Murray's law and the hydraulic *vs* mechanical functioning of wood

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Summary

1. Murray's law states that the hydraulic conductance per blood volume of the cardiovascular system is maximized when the sum of the vessel radii cubed (Σr^3) is conserved.

2. We hypothesize that Murray's law will apply to xylem conduits as long as they only transport water and do not also help support the plant. Specifically, the less volume of wood occupied by conduits, the more the conduits should conform to Murray's law.

3. We tested the applicability of Murray's law along a continuum of decreasing conduit fraction from coniferous (91% conduits) to diffuse-porous (24% conduits) to ring-porous wood (12% conduits), using anatomical and functional tests. The anatomical test compared the Σr^3 conservation across branch points by direct measurements of conduit radii. The functional test compared the hydraulic conductivity between branches of different ages.

4. As predicted, Murray's law was rejected in conifer wood where hydraulic function is coupled to mechanical support. The angiosperm wood did not deviate as strongly from Murray's law, especially the ring-porous type. For comparison we report previously published results from compound leaves and vines which showed general agreement with Murray's law.

5. Deviation from Murray's law was associated with fewer, narrower conduits distally causing a decrease in Σr^3 distally. Although less efficient hydraulically, this configuration is not top-heavy and is more mechanically stable. With the evolution of vessels and fibres, angiosperm wood can more closely approach Murray's law while still meeting mechanical requirements.

Key-words: conduit furcation number, hydraulic architecture, hydraulic conductance, plant-area profile

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Introduction

Carbon dioxide uptake in land plants is associated with large losses of water by evaporation, and land plants are forced to restrict the uptake of CO_2 via stomata to avoid desiccation. Moreover, some assimilated CO_2 must be diverted from reproduction and photosynthetic tissue to construct the vasculature that supplies the transpiration stream. The optimal transport system should minimize the investment of carbon in the vasculature while maximizing vascular conductance, which is proportional to CO_2 uptake (Meinzer & Grantz 1990; Sperry & Pockman 1993; Meinzer *et al.* 1995; Hubbard *et al.* 2001). In this sense, the vascular conductance *vs* investment trade-off constrains the form of the plant. Although it has been assumed that plants have optimized this trade-off (West, Brown & Enquist 1997; West, Brown & Enquist 1999; Enquist, West & Brown 2000), this

assumption has only recently been tested (McCulloh, Sperry & Adler 2003).

Murray's law defines the vascular structure that should maximize conductance per investment for blood circulation in animals (Murray 1926). The optimal structure minimizes the two costs associated with cardiovascular function (Murray 1926; Sherman 1981). The first is the cost of moving the blood through an organism, which is inversely proportional to hydraulic conductance. The second is the cost of constructing and maintaining the vascular system, which is proportional to the vascular tissue volume. These costs are in conflict because, for the generally laminar flow in blood vessels, the length-independent conductivity follows the Hagen–Poiseuille equation and is proportional to the fourth power of the conduit radius, while volume per length increases with the second power of the radius. Murray (1926) demonstrated that the point at which the hydraulic conductivity per volume is maximized is when the volume flow rate (Q) at any point is proportional to the sum of the conduit radii cubed at that point (Σr^3). Q does not

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change in animals, so Murray's law predicts that the optimal transport system will conserve Σr^3 at any cross-section of the system. This solution is independent of vessel length and branching pattern. The validity of Murray's law has been shown in a variety of animal vascular systems (Sherman 1981; LaBarbera 1990).

We have shown that Murray's law applies equally well to the xylem of plants (McCulloh *et al.* 2003). Like blood flow, water flow in xylem is laminar and conductivity is proportional to the conduit radius raised to the fourth power. Also like blood flow, investment in xylem conduits should be proportional to the conduit radius squared. In animals the major investment is in the blood volume itself, and the cost of the thin vessel walls can be ignored. In contrast, in xylem the water is cheap but the conduit walls must be thick. Thickness must be proportional to the conduit diameter to withstand implosion caused by negative pressures in the conduits (Hacke *et al.* 2001). Therefore investment in conduits should still scale with the radius squared, as in animals, and Murray's law should apply.

Although the Murray's law optimum of maximum conductance per vascular volume is always achieved by Σr^3 conservation across branch points, the actual value of the maximum conductance depends on how the number of conduits changes from mother to daughter branches. In animals one mother vessel usually branches into two daughters, and the ratio of conduits between daughter and mother ranks is always ≥2 (Fig. 1a). We refer to this ratio of daughter (distal) to mother (proximal) ranks as the conduit furcation number (F). In plants no such rule applies because the conduits are not continuous. The flow path is made up of multiple conduits in series and in parallel, and the furcation number can be any positive value. For example, the number of conduits can remain the same across ranks (Fig. 1b), or it can increase distally (Fig. 1c). To obtain the greatest conductance per fixed vascular volume, not only must Σr^3 be conserved, but the furcation number should be maximized (McCulloh *et al.* 2003). Higher

furcation numbers with Σr^3 conservation mean fewer, wide conduits proximally and many, narrow ones distally.

Furcation numbers in xylem reach a maximum of 1·4 in compound leaves (McCulloh *et al.* 2003), which is less than the minimum of 2 in animals. Higher furcation numbers in xylem would be more efficient, but would compromise safety by reducing the number of conduits in parallel in the major branches. Multiple pathways are necessary to maintain transport under negative pressure, where a single cavitation or wound embolizes the entire conduit.

Mechanical support requirements may also limit F in plants. An $F > 1$ in combination with Murray's Σr^3 conservation means the cross-sectional area of the conduits increases with height. If the conduit area is proportional to the wood area, a tree with this area profile would fall over. This area profile of an inverted cone was found in our previous study, but the xylem conduits were not involved in structural support because we examined leaves and vines (McCulloh *et al.* 2003). Trunk and branch wood may require an $F \leq 1$ to avoid becoming top-heavy. Moreover, Murray's Σr^3 law may not apply if conduit walls are contributing to support of the shoot. Mechanical support is not considered in the derivation of Murray's law (Murray 1926).

The mechanical limitation on furcation number and Σr^3 conservation should be greater in conifer wood than in angiosperm wood. Conifer wood is 90–95% tracheids by volume (Gartner 1995). These tracheids function simultaneously in transport and support, and one function cannot be optimized at the expense of the other. Angiosperm wood is <55% conduits by volume, the rest being largely fibre cells (Gartner 1995). This more complex xylem has the potential independently to vary vessel structure to optimize transport without sacrificing the mechanical integrity of the fibres. The vessel fraction is especially low in ring-porous trees with their wide-diameter early wood vessels.

Here we test the hypothesis that branch wood of conifers will not follow Murray's Σr^3 law, whereas angiosperm wood will more closely approach Σr^3 conservation, particularly ring-porous wood. We also examine the values of the conduit furcation number (F) exhibited and the degree of the conduit taper to evaluate the area profile. We tested our hypothesis in some of the same species used in our previous study of leaf xylem to compare results between leaf and branch. We also include results from our previous study on vine wood to compare with the results from free-standing trees. As structural parasites, vines provide a natural control to free-standing trees because the xylem of vines should be freed of any role in structural support. We used two methods to test these hypotheses. First, we determined the degree of Σr^3 conservation by making time-consuming anatomical measurements of conduit radii. Second, we developed a more efficient functional test that determined the validity of Murray's law by comparing the ratios of hydraulic conductivity between branch ranks.
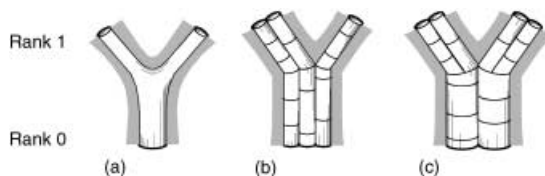

Fig. 1. Vascular networks in animals (a) *vs* plant xylem (b, c). The most proximal rank (0) branches to form more distal ranks (e.g. rank 1). In the animal cardiovascular system (a) a single continuous tube in rank 0 branches to form two daughter tubes in rank 1. The number of tubes increases by a factor ≥ 2 (the conduit furcation number, F) between ranks. In the plant system (b, c) the tubes are not continuous, but divided into individual conduits. (b) The number of conduits is identical at every rank and $F = 1$; (c) $F = 2$ and the number of conduits doubles from rank 0 to rank 1, as in the animal network (a). The value of F in (b, c) represents points in a continuum because, with hundreds of conduits in a single branch (a fraction is shown for clarity), F can be any positive value.

Materials and methods

PLANT MATERIAL

We tested these hypotheses in a ring-porous (*Fraxinus pensylvanica* Marshall), a diffuse-porous (*Acer negundo* L.) and a conifer [*Abies concolor* (Gord. & Glend.) Lindl.] species (Table 1). For the $\Sigma\, r^3$ measurements, three *F. pensylvanica* saplings were collected from Miller Park, Salt Lake City, Utah, USA (111°50′ W, 40°44′ N, elevation 1400 m). Three *A. concolor* saplings and four *A. negundo* saplings were collected from Red Butte Natural Research Area, near the University of Utah campus in Salt Lake City (111°47′ W, 40°47′ N, elevation 1750 m). For the hydraulic conductivity measurements, two branches from each of four mature trees were harvested from individuals growing in the same location as the saplings. The angiosperms are the same species in which we examined compound leaves for our previous study, and the previously published vine data are from *Parthenocissus quinquefolia* and *Campsis radicans* (McCulloh *et al*. 2003).

ANATOMICAL TEST OF MURRAY'S LAW

The validity of Murray's law was tested by directly measuring the radii of 2000–22 000 conduits per individual. Conduit radii (*r*) were measured at the petiolule and petiole rank for leaves (petiole only for the needle-leaved conifer), and at annual bud scars in stems (Table 1) for individual plants. Measurements were made using IMAGEPRO software (Media Cybernetics, Inc., Silver Spring, MD, USA) on digital images taken with a Nikon Coolpix 990 mounted on an Olympus BH2 light microscope. Only the water-transporting sapwood conduits were measured as identified by dye perfusions of 0·5% basic fuchsin.

To account for different branching structures, the raw conduit furcation number (*F′*) for adjacent distal/proximal ranks was standardized using the equation:

$$F = [(F' - 1)/(B - 1)] + 1 \qquad \text{eqn 1}$$

where *F* is the standardized conduit furcation number and *B* is the branch furcation number. This allowed for direct comparison of *F* between individuals with widely variable branching structures.

Due to the large numbers of conduits, a sampling scheme was used to estimate total conduit number and $\Sigma\, r^x$ for each rank. The exponent *x* could be assigned any value, which allowed a comparison of the Murray's law value of *x* = 3 with any other number. For leaves, all conduits in petiole and petiolule ranks were measured in ≥5 leaves. The measurements from all petiolules in a leaf were combined. This gave *n* ≥ 5 measures of $\Sigma\, r^x$ per leaf area for both petiole and petiolule ranks, each of which was multiplied by total leaf area to give ≥5 estimates of rank $\Sigma\, r^x$. For stems, functional conduits in ≥3 radial xylem sectors per branch were measured, with each sector yielding a $\Sigma\, r^x$ per sector area. This was multiplied by total functional xylem area of the rank to obtain *n* ≥ 3 estimates of rank $\Sigma\, r^x$.

To test for a branch effect and determine the independence of $\Sigma\, r^x$ estimates within trees, a two-way ANOVA was performed with the branch from which the measurement was made as the random factor, rank as the fixed factor, and $\Sigma\, r^x$ as the dependent variable. This comparison was made between the most distal rank (petiolule for angiosperm species and petiole for conifer species) and progressively more proximal ranks. This test revealed no significant branch effect, allowing us to treat each $\Sigma\, r^x$ estimate as independent, thus maximizing the $\Sigma\, r^x$ sample size.

To assess the validity of Murray's law, we used a two-way ANOVA to compare the $\Sigma\, r^x$ estimates for the same rank comparisons as the previous two-way ANOVA. In this ANOVA rank was the fixed factor, replicate individual was the random factor and $\Sigma\, r^x$ was the dependent variable. By using the most distal rank as a reference point we could measure any progressive departure from Murray's law moving from leaves to increasingly basal stems. For each paired comparison (most distal rank with progressively proximal ranks) we found the range of *x* over which $\Sigma\, r^x$ between ranks was not significantly different at *P* = 0·05. If this range of *x* did not include 3, Murray's law was rejected for that comparison.

Table 1. Summary of anatomical measurements: rank at which measurements were made; relative change in total conduit number from the most proximal rank (CN); average conduit radius (*r* μm); and relative change in total conduit area from the most proximal rank (CA) for each species. Species abbreviations (given after species names) are used in subsequent figures

Rank	*Fraxinus pensylvanica* (FP) (ring-porous, *n* = 3)			*Acer negundo* (AN) (diffuse-porous, *n* = 4)			*Abies concolor* (AC) (conifer, *n* = 3)		
	CN	*r*	CA	CN	*r*	CA	CN	*r*	CA
Petiolule	2·79	19·88	1·10	1·76	18·42	0·67	na	na	na
Petiole	1·40	26·68	1·00	0·98	23·78	0·64	0·38	4·56	0·11
1-year bud scar	1·05	24·01	0·57	1·03	23·44	0·44	0·84	6·78	0·50
2-year bud scar	0·97	29·50	0·76	1·04	26·24	0·87	1·02	7·07	0·63
3-year bud scar	0·95	30·28	0·90	1	28·07	1	1·01	6·76	0·54
4-year bud scar	1	29·65	1				1	9·12	1

Both angiosperm species (*F. pensylvanica* and *A. negundo*) had compound leaves, both petiolule and petiole ranks were measured. *n* = Number of individuals measured per species.

HYDRAULIC CONDUCTIVITY TEST OF
MURRAY'S LAW

The tediousness of the anatomical measurements prompted us to use hydraulic conductivity measurements to test the applicability of Murray's law. For two ranks with the same frequency distribution of conduit radii, Murray's law predicts that:

$$F'r_2^3 = r_1^3 \qquad \text{eqn 2}$$

where r_1 and r_2 are the mean conduit radii for a proximal and distal rank, respectively, and F' is the raw conduit furcation number, which is the conduit number of the distal rank/conduit number of the proximal rank. Solving for r_2 leaves:

$$r_2 = F'^{-1/3} r_1 \qquad \text{eqn 3}$$

The hydraulic conductivity of a rank, k, is:

$$k = \pi n r^4 / 8\mu \qquad \text{eqn 4}$$

where n is the number of conduits in the rank and μ is the viscosity. Inserting equation 3 for r_2 into an equation for the ratio of conductivities at the two ranks and reducing the constants where possible gives:

$$k_2/k_1 = [F'(r_1 F'^{-1/3})^4]/r_1^4 \qquad \text{eqn 5}$$

Reducing this further allows us to solve for the conductivity ratio predicted by Murray's law:

$$k_2/k_1 = F'^{-1/3} \qquad \text{eqn 6}$$

Fig. 2. The x with the maximum P value from the ANOVA comparing the most distal Rank Σr^x *vs* progressively more proximal ranks on the horizontal axis. na, Rank comparisons for which no x resulted in P values >0. Asterisks mark ranks that were statistically different from Murray's law where $x = 3$ (dashed line). Species abbreviations are as in Table 1; previously published data from PQ (*Parthenocissus quinquefolia*, vine and CR (*Campsis radicans*, vine) are included for comparison (McCulloh *et al.*, 2003).

This derivation assumes that the two ranks being compared have the same conduit radius frequency distribution, which will not necessarily be the case. To test the importance of this assumption we used actual frequency distributions of different ranks from the plants used in the anatomical measurements. Using the conduit number and Σr^3 from one rank, the conduit number from the second rank was adjusted to achieve Σr^3 equality with the first rank. The conductivity ratio was estimated by the ratio of Σr^4 of the two ranks. The slope of a linear regression between the ratio and the Murray's law ratio from equation 6 was 1·01 and was not different from the expected value of 1, indicating that the analysis was insensitive to differences in the frequency distribution of the conduits across ranks.

For each species, hydraulic conductivity was measured on two segments at each rank on branches from four large trees. Ranks in the branched stem were defined by age. Short stem segments between the bud scar and the first leaf scar from 1- to 4-year-old stem ranks in angiosperms and 1- wood to 5-year-old stem ranks in the conifer were measured following the protocol of Sperry, Donnelly & Tyree (1988). Segments were perfused with basic fuchsin after measurement to stain only functional conduits for counting. Conductivity measurements were also made on the petioles in the angiosperms species. All vessels in the petioles were assumed functional for counting.

Hand cross-sections were made near the centre of each segment and photographed on a light microscope. In petioles, all conduits were counted. In stems, all stained conduits in ≥3 radial sectors of xylem were counted to obtain an average conduit density. The total dye-stained area was used to calculate total conduit number from conduit density.

Both hydraulic conductivity and conduit number measurements were compared on a per leaf area basis (leaf weight for *A. concolor*). This allowed us to estimate rank values without measuring all branches on the large trees. The mean hydraulic conductivity per leaf area and mean conduit number per leaf area were calculated for each individual. The mean observed and predicted (from equation 6) conductivity ratios were computed for each rank compared with the most distal rank to detect any progressive deviation from Murray's law. Grand means of the ratios were calculated from $n = 4$ individuals, and individual means were calculated from $n = 2$ branch segments for each rank. Grand mean observed and predicted values for each species were compared using a paired t-test.

Results

ANATOMICAL MEASUREMENTS

The data showed the hypothesized trend towards increased compliance with Murray's law in the continuum from coniferous to diffuse-porous to ring-porous wood types (Fig. 2). The comparison between petiolules and
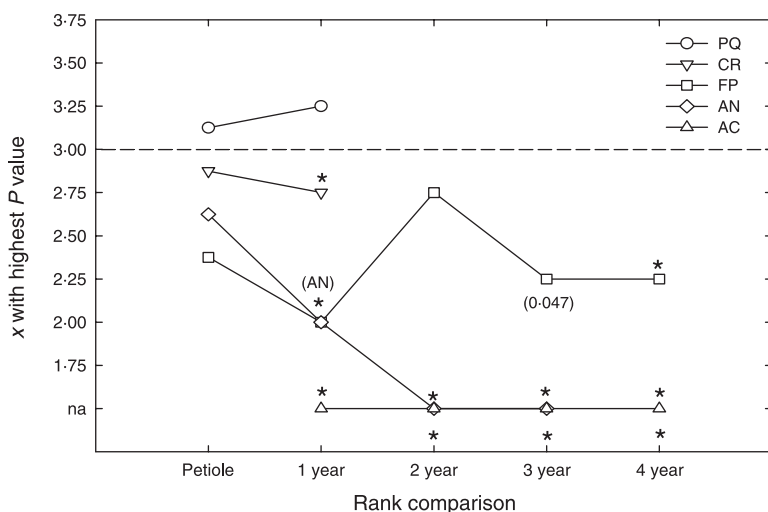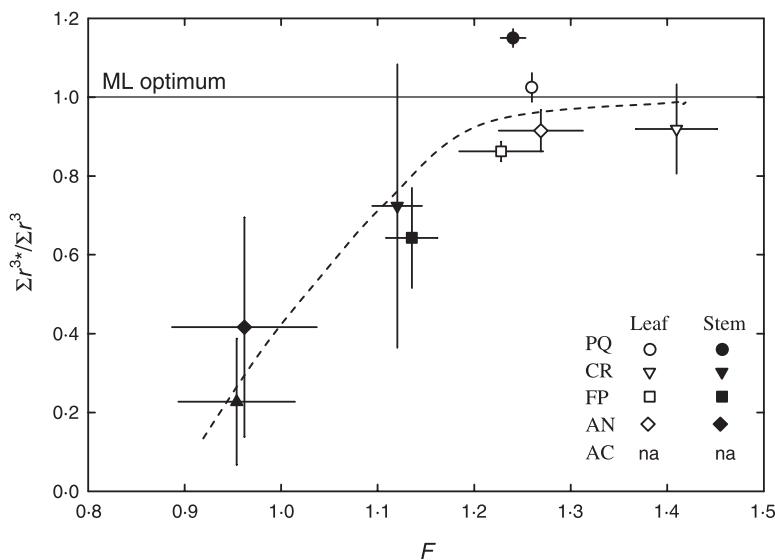
Fig. 3. $\Sigma\,r^3$ ratio *vs* conduit furcation number (F) across leaf ranks (open symbols) and stem ranks (solid symbols). The $\Sigma\,r^3$ ratio is the $\Sigma\,r^3$ for the most distal rank ($\Sigma\,r^{3*}$) over each successively more proximal rank. The most distal rank is the petiolule for the angiosperms and the petiole for the conifer. F is calculated from the distal rank conduit number/proximal rank conduit number for adjacent ranks. No statistical trend with rank was found within stem ranks, so pooled means are shown. Species abbreviations and growth forms are listed in Table 1; previously published data from PQ (*Parthenocissus quinquefolia*, vine and CR (*Campsis radicans*, vine) are included for comparison (McCulloh *et al.*, 2003). Symbols are grand means of all ranks from three to four individuals. Error bars represent standard errors; line represents Murray's law optimum at $\Sigma\,r^3$ ratio = 1.
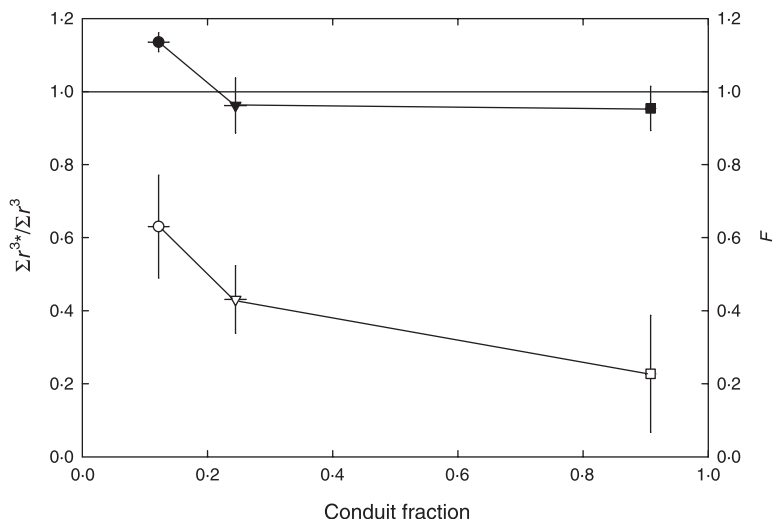

Fig. 4. Trends in $\Sigma\,r^3$ ratio (left ordinate, open symbols) and conduit furcation number (F) (right ordinate, solid symbols) *vs* area of wood occupied by conduits (conduit fraction). The $\Sigma\,r^3$ ratio is the most distal rank, $\Sigma\,r^{3*}$, petiolule for the angiosperms and petiole for the conifer, over each wood rank. F is for adjacent ranks. As in Fig. 3 symbols are pooled means of all ranks from three to four individuals. A trend of increasing conduit fraction exists from the ring-porous species (circles) to the diffuse-porous species (triangles) to the conifer (squares). Along with increased conduit fraction, the $\Sigma\,r^3$ ratio decreased and F fell to ≤1.

petioles showed agreement with Murray's law for all species examined (Fig. 2). When petiolules were compared with stem ranks, Murray's law held in all rank comparisons for the ring-porous species (FP) except the comparison between the petiolules and the stem at

the fourth-year bud scar (Fig. 2). The shoot xylem of the diffuse-porous species (AN) and the conifer (AC) was not consistent with Murray's law (Fig. 2). In most cases there was no x in the 1–5 range that gave $P > 0$ (x = na in Fig. 2). In contrast, the previously published results from vines (Fig. 2; PQ and CR) generally comply with Murray's law, although the wood of *Campsis radicans* was significantly different from the Murray's law optimum.

There was a significant trend for xylem closest to Murray's law to have the greatest furcation number [Kendall's coefficient of rank correlation, $P < 0.05$ (Sokal & Rohlf 1995), Fig. 3, dashed trend line]. For intraleaf comparisons the $\Sigma\,r^3$ ratio was near 1 and F was between 1·2 and 1·4 (Fig. 3, open symbols; McCulloh *et al.* 2003) with the total number of conduits being two to five times higher in petiolules *vs* petioles (Table 1). When the stem ranks were each plotted separately, no statistical trend with rank was found, so the stem data for each species were pooled. The stem comparisons tended to have greater $\Sigma\,r^3$ in proximal *vs* distal ranks, and had lower average F (Fig. 3). The lowest F was 0·95 in the conifer where the total number of functional conduits was approximately constant across stem ranks, but dropped by half from the stem to the petioles (Table 1).

The trends of $\Sigma\,r^3$ conservation and F with the fraction of xylem devoted to conduits were as predicted (Fig. 4). The ring-porous wood had the smallest conduit fraction, and the highest furcation number (ANOVA, LSD test, $P < 0.01$) and greatest $\Sigma\,r^3$ conservation. In contrast, the conifer wood was composed nearly entirely of conduits, had the lowest F (although not statistically different from the diffuse-porous species), and deviated most from Murray's law (Fig. 4).

HYDRAULIC CONDUCTIVITY MEASUREMENTS

The hydraulic conductivity measurements were generally consistent with the anatomical results. The measured hydraulic conductivity ratios (solid symbols, Fig. 5) of the conifer showed complete deviation from the values predicted by Murray's law (open symbols, Fig. 5). The ratios of ring-porous and diffuse-porous species were fairly close to values predicted by Murray's law. The results from the diffuse-porous species indicated more compliance with Murray's law than did the anatomical data.

Discussion

As hypothesized, the results revealed a progressive departure from Murray's law as xylem conduits play an increasing role in mechanical support of the plant. Compound leaves, which are supported hydrostatically, showed $\Sigma\,r^3$ conservation (Figs 2 and 3; McCulloh *et al.* 2003). Similarly vines, which are structural parasites, also showed agreement with Murray's law (Figs 2 and 3). In both these cases F was relatively high, between
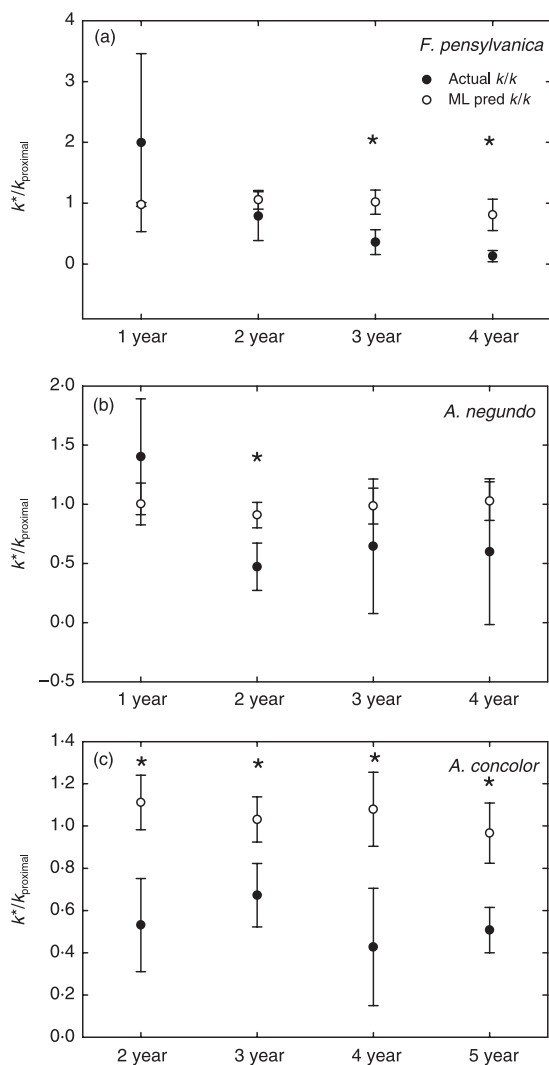
Fig. 5. Comparison of measured hydraulic conductivity/leaf area (or weight for conifer) ratios (solid symbols) with Murray's law ratios (open symbols). In both cases the most distal rank, $k*$ (petiole for angiosperms or 1-year-old wood for conifer) is compared with each proximal rank (indicated on horizontal axis). Murray's law predicted values were calculated from equation 6. Asterisks denote significant difference ($P < 0.05$) between measured *vs* Murray's law ratios (paired *t*-tests).

1·12 and 1·45, and the collective conduit area increased distally, giving a conduit-area profile of an inverted cone (Fig. 3, McCulloh *et al.* 2003). The xylem conduits appear to be optimized for their sole function in transport.

In stark contrast to leaf and vine stem xylem, conifer stem xylem deviated unambiguously from Murray's law according to both the anatomical and conductivity measurements. This deviation was expected because tracheids provide both structural support and water conduction. The conifer deviated from Murray's law because the proximal Σr^3 far exceeded the distal Σr^3 (Fig. 3). The large basal Σr^3 resulted from slightly more conduits proximally than distally, and the conduits narrowed distally (Table 1). This conduit configuration resulted in an area profile of an upright cone, which is consistent with the mechanical requirements of conifer wood, which is built primarily of conduits.

The stem xylem in the diffuse-porous and ring-porous trees was closer to Murray's law than the xylem in the conifer stems. This is consistent with their conduits occupying less wood area and presumably playing less of a role in mechanical support than conifer tracheids. The ring-porous species had the lowest fraction of stem area devoted to conduits and showed the least deviation from Murray's law (Fig. 4). It also exhibited a significantly higher F than the diffuse-porous or coniferous species (Fig. 3). The conduit area declined with rank, but not as sharply as the diffuse-porous or coniferous species (Table 1).

Compared with the ring-porous species, the diffuse-porous species had a higher conduit-area fraction, and the anatomical data indicated greater deviation from Murray's law (Figs 2–4). The deviation was in the same direction as in the conifer, with more Σr^3 basally than distally. The same combination of low F with conduit taper that was found in the conifer resulted in a conduit-area profile of an upright cone in *A. negundo* (Table 1). The results from the conductivity measurements in *A. negundo* contradicted the anatomical data. The discrepancy between methods may have arisen for several reasons. First, the branches used for conductivity measurements were from adult trees, while the anatomical measurements were made on young saplings. Second, the most distal rank for comparison was the petiole in the hydraulic measurements instead of the petiolule rank. Third, the higher level of variability in the hydraulic measurements probably reduced the sensitivity for detecting deviation from Murray's law.

The patterns we observed in conduit-area profiles within a tree are consistent with patterns of sap velocity within trees. If the sap at the top of a tree is moving faster than in the trunk, then the total conduit area must decrease at the top of the tree. Measurements on diffuse porous trees and conifers show increased sap velocity from the trunk to the branch, which is consistent with the upright cone profile for conduit area that we measured for these wood types (Huber & Schmidt 1936; McDonald, Zimmermann & Kimball 2002). In contrast, ring-porous trees tend to show nearly equal velocities in the branches and in the trunk, indicating a constant area profile (Huber & Schmidt 1936). Although the conduit-area fraction declined distally in the ring-porous species examined, it did not decrease as steeply as in the conifer or diffuse-porous species (Table 1), which is consistent with a smaller change in velocity.

Most studies of hydraulic architecture show a decline in leaf-specific conductivity from trunks to branches and to leaves. Accordingly, our conductivity ratios (most distal rank over proximal rank; Fig. 5) would be expected never to be >1, and to decline steadily with older ranks. However, this is not what we found. Instead, we saw a conductivity ratio >1 in the angiosperm species when the petiole was compared with the 1-year-old wood. However, the studies that have found steadily declining leaf-specific conductivities examined many more ranks than we did (Zimmermann 1978; Cochard

et al. 1997; Zotz, Tyree & Patino 1997). When we compare our data with previous results made over a similarly fine scale of branching ranks, the findings are consistent (Tyree & Zimmermann 2002).

Our results indicate that when vascular tissue functions in both transport and mechanical support, it should not and does not follow Murray's law. This raises the question of what law should be followed that would simultaneously optimize conductivity and mechanics. The current dogma consists of Da Vinci's rule of constant area across branch ranks or its modern equivalent in the pipe model (Shinozaki *et al.* 1964; Richter 1970). The latter assumes a constant xylem area per unit leaf area, but contradicts the Da Vinci rule by predicting a monotonic increase in wood area below the canopy from the accumulation of disused pipes connected to shed leaves (Shinozaki *et al.* 1964). However, neither rule was derived from an analysis of hydraulics or mechanics. McMahon's important work showing that tree height scales with trunk diameter to the 2/3 power, as required to preserve elastic similarity, is independent of the distribution of area with height and holds equally well for area-preserving or area-tapering branching (McMahon 1973). Measurements of changes in stem cross-sections across branch points are limited, but show that area is generally preserved except at the petioles, where the area increases (Horn 2000). These findings are not surprising, considering that, for mechanical purposes, the total area of the wood (supporting plus transporting elements) should at the very least not increase with height to avoid a top-heavy structure. It is likely that the optimal area profile would be an upright cone, consistent with mechanical analyses of the shape of the tallest free-standing column for a given volume of material (Keller & Niordson 1966).

We found that as the conduit-area fraction increased, and wood hydraulics and mechanics came more into conflict, there was a trend for F to drop to <1 and for proximal Σr^3 to increase relative to distal Σr^3 (Fig. 3, dashed curve). This configuration achieves a mechanically desirable area profile even in the conifer where nearly all the wood is composed of conduits. However, the same area profile could be achieved at $F > 1$ simply by narrowing the tracheid diameter more steeply from the base to the top of the tree. Although this configuration would not reach the maximum efficiency of Murray's law, it would still exploit the efficiency of fewer, wider conduits proximally. For example, conifer wood could theoretically have maintained the same F as the leaf xylem, achieved the necessary straight area profile for mechanics by disobeying Murray's law through increased tapering of tracheid diameter, and enjoyed higher hydraulic conductivity.

If there is a more efficient option, why should conifers and diffuse-porous trees exhibit such low values of F? We suspect that the geometry of wood development prevents an $F > 1$ in trees where conduits are a significant fraction of wood volume (Fig. 6). Wood grows in concentric rings, and the number of rings decreases
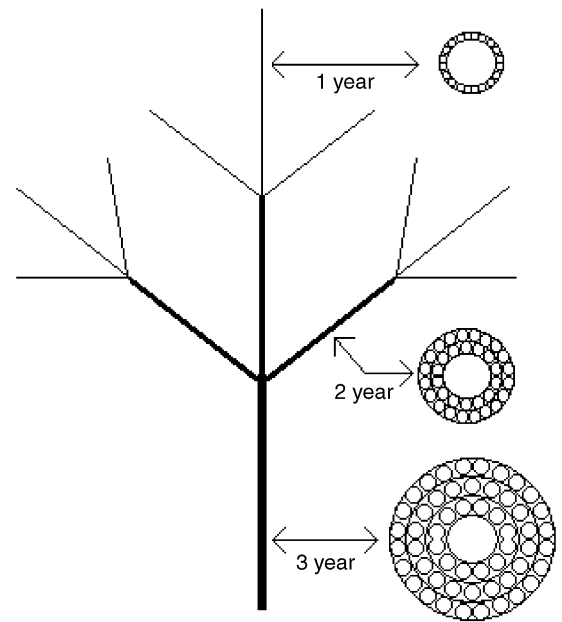
Fig. 6. A simplistic model of wood growth applied to a 3-year-old tree. Growth increments are rings of conduits around the pith, and the number of increments increases with stem age. To preserve a constant wood area from the 3-year-old trunk to the most distal 1-year-old branch rank, conduit diameter must decrease and conduit number must increase. The tree will have a conduit furcation number (F) <1, exhibit a tapering of conduit diameter distally, and deviate from Murray's law by having higher proximal Σr^3. A constraint of this nature may explain the trend for trees with high conduit-area fractions (conifer and diffuse-porous species) to have relatively low F in combination with a departure from Murray's law (Fig. 3).

with increasing branch rank. In a simple simulation we assumed that the conduit diameter is set to the width of a growth increment, and the number of conduits is set by the circumference and number of increments (Fig. 6, cross-sections). For the mechanical requirement of either a straight or upright cone-area profile, our calculations indicate this geometry of growth dictates $F < 1$, a tapering of conduit diameter with rank, and a Σr^3 ratio <1. These predictions are consistent with the data from the conifer. Although a very simplified representation of a complex growth process, this analysis makes the point that growth constraints might limit F where mechanical considerations also constrain the area profile.

We conclude that the optimal area profiles for hydraulics *vs* mechanics of free-standing trees are in direct conflict. Water conduction is most efficient in an area profile of an inverted top-heavy cone, while mechanical support is favoured by a straight column or upright cone. In conifers one cell type must execute these two tasks simultaneously, with opposing optima. We have described how the conducting network in *A. concolor* adjusts to mechanical constraints by a decrease in F to <1 and a conduit diameter taper in excess of the Murray's law optimum. However, with the evolution of vessels and fibres, angiosperms can more closely approach Murray's law while still maintaining a mechanically stable area profile.

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