



Tree Demography and Gap Dynamics in a Tropical Rain Forest

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large gaps clearly could enhance persistence of rare species more light-demanding than the shade-tolerant dominants, especially if, once in the canopy, the former had a high probability of colonizing any new large gaps (e.g., via seed banks).

NORTH–SOUTH ASYMMETRY OF LIGHT

The initial north–south gradient in light levels in the large gap has become reversed over the past 13 yr. This has affected advance recruitment along edges of the gap. Along the northern edge high initial light intensities promoted rapid growth of saplings, shrubs, and herbs, as well as ingrowth (3–5 m) of adjacent beech canopies. Understory light levels have declined from 25% to \approx 2% of full sunlight. Saplings < 10 m are greatly suppressed; recruitment of all species but beech has ceased. In contrast, along the southern edge, where initial light levels were \approx 10% full sunlight, rapid growth of saplings, shrubs, and herbs has not occurred, and ingrowth of beech canopies has only been 1–2 m. Light levels have declined to only \approx 5% full sunlight. Recruitment of many species has continued to occur, and understory beech and maple have continued to increase in size. Asymmetry of light in gaps thus can have important consequences, since new gaps formed along northern and southern edges of older gaps are likely to differ initially in species composition, size structure of cohorts, and degree of suppression.

LIGHT REGIMES IN TEMPERATE AND TROPICAL GAPS

Within forests not subjected to widespread disturbance, patterns of illumination in gaps should change with latitude. Maximum initial light intensities should be lower in temperate than tropical gaps. Also, initial light intensities should decrease from north to south

in north temperate gaps, while in tropical gaps, initially light should be most intense near the center and decrease concentrically (but only twofold; Denslow 1987) toward the edges. Thus, high light levels should occur under much more restricted conditions (and thus less often) in temperate than tropical gaps. In addition, unlike tropical forests, there should be no systematic association of gap microhabitats (mineral soil; tip-up mounds) conducive for germination and rapid growth (see Putz 1983, 1984, Williamson 1984, Wiemann and Williamson 1988) with high light intensities in temperate forests. Such restrictions, especially if coupled with seasonal constraints on responses to variation in light environments (see Runkle 1989), could greatly limit numbers of high-light-demanding pioneer species (*sensu* Swaine and Whitmore 1988, Whitmore 1989) in temperate relative to tropical forests.

The relative importance of within-gap light regimes on the population dynamics of shade-tolerant species in forests not subjected to widespread disturbance is less clear. While advance regeneration occurs at all latitudes, the relative importance of responses to differences in light levels (relative to other phenomena, both prior to and after gap formation; see Brokaw and Scheiner 1989, Martínez-Ramos et al. 1989, Schupp et al. 1989) may change with latitude. We suggest that growth rates at different light levels may increase in importance in temperate compared to tropical forests since within-gap light regimes are more heterogeneous and change more extensively with gap size. Hence, there may be greater predictability of forest composition based on growth responses of shade-tolerant species in temperate than tropical forests because of the increasing importance of variation in light levels within gaps at higher latitudes.

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TREE DEMOGRAPHY AND GAP DYNAMICS IN A TROPICAL RAIN FOREST

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Forests can be considered dynamic mosaics of vegetation patches of different ages produced by disturbances and influenced by different abiotic and biotic conditions. Three main phases (gap, building, and mature) have been recognized in the forest regeneration cycle since initial work by Watt (1947). Each phase

poses particular problems and advantages for the regeneration of different species. Whitmore (1975, 1982, 1989) and Swaine and Whitmore (1988) have placed tropical trees in either of two categories defined by their light requirements for germination and establishment, suggesting two main routes by which trees may attain

maturity in the forest mosaic. Light-demanding pioneer species germinate, establish, and grow to maturity only in gaps, while nonpioneer (climax) species germinate and establish primarily in the shade, but often attain maturity when juveniles are released from suppression.

Whitmore's framework restricts species to one route to maturity and defines this route in terms of light requirements early in the life cycle. This dichotomy uses general (average) demographic patterns and overlooks demographic variability. For example, the occurrence of seeds may be influenced by differential dispersal and/or dormancy. Furthermore, the latter parts of the life cycle are de-emphasized in the model, while in reality successful colonization may be followed by differential survivorship, growth and/or reproduction. Hence, such a dichotomous model may be useful for initial classification, but it may greatly limit analyses of mechanisms involved in the population dynamics. Such analyses must consider all possible routes that individuals of tree species follow to attain maturity, as well as the factors determining the probability of success of each route. It is the composite of all successful and unsuccessful routes to maturity that eventually determines growth rate of a population, which in turn defines its local persistence or extinction.

We have approached the analyses of mechanisms leading to persistence of pioneer and nonpioneer species in the Los Tuxtlas tropical rain forest (Veracruz, Mexico) by combining two types of studies: (1) demographic surveys of species with contrasting life histories, considering all types of forest regeneration phases, and (2) quantitative evaluations of the forest disturbance regime. In this paper we first illustrate some of the individual variability in demographic patterns resulting from local interpatch variation. Then we show how matrix models might be used to integrate analyses of regeneration routes in different forest patch types for estimation of population growth rates. Two abundant tree species, which have contrasting average demographic patterns (Piñero et al. 1984, Alvarez-Buylla 1986), constitute our main examples. The heterogeneous population structure of the shade-intolerant pioneer *Cecropia obtusifolia* (Moraceae), in which cohorts of different ages are highly correlated with ages of gaps (Alvarez-Buylla 1986), contrasts with the almost homogeneous distribution of different-aged trees of the shade-tolerant *Astrocaryum mexicanum* (Palmae) across patches of different age in the Los Tuxtlas tropical forest (Martínez-Ramos et al. 1988a).

DEMOGRAPHIC VARIABILITY

As a result of differences in life histories, interpatch environmental variation is likely to affect all life stages of *A. mexicanum*, but primarily dispersal and survival

of seeds of *C. obtusifolia*. Seed occurrence in *A. mexicanum* is highly correlated with the distribution and fecundity of mature palms. Most seeds fall directly under the palm canopy, and they do not accumulate in the soil (Piñero et al. 1984). In contrast, *C. obtusifolia*'s seeds are dispersed by various frugivores to all forest patches (independently of patch age), but remain dormant in the soil for periods of time that vary in length depending on the patch type. *Cecropia*'s seeds are removed from the soil at higher rates in newly formed gaps and mature patches than in patches dominated by fruiting trees (3–35 yr after disturbance). In the latter, an abundant seed rain (≈ 2000 seeds \cdot m⁻² \cdot yr⁻¹) seems to satiate predators (Alvarez-Buylla 1988, E. Alvarez-Buylla and M. Martínez-Ramos, *unpublished manuscript*). In contrast, the shade-tolerant understory tree *Trichilia martiana* (Illescas 1987) and other species eaten by mammals (V. Sánchez-Cordero, *personal communication*) suffer greater seed losses in mature patches than in gaps.

While seeds of shade-intolerant species germinate mainly in gaps at Los Tuxtlas (Vázquez-Yanes and Orozco-Segovia 1984), seeds of other species are likely to germinate in patches of a range of ages. For example, photoblastic seeds of *C. obtusifolia* germinate at rates >90% in gaps >30 m² (M. Cano, M. Martínez-Ramos and E. Alvarez-Buylla, *personal observation*), but some seeds germinate and establish even in closed forest. Nevertheless, germination is not necessarily synonymous with recruitment into the population: seedlings survived only in gaps with areas >100 m². Moreover, seedlings do not have their journey to maturity insured by being in large gaps, because mortality factors other than shading affect seedling survivorship. For example, all the seedlings established in a well-illuminated area of a large gap (>400 m²) were killed when the trunk of the fallen tree rolled over them (Alvarez-Buylla 1986).

In the Los Tuxtlas forest the population of *Astrocaryum* experiences contrasting demographic conditions in two different patch types: (1) low probability of both recruitment and mortality beneath a closed canopy, and (2) high probability of both recruitment and mortality in gaps. Sources of mortality also differ depending on patch type. Herbivory and damage due to falling debris have greater negative effects on survivorship and growth of *A. mexicanum* and other shade-tolerants beneath a closed canopy than in gaps (Dirzo 1984, Mendoza et al. 1987). Greater recruitment of juveniles of *A. mexicanum* in gaps is followed by higher mortality from intraspecific competition in gaps than beneath the canopy (Martínez-Ramos et al. 1988a). Differences in mortality, growth, and fecundity of this understory species are also related to the type of patch in the forest. Blows by falling trees and debris caused more than one-third of the deaths of adult *A. mexi-*

canum over a 12-yr period (Piñero et al. 1984). Such mortality does not occur in gaps. At the same time, increased light resources and reduced root competition in newly formed gaps enhance growth and fecundity of undamaged plants (Martínez-Ramos and Alvarez-Buylla 1986, Martínez-Ramos et al. 1988a).

Because ages of *Cecropia* roughly coincide with the ages of patches in which they occur, patch effects on survivorship, growth, and fecundity are confounded with effects of tree age and size. We have found that age and size (dbh) of trees explain a significant proportion of the variation in adult growth and fecundity. But there also are some indications that within-patch-type variation may be explained by differences in patch size and intraspecific density of trees. In addition, survivorship and growth rates of *Cecropia* seedlings and saplings vary with light levels within patches (Alvarez-Buylla 1986).

The viability of a gap vs. a non-gap-mediated route to maturity will depend, then, on the action of various biotic and abiotic factors, in addition to responses of seeds and juveniles to light. We have reviewed mainly factors that are either spatially or temporally correlated with gap age, but there is at least one example of a shade-tolerant non-pioneer species (*Virola surinamensis*) becoming gap dependent during drought (Howe et al. 1988).

GAP AND POPULATION DYNAMICS

To integrate all possible routes to maturity for estimation of population growth rates in a forest mosaic we need data on (1) areas covered by patches of different sizes and ages since disturbance, as well as transition probabilities among patches of different age and size, (2) probabilities of occurrence of propagules in these different patches (given by average density of seeds per patch type times area covered by patch), (3) rates of survival, growth, and reproduction of trees in these different patches, (4) probabilities that gaps of a given size and age affect trees in one or more life-cycle stages, and (5) rates of change in demographic parameters as gaps of given sizes and ages change.

Different species will require studies that differ in temporal and spatial scale. For example, an area of 600 m² is large enough to reveal population dynamics of *Astrocaryum mexicanum* (Piñero et al. 1984), but an area as large as 5 ha is required for *Cecropia obtusifolia* (Alvarez-Buylla 1986). Twelve years of demographic studies on *A. mexicanum* are only beginning to reveal patterns of population structure related to the mosaic nature of the tropical forest at Los Tuxtlas. Even longer term studies will be needed to test hypotheses.

Using stems of *A. mexicanum* as a device for dating treefalls, we obtained data for (1) and (4) in a 5-ha plot at Los Tuxtlas (Martínez-Ramos et al. 1988b). These

data and those obtained from a 12-yr population study of *A. mexicanum* and a 1-yr study of *C. obtusifolia* were redescribed using matrix models (Lefkovitch 1965) to combine the forest and population dynamics (Alvarez-Buylla 1988, Martínez-Ramos et al. 1988a). For example, the probability that a seed of *C. obtusifolia* in a mature patch is still present, after 1 yr, will equal the survivorship of seeds in the soil of that patch type times the probability that a mature patch is not affected by a gap in 1 yr. These models were used to obtain patch-specific and entire forest-level population growth rates for *A. mexicanum* and forest-level estimates for *C. obtusifolia*. We found that both populations are close to equilibrium ($\lambda \approx 1$). Such averages may be misleading, however. For example, those portions of the population of *Astrocaryum* found in areas of the forest with a closed canopy were increasing at an annual rate of 1.2%, while those in gaps younger than 12 yr were declining at a similar rate.

Effects of gap dynamics on population growth rates have been examined using sensitivity and elasticity analysis (Caswell 1978, De Kroon et al. 1986). Rates at which demographic values in gaps return to values occurring in closed forest patches (see (5) above) appear particularly important. Gaps of 350–375 m² affect growth and survivorship of *A. mexicanum* seedlings and juveniles for 3 and 6 yr, respectively; fecundities and growth rates of mature palms are modified for ≈ 12 yr by gaps of similar sizes. Hence, the population growth rate of the shade-tolerant *A. mexicanum* is affected by changes in gap dynamics. So, if gaps were > 200 m², slight increases in gap formation rate would provoke a decrease in λ , while if the proportion of area opened to smaller gaps per year is as high as 0.2 the model still predicts growth of the *A. mexicanum* population (Martínez-Ramos et al. 1988a).

Similar analyses are being done for *C. obtusifolia*. For example, the population growth rate of this species is most sensitive to changes in the transition probabilities from seeds to saplings. These are, in turn, determined by both the rate of gap formation and the survivorship of seeds in the soil of different forest patches (E. Alvarez-Buylla and M. Martínez-Ramos, unpublished manuscript).

CONCLUSION

The dichotomous pioneer/climax framework proposed by Whitmore distinguishes species with clearly different average life histories. However, when within-population variability is considered, the critical distinctions between the two classes become diffuse. This variation may well have evolutionary significance; recent studies with *C. obtusifolia* suggest that variability in seed germination responses in natural conditions may have an important genetic component (M. Cano,

M. Martínez-Ramos and E. Alvarez-Buylla, *unpublished manuscript*). Hence, such a dichotomous framework becomes a simplistic classification rather than an ecological and evolutionary categorization.

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REPEATABILITY IN FOREST GAP RESEARCH: STUDIES IN THE GREAT SMOKY MOUNTAINS

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During the late 1970s and early 1980s, J. R. Runkle and I worked independently on gap dynamics in old-growth forests of the southern Appalachians in Great Smoky Mountains National Park (GSMNP) in Tennessee and North Carolina (Barden 1979, 1980, 1981, Runkle 1979, 1981, 1982). We both wanted to find out whether the existing canopy composition could result from tree replacement in small canopy gaps. In addition, Runkle concluded that turnover rates in southern Appalachian forests, which he estimated at $\approx 1\%/yr$, were similar to turnover rates reported for northern coniferous forests and tropical rain forests (Runkle 1982, 1985).

We used different methods, but we independently came to the same primary conclusion: tree replacement in small canopy gaps can account for the existing forest composition of old-growth hardwood forests of the Southern Appalachians. No large disturbances such as fire or windthrow are necessary to perpetuate the existing canopy. However, we differed remarkably in other results. For example, canopy turnover rate was $\approx 1\%/yr$ for Runkle's data and $< 0.4\%/yr$ for mine. I believe that differences in our results were partly caused by differences in our definitions and methods, and that people doing gap research might benefit from a brief discussion of some possible sources of bias. However, I also believe that canopy turnover rates in southern Appalachian forests may be lower than previously thought.

Runkle and I agreed in our definition of "gap," which is an opening in the canopy stratum formed by the

death of a single tree, part of a tree, or a few trees in a group. We differed, however, in the defined height of entry into the canopy stratum; for Runkle gap closure occurs when replacement trees fill the opening at 10–20 m, compared to 18–30 m for my work. We also differed in the minimum diameter of the trunk of a tree that can form a gap when it dies; Runkle used 25 cm as a minimum diameter, while I used 50 cm.

Our gaps differed in closure rates as a consequence of our differing definitions. For comparison of our data I estimated closure rate of gap area by regressing the logarithm of the gap area in each age class of gaps against age. The slope of the line, b , was then converted to closure rate by the transformation, $(1-10^b)$. Runkle's gap closure rate was $\approx 12\%/yr$ (based on ≈ 250 gaps in GSMNP), while the closure rate for my gaps was $\approx 5\%/yr$ (260 gaps). Also, Runkle's gap area had an average longevity (elapsed time before half of the gap area in an age class closes) of 8 yr compared to 20 yr for my data.

The 8-yr average longevity of Runkle's gap area may seem short, but most gaps were filled by upward growth of saplings that were already present at the time of gap formation. For example, I measured the height of replacement saplings in 40 gaps that were 0–15 yr in age and found by linear regression that at gap age 0, when the gap was newly formed, the average height of replacement saplings was 5 m. When gaps were 8 yr old, replacements averaged 10 m tall, at which point they were closing gaps by Runkle's definition.

The turnover rate for the canopy may be calculated