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Growth strategies of the arborescent palm *Iriartea deltoidea* in a western Amazonian forest

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Stem development in palms usually involves the building up of a trunk of maximum diameter before emerging from the ground. Unlike most arboreal palms, the oligarchic palm *Iriartea deltoidea* has been shown to grow in both height and diameter. Nevertheless, the drivers of this unusual growth strategy are poorly known. We examined the growth rates of 554 stems found in 10 ha of the 50-ha Yasuní Forest Dynamics Plot. We explored whether palm growth responds to: (1) the size of individual palms; (2) light availability; or (3) the number of conspecifics and heterospecifics in the surrounding neighbourhood. Individual growth rates were positively related to palm height in the three life stages considered here (seedlings, saplings and adults). The mean annual diameter increment was higher (3.2 ± 4.6 mm year^{-1}) in individuals with a diameter at breast height (DBH) of < 20 cm, and mean vertical elongation of juveniles (0.2 ± 0.2 m year^{-1}) was initiated early in development until they became pre-adults. Growth in *I. deltoidea* was minimally affected by the presence of neighbours (basal area of conspecifics and heterospecifics), suggesting that this species can succeed at high densities with low levels of interspecific competition. Under the forest canopy, growth rates were not significantly different in palms with greater light exposure. Our findings contribute to an understanding of the factors that make *I. deltoidea* a dominant species in western Amazonia. © 2016 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2016

ADDITIONAL KEYWORDS: conspecifics – dendrometers – heterospecifics – light availability.

INTRODUCTION

Although the initial scientific explorers of tropical forests were often overwhelmed by the rich and varied life they encountered (Wallace, 1878; Bates, 1892), it is now apparent that much of the diversity in these systems is composed of relatively few taxa; of the estimated 16 000 tree species in the Amazon, half of all the individual trees come from only 227 species (Pitman *et al.*, 2001; ter Steege *et al.*, 2013). Understanding and explaining this pattern of hyperdominance are therefore prime goals of modern biology.

There appears to be little obvious connection among the suite of species that have attained such high abundance. For example, they are not differentiated from rarer species by seed size (ter Steege *et al.*, 2013), suggesting that neither the pioneer nor extreme shade-tolerant strategies are essential for success. Likewise, hyperdominant species are not especially used by humans (ter Steege *et al.*, 2013), implying that they are not widespread as a result of some form of prehistorical silvicultural management. However, to attain widespread high abundance, hyperdominant species must, almost by definition, meet several criteria. These conditions include: (1) an ability to perform well in a variety of different abiotic conditions, from drier ridge tops to shaded moister valleys, in a range of soil fertilities and nutrient availabilities; (2) an ability to perform well in areas of high conspecific density, less limited by

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negative density dependence; and (3) an ability to grow well in low-shade and high-light environments or to be able to attain the higher light availability in the canopy relatively quickly. In particular, this growth form or trajectory is found in many species of arborescent palms (Arecaceae), several of which are hyperdominant in Amazonia (e.g. species of *Attalea* Kunth, *Euterpe* Mart., *Iriartea* Ruiz & Pav., *Mauritia* L.f., *Mauritiella* Burret, *Oenocarpus* Mart. and *Socratea* H.Karst.). These arborescent palms have a unique stem development and, as a result, have succeeded in competing well with 'conventional' woody trees (Renninger, McCulloh & Phillips, 2013) and continue to represent a significant structural component in many tropical environments (Balslev *et al.*, 2012).

Unlike lignophytes (conifers and arborescent dicotyledons), which are capable of adding secondary vascular or thickening material, arborescent palms can only increase trunk diameter from derived primary tissues (Tomlinson, 1990, 2006). Diameter increment occurs by sustained parenchyma cell expansion, an increase in cell wall thickness and stiffening of stem tissues (especially fibres) by lignification (Rich *et al.*, 1986; Rich, 1987a); growth in height is confined primarily to the production of cells in the apical meristem (but see Renninger & Phillips, 2012). For most arborescent palms, such increment occurs and attains its maximum below ground, with no further increment as palms grow taller (Tomlinson, 1990). These palms (coryphoids, borassoids, phytelephantoids and non-spiny cocosoids) show limited internode distances, slower growth rates and occur in drier, seasonal habitats. Conversely, palms in the tribe Iriarteeae show a remarkable capacity to increase both in height and diameter, have faster growth rates and tend to be found in moister forests (Henderson, 2002). These features are exemplified by *Iriartea deltoidea* Ruiz & Pav. (Rich *et al.*, 1986; Rich, 1987b; Henderson, 1990). The ubiquity of *I. deltoidea* in Amazonian forests is well documented (Pitman *et al.*, 2001; Valencia *et al.*, 2004; Macía & Svenning, 2005; Montúfar & Pintaud, 2006; ter Steege *et al.*, 2013). It is among the five most common trees in Amazonia and is particularly abundant in western Amazonia (ter Steege *et al.*, 2013). It seems likely that growth habit contributes to the success and abundance of iriarteoid palms in these forests. Understanding the growth of *I. deltoidea* in response to a variety of factors, abiotic (e.g. light) and biotic (e.g. neighbouring trees), may shed light on the mechanism of its ecological success.

The abiotic environment often limits the distribution of populations of species because trade-offs in performance prevent organisms being equally fit in all environments. For example, the well-established trade-off between growth in high light and survival in deep shade prevents shade-tolerant species from regenerating in light gaps and pioneers from recruiting into the shaded understorey (Denslow *et al.*, 1990; Montgomery & Chazdon, 2002). Unlike many large palms (Svenning, 2001), *I. deltoidea* does not recruit solely in large forest gaps (Svenning, 1999), suggesting that it can overcome this trade-off to some extent, maybe by growing in diameter underground before growing rapidly in height with sufficient stored resources to reach the canopy (Poorter *et al.*, 2005). Indeed, many arborescent palm species show little to no correlation between stem diameter and height (Goodman *et al.*, 2013).

In addition, many tropical tree species show some degree of habitat association (Harms *et al.*, 2001), often correlated with soil water (Comita, Condit & Hubbell, 2007; Engelbrecht *et al.*, 2007; Comita & Engelbrecht, 2009, 2014) or soil nutrient availability (John *et al.*, 2007; Condit *et al.*, 2013). Drought, certain soil nutrients or other abiotic variables, often associated with variation in topography, exclude species that are not adapted to the specific niche conditions encountered. Some species are restricted to unique and/or rare abiotic environments (e.g. light-demanding pioneer species, such as species of *Cecropia* Loefl., or swamp-adapted species, such as the palm *Mauritia flexuosa* L.f.). Any species that can perform well, or at least better than other species, in a wide variety of microhabitats will probably be able to become widespread and abundant. Hyperdominant species, therefore, are likely to be successful in an abundant habitat or have high growth, survival and reproduction in a number of different microhabitats and can accommodate variation in abiotic conditions (Duque *et al.*, 2002). Moreover, in any one site, hyperdominant species would be expected to show few or no habitat associations and to occur equally in many, if not all, topographic microhabitats.

The abiotic neighbourhood establishes the template for regeneration, but the biotic neighbourhood modifies this potential by limiting germination, recruitment and onward growth and survival (Crawley, 1997), usually by negative density dependence (Barot, Gignoux & Menau, 1999; He & Duncan, 2000; Stoll & Bergius, 2005; Queenborough *et al.*, 2007). Not only the number and physical proximity of neighbours (Uriarte *et al.*, 2004), but also the phylogenetic proximity (Zhu *et al.*, 2015), influence focal tree performance, with larger, closer and more closely related neighbours having more negative effects on growth and survival than smaller, further and more distantly related neighbours, with rarer species suffering more than common species from these negative density-dependent effects (Comita *et al.*, 2010; Mangan *et al.*, 2010).

Hyperdominant species, therefore, are likely to experience little negative effect of conspecific neighbours and grow and survive well in high-density localities.

This study explores how the distribution and growth strategy of individuals of *I. deltoidea* may contribute to an understanding of its success as a dominant species in western Amazonia, focusing on its autecology in a lowland tropical rain forest located in Yasuní National Park, Ecuador. For a population in a large permanent plot, we quantified the allometric relationship between height and diameter and the ontological growth in diameter and height in *I. deltoidea* with the ultimate goal of answering the following questions. (1) Is the hyperdominance of *I. deltoidea* in western Amazonia reflected at a single site? (2) Is *I. deltoidea* distributed uniformly across the site, with no habitat associations or variation in abundance according to topographic habitat? (3) Does light availability or topographic habitat variation affect growth in diameter and/or height? (4) Do conspecific neighbours significantly inhibit growth in diameter and/or height?

MATERIAL AND METHODS

Study site

The Yasuní National Park is located on the western margin of the Amazon Basin, a region located < 100 km from the Andean foothills and running along the line of the Equator (~1°S) (Finer *et al.*, 2009). In conjunction with the Waorani Ethnic Reserve, it is the largest protected area (1.6 million ha) of one of the most biodiverse sites in the Ecuadorian Amazon (Bass *et al.*, 2010). *Terra firme* forest comprises 80% of the terrain, scattered with alluvial floodplains and *Mauritia flexuosa* swamps (Macía & Svenning, 2005). Most of the landscape is covered with evergreen forest, ranging in elevation from 190 to 400 m, with a 10–25-m tall canopy interrupted by occasional emergent trees of 40–50 m. The climate is equatorial humid with a mean annual precipitation of 2826 mm, mean annual temperature of 24–27 °C and high relative humidity (80–94%) (Valencia *et al.*, 2004). Soils are geologically young, resulting from erosion and sedimentation of the Andes (Tuomisto, Ruokolainen & Yli-Halla, 2003).

This research was conducted in the 50-ha Yasuní Forest Dynamics Plot (YFDP), established in 1995 as part of a worldwide network of permanent plots for keeping track of tree populations and carbon dynamics (Anderson-Teixeira *et al.*, 2015). In the plot, *I. deltoidea* is one of the most common species of tree with a diameter at breast height (DBH, measured at 1.3 m) of ≥ 1 cm (mean density of 72.8 stems ha^{-1}, SD = 20.4) and the most abundant species among large trees (1808 individuals ≥ 10 cm DBH, 10.3% of the total; Valencia *et al.*, 2004).

Sampling design

The YFDP has been censused four times, initially in 1994–1999 and in 2002–2003, 2009 and 2015–2016 (exact date varies depending on the location and size of tree; e.g. the most recent census data available for 2015 are for trees > 10 cm DBH, whereas the census for trees 1–10 cm DBH is under way). All woody stems > 1 cm DBH were mapped, tagged and identified to species.

Our allometric census of *I. deltoidea* occurred between 2011 and 2014. These censuses were carried out in ten 1-ha columns (20 m × 500 m) of the 50-ha plot, positioned 80 m apart (Supporting Information, Fig. S1). The sample hectares included the four major habitats: ridge (5.64 ha), valley (3.88 ha), swamp (0.28 ha) and a small area of secondary forest regenerated after a forest clearing occurred on a ridge in *c.* 1987 (0.2 ha; Valencia *et al.*, 2004; Pérez *et al.*, 2014). By the year 2015, the density of large individuals of *I. deltoidea* (DBH ≥ 10 cm) in the ten 1-ha plots was as follows: ridge, 72.3 ha^{-1}; valley, 59.3 ha^{-1}; swamp, 71.4 ha^{-1}; secondary ridge, 40 ha^{-1}).

Our first allometric census was in September–December 2011, after a time interval of 7.12 years since the conclusion of the last main plot census. In each 1-ha column, we measured all the surviving individuals of *I. deltoidea* from previous YFDP censuses, and mapped and tagged all new individuals that had developed stems with adventitious roots (minimum diameter recorded, 4 mm; minimum height recorded, 3 cm), including seedlings and juveniles < 1.3 m tall, which were not included in previous censuses. We included these individuals because stems of *I. deltoidea* can reach up to 7 cm in diameter, but still not 1.30 m in height (M. Ninazunta, pers. observ.), and thus may not be counted as new recruits in the YFDP main plot census. All living individuals of *I. deltoidea*, including previously measured and recruits, were censused four subsequent times: August 2012, January 2013, August 2013 and May 2014.

Data collection

To determine the diameter increment between 2011 and 2014, we measured the diameter of all *I. deltoidea* individuals ($N = 554$), using dendrometer bands rather than tape or calipers as much as possible ($N = 382$; Clark, Wynne & Schmoldt, 2000), because measurement error is often significant in relation to the expected growth over short-term studies (Carvalho & Felfili, 2011). Following the protocol of Muller-Landau & Larjavaara (2009), plastic dendrometer bands were constructed using a 1-cm-wide plastic banding (length: equal to tree circumference plus 35 cm) with both ends folded over the band (leaving one free, mobile end) and attached with metallic seals (length < 25 mm). The free end marks the expansion or contraction of the stem using a cut notch as a reference. Finally, the band is wrapped around the bole and then held with a stainless steel spring (size varied according to palm size) that enables the banding tape to move as the stem expands or contracts. These were installed on 382 individuals: 140 trees with stems ≥ 10 cm DBH selected from 50 equidistant quadrats and 242 individuals with stems < 10 cm DBH (minimum diameter, 41 mm; minimum height, 16 cm) occurring in the remaining 200 quadrats of the sampling area (Fig. S1). Measurements using diameter tape alone were taken for the remaining 109 young palms, the stems of which were unfit for dendrometer installation (e.g. the bole diameter was too small to hold a dendrometer band or was covered by lianas). Diameter measurements were taken with precision calipers (± 0.01 mm) at every census. For palms without dendrometers, the point of measurement (POM) was marked on each stem with permanent paint to ensure accurate repeated measurements. For palms > 130 cm tall, POM was 1.3 m from the ground; for palms with stems 20–130 cm tall, POM was 20 cm; and for stems < 20 cm tall, POM was 5 cm.

Height was recorded using a measuring tape for individuals of < 2 m ($N = 208$) and with a telescopic ruler for palms of 2–7 m ($N = 108$). The heights of taller palms ($N = 175$) were estimated by eye, but could not be estimated repeatedly and accurately (M. Ninazunta, unpubl. data), and so were excluded from further height growth analysis. Stem height was defined as the distance from the ground to the highest point of the leaf sheath, a position that could be assessed with consistency, although it omits the crown height (Terborgh & Davenport, 2001).

CANOPY OPENNESS AND NEIGHBOURHOOD DENSITY

Evaluation of the light environment is challenging, particularly in the tropics. We used a specific method appropriate to the size of the palm. For palms < 3 m tall, we took photographs of the canopy above each palm and obtained an estimate of canopy openness. Photographs were taken with a Panasonic DMC-LZ8 camera, wide-aperture 5-mm focal length lens, ISO-400, f/5.6, exposure time 1/100 s. To capture the light conditions in the immediate vicinity, the camera was stabilized on a tripod and positioned 1 m away to the northern, southern, eastern and western sides of the focal palm. From each of these locations, the camera was pointed towards the sky; thus, four photographs were taken of the overhead canopy openness. Images were processed in the software ImageJ (Rasband, 2012) by converting each of the photographs obtained into a white and black pixel colouring. We obtained an average percentage canopy openness based on the number of white pixels averaged for all the photographs taken for every target palm. For palms > 3 m tall, we assigned a canopy illumination index (CII) score (Clark & Clark, 1992). CII quantifies the light available to a tree by estimating the exposure of the crown on a scale of 1–5: 1, no vertical light and minimal lateral light; 2, no vertical light and medium lateral light; 3, crown exposed to some vertical and some lateral light; 4, crown exposed to vertical and some lateral light; and 5, crown completely exposed vertically and laterally. CII correlates with canopy openness values obtained from hemispherical photographs (Davies *et al.*, 1998) and is a rapid and repeatable way of estimating light availability in tree canopies (Keeling & Phillips, 2007).

For the neighbourhood analyses, we used a dataset corresponding to a census carried out in 2015. The plot census includes trees ≥ 10 cm DBH measured, tagged and mapped to 0.5-m precision. Individuals of *I. deltoidea* with stems that just reached 1.3 m tall by the time of the census usually had DBH > 5 cm (mean, 17.3 cm). We counted the number of conspecific and heterospecific trees > 10 cm DBH located within 10 m of each palm and calculated the total basal area of both around each focal tree. Analyses were performed using the software R 3.2.2 (R Core Team, 2015).

DATA ANALYSIS

Absolute growth rates (AGRs) were calculated as the subtraction of initial (m_i) from final (m_f) measurements divided by the time between censuses ($m_f - m_i/t$) for height and diameter. We evaluated the allometric relationship between $\log_{10}$-transformed height and $\log_{10}$-transformed diameter with a simple linear model for each life stage (seedlings < 20 cm tall, saplings 20–130 cm tall and trees > 130 cm tall). We similarly examined the relationship of AGR to initial size for both diameter and height.

We tested the effects of light and tree neighbourhood on AGR using linear regression. For light availability, we tested small palms (< 3 m tall), using canopy cover as the predictor, and large palms (> 3 m tall), using CII scores as the predictor. For tree neighbourhood, we tested the relative effects of the number of conspecific trees and heterospecific trees > 10 cm DBH and habitat type (ridge, valley, swamp or secondary ridge).

RESULTS

We marked 554 individuals of *I. deltoidea* in 2011, 63 of which had died by our last census in May 2014. Of the 491 living individuals that were recorded, 320 were previously measured from the YFDP main tree censuses, and 90 juveniles and 81 new recruits were included as new records. Of the total number of palms, 63 had died by 2014 and were excluded from growth analyses. A total of 60 palms were < 20 cm tall, 122 were 20–130 cm tall and 333 were > 130 cm tall. The diameter of trees ranged from 4.9 to 247.0 mm (mean ± SD, 102 ± 63 mm). Two hundred and six individuals were > 10 cm DBH. Palm height ranged from 0.03 to 35.00 m (mean, 6.7 ± 8.4 m). One hundred and fifty-one individuals were > 7 m tall.

Palm distribution and habitat associations

Iriartea deltoidea was dominant in the YFDP, with 3166 individuals of *I. deltoidea* > 10 cm DBH recorded in the 50-ha YFDP 2015 tree plot census (Fig. 1). These palms were located throughout the plot and occurred in 1050 (84%) of the 1250 20 m × 20 m (400 m^2) subplots (Fig. S1). The number of palms in each 20 m × 20 m subplot ranged from 0 to 13 (mean = 2.6, median = 2, SD = 2.15).

Iriartea deltoidea occurred at high abundance in all habitat types. In the ten 1-ha plots censused in 2015 (palms with DBH ≥ 10 cm), we found densities of 72.3 individuals per hectare on ridges, 59.3 in valleys, 40 on secondary ridges and 71.4 in swamps. Therefore, all habitats had individuals of *I. deltoidea* and their subplot frequency was proportionally similar (mean of 84% of subplots occupied, $\chi^2 = 3.971$, d.f. = 3, $P = 0.26$). However, valley subplots (mean of 2.76 palms) had a significantly greater mean abundance of palms than did ridge subplots (mean of 2.41 palms; generalized linear model with quasi-Poisson error: $t = 2.775$, $P = 0.0056$). Moreover, the observed total number of palms in each habitat was slightly greater than expected in the valley (1313 observed vs. 1213 expected), but slightly lower on the ridge (1737 vs. 1839), given the abundance of each habitat type in the plot ($\chi^2 = 10.565$, d.f. = 3, $P = 0.014$). The ~0.5-ha secondary forest located on a ridge had individuals of *I. deltoidea* surrounding the centre of the area (Fig. 1).

Palm diameter–height allometry

The allometric evaluation of *I. deltoidea* stems showed strong positive relationships between $\log_{10}$ height and $\log_{10}$ diameter (Fig. 2). Modelling all stems pooled, height was related to diameter as $H = 2.31D + 0.25$ (linear regression, $R^2 = 0.83$, $F_{1,512} = 2577$, $P < 0.001$, Fig. 1, inset). However, because diameter measurements were taken at different POMs for the three different size classes, this single model for all palm individuals is not easily interpretable at all stages, and so we constructed separate models for each stage. For seedlings < 20 cm tall: $H = 0.46D + 0.85$ (linear regression,

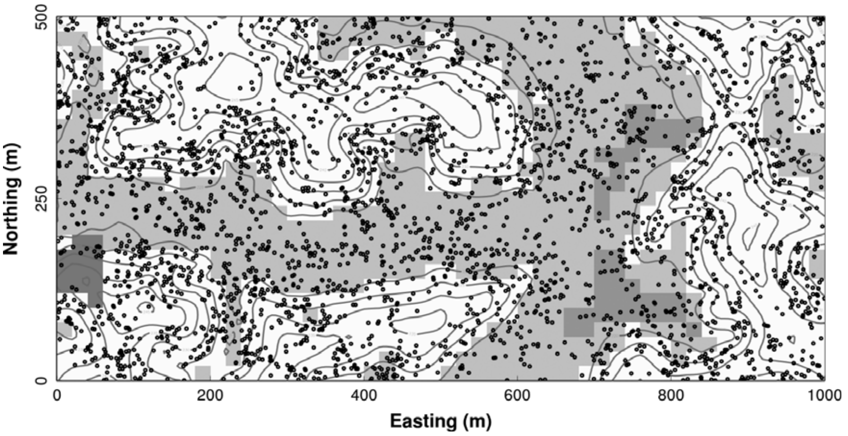

Figure 1. The distribution and abundance of the arborescent palm *Iriartea deltoidea* in a large permanent forest plot in lowland humid forest in western Amazonia. The figure shows individual palms > 10 cm diameter at breast height (DBH) (circles), located in different habitat types (white, ridge; light grey, valley; mid-grey, swamp; dark grey, secondary ridge), defined by the topography (elevation, slope and convexity, see Valencia *et al.*, 2004) of each 20 m × 20 m subplot (6-m contour lines are indicated).

$R^2 = 0.34$, $F_{1,58} = 29.84$, $P < 0.01$). For saplings 20–130 cm tall: $H = 1.30D + 0.80$ (linear regression, $R^2 = 0.27$, $F_{1,120} = 44.0$, $P < 0.01$). For trees > 130 cm tall: $H = 1.68D + 1.03$ (linear regression, $R^2 = 0.82$, $F_{1,330} = 1459$, $P < 0.01$). Thus, three stages of growth could be clearly interpreted. In the seedling stage, plants increased mostly in diameter, but with much variation. This stage was followed by rapid height growth in the sapling stage. Overall, trees appeared to grow similarly in height and diameter with close to a 10 : 1 relationship, which varied depending on the ontogenetic stage.

Palm growth rates

Diameter AGR ranged from −7.4 to 36 mm year^{-1} (mean of 3.2 ± 4.6 mm year^{-1}). Height AGR ranged from 0 to 1.6 m year^{-1} (0.2 ± 0.2 m year^{-1}). Initial height was generally a better predictor than diameter of growth, with higher R^2 values. Further, there was a contrast between diameter AGR and height AGR as a function of initial size (Fig. 3). Despite wide variance, seedlings and saplings grew in diameter and height, with larger individuals having higher AGR (linear regressions, seedlings: $D_{\text{AGR}} = 0.06D + 0.42$, $F_{1,54} = 2.86$, $P = 0.10$, $R^2 = 0.05$; $H_{\text{AGR}} = -0.11H + 0.60$, $F_{1,54} = 11.5$, $P < 0.01$, $R^2 = 0.17$; saplings: $D_{\text{AGR}} = -0.21D + 0.58$, $F_{1,116} = 1.99$, $P = 0.16$, $R^2 = 0.02$; $H_{\text{AGR}} = 0.40H + 0.34$, $F_{1,114} = 5.4$, $P = 0.02$, $R^2 = 0.05$). For height, trees continued to grow taller at a similar rate (Fig. 3B, linear regression, $H_{\text{AGR}} = -0.32H + 0.72$, $F_{1,139} = 15.9$, $P < 0.001$, $R^2 = 0.1$). However, for diameter, the growth rate of larger trees declined as a function of initial size, leading to a negative relationship between diameter AGR and initial diameter (Fig. 3A, linear regression, $D_{\text{AGR}} = 2.71D - 1.01$, $F_{1,315} = 58.2$, $P < 0.01$, $R^2 = 0.16$). There was no trade-off (i.e. a negative relationship) between height growth rate and diameter growth rate (Fig. 3C).

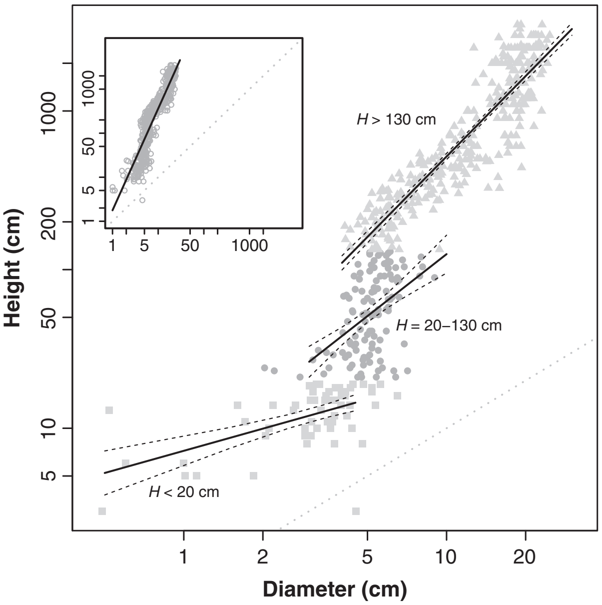

Figure 2. Height–diameter allometry in a natural population of *Iriartea deltoidea* in a lowland rain forest, Yasuní National Park, Ecuador, for 60 seedlings (< 20 cm tall, squares), 122 saplings (20–130 cm tall, circles) and 333 trees (> 130 cm tall, triangles). Full lines indicate fitted values from a linear regression, with 95% confidence intervals shown by broken lines (for seedlings < 20 cm tall: $H = 0.46D + 0.85$, $R^2 = 0.34$, $F_{1,58} = 29.84$, $P < 0.01$; for saplings 20–130 cm tall: $H = 1.30D + 0.80$, $R^2 = 0.27$, $F_{1,120} = 44.0$, $P < 0.01$; for trees > 130 cm tall: $H = 1.68D + 1.03$, $R^2 = 0.82$, $F_{1,330} = 1459$, $P < 0.01$). Both variables are $\log_{10}$-transformed. Inset shows the same data with a single fitted line with both x and y axes of equal ranges (linear regression: $H = 2.31D + 0.25$, $R^2 = 0.83$, $F_{1,512} = 2577$, $P < 0.001$). Dotted grey line indicates the 1 : 1 relationship.

Palm neighbourhoods

The density of conspecific palms within 10 m of focal individuals of *I. deltoidea* ranged from zero to 13 trees > 10 cm DBH (mean ± SD, 3.8 ± 2.6); the density of heterospecific trees within 10 m ranged from nine to 47 trees > 10 cm DBH (23.8 ± 5.7). The basal area of conspecific palms ranged from zero to 376 cm^2 (104.0 ± 74 cm^2) and of heterospecifics from 163 to 3318 cm^2 (975 ± 418 cm^2).

Briefly, in multiple regression models, increasing basal area of conspecifics had a negative effect on both diameter and height AGR, but increasing basal area of heterospecifics had no effect on diameter or height AGR. There were no differences in AGR among habitats (Fig. 4, Table 1; linear regression, D_{AGR}: $F_{5,485} = 5.756$, $P < 0.001$, $R^2 = 0.06$; H_{AGR}: $F_{5,307} = 83.49$, $P < 0.001$, $R^2 = 0.58$).

In more detail, the mean growth rate in the absence of conspecifics was 1.9 ± 1.1 mm for diameter expansion and 2.18 ± 1.1 cm for vertical extension. The addition of 100 cm^2 of conspecific palm basal area (an 11 cm DBH tree) decreased growth by 1.0 mm for diameter (Fig. 4A) and 1.0 cm for height (Fig. 4C). The addition of heterospecific trees had no significant effect (Fig. 4B, D). Habitat had no significant effect on either D_{AGR} or H_{AGR} in either model.

Palm light availability

Canopy closure estimated from photographic images taken over palms < 3 m tall ranged from 73% to

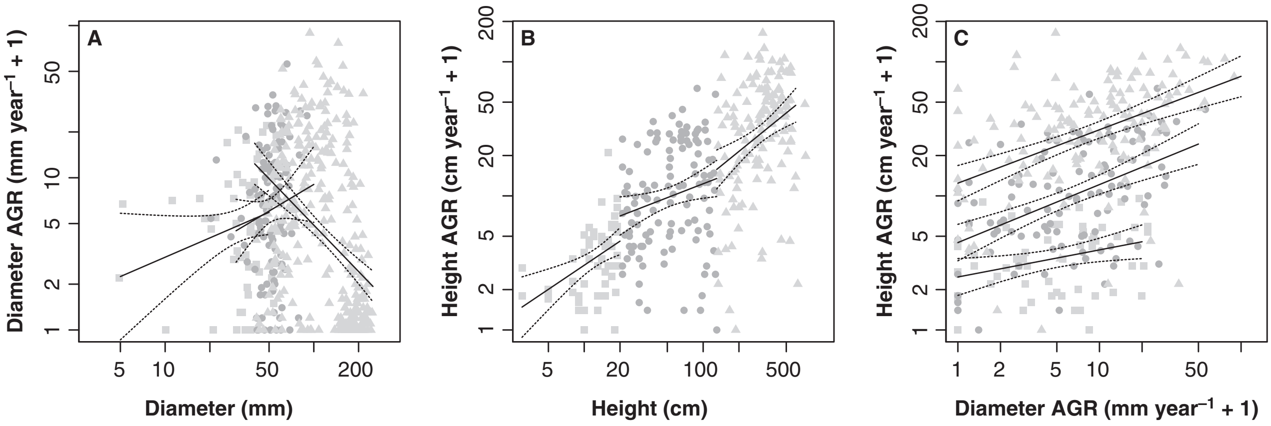

Figure 3. Absolute growth rates (AGRs) in diameter (A) and height (B) increment and the relationship between the two (C) in a natural population of *Iriartea deltoidea* in a lowland rain forest, Yasuní National Park, Ecuador for seedlings (squares), saplings (circles) and trees (triangles). Full lines indicate fitted values from a linear regression, with 95% confidence intervals shown by broken lines. Both variables are $\log_{10}$-transformed. For diameter growth rates (A), the regression equation for seedlings is $0.06D + 0.42$, $F_{1,54} = 2.86$, $P = 0.10$, $R^2 = 0.05$; for saplings $-0.21D + 0.58$, $F_{1,116} = 1.99$, $P = 0.16$; and for trees $2.71D - 1.01$, $F_{1,315} = 58.2$, $P < 0.01$, $R^2 = 0.16$. For height growth rates (B), the equation for seedlings is $-0.11H + 0.60$, $F_{1,54} = 11.5$, $P < 0.01$, $R^2 = 0.17$; for saplings $0.40H + 0.34$, $F_{1,114} = 5.4$, $P = 0.02$, $R^2 = 0.05$; and for trees $-0.32H + 0.72$, $F_{1,139} = 15.9$, $P < 0.001$, $R^2 = 0.1$. There was no trade-off between height growth rate and diameter growth rate (C).

99%, with a mean of 95% (± 4%). CII scores for palms > 3 m tall ranged from 1 to 5, with a mean of 3 (± 1). Just over 50% of palms were found to occur in a low-light environment (CII: 1 or 2), 37% in intermediate levels (CII: 3 or 4) and 13% had a fully exposed canopy (CII: 5). There was no significant effect of canopy cover (CC) on either diameter or height AGR of palms < 3 m tall (Fig. 5A, B; linear regression, $D_{\mathrm{AGR}} = 12.6\mathrm{CC} - 0.1$, $F_{1,163} = 3.86$, $P = 0.05$, $R^2 = 0.02$; $H_{\mathrm{AGR}} = 15.9CC - 0.1$, $F_{1,160} = 0.14$, $P = 0.71$, $R^2 < 0.001$). However, for individuals > 3 m tall, CII scores had a significant effect on AGR, especially in height (Fig. 5C, D, ANOVA, D_{AGR}: $F_{4,303} = 8.7$, $P < 0.001$, $R^2 = 0.1$; H_{AGR}: $F_{3,130} = 3.2$, $P = 0.03$, $R^2 = 0.07$).

DISCUSSION

In agreement with our expectations and its hyperdominance in western Amazonia, *I. deltoidea* was widespread and abundant throughout the 50-ha plot and occurred in all four habitat types. This distribution suggests that these palms are effective at accommodating variation in local abiotic conditions and can overcome the limiting negative density-dependent processes that prevent other species from becoming so abundant. Some clue as to the mechanism lies in the unique growth strategy of *I. deltoidea* and other similar arborescent palms. We found evidence of the onset of simultaneous increments in diameter and height early in the establishment phase of *I. deltoidea*. Absolute annual growth rates were dependent on initial individual size, but differed among life stages. Moreover, the effects of topographic habitat, light availability and nearby trees were minimal, with little ecological effect on the performance of focal individuals, again suggesting that *I. deltoidea* can grow well and succeed in a wide variety of conditions. We consider these various factors in more detail below.

Palm size

Our results suggest that individuals of *I. deltoidea* prioritize stem expansion early in ontogeny until juveniles build up a sufficiently supportive stem to attain greater vertical elongation when approaching adult size. *Iriartea deltoidea* palms grow in diameter and height in pre-adult stages. This strategy might provide a competitive advantage that allows the species to efficiently use light and nutrients to grow in diameter and store resources until sufficient reserves accumulate to allow rapid growth to the canopy; many lignophytes remain in the understorey for decades (Hubbell & Foster, 1986), whereas *I. deltoidea* can grow to a sapling in as few as 14 years and reach the canopy in only 120 years (Stattegger, 2014).

Initial size was a better predictor for height increment than for diameter increment. Trying to model the growth of seedlings to adult palms would

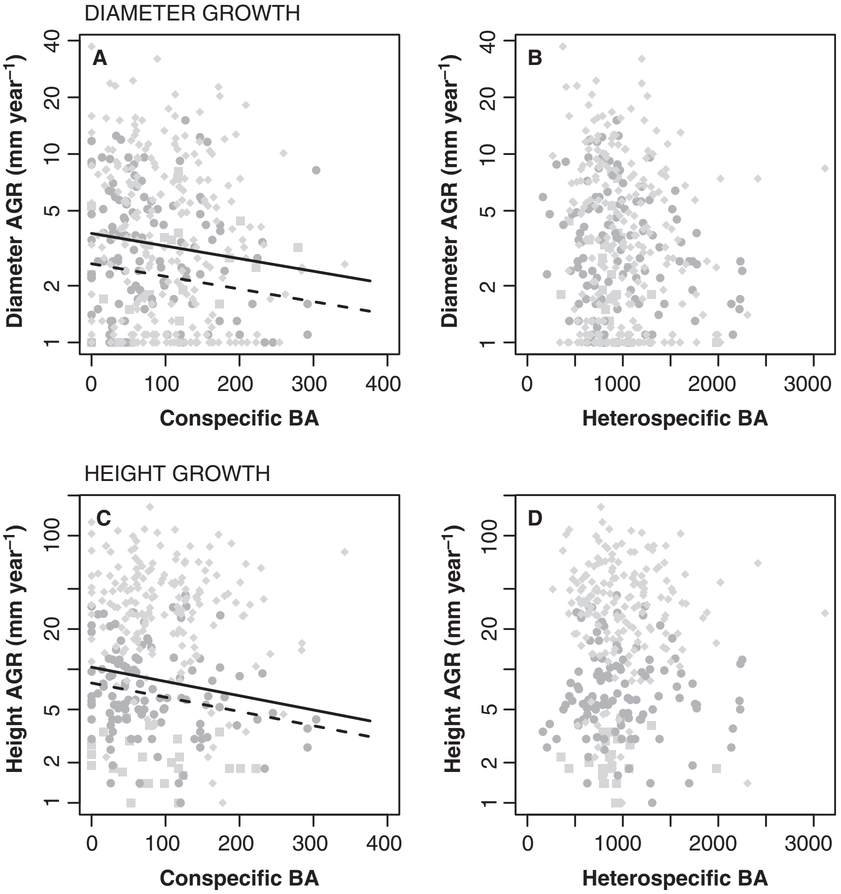

Figure 4. The effect of conspecific and heterospecific neighbouring trees > 1 cm diameter at breast height (DBH) on growth rates of focal *Iriartea deltoidea* palms in a lowland rain forest, for diameter (A, B) and height (C, D) increments. There was no significant effect of heterospecifics on D_{AGR} or H_{AGR}. Full lines in (A) and (C) correspond to the effect of conspecifics in a neighbourhood with zero heterospecifics; the broken line corresponds to a neighbourhood heterospecific basal area (BA) of 3000 cm^2. All fitted lines are for palms 10 m tall. Note the $\log_{10}$ scale of the *y* axis. Equations for linear regression models: D_{AGR}: $F_{5,485} = 5.756$, $P < 0.001$, $R^2 = 0.06$; H_{AGR}: $F_{5,307} = 83.49$, $P < 0.001$, $R^2 = 0.58$. AGR, absolute growth rate.

Table 1. Absolute growth rates in diameter (DGR) and height (HGR) of individuals of *Iriartea deltoidea* in a large forest plot in western Amazonia

DBH (cm)	Mean DBH (cm)	Mean height (m)	*N*	DGR (mm year^{-1}) (± SD)	*N*	HGR (cm year^{-1}) (± SD)
< 5	3.8	0.5	73	1.27 (1.34)	72	3.37 (3.37)
(5–10)	6.8	2.1	191	3.35 (3.17)	183	20.04 (19.41)
(10–15)	12.4	6.3	73	6.32 (4.75)	46	53.47 (23.54)
(15–20)	17.7	12.4	101	2.84 (6.21)	10	70.50 (34.66)
> 20	21.6	19.6	53	1.92 (5.79)	2	102.60 (2.40)

DBH, diameter at breast height.

probably prove to be difficult with linear models, because they imply a constant increment throughout the lifespan of the individual, and obscure the temporal variation in height vs. diameter growth (Paine *et al.*, 2012). As this study considered juvenile individuals for the evaluation of height elongation, as they are believed to grow constantly and quickly (Stattegger, 2014), such an outcome was not

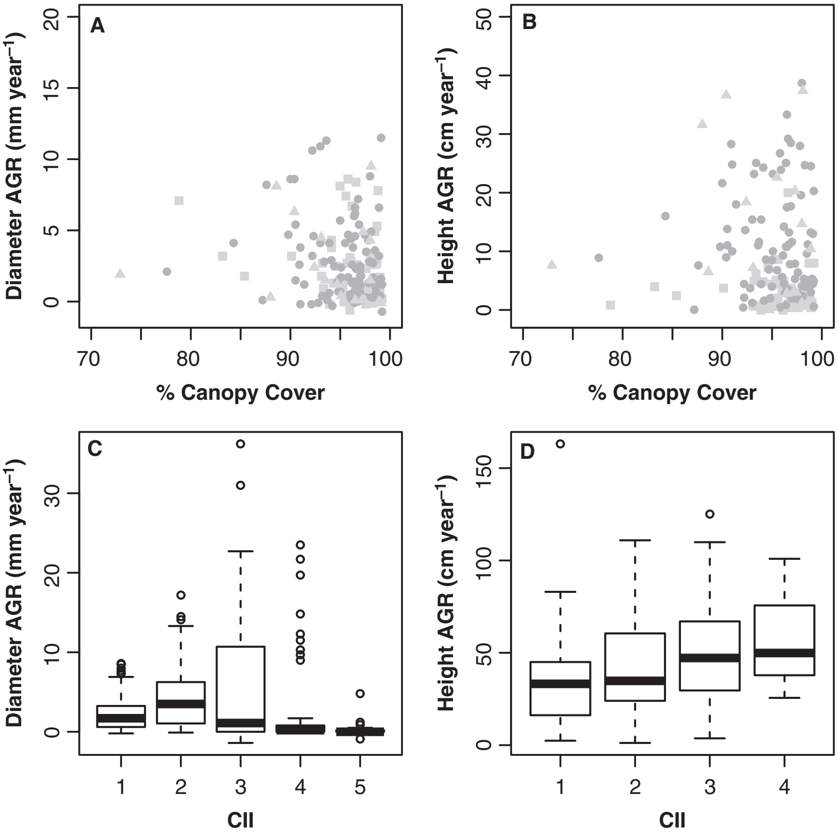

Figure 5. The effect of light availability on growth in diameter (A, C) and height (B, D) increment in a natural population of *Iriartea deltoidea* in a lowland rain forest in Yasuní National Park, Ecuador. Canopy openness had no effect on diameter (A: linear regression, $P = 0.05$, $R^2 = 0.02$) or height (B: $P = 0.71$, $R^2 < 0.001$) growth. However, canopy illumination index (CII) did. Shaded trees grew more in diameter (C: ANOVA, $P < 0.001$, $R^2 = 0.1$), whereas trees with direct light grew more in height (D: ANOVA, $P = 0.03$, $R^2 = 0.07$). Note the $\log_{10}$ scale of the y axis. Class 5 is not included because palms that were assigned to this CII level were all tall adult individuals that were excluded from the analysis. Boxplots show the median (central line) and lower and upper quartiles (box). AGR, absolute growth rate.

surprising. Nevertheless, further conclusions about how growth rates would vary in adult palms could not be made. Rich *et al.* (1986) predicted a linear increase in height AGR rates with taller adult palms; however, given that resources are limited, growth curves are expected to decrease. Thus, this relationship would eventually reach an asymptote. Accordingly, previous studies in *I. deltoidea* have predicted that vertical growth will start to level off with the onset of reproduction (Anderson, 1998; Avalos, Salazar & Araya, 2005) and maintenance of living biomass (Homeier *et al.*, 2002; Stattegger, 2014).

The observed variation in AGR relative to a given size implies that other factors in addition to initial size play a role in determining how quickly palms grow. Certainly, measurement errors accounted for part of this variation, particularly when considering that heteroscedasticity is almost always the rule when dealing with tree size data (Picard, Saint-André & Henry, 2012). For this reason, one of the aims of this study was to reduce such uncertainty by using dendrometer bands and telescopic rules. However, the latter method limited our survey to palms < 7 m, but it could be performed with more precision than with clinometers (Homeier *et al.*, 2002; Avalos *et al.*, 2005; Stattegger, 2014) or range finders.

NEIGHBOURHOOD EFFECTS

The growth of individual plants in densely concentrated populations is expected to be limited by density dependence (Crawley, 1997), but this effect has rarely been tested explicitly in palms (Yeaton, 1979; Barot *et al.*, 1999; Silva Matos, Freckleton & Watkinson, 1999; Barot & Gignoux, 2003). Evidence in support of density dependence has been reported for *Euterpe edulis* Mart. (Silva Matos *et al.*, 1999) and *Socratea exorrhiza* (Mart.) H.Wendl. (Yeaton, 1979). For *I. deltoidea*, negative density dependence has been suggested to regulate seedlings (Norden *et al.*, 2009).

Even as adult palms, *I. deltoidea* can occur at high densities of up to 13 individuals in a 20-m-diameter area and only 6% of focal palms had no conspecific neighbours. Despite the statistically significant negative effect of conspecific basal area on diameter and height growth in our models, the effect size was small, with only a 1 mm (diameter) or 1 cm (height) reduction in growth for every additional neighbour, suggesting that *I. deltoidea* performs well, or at least better than other species, in the presence of high numbers of conspecifics. The strength of negative density dependence is known to be less in common species (Comita *et al.*, 2010), but it appears to be particularly weak in *I. deltoidea*. The question remains as to what limits population growth rates in this and other hyperdominant species.

We expected that heterospecifics would have had some limiting effect, if only in terms of their negative influence on light availability. Height growth is often prioritized as a mechanism to avoid competition for light, perceived as changes in the light environment produced by the presence of neighbours (Stoll & Bergius, 2005). However, we found no negative effect on growth in diameter or height, suggesting that the growth strategy of *I. deltoidea* to increase first in diameter and then height allows it to grow in shaded environments that might limit other species.

LIGHT AVAILABILITY

We found no effect of canopy openness on the growth of palms < 3 m tall, but most of these smaller palms occurred in areas of low openness (Fig. 5A, B). For taller palms, however, height growth increased with greater light exposure (Fig. 5C, D). This pattern was expected, given that increased competition for light favours greater investment in height growth (Crawley, 1997), especially when only about 1–2% of the radiation from the canopy reaches the forest floor (Poorter, 1999). Hence, *I. deltoidea* appears to efficiently use the space and resources in the forest so that the stem elongation is maintained.

Attainment of height via cell division of a constantly active apical meristem (Renninger & Phillips, 2012; Kunert, Barros & Higuchi, 2013), however, would imply a greater energetic investment relative to that of width, which is attained by cellular expansion and intercellular space formation (Tomlinson, 1979; Rich, 1987b). Moreover, bole elongation implies greater costs because of the increased risk of mechanical failure (Rich *et al.*, 1986) and decreased water conduction efficiency (Renninger *et al.*, 2013) as palms get taller. This difference should be borne in mind, particularly when individuals of *I. deltoidea* show signs of ‘growth dormancy’ (i.e. limited change over an extended period of time and/or disproportionate number of internodes on the stem relative to the stem length). In this study, 23.2% of the sampled individuals showed < 1 cm change in diameter over a 10.2 mean year interval, including palms < 20 cm DBH that were expected to expand considerably over such a long period. It has been stated previously that stem development in palms is highly light demanding (de Granville, 1992) and a positive relationship between these two factors is generally expected. The approximations to evaluate the light environment used in this study, however, provided evidence of a significant positive effect of greater light availability on stem growth in *I. deltoidea* once palms start to reach the canopy. However, under shaded conditions, we found no overall significant effect of greater exposure to light during the establishment phase. Furthermore, a wide size range (< 1 m to > 20 m) of individuals was found to occur in closed-canopy sites (Fig. 5). This pattern has been reported previously by Svenning (1999), who also proposed that this species shows attributes that enable it to thrive under shaded conditions. For instance, individuals of *I. deltoidea* have taken > 25 years to prosper in the 0.5-ha secondary forest patch, where they are present near the mature forest border, but they are still absent in the central secondary forest area (Fig. 1). Individuals of *I. deltoidea*, particularly saplings, have an efficient vascular organization that frees space in the stem for cells to function as storage deposits or mechanical support with minimum redundancy and carbon investment (Renninger *et al.*, 2013). These anatomical attributes may account for the growth and survival of *I. deltoidea* under a closed canopy. In addition, leaves in this species show a morphological transition from having horizontally arranged entire pinnae to highly dissected pinnae arranged on multiple axes (Rich, Holbrook & Luttinger, 1995). The former are considered to be well adapted to a low-light subcanopy, whereas the latter are better suited to intercept light once the palm achieves greater heights; such a transition becomes an advantage, particularly when young palms retain the shade-tolerant type for longer periods (Terborgh & Davenport, 2001).

CONCLUSIONS

Although the simultaneous increment of diameter with height has been highlighted as the main feature of growth in this palm, previous studies have exclusively addressed vertical elongation by either measuring actual growth rates (Homeier *et al.*, 2002; Stattegger, 2014) or by some proxy of vertical growth: leaf turnover (Rich *et al.*, 1995; Anderson,

1998) or internode length extension (Renninger & Phillips, 2012; cf. Tomlinson & Quinn, 2013). To our knowledge, width expansion has been mainly inferred from allometric relationships between height and diameter (Rich *et al.*, 1986; Rich, 1987b; Avalos *et al.*, 2005), but not by measuring its actual rate. This study directly quantified expansion and elongation of the stem during early establishment of this palm. By using this method, we were able to discern three main patterns concerning the growth strategy of this palm: (1) AGR is size dependent as proposed previously, but this relationship is not linear with respect to diameter, and disproportionate among seedlings, saplings and juveniles; (2) *I. deltoidea* can succeed at high densities with low levels of interspecific competition; and (3) *I. deltoidea* can grow in shaded environments, probably using stored resources, combined with further increment when approaching the higher light environment of the forest canopy. This combination of traits probably contributes to the ecological success of *I. deltoidea* throughout Amazonia.

Future research on this topic should address whether the growth patterns observed here also enhance the survival of individual trees, and examine non-linear fits of growth rate in response to factors not considered in this study (e.g. direct estimates of soil water and nutrient availability). To that end, long-term plots provide an invaluable tool, particularly because of the longevity of many tree species, *I. deltoidea* included (Stattegger, 2014).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. One-hectare columns and major habitat within the 50-ha Yasuní Forest Dynamics Plot (YFDP). The map shows the four main habitat types (white, ridge; light grey, valley; mid-grey, swamp; dark grey, secondary ridge) defined by the topography of each 20 m × 20 m subplot. Contour lines are indicated each 2 m. In the ten 1-ha columns, we installed dendrometers in *Iriartea* palms with diameter at breast height (DBH) > 4 and < 10 cm, except in 50 subplots (highlighted in green) in which they were installed in palms with DBH ≥ 10 cm alone. We included 5.64 ha of ridge, 3.88 ha of valley, 0.28 ha of swamp and 0.20 ha of secondary forest on a ridge.