of seeds falling in young patches results from the product F_y times W_y plus the seeds dispersed from mature patches [$F_m(pt_{y,m})$]; in the same way, the number of seeds falling in mature patches results from the product F_m times W_m plus the seeds dispersed from young patches [$F_m(pt_{m,y})$] (Figure 2). To estimate pt, we must know the fraction of dispersed seeds (produced by mature individuals found in each patch type) landing in the same or in the other patch type.

The use of a matrix model provides the information necessary to obtain estimates for: (i) population growth rate (usually expressed as $\lambda = e^r$, the finite population rate of increase), and (ii) the sensitivity of λ to small changes in the matrix parameters (Caswell 1989). In our model, each element of the matrix results from the product of demographic and forest dynamic parameters; then, sensitivity of λ depends on changes in one or both of these parameter types. We used elasticity values (de Kroon et al. 1986), a relative sensitivity index, to assess the proportional change in λ that may result from a proportional change in a given matrix parameter value; parameter values with the highest elasticity will be the ones with a greater contribution to λ. Assuming that λ expresses the average population fitness (*sensu* Fisher 1958), elasticity values can be used to construct hypotheses about life-history evolution (e.g., Groenendael 1985, Silvertown et al. 1993). Under this assumption, the intensity of selection on traits affecting demographic rates may be directly expressed by the elasticity values (Caswell 1989).

We illustrate our model by reviewing research on the population ecology of several tree species found in the lowland tropical forest of Los Tuxtlas, Mexico. This forest represents the northernmost rain forest in the

FIGURE 2. *General matrix population model for a tree population growing in two forest patch types. The model includes four* sub-matrixes that correspond to the demographic transitions occurring in: (i) mature patches; (ii) young patches; (iii) the transition from mature to young patches; and (iv) the transition from young to mature patches. The life-cycle stages are the same as defined in Figure 1. Elements of the matrix define: the fecundity values, the *per capita* contribution of mature trees to seeds in mature (F_m) or in young patches (F_y), the proportion of seeds dispersed from mature to young patches ($pt_{y,m}$) and vice versa ($pt_{m,y}$), the probabilities of remaining in the same life-cycle stage (R), and the probabilities of transition (T) to the following stage. Sub-matrices are connected by a Markovian chain defined by the probability that individuals remain in mature patches (W_m), the probability that individuals transit from mature to young patches ($B_{y,m}$), the probability that individuals remain in young patches (W_y), and the probability that individuals transit from young to mature patches ($B_{m,y}$). All transition probabilities are expressed as rates (ind ind^{-1} unit time^{-1}). See text for further details.

$$
\begin{array}{ll|cccc|cccc|}
 & & \multicolumn{4}{c}{\textbf{Young patches } (t=0)} & \multicolumn{4}{c}{\textbf{Mature patches } (t=0)} \\
 & & S & J & PM & M & S & J & PM & M \\
\hline
\textbf{Young patches } (t=1) & S & R_{S,S}(W_y) & & & F_y(W_y) + F_m(pt_{y,m}) & R_{S,S}(B_{y,m}) & & & F_m(B_{y,m}) + F_m(pt_{y,m}) \\
 & J & T_{J,S}(W_y) & R_{J,J}(W_y) & & & T_{J,S}(B_{y,m}) & R_{J,J}(B_{y,m}) & & \\
 & PM & & T_{PM,J}(W_y) & R_{PM,PM}(W_y) & & & T_{PM,J}(B_{y,m}) & R_{PM,PM}(B_{y,m}) & \\
 & M & & & T_{M,PM}(W_y) & R_{M,M}(W_y) & & & T_{M,PM}\,B_{ym} & R_{M,M}\,B_{ym} \\
\hdashline
\textbf{Mature patches } (t=1) & S & R_{S,S}(B_{m,y}) & & & F_y(B_{m,y}) + F_y(pt_{m,y}) & R_{S,S}(W_m) & & & F_m(W_m) + F_y(pt_{m,y}) \\
 & J & T_{J,S}(B_{m,y}) & R_{J,J}(B_{m,y}) & & & T_{J,S}(W_m) & R_{J,J}(W_m) & & \\
 & PM & & T_{PM,J}(B_{m,y}) & R_{PM,PM}(B_{m,y}) & & & T_{PM,J}(W_m) & R_{PM,PM}(W_m) & \\
 & M & & & T_{M,PM}(B_{m,y}) & R_{M,M}(B_{m,y}) & & & T_{M,PM}(W_m) & R_{M,M}(W_m) \\
\end{array}
$$

neotropics (Estrada et al. 1985, Dirzo and Miranda 1991). Forest dynamic data at Los Tuxtlas has been published elsewhere (Martínez-Ramos et al. 1988 and 1989). In the reviewing cases, we designated those forest sites which have suffered treefall disturbances ten or less years ago as young patches. Forest sites with disturbance ages older than ten years were designated as mature patches. We chose this classification because other studies have documented important demographic differences in tree populations between these two age patch categories (Martínez-Ramos et al. 1988 and 1989, Alvarez-Buylla 1994). Patch age determination was made according to Martínez-Ramos et al. (1988). We also discuss several of the mechanisms that interact to determine the observed transitions between life-cycle stages.

THE CASE OF CECROPIA OBTUSIFOLIA

One life-history pattern illustrated by the model is that of a plant species that completes most of its life-cycle in young forest patches. An example from Los Tuxtlas is *Cecropia obtusifolia* (Moraceae), a 35 m canopy tree which is commonly found in recently disturbed areas and has a life-history attuned to conditions in large young patches. This species has been the subject of intensive demographic study since 1982 within a 5-ha permanent plot (Alvarez-Buylla 1986,1994, Alvarez-Buylla and Martínez-Ramos 1990,1992, Alvarez-Buylla and García-Barrios 1991).

Figure 3a shows the life-history pattern proposed for *Cecropia obtusifolia* according to our model. Reproductive plants produce fleshy catkins that are consumed by a wide array of birds and mammals which disperse the seeds widely through the forest (Estrada et al. 1984, Alvarez-Buylla and Martínez-Ramos 1990). Fruit production is asynchronous among individuals, resulting in more-or-less continuous seed production at the population level (Alvarez-Buylla 1986). A single mature plant can produce an estimated annual crop of 10^5-10^7 small (1.5 mm long) seeds (Alvarez-Buylla and Martínez-Ramos 1992). Most seeds are dispersed to mature patches and only about 18% of dispersed seeds reach young sites (Figure 3a). In young and mature forest patches, more than 94% of seed cohorts die within a year, but newly dispersed seeds are continuously replenishing an abundant seed bank in all forest patches (Alvarez-Buylla and Martínez-Ramos 1990). Seeds are photoblastic and germination is triggered by the high red/far red light ratios found in recently opened large gaps (Vázquez-Yanez and Smith 1982). Therefore, only dispersed seeds landing in these sites may reach the juvenile stage (one year old plants 1 to

4 cm in stem diameter; Figure 3a). Alvarez-Buylla and García-Barrios (1991) found that 2-3% of total dispersed seeds land in recently created gaps (forest patches less than two years old since last disturbance), which represent about 15% of total seeds falling in young patches (Figure 3a). Seeds falling in mature patches may become juveniles if a large gap (> 100 m^2) opens overhead; this probability (7×10^{-4} ind ind^{-1} yr^{-1}), however, is two orders of magnitude smaller than the probability of seeds remaining dormant in mature sites (Figure 3a).

Seeds falling in gaps as small as 30 m^2 may have 100% germination when they are protected experimentally from mortality agents (M. Cano, M. Martínez-Ramos, and E. Alvarez-Buylla, unpublished data). In the soil, however, only 4% of the seeds in gaps escape insect predation or pathogen attack and germinate; an additional 2-3% of recently dispersed seeds landing in gaps remain dormant in the soil after one year (Alvarez-Buylla and Martínez-Ramos 1990). Seedlings do not survive in small gaps and juvenile establishment only takes place in gaps larger than 100 m^2 (Alvarez-Buylla and Martínez-Ramos 1992). Seedlings probably require higher light levels to maintain a positive carbon balance than those necessary to trigger germination (Popma and Bongers 1988, Strauss-Debenedetti and Bazzaz 1991). The transition from the seed to the juvenile stage is the most important thinning process operating in the *C. obtusifolia* population; only approximately 0.01% of viable soil seeds in large gaps reach the juvenile stage within a year (Figure 3a). Juvenile recruitment occurs only during the first two years after a gap opening (Alvarez-Buylla and Martínez-Ramos 1992). Therefore, we assumed that at the seed stage every year about 10% of viable seed population found in young patches return to the mature patch conditions (of which 97.3% die). Large gaps, however, are internally heterogeneous and hence not all the space available within a gap is suitable for establishment of *C. obtusifolia* juveniles. Thus, in large gaps, about 55% of juvenile trees die within the first year (Figure 3a) and only juveniles found in full sunlight grow fast (up to 3 m in height per year). As a result of the high mortality rates, less than 4% of juvenile population reaches the pre-mature stage (unbranched trees, two to four years old, and 4.1 to 10 cm dbh) within a year, although some juveniles (1.9%) grow fast enough to attain the mature stage in this period (Figure 3a).

Mortality rates are significantly lower for pre-mature plants (7.3% yr^{-1}) and individual growth rates are maximized (Alvarez-Buylla and Martínez-Ramos 1992). On average about 5% of the pre-mature population reaches the mature stage (> 10 cm dbh, branched trees and older than 5 years) in a year and some of them produce seeds (Figure 3a). Crown expansion coincides with the first reproduction and the demand for direct sunlight persists until individuals reach the mature stage. This is indicated by the fact that the crown of these plants is never beneath other adult trees and *Cecropia obtusifolia* individuals attain their maximum life expectancy (10 yrs) when they reach the upper forest canopy (Alvarez-Buylla and Martínez-Ramos 1992). Presumably, high resource allocation to reproduction and growth, coupled with low investments in maintenance and defense, reduces *C. obtusifolia* longevity and makes it susceptible to disease.

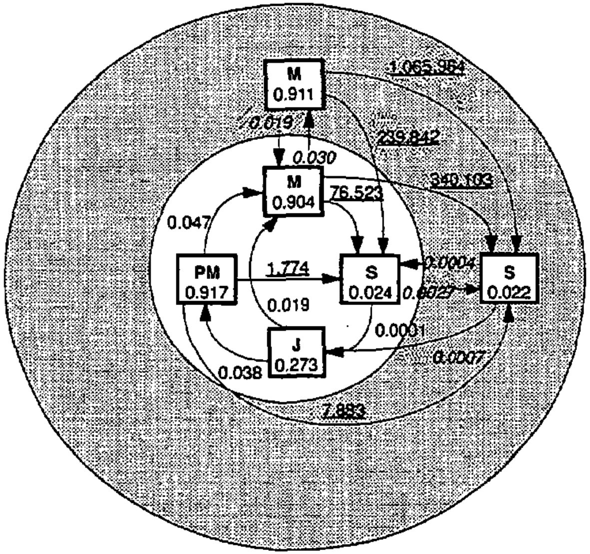
Reproductive trees die at a yearly rate of 4 to 7%, which is a high mortality rate when compared with that of other mature tropical trees (Lieberman et al. 1985a, 1990). Oldest individuals are 35-40 years old (Alvarez-Buylla and Martínez-Ramos 1992). Because reproduction began about three years old (Alvarez-Buylla and Martínez-Ramos 1992), mature populations are structured into the young and mature patches (Figure 3a).

If we assume that demographic and forest dynamic parameter values shown in Figure 3a remain the same through time, we obtain an estimate for λ of 1.684. This estimate suggests that a *C. obtusifolia* population doubles its size in less than 3 years, which is a very fast population rate of increase. Tree species with life-histories restricted to young patches, however, must have populations with structures and dynamics strongly dependent on forest dynamics (e.g., Hubbell and Foster, 1987). Since gap creation rate, and hence the availability of large gaps, changes from year to year (Martínez-Ramos et al. 1988) we can expect to find inter-annual changes in the life-cycle transition values and in the population growth rate of *C. obtusifolia*. We assessed how much these demographic changes could affect λ by performing a elasticity analysis following criteria given by de Kroon et al. (1989; Figure 3b). This analysis suggests that: (i) survival in the mature stage within young patches is the most critical demographic parameter affecting the population dynamics of *C. obtusifolia*; (ii) before maturing, growth rates are more critical than survival, particularly in the transitions from juvenile to mature stages (Figure 3b); (iii) those seeds found in mature patches that germinate and recruit into the juvenile population when a gap opens may have an important contribution to population growth; (iv) seed dispersal to mature patches is relatively more important to population growth than dispersal to gaps; and (v) changes in the forest gap opening rate (that affects the transition for dormant seeds from mature to young patches) may be more critical for λ than the rate of gap closure or the probability for mature patches remaining in the same forest stage.

In conclusion, the above results suggest that at Los Tuxtlas *C. obtusifolia* is a fast growing species whose population dynamic depends on life-history traits and environmental factors that affect the life-span in mature stages, and that favor wide seed dispersal, rapid seed germination, fast

FIGURE 3. Demography of *Cecropia obtusifolia* at Los Tuxtlas rainforest, Mexico. (a) Life-history pattern proposed for *Cecropia obtusifolia*: plain figures within boxes express annual probabilities of remaining in the same life-cycle stage for those individuals that do not experience a change in forest patch type; plain figures outside boxes express transition probabilities between life-cycle stages for those individuals that experience a forest patch change, and underlined figures indicate fecundity values. Data are based on Alvarez-Buylla and Martínez-Ramos (1990, 1992) and Alvarez-Buylla and García-Barrios (1991). (b) Elasticity values for parameters of the population matrix model based on the data of the life-history model. Elasticity expresses the proportional change in the population growth rate (λ) resulting from a proportional change in a given element of a population matrix model (de Kroon et al. 1986). See text for further details.

a)



b)

		Young Patch				Mature Patch			
		S	J	PM	M	S	J	PM	M
Young Patch	S	0.0009		0.0011	0.0262	0.0000			0.0322
	J	0.0595	0.0378			0.1354			
	PM		0.0267	0.0319					
	M		0.1685	0.0207	0.2196				0.0002
Mature Patch	S	0.0001		0.0049	0.1162	0.0018			0.0143
	J								
	PM								
	M				0.0467				0.055

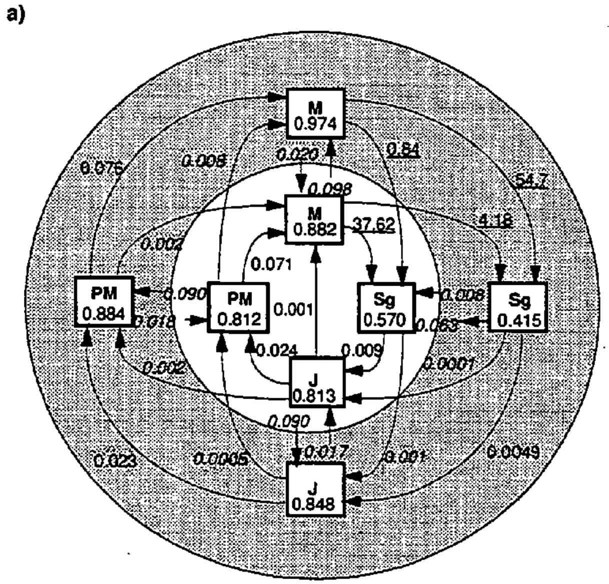
growth, and early reproduction. Given these traits, the population will increase as much as the availability of large gaps increases in the forest. Implicit in our model, however, is the assumption that population growth is density-independent and an assumption which may be unrealistic. *C. obtusifolia* at Los Tuxtlas shows a highly clumped spatial distribution, each clump representing cohorts that established in previously disturbed patches. The number of individuals is positively related to gap size and as the population matures within a gap the growth and fecundity rates of mature individuals decline (Alvarez-Buylla and Martínez-Ramos 1992). Recent studies show that this negative density-dependence effect plays an important regulatory role in the population dynamics of *C. obtusifolia* (Alvarez-Buylla 1994).

THE CASE OF OMPHALEA OLEIFERA

Some long-lived species have individuals of different life-cycle stages distributed through the forest. Depending on the biology of each species, however, one or more life-cycle stages may demographically vary between patch types. For example, some canopy trees grow to the mature stage favored by canopy gaps and will only reproduce when their crowns are exposed to direct sunlight. An example of this life-history pattern at Los Tuxtlas is *Omphalea oleifera* (Euphorbiaceae), a canopy tree that reaches a maximum height of 30 m and lives for more than 150 years. Populations of this species have been demographically studied by Palomeque (1988) during a two year period in a 2-ha permanent plot and by Martínez-Ramos and co-workers since 1982 in a 5-ha permanent plot (unpublished data). Additional information on seedling growth in young and mature patches has been obtained from Popma and Bongers (1988), Dirzo (1984) and Careaga (1989).

Figure 4a shows the life-history pattern proposed for *Omphalea oleifera*. Mature individuals (trees with dbh > 40 cm dbh) produce 50-120 large seeds (4 cm diameter; 5.1 grams dry weight) every year (Palomeque 1988). Because seed germination takes place in a period of two months or less, annual fecundity values are expressed in Figure 4 as the number of seedlings (individuals less than 50 cm in height) produced by a mature tree. On average, 70% of the seeds in the soil germinate successfully and reach the seedling stage (Figure 4a). Scattered fleshy fruits (containing three seeds each) that fall beneath the parent tree create triads of seedlings. The abundance of these triads suggests low seed predation rates. Seed dispersal is very poor, possibly due to the absence of large frugivorous at Los Tuxtlas (Dirzo and Miranda 1991). The result is that very few (if any)

FIGURE 4. Life-history pattern proposed from *Omphalea oleifera* at Los Tuxtlas rain forest, Mexico. Data from Palomeque (1988), Dirzo (1984), Careaga (1989) and M. Martínez-Ramos, E. Alvarez-Buylla and T. Hernández (unpl. data). Note that life-cycle begins with seedlings (Sg) instead of seeds. See Figure 3 and text for further details.



b)

		Young Patch				Mature Patch			
		Sg	J	PM	M	Sg	J	PM	M
Young Patch	Sg	0.012			0.009	0.001			0.001
	J	0.009	0.044			0.000	0.003		
	PM		0.008	0.039			0.000	0.003	
	M		0.001	0.006	0.104			0.000	0.011
Mature Patch	Sg	0.000			0.000	0.012			0.017
	J	0.001	0.004			0.016	0.091		
	PM		0.001	0.004			0.017	0.125	
	M			0.001	0.009			0.019	0.432

seeds are dispersed to young patches. Because some mature trees are found in young patches, however, seeds of these trees fall and germinate in young patches (Figure 4a). Furthermore, some seedlings found in the understory of mature patches may find themselves in young patches if the parental tree or a neighboring tree falls, although the probability of this event is very small (0.008; Figure 4a).

The large *O. oleifera* newborn seedlings (average 30 cm height) have survivorship rates several orders of magnitude higher than the tiny (average less than 0.5 cm height) *Cecropia obtusifolia* seedlings. *Omphalea oleifera* experience extensive herbivore from larvae of the diurnal moth *Urania fulgens* which contribute to seedling and juvenile (plants with 0.5 m in height but with dbh ≥ 1 cm) mortality in the shade but not in sunny conditions (Dirzo 1984, 1987). Seedlings and juvenile populations found in young patches have 21.4% and 4.2% higher annual survivorship rates, respectively, than those populations found in mature patches. (These figures result from summing all transition values for individuals in a given patch type and discounting those for individuals of the same life-stage in the other patch type; Figure 4a.) At Los Tuxtlas, the turnover rate for small gaps (< 100 m^2) is less than 50 years, which suggests that on average *O. oleifera* seedlings and juveniles may be exposed to at least one small gap (and possibly several) during their lifetime. Experimental studies show that heavily defoliated seedlings growing under high light conditions survive much better than those growing in the shade (Dirzo 1984, 1987); maternal reserves in the cotyledons (and probably the succulent, green, presumably photosynthetic stem) may enable totally defoliated seedlings growing under high light conditions to survive for almost one year without producing new leaves (Careaga 1989). Seedling and sapling growth rates are three times faster in large gaps than in mature patches (Pompa and Bongers 1988, Palomeque 1988).

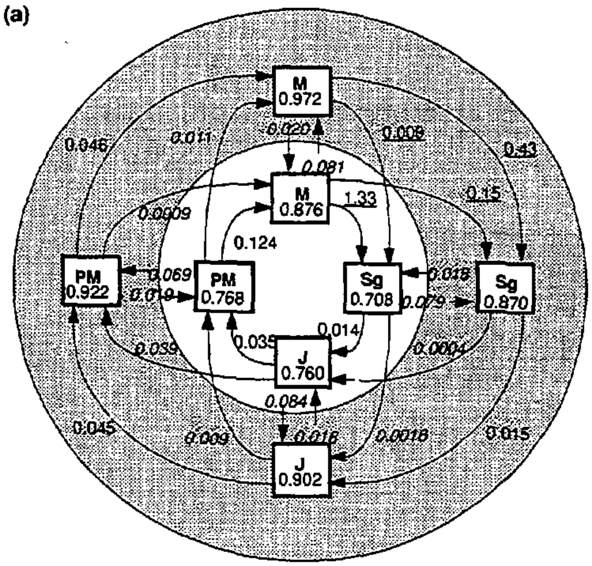
The higher growth and lower mortality rates operating on seedling *Omphalea oleifera* individuals in young patches result in a transition probability to the juvenile stage (1-10 cm dbh) that is twice as high as in mature patches (Figure 4a). Furthermore, some juvenile trees (about 0.1% of the population) in young patches grow fast enough to reach the mature stage during a one year period (Figure 4a). On average, however, juvenile trees have a similar transition probability to premature (10-40 cm dbh) and mature (>40 cm dbh) stages in all forest patches. This is because in mature patches juvenile and individuals growth is stimulated by small canopy gaps (less than 50 m^2), which are very frequent at Los Tuxtlas (Martínez-Ramos et al. 1988). Juvenile individuals that remain shaded for a long time progressively lose their leaves and eventually die, probably because they are unable to replace leaf area lost due to herbivores. As surviving individuals reach the pre-mature stage, the crown expands into canopy areas with high light resources. Thus, the premature to mature transition is similar in young and mature patches (Figure 4). As in *Cecropia obtusifolia*, the maximum future life expectancy of *O. oleifera* is reached when mature individuals reach the forest canopy and are exposed to direct sunlight (Alvarez-Buylla and Martínez-Ramos, 1992). Mature trees die at rates of *c.* 0.010 ind ind^{-1} yr^{-1} (Martínez-Ramos, Alvarez-Buylla, and Hernández, unpublished data) which suggests that *O. oleifera* trees may survive as much as 100 years in the mature stage.

Assuming that demographic and forest dynamic parameter values shown in Figure 4a remain the same through time, we obtain an estimate for λ of 1.038. This estimate is much lower than that estimated for *Cecropia obtusifolia* and suggest that *Omphalea oleifera* population doubles its size in about 25 years. Based on the demographic model discussed above, we suggested that young patches are important for *O. oleifera* life-cycle because gaps facilitate the transition of seedlings and saplings to the premature stage. However, the elasticity analysis (Figure 4b) does not support this idea. Instead, this analysis suggests that survival in the mature stage, mainly within mature patches, is the most critical demographic parameter affecting the population dynamics of *O. oleifera*. Also, traits that favor growth under mature patch conditions are relatively more important for λ than those promoting growth in young patches. Fecundity has a negligible elasticity in the *O. oleifera* population studied. In conclusion, these results suggest that the *O. obtusifolia* population grows at a rate much slower than that of *Cecropia obtusifolia* and that survival, more than growth and reproduction, is the most important demographic trait for population dynamics and fitness.

THE CASE OF ASTROCARYUM MEXICANUM

A life-history pattern incorporating most of the demographic routes shown in Figure 1 is that of the understory palm *Astrocaryum mexicanum* (Figure 5a), the most abundant arboreal species at Los Tuxtlas (300 to 1,200 mature individuals ha^{-1}; Piñero et al. 1977, Bongers et al. 1988). Since 1975, this palm has been the subject of a long-term study on population ecology in eight 20 × 30 m permanent plots (Sarukhán 1978, Piñero et al. 1984, Martínez-Ramos et al. 1988). At Los Tuxtlas, *A. mexicanum* can live for up to 130 years and reach a maximum height of 8 m. This species has a wide distribution in the forest and at a given point in time all life-cycle stages are present in the different forest patch types (Martínez-Ramos et al. 1988).

FIGURE 5. Demography of *Astrocaryum mexicanum* at Los Tuxtlas, Mexico. (a) life-history pattern. Data from Martínez-Ramos et al. (1988). (b) *elasticity values for parameters of the population matrix model based on the data shown in the* life-history model. Note that life-cycle begins with seedlings (Sg) instead of seeds. See Figure 3 and text for further details.



(b)

		Young Patch				Mature Patch			
		Sg	J	PM	M	Sg	J	PM	M
Young Patch	Sg	0.0105			0.0036	0.0008			0.0001
	J	0.0020	0.0110			0.0002	0.0015		
	PM		0.0017	0.0159			0.0003	0.0031	
	M			0.0035	0.1031			0.0002	0.0097
Mature Patch	Sg	0.0022			0.0008	0.0749			0.0093
	J	0.0003	0.0018			0.0113	0.1085		
	PM		0.0002	0.004			0.0115	0.1323	
	M			0.001	0.0091			0.0097	0.4562

Astrocaryum mexicanum palms begin reproducing when they reach one meter in stem height (about 20-30 years old). Annual fruit crops average 20 large seeds (3-4 cm diameter), 40% of which are eaten by arboreal squirrels (*Sciurus aureogaster*) when they are still attached to the palms (Piñero and Sarukhán 1982, Piñero et al. 1984). Ripe fruits are produced between July and November. The majority of fruits that are not removed by frugivorous fall beneath the crown of the parent palm, so there is almost no dispersal between patches (Figure 5a). Approximately 2% of the reproductive palms are found in canopy gaps (Enríquez and Martínez-Ramos, unpublished data), so there is seed input into these patches. Therefore, the transition probability between mature palms and seeds have nonzero values within both mature and young patches (Figure 5a). Seeds remain dormant for eight months in the soil and during this period seed populations experience 90-97% predation by squirrels and other rodents (Sarukhán 1980). Seeds falling in young patches suffer initially lower removal rates than those falling in mature patches (Rodríguez-Velázquez and Martínez-Ramos 1991) but overall, at the end of the germination season, the seed to seedling transition is twice as high in mature patches than in young patches (Martínez-Ramos et al. 1988). Although seed predation rates are very high, the amount of seeds produced by the entire population is enough to satiate predators and the few surviving seeds are eventually covered by litter, which diminishes the risk of predation (Rodríguez-Velázquez and Martínez-Ramos, unpublished data).

As with the case of *Omphalea oleifera*, annual fecundity rates are expressed in the model (Figure 5a) as the seedling produced by mature tree because germination takes less than one year. Seed germination and seedling establishment takes place both in young and mature patches (Figure 5a). In mature patches, the seedlings have enough seed reserves to ensure early survival and growth is possible because they have a low light compensation point (Field and Martínez-Ramos, unpublished data). Juvenile individuals (stemless palms, 1 to 17 years old) die from physical damage produced by limb and treefalls, much in the same way as saplings of other neotropical forest trees (Aide 1987, Clark and Clark 1989, 1991, Samper 1992). Predation by moles and attack by fungal pathogens are also important sources of mortality for juvenile *A. mexicanum* palms (M. Martínez-Ramos, unpublished observations). The mortality rate of juvenile individuals in mature patches, however, is very low (0.082 ind ind^{-1} yr^{-1}) compared with that of *Cecropia obtusifolia* and *Omphalea oleifera*, and the continuous growth exhibited by these palms enables 4.5% of the juvenile population to be recruited into the premature stage (palms with stems $\leq$ 1 m in length, 18-25 years old) every year (Figure 5a). Premature palms grow faster and have lower mortality (0.012 ind ind^{-1} yr^{-1}) than juveniles. Yearly, about 5% of pre-mature individuals attain their first reproductive event (Figure 5a). Maximum growth rates and minimum mortality rates (0.008 ind ind^{-1} yr^{-1}) are obtained at the mature stage (palms > 1 m, 26 to 130 years old). The majority of mature palms die due to mechanical damage produced by limb and tree falls (Martínez-Ramos et al. 1988).

Treefall disturbances have a marked effect on the demography of *Astrocaryum mexicanum*. On average, 2% of closed canopied patches are opened yearly by treefalls at Los Tuxtlas forest (Sarukhán et al. 1984, Martínez-Ramos et al. 1988). Given the high abundance and wide spatial distribution of this palm, we assume that 0.02% of the juvenile, pre-mature and mature populations found in mature patches moves to young patches every year (Figure 5a). Mortality rates are significantly higher in young patches, especially among juvenile palms, which experience thinning associated with an initial increase in density of juvenile palms following the opening of the canopy (Martínez-Ramos, Sarukhán and Piñero 1988). The growth rates of palms in gaps increase, however, so the transition probabilities among life-cycle stages are higher than those operating in mature patches. Also, the opening of a gap leads to a three-fold increase in the fecundity rates of mature palms (Figure 5a).

As a young patch ages, the understory environment changes (Fetcher et al. 1985) and mortality, growth, and fecundity rates of *Astrocaryum mexicanum* palms return to values that are characteristic of mature sites. The rate at which these demographic changes occur depends on the size of the gap. In small gaps (< 50 m^2) these changes take place in less than three years, whereas in large gaps (300-500 m^2) young patch conditions may prevail for as long as twelve years (Martínez-Ramos et al. 1988). This suggests that about 8% of palms in large gaps return to the demographic rates of the populations found in mature sites every year (Figure 5a). Clearly, the time it takes for demographic parameters to return to understory values is also dependent on the stage of the life-cycle under scrutiny. In large gaps, juvenile populations undergo demographic values observed in mature patches after six years since gap opening, whereas the effects on pre-mature and mature palms can last as long as twelve years; therefore, we estimated that 16.7% and 8.3% of juvenile and mature palms found in young patches returns to mature patch conditions on an annual basis, respectively (Figure 5a). This difference is most likely the result of the height of the plants and the speed at which different vertical positions in a patch are covered by canopy overhead.

Demographic transition values included in the life-history pattern shown in Figure 5a give an estimate for λ of 1.012. If transition values remain the same through time, then the population would double its size in 50 years, suggesting that *Astrocaryum mexicanum* has a slower population growth rate at Los Tuxtlas forest in comparison to *Cecropia obtusifolia* and *Omphalea oleifera*. Survival is the most sensitive demographic parameter affecting the population dynamics of *A. mexicanum*, particularly in the mature stage (Figure 5b). Changes in the fecundity and growth rates may have smaller and similar effects on λ, smaller yet than in the case of *O. oleifera* (Figure 4b). The elasticity analysis also shows the high importance of mature patches for the population dynamics of *A. mexicanum* (Figure 5b). Population growth rate of the palm may decline if the probability of remaining in mature patches lowers (Martínez-Ramos et al. 1988). The palm population is much less sensitive to changes in the demographic transitions operating in young patches.

DISCUSSION

The conceptual, graphic nature of the model presented in this paper allows easy visualization of discrete life-history patterns shared by some species, and reveals many possible pathways that can be followed by other species. The model provides a tool for understanding the complex life histories of plants in heterogeneous environments. Plants are sessile and complete their life-cycle in a single location after dispersal. In a limited way, differential growth can allow plants to seek new environments, but the individual is fundamentally restricted to its site of establishment. Given these constraints, tropical forest trees may still experience different patches during a lifetime as a result of disturbance in the canopy overhead and recovery.

Tree Life-History Patterns In Patchy Environments

The model can be extended to other types of organisms and other types of heterogeneity. Three aspects of this model, however, must be pointed out when applied to trees and canopy gaps. First, canopy openings are frequently the result of branch and tree falls which happen very rapidly. Thus, the transition from mature to young patch conditions is much faster and better defined than the transition from young to mature patches, that occur through gradual vertical and horizontal growth of vegetation. Since time for gap closure increases with height above ground (Hubbell and Foster 1986), the young to mature patch transition may have greater effects on those stages which last longer, such as juvenile to mature trees.

Second, in long-lived organisms, such as many trees, the time required for transitions will differ between stages. This is likely to affect the values of the transition probabilities for a given time increment and the relative importance of biotic and abiotic factors that determine them. Third, and perhaps the most important aspect, the different demographic pathways hypothesized in the model are constrained by the time interval used to estimate the transition probabilities among life-cycle stages and forest patches. As the time interval used increases the probabilities of remaining in some stages decreases and in some cases the transitions between stages can approach zero. For example, in fast growing species like *Cecropia obtusifolia*, the use of five years as unit time will reduce the life-cycle only to the seed and mature stages. Conversely, as the unit time is reduced the transition probabilities among stages will be reduced, particularly in populations composed of slow growing trees. Therefore a standard unit of time (e.g., one year) is required in order to use the model to compare life-history patterns between species.

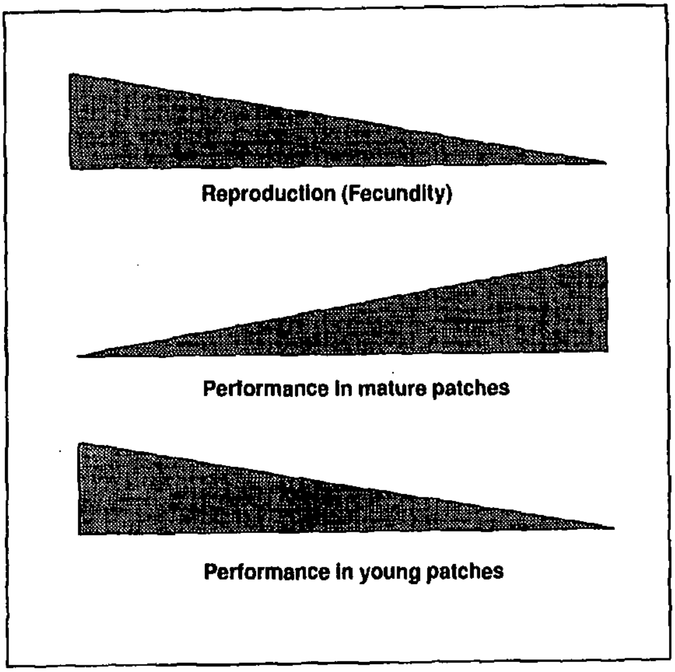
There are other plant life-history components, not discussed here, that can be incorporated into our model to encompass a wider range of life-history patterns. For example, in dioecious species with sex-dependent survivorship and growth rates, demographic pathways can be established by the definition of seeds as a sexually undifferentiated life-cycle stage and the appropriate life-cycle and forest-patch transition probabilities for female and male plants (Caswell 1989). Also, the possibility that some plants may return to earlier life-cycle stages, as when a mature tree snaps and sprouts (e.g., Putz and Brokaw, 1989), can be incorporated in the model by defining the proper return transition probabilities.

Evolution of Life Histories and Forest Dynamics

Are life-history patterns suggested in Figure 1 expected to evolve within a forest? Life-history theory postulates that survivorship, growth, and fecundity patterns express the result of selective forces operating on traits that maximize the individual's genetic contribution to future generations (Stearns 1992). It is proposed that life history evolution takes place only if genetic variability exists in those traits affecting the trade-off between current and future reproduction (e.g., Bazzaz and Ackerly 1992). High investment of energy and resources in one reproductive event may shorten future life, and hence, residual reproduction. On the contrary, a low expenditure of energy and resources in current reproduction could result in an increase in future survival. In this context, different life-history patterns may represent divergent balances in the trade-off between current and future reproduction presumably evolved under different environmental scenarios. For example, short life-spans and high fecundities are expected to evolve within habitats that are ephemeral but rich in resources; on the contrary, longevity and low fecundity can be expected to evolve in habitats where resources are scarce. Genetic evidence for such demographic trade-off has been documented for few short-lived plants (e.g., Law 1979, Venable and Búrquez 1990, Geber 1990). The evaluation of demographic trade-offs, however, mostly relies on the correlative analysis of demographic patterns. This is particularly true for long-lived organisms, such as most trees, for which genetic studies of life-histories are virtually unexplored (Steams 1992).

In tropical rainforests, the low levels of light available in the understory of mature patches limits survival, growth and/or reproduction of most plants (e.g., Augspurger 1984, Sarukhán et al. 1984, Popma and Bongers 1988, Chazdon 1988a, Hubbell and Foster 1991). Large canopy gaps (> 100 m^2) provide high light resource levels that enable positive carbon balance and in turn enhance the probability of reaching the mature stage. In most tropical rainforests, however, these gaps are temporally and spatially scarce and short-lived (review in Clark 1990). At the Los Tuxtlas forest, for example, gaps larger than 100 m^2 created by single and multiple-tree-falls have disturbance return times of more than 50 years; canopy gaps with sizes ranging from 100 to 500 m^2 occur at a frequency of one every year in an area of 10-30 hectares, whereas gaps larger than 500 m^2 occur once each year in 75 hectares (Martínez-Ramos and Alvarez-Buylla 1986, Martínez-Ramos et al. 1988). Under such gap formation regimes tree populations confront more frequently the limited light environment found in the understory. Evolutionary responses to this environmental constraint may include: (a) plant traits that favor wide and abundant seed dispersal so that the probability of seeds landing in recently created gaps is increased, (b) plant traits (including seed dormancy) that enhance survival under shade conditions so that the chance of surviving until a gap opens is increased, and (c) a complex of traits that enables a plant living in the shade to respond and acclimate to the increased light levels of a recently created gap. Figure 6 shows a diagram of some trade-offs expected to be found among these traits. We propose that performance (survivorship, growth or both) under mature patch conditions must show a trade-off with fecundity and performance in young gap conditions; in contrast, fecundity and performance in young patches are expected to co-evolve positively associated. These possibilities may depend on different suites of traits and different combinations of such traits may be related to different life-history patterns as discussed below.

FIGURE 6. An idealized diagram showing relative importance of reproduction (fecundity) and performance (survival, growth, or both) in young and mature forest patches.



(a) Dispersal Across Space

Small seeds inside fleshy fruits easily pass through the digestive tract of frugivorous (Stiles 1992, Wilson 1992) and small seeds inside aerodynamic disperse are dispersed further by wind than heavy, larger seeds (e.g., Jackson 1981, Augspurger 1986). Thus, small seed sizes increase the probability of reaching gaps across space. Small seeds, however, contain lower amounts of maternal resources that can be critical for the survival of new born seedlings in the shade (see below). Under mature patch conditions, large seeds may have higher selective values than small seeds (Foster and Janson 1985). Directional selection for small seed sizes may be associated with evolution of life-histories associated with young patches, as seems to be the case for *Cecropia obtusifolia* (Figure 3a). At the other extreme, evolution of large seed sizes will take place in association with life-history traits that enable juvenile survival under shade conditions as suggested for *Omphalea oleifera* (Figure 4a) and *Astrocaryum mexicanum* (Figure 5a). An intermediate possibility is illustrated by the strong seed size polymorphism exhibited by *Virola surinamensis* (Myristicaceae). Individual trees of this long-lived, canopy species at Barro Colorado Island, Panama, produce mixed crops of large and small seeds; most large seeds fall beneath parental trees while small seeds are more frequently dispersed away by mammals and birds (Howe and Richter 1982). Thus, individual *V. surinamensis* trees producing crops highly variable in seed size may have a greater number of progeny than those trees producing crops of seeds more homogenous in seed size. Species showing such highly polymorphic seed crops are not rare in tropical rainforests (e.g., Dirzo and Dominguez 1986, Careaga 1989).

Evolution of high fecundity rates (the number of seeds produced per mature individual) can be expected to co-evolve with small seeds. The production of copious seeds may guarantee that some seeds will land in young patches and in sites soon to be disturbed. High fecundities, however, may result from a low reproductive effort partitioned in multiple tiny seeds or from a high reproductive effort partitioned in a plethora of small seeds or in a high number of more or less large seeds. High fecundity may often be associated with positive selection for small seed sizes in trees whose fruits are consumed by generalist frugivorous (e.g., Howe and Estabrook 1977) or dispersed by wind. Great numbers of large seeds (< 3 cm diameter) are produced by some canopy trees that are mostly dispersed by one or few large frugivore species (Córdova 1985, Wheelwright 1985, Howe 1990b) or by winged disperse (e.g., Augspurger 1986). At the same time, a high reproductive effort in current reproduction may shorten life-span, growth or future reproduction (Stearns 1992). This trade-off may account for the short-life spans exhibited by copious reproducing, small seeded trees (e.g., Martínez-Ramos 1985), the semelparity of *Tachigalia versicolor*, a long-lived canopy tree (Foster 1977), and the intermittent, mast reproduction exhibited by some long-lived, large seeded tree species (e.g., Janzen 1971, Silvertown 1980).

(b) Survival in Shade

Traits that enhance survival in shade may occur in one or more life-cycle stages. At the seed stage, dormancy is one such trait. In tropical rain forests, the capacity for long-dormancy has been mostly documented in species producing small seeds that require high red/red-far ratios or high soil temperatures to germinate (Vázquez-Yanes and Orozco-Segovia 1984).

Small seeds can remain alive for several years under laboratory conditions (Vázquez-Yanes and Orozco-Segovia 1984) or if excluded from biotic mortality factors in the field (e.g., Holthuijzen and Boerboom 1982, Pérez-Naser and Vázquez-Yanes 1986, Vázquez-Yanes and Orozco-Segovia 1984, Hopkins and Graham 1987, Murray 1988). Under natural conditions, however, the potentially long physiological life-expectancy of these seeds is shortened by predation and pathogenic diseases (e.g., Alvarez-Buylla and Martínez-Ramos 1990). Furthermore, most tropical rain forest tree species produce large seeds that generally experience high seed predation rates (e.g., Janzen 1971, Dirzo and Dominguez 1986), and the short seed dormancy (less than three months) exhibited by most tropical rainforest tree species (Ng 1980, Garwood 1983, Vázquez-Yanes and Orozco-Segovia 1984) has been interpreted as an evolutionary strategy to escape seed predation (Garwood 1983). Thus, evolution of long-lasting seed banks does not seem to be a preponderant life-history trait in most tropical rainforest tree populations. The elasticity analysis for λ in *Cecropia obtusifolia*, whose seeds are physiologically long-lived with some remaining viable in the soil for more than one year (Figure 3), suggests that life-history components other than seed dormancy may have higher selective values.

Short seed dormancy shifts the "waiting for a gap phase" to the seedling and later life-cycle stages. The survivorship of seedlings in shade depends on seedling size (Sarukhán et al. 1984). Tall stems and broad leaf surface areas may enhance interception of ephemeral but energetically rich sunflecks (e.g., Pearcy 1990); large root systems may favor nutrient foraging and mycorrhizal infections (e.g., Janos 1980). Large seedling sizes may also be important to endure physical and biotic damages (Sarukhán et al. 1984, Dirzo 1984). In newborn seedlings, plant size initially depends on the maternal resources found in the seed structures (e.g., Ng 1978, Oberbauer 1990, Hladik and Miquel 1990) and thus the survivorship of seedlings increases with the amount of maternal resources (e.g., Grime and Jeffrey 1965). At Los Tuxtlas, seed dry weight, a possible index for the amount of maternal resources per seed (Fenner 1985), explained more than 50% of the inter-specific variation ($n = 40$ species) found in the annual survival rates of yearly seedlings growing in closed canopied sites (Martínez-Ramos 1991). In the extremes, seedlings of *Cecropia obtusifolia* and *Heliocarpus appendiculants* (Tiliaceae), both of which produce seeds < 1 mg and seedlings < 0.5 cm in height, had zero survivorship whereas all seedlings of *Rheedia edulis* (Guttiferae), which produce seeds > 2,500 mg and seedlings > 15 cm, survived through the study year. Therefore, large seed and seedling sizes are traits that enhance survival in the shade (Foster and Janson 1985) and that would be expected to evolve in association with life-history patterns in mature forest patches.

During and after the seedling stage, a complex of physiological, architectural and morphological traits may enhance survival under mature patch conditions. Low photosynthetic compensation points, low dark respiration rates, high quantum yield, and rapid photosynthetic responses to sunflecks may facilitate positive carbon balances under low light regimes (e.g., Pearcy and Calkin 1983, Langenheim et al. 1984, Chazdon et al. 1988, Hogan, 1988, Pearcy 1990). Lower investment in support structures (e.g., Chazdon 1985, 1988b, Strauss-Debenedetti and Bazzaz 1991), high crown-diameter/stem-height ratios (King 1990, Kohyama 1991), slow crown turn-over rates and leaf longevity (e.g., Williams et al. 1989), and plagiotropic branches (Hallé et al. 1978, King 1990, Kohyama 1991) may facilitate efficient interception and use of light in the understory. Additionally, hard woods (strong stems), well-anchored roots, high recovery capacities following defoliation (Mendoza et al. 1987, Oyama and Mendoza 1990), and the ability to re-sprout after meristem damage (Hallé et al. 1978, Putz and Brokaw 1989, DeStevens 1985,1989, Chazdon 1992) may be important traits to cope with the physical damage caused by frequent debris from the canopy (e.g., Clark and Clark 1990). Finally, the production of secondary metabolites and physical defenses may play a role as defensive mechanisms against pathogens and herbivores (Coley 1983, Coley et al. 1985). Protection of photosynthetic tissues is particularly important for plants producing long-lived shade-leaves that are costly in terms of carbon and nutrients invested and the net carbon gain per unit leaf mass (e.g., Williams et al. 1989).

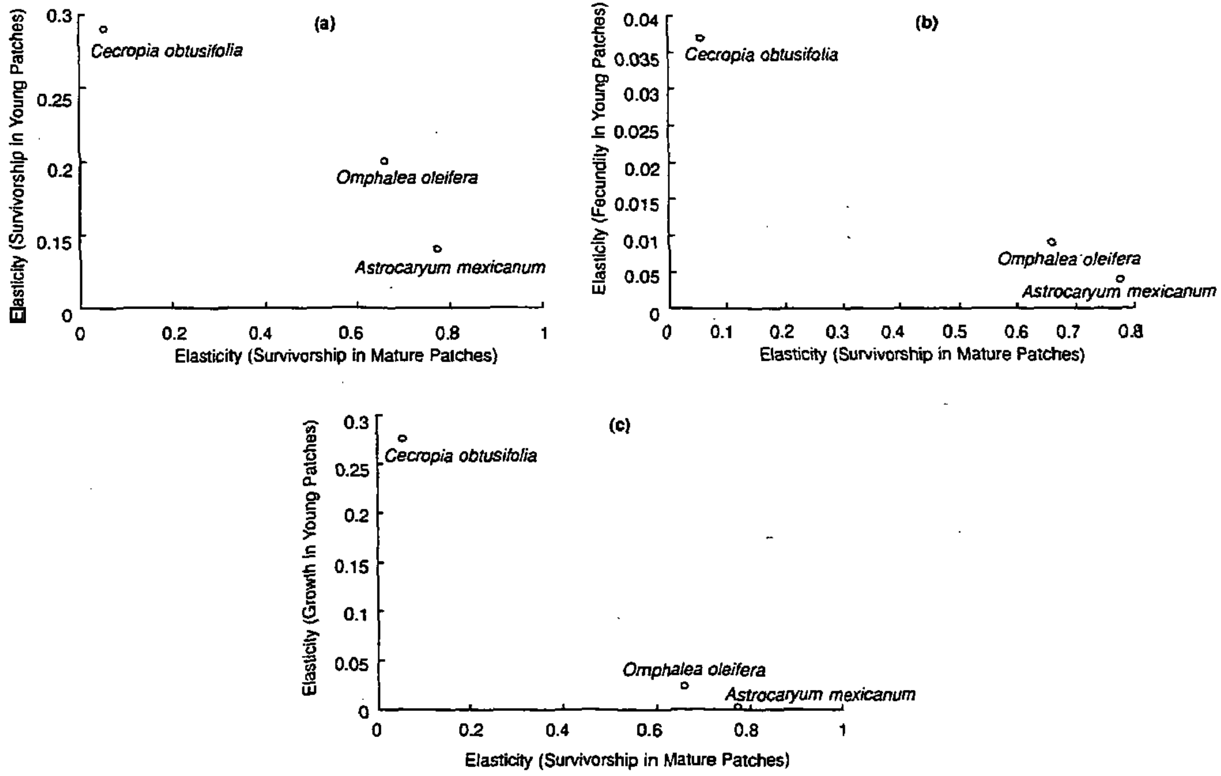
(c) Plant Responses to Gaps

Once a plant reaches a sizable gap either through current seed dispersal or by being present in the understory before gap formation, traits such as early germination and high growth rates have a selective premium because they minimize the risk of shading by neighboring plants and shorten the time to reach the reproductive stage. This expectation is supported by the sensitivity analysis of the *Cecropia obtusifolia* population matrix model: the probability of making a transition to the following stage had higher sensitivity values than that of remaining in the same stage (Figure 3). Plant traits such as high light saturation points, fast leaf turnover, capacity for acclimation to high light conditions, high transpiration rates, high stomatal conductance, the production of low density woods (i.e., high water content per unit volume), small crown-diameter/stem-height ratios, orthotopic branches, and the production of short-lived leaves of low cost (per unit of carbon fixed per unit leaf mass) displayed in a monolayer crown all can favor growth and reproduction under high light environments (Ashton 1978, Bazzaz 1984,1991, Hogan 1988, Williams et al. 1989). The evolution of these traits, however, may be limited by one or more of the traits expected to evolve under mature patch conditions. For example, low compensation points in shade may exhibit a tradeoff with maximum photosynthetic rates so that the high light available in a gap cannot be fully used (e.g., Bazzaz and Pickett 1980, Björkman 1981, Langenheim et al. 1984). A photosynthetic physiology adapted to shade may prevent acclimation to the new, rich light environment and some extreme shade-adapted plants can be photo- or thermo-inhibited under the high light and temperature regimes prevailing in large gaps (e.g., Straus-Debenedetti and Bazzaz 1991). The cost of hard woods may prevent fast growth rates and the canopy forms and architectural characteristics that favor light capture in mature patches may not function well under young patch conditions (Hallé et al. 1978, Givnish 1984, King 1990, Kohyama 1991). Also, the high carbon and nutrient investment in long-lived leaves, and antibiotic defenses can reduce the resource budget available for growth and reproduction.

A formal exploration of trade-offs between life-history traits (as those suggested in Figure 6) can be performed using elasticity values (which are obtained from matrix models for a set of species) and following criteria given by Silvertown et al. (1993). Trade-offs are suggested if elasticity values for survival (S = probability of persistence in the same life-cycle stage), growth (G = probability of progression to further life-cycle stages) or fecundity (F) are negatively correlated. Although the set of species in our case is only of three species, we find a negative correlation between S in young patches and *S* in mature patches (Figure 7a). In a similar way, we find a negative correlations between *F* and *G* in young patches with *S* in mature patches (Figure 7b-c). All these trends suggest that attributes that increase survival (and hence fitness) under mature patch conditions may constrain survival, growth or reproduction under young patch conditions, and vice versa.

In accordance with the above results, seed dispersal (presumably associated with fecundity), performance in mature patches and performance in young patches may represent conflicting life history components that may evolve in the context of forest gap dynamics. Several life-history patterns may result from different combinations of these traits. For example, a life-history pattern matched to large gaps could be the result of selection for wide seed dispersal and high performance in gaps. A contrasting life-history pattern, such as one containing main demographic

FIGURE 7. Correlations between elasticity values for survival (persistence in the same life cycle stage), growth (progression to the next stages) and fecundity in young and mature patches. Elasticity values were obtained from models showed in Figure 7 and expressed as in Silvertown et al. (1994).



routes in mature patches, could result from strong selection for survival under mature patch conditions. Different evolutionary balances between these extremes may produce several of the intermediate life-history patterns hypothesized in our model (Figure 1).

The above point of view, however, is not easy to adopt since many other selective forces, more or less independent of forest dynamics, seem to have played a role in the evolution of tree life-history traits. For example, predation (granivory, herbivory or pathogeny) may have played an important role in the evolution of reproductive schedules, seed dispersal, seed size, and germination behavior in tropical trees (Janzen 1969, 1970, 1978); it is proposed that seed dispersal has evolved to reduce sib competition or increase distances among genetic relatives (Howe and Smallwood 1982, Wilson 1992). Also morphological, architectural, and allometric constraints may prevent the evolution of some life histories (Harper 1982, Alvarez-Buylla and Martínez-Ramos 1992). For example, most tropical rainforest palms depend on a single apical meristem to grow and reproduce and the number of seeds per infructescence is relatively constant (Piñero and Sarukhán 1982, Oyama 1990). Therefore, intrinsically low fecundity rates of palms constrain the evolution of life histories to take advantage of young patches. To the best of our knowledge there are no palm species having a life-history like that of *Cecropia obtusifolia*. Furthermore, we need to take into account possible phylogenetic determinants on the life-history attributes. For example, the suggestion that seed size has evolved in relation to regeneration habitat (Foster and Janson 1985, Foster 1986) was weakened by the fact that seed size is relatively fixed among species of some phylogenetic lineages (Kelly and Purvis 1993).

Life Histories and Regeneration Guilds

By integrating the complete life-cycle with disturbance dynamics, our model bridges the gap between demographic studies and research on successional guilds. The classification of species into guild categories, although useful for an initial broad ecological characterization, may restrict the understanding of the diversity of life-history patterns present in a given forest and the analysis of biological phenomena underlying this diversity. In contrast, the exploration of diversity in life histories may provide important insights for understanding population and community patterns and processes. Even species that follow similar demographic pathways in the forest mosaic (see Figure 1) may differ in life-history traits that affect the abundance and spatial distribution of the species. For example, *Carica papaya* (Caricaceae), a small (< 8 m), fast growing tree (up to 5 m in one year) that completes its life-cycle in large gaps (>200 m^2)

at Los Tuxtlas (Martínez-Ramos 1985), reproduces within one year after germination and has a shorter life span (oldest individuals are less than 8 years) than *Cecropia obtusifolia* (Sarukhán et al. 1985). Although the seeds of *C. papaya* are also widely dispersed by frugivorous, this tree is found at much lower population densities than *C. obtusifolia*, most likely because of lower fecundities, the need for larger (less common) young patches for regeneration, and a lower capacity for seed dormancy.

In spite of the apparent diversity in life histories we can find in a forest, the model presented here may provide two methods for assessing the existence of ecological guilds in forest tree communities. The first method defines the transitions between stages and patches as presence or absence values. This procedure will produce graphical life-history pathways' patterns and the guild idea may be tested by assessing if species fit some life-history patterns more frequently than others. Strong support for the guild concept would include, for example, the existence of different forests exhibiting similar percentages of species having the same life-history patterns. The other method requires that the transition probabilities be expressed in the form of demographic rates followed by sensitivity analyses for population growth rate (Caswell 1989). We can assess the guild idea by determining whether groups of species exist in which λ are equally sensitive to demographic changes in the same life-history transitions. The first approach demands much less field work but the second method provides much richer information for the study of the population ecology and evolution of forest tree populations.

CONCLUSION

Based on the demographic information presented, we believe that much of the debate concerning ecological groups of tropical forest trees derives from over-simplifying the many pathways that can be followed by a species during its life-cycle. The classification of tree species into pioneers and climax species only takes into account the early stage of the life-cycle, namely the transition between seed and seedlings. Furthermore, such classifications are based on studies of the spatial distribution of seedlings and/or saplings, and assume that (i) seed availability is uniform over space, and (ii) patches are discrete over space and time. Future studies should attempt to obtain better data sets on the demography of forest trees. The analysis of demographic and forest patch dynamic rates provides a bridge to study population phenomena in the context of community phenomena. Only when we have comprehensive demographic information on many species from several forests can we confidently look for convergent life-history patterns that would support the existence of discrete guilds among tropical trees.

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