

Murray's law, the 'Yarrum' optimum, and the hydraulic architecture of compound leaves

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Summary

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- There are two optima for maximizing hydraulic conductance per vasculature volume in plants. Murray's law (ML) predicts the optimal conduit taper for a fixed change in conduit number across branch ranks. The opposite, the Yarrum optimum (YO), predicts the optimal change in conduit number for a fixed taper.
- We derived the solution for YO and then evaluated compliance with both optima within the xylem of compound leaves, where conduits should have a minimal mechanical role. We sampled leaves from temperate ferns, and tropical and temperate angiosperms.
- Leaf vasculature exhibited greater agreement with ML than YO. Of the 14 comparisons in 13 species, 12 conformed to ML. The clear tendency towards ML indicates that taper is optimized for a constrained conduit number. Conduit number may be constrained by leaflet number, safety requirements, and the fact that the number of conduits is established before their diameter during development.
- Within a leaf, ML compliance requires leaf-specific conductivity to decrease from petiole to petiolule with the decrease in leaf area supplied. A similar scaling applied across species, indicating lower leaf-specific petiole conductivity in smaller leaves. Small leaf size should offset lower conductivity, and petiole conductance (conductivity/length) may be independent of leaf size.

Introduction

Interest in the link between carbon uptake and water loss has yielded numerous efforts to quantify the efficiency of the water transport network of plants (Banavar *et al.*, 1999; McCulloh *et al.*, 2003, 2004; McCulloh & Sperry, 2005a,b; Anfodillo *et al.*, 2006; Weitz *et al.*, 2006; Atala & Lusk, 2008). Much of this work has focused on the xylem tissue of woody stems, where the xylem conduits (vessels or tracheids) may be providing structural support to the plant in addition to transporting water. The additional support task compromises the potential hydraulic efficiency of water transport (McCulloh *et al.*, 2004). Within leaves, though, substantial structural support is provided by hydrostatic pressure and specialized nonvascular tissues such as collenchyma and sclerenchyma. To the extent that this nonxylary structural support holds up the leaf, this would theoretically leave the xylem conduits free to achieve their maximum transport efficiency. Assessing transport efficiency within the lamina is complicated by the typically reticulate

networks that are losing water to transpiration (Canny, 1993; McCulloh & Sperry, 2005b). By contrast, it is relatively easy to quantify network efficiency in compound leaves because the vascular tissue can be compared at discrete branching levels, the petiole and petiolule. Using these distinct levels in 13 species, we compared compliance with two theoretical optima that maximize the hydraulic conductance of this simple two-ranked vascular network.

The first optimum, Murray's law (ML), predicts how the conduit diameters should change across branching points of a vascular network so as to minimize the power (work/time) driving a given flow rate through a network of fixed total volume (Murray, 1926). As Sherman (1981) demonstrated, a Murray law network also maximizes the hydraulic conductance (volume flow rate per pressure drop). Maximizing conductance (rather than minimizing power at one flow rate) is undoubtedly the real adaptive significance of Murray's law, because a maximum-conductance network is optimal at all flow rates (Sherman, 1981). Murray's law was derived for the specific case of the

cardiovascular system which delivers blood through a single branching tube. The law states that conductance is maximized when the sum of the conduit radii cubed (Σr^3) is conserved at all points along the flow path from aorta to the beginning of the capillaries. Conservation of Σr^3 requires an increase in the cross-sectional area (Σr^2) from aorta to capillaries.

Unlike the cardiovascular system for which it was developed, Murray's law does not define the sole hydraulic optimum for the plant vascular system. In the cardiovascular system the branching of the vascular network equals the branching of a single tube. The ratio of the number of daughter-to-mother tubes (N_R) cannot be varied independently of the network branching structure. Murray's law gives the 'best' daughter-to-mother tube taper ratio (D_R) for the N_R dictated by branching architecture. The evolution of N_R is constrained by the need to deliver fluids spatially, and Murray's law D_R evolved to maximize the conductance of this mammalian vascular topography.

Xylem networks are more complex because they are composed of many conduits in parallel and in series at every branch level, including the trunk. That means that N_R is potentially independent of the branching network. When two daughter arteries join at the aorta, $N_R = 2$. When two petiolules each containing hundreds of conduits join at the petiole, N_R does not have to be 2. N_R can be any number greater than zero or less than the theoretical maximum for a petiole with just one conduit. Optimization of the network conductance is not just a matter of D_R , because N_R can also vary independently of the network branching topography.

The fact that there are at least two variables that are potentially free to vary across the branch junctions of plants means that there are at least two theoretical optima for maximizing conductance. The distinction between the two optima is shown graphically in Fig. 1. The contour lines on this figure are hydraulic conductances of a simple network with one petiole and two petiolules. The tubes within each branch rank are of constant diameter, and the total number of petiolule tubes is constant. All other parameters, including the volume of the network, are constant except for N_R and D_R .

The contours in Fig. 1 describe a diagonal ridge that ascends to greater conductance as N_R increases and D_R decreases. The ascent of the ridge corresponds to fewer, larger tubes in the petiole. The ridge cannot be ascended indefinitely because of limits on permissible values of D_R and N_R . The N_R reaches its maximum theoretical value when the petiole has just a single tube (N_R max on 'y' axis; McCulloh *et al.*, 2003). At $N_R = N_R$ max, the greatest conductance is achieved at the horizontal tangent of the conductance contour where D_R conforms to Murray's law (asterisk on ML diagonal in Fig. 1). This global optimum is represented by the cardiovascular system which is a single branched tube that approximates Murray law taper (Sherman, 1981).

Plants are never plumbed with a single branched tube and so are never at their N_R max. Negative sap pressures make a single-tube network vulnerable to complete failure in the event of a single air leak or cavitation event (Ewers *et al.*, 2007).

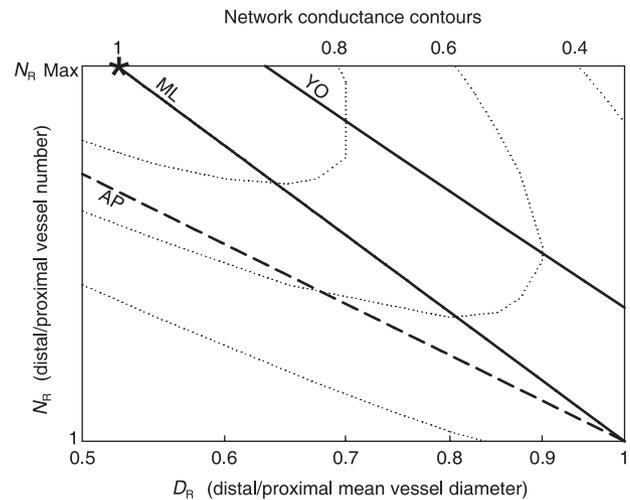


Fig. 1 'Contour map' showing how the conductance of a branch network with fixed vascular volume is influenced by the daughter-to-mother ratio of tube diameters (D_R) and numbers (N_R ; log-log plot). Conductance contours (upper x-axis, arbitrary units) were calculated for a network with one mother-daughter furcation using the reciprocal of Eqn 1. Volume (Eqn 2), lengths (l_0 and l_1), and number of daughter conduits (n_1) were held constant. Murray's law (solid ML diagonal) gives the D_R that maximizes network conductance when $N_R = \text{constant}$. The Yarrum optimum (solid YO diagonal) gives the N_R that maximizes conductance for $D_R = \text{constant}$. The very best conductance is given by the Murray law D_R for the theoretical maximum N_R , which corresponds to a single tube in the mother axis (asterisk on ML line at N_R max). Conduit area preservation (dashed AP diagonal) gives the D_R that results in constant conduit cross-sectional area across ranks.

Greater N_R also results in a greater departure of the xylem network from area preservation (Fig. 1; AP diagonal) towards area-increasing branching at Murray's law. Extreme increases in the cross-sectional area of conduits would result in top-heavy networks that could be mechanically unstable. Hydraulic and mechanical safety considerations combine to keep the N_R of plant xylem well below its theoretical maximum and potentially free to vary independently of the plant's branching system.

The alternative scenario to Murray's law for plant xylem is that D_R is more constrained than N_R for developmental or functional reasons. Such a constraint could result from a developmental link between vessel diameter and branch rank, or a limit to maximum vessel diameter. In this case, the 'best' network would have the minimum permissible D_R , and the greatest conductance would be achieved at the vertical tangent of the conductance contour where N_R conforms to the 'YO' diagonal. Because this optimum is the opposite of Murray's law, we call it the 'Yarrum' optimum (YO; Sperry *et al.*, 2008).

Here, we derive both Murray's law and the Yarrum optimum for a simple network composed of the conduits within a petiolule and two daughter petiolules of equal length. The derivations make explicit the distinction between the two optima. Following Sherman's example (1981), the optima are derived from a maximum conductance criterion because this is more biologically relevant than the equivalent minimum

power derivation. The series conductance of the network is represented as the reciprocal resistances (R), because they are additive in series. The Hagen–Poiseuille equation predicts:

$$R = \left(\frac{8\eta k}{\pi} \right) \left(l_0 n_0^{-1} r_0^{-4} + D_R^{-4} l_1 n_1^{-1} r_0^{-4} \right) \quad \text{Eqn 1}$$

where l is the axis length, n is the number of conduits in parallel, and r is the conduit radius, which is assumed constant within a rank. The subscript ‘0’ denotes petiole values, and subscript ‘1’ denotes the totals for the daughter petiolules. The D_R is r_1/r_0 . The mean radii of petiole or petiolule vessels are assumed to substitute for r_0 or r_1 , and mean petiolule vessel diameters are not expected to differ within a compound leaf when leaflets are of approximately similar size. Constant η is the fluid viscosity and k is the factor by which the resistivity exceeds the Hagen–Poiseuille prediction because of end-walls and other obstructions ($k \geq 1$). The volume, V , of this network is

$$V = \pi r_0^2 \left(l_0 n_0 + D_R^2 l_1 n_1 \right) \quad \text{Eqn 2}$$

Network volume is proportional to the conduit wall volume if wall thickness is proportional to conduit diameter (McCulloh & Sperry, 2006); the latter is approximately true for xylem of a given cavitation resistance (Hacke *et al.*, 2001). In both derivations, we hold the vascular investment, V , constant and solve for the minimum R under either Murray’s law or Yarrum conditions. To derive Murray’s law, we hold the numbers of conduits constant (n_0 and n_1) and vary the conduit taper (D_R) to find the value that minimizes R . Because volume (V) is constant, we must also allow r_0 to vary with D_R . We use the Lagrange multiplier method to find where $R(D_R, r_0)$ (Eqn 1) is minimized subject to the constraint that $V(D_R, r_0) = 0$, where we have subtracted a constant from Eqn 2 to set $V = 0$. At the minimum R , the Lagrange multiplier, λ , defines the two equalities (Edwards & Penney, 1998, p. 864):

$$\frac{\partial R}{\partial D_R} = \lambda \frac{\partial V}{\partial D_R} \quad \text{Eqn 3a}$$

$$\frac{\partial R}{\partial r_0} = \lambda \frac{\partial V}{\partial r_0} \quad \text{Eqn 3b}$$

From Eqns 1 and 2 the partial derivatives in Eqn 3 are:

$$\frac{\partial R}{\partial D_R} = -32\eta k \pi^{-1} l_1 n_1^{-1} r_0^{-4} D_R^{-5} \quad \text{Eqn 4a}$$

$$\frac{\partial V}{\partial D_R} = 2\pi l_1 n_1 r_0^2 D_R \quad \text{Eqn 4b}$$

$$\frac{\partial R}{\partial r_0} = -32\eta k \pi^{-1} r_0^{-5} \left(l_0 n_0^{-1} + l_1 n_1^{-1} D_R^{-4} \right) \quad \text{Eqn 4c}$$

$$\frac{\partial V}{\partial r_0} = 2\pi r_0 \left(l_0 n_0 + l_1 n_1 D_R^2 \right) \quad \text{Eqn 4d}$$

Substituting 4a and 4b into 3a yields

$$\lambda = -16\eta k \pi^{-2} n_1^{-2} r_0^{-6} D_R^{-6} \quad \text{Eqn 5}$$

Substituting λ , 4c and 4d into 3b, and simplifying, yields

$$D_R = (n_0/n_1)^{1/3}$$

or

$$D_R = N_R^{-1/3} \quad \text{Eqn 6}$$

for $N_R = n_1/n_0$. Equation 6 is Murray’s law for the special case where tubes within a rank are of equal diameter. However, we have previously shown that conservation of Σr^3 across branch points is within 3% whether computed from actual vessel distributions or their mean values (McCulloh & Sperry, 2006). Note that the lengths cancel out, indicating that the optimal taper is independent of branch lengths.

To find the Yarrum optimum, we hold the taper constant (D_R) and vary the relative numbers of conduits across ranks (varying n_0 for a constant n_1) to find the value that minimizes R . Because volume (V) is constant, we must allow r_0 to vary with n_0 . As before, we use the Lagrange multiplier method to find where $R(n_0, r_0)$ (Eqn 1) is minimized subject to the constraint that $V(n_0, r_0) = 0$. At the minimum R , the Lagrange multiplier, λ , defines the two equalities:

$$\frac{\partial R}{\partial n_0} = \lambda \frac{\partial V}{\partial n_0} \quad \text{Eqn 7a}$$

$$\frac{\partial R}{\partial r_0} = \lambda \frac{\partial V}{\partial r_0} \quad \text{Eqn 7b}$$

From Eqns 1 and 2 the partial derivatives in 7a are:

$$\frac{\partial R}{\partial n_0} = -8\eta k \pi^{-1} l_0 n_0^{-2} r_0^{-4} \quad \text{Eqn 8a}$$

$$\frac{\partial V}{\partial n_0} = \pi l_0 r_0^2 \quad \text{Eqn 8b}$$

The derivatives for 7b are 4c and 4d. Substituting 8a and 8b into 7a yields:

$$\lambda = -8\eta k \pi^{-2} n_0^{-2} r_0^{-6} \quad \text{Eqn 9}$$

Substituting λ , 4c and 4d into 7b, and simplifying, gives:

$$2D_R^{-4} + (l_0/l_1)(n_1/n_0) - D_R^2(n_1/n_0)^2 = 0 \quad \text{Eqn 10a}$$

or

$$2D_R^{-4} + L_R^{-1} N_R - D_R^2 N_R^2 = 0 \quad \text{Eqn 10b}$$

where the branch length ratio $L_R = l_1/l_0$. Using the quadratic formula to solve for N_R yields the following relevant root (the other root gives negative N_R ; signs in the valid root have been simplified):

$$N_R = \left[L_R^{-1} + (L_R^{-2} + 8D_R^{-2})^{1/2} \right] \left[2D_R^2 \right]^{-1} \quad \text{Eqn 11}$$

which is the Yarrum optimum. Note that the branch lengths do not cancel out, indicating that the optimal N_R depends on the relative lengths of the petiole and petiolule. The shorter the petiolules relative to the petiole (smaller the L_R), the fewer conduits they need in parallel (relative to the petiole) to minimize the total resistance (the smaller the optimal N_R). As L_R approaches zero, the lowest optimal N_R converges on $1.41 D_R^{-3}$. For typical $D_R < 1$, Yarrum's N_R will always exceed 1.4, meaning that petiolule conduits will always be more numerous than petiole conduits at the Yarrum optimum.

The existence of two hydraulic optima raises the question of what variable is most constrained during evolution and development. If the evolution of N_R is more constrained (as in the single-tube mammalian cardiovascular system where it is at N_R max), then the vascular conductance through the branching system can only be optimized by evolving the value of D_R predicted by Murray law. Alternatively, if the D_R and L_R are more constrained, then the vascular conductance through the branch system would be maximized by evolving the Yarrum optimum N_R . To date, the Yarrum optimum has not been recognized, or evaluated, in any system. To address the question of whether leaf vasculature follows Murray's law, or the Yarrum optimum, or conduit area preservation, or none of these patterns, we measured D_R , L_R , and N_R across the petiole vs petiolule ranks of compound leaves and compared them with the predictions. Leaves were studied in six tropical and five temperate angiosperm species, and in two temperate fern species. In addition to evaluating these two optima, we examined the evidence for size- and species-independent scaling patterns in the hydraulic architecture of leaves.

Materials and Methods

Plant material

Compound leaves were collected in the Republic of Panama in April 2005 and in the USA in September 2006 and July 2007. The six tropical species (Table 1) were collected in two seasonally dry tropical forest sites (9°N, 79°W). Three species with leaves exposed in the upper canopy, *Schefflera morototoni* (Aubl.) Maguire, Steyerl. & Frodin (Araliaceae), *Arrabidaea candidans* Dc. (Bignoniaceae), and *Serjania cornigera* Turcz. (Sapindaceae), were accessed using the Smithsonian Tropical Research Institute (STRI) Canopy Crane in the Parque Metropolitan, near Panama City. Leaves from three species growing in the understory, *Dalbergia retusa* Hemsl. (Fabaceae), *Paullinia pterocarpa* Triana & Planch. (Sapindaceae), and

Stizophyllum riparium (H.B. & K.) Sandwith (Bignoniaceae), were collected in Soberania National Park near Gamboa, Panama. The temperate angiosperms were *Daucus carota* L. (Apiaceae), *Rubus discolor* Weihe & Nees (Rosaceae), *Fragaria × ananassa* Duchesne (Rosaceae), *Sambucus caerulea* Raf. (Caprifoliaceae), and *Clematis armandii* Franch. (Ranunculaceae), and the temperate ferns used were *Adiantum pedatum* L. (Adiantaceae) and *Pteridium aquilinum* (L.) Kuhn (Dennstaedtiaceae). All temperate species were collected in and around Corvallis, OR, USA (45°N, 123°W; Table 1). When names were in conflict, International Plant Names Index conventions were followed (IPNI; <http://www.ipni.org/>).

Five leaves from one individual were sampled for each species. For all species, the ranks of petiolule and petiole were compared, except for *A. pedatum*, for which a third, more distal rank was also compared with the petiolule rank. For this species, only four leaves were measured.

For the tropical species, petioles and petiolules were stored in vials containing 50% ethanol and shipped to Oregon State University for sectioning and image analysis. Temperate species were sectioned in fresh condition. Total leaflet area was measured for each leaf using either a leaf area meter (Li-Cor 3100C; Li-Cor, Lincoln, NE, USA), or a flatbed scanner (Hewlett Packard Scanjet 6200C). Scanned leaf areas were measured using IMAGEJ (NIH, USA, <http://rsb.info.nih.gov/ij/>).

Anatomical measurements

Cross-sections were hand-cut near the midpoints of the petioles and petiolules using a sharp razor blade and stained with 0.5% toluidine blue or 0.5% safranin O to clearly distinguish the xylem vessels from surrounding tissues. Images of cross-sections were taken with a Photometrics Coolsnap camera (Tucson, AZ, USA) mounted on a Nikon Eclipse E400 microscope connected to a PC using METAVUE software (Universal Imaging Corp., Downingtown, PA, USA). For all species except *S. morototoni*, all vessels in the petioles and petiolules from all five leaves were measured. Vessel cross-sectional area measurements were made on the images using IMAGEJ, and from these measurements the radius (r) of each vessel was calculated as the radius of a circle with the same area.

The large number of vessels in the petioles and petiolules of *S. morototoni* leaves made it necessary to determine the average conduit number and diameter per vascular bundle area on a subsample and scale up to the whole cross-section from its total bundle area. Every fifth bundle around the circumference of the cross-section was measured to obtain the average number and diameter of conduits per vascular bundle area.

Length ratio measurements

The ratio of petiolule:petiole lengths (L_R) was determined in order to estimate the Yarrum optimum N_R (Eqn 11). Species-specific

Table 1 Abbreviations used in figures and characteristics of the species examined (tropical angiosperms, temperate angiosperms and temperate ferns are grouped separately)

Species	Abbr.	Habit and habitat ^b	Petiole vessel D (μm) (\pm SD) ^c	Petiolule vessel D (μm) (\pm SD)	L_R (\pm SD) ^d	N_R (\pm SD) ^e	YO predicted N_R^f	D_R (\pm SD)	ML predicted D_R^g	ML ^h	Leaf type ⁱ
<i>Arrabidaea candicans</i>	AC	L, Tr	18.2 (1.7)	14.6 (0.9)	0.47 (0.07)	2.9 (0.3)	4.5	0.83 (0.05)	0.70	$P = 0.70$	Palm
<i>Dalbergia retusa</i>	DR	T, Tr	21.0 (1.2)	10.5 (0.8)	0.13 (0.03)	3.7 (0.1)	35.9	0.50 (0.01)	0.65	$P < 0.001^*$	Pinn
<i>Paullinia pterocarpa</i>	PP	L, Tr	17.4 (1.6)	14.5 (1.1)	0.12 (0.01)	1.8 (0.2)	12.6	0.83 (0.04)	0.83	$P = 0.13$	Pinn
<i>Schefflera morototoni</i>	SM	T, Tr	53.9 (2.3)	33.8 (1.7)	0.09 (0.01)	6.0 (0.3)	28.4	0.63 (0.01)	0.55	$P < 0.01^*$	Palm
<i>Serjania cornigera</i>	SC	L, Tr	22.4 (2.5)	16.8 (1.0)	0.15 (0.01)	2.4 (0.1)	13.1	0.74 (0.02)	0.74	$P = 0.18$	Palm
<i>Stizophyllum riparium</i>	SR	L, Tr	21.7 (1.2)	15.2 (1.2)	0.70 (0.03)	2.8 (0.2)	5.5	0.72 (0.02)	0.71	$P = 0.10$	Palm
<i>Clematis arandii</i>	CA	L, Te	17.2 (1.4)	12.8 (1.1)	0.36 (0.08)	1.8 (0.2)	7.2	0.73 (0.04)	0.83	$P = 0.34$	Palm
<i>Daucus carota</i>	DC	H, Te	15.1 (0.4)	12.3 (1.7)	0.13 (0.04)	1.3 (0.1)	11.4	0.86 (0.02)	0.91	$P = 0.41$	Palm
<i>Fragaria</i> \times <i>ananassa</i>	FA	H, Te	7.7 (0.9)	6.1 (0.5)	0.03 (0.01)	2.3 (0.3)	46.9	0.79 (0.04)	0.76	$P = 0.08$	Palm
<i>Rubus discolor</i>	RD	S, Te	18.8 (1.0)	11.6 (0.5)	0.18 (0.04)	3.2 (0.6)	15.9	0.63 (0.03)	0.68	$P = 0.17$	Pinn
<i>Sambucus caerulea</i>	SaC	T, Te	21.9 (4.0)	13.1 (2.0)	0.13 (0.02)	3.3 (0.4)	24.3	0.59 (0.02)	0.67	$P = 0.49$	Pinn
<i>Adiantum pedatum</i>	AP	F, Te	22.4 (1.4)	16.7 (1.8)	0.06 (0.02)	1.5 (0.3)	26.3	0.79 (0.06)	0.87	$P = 0.14$	Palm
<i>Adiantum pedatum</i> * ^a	AP* ^a	F, Te	16.7 (1.8)	15.4 (1.5)	0.70 (0.12)	1.3 (0.1)	2.9	0.92 (0.01)	0.92	$P = 0.46$	Palm
<i>Pteridium aquilinum</i>	PA	F, Te	31.2 (5.3)	25.1 (2.3)	0.09 (0.06)	1.7 (0.1)	18.0	0.80 (0.07)	0.84	$P = 0.84$	Pinn

^aThe asterisk here indicates that, for *Adiantum pedatum*, one rank distal to the petiolule rank was measured in addition to the petiole and petiolule ranks. For this comparison, the petiolule value for vessel diameter is listed under 'petiole,' because it is more basal than the third rank, which is treated as the 'petiolule'.

^bAbbreviations for the habit and habitat: L, liana; T, tree; S, shrub; H, herbaceous plant; F, fern; Tr, tropical; Te, temperate.

^cPetiole and petiolule vessel diameters (D) are the grand mean of the average diameters of the $n = 5$ ($n = 4$ for *A. pedatum*) leaves from each species.

^d L_R is the median ratio for each species of the length of the petiole:petiolule shoots.

^e N_R , the ratio of the number of conduits in the petiolule: petiole, and D_R , the ratio of the mean conduit diameter in the petiolule: petiole, are the median of the ratios from $n = 5$ ($n = 4$ for *A. pedatum*) leaves.

^fThe optimal N_R predicted by the Yarrum optimum (YO) based on the observed D_R .

^gThe optimal D_R predicted by Murray's law (ML) based on the observed N_R .

^hCompliance with ML is based on whether the sum of the conduit radii cubed in petiolules was different from that in petioles as indicated by P -values from paired t -tests greater than 0.05.

Asterisks indicate the two species that deviated from the ML optimum.

ⁱThe compound leaves were separated into pinnate (Pinn), which have a rachis, and palmate (Palm), which do not.

length ratios were estimated from measurements on live material, herbarium sheets of pressed plants, or both. The lengths of petioles and petiolules from four to eight leaves were measured for each species.

Data analysis and statistics

To test whether plants more closely complied with the Murray's law or the Yarrum optimum, the mean predicted error was calculated for each relationship. The mean predicted error from the YO optimum was calculated from the absolute value of the difference: (measured N_R /optimal N_R) - 1 summed across all species. The optimal N_R was calculated from the median D_R and L_R for each species from Eqn 11. The median ratios were used rather than the mean to avoid bias created by the averaging of ratios (Lawren Sack, pers. comm.; Packard & Boardman, 1988; Jasienski & Bazzaz, 1999). The analogous mean square error was calculated for the ML optimum from the difference: (measured D_R /optimal D_R) - 1. The optimal D_R was calculated from the median N_R for each species from Eqn 6. A mean predicted error was also calculated for the deviation of median D_R from the value required for area-preserving branching ('AP', conserved conduit lumen area). In this case the difference was the following: (measured $D_R/D_{R,AP}$) - 1, where $D_{R,AP}$ is the diameter ratio that conserves lumen area for a particular N_R (i.e., $D_R = N_R^{-1/2}$).

Species-specific compliance with the Murray's law optimum was also evaluated by testing the extent of Σr^3 conservation (r = conduit radius) between the ranks of the petiole and the petiolule (McCulloh *et al.*, 2003, 2004). For each leaf and rank, the Σr^3 /distal leaf area was multiplied by the total leaf area of all five leaves for that species. This provided five estimates of the combined Σr^3 for each rank in each species. Cubing the vessel radii strongly skewed the data, so the Σr^3 values were log transformed for statistical analyses. The similarity between the total rank Σr^3 values was assessed using a paired t -test. If the P -value was > 0.05 , Murray's law could not be rejected for that species. The equivalent test for compliance with YO was not possible because of the complexity of the YO optimum (Eqn 11).

Reduced major axis (RMA) regressions were used to compare leaf traits. The slopes were calculated from ordinary least squares (OLS) regression slopes as: RMA slope = OLS slope/ R , where R is the correlation coefficient. RMA intercepts were calculated as $Y - \text{RMA slope } X$, where Y is the mean log y -axis value and X is the mean log x -axis value (Quinn & Keough, 2002). Slope values and y -intercepts from intraspecific comparisons were determined to be different from the pooled, interspecific comparisons when the 95% confidence intervals did not overlap.

Results

On the landscape of possible D_R vs N_R combinations, the species clustered more closely around the ML (Murray's law;

Fig. 2a) optimum than the YO one (Yarrum optimum; Fig. 2b). The RMA regression of the observed D_R vs the Murray predicted D_R was not significantly different from the 1 : 1 line (slope = 1.08). The corresponding regression for observed N_R vs the Yarrum predicted N_R was significantly different from the 1 : 1 line (slope = 0.12), with measured N_R falling far short of the YO optimum. Greater agreement with ML was also supported by the much smaller mean predicted error for the ML optimum than the YO alternative (1.1 vs 10.9, respectively). For the individual species, Murray's law could not be rejected for 11 of the 13 species measured (Table 1). The comparison of the petiolule versus the third rank in *A. pedatum* also was consistent with ML. The two species that deviated from ML were tropical tree species (*S. morototoni* and *D. retusa*). The former had less conduit taper than predicted by ML, and the latter exhibited more taper than the optimum and was quite close to the area-preserving line (Fig. 2c).

Consistent with the tendency towards Murray's law, the data generally fell above the area-preserving line (Fig. 2c). Although the slope of the RMA regression in Fig. 2(c) was not significantly different from the area-preserving slope of 1, the y -intercept was marginally greater than zero, which indicated that the lumen cross-sectional area summed across the petiolule rank was greater than in the petiole for most species. The mean predicted deviation from the AP line was also greater than for the ML optimum (2.0 vs 1.0, respectively). This increase in area occurred despite the decline in vessel diameters from the petiole to petiolule ranks, because the number of vessels increased (Table 1). Area-increasing conduit branching is predicted for Murray's law when $N_R > 1$.

Of most consequence to the plant is how much a given deviation from ML or YO anatomy costs in terms of lost conductivity per investment. Again, ML appears to define the more relevant optimum. Species averaged $97 \pm 5\%$ of the peak conductivity at ML (Fig. 3) vs $47 \pm 26\%$ of the YO value (not shown). Of the two species that deviated statistically from ML anatomy (*S. morototoni* and *D. retusa*), in only one of them did this result in a sizable deviation from ML conductance (Fig. 3; 82% of optimum). Interestingly, this species (*D. retusa*) fell close to the area-preserving condition (Fig. 2c). Excluding *D. retusa*, species averaged $98 \pm 2\%$ of their ML conductivity.

The general agreement with ML suggests that, within a species, D_R adjusts to a 'preset' value of N_R rather than vice versa as would be the case for the Yarrum optimum. In all species, N_R exceeded the often assumed value of 1 (West *et al.*, 1997), ranging from 1.3 in the more distal comparison of *A. pedatum* to ~ 6 in *S. morototoni*, and with a median of 2.4 ± 0.4 (Figs 2b, 4). An advantage of $N_R > 1$ is that, for a given leaf structure and vascular volume, the larger the N_R the greater the conducting efficiency at Murray's law (Fig. 1; McCulloh *et al.*, 2003). Variation in N_R between species was at least in part related to differences in leaf structure:

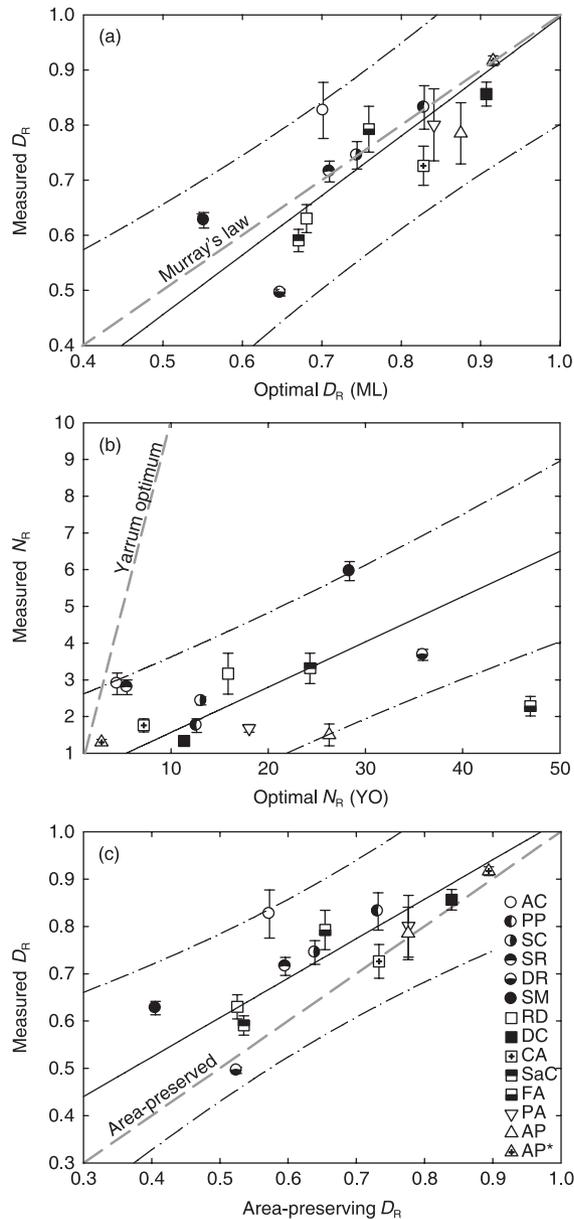


Fig. 2 (a) The median measured D_R , which is the ratio of the mean vessel diameter in petiules: petiole, versus the D_R predicted by Murray's law (ML). The solid line indicates pooled reduced major axis (RMA) regression (slope = 1.08, $R^2 = 0.62$) with dash-dotted 95% confidence intervals. The gray dashed line is the 1 : 1 ML optimum. The asterisks designate the two species that deviated significantly from ML (Table 1). (b) The median measured N_R , which is the ratio of the number of vessels in petiules: petiole, vs the optimum N_R predicted by the Yarrum optimum (YO). The solid line indicates the pooled RMA regression (slope = 0.12, $R^2 = 0.52$) with dash-dotted 95% confidence intervals, and the dashed line is the 1 : 1 YO optimum. (c) The median measured D_R vs the D_R that would result in conduit area preservation between the petiule and petiole. The solid line shows the pooled RMA regression (slope = 0.83, $R^2 = 0.64$) with dash-dotted 95% confidence intervals. The dashed gray line is for area-preserved branching of the vascular network. Error bars on symbols represent standard deviations from the medians among $n = 5$ leaves (or $n = 4$ for *Adiantum pedatum*). Species abbreviations are defined in Table 1.

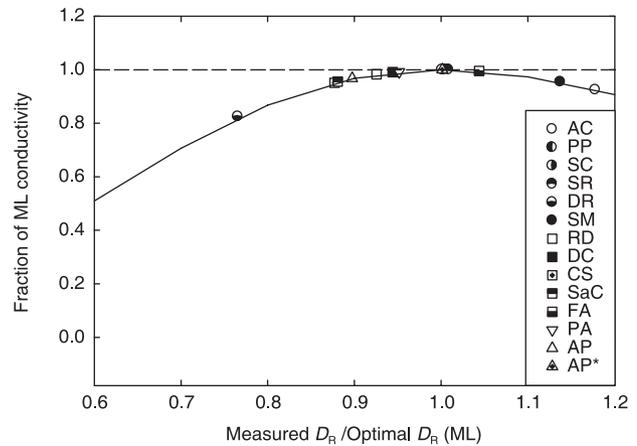


Fig. 3 The fraction of the maximum possible network conductivity for Murray's law (ML) vs the ratio of the measured D_R , which is the ratio of the mean vessel diameter in the petiule: petiole, to the ML predicted optimum D_R . The solid curve shows the shape of the optimum, calculated for the two-rank network depicted in Fig. 1 for $N_R = \text{constant}$. N_R is the ratio of the number of conduits in petiules: petiole. The curve is essentially independent of the particular N_R value. Species conductivities for the same two-rank (petiole–petiule) network were calculated using their measured N_R value, and comparing conductivity for the observed vs the Murray law D_R . Species abbreviations are defined in Table 1.

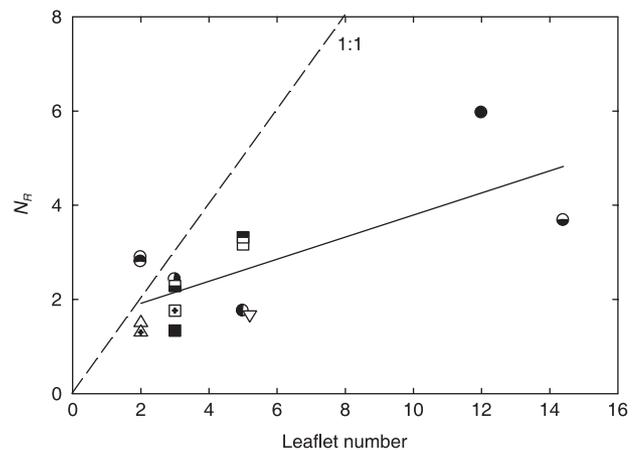


Fig. 4 The median ratio of the number of vessels in petiules: petiole for each species (N_R) versus the average number of leaflets. The dashed line shows the 1 : 1 relationship and the solid line shows the regression of the data. Regression analysis showed that the slope was different from 0 (slope = 0.23; P -value < 0.001; $R^2 = 0.51$). Symbol markings are defined in Fig. 2 for each species, and symbol shapes are: circles, tropical species; squares, temperate angiosperm species; and triangles, temperate fern species. Error bars are not shown for simplicity, but standard deviations in the number ratio are the same as in Fig. 2 and deviation in the average leaflet number ranged from 0 to 9%.

species with more leaflets per leaf tended to have greater N_R (Fig. 4).

Conduit number also scaled significantly with leaf and leaflet area within most species, and also across species (Fig. 5a). In order for N_R to be > 1 across petiole to petiule ranks, the

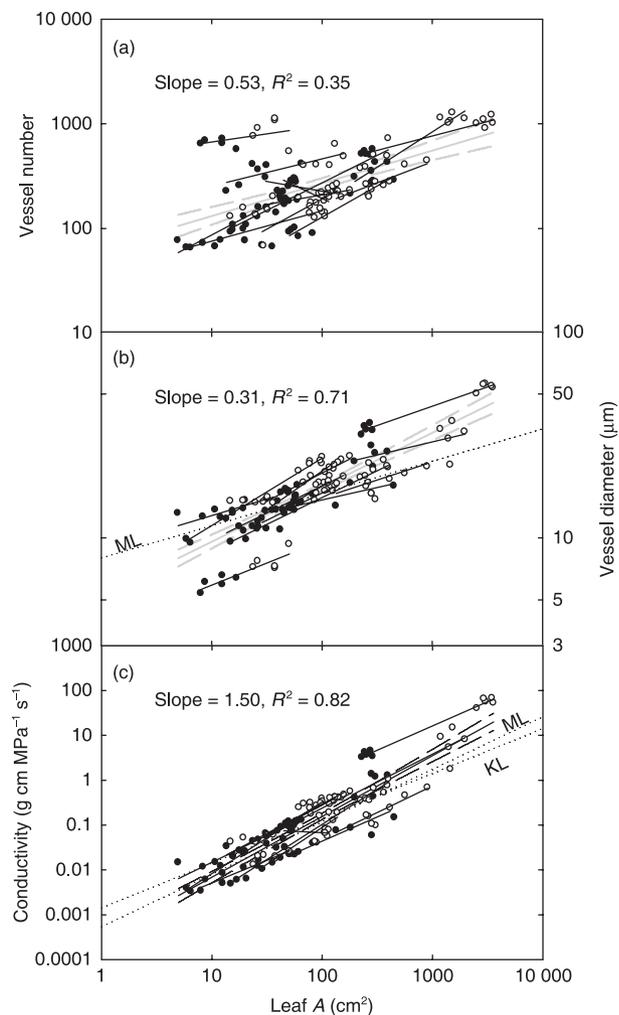


Fig. 5 Intra- and interspecific log–log scaling of petiole and petiolule vasculature with the area of the leaf or leaflet (A) supplied. (a) Number of vessels, (b) the mean diameter of vessels, and (c) the theoretical hydraulic conductivity of petioles and petiolules. Petiole and leaflet data are averages per leaf. Conductivity was calculated from mean vessel diameter and number using the Hagen Poiseuille equation. Solid black lines show intraspecific regressions across petiole (open symbols) and petiolule (closed symbols) ranks. Statistics of these intraspecific regressions are shown in Table 2. Solid gray lines show pooled regressions with 95% confidence intervals (dashed lines). In (b) and (c), the dotted lines show the scaling required for Murray's law ('ML'; see Appendix). In (c), the scaling is also shown for invariant leaf-specific conductivity across leaf size ('KL').

number of conduits must decrease *less* than the drop in leaf area moving from whole leaf to leaflet. Hence, the species-specific regressions of conduit number vs leaf and leaflet area supplied followed power functions with an exponent of < 1 (Fig. 5a; species log–log regressions, all slopes < 1), which is the value required for $N_R = 1$ (Appendix, Eqn A2). Exponents varied from -0.7 to 0.8 (Table 2), with the variation in part reflecting the different numbers of leaflets in the different species (Fig. 4). The negative exponents, for example, corresponded

to the species with the fewest leaflets per leaf (*A. candicans* and *S. riparium*). There was also significant variation between species in the number of conduits for a given leaf area, as indicated by significant differences in the intercepts of the log–log relationships (Table 2). Pooling across all species indicated a significant increase in conduit number with area supplied with an exponent of 0.53. The low R^2 of this pooled regression (0.35) reflects the variation in slopes and intercepts between species: four of the 13 species had slopes significantly different from the pooled regression, and nine species had different intercepts (Table 2).

Average vessel diameter also scaled significantly with leaf area supplied both within and between species (Fig. 5b). Species-specific scaling exponents ranged from 0.1 to 0.4, which corresponds well with the 0.1 to 0.6 range predicted for Murray's law from the N_R scaling in Fig. 5(a) (Appendix, Eqn A7). The pooled data exhibited an exponent of 0.31 for diameter vs leaf area scaling, deviating slightly from the 0.16 value for perfect ML compliance across species (Fig. 5b, dotted ML line; Appendix, Eqn A7). The R^2 of 0.71 for the pooled regression suggests greater convergence of intra- and interspecific scaling for conduit diameters than for conduit numbers (Fig. 5a). Only three of the 13 species had slopes different from the pooled value, and three species had different intercepts (Table 2).

The greatest convergence between intra- and interspecific scaling was in the calculated conductivity vs leaf area (Fig. 5c). Petiole or petiolule theoretical conductivity scaled with leaf area supplied to the 1.50 power across species (Fig. 5c; Table 2). The relatively high R^2 of 0.82 for the pooled regression reflected the fact that only one of 13 species deviated from the pooled regression for slope and one for intercept. The pooled slope of 1.50 is greater than the exponent of 1 for conductivity increasing in direct proportion to leaf area (Fig. 5c; dotted 'KL' line for constant leaf-specific conductivity). An increase in leaf-specific conductivity with leaf area was consistent with the general compliance with ML, which predicts a conductivity vs leaf area exponent of 1.16 (Fig. 5c, ML line; Appendix Eqn A10). Computing conductivities on the basis of the actual conduit distributions rather than the average conduit diameter did not change the indication that conductivity increases disproportionately with leaf area ($R^2 = 0.83$, slope = 1.23; not shown).

Discussion

Compound leaves from a wide range of species complied more closely with Murray's law (ML) than with the Yarrum optimum (YO; Fig. 2a vs 2b). Only two species deviated statistically from ML (Table 1), but even the greatest deviant (*D. retusa*) was within 18% of the broad optimal ML conductivity (Fig. 3; Sherman *et al.*, 1989). These results suggest that vessel diameter ratio (D_R) 'tunes' to a constrained number ratio (N_R) and not vice versa. This sequence makes sense for several reasons. First, the number of conduits (hence N_R) is determined much earlier in development than conduit

Table 2 The slope, R^2 values and y -intercepts from the reduced major axis regressions shown in Fig. 5

Species	Vessel number vs leaf area			Vessel diameter vs leaf area			Theoretical conductivity vs leaf area		
	Slope (\pm CI) ^a	R^2	y -intercept	Slope (\pm CI)	R^2	y -intercept	Slope (\pm CI)	R^2	y -intercept
<i>Arrabidaea candicans</i>	-0.68 (0.38)^b	0.54	3.63	0.36 (0.13)	0.81	0.53	-0.85 (0.68)	0.82	0.43
<i>Dalbergia retusa</i>	0.53 (0.08)	0.97	1.37	0.26 (0.02)	0.99	0.67	1.57 (0.11)	0.99	-4.13
<i>Paullinia pterocarpa</i>	0.62 (0.12)	0.94	0.87	0.14 (0.06)	0.71	0.90	1.14 (0.21)	0.97	-3.64
<i>Schefflera morototoni</i>	0.28 (0.05)	0.96	2.04	0.19 (0.02)	0.98	1.07	1.09 (0.09)	0.99	-2.05
<i>Serjania cornigera</i>	0.21 (0.09)	0.72	1.90	0.28 (0.05)	0.95	0.76	1.29 (0.18)	0.97	-3.20
<i>Stizophyllum riparium</i>	-0.54 (0.42)	0.11	3.38	0.43 (0.17)	0.76	0.48	1.41 (0.42)	0.87	-3.36
<i>Clematis armandii</i>	0.82 (0.48)	0.49	0.68	0.30 (0.11)	0.80	0.63	1.73 (0.47)	0.89	-4.50
<i>Daucus carota</i>	0.62 (0.23)	0.79	1.30	0.22 (0.13)	0.52	0.88	1.42 (0.63)	0.71	-3.28
<i>Fragaria × ananassa</i>	0.39 (0.29)	0.16	2.37	0.24 (0.09)	0.80	0.52	1.08 (0.32)	0.87	-3.40
<i>Rubus discolor</i>	0.32 (0.16)	0.64	2.04	0.29 (0.09)	0.85	0.69	1.35 (0.27)	0.94	-3.22
<i>Sambucus caerulea</i>	0.35 (0.16)	0.70	1.50	0.33 (0.04)	0.98	0.73	1.63 (0.26)	0.96	-3.73
<i>Adiantum pedatum</i>	0.47 (0.24)	0.74	1.26	0.29 (0.23)	0.36	0.55	1.60 (1.07)	0.55	-4.72
<i>Pteridium aquilinum</i>	0.70 (0.13)	0.95	0.84	0.20 (0.13)	0.40	0.88	1.43 (0.58)	0.76	-3.68
Pooled	0.53 (0.08)	0.35	1.38	0.31 (0.03)	0.71	0.62	1.50 (1.12)	0.82	-3.79

^aThe 95% confidence intervals (CIs) of the slope are indicated in parentheses.

^bBold typeface indicates that the slope or y -intercept deviated from the pooled values.

diameter (hence D_R). Yarrum's N_R also depends on the ratio of petiolule-to-petiole length (L_R), which like D_R is determined fairly late in development. Secondly, although plants cannot achieve the theoretical N_R max of a maximally efficient single-tubed vascular network, they may have evolved to achieve the 'next best' N_R within species-specific constraints of leaflet number (Fig. 4) and considerations of transport safety and redundancy. Finally, achieving the Yarrum optimum requires an even more extreme area-increasing branching of conduits than Murray's law (Fig. 1), which may not be possible within the confines of petiole/petiolule architecture. Although it is known that vessel diameters increase basipetally as the vascular auxin concentration declines (Aloni & Zimmermann, 1983), how the plant develops the particular ML diameter ratio is unknown.

Conduits within woody stems tend to be closer to area preserving than the ML optimum, suggesting that the need to avoid top-heavy networks constrains the hydraulic efficiency of trees (McCulloh *et al.*, 2004; Atala & Lusk, 2008). It is worth noting that this area preservation is not da Vinci's rule, which refers to preservation of the total cross-sectional area of branches, not their internal conducting tubes (Horn, 2000). Interestingly, the compound leaf that deviated most significantly from Murray's law (leaves of *D. retusa*; Fig. 2a) was fairly close to the area-preserving line (Fig. 2c). This species had 12–14 leaflets arranged pinnately on a long, rigid axis and perhaps relied more than other species on its xylem conduits for mechanical support. This reliance may have prevented area-increasing branching of vessels which otherwise would have been more hydraulically efficient.

Givnish (1978) suggested that a benefit of compound leaves was as 'throw-away branches' that could achieve the same area

as simple leaves for a smaller investment in woody biomass. Here, we propose that, by following Murray's law more closely than stems, compound leaves are also more hydraulically efficient than the equivalent stem structure. The efficiency is achieved by a greater uncoupling of mechanical support from hydraulic supply, which allows the conduit network to be area-increasing as required for the most efficient Murray law networks.

Intraspecific scaling of the petiole–petiolule network with leaf area did not carry over precisely to a single universal interspecific scaling (Fig. 5). The most variation between species was in how the number of conduits scaled with leaf area (Fig. 5a). However, consistent with N_R being > 1 , all intraspecific exponents were < 1 ; as was the pooled exponent (Table 2). Diameter scaled more consistently across species with leaf area, but still with significant interspecific variation (Fig. 5b). This result is consistent with the strong degree of scaling between the hydraulically weighted vessel diameter and leaf area observed by Coomes *et al.* (2008) across multiple vein orders in leaves of various oak species. The variation in diameter scaling observed in our data partially compensated for variation in conduit number, because theoretical conductivity (calculated from diameter and number) exhibited a fairly strong interspecific relationship with leaf area (Fig. 5c). Actual conductivity tends to be proportional to the theoretical value (Sperry *et al.*, 2006; Choat *et al.*, 2008). These data imply that leaf-specific conductivity of petioles increases with leaf area, a trend consistent with following Murray's law. Experimental data on hydraulic conductivities measured in petioles of simple leaves are consistent with this trend (Sack *et al.*, 2003).

Unlike petiole conductivity, petiole conductance (= conductivity/length) may be relatively invariant with leaf size

because petioles tend to be longer in larger leaves (Niklas, 1994; Sack *et al.*, 2003). A recent survey found that petiole length scaled with leaf area to approximately the 0.5 power (Arcand *et al.*, 2008). Combination of this with the 1.5 scaling of conductivity (Fig. 5c) would predict that petiole conductance scales isometrically with leaf area as does lamina conductance (Sack *et al.*, 2003). Variation in conductivity or conductance by leaf area scaling may be related in part to light environment and the prevailing evaporative gradient, with sunlit leaves or leaves in drier air developing greater conductivity for a given leaf area than shaded leaves or leaves in humid air (Sack *et al.*, 2003).

The petioles and petiolules of compound leaves are discrete branching ranks that provide an opportunity to examine compliance with two distinct optima that both maximize hydraulic conductance per investment in vascular tissue volume. The Yarrum optimum does not seem to represent an achievable optimum, suggesting that N_R is more constrained than D_R in the evolution and development of the leaf vasculature. Most species tracked the alternative Murray law optimum. Convergence on a hydraulic optimum suggests the importance of hydraulic efficiency for maximizing plant fitness. Deviations from the ML optimum in some leaves and in most stems tend to approach the alternative area-preserving behavior, a more adaptive alternative when the xylem conduits are called upon to supply mechanical support in addition to water.

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Appendix: Relations between scaling exponents in Fig. 5

Figure 5(a) shows that the number of conduits (N) is proportional to leaf or leaflet area (A) to the 'x' power:

$$N \propto A^x \quad \text{Eqn A1}$$

Accordingly, the number of conduits per petiole/number of conduits per petiole $\approx (A_i/A_L)^x$, where A_i is the average leaflet area and A_L is the whole leaf area. The approximation is because mean leaflet area is used and the proportionality in Eqn A1 is estimated from a regression. Multiplying $(A_i/A_L)^x$ by the number of petioles ($\approx A_L/A_i$) yields

$$N_R \approx (A_i/A_L)^x (A_L/A_i) \quad \text{Eqn A2.}$$

Using $A_R = A_i/A_L$,

$$N_R \approx A_R^{(x-1)} \quad \text{Eqn A3.}$$

Because $A_R < 1$, it is clear that for $N_R > 1$ as observed, x must be < 1 .

Fig. 5(b) shows that the average diameter of conduits (D) is proportional to leaf area to the 'y' power:

$$D \propto A^y \quad \text{Eqn A4.}$$

This yields

$$D_R \approx (A_i/A_L)^y \approx A_R^y \quad \text{Eqn A5}$$

From Eqn 6, $N_R = D_R^{-3}$ at Murray's law. Equating A3 and A5 at Murray's law gives:

$$A_R^{(x-1)} \approx A_R^{-3y} \quad \text{Eqn A6}$$

Thus, at Murray's law:

$$y = (1 - x)/3 \quad \text{Eqn A7}$$

For $x = 0.53$, the pooled regression exponent from Fig. 5(a), $y = 0.16$ for Murray's law (ML line in Fig. 5b).

Figure 5(c) shows that conductivity (K) scales with A to an exponent 'z':

$$K \propto A^z \quad \text{Eqn A8}$$

Assuming that $K \propto ND^4$, then from A1 and A4:

$$K \propto A^{(x+4y)} \quad \text{Eqn A9}$$

which means $z = x + 4y$. Plugging in y from A7 gives z as a function of x for Murray's law:

$$z = 1.33 - 0.33x \quad \text{Eqn A10}$$

For $x = 0.53$ from Fig. 5(a), $z = 1.16$ at Murray's law (ML line in Fig. 5c).



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