CHAPTER 7

Ecological Life Histories

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Research on the ecological life history (or life cycle) of tropical trees has lagged behind that of other plants, particularly trees of the Temperate Zone. In the Tropics, life-history research has followed two lines of inquiry: demography and succession. Compared to temperate trees, tropical trees (*sensu latus*) appear to have both a shorter timespan to first reproduction and shorter lifespans. Elucidating life-history strategies in species-rich tropical forests is daunting because the traditional dependence on seed and seedling behavior is inadequate, and a complete life-history analysis is required for each species to define appropriate groupings. Analysis of the behavior of seeds, seedlings, and saplings of lowland tropical moist, wet, and rain forest trees suggests two groups of species: pioneer and nonpioneer (or climax). For most trees (nonpioneers), the survival of adults contributes most to fitness, not the number of seeds or seedlings they produce or how fast they grow. For pioneers, the seed bank and the growth of juveniles affects fitness most. More research is needed to validate these trends, however, because the tree species and environmental conditions in the Tropics are diverse. Further division of nonpioneer life histories by functional grouping has proved difficult because a continuum of traits appears to exist among all species.

Formation of tree-fall gaps has been emphasized as the main disturbance event in the life cycle of tropical moist to rain forest trees, and gaps are where most tree life histories experience their critical stages of development. Incident light and, to a lesser extent, nutrients are the factors most responsible for the growth of individuals through gaps or inside a closed canopy. In dry forests, water is more important than light as the factor that determines the success of individuals. Some life-history traits in dry forest trees are small seeds, moisture-related seed dormancy, reliance on root or stem sprouts for regeneration, synchronous growth and reproduction processes, low abundance of seedlings, reduced seed banks, and high density of stems.

Large and infrequent disturbances such as hurricanes instantaneously introduce extreme conditions that significantly alter the stages of the lifecycles of some tropical trees. Sprouting, formation of tree unions, small individuals, short life spans, rapid changes in sun and shade adaptation, explosive establishment of seedling populations, accelerated rates of primary productivity and nutrient cycling, and increased abundance of gap-dependent canopy species, are examples of life-history traits in frequently disturbed areas. In degraded sites, such as those with frequent landslides or human-affected systems, different groups of species—including different life forms and a greater fraction of alient species—achieve success in regeneration. These differences suggest that another set of life-history characteristics is required to overcome these extreme environments. Much research is needed before a clear picture of the diversity of life-history strategies of tropical trees emerges.

INTRODUCTION

> Most plant communities are successional and each species is doomed to local extinction; the two strategies of "escape to somewhere else" or "wait until the right habitat reappears" are alternative ways of meeting the deterioration of the local habitat (Harper 1977).

Harper's words articulate the options available to most plants, including trees in tropical forests. The challenge for scientists is to determine which plants follow which strategy, describe variations of plant response to changing conditions, and examine life-history phenomena in search of patterns of response that can be used to categorize species and improve the capacity to manage tropical forests. Unfortunately, ecological understanding of tropical forests is poor, in part because they are so complex. The complexity of tropical forests comes from the high concentration of tree species per unit area and the wide diversity of ecological conditions that characterize tropical latitudes. On average, tropical trees face more diverse biotic competition and a more varied climate than do temperate and boreal trees. How to address the ecological life histories (or life cycles) of so many tree species growing under so many climatic and edaphic conditions challenges tropical forest ecologists and foresters.

Quantitative analysis of the ecological life history of plants was formalized by Pelton (1953). Before this synthesis, the focus on plants from a population or demographic point of view lagged behind the study of animal populations or that of plant communities (Harper 1967, Hubbell and Werner 1979, McCormick 1995). Moreover, the study of life histories of tropical trees has lagged behind that of temperate trees. In Harper's (1977) 892-page review, fewer than 30 pages contain any reference to tropical tree species, and most of the information is about seed dispersal and predation. Since 1977, many studies have focused on tree regeneration in canopy gaps of tropical-lowland moist and wet forests, but few studies have addressed complete life histories of trees in tropical forests as a whole and dry forests in particular (Alvarez-Buylla and others 1996; Clark and Clark 1992; Garwood 1989; Gómez-Pompa and Vázquez-Yanes 1974; McCormick 1995; Putz and Brokaw 1989; Swaine and Lieberman 1987; Whitmore 1984a, 1984b; Zimmerman and others 1994).

Swaine and others (1987b) observed that most tropical studies do not last long enough to account for the longevity of trees. In Puerto Rico, with some of the longest tree-growth plots in the Neotropics, records now exist covering almost 60 years—the recurrence interval of catastrophic hurricanes (Lugo and others 2000). The situation is compounded by the difficulty in aging tropical trees (Bormann and Berlyn 1981). Wyattt-Smith (1987) regretted the shortage of information on the dynamics of tropical tree populations and added that many long-term tropical studies focused on trees >10 cm d.b.h. Regeneration and establishment through the seedling and sapling phases as well as to flowering and fruiting phases received less attention. He emphasized that understanding the dynamics of large trees of any species requires study of the regeneration and establishment phases. This need exists even though characterizing ecological life histories of tropical trees has usually focused on the short-term responses of seeds and seedlings (e.g., Swaine and Whitmore 1988).

Our review of the literature uncovered two complementary lines of life-history research in tropical forests. One approach is demographic, with a strict focus on individual species (Alvarez-Buylla and others 1996, Hubbell and Foster 1990, McCormick 1995, Silvertown and others 1993). This research can either be comprehensive, based on a population; or fragmented, focused on one or several aspects of the life cycle of a single tree. A second line of research is successional; it focuses on community function and aims to understand the role of tree populations in succession (Bazzaz and Pickett 1980, Clark and Clark 1992, Ewel 1980, Gómez-Pompa and Vázquez-Yanes 1974, Richards 1964). Although demographic techniques are used, this research selects groupings of species with the objective of cataloging functional groups according to their role in succession. In our review, we first place ecological life-history research on tropical trees in context with life-history studies in other plant groups, and then present life-history information according to various lines of research. We end with a review of ecological life- history research in forests that are subjected to large and infrequent disturbances, water limitation, and other ecological stressors. Our objective is to present the paradigms of ecological life-history research for tropical trees and, where possible, propose improvements to these paradigms based on experience in the Caribbean. Throughout the review, we highlight research needs to support improved life-history models for tropical trees.

PARAMETERS OF THIS REVIEW

CAVEATS AND DEFINITIONS

The literature tends to generalize about the Tropics, particularly through comparisons with temperate conditions (Lugo and Brown 1991). Generalizations are useful, but they can lead to pitfalls and myths for two reasons. First, consistency is lacking in the use of such terminology as tropical, tropical forests, rain forests, primary forests, and secondary forests (cf. Brown and Lugo 1990, Lugo and Brown 1991). Readers cannot be sure what environmental conditions or forest states are being referred to without precise definitions. Second, the high richness of species and diversity of life forms that typify the Tropics assure that exceptions to most generalizations will be found. In this review, we retain the terminology on forest types used in the original articles when referring to their findings, and we use those of Holdridge (1967) when expressing our views.

The term "large and infrequent disturbance" is used here *sensu* Romme and others (1998):

> large and infrequent disturbances are defined as those whose intensity exceeds the intensity at which a threshold occurs in the response curve [of ecosystem parameters], and that are statistically infrequent.

Examples are hurricanes above certain intensity scales, large floods, large and intense fires, landslides that exceed certain volume thresholds, and extreme droughts.

METHODS FOR STUDYING ECOLOGICAL LIFE HISTORIES

A life history is defined as the combined changes in expectations for further life and reproduction in an organism as it ages or grows. Life histories are assumed to evolve in response to the organism's environment; life-history tactics are the individual traits of the life history that are selected for or against. The way in which selection and life-history tactics evolve depends on species-specific tradeoffs among tactics (i.e., reproduction vs. survival). How life cycles evolve was shown by Lewontin (1965) using a simple graphical model which was incorporated in Harper's (1977) idealized life cycle of a higher plant (shaded portion of fig. 1). Harper's life cycle diagram showed the reproductive periods of the life cycle that are critical to the demographic success of plants: time of first reproduction, capacity to change the time of onset of the fecundity period, time of peak fecundity, capacity to change the peak period of fecundity, time when fecundity ceases, capacity to change the time when fecundity ceases, and total number of offspring produced.

The fecundity period begins at the age of first reproduction and continues until reproduction ceases because of senescence or death. Age of first reproduction is the most critical aspect of a life history because population growth is a com-

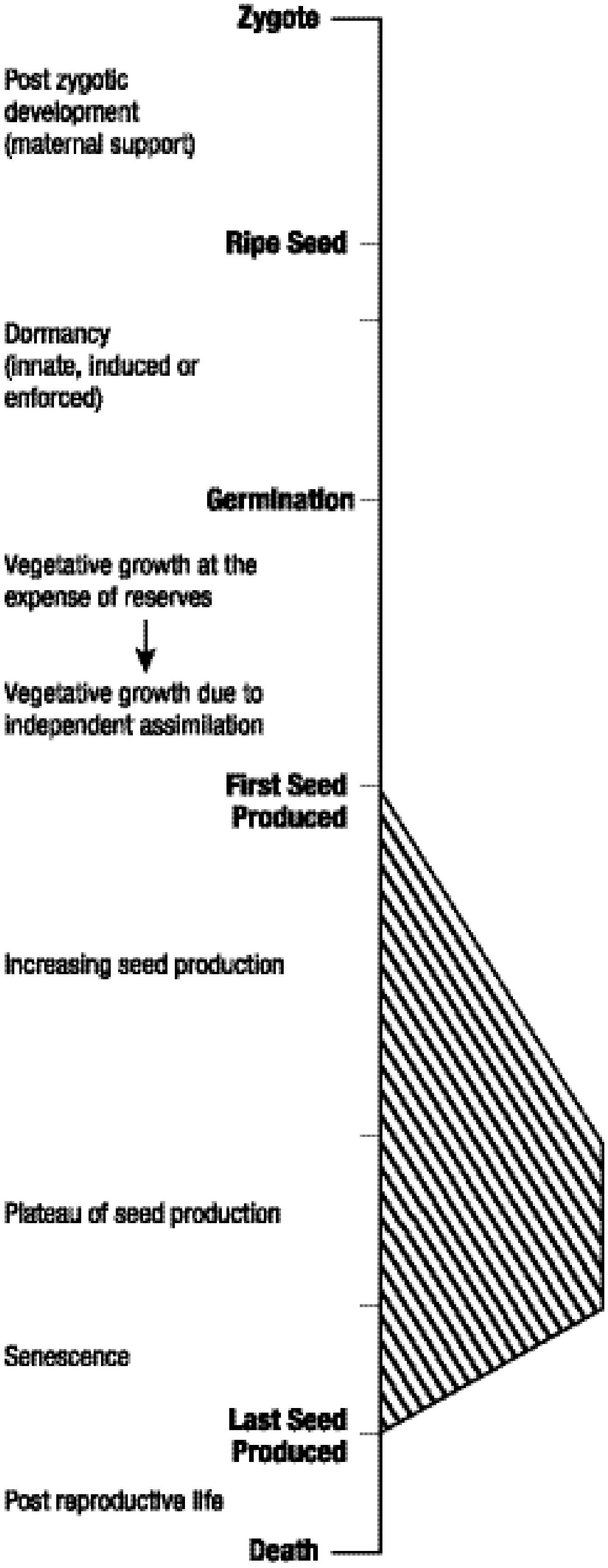


Fig. 1. Idealized life cycle of a higher plant. The shaded portion represents the pattern of production and total amount of seeds produced. From Harper (1977).

pounded variable: the earlier organisms reproduce, the earlier a new generation will be positioned to reproduce themselves and add more individuals to the population. Trees reproduce late relative to other plants as a tradeoff with early growth (Stearns 1992). Reproduction is impossible or difficult until a minimum size is achieved; thus, early growth allows trees to reach the canopy where reproduction is maximized.

A life history can be best analyzed as a life table, a square matrix providing the age- (or size-) specific probabilities of death and amount of reproduction in each age (or size) class. Age-based matrices are termed Leslie matrices (Leslie 1948) in which the only nonzero entries are on the first row (fecundities) and along the diagonal (survivorship). Nonzero entries reflect impossible transitions such as going from age 7 to 9 in a single time step. Stage-based (population transition) matrices are called Lefkovitch matrices (Lefkovitch 1965) in which any element of the matrix may be nonzero because any class could contribute to any other class in the next time interval.

A life cycle graph (fig. 2a) includes all relevant demographic data for a tree, which is readily translated into a population transition matrix (fig. 2b). The transition matrix provides quantitative data on a yearly time step for transition probabilities from one stage to another (Caswell 1989). For tropical trees, a stage-based or Lefkovitch matrix rather than an age-based matrix is most appropriate because tropical trees are difficult to age and, more importantly, except in senescent trees, the size of a tree rather than its age best determines its future behavior.

Columns in the transition matrix indicate, for each stage, the combined probability of surviving and of growing, of declining in size, or of remaining in the same stage by the next time step (usually a year). Seed production (F = fecundity) is depicted in the top row (number of seed produced by the average small or large adult tree). The probability of remaining a seed in the seed bank, a seedling, a sapling, and so on, is provided by the diagonal (L). The chances of surviving and growing to the next stage are below the diagonal (G), and the chances of declining in size because of catastrophe (D) appear above the diagonal. Each row looks backward, defining each stage in terms of the fecundity, survival, and growth of the contributing stages during the previous year. The matrix has great flexibility in terms of the type of life-history information available. For example, clonal growth would be indicated by arrows from any of the adult classes to the juvenile class and would appear in the transition matrix above the diagonal position (combined with D). With a seed pool, or if a seed pool does not exist in the population for more than a year, then the seed stage should be omitted (Caswell 1989, Silvertown and others 1993); reproduction is then described as the average seedling production by each adult stage. This procedure is used in cases when the time step of the transition matrix is a year.

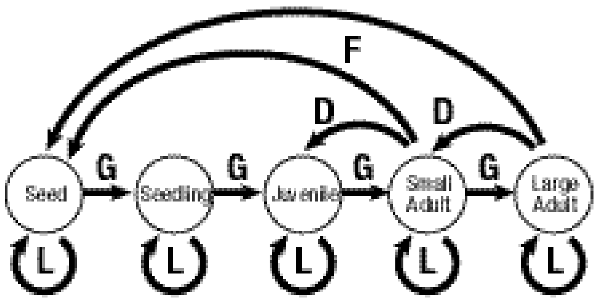
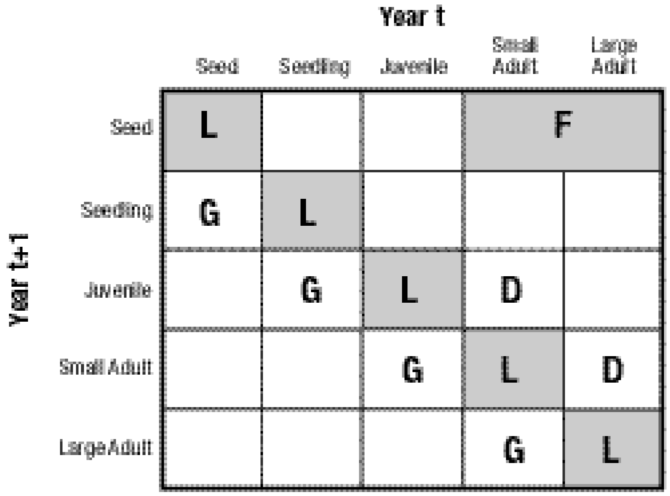


Fig. 2a. A five stage (seed to large adult) model of a life cycle of a tree showing critical demographic processes (a). Survival is L, growth is G, size reduction due to catastrophe is D, and fecundity by seed production is F.



		Year t				
		Seed	Seedling	Juvenile	Small Adult	Large Adult
Year t+1	Seed	L			F	
	Seedling	G	L			
	Juvenile		G	L	D	
	Small Adult			G	L	D
	Large Adult				G	L

Fig. 2b. The same diagram in matrix form (b) suitable for analysis by the power method of Caswell (1989). From Hubbell and Werner (1979).

In mathematical terms, the transition or projection matrix **A** provides the average contributions of an individual in a particular stage (*j*) to another stage (*i*) in a predefined time interval. Each element is termed *aij*; these values are whole numbers in terms of fecundity, and range from 0 to 1 in the remainder of the matrix. A variety of population measures can be derived from **A** (Caswell 1989). The most important of these is lambda (l), the population growth rate or the change in the number of individuals at each stage over time (assuming the relative number of individuals at each stage is the same over time). The value l is important because it also provides a definition of fitness in evolutionary studies–the expected number of offspring to be produced by an organism with a particular set of traits in a particular environment. One set of indices that are frequently derived from **A** are the elasticities. Elasticity (e*ij*) is a measure of the proportional sensitivity of l to small changes in the a*ij*’s, and it thus provides a clear measure of the relative importance of different life stages to the organism’s fitness. Because of bottlenecks between life stages, a 10-percent increase in seedling survivorship will not have the same effect as a 10-percent increase in adult survivorship or a 10-percent increase in fecundity.

SEED LONGEVITY IN TROPICAL FORESTS

To show how recent research is modifying early pantropical generalizations, we use information on seed longevity. The accepted generalization is that tropical tree seeds have short spans of viability (Harper 1977, Mabberley 1983, Ng 1983). Many species conform to the accepted generality, particularly in true rain forests, but many seeds do not have short spans of viability and others have some kind of dormancy (Gómez-Pompa and others 1976, Smith 1970, Whitmore 1984b). Ng (1980) found an exponential decline in the relation between number of species and time required for germination in Malaysian rain forests, with 50 percent of 335 species completing their germination in 6 weeks. About 15 percent of the species exceeded 20 weeks before they began germination.

Vázquez-Yanes and Orozco-Segovia (1993) found that seed crop, seasonality of production, and number of seeds per fruit vary greatly, due to the enormous diversity of plant taxa and life forms in tropical rain forests. They also observed that the seeds are remarkably diverse in size, shape, morphology, anatomy, moisture content, nature of reserves, and presence of secondary compounds. They reported that the mean longevity of seeds in tropical rain forests, where the forest floor is wet, dark, and hot, may be one of the shortest of any plant community because seeds tend to germinate soon after dispersal. Seeds of pioneer species in rain forests, however, show long longevity, reaching turnover times of more than 1 year. In seasonal tropical forests, some seeds may be released with low moisture (wind-dispersed seeds such as those of *Swietenia macrophylla*) and can remain quiescent until moisture becomes available. A large data set on seed production, size, and dispersal mechanisms is available for Amazonian forests in Knowles and Parrotta (1995, 1997).

The factors that independently or in combination may extend the ecological longevity of seeds are: dormancy mechanisms, delayed germination, metabolic interruption, presence of a hard or impermeable coat that prevents fast rehydration and diminishes predation, abundant seed production that allows many seeds to survive predators and parasites, and strong chemical defenses against parasitism and predation. Vázquez-Yanes and Orozco-Segovia (1993) suggested that plants that become established in the undisturbed forest floor have less complex, environmentally regulated dormancy mechanisms than those established in scattered gaps. Garwood (1989) gave examples of the diversity of seed germination and seed-dispersal patterns along gradients of regeneration strategies in the lowland Tropics (table 1). Unfortunately, the amount of information available on the physiology of dormancy of rain forest seeds is too limited to allow generalizations on the mechanisms for different ecological groups of plants.

Table 1

The expected distribution of tropical seed-bank strategies among regeneration strategies, based on the distribution of germination behaviors and frequency of dispersal

(Source: Garwood 1989)

	Regeneration Strategy[a]			
Seed-bank Strategy	Weedy Species	Short-lived Pioneers	Long-lived Pioneers	Primary species
Transient	R + A	R + A	R + A/I	R + A/I
Transient with seedling bank	—	—	—	R + A/I
Pseudo-persistent	R + C	R + C	—	—
Delayed-transient	—	—	D + A/I	D + A/I
Seasonal-transient	S + C/A	S + C/A	S + A/I	S + A/I
Persistent	F + C/A	F + C/A	—	—

[a] Germination behavior + dispersal frequency. Germination behavior denoted by: R, rapid germination and short-term viability; S, seasonal dormancy and intermediate-term viability; D, delayed germination and intermediate-term viability; and F, facultative dormancy and long-term viability. Dispersal frequency denoted by: C, continuous; A, annual; and I supra-annual (intermittent).

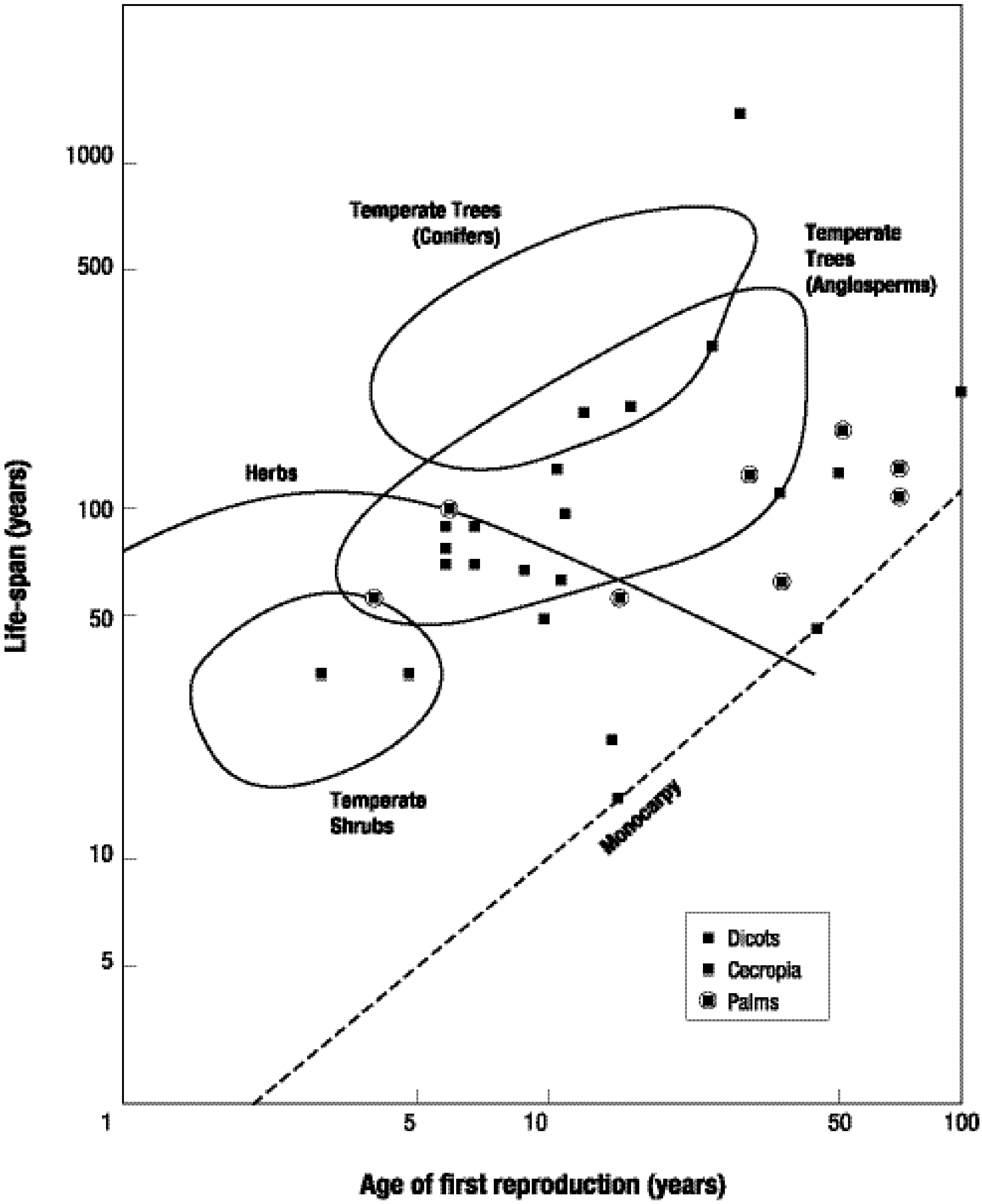


Fig. 3. Relationship between juvenile period (age of first reproduction) and total life span for perennial plants. Modified from Harper (1977). Original data are from Harper and White (1974) with additional data for tropical trees obtained from Alvarez-Buylla and Martínez Ramos (1992), Bullock (1980), Francis (1989), Francis (1991), Hartshorn (1972 and personal communication), Muñiz Meléndez (1978), Olmstead and Alvarez-Buylla (1995), Piñero and others. (1984), Sastre de Jesús (1979), Silander (1979), Van Valen (1975), You (1991), [two from silvics manual: *Mammea americana* and *Swietenia mahogoni*]

LIFE HISTORIES OF TROPICAL TREES COMPARED TO OTHER PLANTS AND TREES

Harper and White (1974) compiled data on the age of first reproduction of seed plants. They differentiate between semelparous plants (those that reproduce once and die, i.e., age of reproduction is the same as lifespan), herbs, shrubs, and trees–both angiosperms and gymnosperms (fig. 3). Compared with other plants, trees have long lifespans and tend to reach the age of first reproduction late. We added new data on tropical trees (Dicots, *Cecropia,* and palms) to Harper and White's figure and included them with those in their original diagram. The results suggest that tropical trees (*sensu latus*) tend to reproduce at younger ages and have shorter lifespans than temperate trees. In addition, some understory tropical palms appear to have long juvenile periods relative to their lifespan (Bullock 1980, Olmstead and Alvarez-Buylla 1995, Van Valen 1975). The only tropical pioneers in the figure (*Cecropia*) behaved like temperate shrubs: they had very short lifespans and early ages of first reproduction. More research is needed to verify these tendencies.

Grime (1979) identified the environmental extremes of evolutionary specialization in plants in terms of stress, competition, and disturbance. From these extremes, he described three main strategies of plant response: stress tolerators (S), competitors (C), and ruderals (R). Stress tolerators grow in competition-free environments where resource availability is low. Competitors grow in areas where resource availability is high and where competition from established vegetation is also high. Ruderals are weeds that grow in competition-free environments where resource availability is high. Grime identified secondary strategies that develop from a combination of these three strategies and placed various plant groups in the context of these response strategies (fig. 4).

Most trees occupy the range of conditions largely defined as stress-tolerance competitors, which adapt to relatively undisturbed conditions with moderate intensities of stress. From these determinations, we can generalize regeneration strategies that best adapt trees to the conditions they face. For example, as stress increases, trees rely more on persistent seedling banks than on seed banks (Garwood 1989). Mangrove trees are tropical trees without a seed bank; their viviparous seedlings form a seedling bank (Tomlinson 1986). In this view, pioneer trees exist near the ruderal corner of the triangle where resources (light) are relatively high and competition relatively low. Unfortunately, Grime developed his scheme primarily for herbaceous plants in the temperate zone; the utility of this scheme for discriminating among life histories of trees remains untested, as does the distinction between temperate and tropical trees.

The demographic approach to tree life histories has been more fruitful and produced a scheme similar to Grime's. Silvertown and others (1993) analyzed Lefkovitch matrices for 66 species of plants, calculating the summed elasticities for fecundity (F), survival (L), and growth (G) for each species. The results were depicted on triangular diagrams similar to Grime's habitat classification scheme. Species differed in their demographic parameters in a manner that would meet expectations. Elasticities for semelparous (biennial) herbs were highest on the F and G axes and those for perennial herbs appeared in the middle of the diagram. Understory herbs were intermediate for L and G, and low on the F axis. Woody plants, including a few tropical trees, were almost entirely restricted to one corner of the triangle, where F and G were both near 0 and L was near 1. Thus, for most trees, the survival of adults contributes most to fitness, not the number of seeds or seedlings they produce or how fast the trees grow. The few exceptions to this pattern were shrub species in the fire-prone habitats where F and G were intermediate.

With the same approach, Alvarez-Buylla and others (1996) focused on 13 tropical tree and palm species; they found that the highest elasticities in 12 of these species were found in the survival of adults or preadults, a finding similar to the global analysis of Silvertown and others (1993). The one exception was *Cecropia obtusifolia*, the only pioneer species on the list, for which the survival of seeds in the seed bank and the growth of juveniles showed the highest elasticities. This finding agrees with the accepted expectation that pioneer and nonpioneer species would differ. *Cecropia obtusifolia* would occur toward the center of the G-L-F space (Silvertown and others 1993), with temperate shrubs in fire-dominated habitats. Therefore, the life histories of the temperate and tropical

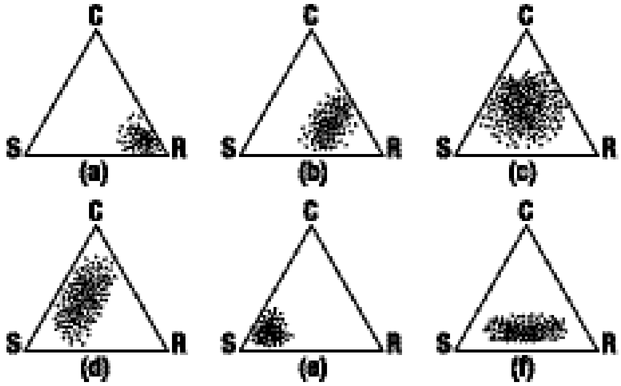


Fig. 4. Diagram describing the range of strategies encompassed by (a) annual herbs, (b) biennial herbs, (c) perennial herbs and ferns, (d) trees and shrubs, (e) lichens, and (f) bryophytes. From Grime (1979).

angiosperm trees studied tend to be similar, except for fast-growing tropical pioneers. However, a large sample of matrices is needed to confirm this pattern. This approach could also be used to determine whether nonpioneer species show any distinctive pattern of change in their elasticities.

THE ECOLOGICAL LIFE HISTORY OF TROPICAL TREES

Schimper (1903) distinguished between sun- and shade-adapted plants, and Richards (1964) contrasted species that grew in open areas or gaps in rain forests (light demanding or intolerant [of shade]) with those that regenerated inside the forest (shade bearing, tolerant, or primary forest dominants). These observations formed the basis for a variety of ecophysiological studies at leaf, seedling, and whole-tree scales (Bazzaz and Pickett 1980, Fetcher and others 1987, Kitajima 1994, Lugo 1970, Medina in press, Odum and others 1970). Sun-adapted plants are distinguished by photosynthetic light-response curves that saturate at high light intensities; photosynthesis rates of shade-adapted plants saturate at low light intensities. Respiration rates in shade-adapted plants are low, allowing them to persist for long periods in the shade.

Fetcher and others (1987) found that the metabolism of early successional species is less affected by the previous environment after being moved to a new environment than are late-successional species. Therefore, they surmised that early successional species are able to acclimate to new environments more rapidly than are late-successional species. When response variables were considered separately, however, Fetcher and others (1987) found that species with apparently similar ecological roles do not necessarily have similar acclimation responses. Kitajima (1994) found that traits that maximize carbon gain in seedlings do not necessarily lead to a higher survival in shade, and that acclimation responses of individual photosynthetic traits do not necessarily differ between shade-tolerant and shade-intolerant species. Instead, she found that morphological traits were negatively correlated with the survival of individuals in shade. The explanation is that faster growth rates are achieved at the expense of defense or storage allocation. Morphological traits achieve a degree of protection and storage allocation that assures shade survival even at slow rates of growth.

The dichotomy in light response (sun-adapted or heliophytic vs. shade-adapted or non-heliophytic) is the basis of the quotation from Harper (1977) at the beginning of this review. The dichotomy has led to the many name pairs critically reviewed by Swaine and Whitmore (1988), such as pioneer vs. nonpioneer, colonizing vs. climax, secondary vs. primary, shade bearers vs. light demanders, nonequilibrium vs. equilibrium, r-selected vs. k-selected, weeds vs. species of closed vegetation, ephemerals vs. persistents, nomad vs. dryad. Swaine and Whitmore (1988) used seed germination and seedling establishment as the basis for proposing two ecological groups to substitute for all the commonly used name pairs. Their proposed nomenclature was pioneers vs. nonpioneers (or climax).

We agree with Swaine and Whitmore (1988) and Clark and Clark (1992) that the only classification scheme for tropical tree life histories that is supported by data is the contrast between pioneer and nonpioneer species. Whether these two types of species form distinct groups (Clark and Clark 1992, Swaine and Whitmore 1988, Zimmerman and others 1994) or are the end points in a continuum of life-history types (Alvarez-Buylla and others 1996, Gómez-Pompa and others 1976) is presently unclear and deserves further research. The distinguishing characteristics of these two life-history types were summarized by Swaine and Whitmore (1988) but a different listing of characteristics was provided earlier by Gómez-Pompa and Vázquez-Yanes (1974) (fig. 5). The character syndrome of pioneer tree species in tropical rain forests as proposed by Swaine and Whitmore is tabulated below.

- Seeds germinate only in canopy gaps that are open to the sky and receive some full sunlight.
- Plants cannot survive in shade–young plants never found under a closed forest canopy.
- Seeds small and produced copiously and more-or-less continuously.
- Seeds produced from early in life.
- Seeds dispersed by animals or wind.
- Dormant seeds usually abundant in forest soil (especially fleshy-fruited species); seeds orthodox (no recalcitrant species known).
- Seedling carbon-fixation rate high; compensation point high.
- Height growth rapid.
- Growth indeterminate with no resting buds.
- Branching relatively sparse.
- Leaves short-lived.
- Rooting superficial.
- Wood usually pale, low density, not siliceous.
- Leaves susceptible to herbivory; sometimes with little chemical defense.
- Wide ecological range; phenotypically plastic.
- Often short-lived.

All pioneers are expected to have the first two characteristics but not all pioneers have all the others in the list.

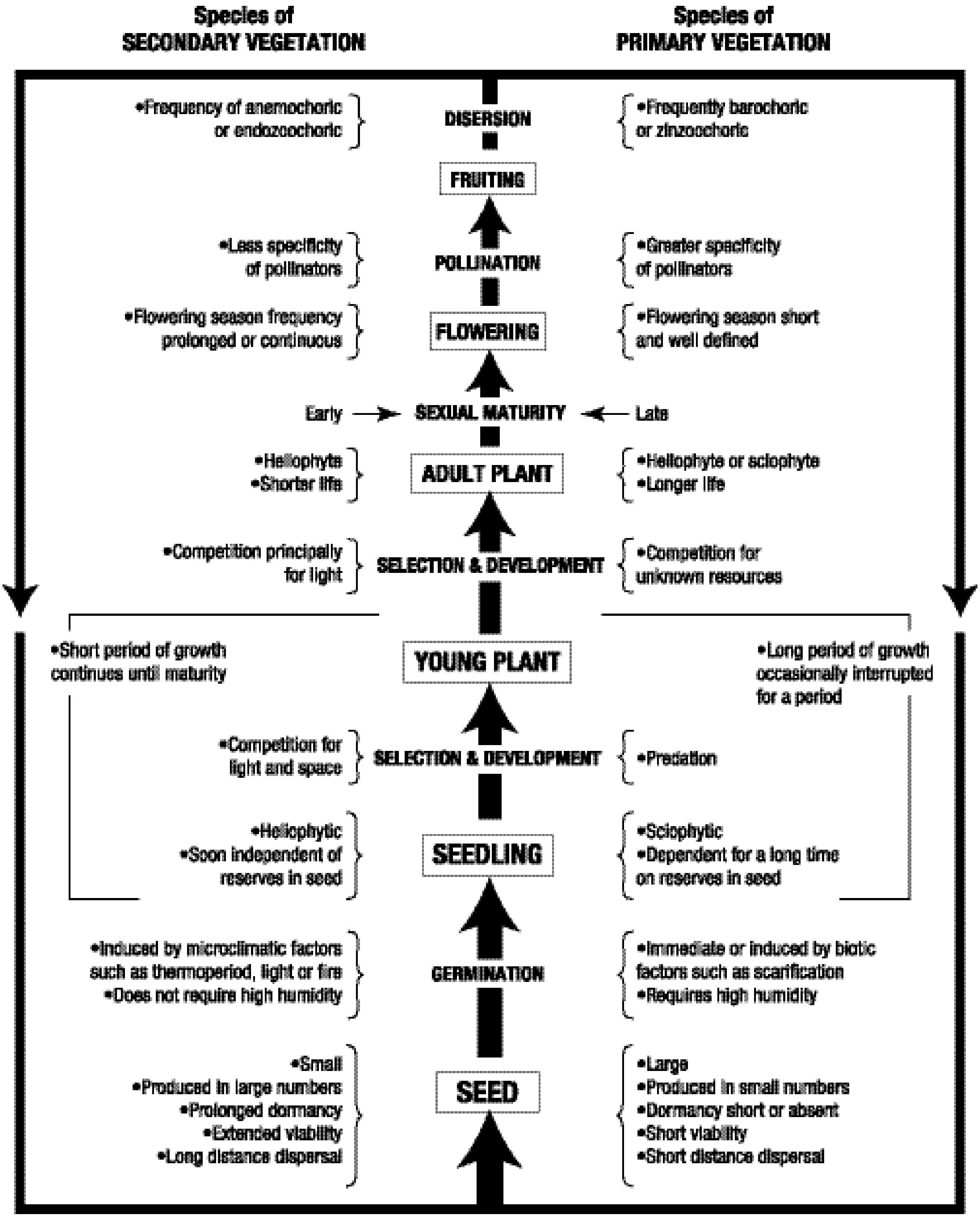


Fig. 5. Life cycle of secondary and primary plant species of tropical forests. Each step of the diagram can be isolated for research purposes. From Gómez-Pompa and Vázquez-Yanes (1974).

Successional viewpoints of tree life cycles consider the role of the species in the recovery from disturbance. Historically, this recovery has been viewed primarily in the context of gap-phase regeneration in tropical moist, wet, and rain forests. Secondary species respond to disturbance (light gaps) by increasing local numbers. Secondary species are ephemeral in space and time. Populations of primary or climax species become predominant long after a disturbance event or persist through a disturbance, recovering after the disturbance through direct regeneration (Yih and others 1991, Zimmerman and others 1994). We present a guide (fig. 6) for some of the schemes used to classify tropical trees according to successional functional groups for the variety of tropical tree life histories discussed in the following pages.

Whitmore (1984b) formalized the description of the life cycle of tropical trees in the Far East by describing the development of trees from seeds to senescence. He described growth after formation of a gap as going through gap, building, and mature phases. This sequence summarizes the model of gap phase dynamics from beginning to end. However, Whitmore cautioned against the generalization that gap-phase and mature-phase species can be identified, because a tropical rain forest has a suite of species that can complete their life cycles along a gradient of conditions from closed forest to very large gaps. Gap size is critical in determining the microclimatic conditions that seedlings face in developing into trees. Species can be categorized by their light demand or shade tolerance and their capacity to growth through the tangle of competing vegetation that invades forest gaps. Whitmore identified two types of pioneer species: short-lived, which mature in 10 to 30 years, and long-lived, which mature after 80 years. However, no sharp distinction exists between these two groups.

Whitmore (1984b) arranged 12 tree species in the Solomon Islands into four groups according to their response to gaps: seedlings that establish and grow inside the canopy shade; seedlings that establish and grow inside the canopy but show

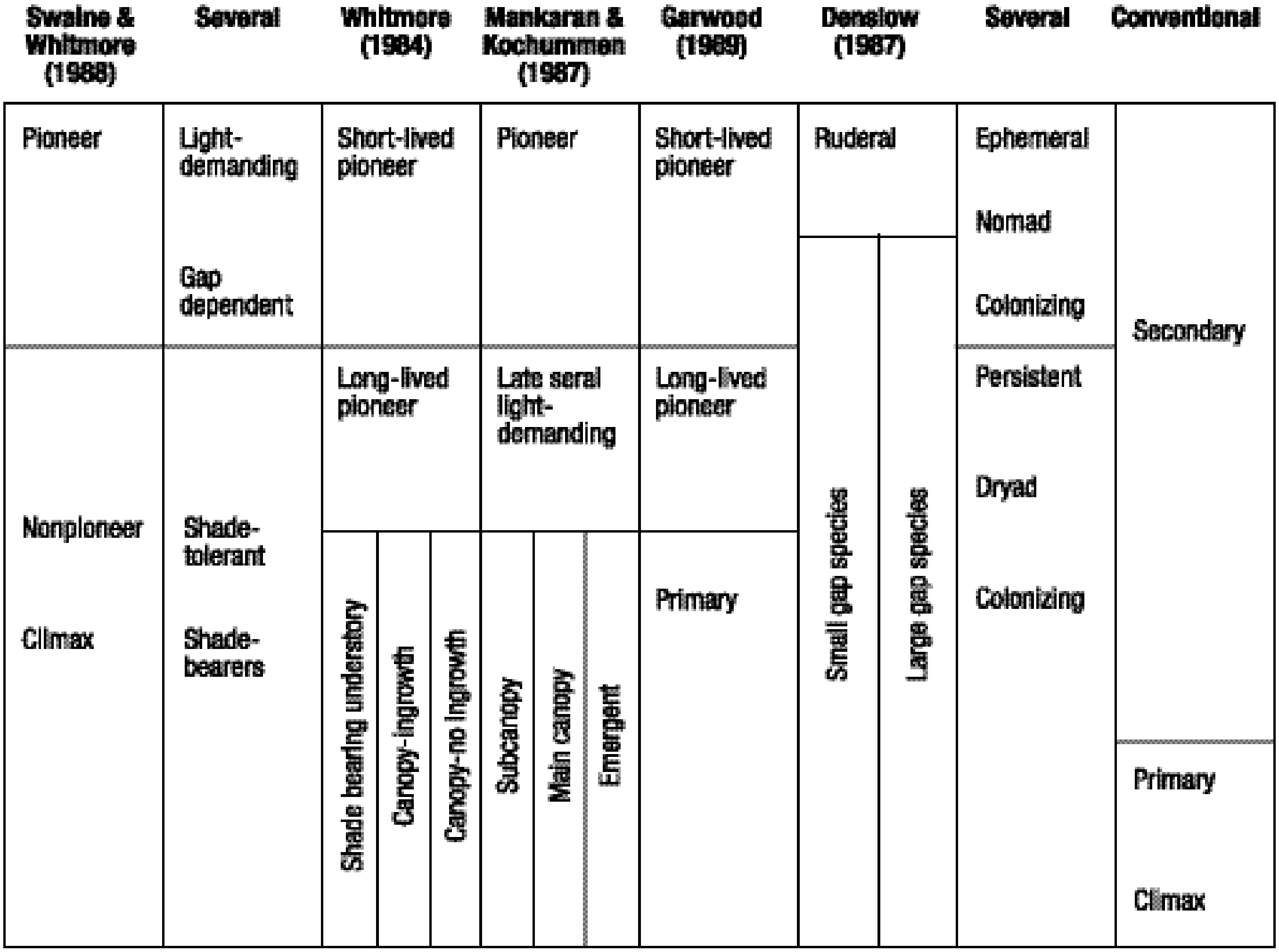


Fig. 6. Some common schemes used to classify tropical forest trees. Cross comparisons among schemes are only approximate and numerous exceptions exist (see text).

some signs of benefiting from gaps; seedlings that establish mainly inside the canopy, but definitely require gaps to grow; and seedlings that establish mainly or entirely in gaps and grow only in gaps (the pioneer species). This arrangement illustrates the continuity of response to environmental gradients.

Using tree mortality and recruitment data collected in Malaysia by Wyatt-Smith, Whitmore (1984b) grouped the trees of a mature forest into five groups according to life-history strategy: short-lived pioneer and long-lived pioneer species without recruitment under a closed canopy, shade-bearing or shade-tolerant understory species not reaching the canopy, canopy species without ingrowth, and canopy species with ingrowth (fig. 6). Ingrowth means that the seedlings of the population were able to develop into trees inside the canopy. This analysis showed that emergent trees were light demanding, and the main canopy species were strongly so. Shade bearers failed to reach the canopy. Periodic gap formations or large-scale disturbances create conditions for the regeneration of crown-dominant species.

A similar categorization was used by Manokaran and Kochummen (1987) for trees in long-term plots in a dipterocarp forest in Peninsular Malaysia (fig. 6). They placed species in five groups according to their characteristics: pioneer–short-lived tree species requiring a gap to germinate and establish, showing rapid growth, extremely light demanding, and intolerant of shade; late-seral–light demanding tree species but relatively tolerant of shade and prominent during the late stages of succession (can persist into the mature forest); emergents–mature phase, light demanding, long-lived species growing above the main canopy of primary forests to more than 30 m, usually with spreading crowns; main canopy–mature phase, light demanding, relatively long-lived species that form the main canopy of primary forest, growing to heights between 20 and 30 m; and understory–mature phase, shade-tolerant tree species forming the lower strata of the primary forest, with maximum heights below 20 m.

Garwood (1989) grouped life-history strategies into four regeneration groups to analyze the role of seed and seedling banks, advanced regeneration, and sprouting in lowland tropical forests (fig. 6). The four groups follow: (1) primary species–germinate and establish in the shaded understory of undisturbed forest; (2) long-lived pioneer species or late secondary species–germinate in shade or sun but grow only in forest gaps, are intermediate between short-lived pioneers and primary species, and dominate secondary forests but are also components of primary forests; (3) short-lived pioneer species–germinate and establish only in large forest gaps or human-produced clearings and are small-seeded, shade intolerant, and fast growing; and (4) weedy species (*sensu* Gómez-Pompa and Vázquez-Yanes 1974). Weedy species are not shown in fig. 6. These regeneration groupings were matched to six seed-bank strategies (transient, transient with seedling bank, pseudo-persistent, delayed-transient, seasonal-transient, and persistent (fig. 7), and the resulting matrix is shown in table 1. Rapid germination and short-term viability are found in all regeneration strategies, as are seasonal dormancy and annual dispersal frequency. Primary species are the only species with transient seedling banks. Long-lived pioneers and primary species are the only species with delayed seed germination, intermediate-term viability, and intermittent dispersal frequency. The diversity of regeneration and seed-bank strategy combinations is obvious, and the seed bank changes in density and composition through succession.

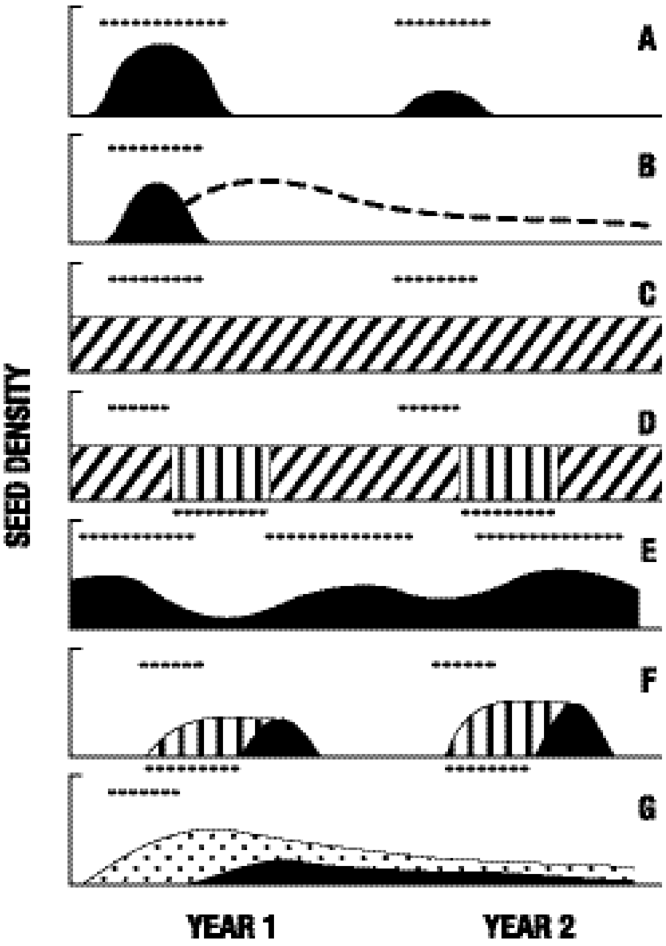


Fig. 7. Tropical soil seed bank strategies. (A) transient. (B) Transient replaced by seedling bank. (C) Persistent. (D) Persistent with periodic seasonal dormancy. (E) Pseudopersistent of fluctuating size. (F) Seasonal-transient. (G) Delayed-transient. Fruiting periods are denoted by asterisks, dry season by small open circles, seedling banks by dashes, germinable seeds without dormancy that must germinate or die, by black areas, seeds with seasonal dormancy by vertical lines, seeds with facultative dormancy under forest canopy by slanted lines, and seeds with delayed germination by stippling. From Garwood (1989).

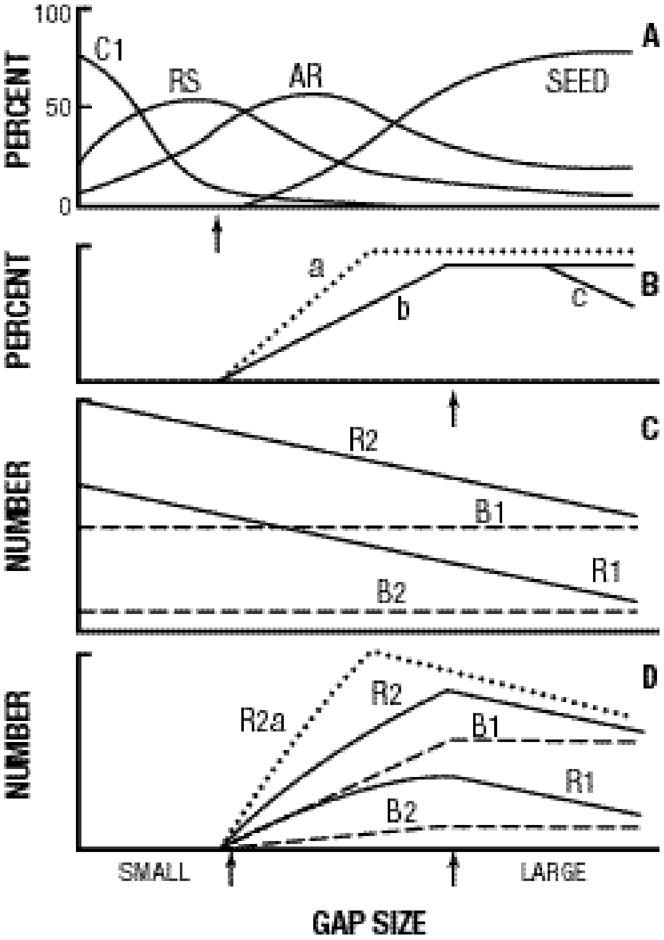


Fig. 8. Relationship of gap size to changing roles of different regeneration pathways in lowland tropical forests. (A) percentage contribution to regeneration from different pathways: canopy ingrowth (CI), root and shoot sprouts (RS), seedling bank and advance regeneration (AR), and seed bank and seed rain combined (SEED). The arrow indicates the minimum gap size for establishment of pioneers from seed. (B) Percentage of available pioneer seeds from the seed bank or seed rain that will germinate, successfully establish, and contribute to regeneration. The arrow indicates the gap size at which the maximum contribution to regeneration first occurs. The maximum contribution and gap size at which this occurs may differ among taxa (a vs. b). If mortality is greater in larger, more environmentally stressful gaps, the percentage of seeds contributing to regeneration will decrease (c). (C) Number of seeds available for regeneration at the time of gap creation. The number arriving in the seed rain (R1 or R2) will decrease as gap size increases because distance from forest edge and seed sources increases. The number of seeds in the seed bank (B1 or B2) will be independent of size of the gap just created. (D) Number of seeds contributing to regeneration from seed rain and the seed bank. Number contributing at each gap size is the product of number available (Fig. 8 C) and percentage contributing (Fig. 8 B: b for R1, R2, B1, B2; a for R2a). In B-D, percentage and number increase in arbitrary units along the axes. From Garwood (1989)

Gap size influences regeneration pathways in lowland tropical forests (fig. 8). Garwood (1989) proposed an increased dependence on seed rain and seed bank, and a sharp reduction in the role of root and stem sprouts as gap size increases. Advanced regeneration (AR) peaks at intermediate gap sizes (fig. 8a). Pioneer seeds are increasingly capable of germinating and completing their life cycles with increased gap size, unless environmentally stressful conditions develop in the large gaps (fig. 8b). Seed rain decreases with increased gap size as dispersal mechanisms limit seed rain in the very large gaps (Greene and Johnson 1995, 1996), but the number of seeds that can germinate in the seed bank is independent of gap size at the time of gap formation (fig. 8c). As a result of the previous two trends (figs. 8a and 8b), the number of seeds contributing to regeneration peaks toward large gaps and diminishes in the very large or small ones (fig. 8d).

Denslow (1980, 1987) suggested that most tropical tree species have different regeneration properties keyed to particular gap sizes, and that gap-size frequency distribution influences the types and richness of species in tropical forests. Life-history strategies for tropical forest trees could then be grouped according to light responses. She arrayed species in a continuum of light availability from high light requiring, shade intolerant, ruderal species; through light-requiring species with some shade tolerance; to highly shade-tolerant, slow-growing species. These categories conform to Grime’s ruderal, competitive, and stress-tolerant types, but Denslow noted that the resource (incident light) that regulates the response is always related to disturbance.

The light response of tropical trees is complex because light requirements change over the life cycle of individuals. These changes in turn have implications for life history groupings of trees (Augspurger 1984). In a study of gap-phase regeneration, Brokaw (1985, 1987) found evidence of gap-size specialization in only three of the many pioneer species he studied. Moreover, Clark and Clark (1992) showed that grouping of species according to the response of seeds and seedlings to light can differ when all stages of the life cycle are considered.

Gómez-Pompa and Vázquez-Yanes (1974) focused attention on secondary species, especially those with short lifespans which they termed nomads. Their life cycle model (fig. 5) contrasts secondary and primary tropical trees in life-history attributes such as periods of growth, lifespan, dispersal, pollination, flowering, time to reach sexual maturity, selection and development, germination, and seed characteristics. Although Gómez-Pompa and Vázquez-Yanes were using a dichotomy to contrast tree life histories, they segregated 21 life-history groups along an axis of successional time (fig. 9). A subsequent summary of demographic data for species in Mexico underscored the absence of a dichotomy between climax and pioneer species. Instead, a

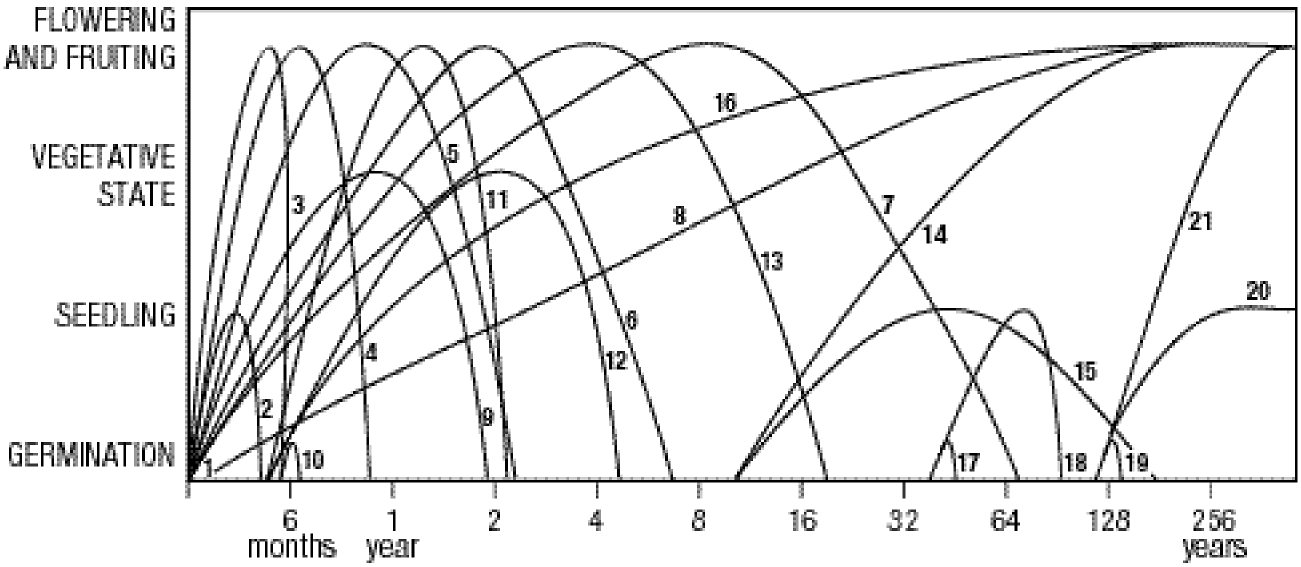


Fig. 9. A model of life-cycle patterns along a time gradient in the successional process. Each one represents a complete or an incomplete life cycle. (1) Species that germinate and die. (2) Species that germinate, produce a few leaves, and die. (3) Species that complete their life cycle in a few months. (4) Annual species. (5) Biennial species. (6) Species with life cycles of few years (<10 yr). (7) Species with a long life span, several decades, but eventually dying (species from old secondary forests). (8) Primary species with life spans of hundreds of years that have lived since the beginning of the succession. (9) Species that never reach the stage of sexual reproduction. (10) Species that germinate a few months after the succession begins and soon die. (11) Annual species that germinate after the succession begins. (12) Species that germinate after the succession begins but do not reach the stage of sexual reproduction. (13) Species with a short life cycle (<30 yr). (14) Species with a long life cycle that germinate when the succession is well advanced. (15) Species that germinate when the succession is well advanced and remain in the seedling or "young" plant stage for a few years. (16) Species that germinate a few months after succession begins and then have a life cycle hundreds of years long (primary species). (17) Species that germinate and die in old successional stages. (18) Species that germinate and live at the seedling or "young" plant stage in old successional stages, and then die. (19) Species that germinate and die in the primary forest.(20) Species that germinate and grow to a seedling or young plant stage inside the primary forest and remain there waiting for suitable conditions for continuing growth. (21) Species that germinate and grow in the primary rain forest and may reach reproductive stage after having long life cycles (primary species). From Gómez-Pompa and Vázquez-Yanes (1974).

continuum of tree life histories between these two extremes was found (Alvarez-Buylla and Martínez-Rámos 1992).

Gap processes appear to be a major determinant controlling which trees reach the canopy and form the mature stages of tropical moist, wet, and rain forests. Swaine and others (1987a) gathered evidence to show that fast-growing trees are more likely to reach the canopy and to have lower rates of tree mortality than slower-growing trees. They also found that large-diameter trees had faster growth rates than small-diameter trees. Hartshorn (1980) found that more than two-thirds of the tree species at La Selva, Costa Rica are shade intolerant and almost half of 320 tree species depend on gaps for their regeneration.

Clark and Clark (1992) observed that, for tropical wet forests, only one group of species has been clearly identified as sharing a common life history: short-lived pioneers *sensu* Whitmore (1984b). These species are characterized by high fecundity, small seeds, dependence on large openings for germination and establishment, high growth rates, short life spans, and high mortality in the shade (table 2). Representative genera are *Trema*, *Ochroma*, and *Macaranga*. Clark and Clark (1992) noted that the data are not sufficient to justify classifying the remaining tropical trees as shade tolerant or gap dependent, as if these categories were as well established as short-lived pioneer. The absence of documented operational criteria to justify the groupings limits grouping species by life-history characteristics. Clark and Clark list the following steps as needed to understand tropical tree regeneration: (1) evaluating requirements for germination and seedling establishment; (2) studying all juvenile size classes; (3) assessing performance in measured microsite conditions over the range of sites occupied by the species; (4) observing over a long term, particularly for analysis of suppression, survival, and microhabitat dynamics; and, preferably, (5) comparison of species in the same forest.

When Clark and Clark (1992) applied their criteria for 6 years to nine species in a wet forest of La Selva, they found that juveniles were associated with four patterns of microsite

Table 2

Character syndrome of pioneer tree species in tropical rain forest. Not all pioneer possess all the characters below the second listing.

From Swaine and Whitmore (1988).

1. Seeds only germinate in canopy gaps open to the sky and which receive some full sunlight.
2. Plants cannot survive in shade—young plants never found under a closed forest canopy.
3. Seeds small and produced copiously and more-or-less continuously.
4. Seeds produced from early in life.
5. Seeds dispersed by animals or wind.
6. Dormant seeds usually abundant in forest soil (especially fleshy-fruited species).
   Seeds orthodox (no recalcitrant species known).
7. Seedling carbon-fixation rate high; compensation point high.
8. Height growth rapid.
9. Growth indeterminate with no resting buds.
10. Branching relatively sparse.
11. Leaves short-lived.
12. Rooting superficial.
13. Wood usually pale, low density, not siliceous.
14. Leaves susceptible to herbivory; sometimes with little chemical defense.
15. Wide ecological range; phenotypically plastic.
16. Often short-lived.

occupancy. Among the six nonpioneer species that reached the canopy and lived as emergent trees when mature, two species were associated with low crown illumination and mature-phase forest in all juvenile stages. The two species with the smallest saplings were in predominantly low-light mature sites, but crown illumination and association with gap or building phases increased with juvenile size. Two species were strongly associated with gap or building phases as small juveniles and again as subcanopy trees, but were predominantly in mature-phase sites at intermediate sizes. Juveniles of two pioneer species showed the highest crown illumination and association with gap or building phases.

Clark and Clark (1992) concluded that life-history classification based on generalized concepts such as gap dependence and shade tolerance is inadequate to describe the complex size-dependent patterns of life-history differences and similarities among nonpioneer tropical tree species (*sensu* Swaine and Whitmore 1988). The task of elucidating the number of life-history strategies in tropical forests is daunting because the traditional dependence on seed and seedling behavior to make these determinations is inadequate; whole-life history and analysis are required to reach appropriate groupings.

Clark and Clark (1992) also observed that the regeneration of some emergent canopy trees was not gap dependent. Others have proposed (Denslow 1980, 1987) or found (Hartshorn 1978, 1980; Whitmore 1984b) that gap-dependent regeneration is common in tropical forests of the Neotropics and the Far East. These observations question the relative importance of high light adaptation (heliophytes) in the life history of mature and emergent trees in tropical forests. For emergent canopy trees at La Selva (Clark and Clark 1992), gap-dependent regeneration is not always as important as it is for other functional groups of species, such as pioneers or too many mature forest and emergent canopy trees in the wet forests of Puerto Rico (Zimmerman and others 1994). This difference brings attention to the importance of large-scale disturbances in the life histories of tropical trees.

ECOLOGICAL LIFE HISTORY IN RELATION TO LARGE AND INFREQUENT DISTURBANCES

Describing the life cycle of tropical trees commonly involves three phases (Hallé and Oldeman 1975). Phase I begins with germination, perhaps inside a gap, and continues until definitive morphological mechanisms and rhythms appear in the vegetative apparatus. Phase II begins when the specific vegetative architecture is qualitatively acquired; it proceeds as long as the young tree remains in the constant ecological conditions, often nearly optimal, that characterize tropical undergrowth. This phase can be called the microclimatic phase; the young tree can expand freely, sheltered from ecological traumas and directed by its genetic constitution. Phase III (influenced by macroclimate) begins when the tree, having acquired comparatively large dimensions, penetrates the canopy of the forest and, in full sun, develops a large, hemispherical crown of foliage. This narrative of tree development occurs in tropical moist, wet, and rain forests not subjected to large and infrequent disturbances. The absence of large and infrequent disturbances provides trees with ample time to reach and dominate canopy space.

Large and infrequent disturbances can significantly modify the chain of events implied by Hallé and Oldeman. Storms and hurricanes increase the area of canopy openings and can lessen the time the developing tree is protected from the macroclimate of the site. Vandermeer and others (1996) found that a hurricane in Nicaragua acted as a density-independent factor that eliminated competitive dominance of species, thus preserving species diversity by retarding competitive exclusion. In the following discussion we examine how large and infrequent disturbances affect ecological life histories of trees, and ask what effects they might have as agents of evolution.

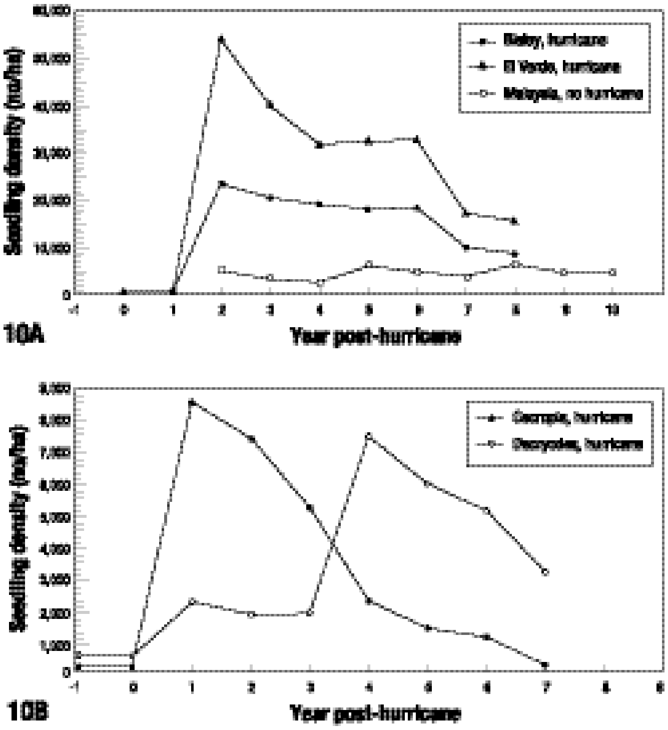


Fig. 10. A. Fluctuation of seedling populations of *Parashorea tomentellas* in Sepilok, Sabah and of seedlings after Hurricane Hugo in Puerto Rico. From Whitmore (1984) for Sabah from Brokaw, Haines, Walker, and Lodge, (unpublished) for El Verde, and from Scatena and others (1996) and Scatena (unpublished) for Bisley. The minimum seedling height for El Verde was 10 cm; for Bisley, it was 23 cm. **B.** Fluctuation of seedling populations of two species at El Verde, Luquillo Experimental Forest, Puerto Rico. *Cecropia peltata* is a pioneer species and *Dacryodes excelsa* is a primary forest species. **A and B.** Posthurricane data are from Brokaw, Haines, Walker, and Lodge (unpublished). Prehurricane data are from Lugo (1970) and Smith (1970).

HURRICANES, LANDSLIDES, AND OTHER LARGE AND INFREQUENT DISTURBANCES

Hurricanes, landslides, and other large and infrequent disturbances are significant because they can change the landscape or spatial matrix on which trees must complete their life cycles. Under the model of gap-phase dynamics, gaps are part of a large matrix of closed forests. Typically, about 0.7 to 1.2 percent of the forest area is converted to gaps annually (Denslow 1987), and gaps may cover no more than 10 percent of the landscape at any one time (Brokaw 1982, Hartshorn 1978, Lang and Knight 1983). Compared to sites subject to hurricanes or landslides, conditions for regeneration in gaps are fairly predictable (Denslow 1987). With the passage of a high-intensity hurricane, however, the landscape matrix is inverted, and gaps become the rule rather than the exception (Boose and others 1994, Brokaw and Grear 1991). Closed forest fragments can now cover less than half of the landscape. After these disturbances, microclimate and seed sources differ from those in normal forest gaps (Fernández and Fetcher 1991, You and Petty 1991). As a consequence, tree regeneration may take a different trajectory and involve species substitutions, especially if site conditions change significantly (Dittus 1985, Lugo and Scatena 1996, Walker and others 1996a). Processes are much faster. For example, tree mortality increases from 1 to 5 percent per year to 5 to 40 percent instantaneously (Lugo and Scatena 1996). Seedling abundance and temporal dynamics also change dramatically (fig. 10). Before the hurricane, seedling density in the forest as a whole averaged about 540 seedlings per ha (Smith 1970). Seedlings could reach densities of up to 1600 per ha, but they covered only 2 percent of the forest floor. After experimental disturbances, Smith (1970) counted as many as 3,000 seedlings per ha. Variability was high, with standard deviations ranging from 400 to 8,000 seedlings per ha. After the hurricane, seedling densities increased to about 55,000 per ha in highly affected areas (fig. 10a, b), and they covered the forest floor.

Landslides occupy a small fraction of the landscape (<3 percent of a subtropical lower montane wet forest) (Walker and others 1996a), but they change soil and light conditions so

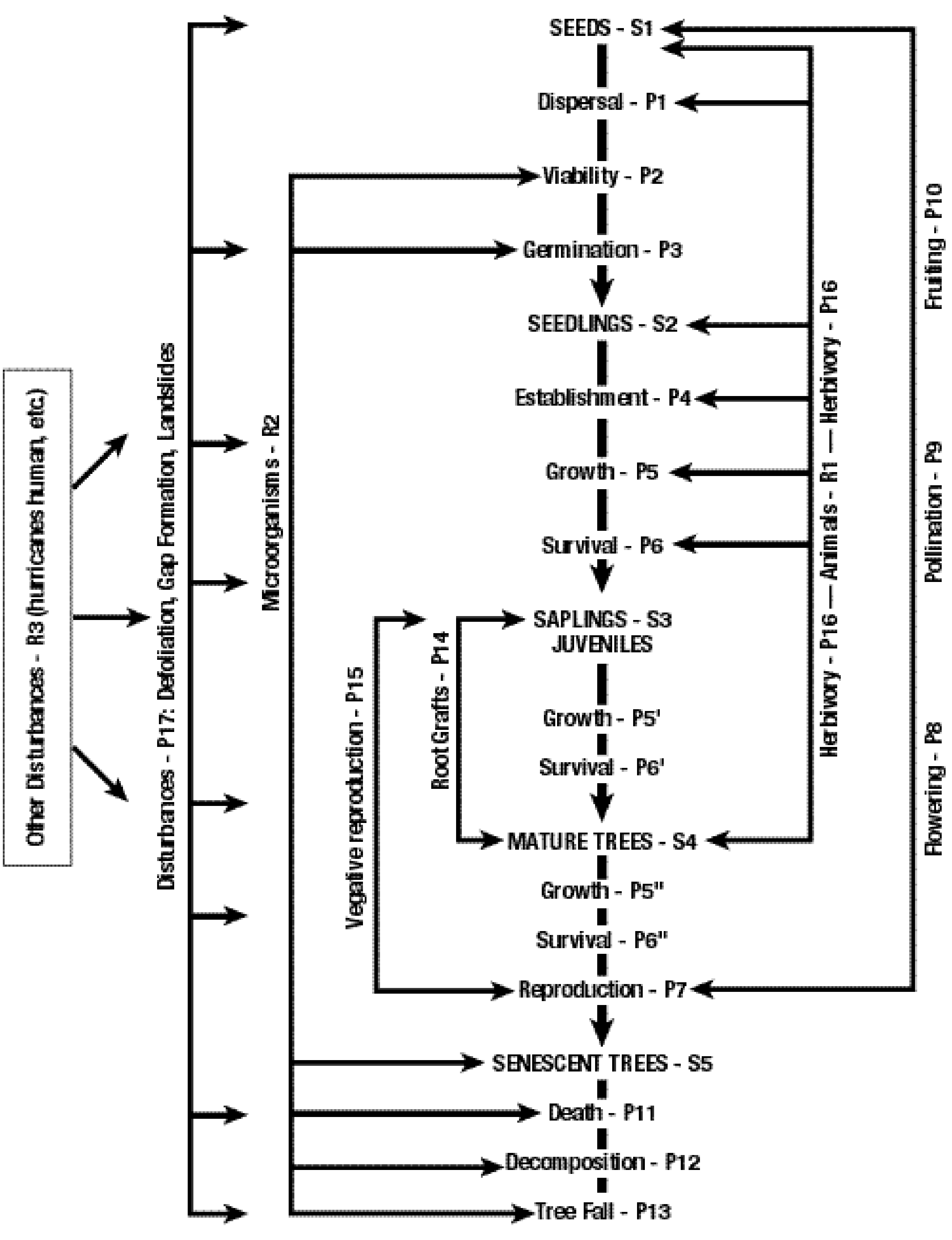


Fig. 11. Conceptual model of the ecological life-cycle of tree species in a subtropical wet forest in Puerto Rico. Life-cycle stages are S, processes are P, and population regulators are R. The number of each stage, process, or population regulator is shown after each letter code. From McCormick (1996).

much that different flora become established at the site (Walker and others 1996a). Succession can be arrested on landslides (Walker 1994), and tree establishment can be delayed, depending on the conditions of the substrate (Walker and others 1996a).

Human-caused disturbances associated with deforestation and site degradation also influence successional trajectory (Thomlinson and others 1996). Conditions for establishing species can be extreme, and, again, different species can invade as a result of human disturbances. When site degradation accompanies the disturbance, the possibility of invasion by alien species increases in both the seed bank (Garwood 1989) and the aboveground vegetation (Aide and others 1996). The reasons alien species tend to invade highly degraded sites but seldom invade undegraded natural areas are not clearly understood, but they have been the subject of much analysis (cf. Williamson 1996).

The Caribbean experience with its large, infrequent disturbances and degraded landscapes (Lugo 1996) provides a new dimension to the analysis of life histories of tropical trees because the classic work in the Far East (Whitmore 1984b) and Central America (Clark and Clark 1992, Gómez-Pompa and Vázquez-Yanes 1974) was conducted outside the hurricane belt in mature forests long removed in time from major disturbances. In the Caribbean and other parts of the Tropics, abiotic disturbances change conditions so much and so frequently that individuals must somehow complete a life cycle without the benefit of long periods of environmental stability. Life-history traits approaching those of pioneer species (*sensu* Swaine and Whitmore 1988) should be more common than those similar to shade-tolerant climax species. Similarly, the importance of heliophyte species and other life forms, such as vines, should increase. Differences between the climax and pioneer species may not be as wide ranging as those in tropical climates that do not experience large and infrequent disturbances.

RESULTS FROM WET FORESTS IN THE LUQUILLO MOUNTAINS

The tree species of the Luquillo Mountains have been classified as successional or primary according to their seed size, wood density, ratio of understory relative density to canopy relative density, and ratio of seedling relative density to canopy relative density (Smith 1970, Weaver 1995). Seed size and wood density indicators failed to produce a clear-cut dichotomy among species and yield; instead, the characteristics form a continuum, with pioneer and primary species characteristics at each end of the spectrum. The relative-density ratios of the understory and seedlings had some discontinuities that allowed three groupings of species among the 29 studied by Smith (1970). Weaver (1995) found similar results in his analysis of 20 species in a *Cyrilla racemiflora* forest. Weaver's results were notable because the dominant species in the forest (*Cyrilla*) was classified as a successional or gap species. When examining the response of tree species to Hurricane Hugo, Zimmerman and others (1994) found some evidence of a distinction between pioneer and nonpioneer species. Detailed study of the demography of more species as well as their role in succession might help explain why classifying species as pioneer or nonpioneer in the Luquillo Mountains is so difficult.

Building on the work of Pelton, McCormick (1995) developed a model of the ecological life history of trees in subtropical wet forests in the Caribbean (fig. 11). McCormick's life-cycle model was used explicitly to gather demographic data on a variety of tree species (Bannister 1967, Lebrón 1977, Muñíz Meléndez 1978, Sastre de Jesús 1979, Silander 1979, You 1991) to understand the role of tree populations in the plant community. The model includes five life-cycle stages from seeds to senescent trees, 17 processes (three associated with seeds, three with seedlings, two with saplings, three with mature trees, three with senescent trees, and six that feed back from one stage to a previous stage of development), and three classes of population regulators such as animals, microorganisms, and disturbances.

This model, like that of Gómez-Pompa and Vázquez-Yanes (fig. 5), is useful as a checklist for the kinds of measurements needed to evaluate the parameters of the life cycle of a species. In addition, McCormick's model includes disturbances as a regulatory process in the life history of tropical trees. Similarly, even though the importance and consequences of the three processes of tree senescence in the Tropics are poorly understood, they provide valuable insight into forest development and functioning (Lugo and Scatena 1996, Scatena and Lugo 1995).

Each of the six species studied (table 3) exhibits complex life-history traits with strategies that are considered pioneer in one stage of development and nonpioneer in another. *Manilkara bidentata* has deep-shade-bearing seedlings that survive for decades under a closed canopy and exhibit slow growth, but mature individuals dominate in the canopy. These traits suggest a nonpioneer strategy. However, *Manilkara bidentata* grows explosively after a disturbance, much like pioneers (You and Petty 1991). Even more notable are species that behave as primary species in some locations and as pioneer species in others (e.g., *Prestoea montana*) (Bannister 1967, Lugo and others 1995). The establishment of *Buchenavia capitata* (Sastre de Jesús 1979), a late-successional species, is furthered by hurricanes. The species thrives in riparian areas where continuous disturbances cause high turnover rates of individuals of all species (Scatena and Lugo 1995). *Palicourea*

Table 3

Summary of Ecological Life Cycles of Six Tree Species in the Luquillo Experimental Forest

	Cecropia peltata	*Prestoea montana*	*Buchenavia capitata*	*Palicourea riparia*	*Inga vera*	*Manilkara bidentata*
Stages						
Seed	Numerous (6.7 x 10^6 per individual), small (2 mm length), long viability (2 to 6 mo.). Germination favored by forest disturbance (76% vs. 0.3%)	Large (fruit approx. 1 cm, wt 0.07 g), numerous (mean = 1.4/m^2 throughout forest). Short viability. Long maturation (>3 mo). High predation.	Large fruit, high production (22.4 x 10^6/ha/yr), but high predation (>20% eaten by rodents).	Prolonged dormancy and viability.	Large, few survivors, and poorly dispersed. Poor viability (1 week of “dry days” = no germination).	Large and few (0.3/m^2); no dormancy.
Seedling	High survival in gaps (80% vs. closed forest 0%). Rapid height growth.	Relatively long-lived (3 x longer than mean for all species). Slow growth (mean height growth = 0.1 mm/mo in forest.	High mortality (86%).	Acclimate quickly to new light conditions.	Shade adapted but respond to increased light. Sixfold increase growth in gaps.	Very long lived (35 to 50 yr), shade adapted, and strong (survive burial by litter).
Juvenile	Rapid growth in gaps (max. 2.2 m/yr height and 3.0 cm/yr diameter.	High mortality (sapling survival is no greater than seedling).	High survival to maturity (59%).	Shade adapted.	Growth is light limited. High mortality (>99% from seedling to juvenile).	Low mortality. Very shade tolerant.
Mature tree	Growth shifts more to radial increase (mean = 0.6 cm/yr, max. = 1.5 cm/yr. Short-lived (<30 yr).	Intermediate life span (mean 61 yr). Intermediate reproductive maturity (25 yr). Long time to reach canopy (50 yr).	Apparent high survival (87%) once trees reach subcanopy (10 m or more, 30 to 50 yr).	Reproductive maturity within 2.5 yr.	Early senescence (35 yr).	Long lived: 50 yr to canopy >100 yr life span.
Process						
Germination	Requires light or disturbance (76% in gaps, 0.3 in closed forest).	Intermediate success (53%). Slow (3 to 6 mo).	During dry season, mesocarp removal requires 45 days.	Very low and limited by light (14% in gaps vs. 6% in forest).	Initially high (83%) but diminishes rapidly (20% after 3 mo). Restricted to gaps.	No dormancy, 42% germination of viable seed.
Growth	Explosive (trees ≥2 m/yr). Reach canopy <10 yr.	Shade-adapted, light- limited (10-fold greater in light, 10- fold greater growth).	Light limited. Seedling growth 3.7 cm/mo in gaps vs. 0.7 cm/mo in closed forest.	Rapid and extreme response to light. High photosynthetic rates but low quantum yield.	Light limited.	Shade adapted. Seedling growth >40-fold in gaps vs. forest.
Reproduction	Prolific (>10^6 seeds/yr/ tree). Wind pollinated. Early maturity (<4 yr).	Bee and fly pollination. High seed production (>5000/individual/yr).	Prolific seed production (448,000/tree/yr). Wind damage to flowers.	Pollination by bees and hummingbirds. Light-limited (95% fewer seeds produced in forest vs. gaps).	Vivipary results in high seed loss to predators. Prolific flowering but few seeds (one seed per 255 flowers). Damage by pollinators. Very inefficient.	Late maturation. Bee pollination. Few seeds/fruit. Few seeds produced.

Table 3 (continued)

	Cecropia peltata	*Prestoea montana*	*Buchenavia capitata*	*Palicourea riparia*	*Inga vera*	*Manilkara bidentata*
Dispersal	Widely in forest (mean 300/m^2 throughout forest). Birds and bats.	Poor; birds and rats (density under parent tree 5.5m^2 vs. 1.4m^2 throughout forest).	Nearly nonexistent (5.2 seeds/m^2 under parent tree vs. 0.6/m^2 in forest.	Birds, well-dispersed.	Birds, rodents, and water. Very poor. No seed in forest except under parent tree.	Bat-dispersed seed (95% of eventual seedlings). High mortality under parent (70% over 3 yr).
Survival	Short-lived (30 yr). Gaps only.	Intermediate life span (mean 61.1 yr). Seed to seedling 53%. Seedling to juvenile 32%. Seed to mature tree 0.05%.	Furthered by hurricanes.	Light limited (77% in gaps vs. 53% in forest).	Seed and seedling survival very poor.	Long-term seedling survival >35 yr. High post-hurricane survival of seedlings provides recruitment to tree size class.
Phenology	Flower all year. Max. Jan. to Mar. Dry season.	Flower all year. Max. June to Sept. Max. fruit Oct. to Jan.	Flowering at leaf fall during dry season.	Reproduction all year but not prolific.	Max. fruit Mar.-June.	Extremely sporadic flowering, tree to tree, branch to branch.
Special Adaptations	Rapid growth. High reproduction. Good dispersal.	Prop. roots, shade-adapted.	Pollination benefits from leaf fall. Excellent wood quality.	Reversible acclimation to light. No ecotypes.	Vivipary and pollination very inefficient. Suspect loss of original pollinators and dispersal species	Bat dispersal to favorable sites. Long- lived seedlings and acclimation to increased light contribute to hurricane resistance. Benefits from hurricanes and bat dispersal.
Habitat Preference	Obligate gaps.	Boulder fields, ravines.	Throughout forest.	Gaps.	Mesic sites.	Excellent wood. Mesic plateaus and slopes.

riparia (Lebrón 1977) is a gap species that thrives after hurricanes and other disturbances, such as exposure to ionizing radiation, but grows as a small tree under the canopy of the mature forest. *Palicourea* reaches reproductive maturity in 2.5 years. *Inga vera* is a nitrogen fixer with vivipary, gap dependency in its early stages of regeneration and shade tolerance in the seedling stage (Muñíz Meléndez 1978). *Cecropia peltata* (now *C. schreberiana*) is a typical pioneer species throughout moist and wet forests in Puerto Rico (Silander 1979), but not in rain or floodplain forests or in pastures (Aide and others 1996, Frangi and Lugo 1998, Walker and others 1996b).

The following short summaries of the life-history traits of two species in the wet forests of the Luquillo Mountains illustrate some of the previous generalizations, show the complexity of life-history strategies, and highlight characteristics that could be construed as responses to a high-disturbance regime. The canopy tree *Manilkara bidentata* is considered a primary forest species based on its shade tolerance in the seedling stage, slow growth inside the forest canopy, high-density wood, large seeds, and few seeds (You 1991, table 2). Seeds have a short period of viability and no dormancy mechanism. Seedlings of this species are large, woody, and can live >40 years in the forest understory. Mature trees are also long lived. Saplings are shade tolerant, have a low mortality rate, and are considered the critical point of the life cycle (You 1991, You and Petty 1991). In spite of these characteristics, transplanted seedlings can grow up to 24 times faster in tree fall gaps than they grow in the shade (You 1991).

Table 4

Effects of Hurricane Hugo on the Life Cycle of *Manilkara bidentata*, a Primary Forest Tree Species

	From young to old seedling		**From old seedling to sapling**	
Parameter	Pre-hurricane	Post-hurricane	Pre-hurricane	Post-hurricane
Recruitment cost[a]	168.3	7.5	4.0	0.3
Transition period (months)	140	28	292	16

[a] Number dead/number recruited to next size class.

Source: You and Petty (1991); data from El Verde.

Hurricane Hugo caused a pulse in the mortality of large *Manilkara* trees (4 percent), young seedlings (61 percent), and old seedlings (30 percent) (You and Petty 1991). Mortality below the canopy was the result of crushing by wood fall and burial by litter. No flowers, fruits, or seeds were found for 9 months after the hurricane. As a result, new recruitment was expected to be delayed for at least 2 years after the hurricane. Those individuals that survived the hurricane, however, adjusted to new light conditions, grew faster, and moved into larger size classes with greater efficiency in less time than before the hurricane (table 4). Given the low mortality of the advanced life stages in this species, the hurricane actually increased the presence of *Manilkara bidentata* in the forest. Hurricane disturbance also boosted the number of saplings in the forest to higher values than before the hurricane. The result was that a single hurricane was sufficient to overcome both its own instantaneous effects and those of past selective logging on the populations. To take advantage of this disturbance event, the individuals involved changed from deep-shade tolerance to a strong, sun-adapted growth pattern, which required discarding old leaves and forming new ones (You and Petty 1991).

Dacryodes excelsa (tabonuco) is another primary forest species (Smith 1970). Its seedlings are shade adapted and incapable of adjusting to full sunlight (Lugo 1970). The seedlings depend on mychorrhizae for their establishment (Guzmán Grajales and Walker 1991) and respond positively to the presence of litter on the ground and negatively to its absence. During the 1960's and 1970's, finding saplings and poles of the species was difficult when the forest canopy at El Verde was closed and the forest was in an apparent steady state (Lugo and others 2000; Odum 1970). Many fruit crops were sterile year after year. Periodically, however, large seedling explosions occurred, with average seedling densities of 481 per ha (Lugo 1970). Seedlings were more common in ridges where densities reached 8,776 per ha ±1,240 in high years and 728 per ha ±307 in low years. In valleys, seedling densities reached 4,304 per ha ±1010 in good years and 2,334 per ha ±118 in low years (Lugo 1970). Without significant disturbances, tabonuco seedling populations have a half-life of 6 months and their growth is limited to increasing leaf numbers and some stem thickening (Lugo 1970). With canopy opening by Hurricane Hugo and closure 5 years later, seedlings, saplings, and poles became common (fig. 10b), although the peak densities lagged the hurricane by 4 years. In contrast, the pioneer *Cecropia peltata* peaked in seedling density less than 1 year after the hurricane (fig. 10b).

Seedlings of *Dacryodes excelsa* had more and larger leaves than before the hurricane, and height growth was explosive (authors' personal observations). We estimate that for the *Dacryodes excelsa* population at El Verde, seedling explosions occur at about 60-year intervals after major hurricanes. In the regeneration strategy of *Dacryodes excelsa*, seedlings are constantly turning over until a hurricane event creates the conditions under which a particular seedling crop will successfully reach the canopy, while in the *Manilkara bidentata* strategy seedlings survive the interhurricane interval in the forest as advanced regeneration.

Seedling populations of *Dacryodes excelsa* tend to concentrate on ridges (Lugo 1970) where adults dominate and form tree unions by interconnecting all individuals through root grafts (Basnet and others 1993). These tree unions effectively exclude competitors from these locations, which have the best aerated soils in the forest (Silver and others 1999). Tree unions provide effective resistance to wind storms because trees on ridges survive the highest winds observed in Puerto Rico (Basnet and others 1992, Scatena and Lugo 1995, Wadsworth and Englerth 1959). Another mechanism of wind tolerance is the disposal of branches during the storm, followed by vigorous resprouting after the event (Zimmerman and others 1994). As a result, many species in the tabonuco forest have low ratios of canopy area to stem area (Pérez 1970). Because the root connections of the tree union allow materials to interchange among trees, suppressed and dead trees and stumps resprout after the disturbance event (Basnet and others 1992, 1993; Scatena and Lugo 1995). This resprouting assures that the tree union will continue to exert dominance over ridge sites regardless of the fate of particular individuals within the union.

After hurricanes in Nicaragua and Puerto Rico, many species resprouted new branches from delimbed trunks within a few months of the disturbance, and this was an important component of post-hurricane recovery (Yih and others 1991, Zimmerman and others 1994). Yih and others (1991) called this resprouting direct regeneration, and Zimmerman and others (1994) showed how it was tied to plant life histories. Trees showed clear tradeoffs in hurricane damage and recovery. Many species had low mortality in the hurricane, lost many branches, and resprouted at high frequency after the hurricane. Pioneers suffered high mortality (30 to 60 percent of the trees >10 cm d.b.h.) due to high frequencies of broken stems; survivors exhibited low frequencies of sprouting. These frequencies, summarized using principal components analysis, suggested that the responses of pioneers were separate from those of the remaining nonpioneers. The primary differences, reflecting the tradeoffs mentioned above, fell along the first principal axis. This axis correlated with an index of shade tolerance for these same species, developed from data in Smith (1970), which indicates a connection between seedling and adult life-history traits.

RESULTS FROM LANDSLIDES IN THE LUQUILLO MOUNTAINS

Landslides expose large areas of mineral soil, depositing the organic surface soil at the bottom of the landslide. These two regions of the landslide often have differing successional trajectories because of different nutrient availability (Walker and others 1996a). Fetcher and others (1996) studied the growth and physiological responses of two pioneer and two nonpioneer species to fertilization in the exposed mineral soils of a landslide. The two nonpioneer species (*Manilkara bidentata* and *Palicourea riparia*) (table 2) responded to increased phosphorus availability but not to increased nitrogen, but the two pioneer species (*Cecropia schreberiana* and *Phytolacca rivinoides*) responded to both phosphorus and nitrogen. Pioneer species appear to be highly nutrient demanding, which might help explain why they do not successfully invade degraded sites. Landslides also pose conditions–hot and organic matter-free substrates with little soil structure–that are extreme for tree seed germination, but benefit from the establishment of ferns and other herbaceous species. These latter species can dominate the site for long periods while soils rehabilitate, resulting in periods of arrested succession (Walker 1994).

RESULTS FROM RAIN FORESTS IN THE LUQUILLO MOUNTAINS

In elfin and *Cyrilla* forests in the subtropical rain forest and subtropical lower montane rain forest life zones, excessive moisture and poor dispersal conditions create difficulties for plant regeneration (Brown and others 1983). Cloning, a regeneration strategy observed under these conditions, is seen in *Tabebuia rigida* at high elevations in the Luquillo Mountains. After observing a plane-crash scar in an elfin forest for 23 years, Weaver (1990b) suggested that these forests lacked pioneer tree species. The grasses that invaded the site were slowly being replaced by the previously common tree species without an intervening stage of highly abundant pioneer trees. Walker and others (1996b) found evidence to support the hypothesis that pioneer species do not grow in the elfin forest. After Hurricane Hugo, fertilized plots in low-elevation forests were dominated by *Cecropia schreberiana*, but the only species available to respond to increased nutrient availability in the hurricane-damaged elfin forest were grasses, which grew in great abundance. No pioneer tree species invaded after the hurricane. Lugo and Scatena (1995) interpreted this as allogenic autosuccession resulting from the wetland conditions of forests, such as elfin, palm, *Cyrilla*, and mangroves. Under these wetland conditions, species like *Prestoea montana, Tabebuia rigida, Cyrilla racemiflora*, and *Rhizophora mangle* can be interpreted as successional or climax species depending on where they grow (Lugo 1980, Lugo and others 1995, Weaver 1995).

RESULTS FROM DRY FORESTS IN PUERTO RICO AND CENTRAL AMERICA

Dry forest plants face conditions that are very different from those in moist, wet, and rain forests. In dry forests, plants do not appear to compete for light, but they must secure a reliable water supply under conditions of high air temperature, high atmospheric saturation deficit, and irregular and low amounts of rainfall. Seedling establishment and tree growth under these conditions require life-history strategies different from those that are successful in moist to rain forests (Bullock 1995; Castilleja 1991; Gerhardt 1994; Lugo and others 1978; Medina, in press; Molina Colón 1998; Murphy and Lugo 1986a, 1986b; Murphy and others 1995). The concentration of sap in dry forest species, which is high compared to that of species from moist to rain forests, tends to increase with aridity (Medina 1995). This concentration allows dry-forest trees to secure water from soils with low water content. Succulent tree species like *Clusia* sp. maintain lower osmotic pressures in their sap and survive dry forest conditions by storing water and conducting crassulacean acid metabolism (CAM) (Medina 1995). Bullock (1995) noted that, contrary to the situation in wetter forests, trunk size is a mediocre predictor of reproduction in dry forests. He also suggested that greater density of individuals may favor outcrossing in dry forests.

In spite of the water limitation in dry forests, plants there face a highly heterogeneous environment. The basis for environmental heterogeneity rests on edaphic gradients such as soil depth, fertility, and moisture, as well as seasonal variation in most environmental factors including rainfall. Medina (1995) has shown that dry forests harbor more plant life forms than do moist to rain forests. Each of these different life forms has different metabolic strategies (from evergreen to deciduous to succulent), different functional attributes (Ewel and Bigelow 1996), and different life-history characteristics. Unfortunately, this diversity of ecological life histories has not been documented in detail. Molina Colón (1998) classified dry forest species into pioneer or primary based on propagule size, fruiting periods, soil conditions required for germination, shade tolerance, gap size preferences, growth rates, and length of vegetative period. With these criteria, she placed *Leucanena leucocephala, Croton astroites, C. rigidus, Guazuma ulmifolia,* and *Lantana arida* as pioneer species, and *Bursera simaruba, Bucida buceras, Machaonia portoricensis,* and *Eugenia fortida* as primary species.

Seeds in the Guánica Forest, Puerto Rico, are dispersed primarily by birds and ants and germinate only when adequate moisture is available (Castilleja 1991). The seed bank is low in number of seeds and species represented (Castilleja 1991, Molina Colón 1998, Murphy and others 1995). Seedlings are uncommon on the forest floor and limited to shaded sites. Seedling recruitment is an infrequent event and most trees can coppice by either roots or stems (Dunevitz 1985, Dunphy 1996, Ewel 1971, Molina Colón 1998, Murphy and others 1995). Most life-history events in the Guánica Forest (such as flowering, fruiting, leaf fall, leaf growth, tree growth, and seed germination) are synchronized with the cycles of rain and drought (Murphy and Lugo 1986a, 1986b; Murphy and others 1995). However, because access to water differs in these areas, some trees may have a complete complement of green foliage, flower in the midst of extended drought, and be completely deciduous.

Castilleja (1991) compared the seeds from the Guánica Forest with those from Luquillo (dry vs. wet forest) and found that dry-forest seeds tend to be remarkably small. Although fruiting seasons occur, they do not appear to be timed as a moisture avoidance mechanism, as they are in Costa Rica (Frankie and others 1974). Seeds are dispersed by birds year round, which represents a positive adjustment to highly variable rain. In other tropical dry forests, seeds are predominantly wind dispersed (Frankie and others 1974). Seeds in Guánica Forest have impermeable coats and delayed hypogeal germination; they germinate in response to adequate moisture supply. Seedling density varies according to forest cover, increasing in closed-canopy deciduous forests and decreasing toward the cactus scrub. Seedling banks, like seed banks, are sparse and reflect the canopy dominants. Seedling recruitment is very infrequent and responds to moisture availability. One species, *Bursera simaruba*, showed higher recruitment rates and growth rates when emerging from crevices on exposed limestone; it grew faster in exposed areas than in shaded locations where other species tended to grow better. Most species in Guánica Forest avoid drought, and both the seedling and seed banks fail to exhibit the abundance and diversity of trees in the overstory (Castilleja 1991, Molina Colón 1998). These findings highlight the importance of resprouting as an important regeneration strategy in this forest (Dunevitz 1985; Dunphy 1996; Ewel 1971; Molina Colón 1998; Murphy and Lugo 1986a, 1986b; Murphy and others 1995).

In dry forests with greater rainfall and deeper soils than in the Guánica Forest, the forest is taller (Murphy and Lugo 1995), and seedlings are larger and represent a more diverse group of species. More moisture, shade, and nutrients are available, which allows for a more diverse set of strategies for seedling establishment and growth. Gerhardt (1994) studied seedling development strategies for four tree species (*Hymenaea courbaril, Swietenia macrophylla, Manilkara chicle*, and *Cedrela odorata*) and found significant differences in their response to light and moisture. Drought was the main cause of mortality, and some species invested in developing deep root systems before elongating. Root competition increased the effect of drought and when it was reduced by trenching, seedling development was improved. Some evergreen cover reduced mortality during the dry season. Thinning the canopy benefited *Hymenaea courbaril* and *Swietenia macrophylla* but lowered the survival of *Manilkara chicle* and *Cedrela odorata*. Attaining large seedling size before the onset of the dry season improved the chances of survival. *Hymenaea courbaril* and *Swietenia macrophylla* established well in pastures and young secondary forests. *Manilkara chicle* had low survival in these environments, and *Cedrela odorata* failed in most environments, limiting its recruitment to wet years.

CONCLUDING REMARKS

Available results suggest notable differences when species from contrasting forest types are compared (i.e dry forests with moist to rain forests, or wetland forests with nonwetland forests) as well as differences of degree between forests with similar climate but different disturbance regimes (i.e. wet forests having only tree-fall gaps, with wet forests subjected to hurricanes). These differences are presented below as generalizations, but they actually represent hypotheses to be tested through further research.

The major difference between dry and moist forests is the overwhelming role of water in dry forests versus that of light in moist, wet, and rain forests. Tree life histories in tropical dry forests are thus more responsive to water than they are to light, and the opposite is true in moist to rain forests. Timing and rate of life-history processes are synchronized to intensity, timing, and variability of rainfall in dry forests; but in moist to rain forests, the life histories are synchronized to intensity and duration of incident light.

In wetland tropical forests, low soil oxygen is a factor that influences seed germination and, as a result, life-history traits include vivipary, seedling banks, absence of seed banks, cloning, adventitious tissues, pulsed regeneration tied to favorable periods, frequent sprouting, and short successions culminating in autosuccession.

Life histories of trees influenced by hurricanes are characterized by short life spans, early age of first reproduction, leaf heterophylly, ability to change quickly from shade tolerance to shade intolerance, advanced regeneration, conspicuous sprouting, tree unions, and low crown-area to stem-area ratios. As stressors increase (from moister forests without hurricanes, to forests of the same climates with hurricanes, to wetland forests), the number of species capable of completing their life cycles decreases.

The sequences described in figure 8 for gap dynamics do not apply to sites with hurricane regeneration, in part because the conditions after a hurricane differ from those predicted for large gap size. In large gaps, advanced regeneration and resprouting are supposed to be at minimal values, but after a hurricane, these two mechanisms of regeneration achieve predominance. Moreover, compared to sites with gap-phase dynamics as the main disturbance regime, the time available for uninterrupted growth is dramatically reduced in sites with large and infrequent disturbances. Interruption of growth conditions may act as a selective force for life-history traits that include shorter life spans, earlier reproductive age, smaller biomass accumulation, sprouting, and morphological and physiological plasticity in early stages of the life cycle. Similarly, the observed changes in species and life-form composition in landslides and sites degraded by human-caused factors signal the limits of adaptation of the life histories of normal tree species. These changes also suggest the selection of more extreme biotic adaptations for establishment and survival in these disturbed environments, perhaps analogous to the concept of the supertramp in birds (Arendt 1993).

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