Is dominance of *Pentaclethra macroloba* limited by density-dependent seedling recruitment?

Cory A. Donovan and Nira L. Salant

Abstract: High diversity of rain forest trees may not be maintained if there are no limits to the dominance of common species. Dominance of the most abundant canopy tree, *Pentaclethra macroloba*, in the primary forests of La Selva, Costa Rica may be limited by density-dependent seedling survival and recruitment. We found a significant relationship between local adult canopy cover (a measure of local canopy tree abundance) and seedling stage class structure of *P. macroloba*. We found a lower proportion of individuals in the largest seedling size class in areas where *P. macroloba* dominated the canopy, suggesting that local adult dominance may reduce seedling survival and/or growth rates. Such dynamics may stabilize the population of adult *P. macroloba* in the forest canopy, preventing exclusion of the diverse assemblage of less common tree species.

Key Words: density-dependence, population dynamics, seed dispersal

Introduction

The population structure of a forest tree species can provide insights into the underlying population dynamics. Tree mortality rates decline considerably with size, and seedling survival may be critical to the success of a tree species (Hartshorn 1972). The canopy of primary forests in La Selva Biological Reserve, Costa Rica, is dominated by *Pentaclethra macroloba* (Fabaceae), a slow growing, shade-tolerant, leguminous tree. *P. macroloba* is tolerant of poor soils and high soil moisture, possibly explaining its competitive dominance in the rain forests of the Caribbean slope (Hartshorn 1972). Reproductive trees have large pods that explosively disperse seeds up to 10 m from the base of the tree, resulting in high concentrations of seeds and seedlings in the area beneath the tree's crown (Hartshorn 1972). This method of seed dispersal potentially limits the spread and success of this species, however, and slow growth rates may reduce its ability to colonize forest gaps. *P. macroloba* dominance and distribution throughout the forest canopy may depend on factors that influence seedling recruitment, growth, and survival.

We examined the relationship between local adult canopy cover and seedling stage class composition of *P. macroloba*. We predicted that in areas under a canopy dominated by *P. macroloba*, there would be a lower proportion of seedlings in later stage classes. This pattern could result from reduced survival and/or reduced growth rates in areas of high *P. macroloba* canopy cover. Any combination of these trends in growth and survival would tend to limit the abundance of this most common species in the canopy.

Methods

We examined *P. macroloba* seed and seedling abundance in the primary forest of La Selva Biological Reserve, Costa Rica on 15 and 16 February 2003. We sampled 25 m^2 plots along transects, choosing plots under either high (n = 8) or low (n = 26) local *P. macroloba* canopy cover. All plots were at least 5 m from the nearest trail, and all had > 90 % total canopy cover. We measured *P. macroloba* and total canopy cover using a spherical densiometer. High adult canopy cover plots had *P. macroloba* canopy cover > 85%, while low adult canopy cover plots had *P. macroloba* canopy cover < 15%.

In each 5 x 5 m plot, we counted the number of seedlings > 30 cm tall (Stage class 3). In a 2 x 5 m nested plot, we counted the number of seedlings < 30 cm tall, excluding recent germinants (Stage class 2). In a 1 x 5

m nested plot, we counted the number of seeds (Stage class 0) and recent germinants (Stage class 1; distinguished by the attached cotyledons and lack of true leaves). We used the counts from the nested plots to estimate the total number of individuals in stage classes 0 - 2 for the entire 5 x 5m plot. We used these values to determine the proportion of individuals in each stage class (stage class proportion = number of individuals in each stage class / total number of individuals). We used a G-test on raw counts to determine if the number of individuals in each stage class differed between areas of high and low *P. macroloba* canopy cover.

Results

High adult canopy cover sites had significantly more seeds and seedlings per unit area than low adult canopy cover sites, with mean values (± SE) of 4.52 ± 0.29 individuals / m^2 and 0.88 ± 0.16 individuals / m^2, respectively ($F = 119.3$, $df = 2,32$, $P < 0.001$). The proportion of individuals in stage classes differed significantly between areas of high and low *P. macroloba* canopy cover (Table 1; $X^2 = 8.93$, $df = 3$, $P = 0.03$). The proportions of individuals in stage classes 0, 1, and 2 were similar between high and low adult canopy cover sites. However, the proportion of individuals in stage class 3 was higher in low adult canopy cover sites (Fig. 1).

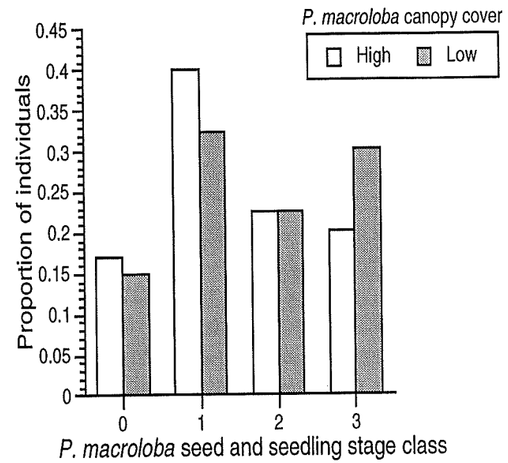

FIG. 1. Proportion of *P. macroloba* recruits in seed and seedling stage classes, under high and low canopy cover of *P. macroloba*, at La Selva Biological Reserve, Costa Rica. Stage class 0 = non-germinated seeds; stage class 1 = recent germinants; stage class 2 = seedlings < 30 cm tall; stage class 3 = seedlings > 30 cm tall. Proportion = number of individuals in each stage class / total number of individuals counted.

Discussion

As expected in a species with limited dispersal ability, the density of *P. macroloba* seeds and seedlings was much greater in high adult canopy cover sites. *P. macroloba* seeds are dispersed mechanically, therefore the majority of seeds fall beneath the tree crown (Hartshorn 1972).

Our results supported our hypothesis that plots under high adult canopy cover had a lower proportion of large seedlings

TABLE 1. Counts of individual *P. macroloba* in seed and seedling stage classes under high and low canopy cover of *P. macroloba* adults, at La Selva Biological Reserve, Costa Rica. Counts in areas of high (n=8) and low (n = 26) adult densities were taken in 25 m^2 plots. Within each plot, Stage classes 0 and 1 were counted in one 1 x 5 m subplot; Stage class 2 was counted in one 2 x 5 m subplot; Stage class 3 was counted in the entire 5 x 5 m area. See Fig. 1 for definitions of stage classes.

P. macroloba canopy cover	Stage Class				Total
	0	1	2	3	
High	38	87	49	67	241
Low	17	37	26	59	139
Total	55	124	75	126	380

(Stage class 3). This finding has two potential explanations. Seedlings in areas of high adult canopy cover may have lower survival rates from Stage class 2 to Stage class 3. Alternatively, seedlings in Stage class 2 may have slower growth rates under high adult canopy cover.

The soil beneath adult *P. macroloba* is more acidic than the surrounding soil, presumably because these trees have root symbionts that fix soil nitrogen, which is subsequently nitrified (Parker 1994). Soils with a lower pH have a lower retention of cations and other nutrients (Parker 1994). Thus, low soil pH has potentially negative consequences for *P. macroloba* seedling growth and survival.

In addition, *P. macroloba* leaves decompose at slower rates than the leaves of many other tropical forest canopy trees (Parker 1994). Therefore, *P. macroloba* seedlings beneath the canopy of conspecifics may have lower available nutrients, contributing to lower growth rates and reduced survival. High local conspecific seedling density may also negatively influence seedling growth and survival. Seedlings at higher seedling densities may be more susceptible to herbivory and pathogens, factors that potentially stress seedlings, limit growth, and increase mortality rates (Deem 1998, Dallison 1999). Based on our findings, we cannot separate the effects of adult density and seedling density on seedling survival; adult canopy cover and seedling density are spatially correlated. Through manipulation of seedling density or larger sample sizes, future studies could potentially separate these factors.

Lower survival and growth rates of conspecific seedlings under a canopy dominated by *P. macroloba* may help to explain the limitation of dominance of this species in the La Selva forest. In areas of low adult canopy cover, higher survival of seedlings may increase the recruitment of *P. macroloba* to the canopy. In contrast, where *P. macroloba* already dominates, adult replacement rates may be lower. Over time, these dynamics may help stabilize the population of adult *P. macroloba* and prevent complete canopy dominance by this species.

We suggest that these questions are of sufficient interest to warrant more extensive studies to confirm the patterns we found. Long-term demographic studies using marked individuals would distinguish between the effects of growth and survival on stage structure. Such studies could also elucidate the mechanisms responsible, e.g. by quantifying herbivore damage in areas of high and low conspecific density.

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