

## Endogenous and exogenous control of leaf morphology in *Iriartea deltoidea* (Palmae)

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**ABSTRACT.** Like many other palms, *Iriartea deltoidea* undergoes ontogenetic transitions in leaf morphology. It has been asked whether the transition to adult leaf form in *Iriartea* was a fixed developmental pattern or a more plastic response to changes in environmental conditions, but studies so far have not resolved the question. We re-examined the question by taking measurements on palms growing under the full range of conditions experienced in the natural environment. Using trunk height as a surrogate variable for ontogenetic stage, we found that individual palms undergo the transition to adult morphology over a wide range of heights from < 10 m to > 20 m. Palms growing in gaps undergo the transition early, whereas those growing under a closed canopy undergo the transition late. Noting this, we asked whether the transition occurred in individuals that were growing faster than a critical minimum rate, and found no correlation between growth and morphological stage. A post-hoc hypothesis, that structural support of the crown (measured as trunk diameter) could limit or delay the transition, was confirmed. Our results indicate that multiple conditions must be satisfied before the transition can be completed. The complex requirements for leaf morphogenesis in *Iriartea* confer an ability to respond flexibly to spatially and temporally varying environmental conditions.

**KEY WORDS:** Amazon, environmental control of morphology, *Iriartea deltoidea*, leaf morphology, morphogenesis, palm

Like many other palms, *Iriartea deltoidea* Ruiz & Pavon (hereafter simply *Iriartea*) undergoes ontogenetic transitions in leaf morphology. The first post-cotyledonary leaves are simple, entire-margined structures, consisting of a broad (nearly round) slightly pleated blade (Rich *et al.* 1995). After producing about a half-dozen of these seedling leaves, juveniles produce more elaborate leaves consisting of a terminal blade (resembling a seedling leaf) plus several narrow pinnae distributed along the rachis. At this stage *Iriartea* palms begin

to develop a slender trunk. As individuals increase in height, successively produced leaves become longer and carry more pinnae. These ordinary pinnae are broad and triangular, fin-like, with a pleated surface.

Plants with juvenile morphology continue to increase in height and girth until they attain the adult condition in a second morphological transition. The change in leaf morphology at this transition is dramatic. Juvenile leaves are light, slender structures. The pinnae are arrayed along the gently arching rachis with the blades held approximately in the horizontal plane (monolayer). Adult leaves, in contrast, are massive structures up to 6 m long and weighing many kg each (Rich 1986). They are held in place by a tough, 1-m-long petiolar sheath that fully envelops the trunk. The pinnae are highly elaborated, consisting of large numbers of fin- and strap-like elements arrayed over a wide range of angles in the plane perpendicular to the rachis, creating a bottle-brush (multilayer) arrangement. Reproducing adults carry an average of six of these massive leaves held at angles both above and below the horizontal.

Rich *et al.* (1995) asked whether the transition to adult leaf form in *Iriartea* was a fixed developmental pattern or a more plastic response to changes in environmental conditions. They found that *Iriartea* palms at La Selva Biological Station in Costa Rica displayed juvenile leaves up to heights of 10–12 m, and carried increasing numbers of transitional or adult leaves at greater heights up to 25 m. The evidence presented by Rich *et al.* (1995) suggested a role of both developmental stage (height) and light availability in determining when monolayer vs. multilayer leaves are produced. However, the data analysed by these authors left open the question of whether increased light levels encountered as an individual palm grows upwards act as an ontogenetic switch that triggers the production of multilayered leaves, or whether the transition is a graded response to gradually increasing resource availability (Rich *et al.* 1995).

This question attracted our attention at the Cocha Cashu Biological Station in Amazonian Peru when we noticed that relatively tall *Iriartea* palms carrying juvenile leaves could sometimes be found within a few metres of much shorter individuals carrying leaves of transitional or adult morphology. Tall juveniles were nearly always found in shady situations, whereas short adults were nearly always located in gaps. We therefore decided to re-investigate the question posed by Rich *et al.* (1995) to see whether a different sampling approach would yield new insights into the transition from juvenile to adult leaves. We shall see below that environmental control of the morphological transition is more complicated than suggested by the simple dichotomy posed by Rich *et al.* (1995).

*Iriartea deltoidea* is widespread in the neotropics, being distributed from Costa Rica to Bolivia. In the forests of Madre de Dios, Peru, where this research was done, it is the most abundant tree, occupying all major habitats: successional

forests, swamps, mature floodplain forests and terra firme forest (Pitman *et al.* 1999, Terborgh *et al.* 1996). The species displays similar versatility in Ecuador (Svenning 1999a). Juvenile trees are scattered throughout the understory, in shady as well as sunny microsites (Svenning 1999b). Large individuals attain heights of over 30 m, and are conspicuous for their stilt roots and a large bulge in their trunks at mid-height (Rich 1986).

## METHODS

### *Study site*

We conducted the research in the floodplain forest surrounding the Cocha Cashu Biological Station in Peru's Manu National Park. This is a seasonal tropical moist forest of large stature and high species diversity that receives around 2000 mm of rain a year in a 7-mo wet season (Terborgh 1983). Data on the climate, species composition and dynamics of this forest are contained in Gentry (1990).

### *Developmental stages in the transition to adult leaf morphology*

Following Rich *et al.* (1995) we assigned individuals to one of four classes: (1) juvenile, (2) early transitional, (3) late transitional and (4) fully adult. Juveniles were recognized by leaves carrying simple, undivided pinnae. Class 2 transitional individuals displayed pinnae subdivided into a small number of discrete elements (usually 3 to 5), most or all of which were held in roughly the horizontal plane. Class 3 transitional individuals were distinguished by having pinnae subdivided into many elements, some of which were held at high angles (near vertical). Finally, palms displaying adult leaves (Class 4) were distinguished by having pinnae subdivided into numerous elements and by possessing the fully developed bottle-brush condition. Most individuals fell unambiguously into one class or another, but inevitably, some individuals displayed borderline characteristics. We resolved borderline cases by carefully examining the youngest (topmost) leaf and then assigning the tree to a class based on the characteristics of that leaf. Two of us independently evaluated each tree and made an assignment to class, and in the great majority of cases, we agreed. When at first we did not agree, we re-examined the tree and discussed the relevant features until we came to an agreement.

### *Light environment*

We evaluated the light environment of trees by counting, in increments of 0.5, the number of crowns superimposed in the cylindrical projection of the crown of a given *Iriartea* to the open sky. Thus, a palm that was directly beneath the overtopping crown of a single canopy tree was assigned a light score of 1.0, etc. Most old (tall) adults had scores of 0.0 or 0.5, whereas most small juveniles had scores  $\geq 2.0$ . The scale is admittedly a crude one because the crowns of different canopy trees intercept varying amounts of light and lateral light

sources are not taken into account, but there are no available technological alternatives to an improvised light scale for use with trees attaining heights up to 35 m (Rich *et al.* 1995, Svenning 1999b, Welden *et al.* 1991). We realize that a given score can imply different amounts of light at low and high positions in the forest. Nevertheless, our ad hoc scale should represent available light in some approximate way, especially in comparisons of extremes. Since light attenuation is an exponential process (Beer's Law), we used the logarithm of the scores in all analyses.

#### *Selection of a stratified sample*

To re-address the question of what triggers the transition to adult leaf morphology in *Iriartea* palms, we designed a stratified sampling procedure based on the improvised light scale described above. Specifically, we selected Class 1, 2, 3 and 4 palms that were judged to have light scores of  $\geq 2.0$  and  $\leq 1.0$ . It was relatively easy to find well- and poorly illuminated individuals of Classes 2 and 3, but difficult to find well-illuminated Class 1 individuals and poorly illuminated Class 4 individuals. Nevertheless, we persisted in searching until we had accumulated a sample of 139 palms, including approximately equal numbers of individuals representing the four morphological classes.

#### *Height and growth measurements*

Fortuitously, *Iriartea* palms inscribe a record of their individual growth histories in the form of leaf scars that are easily visible on the trunks of trees of all ages. Measurements on *Iriartea* carried out at La Selva indicated that the annual rate of leaf production increased from 1.58 in 5-m-tall individuals to 2.13 in those 10 m tall (Rich 1986). Inter- and intra-individual variation in growth rates are clearly evident in the wide range of intervals between successive leaf scars that can be seen in a population (for other examples, see King 1993, Lieberman & Lieberman 1988, Oyama 1993).

For each tree included in our sample, we measured its current height and its recent growth performance, using a hand-held electronic hypsometer (Forester Vertex). Hypsometer readings are repeatable to  $\pm 0.1$  m. Height was measured at the bottom of the sheath of the lowest green leaf, a position that could be determined with high precision and consistency, although it underestimates full height by omitting the entire crown. We represented recent growth performance as the mean interscar interval over the top five intervals below the base of the lowest green leaf sheath, the point at which height was measured. Analyses were conducted with data from pre-reproductive trees only. If the rate of leaf production increases with height (see previous paragraph), then our measure of growth will somewhat underestimate the performance of tall palms relative to shorter ones. Finally, we noted whether trees had reproduced or not, as determined by the presence on the trunk of scars representing past inflorescences.

## RESULTS

*Morphological class vs. height*

If the transition to adult leaf morphology was triggered simply by the attainment of a certain developmental stage (for which we shall use height as a proxy), one would expect that the ranges of heights represented by individual trees assigned to morphological Classes 1, 2, 3 and 4 would be non-overlapping, or nearly so. Instead, the ranges are broadly overlapping, so much so that the tallest Class 1 trees we found were as tall as some Class 4 individuals (Figure 1). Clearly, the morphological transition is triggered by something other than attainment of a critical height, but what is it? The possibilities we can evaluate are that the transition is a response to the attainment of a critical growth rate or exposure to a threshold light level.

*Interscar intervals*

To compare growth rates we used the mean interval between the five uppermost scars visible on the trunk. We compared interscar intervals of non-reproductive Class 1, 2, 3 and 4 individuals and found that variation in height growth within classes far exceeded that between classes, accounting for 97% of the sum of squares (Table 1). Thus, there is no direct link between growth rate

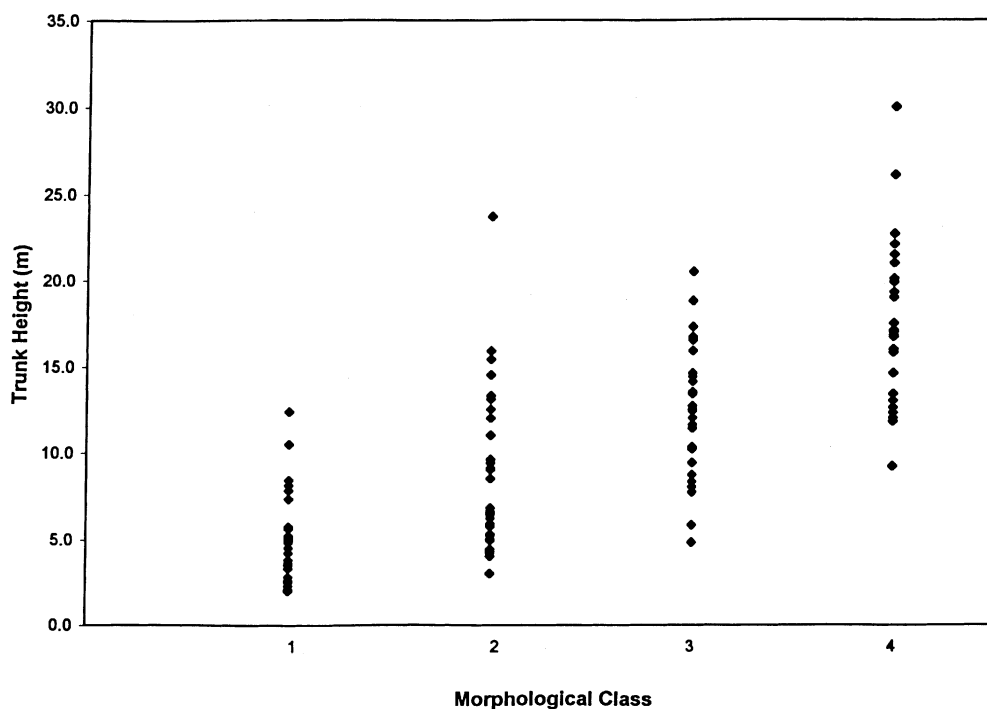


Figure 1. Trunk heights (to base of leaf sheaths) of *Iriartea deltoidea* palms bearing Class 1, 2, 3 and 4 leaves.

Table 1. Height growth of *Iriartea* palms carrying leaves of four morphological classes

Morphological class	n	Mean intermode length (cm)	Standard error
1	31	23	0.017
2	37	27	0.022
3	27	26	0.022
4	12	26	0.026

per se and the morphological transition, at least when growth is represented by the mean interval between the uppermost leaf scars.

To investigate the effect of reproduction on growth, we compared interscar intervals in pre- and post-reproductive Class 4 (adult) palms. Mean length of interscar intervals in post-reproductive trees was only 60% of that of pre-reproductive individuals ( $P < 0.001$  by one-tailed t-test), indicating that growth slows when resources are allocated to reproduction. Prior to the onset of reproduction, there is no decrease in interscar intervals, even in Class 4 individuals.

#### *Light index*

There appears to be no direct link between light and the morphological transition. We found individuals of all classes, including Class 1 (juveniles) growing in openings (light index of 0.0 or 0.5), indicating that exposure to high light, in itself, is not a sufficient condition for the onset of morphogenesis.

#### *Growth $\times$ light interaction*

The growth of autotrophic plants is inevitably constrained by light below some critical level, so a positive relationship between light and growth can be expected. Pooling all non-reproductive individuals and regressing the square root of their mean interscar intervals against the log of the light index, we found a strong and significant negative relationship (less light, less growth) but a low value of r-square (0.22) which is no doubt indicative of the crudeness of our index as a measure of available light. When height is added to the model as a cofactor, the value of r-square increases to 0.38, presumably reflecting the general increase in light availability with increased height above the forest floor (Terborgh & Mathews 1999).

Whereas the data do not support the conclusion that high light or high growth rates per se directly induce the morphological transition, we can ask whether low light and low growth delays it. To answer this question, we subdivided the samples of the four classes into thirds, based on height, and then compared interscar intervals of the tallest third of the trees in each class with those of the shortest third in the next class. In each case, 1s vs. 2s, etc., the tallest third of the trees in one class were growing significantly more slowly than the shortest third of the next higher class, indicating that morphogenesis is accelerated (with respect to height) in fast-growing individuals and delayed in slow-growing individuals ( $P < 0.05$  in all comparisons). Similarly, the mean

light index for the tallest third of the trees in each class is higher (less light) than that of the lowest third of the next higher class ( $P \leq 0.6$  in two of three cases), as would be expected inasmuch as light and growth are related.

#### DISCUSSION

Mean values indicate central tendency, but convey little information about the tails of a population. Here, it is the tails that are of interest, because the morphological transition clearly occurs earlier (at lower height) in individuals that are exposed to the 'best' available conditions (high light) and later among individuals exposed to deep shade. Thus, by examining individuals representing the tails of a population, instead of individuals taken at random, we investigated whether the transition from juvenile to adult leaf morphology in the palm, *Iriartea deltoidea*, is a response to (1) developmental stage as proxied by height, (2) exposure to a minimum light level or (3) attainment of a minimum growth rate. We found that none of these conditions by itself is sufficient to induce the morphological transition. Rapidly growing individuals exposed to relatively high light experienced accelerated development (with respect to height) relative to slow-growing individuals exposed to low light. But there is more involved in triggering the morphological response than light or growth or some interaction of the two, because palms with juvenile morphology can be found growing rapidly in well-illuminated sites and palms with adult morphology can be found growing more slowly in partial shade. Is there some additional requirement that we did not investigate?

Some insight into the question can be gained from the observation that even the best-illuminated, fastest-growing individuals do not acquire adult leaf morphology without going through the succession of stages we have described in Classes 1, 2, and 3. Individual crowns can carry Class 1 and Class 2, or Class 2 and Class 3 leaves, etc. but we failed to note any trees with leaves representing more than two of the four classes, suggesting that the transition can be accelerated only to a limited degree, even under the most optimal conditions.

There are at least two factors that might come into play in imposing a limit on the acceleration of morphogenesis: one is an evolved strategy of bet hedging and the other is a structural requirement.

There might be an evolved brake on the acceleration of development. Many fast-growing juveniles are situated in small light gaps that are subject to canopy closure by the lateral ingrowth of nearby trees (Kahn 1986). An *Iriartea* that completed the transition to adult morphology at a low height would risk entering a zone of decreasing light as it grew up toward the overtopping branches of a taller neighbour. If adult morphology carries with it the higher respiration rate of sun-adapted foliage, then possessing such foliage could be lethal in a shaded situation. Therefore, it might be the best strategy to proceed slowly through the transition to adulthood so commitment to a high light



requirement is not made until there is a good probability that access to sufficient light will be permanent. Whether there is such an endogenous brake on the acceleration of development cannot be determined from the data at hand.

However, there does appear to be a structural requirement for the production of adult leaves, which can be reasoned as follows. Adult leaves are large structures weighing many kg each (Rich 1986). One can thus doubt that the slender, soft (incompletely lignified) trunk of a Class 1 juvenile could support the 40 kg mass of a crown of adult leaves (Rich 1986). To substantiate this possibility, we measured the diameters of the three tallest Class 1 individuals in our sample (mean height 10.4 m, mean dbh 26.8 cm) and the three shortest Class 4 individuals (mean height 10.9 m, mean dbh 43.4 cm). Although the heights were almost the same, the mean diameters of the Class 4 trees were 62% greater than those of the Class 1 trees. The diameter vs. height relationships of the tallest Class 1 palms fell precariously close to the theoretical limit at which a trunk buckles under the mass of the crown (McMahon 1973, Rich 1986, Rich *et al.* 1986). Thus, the development of a massive crown of adult leaves is ultimately constrained by allometric scaling limits, a fact that can explain why, even under the best circumstances, individual trees do not saltate into adulthood but instead progress methodically through ontogenetic classes 1–4.

We conclude that the transition to adult leaf morphology in *Iriartea deltoidea* is an ontogenetically flexible response to environmental conditions that can be accelerated or delayed within bounds in accordance with the circumstances of individual trees. No simple endogenous or exogenous trigger appears to be involved. Instead, multiple requirements for light, growth, and structural support must all be satisfied. By maintaining monolayer architecture and relatively low leaf area through the juvenile phase, internal shading within the crown and respiratory costs are held to a minimum. More efficient height growth is ensured because the relatively light mass of a juvenile crown allows the trunk to maintain a smaller diameter than would be possible with a crown of adult leaves (Chazdon 1986). *Iriartea* and other Iriartoid palms, such as *Socratea*, are thus able to rise into the high light zone of the canopy much more rapidly than the more conventional palms which develop a full-sized trunk before beginning to gain height. The complex requirements for leaf morphogenesis in *Iriartea* thus confer an ability to respond flexibly to spatially and temporally varying environmental conditions.

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## LITERATURE CITED

- CHAZDON, R. L. 1986. The costs of leaf support in understory palms: economy versus safety. *American Naturalist* 127:9–30.
- GENTRY, A. H. (ed.) 1990. *Four neotropical rainforests*. Yale University Press, New Haven.
- KAHN, F. 1986. Life forms of Amazonian palms in relation to forest structure and dynamics. *Biotropica* 18:214–218.
- KING, D. A. 1993. Growth history of a Neotropical tree inferred from the spacing of leaf scars. *Journal of Tropical Ecology* 9:525–532.
- LIEBERMAN, M. & LIEBERMAN, D. 1988. Age-size relationships and growth behavior of the palm *Welfia georgii*. *Biotropica* 20:270–273.
- MCMAHON, T. A. 1973. Size and shape in biology. *Science* 179:1201–1204.
- OYAMA, K. 1993. Are age and height correlated in *Chamaedorea tepejilote* (Palmae)? *Journal of Tropical Ecology* 9:381–385.
- PITMAN, N., TERBORGH, J., SILMAN, M. R. & NUNEZ, P. 1999. Tree species distributions in an upper Amazonian forest. *Ecology* 80:2652–2661.
- RICH, P. M. 1986. Mechanical architecture of arborescent rain forest palms. *Principes* 30:117–131.
- RICH, P. M., HELENURM, K., KEARNS, D., MORSE, S. R., PALMER, M. W. & SHORT, L. 1986. Height and stem diameter relationships for dicotyledonous trees and arborescent palms of Costa Rican tropical wet forest. *Bulletin of the Torrey Botanical Club* 113:241–246.
- RICH, P. M., HOLBROOK, N. M. & LUTTINGER, N. 1995. Leaf development and crown geometry of two iriarteoid palms. *American Journal of Botany* 82:328–336.
- SVENNING, J.-C. 1999a. Microhabitat specialization in a species-rich palm community in Amazonian Ecuador. *Journal of Ecology* 87:55–65.
- SVENNING, J.-C. 1999b. Recruitment of tall arborescent palms in the Yasuní National Park, Amazonian Ecuador: are large treefall gaps important? *Journal of Tropical Ecology* 15:355–366.
- TERBORGH, J. 1983. *Five New World primates: a study in comparative ecology*. Princeton University Press, Princeton.
- TERBORGH, J., FOSTER, R. B. & NUNEZ, V. P. 1996. Tropical tree communities: a test of the nonequilibrium hypothesis. *Ecology* 77:561–567.
- TERBORGH, J. & MATHEWS, J. 1999. Partitioning of the understorey light environment by two Amazonian treelets. *Journal of Tropical Ecology* 15:751–763.
- WELDEN, C. W., HEWETT, S. W., HUBBELL, S. P. & FOSTER, R. B. 1991. Sapling survival, growth and recruitment: relationship to canopy height in a Neotropical forest. *Ecology* 72:35–50.

