

SEED SUCCESS OF *PENTACLETHRA MACROLOBA* ACROSS SOIL TYPES AND SEED DENSITIES

LINDSAY V. REYNOLDS AND MICHAEL L. BROSNAHAN

Abstract: Seed dispersal and germination are critical to the fitness of all tree species. Moreover, among most trees the percentage of seeds that become seedlings, or “seedling success”, is very low. We examined seed success of a dominant lowland rainforest species, *Pentaclethra macroloba*, across a soil moisture gradient. Previous studies have established that *P. macroloba* has reduced seed germination rates in areas of low moisture and also has density dependant population dynamics. Results from these studies suggest that these density dependent population dynamics may be due to fungal pathogens. We hypothesized that if fungal pathogens are regulating the population but seed germination rates are greater in areas of higher moisture, seed success will be greatest in areas of low seed density and high soil moisture. We surveyed quadrats for seedlings and estimated seed abundance dispersed using seed pods found within quadrats. Our results indicate that seed success is density dependant in alluvial soils but not in non-alluvial. It appears that *P. macroloba* seedling density is more clumped in non-alluvial soils. Other studies have documented even distributions of adult trees across the landscape. Future studies may consider mechanisms of increasing mortality at intermediate life-stages in non-alluvial habitats that might compensate for the clustered distribution of seedlings.

Key Words: alluvial soils, Janzen-Connell Hypothesis, seed survivorship

INTRODUCTION

Few of the seeds produced by trees ever grow to become trees themselves. Seeds are preyed upon by many animals and are also vulnerable to disease. The success rate of seeds is therefore quite low, but is critical for the persistence of any tree species. The Janzen-Connell hypothesis predicts that seed success will be highest where seed density is low, but that most seeds tend to be aggregated (high seed density) in the immediate vicinity of the parent tree. Therefore, the hypothesis predicts that a

disproportionately high number of young trees will be the result of relatively few seeds that disperse far enough to be in patches of low seed density.

Hartshorn (1972) has found support for the Janzen-Connell hypothesis in the tropical leguminous tree, *Pentaclethra macroloba*. This tree is extremely abundant in the forests near La Selva Biological Station, comprising over 30% of all trees. *P. macroloba* is highly resistant to herbivores and seed predators because of the high alkaloid content of its seed and leaf tissue. Nonetheless, seed success apparently still decreases with increasing seed density because of specialist pathogens or resource competition. If fungal pathogens are regulating the population at the seed or seedling stage, then wetter soils (that are conducive to fungal growth) should enhance these density dependent effects. On the other hand, Hartshorn also suggests that seed germination of *P. macroloba* in the absence of pathogens is greater in areas of high moisture. We hypothesized that seed success within the forest at La Selva is influenced by the interaction between soil moisture and seed density, such that the success of seeds would be greatest in areas of low density and high moisture, but least in areas of high density and high moisture. We tested this hypothesis by evaluating the probability of seeds becoming seedlings at high and low seed densities across a soil moisture gradient.

METHODS

On 14 - 16 February we sampled along the Camino Circular Lejano (CCL) and Sendero Sura (SUR) trails near the La Selva Biological Station, Costa Rica. We sampled in areas identified as alluvial and non-alluvial soil types based on flooding history data from the La Selva GIS database. Alluvial soils have greater moisture content through the year than do non-alluvial areas (A. Trabucco, pers. comm.). There were 4 replicate plots in each of 4 treatments: alluvial soil and high seed density, alluvial soil and low seed density, non-alluvial soil and high seed density and non-alluvial soil and low seed density. Within each soil type, we haphazardly identified high and low seed densities along the trail. Each plot was at least 10 m away from any adjacent plot. Once a high or low density site was identified, we measured 10 m perpendicularly out from the trail and identified a 5 x 5 m plot for high density sites and a

10 x 10 m plot for low density sites. Within each plot, we gathered all the seed pods, counted the number of viable seed indentations for each seed pod and counted the number of seedlings less than 50 cm. Seed pods last no longer than 6 - 8 months and seedlings less than 50 cm represent trees less than one year old (Hartshorn 1972). Thus all the pods we found and seedlings we counted represent a recent seed set. We also quantified the number of unopened (aborted) seed pods.

We estimated the total number of seeds dispersed into an area by dividing the total number of viable seed indentations per area by 2 because each viable seed creates indentations on 2 pods (i.e. any 2 pods we collected might have been halves of one structure containing seeds). Seed success was measured by dividing total number of seedlings by the total number of seeds. We tested for effects of soil type and seed density on seed success, aborted seed pods and total seeds per pod with 2-way ANOVA tests. Linear regressions were used to evaluate relations between seed success and seed density within soil types.

RESULTS

Overall, seed success was <10% for all treatments (Table 1). Average number of seeds per pod ranged from 2.76 - 3.46 across soil treatments and 2.98 - 3.22 across density treatments (Table 1). Average proportion of pods aborted was <20%. There was no overlap in seed density among high and low density quadrats, so that variation in seed density between high and low density quadrats was highly significant ($F_{1,14} = 82.37$, $P < 0.001$).

Seed success was greater in areas of low seed density than in areas of high seed density and was greatest in alluvial, low seed density quadrats. This trend was strongest across alluvial quadrats alone and was not significant across non-alluvial quadrats alone (Fig. 1, Table 2). Similarly, seed density and seed success were strongly correlated among alluvial quadrats ($r = 0.82$, $df = 6$, $P = 0.013$), but not among non-alluvial quadrats ($r = 0.3$, $df = 6$, $P = 0.47$).

The mean number of seeds per pod was greater in non-alluvial quadrats than alluvial quadrats. Percentage of pods aborted was greatest in alluvial, high density areas and lowest in non-alluvial, low density areas (Table 1).

DISCUSSION

Seed success increased with decreasing density of seeds. If we assume that low density areas are generally farther from parent trees than high density areas, our results support the Janzen-Connell hypothesis for *P. macroloba*. However, this pattern was only significant in alluvial soils. In non-alluvial soils, there was no change in seed success between areas with high and low seed density. This supports our hypothesis that seed success is influenced by interactions between soil type and seed density. However, our results run counter to the hypothesis that alluvial areas would be more susceptible to fungal pathogens as seed success was actually slightly greater in alluvial areas than in non-alluvial areas. This indicates that alluvial soils provide a benefit to *P. macroloba* by improving germination success as suggested by Hartshorn.

Our results suggest that the distribution of seedlings would be more even in alluvial habitat than in non-alluvial habitat. If *P. macroloba* has similar seedling-to-adult survivorship in both soil types, we might expect that adult *P. macroloba* trees would have a clumped distribution in the non-alluvial soils because their seed success does not necessarily decrease with increasing density. However, previous studies have found that the distribution of *P. macroloba* adult trees is not clumped (Leiberman and Leiberman 1987, Deem et al. 1998). While these studies did not attempt to sample across alluvial and non-alluvial soils, their results could be due to greater abundance of non-alluvial soils. Alternatively, there could be greater mortality in intermediate life stages of *P. macroloba* in non-alluvial habitat leading to evenness in the adult distribution (Janzen-Connell hypothesis). Further studies could investigate potential mechanisms for greater mortality of intermediate life stages in non-alluvial habitat (e.g. intraspecific competition or increased herbivory due to optimal foraging).

Seedling distribution in alluvial soils appears to be more even than in non-alluvial soils. The evenness of *P. macroloba* seedling distribution in alluvial habitats may be enhanced by flooding and the movement of seeds by water. Surprisingly, we found a lower number of seeds per pod and higher rates of pod abortion in alluvial habitats. This may be caused by resource or pollinator limitation in alluvial habitats. Further studies may investigate these two factors by measuring resource allocation to seeds and/or observing pollinator behavior.

P. macroloba comprises a large proportion of adult trees in the forests of La Selva. However, the high abundance of this tree does not preclude it from variability in seed survivorship within this forest. The strength of density dependence regulation of *P. macroloba* at the seed stage appears to be strongly affected by abiotic factors. The uniform distribution of adult individuals across the landscape and the greater clumping of seedlings in non-alluvial soils indicates significant variation across moisture gradients for survivorship in other life stages. Additional studies are needed to understand the abiotic factors that cause density dependence variability in *P. macroloba* and how the strength of these factors may differ across a heterogeneous landscape.

LITERATURE CITED

- Deem, K. C., K. E. Weir, E. A. Wright and G. K. Eaton. 1998. Density dependent mortality in *Pentaclethra macroloba*. Pp. 89 - 91 in E. S. Berg and R. F. Douzinas eds. Dartmouth Studies in Tropical Ecology. Dartmouth College, Hanover, NH.
- Hartshorn, G. S. 1972. The ecological life history and population dynamics of *Pentaclethra macroloba*, a tropical wet forest dominant and *Stryphnodendron excelsum*, an occasional associate. Ph. D. diss., University of Washington, Seattle, WA.
- Hartshorn, G. S. 1983. *Pentaclethra macroloba*. Pp. 301 - 303 in D. H. Janzen, ed. Costa Rican Natural History. Chicago, IL: University of Chicago Press.
- Liebermann, M. and D. Lieberman. 1987. Patterns of density and dispersion of forest trees. Pp. 106 - 127 in L. A. McDade et al. eds. La Selva: ecology and natural history of a Neotropical rain forest. Chicago, IL: University of Chicago Press.

TABLE 1. Mean values (\pm SE) of seed success, seeds/pod and proportion of pods aborted

Treatment	seed success	seed/pod	Proportion of pods aborted
alluvial	0.07 \pm 0.03	2.76 \pm 0.22	0.17 \pm 0.07
non-alluvial	0.02 \pm 0.05	3.46 \pm 0.28	0.03 \pm 0.01
high	0.015 \pm 0.002	2.98 \pm 0.18	0.11 \pm 0.06
low	0.07 \pm 0.03	3.22 \pm 0.36	0.09 \pm 0.06

TABLE 2. ANOVA results testing for patterns in seed success with respect to soil type and seed density.

Source	df	F	P
Soil type	1, 12	2.86	0.12
Seed density	1, 12	4.46	0.05
Soil type x seed density	1, 12	3.35	0.09

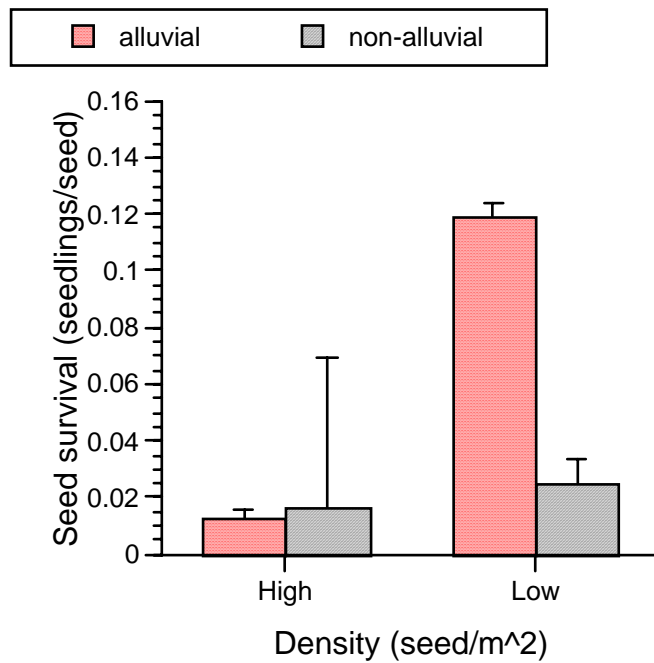


FIG. 1. Seed success at high and low seed densities on alluvial and non-alluvial soils.