Axial vessel widening in arborescent monocots

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Dicotyledons have evolved a strategy to compensate for the increase in hydraulic resistance to water transport with height growth by widening xylem conduits downwards. In monocots, the accumulation of hydraulic resistance with height should be similar, but the absence of secondary growth represents a strong limitation for the maintenance of xylem hydraulic efficiency during ontogeny. The hydraulic architecture of monocots has been studied but it is unclear how monocots arrange their axial vascular structure during ontogeny to compensate for increases in height. We measured the vessel lumina and estimated the hydraulic diameter ($D_h$) at different heights along the stem of two arborescent monocots, *Bactris gasipaes* (Kunth) and *Guadua angustifolia* (Kunth). For the former, we also estimated the variation in $D_h$ along the leaf rachis. Hydraulic diameter increased basally from the stem apex to the base with a scaling exponent ($b$) in the range of those reported for dicot trees ($b = 0.22$ in *B. gasipaes*; $b = 0.31$ and $0.23$ in *G. angustifolia*). In *B. gasipaes*, vessels decrease in $D_h$ from the stem’s centre towards the periphery, an opposite pattern compared with dicot trees. Along the leaf rachis, a pattern of increasing $D_h$ basally was also found ($b = 0.13$). The hydraulic design of the monocots studied revealed an axial pattern of xylem conduits similar to those evolved by dicots to compensate and minimize the negative effect of root-to-leaf length on hydrodynamic resistance to water flow.

**Keywords**: hydraulic limitations, hydraulic optimization, monocot anatomy, palm anatomy, plant hydraulics, tapering, vascular bundles.

**Introduction**

Among land plants, tracheophytes account for a wide range of variability in terms of form, structure, size, lifespan and reproductive strategies. As a tree gets taller, the distance between leaves and roots becomes longer and the tensile strength of ‘pulling’ water to the transpiring leaves increases accordingly. This should negatively affect the efficiency of water flow and thus assimilation and photosynthesis, and ultimately biomass production and growth (Ryan and Yoder 1997). However, every arborescent plant species has evolved anatomical adjustments to the xylem architecture to compensate for the hydraulic limitations imposed by the increased tree height. The actual hydrodynamic resistance to water flow and its variation during ontogeny are strongly dependent on tree size and spatial configuration of the network of xylem conduits (Becker et al. 2000, Petit et al. 2009), with conduit diameters being strictly dependent on the distance to the peripheral parts of the crown (Anfodillo et al. 2006, Olson and Rosell 2012). In dicot trees, cambial activity is under hormonal control (Aloni 1987, Anfodillo et al. 2012) and conduit elements increase in size from the stem apex downwards following a pattern that is maintained throughout ontogeny (Weitz et al. 2006). The axial pattern of basal increase in xylem element diameter (conduit widening) can be found along the whole axial xylem path from leaves (Coomes et al. 2008) to roots.

†Both these authors made equal contributions to data analyses and manuscript preparation.
Conduit widening in the stem is rather similar across dicot species and follows a power scaling with exponents ranging roughly from 0.15 to 0.33 (Anfodillo et al. 2006, Coomes et al. 2007, Petit et al. 2008, 2009, 2010, 2011, Lintunen and Kalliokoski 2010, Bettiati et al. 2012). As a consequence, most of the total hydraulic resistance to water flow is confined to the first 20–40 cm of stem length from the apex (Yang and Tyree 1993, Becker et al. 2000, Petit et al. 2008, 2010, Petit and Anfodillo 2009). In this way, dicot trees have evolved an effective xylem production strategy that minimizes the negative effect of increasing hydraulic resistance with increased height by simply enlarging the conduit elements towards the base.

In spite of the increasing literature documenting the size-mediated adjustments to the xylem network to sustain an efficient leaf physiology in dicot trees, no investigations have been carried out to verify whether the mechanism has evolved in arborescent monocots.

Among upright plants, dicots are characterized by the evolution of secondary growth carried out by a secondary meristem (the cambium). The cambium is wrapped around the longitudinal axes of above- and below-ground organs and continuously (or periodically) produces new xylem tissues that meet the water transport demand and mechanical requirements produced by further growth and crown development. This differs from monocots, which are characterized by the absence of a secondary meristem. The vascular system is organized in independent vascular bundles, i.e., aggregates of a few large vessels (typically one to three, plus some minor tracheary elements), phloem elements, fibres and parenchymal cells (Zimmermann and Tomlinson 1972). In light of the absence of a vascular cambium sustaining plant growth, monocots have evolved alternative strategies to grow and efficiently deliver water to remarkable heights, up to 60 m in the case of the world’s tallest palm species Ceroxylon quindiuense Karsten (the wax palm of high-altitude Andean regions) (Sanin and Galeano 2011).

Palm growth substantially differs from dicot trees and is characterized by peculiar developmental phases during ontogeny (Tomlinson 1990). After germination, the seedling enters an extended period of early development with a gradual expansion of the longitudinal axis to the maximum stem diameter attained by the individual (establishment growth). In this phase, the plant is required to build up all the vasculature needed to sustain the water demand for its entire life. After the achievement of the definitive basal diameter, the stem elongates, maintaining a nearly cylindrical form. The stem diameter and crown size do not change much for the remainder of the plant’s life (Tomlinson 1990, Renninger and Phillips 2010, 2011). Because of these peculiarities, palms are considered unique among plants for their ability to keep their xylem system functioning by preventing dysfunctions and for maintaining early differentiated living cells (e.g., parenchyma) active for their entire lifespan (Tomlinson 2006, Tomlinson and Huggett 2012). Not all palms are restricted to this growth pattern; some species continuously increase stem diameter during ontogeny (Tomlinson 1990). However, this increased diameter is not attributed to a secondary meristem, but rather is thought to be the consequence of the continuous expansion of the sclerenchymatic cap of the vascular bundles with increasing size and/or age as well as increased space between parenchyma cells (lacunae) in the stem and an enlargement of the parenchyma cells themselves (Rich 1986, Tomlinson 1990). Structural properties of palm stems can vary among species, but some important common features can be outlined (Tomlinson 1990). Tissue density often increases from the centre towards the periphery according to an increase in fibre content in the bundle sheath. The centre is characterized by a soft and spongy parenchyma, whose cells are connected to form a loosely packed network (central cylinder). Within this central ground tissue vessel bundles are randomly oriented with poorly lignified bundle sheaths. The peripheral region of the stem is the cortex, where all bundles are well aligned and packed towards the stem circumference with the fibrous bundle sheaths hardly lignified (forming the fibrous cap) and the surrounding parenchyma highly packed with no space between cells. The region between the soft central cylinder where the fibrous cap of bundle sheaths is not yet developed and the very stiff cortex (transition zone) shows a gradual variation of the anatomical features of parenchymatic ground tissue and bundle sheaths. Cortex thickness and the spread of the transition zone increase from the stem apex towards the base (Rich 1987, Bhat et al. 1990). Vessel dimensions have been reported as decreasing from the stem base to the apex and radially from the central cylinder to the cortex (Tomlinson 1990). In addition, vessel lumina decrease smoothly further up the rachis, after a ‘bottle-neck’ at the point of rachis insertion into the stem, where conduits are typically smaller (Tomlinson 1990).

In early palm anatomy studies, it was proposed that bundle courses connect the leaf vasculature with the central bundles at the stem base according to a so-called ‘endogenous growth’ (i.e., the continuous production of vascular bundles from the interior of the stem, which produces a centrifugal packing of bundles towards the periphery) (Desfontaines 1798, Tomlinson 2006). On the contrary, most recent studies reject this hypothesis in favour of predetermined proliferation of vascular bundles before height growth because there is no evidence of secondary meristems in palms (Zimmermann and Tomlinson 1972, Tomlinson 1990). According to this latter hypothesis, the hydraulic network system of vascular bundles can be simplified as a series of overlapping modules (like internodes) where vascular bundles originate from those of the module below at the level of leaf traces and extend upward before bending outwards into newer leaf traces. With this modular hydraulic design, palms are thought to overbuild their vasculature in terms of cell size and
number during the establishment phase, thereby accounting for the future water demand of leaves (Tomlinson 1990, 2006).

The above hypothesis, although supported by extensive literature based on palm anatomy, would seem to conflict with the increasing literature in favour of size-mediated modifications that compensate for the negative effect of increased plant height and thus sustain an efficient leaf physiology during ontogeny.

Given the importance of the whole-tree xylem architecture for the efficiency of water transport and the apical control of xylogenesis in dicot trees, here we tested the hypothesis that, in arborescent monocots, vessel diameter should progressively increase basally along the longitudinal axis of the leaf rachis and stem similarly to dicots, in such a way as to sustain an efficient water supply to the leaves during all stages of ontogeny. In particular, we carried out measurements of vessel dimensions along the longitudinal axis of the stem and leaf rachis in an arborescent palm (Bactris gasipaes Kunth) and a bamboo species (Guadua angustifolia Kunth).

Materials and methods

We selected two arborescent monocotyledon species for this study: peach palm (B. gasipaes Kunth) and guadua bamboo (G. angustifolia Kunth). Both species are native to and widely cultivated in Central America.

In March 2011, we harvested two stems of G. angustifolia and a single B. gasipaes individual (Table 1) from the CATIE farm located on the outskirts of Turrialba, Costa Rica (9° 54’ 0” N, 83° 41’ 0” W). All specimens were healthy. Turrialba is located on the Caribbean slopes of Costa Rica with an elevation of 600 m above sea level. The region is slightly seasonal with a mean annual precipitation of 2600 mm, with at least 85 mm of rainfall per month. The mean annual temperature is 21.5 °C, with little variation through the year.

For each plant, 2-cm-thick discs were cut every metre from the stem base to the apex. Diameter (D) and distance from the apex (L) were carefully measured for each stem disk. In addition, samples were taken from along the rachis of a leaf of the peach palm and their distance from the rachis apex (LR) recorded. Samples were then dried in an oven for 48 h at 70 °C.

For the peach palm, the transverse section of each stem disk was divided into up to seven distinct radial sectors with each zone encompassing 1 cm of the radius of the transverse section starting from the periphery, and moving towards the interior (sector from periphery: SP). Because of stem taper, central sector 6 was absent from the most apical sample, whereas the large section at the stem base accounted also for sector 7.

The stem structure of arborescent monocots is of highly variable density and characterized by a very fibrous texture. In addition to this, the presence of a strongly lignified sclerenchyma and of inclusions of silica bodies make extremely difficult (if not impossible) the preparation of thin sections with common methodologies used in wood anatomy (Tomlinson et al. 2011). Therefore, we settled on manually preparing clean cuts of sample surfaces with a straight edge razor blade. Samples were then observed under a Nikon Eclipse 80i light microscope (Nikon, Tokyo, Japan) at ×100–250 magnifications. The length of both major and minor axes of vessel lumina was measured with a digital caliper provided with the microscope. We restricted our measurement to vascular bundles that were intact. Collapsed or crescent-shaped vessel lumina were excluded from the measurements. We measured the two vessels of six bundles per segment height and per radial sector in the palm samples. We followed the same procedure for the bamboo species, but we measured the two vessels of six bundles in the third cell row from the inside of the stem. For both species we avoided vascular bundles that were located on the very periphery of the stem. For the bamboo species, we also avoided measurements for segments that contained nodal tissue and focused on internodal segments only. Vessel lumina were considered to be circular and the mean hydraulic diameter (Dn) (Kolb and Sperry 1999) was calculated as

\[
D_n = \frac{\sum d^5}{\sum d^4}
\]

where d is the conduit diameter of the n cell.

Statistical analysis

Data were log_{10}-transformed as is typically done in allometric analyses to meet assumptions of normality and homoscedasticity. We used a type II regression with a reduced major axis to determine the scaling exponents and allometric constants (regression slope and y intercept, b and a, respectively) of pairwise comparisons of the log_{10}-transformed data. Regression coefficients, their significance and 95% confidence intervals (CIs) were computed using standard methods (Sokal and Rohlf 1981), using a bootstrap procedure with 100,000 replications (Davison and Hinkley 1997).

Results

Qualitative observations

The anatomy of the stem and rachis of our B. gasipaes palm trees corresponded well to descriptions in the literature (Tomlinson 1990, Tomlinson et al. 2011). In the stem, tissue
density and vascular bundle orientations varied from the centre towards the periphery. The centre was characterized by a soft and spongy parenchyma, whose cells were connected together to form a loosely packed network (central cylinder). Here, vessel bundles were randomly oriented and bundle sheaths did not have lignified structures. In the peripheral region of the stem we distinguished the cortex: here, all bundles had a thick fibrous cap and were well oriented towards the stem circumference. In addition, the surrounding parenchyma was highly packed, thus leaving no space between cells. Between the central cylinder

Figure 1. Spatial patterns of $D_h$ in the stem of *B. gasipaes*. (A) Variation of $D_h$ in the different radial sectors (SP = 1 is the most peripheral) at the different heights along the stem. (B) Hydraulic diameter of the innermost sector (filled circles) at the different heights along the stem. (C) Variation of $D_h$ of the innermost sector (filled circles) with the distance from the stem apex ($L$) (log–log scale). Solid, dashed and dotted lines in (B) and (C) are the regression line, the 95% CIs and 95% prevision intervals, respectively (details in Table 2).
and the cortex we distinguished the transition zone where, going outwards, vessel bundles increased their centrifugal orientation along the circumference, the fibrous cap progressively increased in thickness (darker colour) and parenchyma cells became more tightly packed. As already reported in other studies (Rich 1987, Bhat et al. 1990), the thickness of the cortex and the transition zone increased from the stem apex towards the base.

In the bamboo *G. angustifolia*, the stem internodes were thin-walled hollow cylinders (~0.5–1.5 cm thick). Stem nodes were solid, providing additional structural support. The vascular bundles of the stem were sharply oriented towards the stem periphery, tightly packed together and each had a well-developed fibrous cap.

In *B. gasipaes* we noted that the peripheral sections (1 and 2) near the base of the stem included vascular bundles with larger fibrous caps, likely due to a more important structural role for the plant stability. Something similar was observed in the bamboo, in which peripheral cells were highly modified to provide more mechanical support, and there was a noticeable decrease in vascular bundle diameter and an increase in frequency from the interior of the stem towards the periphery.

**Quantitative analysis**

Vessel allometry was analysed in terms of variation in \( D_h \) with \( L \), as is commonly done for dicot trees, and anatomical analyses revealed clear axial patterns of basal increase in vessel diameter along the stem of both species and further along the leaf rachis of the peach palm.

In the stem of *B. gasipaes*, \( D_h \) increased from the stem apex towards the base with a similar trajectory between the different radial sectors analysed (Figure 1, Table 2). \( D_h \) increased with \( L \) as a power function, whose exponent \( (b) \) varied from 0.19 in the most peripheral sector (1) to 0.23 in the innermost sectors. However, differences between sectors were not significant when comparing the 95% CI. The models explained most of the variance \((0.64 < R^2 < 0.85)\) and the amount of explained variation increased from the stem periphery inwards. The axial patterns in \( D_h \) variation were parallel across sectors, but a radial increase in \( D_h \) was observed from the periphery to the centre at each stem height (Figure 1).

We observed highly variable tissue density in the outermost region of the stem along its length. When the cortex was too hard to cut, the vascular bundles in that area were not taken into account for anatomical measurements because of practical difficulties in flattening the surface of this highly sclerified region. In any case, vessels in the very peripheral cortex appeared as the smallest of the total stem cross-sectional area. Hydraulic diameter in the outermost sector (SP 1) increased from the stem apex to the base (Figure 1, Table 2) in parallel with an increase in tissue hardness (not measured directly) that hampered measurements in the smallest peripheral vascular bundles. In absolute terms, the smallest vessel dimensions were recorded for the peripheral sector SP 1 \((D_h = 130 \mu m)\) of the two most apical disks, where the presence of sclerified tissues was minimal. In turn, the widest xylem conduits were found at the centre of the stem base \((D_h = 290 \mu m)\).

Measurements of vessel size along the leaf rachis of *B. gasipaes* revealed that \( D_h \) decreased progressively towards the apex of the leaf, describing a pattern that was a clear continuation of the \( D_h \) observed at the stem apex (Figure 2). The xylem architecture of the rachis alone seemed to show a slower increase in \( D_h \) with \( LR \) (i.e., a lower slope, Table 3), when compared with the change in \( D_h \) per unit of length observed for the stem. However, these differences were not statistically significant (cf. 95% CI in Tables 2 and 3), as opposed to dicot trees, where conduits in leaf venations widen at a faster rate than along the stem (Coomes and Allen 2009).

The vasculature of *G. angustifolia* also exhibited a basal increase in vessel diameter (Figure 3). This was well fitted by power functions (Table 4), which explained 88–89% of the total variance. However, some differences in the actual pattern of variation were found between the two individuals examined (see 95% CIs in Table 4), with the smaller individual (G1, with \( H = 25 m \)) showing a higher scaling exponent \( (b = 0.31) \) compared with the bigger individual (G2, with \( H = 30 m; b = 0.23) \).

**Discussion**

We analysed the axial pattern of vessel \( D_h \) in terms of tip-to-base variation. This is an observational point of view that does

<table>
<thead>
<tr>
<th>SP</th>
<th>( N )</th>
<th>( a )</th>
<th>( b )</th>
<th>( R^2 )</th>
<th>( P )</th>
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<tbody>
<tr>
<td>1</td>
<td>7</td>
<td>1.69 (1.16–1.91)</td>
<td>0.19 (0.11–0.37)</td>
<td>0.64</td>
<td>0.0173</td>
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<tr>
<td>2</td>
<td>8</td>
<td>1.79 (1.34–1.96)</td>
<td>0.17 (0.11–0.33)</td>
<td>0.68</td>
<td>0.0064</td>
</tr>
<tr>
<td>3</td>
<td>8</td>
<td>1.72 (1.21–1.86)</td>
<td>0.22 (0.17–0.38)</td>
<td>0.80</td>
<td>0.0012</td>
</tr>
<tr>
<td>4</td>
<td>8</td>
<td>1.81 (1.50–1.93)</td>
<td>0.19 (0.14–0.29)</td>
<td>0.85</td>
<td>0.0004</td>
</tr>
<tr>
<td>5</td>
<td>7</td>
<td>1.72 (1.31–1.90)</td>
<td>0.22 (0.16–0.36)</td>
<td>0.81</td>
<td>0.0008</td>
</tr>
<tr>
<td>Im</td>
<td>8</td>
<td>1.70 (1.27–1.90)</td>
<td>0.23 (0.16–0.38)</td>
<td>0.81</td>
<td>0.0010</td>
</tr>
<tr>
<td>All</td>
<td>8</td>
<td>1.70 (1.31–1.86)</td>
<td>0.23 (0.17–0.31)</td>
<td>0.83</td>
<td>0.0006</td>
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</table>

Table 2. Parameters of the linear relationship \( \log_{10} D_h = a + b \log_{10} L \) along the different sectors from the stem periphery (SP 1–5), along the innermost sector (Im) and on average along the stem (All: average of all the vessels measured at each height) in *B. gasipaes*. \( N \) is the number of sampling points. The 95% CIs of \( a \) and \( b \) are in parentheses.
not necessarily refer to an ontological process. From a purely descriptive point of view, it makes no difference whether a form, say a cone, tapers to a point or widens to its base. However, from a functional point of view, selection favours wider vessels at the base of the stem in order to maintain hydraulic resistance as constant (West et al. 1999, Petit and Anfodillo 2009). If hydraulic resistance does not accrue with increasing path length, then there is no reason to expect basal conduits to be wider than those found in leaf terminal veins. As a result, ‘axial widening’ best captures the important idea from the point of view of the functional outcomes of natural selection.

Our analyses of arborescent monocot vessel anatomy revealed a general hydraulic vasculature design that mimics the scaling of dicot trees. In dicot trees, xylem conduits widen from the crown periphery towards the stem base and further down along the roots to rootlets, following a characteristic pattern consistent with a hydraulic optimization of water transport (Anfodillo et al. 2006, Petit et al. 2008, 2009, Petit and Anfodillo 2009). The leaf physiological performance does not vary much with increasing tree size given that the vascular architecture compensates for the negative effect of the increase in the path length resistance via conduit widening (Becker et al. 2000, Petit et al. 2009). Dicot trees have evolved a mechanism to perform this compensation by subjugating the final size of xylem elements to apical control. It has been recently demonstrated that conduit size strictly depends on the time that the cell remains in the enlargement phase (Anfodillo et al. 2012) and that this phase is much longer at the stem base. In such a way, conduit elements widen from the stem/branch apices downwards, confining most of the hydraulic resistance to the first tens of centimetres from the apices (Becker et al. 2000, Petit and Anfodillo 2009). Consequently, as a tree grows in height and the cambium produces new xylem tissue along the circumference, the stem conduits of dicots (vessels or tracheids) increase in size from the pith to the bark (Anfodillo et al. 2006, Olson and Rosell 2012).

Pioneering studies on palm anatomy reported axial and radial patterns of increase in vessel length (Tomlinson 1990) comparable to those of vessel diameter observed in this study. Our results from the palm B. gasipaes showed that vessels from the centre of the stem increase in diameter from the apex to the base according to a power function with an exponent in the range of those reported for dicot trees (on average $b = 0.2$) (Anfodillo et al. 2006, Weitz et al. 2006, Coomes et al. 2007, Mencuccini et al. 2007, Petit et al. 2008, 2009, 2010, 2011,

Figure 2. Variation of $D_h$ with $LR$ (log–log scale) along the leaf rachis (triangles) and stem (circles). Hydraulic diameter at the different heights along the stem are those measured in the innermost sector. Solid, dashed and dotted lines are the regression line, the 95% CIs and the 95% prevision intervals, respectively (details in Table 3). Linear scale in shown the inset.

Table 3. Parameters of the linear relationship $\log_{10} D_h = a + b \log_{10} L$ along the longitudinal axis of the rachis ($R$) and along the rachis plus stem ($R + S$) in B. gasipaes. For the $D_h$ estimates at the different heights along the stem, $S(\text{All})$ accounts for the $D_h$ average of all the vessels in the different sectors, and $S(\text{Im})$ for the $D_h$ relative to the innermost sector. $N$ is the number of sampling points. The 95% CIs of $a$ and $b$ are in parentheses.

<table>
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<tr>
<th>Path ID</th>
<th>$N$</th>
<th>$a$</th>
<th>$b$</th>
<th>$R^2$</th>
<th>$P$</th>
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<td>0.13 (0.11–0.22)</td>
<td>0.75</td>
<td>0.0003</td>
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<tr>
<td>$R + S(\text{All})$</td>
<td>19</td>
<td>1.82 (1.73–1.89)</td>
<td>0.17 (0.14–0.21)</td>
<td>0.85</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>$R + S(\text{Im})$</td>
<td>19</td>
<td>1.79 (1.68–1.86)</td>
<td>0.19 (0.15–0.23)</td>
<td>0.86</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>

Figure 3. Variation of $D_h$ with $L$ (log–log scale) along the stem of the bamboos G. angustifolia G1 (diamonds) and G2 (triangles). Solid, dashed and dotted lines are the regression line, the 95% CIs and the 95% prevision intervals, respectively (details in Table 4). Linear scale shown in the inset.
Lintunen and Kalliokoski 2010, Bettiati et al. 2012). The same pattern was observed along each radial sector (SP). Notably, the smallest vessels were found at the periphery of the most apical section, whereas the widest ones were located at the centre of the stem base.

Analyses of vessel diameter variation in bamboo stems provide additional evidence that the pattern of hydraulically optimized xylem anatomy can also be found in other arborescent monocots. We found that in *G. angustifolia*, as was the case with dicots and *B. gasipaes*, vessel diameter increases from the stem apex to the base following a power trajectory with an exponent consistent with those reported for dicot trees. In addition, the xylem anatomy observed along the palm leaf rachis revealed that its conduits increase in diameter basally. Regarding leaf vessel size variation, monocots seem to differ from dicots: while in dicots the axial scaling of leaf venation conduits is higher (Coomes et al. 2008) than that of the stem (Anfodillo et al. 2006), our measurements suggested no significant differences in the rate of axial *Dv* variation between the leaf rachis and the stem. The development of the axial pattern of vessel dimensions in arborescent monocots can be explained by two alternative hypotheses. According to the ‘overbuilt scenario’ xylem vasculature is concluded with the establishment phase because palms lack any form of secondary vascular development and therefore the hydraulic requirements of the later-formed tall stem have to be anticipated in early development (Tomlinson 1990, Tomlinson and Huggett 2012). This implies that the production of new vessels would follow a tapered axial pattern with decreasing xylem conduit diameters as the stem height increases during ontogeny. Consequently, the ‘overbuilt hypothesis’ predicts either a strong reduction in leaf area and metabolism during ontogeny, or that the trade-off mechanism between hydraulic efficiency and construction costs for the build-up of the xylem transport network (Mencuccini et al. 2007) does not affect arborescent monocot ontogeny.

However, we observed in our arborescent monocots a typical pattern of vasculature for stem-apex-to-base length with elements increasing basally in agreement with the universal pattern of hydraulic efficiency observed for dicot trees (West et al. 1999, Anfodillo et al. 2006, Weitz et al. 2006, Mencuccini et al. 2007, Petit and Anfodillo 2009).

In the palm, we observed changing patterns of vascular bundle arrangements from the stem core to its periphery where the core was comprised of loosely packed, spongy ground tissue, with randomly oriented vascular bundles. This sponginess decreases towards the stem periphery because of a centrifugal packing of vascular bundles that increases from the core to the periphery. The bundle sheaths near the periphery harden over because of progressive development of the fibrous cap. Packing and hardness increase towards the stem periphery, bearing the extremely hard tissue forming the cortex. In addition, the thickness of the cortex and the transition zone increased along the stem from the apex to the base, in agreement with previous reports (Rich 1987, Bhat et al. 1990).

Considering the vasculature as a whole of bundles independent of one another (Shinozaki et al. 1964), we can therefore propose an alternative and speculative hypothesis consistent with principles of hydraulic optimization (West et al. 1999, Anfodillo et al. 2006, Petit and Anfodillo 2009). According to this, the observed patterns of vessel size and distribution would be the consequence of the continuous production of new root-to-leaf xylem bundles and their progressive displacement towards the periphery of the stem apex with leaf ageing.

Therefore, can we assert that the principles of water transport optimization that led dicot trees to evolve a vasculature with conduits enlarging basally can be applied to monocots as well? Conduits near transpiring leaves are narrow to avoid embolism formation (Hacke et al. 2001, Tyree and Zimmermann 2002) and widen basally to compensate for path length resistance (Becker et al. 2000, Petit and Anfodillo 2009). This interpretation of monocot vascular development conflicts with the ‘overbuilt hypothesis’ (Zimmermann and Tomlinson 1972, 1990, 2006, Tomlinson et al. 2011). Since stem development of palms accounts for the early ‘establishment growth’ phase (Tomlinson 1990), where stem enlargement achieves the final diameter, a good test to challenge our novel hypothesis is to compare the anatomy at the stem base on chronosequences (i.e., with different height classes) of different palm species of similar stem diameters. According to the established knowledge (Tomlinson 1990), vessels should have achieved their maximum size and number already in the shorter and younger plants. On the contrary, if the widest vessels in the central cylinder scaled with the tree height according to the universal design for hydraulic optimization (Anfodillo et al. 2006), this would implicitly open a new frontier in monocot anatomy aimed at understanding how the average vessel diameter can vary during ontogeny in plants without secondary meristems.

Table 4. Parameters of the linear relationship Log10 *Dv* = *a* + *b* Log10 *L* along the stem of the two *G. angustifolia* species (B1 and B2). *N* is the number of sampling points. The 95% CIs of *a* and *b* are in parentheses.

<table>
<thead>
<tr>
<th>Bamboo ID</th>
<th><em>N</em></th>
<th><em>a</em> (CI)</th>
<th><em>b</em> (CI)</th>
<th><em>R</em>^2^</th>
<th><em>P</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>G1</td>
<td>36</td>
<td>1.39 (1.28–1.52)</td>
<td>0.31 (0.26–0.36)</td>
<td>0.89</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>G2</td>
<td>31</td>
<td>1.63 (1.56–1.71)</td>
<td>0.23 (0.20–0.25)</td>
<td>0.88</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>G1 + G2</td>
<td>67</td>
<td>1.51 (1.41–1.60)</td>
<td>0.27 (0.24–0.31)</td>
<td>0.87</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>
To summarize, our observation of the tapered/widened hydraulic system of monocots opens the question of how this pattern is ontogenetically constructed. In the absence of secondary growth it is clear that apically produced vessels must become narrower. Thus the ontogenetic trajectory is from wide to narrow. The ontogenetic mechanisms remain hypothetical however. Here we present two hypotheses to be explored. First, basal vessel diameter is determined during the establishment phase (Tomlinson 1990, 2006); however, this would require that the plant ‘know’ how tall it will be later in life. An alternative explanation is that bundles are initiated during a post-proliferation phase. Future work on woody monocot morphology should test these hypotheses of interest.

In conclusion, despite differences in the anatomical organization of stem anatomy, our study suggests that both dicots and monocots may have responded to specific hydraulic pressures by evolving a pattern of xylem vasculature that follows the same principles of hydraulic optimization.

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Conflict of interest

None declared.

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References