

Hydraulic architecture of *Monstera acuminata*: evolutionary consequences of the hemiepiphytic growth form

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SUMMARY

The hydraulic architecture of the secondary hemiepiphyte *Monstera acuminata* was examined in native plants from Los Tuxtlas, Veracruz, Mexico, to determine how it compared to better-known growth forms such as trees, shrubs, lianas and primary hemiepiphytes. *Monstera acuminata* starts its life cycle as a prostrate herb. As it ascends a tree or other vertical support, the stem becomes thicker, produces larger leaves, and may die back from the base upwards until only aerial feeding roots serve to connect the stem to the soil. Unlike the pattern of vessel-size distribution along the stems of woody dicotyledons, *M. acuminata* has its wider vessels at the top of the stem, decreasing in diameter towards the base. Also peculiar is the fact that Huber values (axis area/distal leaf area) tend to increase exponentially at higher positions within the plant. Based on the hydraulic conductivity (k_h) and leaf-specific conductivity (LSC, k_h /distal leaf area), the base of the stem potentially acts as a severe hydraulic constriction. This constriction is apparently not limiting, as aerial roots are produced further up the stem. The plants have remarkably strong root pressures, up to 225 kPa, which may contribute to the maintenance of functional vessels by refilling them at night or during periods of very high atmospheric humidity, as in foggy weather and rain. In common with dicotyledonous plants, vessel length, vessel diameter, k_h , specific conductivity (k_s , k_h /axis area) and LSCs were all positively correlated with axis diameter. The features of the hydraulic architecture of *M. acuminata* may be an evolutionary consequence of an anatomical constraint (lack of vascular cambium and therefore of secondary growth) and the special requirements of the hemiepiphytic growth form.

Key words: *Monstera acuminata*, Araceae, secondary hemiepiphytes, root pressure, hydraulic architecture, xylem vessels, functional morphology, climbing plants.

INTRODUCTION

The hydraulic architecture is the design of the water-conducting tissue, the xylem, used by plants in order to distribute water through the root–stem–leaf continuum. In trees the highest resistance to water flow is at the periphery (i.e. minor branches) and decreases towards the trunk, which ensures an almost equal distribution of water from the trunk to the many leaves (Tyree, 1988; Tyree & Ewers, 1991; Tyree *et al.*, 1991; Yang & Tyree, 1993, 1994). As woody plants grow, wider and longer vessels are produced, balancing an increasing evaporative demand. This is accomplished by the production of

secondary xylem in stems and roots (Zimmermann, 1983). Lianas (woody vines) also produce secondary xylem, but invest relatively less in supporting tissue as they are structural parasites (*sensu* Stevens, 1987). Comparatively wider and longer vessels are found in lianas than in trees or shrubs. For this reason, liana stems are much more efficient per stem transverse area than are stems of trees and shrubs (Ewers *et al.*, 1989; Ewers & Fisher, 1991). Other than for the palm *Rhapis excelsa* (Sperry, 1986), for sugarcane (Meinzer *et al.*, 1992) and, to a lesser extent, bamboo (Cochard *et al.*, 1994), relatively little is known about the hydraulic architecture of large plants that lack secondary growth.

Certain plants, important in moist tropical forests, live a portion of their life cycle as epiphytes (*sensu*

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lato; Madison, 1977a), and thus gain access to light in crowded environments. These are the hemiepiphytes (Richards, 1952; Kress, 1986), of which there are two types; primary, which start as epiphytes and later establish contact with the soil, and secondary, which germinate in the ground, grow as a vine up a host plant or other vertical substrate, and then lose stem contact with the soil. Examples of secondary hemiepiphytes occur in various families, particularly the monocotyledonous families Araceae and Cyclanthaceae, and the dicotyledonous family Marcgraviaceae (Williams-Linera & Lawton, 1995). The genus *Monstera* (Araceae) comprises 22 species distributed in the neotropics (Madison, 1977b). In *Monstera gigantea* (*M. tenuis* or *M. dubia* according to Madison, 1977b), the juvenile prostrate herb 'searches' for vertical substrates to climb by means of skototropism, growth towards the darker areas (Strong & Ray, 1975). In this genus, adventitious anchoring roots hold the appressed climber (Croat, 1988) to the bark of the host tree. After vertical ascent, the base of the stem of the hemiepiphyte dies and rots. Direct contact between stem and soil is thus lost, but by that time one or more adventitious aerial feeding roots have contacted the soil to allow for water and mineral uptake (Madison, 1977b; Croat, 1981). Although there have been recent advances in understanding the hydraulic architecture and water relations of primary hemiepiphytes (Zotz *et al.*, 1994; Patiño *et al.*, 1995; Holbrook & Putz, 1996), there are no reports concerning secondary hemiepiphytes. In this paper we discuss the pattern of xylem distribution, hydraulic conductivity and root pressure in the secondary hemiepiphyte *M. acuminata*, contrasted with those of other growth forms.

MATERIALS AND METHODS

Study site

The study site (95° 04' W, 18° 35' N, 180 m altitude) is located around the Estación de Biología Tropical Los Tuxtlas, Veracruz, Mexico, within a tropical evergreen forest (*Selva alta perennifolia*; Miranda & Hernández-Xolocotzi, 1963). Average annual rainfall is 4725 mm, mean annual temperature 24.3°C, and the rainfall of the driest month 60 mm (Ibarra-Manríquez & Sinaca-Colín, 1987).

Plant material

The growth habits of *Monstera acuminata* C. Koch (Araceae) and other species of this genus have been detailed by Madison (1977b). This species germinates in the ground and grows horizontally as a low prostrate herb up to 10 m in length, with a stem diameter of *c.* 5–8 mm, and with relatively small leaves and long internodes. When it encounters a tree trunk, it attaches firmly to the bark by means of

ageotropic anchoring roots, and grows vertically with shorter internodes and a progressively thicker stem. The upper leaves are larger and have fenestrations. New feeder roots are progressively formed further up the stem as the plant ascends its host (Madison, 1977b; Ray, 1988). All the plants used were native plants vertically attached to host trees. The *M. acuminata* plants lacked their original connection to the soil through the stem, but in each case there was at least one aerial feeder root attached to the soil. The prostrate juvenile stage of the life cycle was not examined.

Root pressure

Root pressures were measured in aerial roots that we cut off with a sharp razor. In December 1996, during the rainy season, eight *M. acuminata* individuals were chosen ranging in stem height above soil from 1.23 to 6.9 m, and in their number of leaves from 14 to 90. For seven of the plants, xylem sap pressures (P_x) were recorded at the proximal end of one aerial feeding root (severed at 0.2 m height) of each of the seven plants. For one plant that was 4.5 m in height pressures were measured in two feeding roots, both of which were severed near their point of insertion to the stem (1.0 and 2.0 m above soil level). Bubble manometers made with glass micropipettes were used (Fisher *et al.*, 1997). The length of the bubble was measured at equilibrated xylem pressure (L_{pd}) and then the tubing quickly cut to measure the bubble length at atmospheric pressure (L_{atm}). Four measurements were made in a 24 h period starting at 07.00 hours, fitting a new manometer after the cut was done and allowing at least 5 h for pressure equilibration. Xylem water pressure was calculated as $P_x = 100 [(L_{atm}/L_{pd}) - 1]$ (Fisher *et al.*, 1997).

Root pressure was also measured in June 1998, during one of the longest recorded dry spells at Los Tuxtlas which was due to the El Niño Southern Oscillation. It had not rained for at least 2 months and relative humidity was 63–75%, in contrast to 90% in December 1996. One feeding root was selected for each of eight plants. The bubble manometers were attached to the severed feeding roots on a previous night at 20.00 hours, and root pressures were measured at predawn the next day.

Vessel dimensions

In July 1995, 16 *M. acuminata* individuals were selected with stems ranging from 0.3 to 11.3 m (median 3.6 m) above soil level for measurements of maximum vessel lengths in 19 stem and 19 feeder root segments, via the pneumatic method (Ewers & Fisher, 1989a). A tygon tube was clamped to the proximal end of a long stem or root segment, and the distal end of the root or stem segment was immersed

in a deep pan filled with clean water. Compressed air (40 kPa) was fed through the tygon tube while sequentially removing 0.05 m segments from the distal end of the axis using a sharp razor blade or pruners, until a steady stream of air bubbles emerged from the freshly cut end, indicating a continuous open vessel. Maximum vessel length was then recorded as the length of the remaining axis plus 0.025 m. Axis and central cylinder (stele) diameters were measured at the proximal and distal end of the remaining axis. The stele is well defined by a sclerotic layer in this species (French & Tomlinson, 1981). A median portion of the remaining axis was used for measurements of maximum vessel diameter in a fresh, freehand, transverse section stained with 0.1% toluidine blue. We used an ocular micrometer on a compound microscope to determine the diameter (= mean of radial and tangential lumen diameter) of the five widest vessels for each section. The average of the five widest vessels was considered the maximum vessel diameter, which was correlated with the maximum vessel length in that segment. For stems, measurements of stele, axis and vessel diameters were always made at internodes rather than at nodes.

Maximum vessel lengths were found to be quite low in three roots that were interrupted by a gall. From follow-up experiments with the pneumatic method, it appeared that all vessels ended at a gall. As this was apparently a pathogenic condition, the roots with galls were excluded from the data sets comparing vessel length versus vessel diameter.

Hydraulic architecture parameters

These measurements were made on four plants between 21 and 26 July, 1995. We carefully removed the plant from its host tree, then we cut the feeder root(s) under water, near soil level. We kept the cut, distal ends of the roots immersed to minimize the introduction of embolisms in transit to the laboratory. Depending on the size of the plant, 8–11 equally spaced stem segments, 6–12 feeder root segments, and leaves were numbered. The segments were immersed while they were cut to 10 cm lengths. Leaf areas were measured with a LI-COR LI-3100 area meter.

We measured hydraulic conductivity (k_h , flux per pressure gradient), specific conductivity (k_s , k_h /axis area), leaf-specific conductivity (LSC, k_h /distal leaf area) and Huber value (axis area/distal leaf area) in each of the 10-cm-long segments (Tyree & Ewers, 1991). The k_h values ($\text{kg m MPa}^{-1} \text{s}^{-1}$) were measured using a dilute solution of oxalic acid (0.15 M) with a pressure head of 10 kPa (pressure gradient in segments 0.01 MPa m^{-1}) while the flux (in kg s^{-1}) was followed with a graduated pipette and a stopwatch. The k_s ($\text{kg m MPa}^{-1} \text{s}^{-1} \text{m}^{-2}$) and Huber values (HV, $\text{m}^2 \text{m}^{-2}$) were calculated using the

average of the axis areas of the distal and proximal ends of the 10 cm segment.

To mark the conductive vessels, after flux measurements were completed the segments were perfused with 1% safranin in oxalic acid, chased by a clear 0.15 M oxalic acid solution to remove excess of safranin and to minimize lateral diffusion (Ewers *et al.*, 1989). Thin, freehand sections taken from the median part of the segments were mounted with water on slides and covered with a coverslip. Sections were examined with a compound microscope. Vessels were measured, marking those stained with safranin, by projecting them on paper via a camera lucida. When it was not possible to see the whole stem section because of the large size of the stele, we chose a 'pie-shaped' section representing no less than 12.5% of the stele area. The vessel counts thus obtained were then converted to the expected value for 100% of the stele.

For analysis of root versus shoot contributions at various heights (path lengths) along the plant, the values for the feeder roots of a plant were combined to determine total root axis and stele area, vessel number, k_h , etc. For analysis of Huber values and possible pressure gradients along the length of the plant, the corresponding values at each equivalent height above the soil were pooled for roots plus stem. For example, if three roots and one stem segment of a plant coincided in height, their axis areas or k_h values were added in order to calculate total HV, k_s and LSC.

We calculated stepwise multiple regressions between \log_{10} -transformed values of k_h , k_s and LSC and \log_{10} -transformed maximum vessel diameter or axis diameter. The plant organ (feeder root or stem) was considered as a categorical variable.

Theoretical pressure gradients (MPa m^{-1}) are equal to E/LSC , where E = transpiration rate. To determine the effectiveness of the feeding roots and stem at supplying their leaves when actively transpiring, the pressure gradient was related to LSC by calculating the predicted water potential difference with respect to path length (i.e. plant height) of every segment i as:

$$\psi_i = -[(E_i/\text{LSC}_i \times L_i) + (dP/dx \times L_i)]$$

(Ψ , water potential (MPa); E , transpiration rate ($\text{m}^3 \text{water s}^{-1} \text{m}^{-2} \text{leaf area} = \text{m s}^{-1}$); LSC, leaf-specific conductivity ($\text{m}^2 \text{MPa}^{-1} \text{s}^{-1}$); L , length of segment (m); dP/dx , the hydrostatic gradient (0.01 MPa m^{-1})).

Three transpiration rates reported for the liana *Bauhinia fassoglensis* from Ewers *et al.* (1989) were used. To obtain the water potential at each segment height, the drop in water potential for that segment was added to the water potential of the subtending segment.

Taper is defined as ((distal axis diameter – proximal axis diameter)/axis length). Taper was

calculated for each of the axes used to determine vessel length, and also in the stems and in the longest aerial root of each of the four individuals used for conductivity measurements. For the stem and longest feeding root of each individual, the most distal and most proximal segments used for conductivity were used to calculate taper.

RESULTS

Dimensions of axes and steles

Axis diameter was significantly correlated with stele diameter for both stems ($r = 0.96$, $df = 33$, $P < 0.0001$) and roots ($r = 0.85$, $df = 37$, $P < 0.0001$). The slopes of the regression lines indicate an axis : stele proportion of 1 : 0.7 in stems and 1 : 0.6 in roots. For taper, root parts were compared in terms of their relative proximal or distal position to the stem, and stem parts were compared in terms of their relative proximal or distal position to the root. Based upon paired two-tailed t tests, mean proximal axis diameter was significantly less than mean distal diameter for roots as well as stems. The tapers were negative in 83 % of the stems and in 74 % of the roots sampled. Stem axes were, on average, two or three times wider than root axes, but their negative taper was 6.7 times steeper than for roots, with mean values of -3.69 mm m^{-1} for stems versus just -0.56 mm m^{-1} for roots (Table 1).

Stele tapers were negative in 91 % of the stems but in just 65 % of the roots. Based on paired two-tailed tests, for stems the mean proximal stele diameter was significantly less than the mean distal diameter (Table 1). However, for root steles the difference between distal versus proximal stele diameter was not statistically significant ($P = 0.18$).

Root pressure

In December 1996, during the wet season, we registered positive xylem pressures in the root stumps of all eight plants sampled. In the seven plants that were monitored over a 24 h period, pressures fluctuated between 10–200 kPa, with

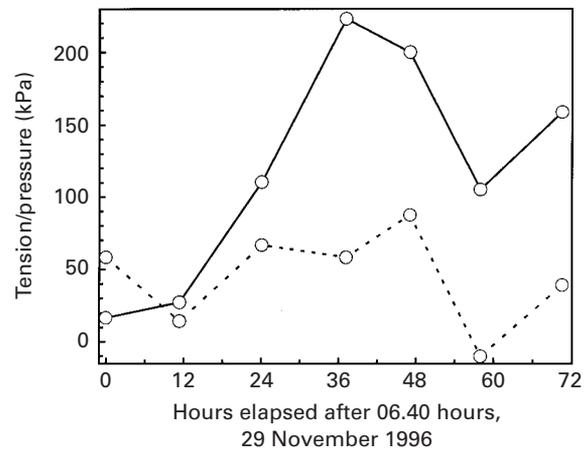


Fig. 1. Root pressure in two roots (root stump at a height of 1 m, solid line; 2 m, broken line) of a *Monstera acuminata* individual 4.5 m tall growing on a remnant tree in pastureland. Abscissas indicate hours elapsed since the roots were severed from the stem.

positive pressures being recorded at all times of day. The xylem pressures varied considerably over time, as illustrated by the plant in which we monitored two feeding roots at different heights for a 70 h period, with a maximum pressure of 223 kPa recorded (Fig. 1).

In June 1998, during the dry season, all eight plants failed to show positive root pressures. The bubble manometers became completely air-filled and empty vessels could be seen on the cut surface of the root stumps before dawn.

Vessel diameter and length

Linear regressions between maximum vessel length and stele diameter (Fig. 2a) and maximum vessel diameter and stele diameter (Fig. 2b) were statistically significant for stem and root axes (Fig. 2; $P < 0.005$). It can also be seen that vessel diameters and lengths were much greater in roots than in stems for a given stele diameter. As with maximum vessel diameter, maximum vessel length tended to increase with stele diameter in roots and stems ($P < 0.02$), the slope (m) being significantly higher in roots than in stems ($m_{\text{roots}} = 0.04$; $m_{\text{stem}} = 0.007$). Thus the

Table 1. Summary of the root and stem dimensions of *Monstera acuminata* plants sampled

	Stems		Roots	
	Axis	Stele	Axis	Stele
Distal diameter (mm)	$10.38 \pm 0.95^{**}$	$6.42 \pm 0.84^{**}$	$4.01 \pm 0.36^*$	2.65 ± 0.19
Proximal diameter (mm)	7.83 ± 0.75	4.73 ± 0.64	3.63 ± 0.32	2.53 ± 0.22
Length of segment (m)	1.14 ± 0.36	1.14 ± 0.36	1.49 ± 0.31	1.49 ± 0.31
Taper (mm m^{-1})	-3.69 ± 1.27	-2.04 ± 0.60	-0.56 ± 0.15	0.40 ± 0.19

Values are means \pm SE, $n = 23$.

*, Significantly different from proximal at $P < 0.02$; **, significantly different from proximal at $P < 0.002$.

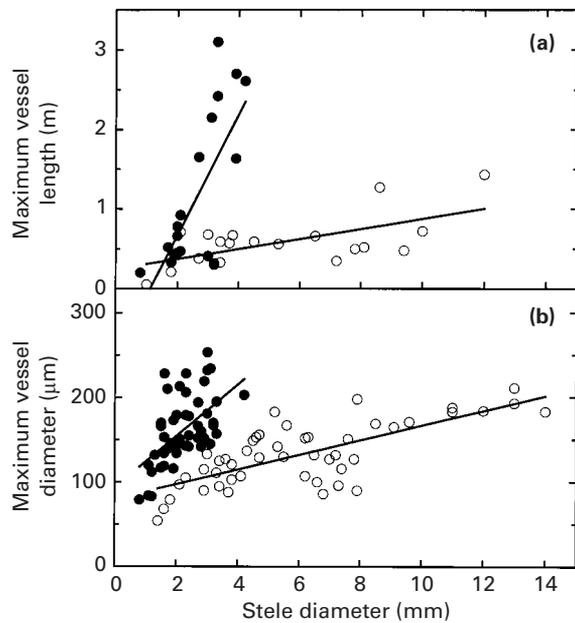


Fig. 2. Relation between maximum vessel length, maximum vessel diameter and stele diameter of stem (open circles) and root (closed circles) segments for 16 *Monstera acuminata* plants. Linear regressions, df , correlation coefficients and P values: (a) $y = -0.86 + 0.76x$, 17, 0.71, 0.0001 (roots), $y = 0.25 + 0.06x$, 17, 0.62, 0.0001 (stems); (b) $y = 94 + 30.4x$, 50, 0.56, 0.0001 (roots), $y = 80 + 8.6x$, 46, 0.73, 0.0001 (stems).

widest roots tended to have longer and wider vessels than the widest stem segments.

Hydraulic architecture parameters

Fig. 3 shows the relationships between maximum vessel diameter (a–c) or axis diameter (d–f) and several hydraulic architecture parameters in stem and root segments in four *M. acuminata* individuals. Multiple regression analyses indicate that when vessel diameters are taken into account (Fig. 3a–c), the difference between stems and roots is either non-significant ($P > 0.05$, as in k_h and LSC), or explains only a low proportion of total variability in the data sets (c. 5% in k_s ; $P < 0.001$). When axis diameter is plotted against k_h , k_s and LSC (Fig. 3d–f), stem and root segments are segregated and these organs account for a higher percentage of total variability of the data set (c. 20–47%; $P < 0.0001$). The intercepts of the regression lines were significantly different between plant parts ($P < 0.0001$) but the slopes were not, as indicated by a non-significant interaction term (stem \times plant part; $P > 0.05$). Axis diameter accounts for 15–36% of the total variability ($P < 0.0001$). For a given axis diameter, k_h , k_s and LSC values were significantly greater in roots than in stems.

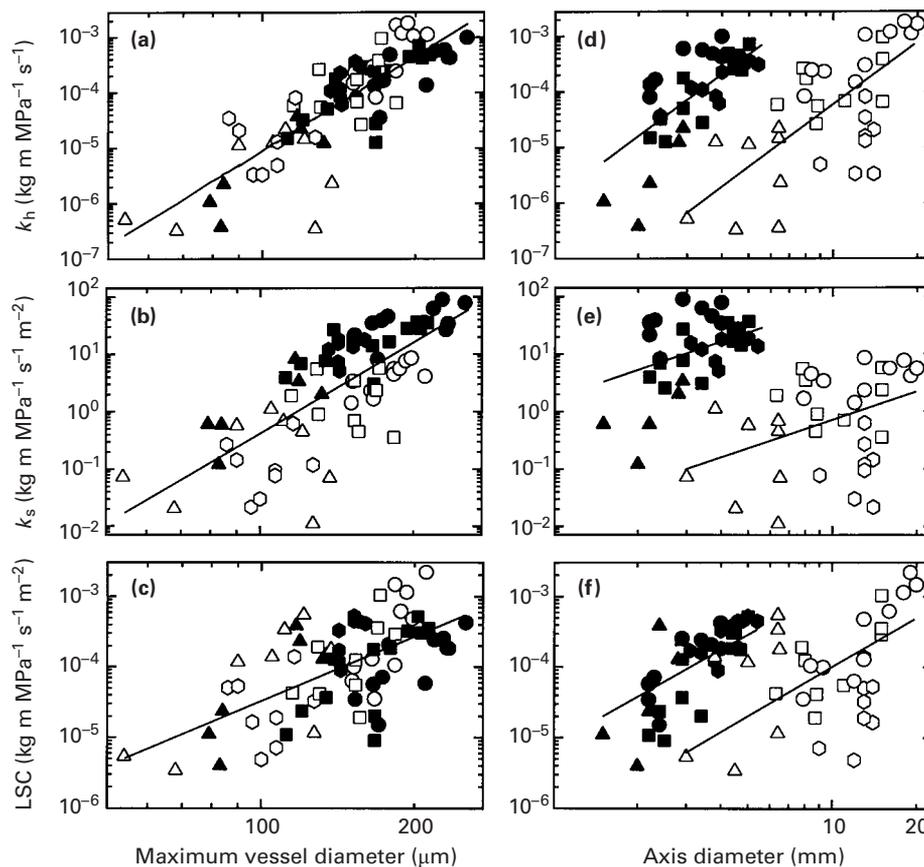


Fig. 3. Relationships between maximum vessel diameter (a–c) or axis diameter (d–f) and hydraulic conductivity (k_h), specific conductivity (k_s) and leaf specific conductivity (LSC) of stem (open symbols) and root (closed symbols) segments for four *Monstera acuminata* individuals (as indicated by different symbols).

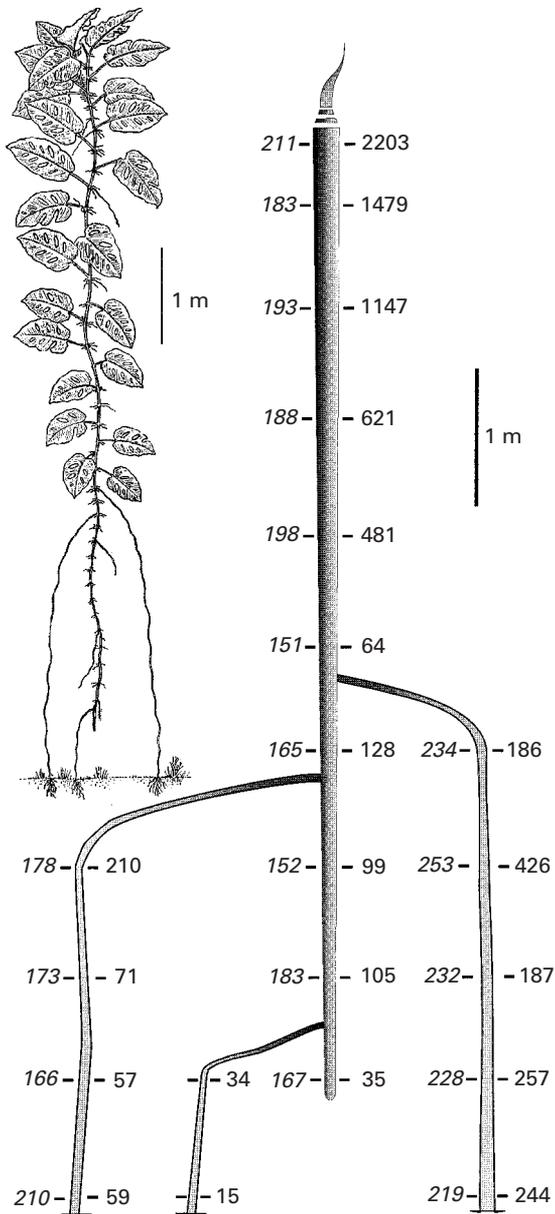


Fig. 4. Maximum vessel diameter (μm , left side, in italics) and leaf-specific conductivity (LSC in $10^{-6} \text{ kg m MPa}^{-1} \text{ s}^{-1} \text{ m}^{-2}$, right side) for one representative *Monstera acuminata* plant, including three adventitious feeding roots with soil contact. Note that the highest LSC values are towards the top.

The LSCs and maximum vessel diameters are mapped for the most extensive shoot-feeding root system we studied (Fig. 4). The difference in maximum vessel diameter between the lowest (most proximal) and highest stem sections was $44 \mu\text{m}$. Although the vessel diameters and LSCs tended to increase acropetally in stems, the patterns in roots were less clear.

Fig. 5 shows the increase in stele area, the number of vessels $> 80 \mu\text{m}$, the proportion of stained vessels, k_h and k_s along the root or stem path length in the largest plant in the data set (Figs 6d, 7d; 2.3 m^2 total leaf area). The trends shown were similar in the four plants analysed in this manner. It can be seen that

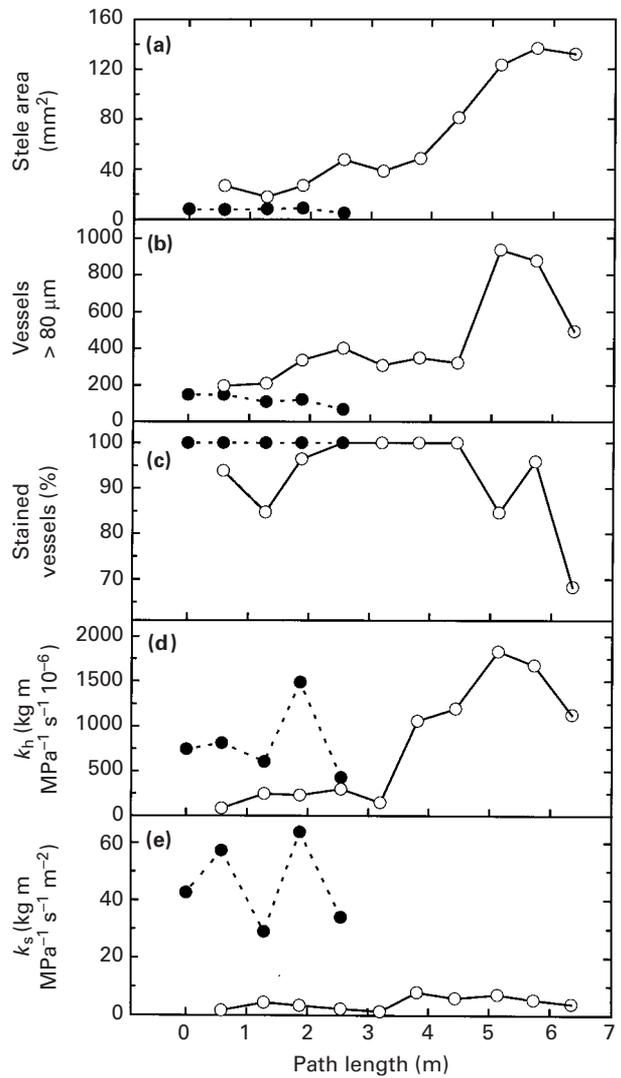


Fig. 5. Stele area, number of vessels with lumen diameters $> 80 \mu\text{m}$, percentage of stained vessels, hydraulic conductivity (k_h) and specific conductivity (k_s) as a function of plant length in feeding roots (closed symbols) and stem (open symbols) of one *Monstera acuminata* plant.

while stele area is mostly similar along the path of feeding roots, it increases steadily in the stem, attaining maximum values just before the plant tip (Fig. 5a). The number of wide vessels is comparatively smaller in feeding roots when compared to those of the stem, and increases acropetally in the stem, where it reached a peak *c.* 1 m before the tip (Fig. 5b). The 1% safranin was perfused through the segments. All vessels stained with safranin were assumed to be conductive. All vessels (100%) were stained in root segments and in the three stem segments distal to the point of insertion of the highest feeding root. At the position just below the insertion of this root, up to 15% of vessels in stem segments were not conductive. The decrease in stained vessels in the top metre of the stem was probably a consequence of their immaturity: most of their perforation plates were still intact (Fig. 5c). The decrease in both vessel number and number of

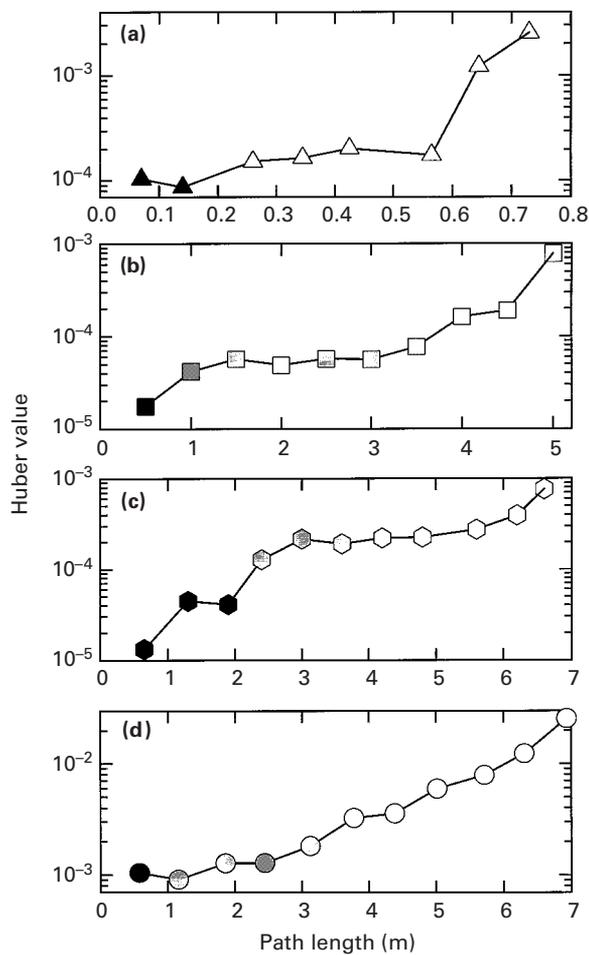


Fig. 6. Huber values along path length in four *Monstera acuminata* plants (indicated by different symbols) differing in height. Open symbols, stem parts; closed symbols, feeding root parts; grey symbols, sections of plants where roots and stem parts coincide.

stained vessels near the tip of the shoot corresponded with a decrease in k_h (Fig. 5d).

Comparing conductivity in root versus stem components of the plant, the k_h values were larger in the roots than in their stem segment counterparts. In the stem, the k_h values were smallest near the base and increased acropetally, especially at two segments above the insertion of the highest root. Thus, considering root plus stem k_h at each position along the path length, the smallest total k_h would be along that portion of the stem which is immediately above the insertion of the uppermost root. That area could represent a hydraulic constriction and was associated with low vessel diameters as well as with a low total number of vessels. Finally, k_s values (Fig. 5e) were variable but much greater in the root segments than in stem segments. In stems, k_s was lower in the more basal stem segments, but about twice as high in the more distal segments.

The relationships between Huber values and path length are shown for four *M. acuminata* plants (Fig. 6). Note the log scale of the y axis. Huber values increase exponentially from roots to stems (Fig.

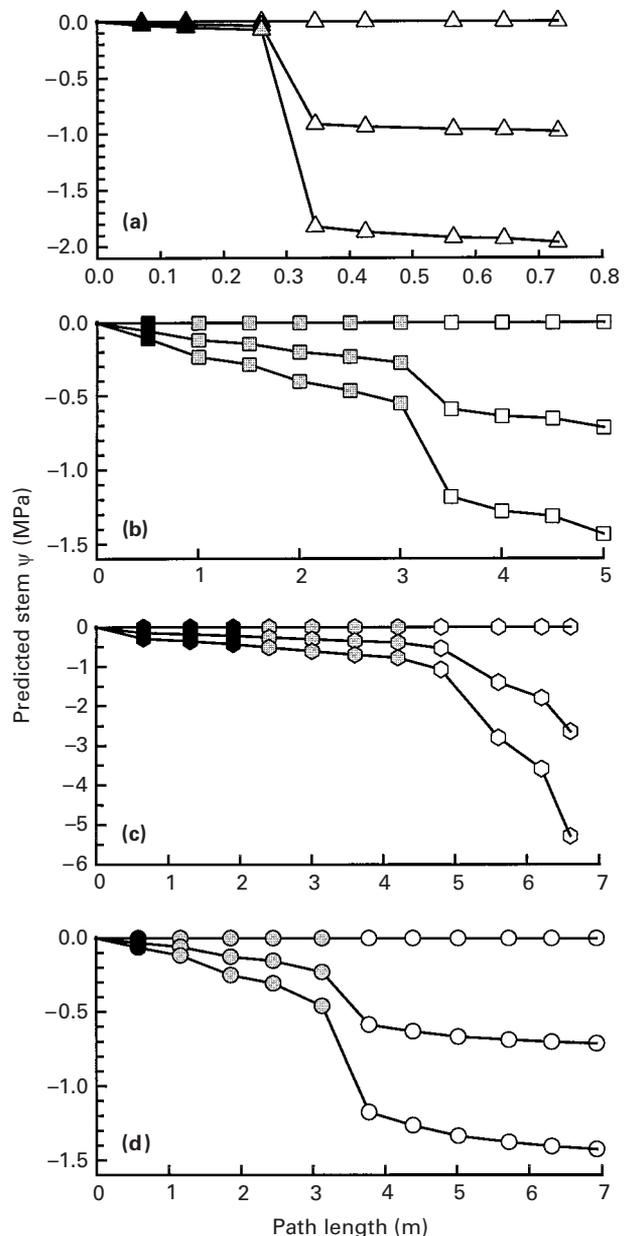


Fig. 7. Predicted stem xylem water potential (Ψ) along the feeding root–stem path in four *Monstera acuminata* plants of different sizes. Results are shown for three different transpiration rates ($E = 0, 3.5$ and $7 \times 10^{-8} \text{ m s}^{-1}$) taken from Ewers *et al.* (1989), and are based on leaf-specific conductivities (LSC) shown in Fig. 3. Open symbols, stem parts; closed symbols, feeding root parts; grey symbols, sections of plants where roots and stem parts coincide.

6a–d), indicating that much more axis cross-sectional area per leaf area is invested as the hemiepiphyte ascends the host.

Fig. 7 shows the predicted xylem water potential along the feeding roots and stem, based upon root plus stem LSCs of four individuals of *M. acuminata*. For transpiration rates > 0 , water potential (Ψ) decreased acropetally, but in three plants (Fig. 7a, b, d) there was a particularly steep dip in Ψ just after the insertion of the highest feeding root (last grey symbols in Fig. 7). The Ψ values in the roots as well

as in the higher stem segments decreased only gradually, as opposed to the steep drop in predicted water potentials in the lower stem just above the insertion of the uppermost root. The plant in Fig. 7c showed a different pattern, with steep drops in predicted water potentials occurring all along the stem, not just in the basal stem portions.

DISCUSSION

In conifers as well as in dicotyledonous trees and shrubs, it is well known that tracheid or vessel diameters increase in the basipetal direction from the top of the plant to the soil, as do k_n and k_s values (Zimmermann, 1983; Ewers & Zimmermann, 1984a,b; Tyree & Ewers, 1991, 1996). These patterns are reversed in *M. acuminata*, as are some other features of the hydraulic architecture of this secondary hemiepiphyte.

The LSCs may be the best measure of the hydraulic sufficiency of an axis in transporting water to its leaves. They can be analysed by the following relationship:

$$\text{LSC} = \text{Huber value} \times k_s$$

In conifers and dicotyledons, as stems and roots increase in diameter via secondary growth, they produce wider tracheids or vessels resulting in higher k_s values. By the pipe model theory of plant form (Shinozaki *et al.*, 1964), Huber values normally remain fairly constant at higher positions within the tree. Therefore it is not surprising that the largest LSCs are normally found in the stems with largest diameter, which are near the base of the plant. Exceptions occur, as in the coniferous tree *Abies balsamea*, where there is a sharp acropetal increase in Huber values in the central stem which counteracts the acropetal decrease in k_s values. The result in *A. balsamea* is that LSCs of the trunk can remain fairly constant up to the stem tip, and the trunk thus has a hydraulic advantage over lateral branches (Ewers & Zimmermann, 1984b). In *M. acuminata* not only is there a sharp acropetal increase in Huber values, there is also an acropetal increase in k_s values, both of which contribute to increased LSCs. This is the first report of a plant with acropetal increases in both k_s and Huber values, both of which increase the hydraulic sufficiency of the stem of *M. acuminata* as it ascends the host plant.

In common with previous reports in dicotyledonous trees, shrubs, lianas and primary hemiepiphytes, the stem diameter of *M. acuminata* is positively correlated with vessel diameter, k_n , LSC and k_s (Tyree *et al.*, 1983, 1991; Ewers *et al.*, 1990; Machado & Tyree, 1994; Yang & Tyree, 1994; Patiño *et al.*, 1995). An unusual feature of *M. acuminata* is that the stems show negative taper and so the wider stems are positioned further up the plant. To a lesser extent the aerial feeder roots also

show negative taper, and so they become wider further from the stem as they grow down towards the soil.

Monstera acuminata is not unique in showing inverse taper. In many plants, there is a progressive increase in primary tissues at the shoot tip during shoot growth. In gymnosperms and dicotyledons with inverse taper in their primary tissues (also termed 'establishment growth'; Bell, 1991), it is usually masked by secondary growth. In some plants inverse taper can be externally visible (e.g. stilt rooted palms), or masked by external roots (e.g. tree ferns) (Hallé *et al.*, 1978). In both cases the adventitious roots have both a mechanical and a hydraulic function. Unlike stilt palms and tree ferns *M. acuminata* overcomes its mechanical limitations by adhering to the host plant via anchoring roots. The feeder roots of *M. acuminata* lack mechanical function but their hydraulic conductivity overcomes the hydraulic limitation imposed by the lack of secondary growth.

Less is known about conductivity of roots than stems of angiosperms, but the results for *M. acuminata* are in agreement with the general rule that roots have wider vessels and higher k_s values than stems (Gartner, 1995). An exception is in lianas, where vessels are as wide, or wider, in stems than in roots (Ewers *et al.*, 1997a).

The various hydraulic architecture parameters measured in *M. acuminata* are within the range of values published in the literature for angiosperms (Tyree *et al.*, 1983, 1991; Shumway *et al.*, 1993; Yang & Tyree, 1994; Sobrado, 1997). Tyree & Ewers (1996) show the ranges in HV, LSC and k_s of several life forms of tropical and temperate plants based on stems 15 mm in diameter – this is in the size range of some of the wider stems, but not the roots, in our *M. acuminata* data set. However, the Huber values of the upper stems of *M. acuminata* were at the higher end of the range of Huber values previously reported for angiosperms. The k_s values of the larger roots were at the higher end of the range of k_s values reported for angiosperm stems, comparable to those found in the stems of tropical lianas. In contrast, all the stem k_s and LSC values of *M. acuminata* were in the lower half of the range reported for angiosperms, and well below those reported for liana stems.

There is little published information on vessel lengths in monocotyledons, but the results for *M. acuminata* are within the range reported for wide-vesselled dicotyledons including lianas and ring-porous trees. Also in common with results for dicotyledons, vessel length was correlated with vessel diameter (Zimmermann & Potter, 1982; Zimmermann, 1983; Ewers & Fisher, 1989b, Ewers *et al.*, 1990). The evolutionary reason for this correlation may be that the summation of vessel diameters to the fourth power is proportional to theoretical k_s , but

measured k_s could be limited also by vessel length. To make an analogy to tracheid systems (Gibson *et al.*, 1985), in narrow vessels the vessel width might limit k_s but in wider vessels the length might be more limiting.

Monstera acuminata, like most monocotyledons, lacks secondary growth. It has discrete vascular bundles and does not form a closed cylinder of vascular cambium. Plants with a closed vascular cambium (dicotyledons and conifers) increase their water conductance by the addition of new secondary xylem. As it grows from a shade-dwelling creeper to an erect climber, the water needs of *M. acuminata* must change dramatically, but the lack of secondary growth might be an evolutionary constraint. In this context, some of the peculiar features of the hydraulic architecture of this plant are not surprising, and they might be representative for other monocotyledonous hemiepiphytes. Secondary hemiepiphytes usually lose the original soil–stem contact, but not before adventitious feeding roots are active. Why does the basal portion of the stem die? As it is hydraulically limited relative to the newer parts of the plant, it may be of no further service. However, the control mechanisms for the death and decay of this plant part are unknown.

With the production of a progressively wider, more hydraulically efficient stem as it ascends the host plant, the basal part of the stem of *M. acuminata* becomes a hydraulic bottleneck. But could the bottleneck actually limit water relations? Transpiration data for *M. acuminata* are not presently available, so we used published transpiration rates from a liana (Ewers *et al.*, 1989) to model theoretical pressure gradients. We found that in three of the plants modelled, at maximum transpiration rates the stem segment just above the insertion of the uppermost feeder root showed a pressure drop of from 0.6 to 1.8 MPa, certainly enough to affect water relations in most mesophytic plant species.

What might be the impact of variations in the hydraulic architecture of individuals on their water relations? As an example, at maximum transpiration rates one of the four plants modelled (plant C, Figs 6 and 7) had sharp pressure drops all the way to the stem tip, with theoretical pressures dropping as low as -5 MPa, which is below the tolerance level of most mesic plants. In this case, the entire stem was effectively a bottleneck. Compared with other specimens of *M. acuminata* which were of comparable length, plant C had small Huber values in its stem, and only a very slightly negative taper (-1.22 mm m^{-1} vs a species mean of -3.69 mm m^{-1}). By analogy, in the conifer *A. balsamea* vigorous specimens have a much larger Huber value in the central leader than do slow-growing individuals (Ewers & Zimmermann, 1984b). Perhaps more shaded, slower-growing individuals of *M. acuminata* do not produce the thicker, more transport-efficient stems that are

needed in higher-transpiration environments. As a shaded climbing plant begins to reach a higher light environment, it can produce thicker, more hydraulically efficient stems at the top of the plant, with many new aerial roots. The models of the theoretical pressure gradients suggest that the upper stem segments must then be connected to the soil by means of one or more new feeder roots, in order to bypass the potentially lethal hydraulic constriction of the lower stem. When aroid hemiepiphytes are very suddenly exposed to a high light environment (e.g. due to felling of adjacent trees) they often die back very quickly, possibly because their hydraulic architecture is not prepared for a high light environment.

The root pressures found in *M. acuminata* during the rainy season, up to 225 kPa, are among the strongest root pressures reported in the plant kingdom. Positive root pressures were found in this study in all eight *M. acuminata* plants sampled during the rainy season. This is consistent with results from a survey which included this and many other tropical and subtropical species (Fisher *et al.*, 1997). As a caveat, the technique used in this study does not show what the pressures might have been in actively transpiring, intact plants. Severing the feeder roots shows only the pressures that can be attained if transpiration is eliminated, such as during rain and foggy weather (Sperry, 1983), or at night. In addition, root pressures could not be detected during the severe dry season of the 1998 El Niño Southern Oscillation. However, it is noteworthy that in a survey of root pressures all ten species of the Araceae sampled had positive root pressures (Fisher *et al.*, 1997). What is the significance of the positive root pressures in *M. acuminata* and other secondary hemiepiphytes? In addition to making the xylem pressures somewhat less negative than they might otherwise be in rapidly transpiring plants, the root pressures could have two roles: (1) rehydrating the stems when water is plentiful, which could then establish an important water storage (capacitance) for when water potentials decline; and (2) reversing embolisms (air blockages) in the xylem at night or during rainstorms.

(1) *Monstera acuminata*, like other members of the Araceae, has a rather succulent stem. During periods of water stress, such as during the dry season or when feeder roots are damaged, the plant may depend on water stored in its stem for survival. When water is plentiful in the soil, root pressures could allow parenchyma in the stems to become fully recharged at night or during rainstorms.

(2) If a vessel becomes embolized because of water stress, it may be critical for the plant to be able to repair that embolism. This is especially true in monocotyledons which lack secondary growth; unlike dicotyledons and conifers, monocotyledons cannot produce new vessels along the length of the

stem. The dyes used can give an assessment of embolism. We found that in *M. acuminata* during the rainy season, all along the length of the roots and for the stem segments just above the aerial roots, 100% of the vessels were conductive. Towards the growing tip of the stem some of the vessels were not conductive, a possible consequence of vessel immaturity. The lack of embolism in roots and lower stem segments above feeding roots may have been due to strong root pressure, an efficient mechanism for repairing embolisms in plants (Sperry *et al.*, 1987; Cochard *et al.*, 1994; Ewers *et al.*, 1997b).

The Araceae is a remarkable family. About 49% of all aroids are secondary hemiepiphytes and possess distinctive characteristics when compared with other life forms. It was in these hemiepiphytes that Strong & Ray (1975) found skototropism, and Moodie (1976) reported production of heat during anthesis. We have also found that *M. acuminata* has one of the highest root pressures yet reported. To these relatively rare phenomena another should be added: a reversal from known patterns in plant hydraulic architecture, with the aerial roots bypassing the major limitation of a lack of secondary growth.

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