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Photosynthetic Characteristics of Tropical Trees Along Successional Gradients

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Patterns of tropical succession and species replacement are shaped and determined by the dynamic nature of these forests. Gap-phase succession in tropical forests is driven by changes in resource availability arising from canopy disturbances and associated soil disturbances. Large gaps result primarily from major storms that cause the blowdown of numerous trees, while smaller gaps are created as individual trees lose branches, topple, or die standing (reviewed in Den­slow, 1987). When such breaches in the canopy occur, light, temperature, humidity, and nutrients are altered (Chazdon & Fetcher, 1984a; Chiariello, 1984; Fetcher, Oberbauer & Strain, 1985; Ashton, 1992; Vázquez-Yanes & Orozco-Segovia, Chapter 18). Consequently, it is common to find all stages of forest succession occurring within the same forest at any given time along the understory-gap center con­tinuum.

The ensuing differences in light quantity— and to a lesser extent, quality—between the undisturbed forest and the newly created gap
environment play a crucial role in influencing species establishment, growth, and reproduction (Fetcher, Oberbauer & Chazdon, 1994; Den­slow, 1987; Chazdon et al., Chapter 1; Fredeen & Field, Chapter 20). Tropical forest species differ in the extent to which gaps are required for successful regeneration. Based on their contrasting life-histories, tropical forest species have been categorized into two successional groups: light demanding or early successional, on the one hand, and shade tolerant or late successional, on the other. Many researchers have attempted to refine these criteria and make them more sensitive to the array of regeneration and life-history patterns found among tropical species (e.g., Martínez-Ramos, 1985; Whitmore, 1989; Swaine & Whitmore, 1989; Clark & Clark, 1992). In the absence of reliable data on species distributions along a successional sequence, however, no clear consensus has emerged on how to gauge the successional status of tropical species in relation to gap dynamics.

In this chapter, we evaluate the photosynthetic traits of tropical tree species to determine whether predictable patterns emerge between species broadly identified as early and late successional (pioneers vs. shade-tolerant species), within the framework of gap-phase succession. Our starting point in this analysis is the hypothesis that early successional, gap-requiring species exhibit a high degree of physiological flexibility (Bazzaz 1979 1984; Bazzaz & Pickett, 1980). We first describe the environment of early and late successional habitats within tropical forests, noting that these habitats require distinct physiological responses for survival and growth. We then focus on a comparison of the photosynthetic characteristics of seedlings of purported early and late successional species under an array of light conditions. Finally, we speculate on differences in responses of seedlings and mature trees and expand the original paradigm describing the photosynthetic performance of tropical trees to incorporate ontogenetic changes in performance. In concluding, we present a series of guidelines and suggestions for further research in the field.

6.1 PHOTOSYNTHESIS IN TROPICAL TREES: HYPOTHESES

The recognition that early and late successional species experience contrasting levels and scales of environmental heterogeneity has led to the formulation of hypotheses predicting their performance. The leading paradigm guiding much of the research on the ecophysiological patterns in tropical forest succession focuses on the assumption