

## MICROHABITAT-DEPENDENT RECRUITMENT OF *IRIARTEA DELTOIDEA* (ARECACEAE) IN AMAZONIAN ECUADOR

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### INTRODUCTION

Tree species diversity at the local scale (10–1000 m) is extremely high in the lowland rain forests of western Amazonia (Gentry 1988, Valencia *et al.* 1994, Romoleroux *et al.* 1997). One important hypothesis proposed to explain the maintenance of this high local-scale tree species richness is differentiation of the regeneration niche (Grubb 1977). According to this model, tropical tree species should have highly specialized demands for successful recruitment. Regeneration niche differentiation has been proposed with regard to light, litter cover, and edaphic requirements (Grubb 1977, 1996; Denslow 1987). Environmental heterogeneity corresponding to these factors has been documented as influencing the local distribution and/or demography of numerous tropical plant species (e.g., Baillie *et al.* 1987; Denslow 1987; Poulsen & Balslev 1991; Welden *et al.* 1991; Basnet 1992; Clark & Clark 1992; ter Steege *et al.* 1993; Clark *et al.* 1995, 1998; Duivenvoorden 1995; Tuomisto *et al.* 1995; Cintra 1997; Sollins 1998; Svenning 1999).

In the study reported here we investigate the local-scale spatial distribution of an abundant arborescent palm species, *Iriartea deltoidea* Ruiz & Pavón, at a site in Amazonian Ecuador. We specifically test the following two hypotheses which are relevant to the regeneration niche differentiation hypothesis:

1. Seedling recruitment rate of *Iriartea deltoidea* is influenced by environmental heterogeneity at the scale of 10 x 10 m (i.e., microhabitat heterogeneity).

2. Microhabitat heterogeneity influences the survival probability of immature *Iriartea deltoidea* individuals after initial germination and early seedling establishment phase.

We conclude with a discussion of the results in the context of the habitat requirements of the species throughout its range.

### STUDY SITE, STUDY SPECIES, AND METHODS

*Study area.* The study was carried out in old-growth tropical rain forest 1.2 km north of the Laguna Grande in the Cuyabeno Wildlife Production Reserve in Amazonian Ecuador (00°00', 76°12' W). The area is a flat *terra firme* bottomland c. 265 m above sea-level, crossed by a small stream and with shallow depressions which form temporary pools after heavy rain. Annual precipitation and mean daily temperature were 3555 mm and 24°C respectively (Valencia *et al.* 1994). More information about the study area can be found in Paz y Miño C. *et al.* (1991), Poulsen & Balslev (1991), Valencia *et al.* (1994, 1997), and Svenning & Balslev (1997). One interesting feature of this area is that the highest tree species diversity ever recorded for a 1.0 ha plot, 307 species with DBH ≥ 10 cm, was reported from a plot within 500 m of the study site used for this research (Valencia *et al.* 1994).

*Study species.* *Iriartea deltoidea* (hereafter *Iriartea*) is a tall arborescent palm which reaches more than 30 m in height and 30 cm stem diameter. It occurs in lowland and premontane rain forests of western South America and Central America (Henderson 1990, 1995). It is often abundant, and in many forests it is among the five most abundant tree species (Lieberman *et al.* 1985, Balslev *et al.* 1987, Gentry 1988, Wattenberg & Breckle 1995, Cerón & Mortalvo A. 1997, Romoleroux *et al.* 1997). *Iriartea* is

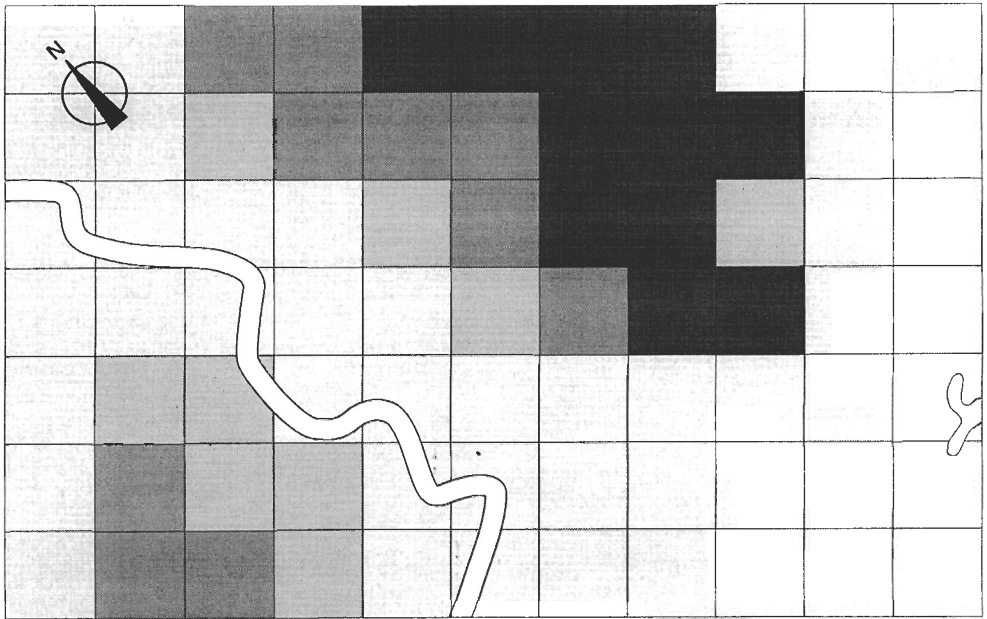


FIG. 1. A map of the study plot showing the streams and the shallow depressions that form temporary pools after heavy rain. The darker a subunit is colored, the higher is the proportion of its area formed by depressions (0%, 1–20%, 20–80%, and > 80%).

restricted to poorly drained streambanks in eastern and southern Amazonia, but is abundant on well-drained *terra firme* in the rest of its range (Balslev *et al.* 1987, Henderson 1990, Pinard 1993, Peres 1994, Clark *et al.* 1995, Chavez 1996, Svenning, in press). In Cuyabeno, *Iriartea* appears to occur mainly in bottomlands and creeks.

**Methods.** A 0.77 ha plot was established (Fig. 1). The number of seedlings, small juveniles, large juveniles and adults in each 10 × 10 m subunit were recorded. Seedlings were defined as having only entire leaves. Small juveniles were defined as individuals with pinnately divided leaves and stem height < 2 m. Large juveniles were 2–14 m tall, while adults were ≥ 14 m tall, which is the stem height at which reproduction begins (Pinard 1993, Svenning & Balslev 1997).

For each subunit, a record was made of whether it was dissected by a stream and the proportion of its area accounted for by the shallow depressions (0 = 0%, 1 = 1–20%, 2 = 20–80%, 3 = > 80%) (Fig. 1). The first variable, location on the bank of a small stream versus away from the stream, reflects two covarying environmental variables. As the stream

was in a deep channel, drainage was better on the stream bank than further away. Since no trees grow in the stream, there was only a broken canopy coverage immediately above it and light availability on the stream bank was in general higher than further away. The second variable, coverage by temporary pools after rain, represents a gradient in drainage.

Spatial distribution of the different life-history stages was analyzed using Mantel path analysis (Legendre & Fortin 1989, Leduc *et al.* 1992, Fortin & Gurevitch 1993). The significance of the Mantel coefficients was assessed using Mantel's *t*-test, an asymptotic *t*-approximation test (Fortin & Gurevitch 1993). Our sample size of 77 quadrats is well over the minimum of 40 required for this test (Fortin & Gurevitch 1993). Distance matrices for cover by depressions, and the number of seedlings, small juveniles and adults, were calculated using the Euclidean distance (Legendre & Legendre 1983). Before calculating the distance coefficient, the seedling numbers were transformed into a five-state ordinal index (0 = 0, 1 = 1–5, 2 = 6–10, 3 = 11–20, 4 = 21–40, and 5 = > 40 individuals) (Leduc *et al.* 1992). Dis-

tance matrices for the occurrence of streams and the number of large juveniles (always just 0 or 1) were calculated using the simple matching coefficient and subtracting it from 1 (Legendre & Legendre 1983). To be able to control for a spatial gradient in the variables, e.g., a gradient away from the neighboring hill, we also included a distance matrix for spatial location, calculated using the Euclidean distance between subunit centers (Legendre & Fortin 1989).

## RESULTS

*Iriarte* was very abundant in the 0.77 ha study plot: 981 seedlings, 29 small juveniles, 7 large juveniles, and 45 adults. For large juveniles and adults combined this corresponds to a density of 67.5 ha<sup>-1</sup>.

**Mantel correlations.** The seedlings and small juveniles are correlated with the presence of streams and the abundance of adults (Table 1). Large juveniles show a very slightly significant and weaker correlation with the abundance of adults and a stronger and very significant correlation with the presence of streams. The abundance of adults is also highly and very significantly correlated with the presence of streams. None of the four life-history classes is correlated in abundance with temporary pool cover, and no spatial autocorrelation was detected (Table 1).

**Comparison of density in streamside and non-streamside subunits.** Although the variability in the density of the different life-history stages is high, all have a higher average density in the stream subunits (Fig. 2).

**Partial Mantel correlations.** Since we found significant correlations of the abundances of seedling and juvenile stages with both the presence of streams and the abundance of adults, we calculated the partial Mantel correlations controlling for the effect of either the

TABLE 2. Smouse, Long & Sokal partial Mantel correlation coefficients among similarity matrices for streams, *Iriarte* adults (AD), large juveniles (LJ), small juveniles (SJ), and seedlings (SE). The coefficients are calculated controlling for the effect of the matrix given in parentheses. Probability levels are calculated using Mantel's t-test and Bonferroni-corrected for 18 simultaneous tests. ns  $P \geq 0.10$ , (\*)  $P < 0.10$ , \*\*\* $P < 0.001$ .

	LJ	SJ	SE
AD (streams)	0.11 ns	0.35***	0.29***
streams(AD)	0.31***	0.27***	0.21***

abundance of adults or the presence of streams (Legendre & Fortin 1989, Leduc *et al.* 1992, Fortin & Gurevitch 1993). The abundances of seedlings and small juveniles were independently correlated with both the abundance of adults and the occurrence of streams (Table 2). The abundance of large juveniles was only correlated with the occurrence of streams, and not with the abundance of adults when the effect of the other variable was controlled for (Table 2). The partial correlation coefficients of abundance of the immature stages and the correlation coefficient of adult abundance with the presence of streams also show that the association increases from the seedling to the large juvenile stage, but not between the large juvenile and adult stage (Table 1, 2).

## DISCUSSION

The hypothesis that variation in microhabitat variables influences the seedling recruitment rate of *Iriarte* is confirmed. The positive association of the seedlings with the stream bank is to a large degree independent of the association with adult abundance,

TABLE 1. Mantel correlation coefficients among similarity matrices for spatial location (space), streams, pools, *Iriarte* adults (AD), large juveniles (LJ), small juveniles (SJ), and seedlings (SE). Probability levels are calculated using Mantel's t-test and Bonferroni-corrected for 18 simultaneous tests. ns  $P \geq 0.10$ , (\*)  $P < 0.10$ , \*\*\* $P < 0.001$ .

	streams	pools	AD	LJ	SJ	SE
space	0.02 ns	-0.01 ns	-0.01 ns	-0.07 ns	-0.02 ns	0.05 ns
streams		-0.09 ns	0.30***	0.35***	0.36***	0.30***
pools			-0.06 ns	-0.03 ns	-0.10 ns	-0.02 ns
AD				0.20 (*)	0.42***	0.36***

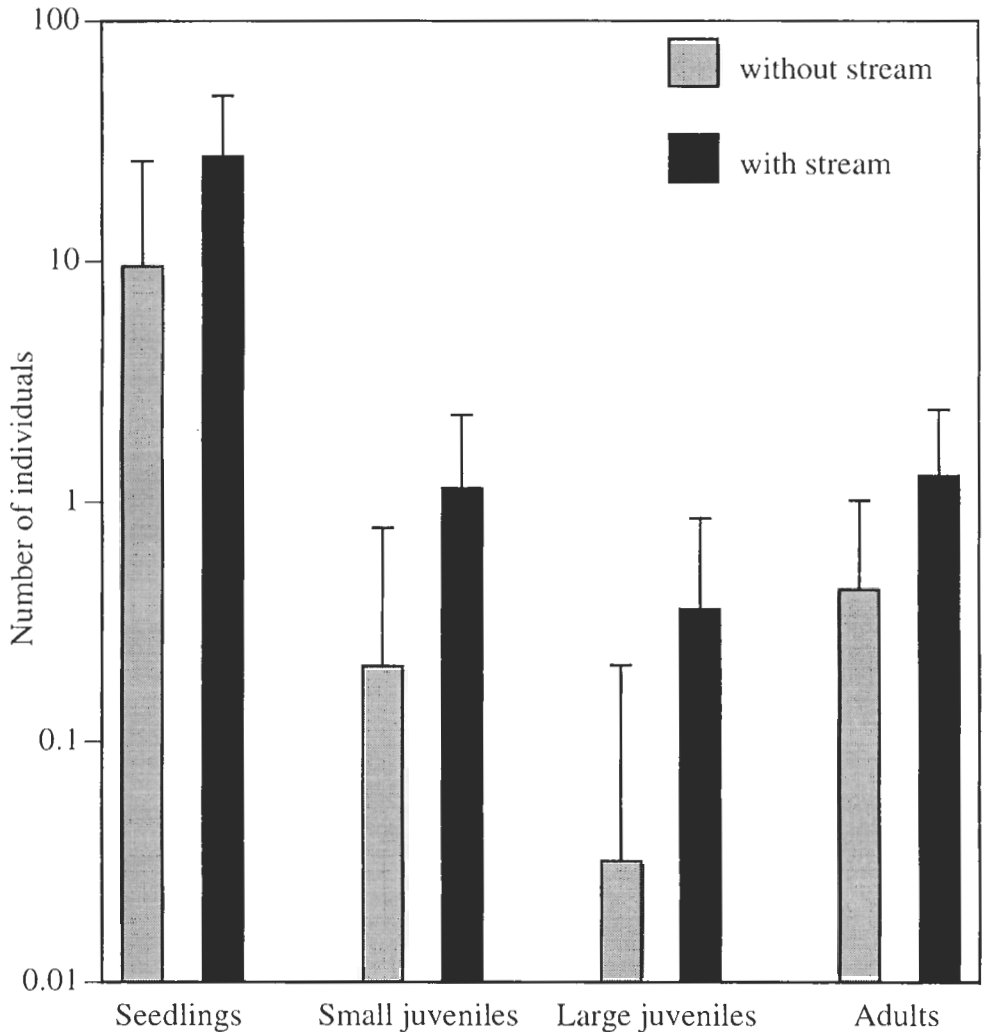


FIG. 2. The density per 10 x 10 m subunit of seedlings, small juveniles, large juveniles, and adults. Columns show the density, while error bars indicate the sample standard deviation. Black columns represent the stream-containing subunits (+S), while gray columns represent the subunits not containing a stream (-S).

and thus does not merely reflect limited propagule dispersal, but also a microhabitat effect already present at germination and/or early establishment. Whether the ultimate environmental factor causing this pattern is the higher light availability and/or better drainage conditions at the stream bank cannot be judged from our results. An experimental design including watering treatments and varying light intensities would be needed to distinguish these

possibilities. It is, however, noteworthy that a negative effect of flooding on seedling survivorship in *Iriartea* has been documented (Losos 1995).

The fact that the positive association with streams increases from the seedling to the large juvenile stage confirms our second hypothesis of differential mortality after the germination and initial seedling establishment phases. Mortality rates for seedlings and small juveniles must differ among the stream and

non-stream subunits, being higher in the latter, to produce the observed pattern. Since the associations of large juveniles and adults with streams are similar, no differential mortality can be documented for these stages. It has been suggested by Kahn & de Granville (1992) that high light availability is crucial for growth and survival of large juveniles of arborescent palms. Again, experiments would be necessary to establish whether light availability or drainage is the ultimate environmental factor causing the differential mortality.

Thus, variation in microhabitat conditions not only acts as a filter on germination and initial seedling establishment, but also on the survival through the seedling and small juvenile stages. Our results thereby provide evidence for microhabitat specialization in two of those processes where Grubb (1977) argued that regeneration niche differentiation could occur: germination and/or seedling establishment and further development of the immature plant.

Our impression that *Iriartea* had a larger-scale preference for streamside habitats in Cuyabeno was confirmed both by its small-scale preference for the streamside documented here and by comparing the high density of individuals found in our study plot with the density in a nearby 1.0 ha plot located on *terra firme* away from streams. Here, only 11 individuals with DBH  $\geq 5$  cm were found (Valencia *et al.* 1994). This density is very low compared to the 67.5 individuals  $\geq 2.0$  m tall  $\text{ha}^{-1}$  found in our bottomland plot. The height limit of  $\geq 2.0$  m corresponds well with the DBH limit of  $\geq 5$  cm. Thus, in Cuyabeno *Iriartea* appears to show the same preference for poorly drained streamside habitats as has been reported from Brazil and southern Peru (Henderson 1990, Pinard 1993, Peres 1994). This contrasts with its abundance on well-drained hill tops and slopes as well as in bottomlands in the Yasuní area in the Ecuadorian Amazon south of Cuyabeno (Balslev *et al.* 1987, Svenning 1999), the Andes (Henderson 1990), and Costa Rica (Clark *et al.* 1995). As the Yasuní area receives the same or less precipitation (Yasuní Scientific Station, unpublished data) than Cuyabeno, climatic differences cannot explain the differences in the habitat requirements of *Iriartea* between these areas. Thus it is possible that the differences might be genetically based.

Our results show that environmental heterogeneity strongly influences the local distribution of *Iriartea* in Cuyabeno. At the local scale, the effect is established both through differential germination or

seedling establishment and differential mortality until the large juvenile stage. These results are consistent with the regeneration niche hypothesis, which predicts that such fine-tuned environmental preferences maintain the high local-scale tree species richness found in many tropical rain forests (Grubb 1977, 1996; Denslow 1987).

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