DISCUSSION

Heliconia flower morphology appears to serve as a mechanism for reducing floral herbivory. *H. latispatha* inflorescences in the arid sites had three times more herbivory damage to their bracts than plants in the mesic site. Although few Heliconia inflorescences contained water at the time of our measurements, higher soil moisture at the mesic site and more water in the *C. lutea* bracts suggest that Heliconia bracts at the mesic site contained water more recently than those in the arid site. Presumably, the patterns in herbivory that we recorded were the result of herbivory that partly occurred before the bracts were dried out. The benefits incurred by the plant from reducing herbivory of reproductive plant parts must outweigh the cost of actively transporting water to keep the bracts full, even when water resources are quite low.

The amount of herbivory damage to *C. lutea* inflorescences did not differ between the arid and the mesic sites, despite the difference in bract water content between the two sites. It could be that although inflorescences of Heliconiaceae and Marantaceae have similar morphology, the water-filled bracts in Marantaceae require a different explanation than herbivore defense. For example, the water in the bracts, possibly sweetened with glucose or containing insects, might serve as an attractant to insects or birds who pollinate the flower in the process of visiting the bract, but this seems unlikely given the positioning of the flower as it emerges from the bract. The slightly viscuous water solution might serve to protect the flowers from desiccation during development (R. Rojas, pers. comm.), or perhaps the water-filled bracts of the Marantaceae are an anachronism from selection by some now extinct herbivore.

Alternatively, water-filled bracts in the Marantaceae may reduce floral herbivory, but we may have been unable to detect the response because their bracts only recently dried up. We cannot assess exactly when these bracts dried up nor when herbivory occurred. Given that most *H. latispatha* bracts in the mesic site were dry, whereas *C. lutea* bracts still contained water, it must be that *C. lutea* had greater water reserves (perhaps due to deeper roots) or were allocating more of their water to the bracts. If bract water is an anti-herbivore defense in *C. lutea*, sampling later in the dry season, or across a steeper gradient in soil moisture, should yield differences in herbivory damage.

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DENSITY-DEPENDENT MORTALITY IN *PENTACLETHRA MACROLOBA*

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Abstract. Tropical rainforest trees generally occur in low abundance and densities, however *Pentaclethra macroloba* is the most abundant tree species in the La Selva forest preserve and represents more than half of the individuals in the canopy. We hypothesized that mortality in *P. macroloba* is density dependent, especially between the seedling and juvenile life stages. We measured densities of four stage classes of *P. macroloba* (seeds, seedlings, juveniles, and adults) across 16 primary forest plots. The uniform dispersion of *P. macroloba* adults is apparently the result of density-dependent mortality acting upon trees in the juvenile stage class. Further study is needed to determine spatial patterns of seedling mortality due to herbivory, pathogens, and intraspecific competition, as these seem to be the major factors producing spatial density dependence in *P. macroloba*.

Key Words: Janzen-Connell model, seedling mortality, uniform dispersion

INTRODUCTION

Many tree species in tropical forests are characterized by low population densities and a uniform dispersion. *Pentaclethra macroloba* (Fabaceae), is reported to be uniformly dispersed (Lieberman and Lieberman, 1994) in accord with this generalization, but is remarkably abundant in the primary forest of La Selva: it contributes 14% of stems > 10 cm dbh and 51% of individuals in the canopy (Hartshorn, 1972). Models of spatial density dependence, e.g. the Janzen-Connell model, can potentially explain this pattern of over-dispersion. We tested whether mortality in *P. macroloba* is density-dependent. The Janzen-Connell model predicts greater attrition from seedlings to juvenile stages in sites with high adult density. An alternative formulation of the model that could also produce a uniform adult dispersion predicts greater attrition from seedlings to juveniles in sites with high seedling density.

METHODS

We collected data from the primary forest adjacent to La Selva biological station, Heredia Province, Costa Rica, on 15-18 February 1998. We assessed the populations of four stage classes of *Pentaclethra macroloba:* (1) seeds, (2) seedlings (5 - 50 cm in height), (3) juveniles (1 - 15 m in height), and (4) adults (trees reaching canopy height). Most seedlings still had cotyledons so were classed as both seeds and seedlings. We counted the number of adults and juveniles in 16 haphazardly chosen 30 x 30 m plots. All trees with any part of its canopy overhanging the plot perimeter were included in the count. Within each plot we randomly selected three 2 x 2 m subplots and counted the number of seeds and seedlings within each. Each seed was classified as healthy, rotten, or damaged by herbivory, and each seedling was classified as healthy, diseased (marked by discoloration of leaves), damaged by herbivory, or damaged by fallen debris (e.g. tree limbs, palm fronds).

Three indices of survival were calculated from the ratio of the number of individuals in a stage class to the number of individuals in the previous stage class: (1) seedlings to seeds, (2) juveniles to seedlings, and (3) adults to juveniles. The dispersion of each stage class was compared with a Poisson distribution (= null model of random dispersion) and evaluated by inspection of the coefficients of variation (uniform dispersion indicated by variance / mean < 1, and clumped dispersion indicated by variance / mean > 1). Regression analyses were used to examine the effect of both seedling and adult densities on the three indices of survival. Measures of seed and seedling damage were compared with seedling and adult densities using correlation analyses.

RESULTS

We observed a total of 469 *P. macroloba* individuals in 16 30 x 30 m plots (272 seeds, 218 saplings, 81 juveniles, and 139 adults). Comparison with the Poisson distribution in each stage class shows a change from highly clumped dispersion in the seed and seedling stage classes to uniform dispersion in the adult stage class (Table 1).

The ratio of juveniles to seedlings decreased as seedling density increased (slope = -1.16), while the ratio of seedlings to seeds and adults to juveniles exhibited no effect of density (Figure 1; Table 2). As adult density increased, the ratio of seedlings to seeds decreased (P = 0.077), while the ratio of juveniles to seedlings and adults to juveniles did not change (Figure 1; Table 2). A higher proportion of seedlings were knocked-down in areas of higher seedling density (Spearman rho = 0.63, P = 0.008). Proportions of seedlings with signs of herbivory or disease did not change with seedling density (all P > 0.05), and none of the measures of damage changed with adult density (all P > 0.05). Of the seeds we observed, 5.5% showed signs of herbivory, and 2.2% were rotten. Nearly 20% of observed seedlings showed signs of herbivory, while 6.4% were diseased and 6.0 % were knocked-down by falling debris.

TABLE 1. Mean density and dispersion (as compared to Poisson distribution) of *P. macroloba* seeds, seedlings, juveniles and adults within the 16 plots studied.

	Density (individual / 900 m^2)			
Age class	Mean	Variance	Coeff. of variation	Dispersion
Seed	1275	1.44×10^6	1133	Clumped
Seedling	1022	9.18×10^5	898	Clumped
Juvenile	5.06	9.24	1.83	Clumped
Adult	8.69	6.92	0.80	Uniform

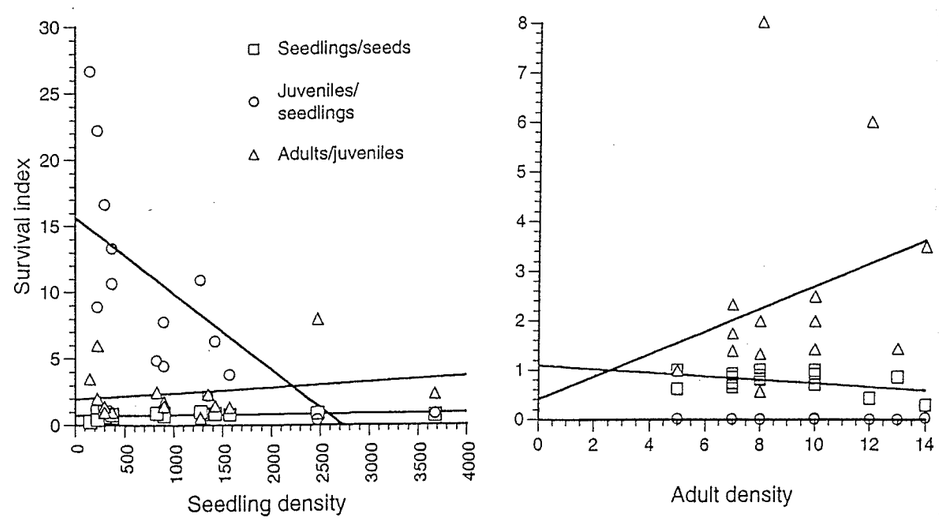

FIG. 1. Ratio of the number of individuals in one stage class to the previous stage (an index of survival between stages). Density refers to the number of individuals within a 900 sq. meter plot. Levels of juvenile/seedling survival as seedling density incresed were multiplied by 1000 to allow them to be shown on the same scale.

TABLE 2. Results of regressions comparing survival indices with seedling and adult density.

	$F_{1,14}$; P – value	
Index of survival	Seedling density	Adult density
Seed to seedling	0.80; 0.39	3.76; 0.073
Seedling to juvenile	14.99; 0.002	0.92; 0.35
Juvenile to Adult	0.68; 0.42	1.46; 0.25

DISCUSSION

The density of individuals in each stage class decreased dramatically between seeds and adults. Population dispersion changed from highly clumped in seedlings to overdispersed in adults (nearly 400-fold decrease in coefficient of variation). Our estimates of adult dispersion support those of Lieberman and Lieberman (1994). Given that few seeds are predated upon (we found < 6% herbivory damage), seed dispersal is limited to the propulsion of the seeds when the seed pod opens. Therefore, the 5-8 seeds per pod are likely to travel a short distance and exhibit patchy seed and seedling growth.

Adult density had a slightly negative effect on the seed survival index, possibly due to an increased transmission of pathogens to seeds, but the mortality incurred between seeds to seedlings is small and does not appear to greatly impact the *P. macroloba* population. Seedling density was inversely related to the attrition between seedling and the juvenile stage classes. Although seed toxicity appears to limit herbivory of seeds, herbivore damage increased ≈ five-fold between the seed to seedling stage classes. As the optimal foraging theory would predict, aggregated clumps of seedlings may attract more herbivores. However, neither herbivory nor disease were correlated with seedling or adult density. We found that damage caused by fallen debris was correlated with seedling density, but an individual seedling's chance of being struck by falling debris should not be affected by the presence of conspecific neighbors. It could be that resource competition leads to the observed density-dependent mortality or that our measures of herbivory or disease were not sufficiently powerful to detect the density dependence. Further studies are needed of spatial patterns in seedling mortality due to herbivory, pathogens, and intraspecific competition, as these seem to be the chief processes that could produce spatial density dependence in *P. macroloba*.

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