

# **A comparison of the hydraulic efficiency of a palm species (*Iriartea deltoidea*) with other wood types**

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## Summary

Palms are an important component of tropical ecosystems, living alongside dicotyledonous trees, even though they have a very different growth pattern and vascular system. As monocots, vessels in palms are located within vascular bundles and, without a vascular cambium that many dicotyledonous trees possess, palms cannot add additional vessels to their vascular system as they get older and taller. This means that hydraulic architecture in palms is more predetermined, which may require a highly efficient hydraulic system. This preset nature, along with the decoupling of hydraulic and mechanical functioning to different cell types, may allow palms to have a more efficient hydraulic system than dicotyledonous trees. Therefore, this study seeks to determine the efficiency of the hydraulic system in the palm *Iriartea deltoidea* (Ruiz & Pav.) and compare this efficiency with other tree forms. We measured cross-sectional areas of roots, stems and fronds as well as leaf areas of *I. deltoidea* saplings. Likewise, cross-sections were made and vessel diameters and frequencies measured. This allowed for the calculation of theoretical specific-conductivity ( $K_{S, calc}$ ), theoretical leaf-specific conductivity ( $K_{L, calc}$ ), and vessel diameter and vessel number ratios between distal and proximal locations in the palms. *I. deltoidea* palms were found to have the largest, least frequent vessels that diverged most from the square packing limit (maximum number of vessels that fit into a given area) compared with other major tree forms, and they therefore invested the least space and carbon into water transport structures. Likewise, conduits tapered by approximately one third between ranks (root, bole, petiole), which represents an efficient ratio with regard to the trade-offs between safety and efficiency of the conducting system. Conduits also exhibited a high conservation of the sum of the

conduit radii cubed ( $\Sigma r^3$ ) across ranks, thereby approximating Murray's Law patterning. Therefore, our results indicate that the palm, *I. deltoidea*, has a very efficient hydraulic system in terms of maintaining a large conducting capacity with a minimal vascular investment. This efficiency may allow palms to compete well with dicotyledonous trees in tropical and subtropical climates but other developmental factors largely restrict palms from regions that experience prolonged freezing temperatures.

**Keywords:** Hydraulic architecture, Vascular anatomy, Palms, Murray's law, Conduit tapering

## **Introduction**

Palms make up a significant portion of many tropical forests (Dransfield 1978, Pitman et al. 2001, Montufar and Pintaud 2006) growing alongside dicotyledonous trees and in some cases outcompeting them in locations like palm swamps where one or two species of palms tend to dominate (Myers 1990, Kahn 1991). While the hydraulic system in palms is analogous to dicotyledonous trees in that water is pulled from the ground to the leaves traveling through vascular conduits, their growth structure and conduit organization is very different. Palms are monocots and therefore their vascular system is composed of thousands of vascular bundles that contain primary xylem vessels, fibers and phloem sieve tube cells. Likewise, palms lack a secondary vascular cambium that is present in dicotyledonous trees, and therefore, cannot add a new outer layer of vascular tissue each season. Palms add new vascular tissue only at their tips via a primary thickening meristem and through the addition of new roots and leaves (Tomlinson 1962, Schatz et al. 1985, Tomlinson 1990, Tomlinson et al. 2011). Therefore, palms cannot adjust their hydraulic architecture each season as dicotyledonous trees do, and instead must rely on a certain amount of predetermination as they continuously use the oldest, first-formed vascular bundles at their bases throughout their entire lifespan which can reach and exceed one hundred years of age (Lugo and Rivera Batlle 1987, Bullock and Heath 2006).

In order to maximize carbon gain for a given amount of water use, plants must transport water sufficiently to maximize photosynthesis and allocate carbon efficiently between the vascular conduits, the cells that provide structural support, storage cells and the photosynthetic leaves. Therefore, if less carbon can be allocated to the water

conducting tissues while yielding a similar transport capacity, this would be a more efficient hydraulic system than one in which more carbon was required (McCulloh et al. 2010). The Hagen-Poiseuille law states that hydraulic conductivity increases by a magnitude of 16 for every doubling of a conduit radius (Zimmermann 1983) due to the fourth power relationship between these two parameters. Likewise, longer conduits are generally more efficient as these contain fewer pit membranes to be crossed in the transport pathway (Zimmermann 1983, Tyree and Ewers 1991, Comstock and Sperry 2000, Sperry et al. 2005). Large but widely spaced conduits would provide a large transport capacity while minimizing the carbon requirements needed to make these conduits, thereby increasing the hydraulic efficiency of the system. However, tradeoffs exist that may limit the size of vascular conduits, including vulnerability to embolism (Hacke et al. 2006, Sperry et al. 2006, Christman et al. 2009, Cai and Tyree 2010), mechanical stability against implosion (Hacke et al. 2001, Jacobsen et al. 2005) and refilling potential (Holbrook and Zwieniecki 1999, Sperry 2003, Vesala et al. 2003).

While vessel size and frequency are the main determinants for the hydraulic efficiency of a particular tissue, on a whole tree level, the vascular arrangement or hydraulic architecture also contribute to hydraulic efficiency. Regarding whole tree hydraulic architectures, the distribution of vascular tissue considered most efficient is one in which the sum of the conduit radii cubed ( $\Sigma r^3$ ) across a given horizontal rank within a tree is conserved across ranks from the roots to the trunk to the leaves (McCulloh and Sperry 2005, Sperry et al. 2008). This pattern approximates Murray's law (Murray 1926) which was derived as the optimum distribution of vascular tissue volume to maximize hydraulic conductance in the vascular systems of animals. McCulloh et al.

(2004) found that along a continuum of increasing reliance on vascular conduits for structural support, species tended to deviate more from Murray's law. In addition to Murray's Law, hydraulic systems where a few large conduits branch into many small conduits are more hydraulically efficient (McCulloh et al. 2003, McCulloh et al. 2004, McCulloh and Sperry 2005, Sperry et al. 2008) than other patterns. However, again tradeoffs exist and trees with this hydraulically efficient system may be mechanically unstable and top-heavy if they approximate Murray's law with this hydraulic design (McCulloh and Sperry 2005, McCulloh et al. 2009). Although hydraulic architecture has been studied in many dicotyledonous tree species, it has yet to be studied in palms, a tree form which, given its growth pattern, has the potential to have a very efficient hydraulic system.

This study sought to determine the hydraulic efficiency of the roots, trunk and petiole tissue of the palm *Iriarteia deltoidea* (Ruiz & Pav.) as well as the efficiency of the vascular system on a whole tree level. *I. deltoidea* grows in lowland tropical rain forests, reaches approximately 30 m tall, and is widespread throughout the northwestern Amazon (Henderson et al. 1995). In rainforest locations in Peru and Ecuador, *I. deltoidea* was found to be the most abundant tree species (Pitman et al. 2001, Montufar and Pintaud 2006). Palms are an interesting growth form to study hydraulic efficiency because, while the vascular conduits provide little mechanical support, palms are free-standing and can reach significant heights of up to 60 m tall (Henderson et al. 1995). In palms, the primary source of mechanical support comes from the fibers, other sclerenchyma cells and thick-walled parenchyma cells (Rich 1987b, Niklas 1992, Kuo-Huang et al. 2004, Rüggeberg et al. 2008). The relatively small crowns of palms also mean their mechanical

requirements are not as great as dicotyledonous trees (Rich 1986). Likewise, the lack of branching and simple tree form may allow palms to maintain a greater taper between vascular conduits across ranks, as well as fewer, larger conduits in the trunks that branch into smaller, more numerous conduits in the fronds. We expected that because palms do not rely on their vascular conduits for mechanical support and the crowns of *I. deltoidea* palms are relatively simple, they would be more hydraulically efficient in terms of conduit size, taper and hydraulic architecture than similar-sized conifer and angiosperm trees and will more closely approximate Murray's Law predictions for optimum transport architecture.

## **Materials and Methods**

### ***Site description***

This research was conducted at Tiputini Biodiversity Station (0° 36' S, 76° 27' W), a 650 ha research facility located within the Yasuní National Park and Biosphere Reserve in eastern Ecuador. Yasuní receives approximately 2800 mm of rainfall per year with no month receiving less than 100 mm of rainfall and has a mean monthly high temperature of 34 °C and low of 22 °C (Valencia et al. 2004). This closed-canopy primary forest is approximately 30 m tall and contains numerous tree-fall gaps. *Iriartea deltoidea* saplings were found in the understory growing on terra-firme soils.

### ***Tree harvesting and collection***

Five *I. deltoidea* palms with trunks between 0.3 and 3.5 m tall were harvested. The study was focused on saplings because it was not logistically possible to cut larger palms. *I. deltoidea* palms possess an above-ground trunk very early in their development that expands in diameter as palms grow taller. This contrasts with many other palm

species whose trunks grow in diameter underground and only emerge when a final diameter is reached. Four bole tissue samples measuring  $1\text{cm}^2$  were collected from mid-height on the bole. Two were cut from the outer part of the central cylinder (where vascular bundles are more numerous) and two were cut from the inner part of the central cylinder (where vascular bundles are less frequent). A small area around the trunks was dug so that all underground roots attached to the trunk could be cut and returned to the lab. While this species eventually develops stilt roots, the individuals collected for this work had not yet formed them. All fronds were cut from the trunk and the leaves were removed. Cross-sectional areas of the bole, all attached roots and all petioles from expanded fronds were measured. *I. deltoidea* has pinnately-compound leaves and leaf areas were estimated by weighing leaves and taking a photograph of one representative leaflet per palm. The fresh mass and area of this leaflet was used to convert the total leaf mass of the palm to an area.

### ***Anatomical measurements***

Thin cross-sections from the bole samples, roots and fronds were hand-cut with a razor blade and stained with 1% Toluidine blue. They were then placed on a slide, the excess water dried, and Permout and a coverslip added. Slides were viewed with either a dissecting scope ((Leica MZ12) or a compound light microscope (Leica CME, Bannockburn, Illinois, USA) at 10X and 40X magnification respectively and several photographs were taken with a digital camera (Olympus SP-550 UZ, Center Valley, Pennsylvania, USA) at various positions within the sections. Using Image J (Scion Image, Frederick, Maryland, USA) software, metaxylem vessel diameters were measured and the numbers of metaxylem vessels per unit area (conduit frequency) were counted.

Only metaxylem vessels were included because they are much larger than protoxylem vessels and therefore perform the bulk of the water conduction (Zimmermann 1983).

Theoretical specific-conductivities ( $K_{S, calc}$ ) were also calculated using the Hagen–Poiseuille equation by measuring all metaxylem vessel diameters within a given microscopic field of view as follows:

$$K_{S, calc} = \frac{\pi(\sum r^4)}{8\eta A_s} \times \rho$$

Where  $\rho$  is the density of water,  $r$  is the radius of metaxylem vessels,  $\eta$  is the viscosity of water, and  $A_s$  is the cross-sectional area of the field of view, with the summation over all metaxylem vessels in the field of view (Zimmermann 1983). Theoretical leaf-specific conductivities ( $K_{L, calc}$ ) were also calculated by multiplying  $K_{S, calc}$  by the cross-sectional area of the organ and dividing by the distal leaf area.

### ***Data and statistical analyses***

To determine the relationship between conduit diameter and conduit frequency (Fig. 1), area-weighted mean vessel diameters ( $D_A$ ) that correspond to the diameter of an average lumen cross-sectional area were calculated as follows:

$$D_A = \left( \frac{\sum D^2}{n} \right)^{\frac{1}{2}}$$

where  $D$  are measured vessel diameters and  $n$  is the number of vessels measured.

Histograms of the distributions of vessel diameters, conduit frequencies and  $K_{S, calc}$  were plotted to ensure that all distributions were normal. While the distributions of vessel diameters were normally distributed for all bole, frond and root samples, distributions of conduit frequency and  $K_{S, calc}$  were skewed with a long tail extending toward higher values. Transforming the data by calculating the natural log resulted in normal

distributions of all bole, frond and root samples. Once normal distributions were confirmed, averages and standard errors were calculated. Ratios of distal to proximal vessel diameters ( $D_R$ ) were calculated between fronds/bole and bole/roots for each of the five palms. Likewise, conduit frequencies in a given area for each organ were multiplied by the cross-sectional area of the organ (or sum of areas for the fronds and roots) to calculate the total numbers of vessels at each cross-sectional rank (roots, bole, fronds). Ratios of distal to proximal total vessel number (conduit number ratio) were calculated between fronds/bole and bole/roots. Ratios of distal to proximal  $K_{S, calc}$  and  $K_{L, calc}$  were also calculated for each organ combination.

In order to determine the efficiency of the hydraulic system in *I. deltoidea* (expressed as the maximum hydraulic conductance for a given volume of vascular tissue) the sums of all conduit radii cubed ( $\Sigma r^3$ ) for each organ were calculated from the roots, the trunk and the fronds. This calculation was performed by measuring the radii of all conduits within a cross-sectional area, raising each to the third power and summing for all conduits. An average from many microscopic sample views was calculated for fronds, roots, and bole material from the inner and outer central cylinder and multiplied by the area of the plant organ to scale values to the whole palm level. These values of  $\Sigma r^3$  were then compared between fronds vs. bole and bole vs. roots using paired t-tests (R version 2.5.1, 2007, The R Foundation for Statistical Computing). Conservation of  $\Sigma r^3$  across organs (in accordance with Murray's law) is indicative of an efficient hydraulic system.

For the comparison between conduit diameter and conduit frequency (Fig. 1), standard major axis (SMA) line-fitting methodology was used and SMA slopes and p-

values were calculated using SMATR freeware ((Warton et al. 2006); <http://www.bio.mq.edu.au/ecology/SMATR/>). All other regressions were calculated using Sigmaplot (version 10, Systat software Inc, Chicago, IL, USA). Tukey HSD tests were performed using R to determine whether variable averages for the different organs (fronds, trunk, roots) were significantly different from one another (Table 1).

For comparison with other tree types, conduit diameter and frequency of *I. deltoidea* were plotted with data from McCulloh et al. (2010). This study included data from three to eight, 1-4 m tall saplings from tropical diffuse-porous (4 species), temperate diffuse-porous (4 species), temperate ring-porous (3 species) and temperate conifers (5 species) tree functional types. Grand means were calculated from each tree functional type (trunk and branch separately) and compared with means of *I. deltoidea* trunk, frond and stilt root material from the five harvested individuals.

## Results

In *I. deltoidea*, conduit diameters were significantly larger in the roots than in the trunk and in the trunk compared to the fronds (Table 1,  $\alpha < 0.05$ ). Conduit diameters were approximately one third smaller in the fronds compared to the trunk and one third smaller in the trunk compared to the roots. As conduit diameters increased, conduit frequencies decreased (Fig. 1) but were similar in frequency between trunks and fronds and about half as frequent in roots (Table 1). The slope of the relationship between conduit frequency and conduit diameter in *I. deltoidea* was  $-1.4$  ( $r^2 = 0.51$ ) and differed significantly ( $P = 0.002$ ) from a slope of  $-2$  which represents the condition where conduit area is conserved across the relationship between conduit diameter and frequency. When compared with other tree growth forms, *I. deltoidea* palms had the largest conduit

diameters and the lowest conduit frequencies that were furthest from the square packing limit ( $1/\text{diameter squared}$ ) or the maximum number of vessels of a given diameter to fit into a given area (Fig. 2). Conduits comprised about 2% of the cross-sectional area in the fronds of *I. deltoidea* and about 5% of the cross-sectional area of the trunks and the roots.

Within an organ (frond, trunk, root), wider organs exhibited wider vessels. Roots exhibited the greatest increase in conduit diameter for a given change in organ diameter followed by the fronds and the trunk (Fig. 3A). Conversely, conduit frequencies decreased as organ diameters increased with data from fronds and roots falling on the same line (Fig. 3B) and exhibiting a shallower slope than within the trunk. Theoretical specific-conductivities ( $K_{S, \text{calc}}$ ) were about twice as large in roots as trunks, which, in turn, had conductivities that were about five times larger than fronds (Table 1).  $K_{S, \text{calc}}$  displayed a non-linear relationship with organ diameter (Fig. 3C), with fronds and trunks having roughly equivalent values. Total palm leaf areas increased as trunks increased in diameter and individual frond leaf areas increased as fronds increased in diameter (Fig. 3D) with fronds having significantly greater leaf area for a given cross-sectional area than trunks and roots, which did not differ significantly from one another (Table 1). However, theoretical leaf-specific conductivities ( $K_{L, \text{calc}}$ ) were significantly smaller in fronds than in the trunks and roots of *I. deltoidea* palms (Table 1).

In order to determine the maximum hydraulic conductance for a given volume of vascular tissue, the sums of all conduit radii cubed ( $\Sigma r^3$ ) for each organ were calculated with a conservation of the  $\Sigma r^3$  ratio across organs (in accordance with Murray's law) being indicative of an efficient hydraulic system. *I. deltoidea* was found to conform to Murray's law in that the  $\Sigma r^3$  did not differ significantly between the fronds and trunk ( $P =$

0.85) or between the trunk and roots ( $P = 0.73$ ) based on paired t-tests. The average ratio of  $\Sigma r^3$  for each harvested palms' organ pairs (fronds/trunk, trunk/roots) was 0.81 (SE = 0.10; excluding the outlier) and fell slightly below the optimum of 1 which indicates conservation of this ratio across organs. Likewise, the ratio of total conduit number for distal/proximal organs was similar to the ratios of  $K_{L, calc}$  for these organs, with the data closely matching the one to one line (Fig. 4A). This contrasts with the ratios of conduit diameter ( $D_R$ ) where similar diameter ratios between organs yield a large range of  $K_{L, calc}$  ratios (Fig. 4B).

### Discussion

The palm, *I. deltoidea*, has been shown to have an efficient hydraulic system compared with other woody saplings studied, investing a small amount of carbon into its vasculature while maintaining a large capacity for photosynthesis with high leaf area. Compared to the other major tree types (conifers, ring-porous, and temperate and tropical diffuse porous species; Fig. 2) *I. deltoidea* had the largest diameter vessels as well as the lowest frequency of vessels. *I. deltoidea* also deviated most from the square packing limit line for conduits (Fig. 2), suggesting that its stems contain more space for cells that perform functions other than water conduction, such as storage and mechanical support, and that its highly efficient vascular network minimizes redundancy. Although making the least investment to its vascular system with conduits occupying 2 and 5% of the area of fronds and trunks respectively, *I. deltoidea* palms support the largest amount of leaf area compared to the other dicotyledonous tree forms at the sapling stage studied by McCulloh et al. (2010). *I. deltoidea* palms also had the shallowest negative slope (-1.4; Fig. 1) in the relationship between conduit size and frequency compared with the other

major tree forms studied by McCulloh et al. (2010) meaning that there is less conduit area in fronds compared to trunks and roots (with a constant conduit area represented by a slope of -2). Palms may not be able to support as much vascular tissue in their fronds because they are non-woody and their fibers do not lignify to the same extent as trunks (Tomlinson et al. 2011). This lack of lignin means that fronds are more flexible to external forces (Winter 1993, Duryea et al. 1996) but could ultimately compromise the total cross-sectional area of fronds, and in turn, total conduit areas.

Perhaps *I. deltoidea* saplings are exceptionally efficient hydraulically because the growth pattern of palms requires them to be overbuilt hydraulically when they are young so that they have the capacity to supply an expanding crown that is located progressively further from the ground. It should be noted that *I. deltoidea* contains an aboveground trunk that, from a young age, increases in diameter as palms get taller (Renninger and Phillips 2010) largely through expansion of parenchyma cells and the spaces between them (Rich 1987a, Tomlinson et al. 2011) unlike palms which produce a below-ground stem until a final diameter is reached (Tomlinson et al. 2011). This means that in *I. deltoidea*, the relationship between stem diameter and vessel diameter (Fig. 3A) is contingent on the age class of the palm and the location of the sample. Likewise, it could be argued that *I. deltoidea* saplings may be hydraulically efficient while young, but become progressively more and more inefficient as adults. This could also explain the very shallow slope seen in the relationship between conduit diameter and frequency with trunk and root tissue being overbuilt for conducting capacity compared with fronds. However, Renninger and Phillips (2010) found that *I. deltoidea* palms varying in height from 1 m to 22 m tall maintained similar rates of sap flow per unit leaf area. Likewise,

vessel diameters in the trunks of these palms have been shown to increase with increasing height from the sizes seen in these saplings (*ca.* 120  $\mu\text{m}$ ) to approximately twice that size at the tops of tall palm trunks (Renninger and Phillips 2010). With vessels in their trunks around 240  $\mu\text{m}$  in diameter, *I. deltoidea* also has some of the largest mean trunk vessel diameters when compared with several reported mature tropical species and growth forms (Ewers et al. 1990, McCulloh et al. 2011). Vessel sizes in the petioles were also found to increase (from 80 to 120  $\mu\text{m}$  in diameter) in larger, taller *I. deltoidea* palms (Renninger and Phillips 2011) and are among the largest of the measured vessel diameters in the branches of early- and late-successional trees (McCulloh et al. 2011).

In terms of whole plant hydraulic structure, *I. deltoidea* also has an efficient system compared with other woody groups. For example, vessels taper by approximately 1/3 from roots to trunk and from trunk to fronds and this fraction was found to be the most efficient given the tradeoff between conducting efficiency and safety (Savage et al. 2010). Likewise, the conducting system in *I. deltoidea* closely approximates one with maximum hydraulic conductance for a given volume of vascular conduits (Murray's law) with the  $\Sigma r^3$  being statistically similar between the fronds and the trunk and the trunk and the roots. Therefore, this palm species conforms to the Murray's law predicted optimum of a conservation of  $\Sigma r^3$  across ranks as well as or better than ring-porous angiosperms and the vine *Campsis radicans* (Seem.) (McCulloh et al. 2004) and the compound leaves of temperate and tropical species (McCulloh et al. 2009). It is also notable that the ratio of theoretical leaf-specific conductivities ( $K_{L,calc}$ ) between fronds vs. trunk and trunk vs. roots seems to be driven by the ratio in conduit number between proximal vs. distal organs and not by the conduit diameter ratio which appears to be relatively fixed (Fig. 4).

This contrasts with McCulloh et al. (2009) who found that, in compound leaves, the conduit number ratio between ranks was more constrained than the vessel diameter ratio, which matched more closely with the ratios of leaf-specific conductivity between ranks. This reversal may be related to the differences between the dicot and monocot vascular bundle arrangement, because bundles are located in a fixed cylindrical pattern in dicot primary tissues whereas monocots contain a more random pattern of bundles located throughout their tissues.

Palms likely owe their hydraulic efficiency to their predetermined growth pattern and the location of their vessels within vascular bundles. The fact that all leaves emerge from a single apical meristem leads to a more compact crown that is more mechanically stable than the larger, more spreading crowns of many dicotyledonous trees (Rich 1986). Although palms lack a secondary cambium in their trunk, they still maintain the ability to alter the mechanical strength of their stems allowing tall palms to exceed theoretical buckling limits of dicotyledonous trees (Rich 1986). These factors decouple the burden of mechanical support from the vascular system (McCulloh and Sperry 2005) in palms, allowing optimal hydraulic efficiency to be achieved. The other main tradeoff that affects the efficiency of a hydraulic system in trees is that of safety from malfunction due to embolism and optimal conductance (Wheeler et al. 2005, Hacke et al. 2006, Sperry et al. 2008, Meinzer et al. 2010). *I. deltoidea* palms maintain fairly large vessels within all major organs and their petioles of their fronds have been shown to be fairly vulnerable to embolism with 50% loss of conductivity at -1.4 MPa (Renninger and Phillips 2011). However, vessels throughout tall palms (fronds, trunk, roots) may refill once embolized rather easily due to their close proximity to living parenchyma cells and phloem tissues

(Salleo et al. 1996, Zwieniecki and Holbrook 1998, Salleo et al. 2004, Zwieniecki et al. 2004, Salleo et al. 2006) within the vascular bundle, and possibly root pressure (Davis 1961, Milburn and Davis 1973). One other feature of note in the hydraulic system of palms is the large hydraulic constriction that occurs at their leaf bases because only the small protoxylem vessels connect the trunk and fronds hydraulically (Zimmermann and Tomlinson 1965, Zimmermann 1973, Sperry 1985). This hydraulic constriction may protect the irreplaceable trunk tissue from damage due to embolisms (if embolisms cannot be reversed in stems) but also adds a large amount of resistance to the hydraulic pathway that may decrease the efficiency of the hydraulic network in palms from a whole tree perspective.

In conclusion the palm, *I. deltoidea*, has been found to have an efficient hydraulic system both in terms of vessel sizes and density but also in terms of overall hydraulic architecture. Although the unique growth form and vascular organization of palms have led to an efficient hydraulic system, it also introduces some drawbacks relative to dicotyledonous trees. The lack of plasticity in the crown form of palms may make palms less adaptable to changes in light regimes compared to the more spreading crowns of many dicotyledonous trees. Likewise, the increased proportion of living cells within the roots, stems and fronds of palms compared to dicotyledonous trees may incur a larger respiration burden (Breure 1988, Henson 2004, Navarro et al. 2008). The other obvious limitation that palms face is a lack of a dormancy mechanism which restricts them largely to places without an extended period of freezing temperatures (Tomlinson 2006). Yet despite these drawbacks, palms continue to be an important component of tropical and

subtropical ecosystems and the efficiency of their hydraulic system likely contributes to this success.

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**Table 1:** Hydraulic and biometric variables for fronds, trunks and roots of five *Iriartea deltoidea* palms. Standard errors are in parentheses where  $n = 24$  for fronds,  $n = 5$  for boles and  $n = 13$  for roots. Different superscript letters denote statistically significant differences at  $\alpha = 0.05$  within each row.

	<b>Fron</b>	<b>Trunk</b>	<b>Root</b>
Organ diameter (mm)	14.6 (0.56) <sup>a</sup>	68.6 (12) <sup>b</sup>	23.2 (1.8) <sup>c</sup>
Total cross-sectional area (m <sup>2</sup> )	0.075 (0.015) <sup>a</sup>	0.41 (0.13) <sup>b</sup>	0.20 (0.076) <sup>c</sup>
Conduit diameter (μm)	77.7 (1.9) <sup>a</sup>	119.9 (5.9) <sup>b</sup>	179.1 (8.8) <sup>c</sup>
Conduit frequency (mm <sup>-2</sup> )	3.4 (0.33) <sup>a</sup>	3.8 (1.1) <sup>a</sup>	1.5 (0.16) <sup>b</sup>
Theor. specific-conductivity ( $K_{S, calc}$ )(kg m <sup>-1</sup> s <sup>-1</sup> MPa <sup>-1</sup> )	4.8 (0.35) <sup>a</sup>	24.0 (6.3) <sup>b</sup>	41.8 (6.5) <sup>c</sup>
Leaf area (m <sup>2</sup> )	1.1 (0.10) <sup>a</sup>	4.7 (1.3) <sup>b</sup>	—
Leaf area/x-sect area (m <sup>2</sup> m <sup>-2</sup> )	6000 (180) <sup>a</sup>	1300 (210) <sup>b</sup>	1800 (290) <sup>b</sup>
Theor. leaf-specific conductivity ( $K_{L, calc}$ )(kg m <sup>-1</sup> s <sup>-1</sup> MPa <sup>-1</sup> )	8.2x10 <sup>-4</sup> (0.7x10 <sup>-4</sup> ) <sup>a</sup>	0.021 (0.007) <sup>b</sup>	0.045 (0.03) <sup>b</sup>

### Figure Captions

**Figure 1:** Area-weighted conduit diameter ( $D_A$ ;  $\mu\text{m}$ ) vs. conduit frequency ( $\text{mm}^{-2}$ ; note the log scale) for trunk, fronds and roots from *Iriartea deltoidea* individuals. Solid line is the packing limit ( $1/\text{diameter}^2$  assuming square packing) or the maximum number of conduits of a given diameter that can fit into a given area and dashed line is the best fit regression ( $-1.4x + 7.4$ ;  $r^2 = 0.51$ ).

**Figure 2:** Area-weighted conduit diameter ( $D_A$ ;  $\mu\text{m}$ ) vs. conduit frequency ( $\text{mm}^{-2}$ ) for representative tree types (data from McCulloh et al. (2010)) and *Iriartea deltoidea* palms. Solid line is the packing limit ( $1/\text{diameter}^2$  assuming square packing) or the maximum number of conduits of a given diameter that can fit into a given area and dashed line is the best fit regression ( $-2.68x + 6.13$ ;  $r^2 = 0.95$ ). Data are plotted on log-log axes.

**Figure 3:** Stem diameter (mm) of fronds, trunks and roots of *Iriartea deltoidea* vs. A) conduit diameter ( $\mu\text{m}$ ) including best fit regression for the fronds ( $y = 1.7x + 54$ ,  $r^2 = 0.25$ ), trunks ( $y = 0.26x + 102$ ,  $r^2 = 0.27$ ) and roots ( $y = 3.4x + 101$ ,  $r^2 = 0.47$ ), B) conduit frequency ( $\text{mm}^{-2}$ ) where best fit lines are fitted to both fronds and roots ( $y = 20 * e^{-0.13x}$ ,  $r^2 = 0.71$ ) and trunks ( $y = 23 * e^{-0.03x}$ ,  $r^2 = 0.97$ ), C) theoretical specific-conductivity ( $K_{S, \text{calc}}$ ;  $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$ ) where one line is fitted to all organs ( $y = -76 + 117 * (1 - e^{-0.10x})$ ,  $r^2 = 0.36$ ) and D) distal leaf area ( $\text{m}^2$ ) for fronds ( $y = 0.0003 * x^{3.05}$ ,  $r^2 = 0.95$ ) and trunks ( $y = 0.0086 * x^{1.5}$ ,  $r^2 = 0.79$ ). Stem diameters are plotted on a natural log scale.

**Figure 4:** Distal/proximal ratios of theoretical leaf-specific conductivity ( $K_{L, \text{calc}}$ ) vs. A) distal/proximal ratios of total conduit numbers at each rank (i.e. within the total cross-sectional area of all fronds, total cross-sectional area of the trunk, and total cross-

sectional area of all roots) and B) distal/proximal ratios of conduit diameter (taper). The solid lines are the one to one lines.

FIGURE 1

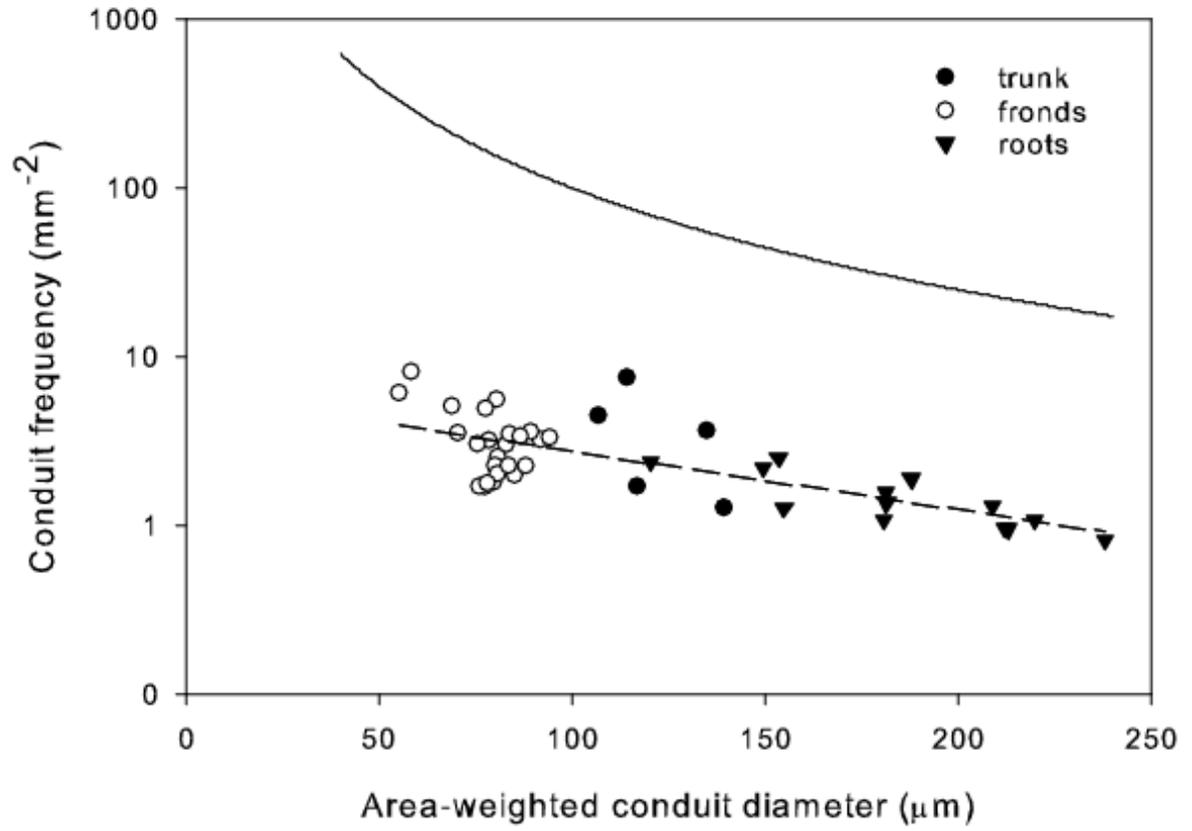


FIGURE 2

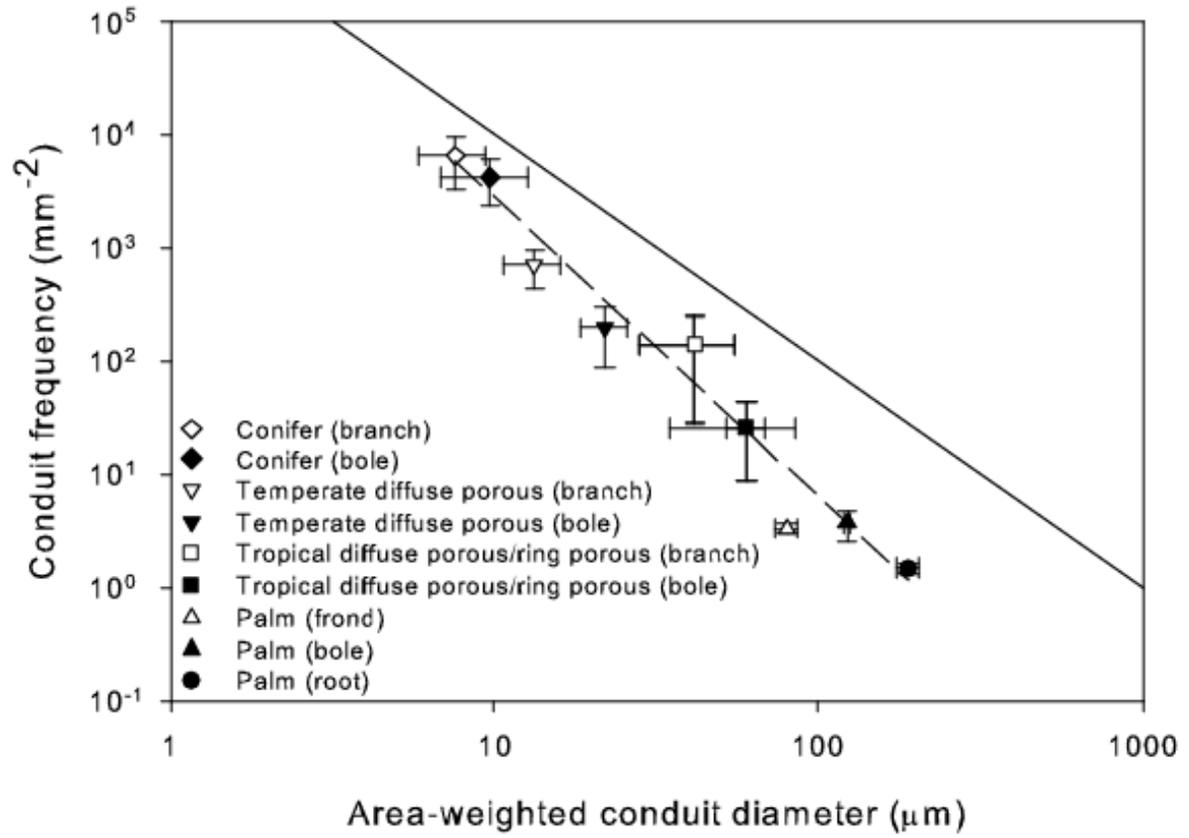


FIGURE 3

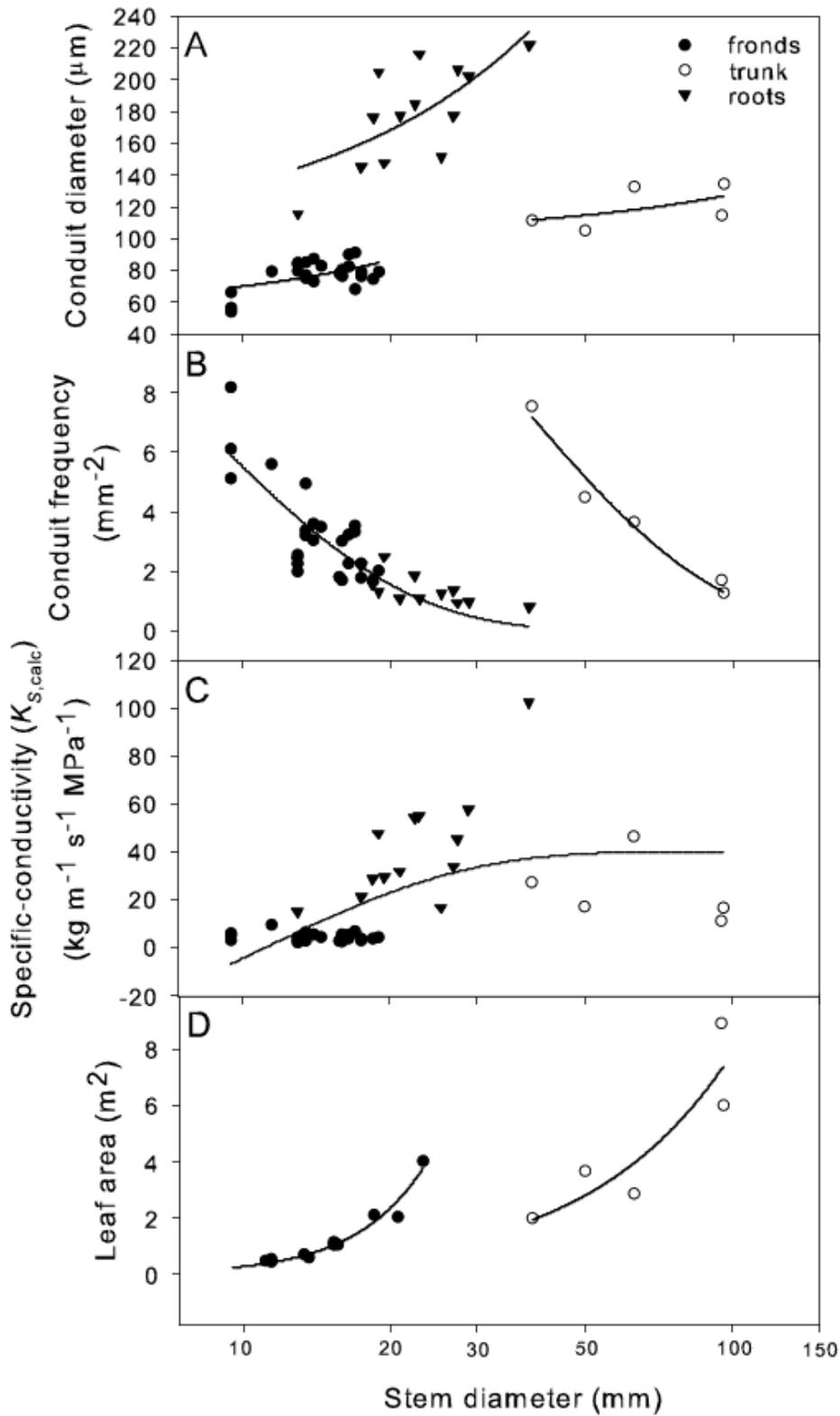


FIGURE 4

