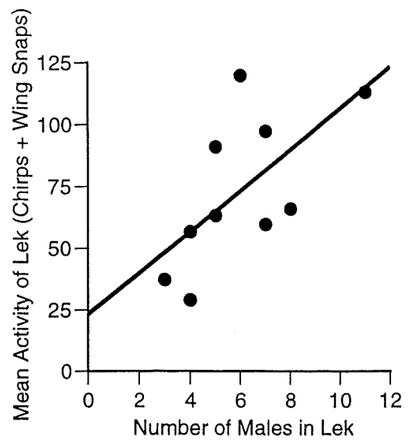

Fig. 3. Mean activity (Chirps + Wing Snaps in a 5 min period) in white-collared manakin leks at Estacion Biologica La Selva was positively correlated with the number of males (P = 0.045).

DISCUSSION

As predicted, the distribution of white-collared manakin leks indicates a preference for secondary growth, especially areas near abandoned pasture edges. Although not quantified, we observed more small saplings, brush, and vines in these habitats, which may provide the physical structures preferred by displaying males. The absence of leks in primary forests may be due to the lack of these physical characteristics. It is also possible that secondary forests are preferred for lek locations because the early successional vegetation provides manakins with the small fruits they eat.

Alternatively, the preference of secondary growth areas for leks may be related to the number of females present in those areas. The hotspot hypothesis suggests that males cluster in areas with certain physical characteristics that are attractive to females, allowing males increased access to potential mates (Westcott 1995). If so, the number of males per lek may be related to the number of females immediately surrounding the lek, which might explain why there are no significant differences in the number of males in each lek. An examination of female density and activity in these areas may provide more support for this hypothesis.

The mean activity per individual increased with lek size. Since most males in a white-collar manakin lek display (i.e., there are no inactive subordinates - Wray and Osterling 1995), when more males congregate together it would be expected that individuals would display even more to out-compete each other. Thus it seems that there is an optimal lek size and males would join leks that are large enough to attract females but not so big as to require a disproportionate expenditure of energy in display.

Though the factors controlling lek location are still largely unknown, white-collar manakins do show preference for specific habitat types, which suggests that the vegetative structure of available habitats influences the placement of leks.

ACKNOWLEDGMENTS

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Mechanisms of density-dependent mortality in *Pentaclethra macroloba* seedlings

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Abstract. Density-dependent mortality may be an important factor influencing the population structure of *P. macroloba.* We examined whether herbivory, infection by pathogens, and/or intraspecific competition were important mechanisms of density-dependent mortality between seedlings (<1 m tall) and juveniles (1-5 m tall) of *P. macroloba.* We found no correlation between herbivory or infection by pathogens with seedling density. Further, intraspecific competition did not seem to affect the seedling stage, as root and canopy overlap between *P. macroloba* seedlings was minimal. We found that young seedlings had significantly less herbivory and pathogen infection than old seedlings. Therefore, we refined Deem et al.'s 1998 finding of density-dependent mortality between the seedling and juvenile stages by subdividing the seedling stage into "young" (with cotyledons) and "old" (cotyledons shed) seedlings. The ratio of old to young seedlings, an index of survivorship, was negatively correlated with the density of young seedlings. This suggests that there is density-dependent mortality acting between the young and old seedling stages, although the mechanisms remain unknown. We did find that pathogen infection increased with decreasing nearest neighbor distance in old seedlings, suggesting that pathogens may impose density-dependent mortality on the older seedlings. We recommend that young and old seedlings should be considered as two separate life stages in studies of population dynamics in *P. macroloba*, since they seem to play distinct roles in the population dynamics of this species.

Key Words: herbivory, intraspecific competition, pathogens

INTRODUCTION

Pentaclethra macroloba (Mimosaceae) is an abundant emergent tree species in lowland neotropical rainforests, constituting 34.6% of the forest basal area at La Selva Biological Reserve, Costa Rica (Hartshorn and Hammel 1994). Deem et al. (1998) examined the population stage structure of *P. macroloba* and found evidence of density-dependent mortality between the seedling and juvenile stages in areas of high seedling density. The density dependence found by Deem et al. must have a mechanism operating in the seedling stage. They investigated three possible mechanisms for this density-dependent mortality: herbivory, pathogens and intraspecific competition, but did not find evidence for any of them.

We examined these three mechanisms more comprehensively than the 1998 study. If herbivory was an important factor, we predicted that it would be greater in areas of high seedling density due to herbivore preference for dense food patches. Similarly, if pathogens were causing the density-dependent mortality, we predicted that infection by pathogens would be greater in areas of high seedling density. Finally, if intraspecific competition was important, we predicted that it would increase with conspecific seedling density.

In the field we observed a distinct difference between individuals within the seedling stage. We distinguished "young" seedlings, which had green cotyledons, and "old" seedlings, which had shed their cotyledons (all <1 m tall). We investigated differences in herbivory and pathogens between the two types of seedlings.

Finally, we evaluated whether density-dependent mortality acts within the seedling stage, i.e., between young and old seedling classes. We investigated whether the mechanisms proposed above (herbivory and pathogens) are possible causes of density-dependent mortality in the young seedling stage.

METHODS

We conducted our study on 16-18 February 1999 at La Selva Biological Station, Costa Rica. We counted the number of young and old

seedlings of *P. macroloba* in 24 randomly selected 4 x 4 m quadrats, located along the Camino Experimental Sur and the Sendero Sura.

We took measurements on four young and four old seedlings (chosen randomly in each plot), or as many as were present when there was less than four of each stage. For each of the seedlings, we recorded the distance to the two nearest conspecific neighbors, and took the mean for each individual ("nearest neighbor distance"). We also assessed the condition of the apical meristem (intact or not intact). We measured percent leaf area missing ("herbivory", see Brayce et al. 1999 for methods), and percent remaining leaflets with discoloration ("pathogens") on the two youngest leaves of each seedling.

Since intraspecific competition can only act if conspecific canopies or roots overlap, we measured the extent of the crown and the roots. We randomly chose 20 *P. macroloba* seedlings and measured the radius of the crown at its widest point. For 10 randomly chosen seedlings, we excavated their roots and measured the radius of the root system at the widest extension of the fine root hairs from the central tap root.

For analysis of mechanisms of density-dependent mortality between seedlings (< 1 m tall) and juveniles (1-5 m tall), we grouped young and old seedlings as one life stage (consistent with Deem et al. 1998). We tested the correlation of percent herbivory and percent pathogens with total seedling density.

We used the ratio of old seedling density to young seedling density as an index of survivorship between these two stages. We correlated this index of survivorship with young seedling density to determine whether density-dependent mortality exists between these two classes of the seedling stage. We assumed that there is no fluctuation in the production and germination of seeds between years, since Hartshorn (1972) found the population growth rate, λ = 1.002 for *P. macroloba* at La Selva.

For evaluation of the mechanisms of density-dependent mortality on young seedlings, we tested the correlation of percent herbivory and percent pathogens with young seedling density. In a similar manner, we looked for density-dependent characteristics in the old seedling stage.

RESULTS

Total density of *P. macroloba* ranged from 2-130 seedlings/16 m^2 in the 24 quadrats we sampled. Of the 374 individuals counted, 136 (36%) were young seedlings and 238 (64%) were old seedlings. We took measurements on 38 young and 79 old seedlings.

There were no trends in percent herbivory or degree of pathogen infection with seedling density in the 4 x 4 m plots (correlation; herbivory: r^2=0.00, df=1, 115 P=0.81; pathogens: r^2=0.01, df= 1, 115, P=0.35). The percent herbivory was 30.6 ± 2.3% (mean ± 1 SE) and percent pathogens was 7.9 ± 1.1%.

Likewise, intraspecific competition in the seedling stage does not appear to act as a mechanism of density-dependent mortality. Because the average canopy radius is 15 cm, seedlings must be < 30 cm apart to experience shading by conspecifics. Because the radius of the average root system was 4.2 cm, seedlings must be < 8.4 cm apart to experience root overlap. The range of nearest neighbor distance was 12.5 – 315.0 cm and the mean was 78.2 ± 57.3 cm. Only 13.7% of individuals were close enough for leaf overlap, and no seedlings were close enough for root overlap.

Our investigation into the differences between young and old seedlings revealed that young seedlings had significantly lower herbivory and fewer signs of pathogens than old seedlings (Wilcoxon/Kruskal-Wallis; herbivory: X^2=55.66, df=1, P<0.0001; pathogens: X^2=61.54, df=1, P<0.0001; Fig. 1). Additionally, all the young seedlings had intact apical meristems, while 54% of the old ones had damaged meristems (X^2=35.53, df=1, P<0.0001).

We found evidence consistent with density-dependent mortality operating between young and old seedlings, using our index of survivorship. Using natural log transformed data, we found a negative correlation between our index of survivorship of young seedlings (ratio of old to young seedling density) and young seedling density (r^2=0.20, df=1, P=0.07; Fig. 2). Neither herbivory nor pathogens were correlated with young seedling density. There was, however, a significant negative correlation of percent pathogens on old seedlings with increasing nearest neighbor distance (r^2= 0.19, df = 1, P = 0.006; Fig. 3).

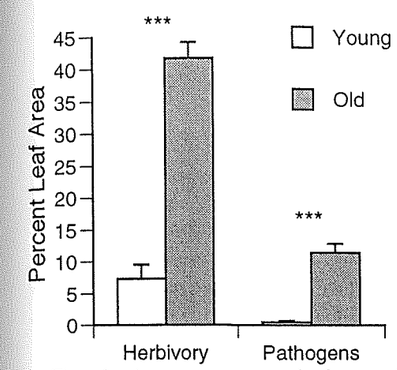

Fig. 1. Average percent leaf area lost to herbivory and average percent leaf area affected by pathogens in young and old seedlings of *P. macroloba*, at La Selva Biological Station, C osta Rica. Means for all individuals of each type ± 1 SE, young: n = 38; old: n = 79. Pairs with *** indicate P <0.0001.

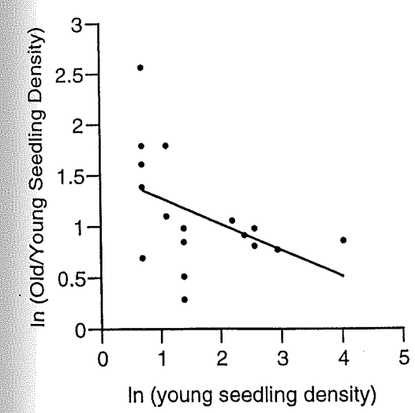

Fig. 2. Index of survivorship from young to old seedling stages of *P. macroloba* as a function of the density of young seedlings in 16 m^2 plots, at La Selva Biological Station, Costa Rica. Data were log transformed (P=0.07, n=17).

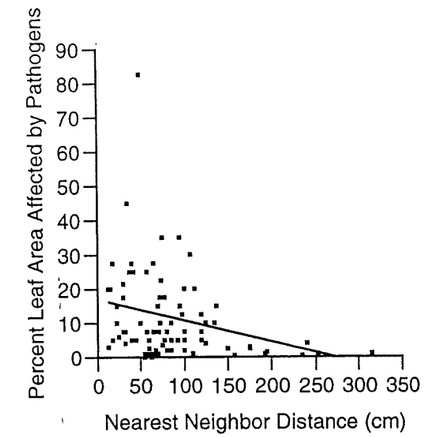

Fig. 3. Percent leaf area discolored by pathogen infection for old seedlings of *P. macroloba* as a function of nearest neighbor distance, at La Selva Biological Station, Costa Rica (P = 0.0064, n=117).

DISCUSSION

We tested for the mechanisms that cause patterns of density-dependent mortality between the seedling and juvenile stages found by Deem et al. (1998). We found no evidence that herbivory, pathogens or intraspecific competition are mechanisms of density-dependent mortality between seedling and juvenile stages of *P. macroloba*. Perhaps most herbivores on this species are generalists, and therefore, prefer areas of high plant density rather than congregate in areas of high *P. macroloba* seedling density. Also, some of the seedlings had recently flushed new leaves (indicated by their tenderness and light green color), which may not have been exposed to herbivory or pathogens yet, masking possible effects of these density-dependent mechanisms. Intraspecific competition for light, nutrients or water does not seem to affect *P. macroloba* seedlings, since only 13.5% of individuals were close enough to experience shading from conspecifics, and no individuals were close enough to experience root overlap. Other

factors such as interspecific competition or damage by litter fall (Hartshorn 1972) may be more important influences on *P. macroloba* seedling mortality.

Our investigation into the differences between young and old seedlings yielded interesting results. In general, herbivores prefer young and tender leaves (which were more abundant on young seedlings) over old, more lignified leaves (Coley and Aide, 1991). However, we found less evidence of herbivory on young compared to old *P. macroloba* seedlings. Young seedlings may be less palatable than old ones because they have fewer nutritious nitrogenous compounds such as chlorophyll. This is consistent with our observation that young seedlings had lighter green or reddish leaves compared to the dark leaves of old seedlings. And, obviously, young seedlings may not have been exposed to herbivory and pathogens as long as old seedlings. Furthermore, they may contain defensive compounds contributed by maternal reserves in the seed, which are known to be toxic (Hartshorn 1972).

Since herbivory and pathogens were so different between young and old seedlings, we considered these two stages separately. We found evidence of density-dependent mortality between the young and old seedling stages, since the ratio of old to young seedlings decreased with increasing density of young seedlings. This implies that the population structure of *P. macroloba* may be more complex than previously thought, and perhaps that the young seedling life stage plays an influential role in the population dynamics of this species.

In examining the mechanisms of this density-dependent mortality, there was no correlation of herbivory and pathogens on young seedlings with young seedling density. It is plausible that mechanisms generating mortality of young seedlings act at different times of the year than our study period. For example, pathogens of young *P. macroloba* seedlings may be more easily transferred during the wet season. Also, the cotyledons of young seedlings may provide a reserve of nutrients and energy when resources are limiting, and when this reserve runs out, the young seedlings may be subject to high mortality.

Pathogens may act as a source of density-dependent mortality between old seedlings and juveniles, since infection by pathogens on old seedlings increased with decreasing nearest neighbor distance. Thus, the proximity of seedlings to conspecifics may increase the transfer of fungal pathogens. The fact that we didn't find this trend with density in the 4 x 4 m plots suggests that herbivores and pathogens may act on a finer spatial scale than 16 m^2. On a more localized scale, infection by pathogens could be an important mechanism of density-dependent mortality in this size class. However, further studies should examine density-dependent mortality between the old seedlings and juveniles.

It is apparent that young and old *P. macroloba* seedlings should be considered as separate life stages since herbivory and pathogens appear to affect these stages differently. However, our data did not show the relative importance of these density-dependent mechanisms. Also, density-dependent mortality exists between the young and old seedling stage. Infection by pathogens is the most likely mechanism operating on the older seedling stage, but factors operating on the young seedlings remain to be elucidated. In future population studies of *P. macroloba* young and old seedlings should be considered separately, since the dynamics between young and old seedlings play an important role in determining the population dynamics of *P. macroloba*.

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