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How are leaves plumbed inside a branch? Differences in leaf-to-leaf hydraulic sectoriality among six temperate tree species

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Abstract

The transport of water, sugar, and nutrients in trees is restricted to specific vascular pathways, and thus organs may be relatively isolated from one another (i.e. sectored). Strongly sectored leaf-to-leaf pathways have been shown for the transport of sugar and signal molecules within a shoot, but not previously for water transport. The hydraulic sectoriality of leaf-to-leaf pathways was determined for current year shoots of six temperate deciduous tree species (three ring-porous: *Castanea dentata*, *Fraxinus americana*, and *Quercus rubra*, and three diffuse-porous: *Acer saccharum*, *Betula papyrifera*, and *Liriodendron tulipifera*). Hydraulic sectoriality was determined using dye staining and a hydraulic method. In the dye method, leaf blades were removed and dye was forced into the most proximal petiole. For each petiole the vascular traces that were shared with the proximal petiole were counted. For other shoots, measurements were made of the leaf-area-specific hydraulic conductivity for the leaf-to-leaf pathways (k_{LL}). In five out of the six species, patterns of sectoriality reflected phyllotaxy; both the sharing of vascular bundles between leaves and k_{LL} were higher for orthostichous than non-orthostichous leaf pairs. For each species, leaf-to-leaf sectoriality was determined as the proportional differences between non-orthostichous versus orthostichous leaf pairs in their staining of shared vascular bundles and in their k_{LL}; for the six species these two indices of sectoriality were strongly correlated ($R^2 = 0.94$; $P < 0.002$). Species varied 8-fold in their k_{LL}-based sectoriality, and ring-porous species were more sectored than diffuse-porous species. Differential leaf-to-leaf sectoriality has implications for species-specific co-ordination of leaf gas exchange and water relations within a branch, especially during fluctuations in irradiance and water and nutrient availability.

Introduction

The transport of resources within a plant can be constrained by its vascular system, and may result in the semi-isolation of plant parts (also known as sectoriality; Murray *et al.*, 1982; Watson and Casper, 1984; Marshall, 1996; Vuorisalo and Hutchings, 1996; Orians and Jones, 2001). An extremely sectored plant would behave as if constructed of autonomous subunits while an integrated plant would behave as if it were a single unit. In sectored plants, restricted transport of resources within these subunits can lead to differential rates of water and nutrient supplies between parts, such as between specific roots and leaves or branches, and between leaves on a branch (Rinne and Langston, 1960; Stryker *et al.*, 1974; Horwath *et al.*, 1992; Larson *et al.*, 1994; Hay and Sackville Hamilton, 1996;

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Fort *et al.*, 1998; Orians *et al.*, 2000, 2002, 2004). Restricted transport of sugars, nutrients, and signal molecules can lead to within-plant variation in tissue development, chemistry, and systemic induction (Watson and Casper, 1984; Orians *et al.*, 2000, 2002; Schittko and Baldwin, 2003). Interspecific variation in sectoriality may have ecological consequences, affecting plant responses to environmental heterogeneity and plant–consumer interactions (reviewed by Orians and Jones, 2001).

While, most generally, water moves in trees from roots to the leaves in a pathway that ends with the most distal leaves on a shoot, water transport in leaf-to-leaf pathways has potentially important implications in processes including leaf development, growth, and responses to fluctuations in light or to drought and herbivory. Leaf-to-leaf pathways may reflect the degree to which leaves are plumbed to different sources of water in the branch; leaf-pairs plumbed to different water supplies in the shoot would express relatively low leaf-to-leaf hydraulic conductance. Such leaves would be expected to respond relatively independently during development as well as at maturity, during localized fluctuations in irradiance, water or nutrient supply, or during herbivory. Such consequences have previously been shown from the point of view of the phloem transport of sugars and of signal molecules between leaves (Watson and Casper, 1984; Novoplansky, 1989; Dickson, 1991; Schittko and Baldwin, 2003). The sectoriality of leaf-to-leaf hydraulics has never been previously quantified. However, anatomical studies of stem–leaf vascular connections indicate the potential for differential plumbing of leaves on a shoot (Dimond, 1966; Larson, 1977). Studies of branch junctions, and of branchlets within branches show that hydraulic sectoriality may be substantial, and, importantly, variable across species (Kozlowski and Winget, 1963; Brooks *et al.*, 2003; Schulte and Brooks, 2003).

Patterns of leaf-to-leaf hydraulic sectoriality are reported for six temperate tree species common in the north-eastern United States. It was hypothesized that patterns of sectoriality would reflect phyllotaxy, because orthostichous leaves (those vertically aligned; Fig. 1) have repeatedly been shown to exhibit greater phloem connectivity than non-orthostichous leaves (Watson and Casper, 1984). As a consequence, differences were expected among species in the relative connectivity of orthostichous leaf pairs and non-orthostichous leaf pairs to provide a robust measure of sectoriality. It was further hypothesized that leaf-to-leaf hydraulic sectoriality would be highly variable across species, reflecting differences in vascular anatomy, as sampled across ring-porous and diffuse-porous trees.

Materials and methods

Species and site

The experiments were performed from June to August 2002 at Harvard Forest in Petersham, MA (42.54° N, 72.18° W). Six common
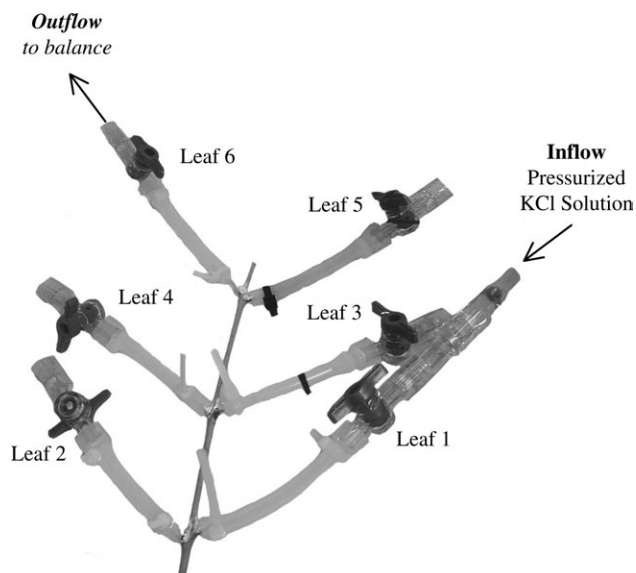

Fig. 1. The hydraulic system used to measure conductance. Flow solution (10 mM KCl) was forced into the petiole of leaf 1. Outflow to a balance was measured individually for petioles of leaves 2–6; the outflow from other leaves was blocked by stopcocks. The diagram illustrates flow from leaf 1 to leaf 6. Note that leaves 1 and 5 are an orthostichous pair.

deciduous tree species were examined: diffuse-porous species *Acer saccharum* Marshall, *Betula papyrifera* Marshall, and *Liriodendron tulipifera* L.; and ring-porous species *Castanea dentata* (Marshall) Borkh., *Fraxinus americana* L., and *Quercus rubra* L. (nomenclature follows Gleason and Cronquist, 1991).

Current-year shoots with at least six mature leaves, of lengths 0.2–0.6 m, were collected from each species. For each species, shoots were collected from four different trees, and recut under water. Leaf-to-leaf connections and hydraulic resistance were determined using safranin O dye and hydraulic techniques.

Dye studies

Dye staining was used to map the vascular connections among leaves. The shoot, one per species, was first cut below and above the six leaves of interest. The base of the recut shoot was sealed with acrylic-based glue (Super Bonder Loctite 409; Loctite Corporation, Rocky Hill, Connecticut). The most proximal leaf was cut underwater, midway along the petiole, and sealed to tubing filled with 0.5% safranin O dye (Sigma, St Louis, Missouri) running to a dye-filled syringe. The other leaves on the shoot were then cut mid-way along the petioles, and the dye in the syringe was pressurized to 0.1 MPa. After 10–20 min, when dye exited the shoot apex, the pressure was released, the bark removed, and the number of dyed and undyed vascular traces in each leaf petiole was counted.

Hydraulic measurements

Hydraulic connectivity was measured for each shoot between the proximal leaf (henceforth 'leaf 1') and each distal leaf on the shoot. For each shoot, the stem was cut 6 cm below leaf 1 and 6 cm above leaf 6, and leaves were excised, leaving 2 cm of petiole. Both ends of the stem were sealed with the acrylic-based glue (see above). Petioles were wrapped with parafilm and sealed with small cable ties into tubing ending with a stopcock (Fig. 1). Flow was generated by forcing a solution of degassed filtered water as 10 mM KCl into the petiole of leaf 1 and measuring the outflow from the petioles of leaves

2 to 6 in sequence, with the stopcocks attached to the other petioles closed. 10 mM KCl solution was used to maximize the conductivity of bordered pit fields (Zwieniecki *et al.*, 2001*a*, 2003). The solution was pressurized at approximately 0.2 MPa in a coil of tubing connected to the petiole. A pressure transducer (PX26-005, Omega, Stamford, Connecticut) connected to the tubing proximal to the petiole reported the flow pressure. The outflow from the petiole ran through solution-filled tubing to an analytical balance (±0.01 mg; Denver Instruments MD210; Arvada, Colorado), logging to a computer each 30 s; the final flow rate was noted when five consecutive readings had stabilized (CV <5%; approximately 10–20 min). Close observations were made for declines in flow rate due to wounding responses, but none were detected. The reported measurements were made with flow driven from leaf 1 to the distal leaf; the values did not differ significantly for flow driven in the reverse direction, from the distal leaf to leaf 1 (CM Orians, unpublished data).

Hydraulic conductance was calculated as the flow rate divided by the pressure driving force. To control for the fact that larger leaves typically have proportionally larger water supply (Sack *et al.*, 2002, 2003), as well as for the dependence of conductance on distance, leaf-area-specific leaf-to-leaf hydraulic conductivities (k_{LL}) were determined for each leaf-to-leaf pathway by dividing hydraulic conductance by the area of the lamina (m²; measured using CI-203 portable laser area meter; CID, Vancouver, Washington) previously attached to the outflow petiole and multiplying by the distance (m) between the two leaf positions. The precise path length of water is in fact not a simple parameter, as water very likely moves laterally between conduits all along the axial pathway between the two leaves. Thus, k_{LL} cannot be standardized by a fully characterized path length, and differences in axial versus lateral conductance are an important source of variation among leaf-to-leaf pathways, and may differ among species (see Discussion). From the same raw data, leaf-to-leaf hydraulic conductances were calculated (i.e. without normalizing by distance); the patterns were similar, and are not presented here.

Analyses

Differences in connectivity between flow from leaf 1 to its orthostichous leaf (orthostichous connectivity) and between leaf 1 and its most distal non-orthostichous leaf (non-orthostichous connectivity) were tested using paired *t*-tests with one tail according to the expectation of greater connectivity between orthostichous leaf pairs (Sokal and Rohlf, 1995). In *A. saccharum* and *F. americana*, leaf 5 is orthostichous to leaf 1 and leaf 6 is the most distal non-orthostichous leaf. In *B. papyrifera*, *C. dentata*, *L. tulipifera*, and *Q. rubra* the reverse is true. Data were log-transformed when necessary to fulfil the assumption of normality (assessed using the Anderson–Darling normality test; Minitab Release 14; Sokal and Rohlf, 1995).

To compare species' empirical values for sectoriality, an index of sectoriality ranging between 0 and 1 is presented, calculated as: (orthostichous connectivity–non-orthostichous connectivity)/orthostichous connectivity. In a fully sectored species, the ratio would be 1 (as non-orthostichous connectivity is zero), and in fully integrated species, the ratio will be 0 (as non-orthostichous connectivity = orthostichous connectivity). The index for sectoriality was calculated in two ways, with orthostichous and non-orthostichous connectivities either (i) based on the proportion of stained vascular bundles in common, or (ii) represented by k_{LL}. Differences in hydraulic sectoriality (based on k_{LL}) among species were tested first with a one-way ANOVA, and second with a nested analysis of variance with species nested within porosity (ring-porous versus diffuse-porous xylem structure). Finally, tests were made for correlation across species of the sectoriality indices calculated in the two ways, and for correlation between the k_{LL}-based index of sectoriality and orthostichous connectivity.

Results

Patterns of dye flow from petiole-to-petiole differed strongly across species (Fig. 2). In some species dye flowed up along the same side of the shoot (especially *Fraxinus* and *Quercus*) while in others it spread quickly around the stem from the point of entry (especially *Betula*). Dye flow was highly restricted in ring-porous species (Fig. 2). When dye was pushed into leaf 1, the orthostichous leaf petiole accumulated dye in all three of its vascular bundles while in non-orthostichous leaf petioles a single (*Castanea*) or none (*Fraxinus* and *Quercus*) of the vascular bundles accumulated dye. By contrast, staining in diffuse-porous species was more uniform (Fig. 2). In *Acer*, all three vascular bundles accumulated dye in both the orthostichous and adjacent leaves; only the central vascular bundle for petioles on the opposite side of the stem (leaves 2 and 6) failed to accumulate dye. In *Betula*, nearly all vascular bundles of petioles 2–6 accumulated dye (only a single bundle in leaf 5 failed to do so). In *Liriodendron*, the orthostichous leaf petiole accumulated dye in all seven vascular bundles, and the other petioles accumulated dye in 3–6 vascular bundles; the most distal non-orthostichous
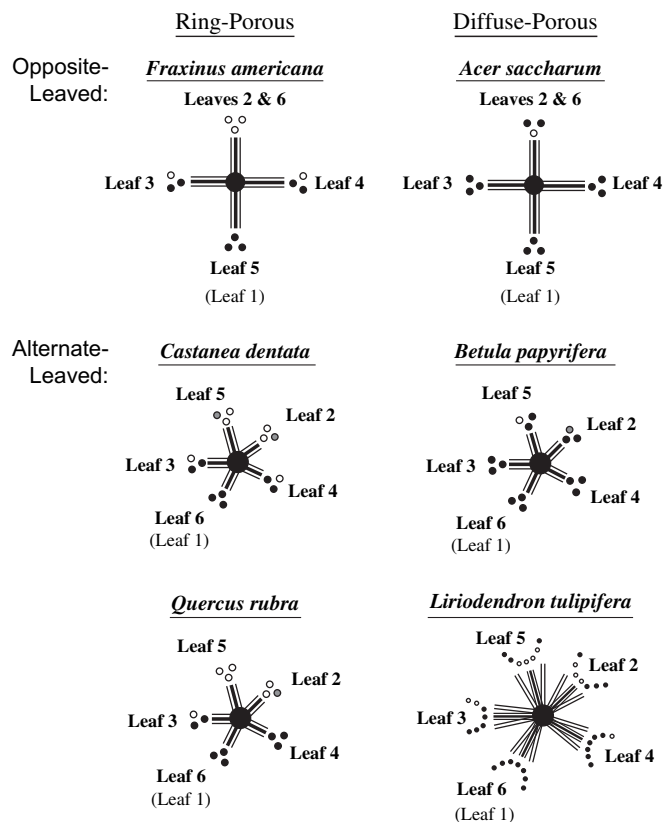

Fig. 2. Dye-staining maps of water flow pathways from the petiole of leaf 1 to the petioles of distal leaves (positions 2–6). Three vascular traces entered each petiole from the stem for all species except *Liriodendron tulipifera* (seven vascular traces). Vascular traces were scored as extensively stained (filled circles), lightly stained (grey circles), or unstained (open circles).
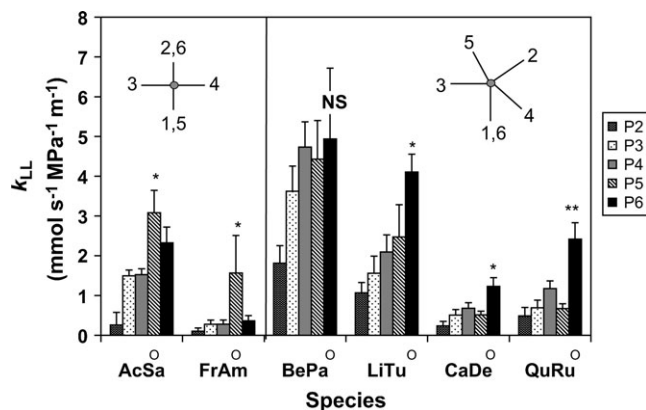
Fig. 3. Mean values ±SE for leaf-specific leaf-to-leaf conductivity (k_{LL}) from leaf 1 to petioles of distal leaves on the shoot for AcSa=*Acer saccharum*, FrAm=*Fraxinus americana*, BePa=*Betula papyrifera*, LiTu= *Liriodendron tulipifera*, CaDe=*Castanea dentata*, and QuRu=*Quercus rubra* (n=4 individuals per species). Inset diagrams show the phyllotaxy: opposite arrangement for AcSa and FrAm; alternate for BePa, LiTu, CaDe, and QuRu. 'O' below columns identify the leaf orthostichous to leaf 1. For each species, significant differences between orthostichous k_{LL} and non-orthostichous k_{LL} are indicated by symbols above the bar (NS not significant; * P <0.05; ** P <0.01; one-tailed paired *t*-test). n=4 per species.
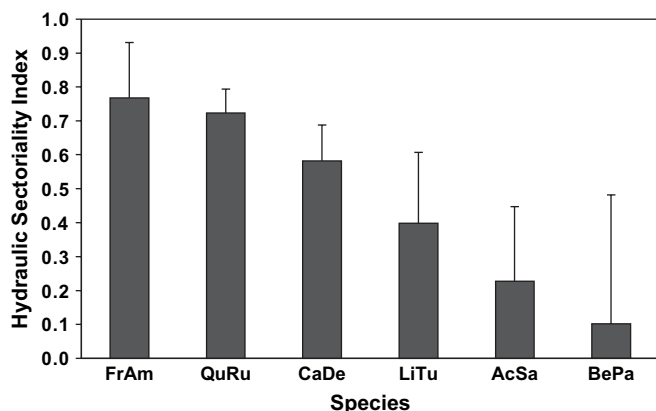

Fig. 4. Mean values ±SE for hydraulic sectoriality index for six temperate tree species. The hydraulic sectoriality index was calculated as: [(orthostichous k_{LL}–non-orthostichous k_{LL})/orthostichous k_{LL}]. Species abbreviations are as in Fig. 3. n=4 per species.

leaf petiole accumulated dye in only 3 out of 7 vascular bundles.

Patterns of hydraulic connectivity generally reflected phyllotaxy. For all species but *Betula*, k_{LL} was significantly higher between orthostichous leaves (i.e. leaf 1 to leaf 5 for opposite phyllotaxy; leaf 1 to leaf 6 for alternate phyllotaxy) than between non-orthostichous leaves (i.e., leaf 1 to leaf 6 for opposite phyllotaxy; leaf 1 to leaf 5 for alternate phyllotaxy; Fig. 3). k_{LL} was lowest for the pathway between leaf 1 and its leaf 2 for all species. In *Betula*, k_{LL} was high for all other leaf positions (Fig. 3).

Species differed in their overall k_{LL} values and in their orthostichous and non-orthostichous connectivities (Fig. 3). The three ring-porous species had lower k_{LL} values than the diffuse-porous species (Fig. 3). Species varied 8-fold in
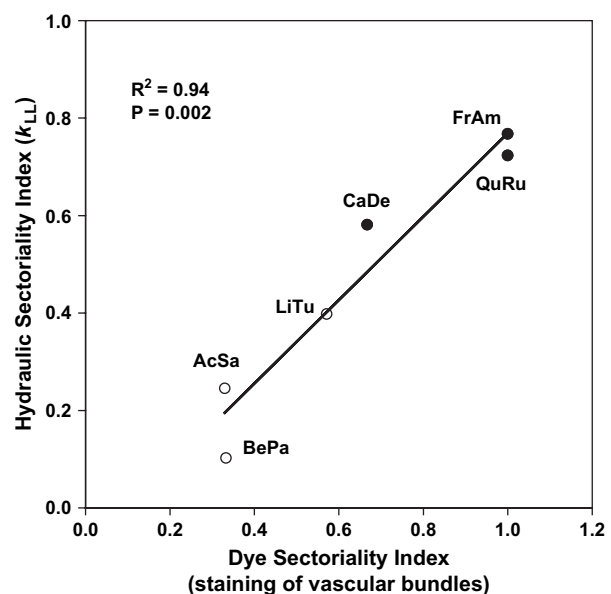

Fig. 5. Relationship between the two indices of sectoriality based on dye accumulation or on the hydraulic conductivity of leaf-to-leaf pathways. Indices were determined by proportional similarity between connectivities of orthostichous and non-orthostichous leaf pairs. Species abbreviations as in Fig. 3. Open circles represent diffuse-porous species; filled circles represent ring-porous species.

the index of hydraulic sectoriality based on k_{LL}, from *Betula* to *Fraxinus* (Fig. 4; F=4.28, P=0.008; one-way ANOVA). The ring-porous species were significantly more sectored than the diffuse-porous species (F=14.6, P=0.001 for porosity, and F=1.83, P=0.158 in an ANOVA testing for species nested within porosity). Across all species, the two calculated indices of sectoriality (i.e. based on staining or on k_{LL}) were highly correlated (Fig. 5), with both indicating that the three ring-porous species were more sectored than the three diffuse-porous species. Because ring-porous species had lower k_{LL} values as well as higher hydraulic sectoriality, a negative correlation was found across species in these traits (R^2=0.67; P=0.045).

Discussion

The hydraulic connectivity of leaf-to-leaf pathways varied strongly within shoots in all species. In 5/6 species, excluding *B. papyrifera*, these patterns reflected phyllotaxy, with orthostichous leaf pairs having higher k_{LL} than non-orthostichous leaf pairs. This matching of hydraulic connectivity with phyllotaxy is consistent with patterns of carbon transport in the phloem (Watson and Casper, 1984) and with patterns of systemic induction following localized damage (Davis *et al.*, 1991; Jones *et al.*, 1993; Orians *et al.*, 2000; Schittko and Baldwin, 2003).

What are the implications of sectored leaf-to-leaf water (and nutrient) transport? Leaves with high leaf-to-leaf connectivity share their plumbing more than leaves with

lower leaf-to-leaf connectivity. Thus, orthostichous leaves will tend to share (or to compete for) water to a greater extent than non-orthostichous leaves. Under bright illumination, or higher evaporative demand, upper leaves would be expected to reduce water supply to lower orthostichous leaves to a much greater extent than to non-orthostichous leaves (see Brooks *et al.*, 2003, for this idea in relation to branchlets on a branch). The design of such plumbing of leaf-to-leaf pathways is consistent with the fact that orthostichous leaves, being vertically in-line, may self-shade each other maximally; this arrangement will minimize the detrimental effect of maximal competition for water. Future experiments could test this phenomenon by examining the consequences of covering leaves on the stomatal conductance and photosynthetic performance of orthostichous and non-orthostichous leaves.

The hydraulic connectivity of leaf-to-leaf pathways, as quantified with k_{LL} values, are also physiologically significant for water movement between leaves. This is true even accounting for the fact that the flow pathways across the leaf lamina constitute a major hydraulic bottleneck in the flow from stem xylem to sites of evaporation in the leaf. Recent work has found that the leaf lamina hydraulic conductance values (K_{leaf}) range from 7–15 mmol m^{-2} s^{-1} MPa^{-1} for sun leaves of temperate tree species (Sack *et al.*, 2003). Notably, the conductances of the flow pathways between leaves determined in this study are of the same order, ranging 2.5–29 mmol m^{-2} s^{-1} MPa^{-1} (i.e. as calculated from k_{LL} values, removing the normalization by axial distance). Thus, leaf-to-leaf connectivity will play a major determining role in the capacity for flow from the mesophyll of one leaf to that of a second leaf.

There was extensive variation among species in leaf-to-leaf hydraulic sectoriality. The hydraulic connectivity index, based on k_{LL} has the advantage of providing a high-resolution quantitative measurement. This measure agreed strongly with the findings of the more qualitative dye-staining method. Across species, an 8-fold variation in sectoriality was observed. The three ring-porous species were more sectored than the three diffuse-porous species, but even among the diffuse porous species there were 4-fold differences in sectoriality. How do such different patterns of leaf-to-leaf hydraulic sectoriality arise? It was noted that xylem conduits in the leaf petioles insert in the stem next to stem xylem vessels (Esau, 1965; Tyree and Zimmermann, 2002). In first-year dicotyledon tree shoots, resources or dye moving from one leaf to another move through the xylem conduits in the vascular bundles of one petiole, and then across intervessel pits into vessel elements within the vascular bundles of the stem. Resources then move axially up the stem and across intervessel pits into the xylem conduits that supply the second leaf. Thus, k_{LL} is expected to depend on (i) the plumbing of leaves to common vascular bundles in the stem, as water presumably moves much more easily between nearby conduits within the bundles

than among bundles that are set off among parenchyma. Thus, k_{LL} will be higher for leaves that are plumbed to a common bundle in the stem, and lower if the leaves are plumbed to separate bundles. In addition, k_{LL} will depend on the xylem features *within* the bundles, especially (ii) the axial xylem conductance between the two leaves, which depends on xylem conduit dimensions as well as the number and size of intervessel pits, and (iii) the lateral conductance, which depends on the number and size of intervessel pits between adjacent vessels. These characters are fundamental in determining leaf-to-leaf sectoriality, and merit direct measurement (*sensu* Zwieniecki *et al.*, 2001*b*).

The correlation of the indices of sectoriality based on staining of vascular bundles and on k_{LL} implies that leaf plumbing to common vascular bundles is the principal determinant of leaf-to-leaf hydraulic sectoriality for first-year shoots of all six species. However, it was noted that, among species with similar sectoriality according to staining of vascular bundles, there was still differential sectoriality based on k_{LL} (e.g. *A. saccharum* is more sectored than *B. papyrifera*; Fig. 3). Such differences are expected if species vary in the lateral and the axial components of the flow path within bundles. Indeed, there is evidence that these pathways differ for some of these species. Orians *et al.* (2004) showed that *A. saccharum* has a much lower percentage of vessel wall as intervessel pits relative to *B. papyrifera* (9% and 26%, respectively), and that this difference would lead to lower lateral flow relative to axial flow in *A. saccharum*. Such differences in lateral flow relative to axial flow would increase the variation in k_{LL} within a shoot (Zwieniecki *et al.*, 2003). The frequency of vessel-to-vessel contact would also influence lateral flow, and contribute to further variation. Overall, species with wide and long conduits that are more isolated from one another, such as ring-porous trees, would tend to be more sectored (Orians *et al.*, 2005). It was noted that, as shoots age, the distinct vascular bundles in the stem become tangentially elongated and, eventually, a continuous vascular ('hollow') cylinder is formed, in cross-section, a ring of xylem. Thus, factors beyond the vascular bundle patterns in the stem, i.e. the conduit numbers and dimensions and the number and sizes of intervessel pits *per se*, would increasingly determine patterns of sectoriality in older shoots that have developed continuous vascular cylinders (reviewed by Orians *et al.*, 2005). Change in sectoriality across different ages of woody shoots is an interesting avenue for further study.

Whether the strong (8-fold) difference across species in their leaf-to-leaf hydraulic sectoriality reflects historical selective pressures or is a by-product of xylem evolution is unknown. Sectoriality may have an adaptive function. An advantage of a sectored vasculature may be for tolerance of a low water supply. Embolism of xylem conduits is rendered more likely by high evaporative demand and by dry soil (Tyree and Zimmermann, 2002). Because emboli

probably spread much more strongly within than across vascular bundles in the stem, the plumbing of leaves to different supplies will limit the lateral spread of emboli. Being sectored may be more important for ring-porous species than for diffuse-porous species. Ring-porous species rely extensively on relatively isolated large vessels for water and mineral transport early in the growing season and smaller isolated vessels late in the year (Carlquist, 2001; CM Orians, unpublished data); plants with large vessels can be more susceptible to drought or freeze–thaw-induced embolism (Sperry *et al.*, 1994; Hacke and Sperry, 2001). Embolism of the scattered large vessel elements in ring-porous wood is a major threat, and sectored leaf-to-leaf pathways may be advantageous by minimizing this threat (Zimmermann and Brown, 1971; Thomas, 2000). There are also potential disadvantages of being sectored. Greater integration allows effective transport of water and nutrients from one sector to impoverished tissues in another sector. The most effective system for exchange of water and nutrients within the shoot would be high leaf-to-leaf conductance for every leaf pair. The disadvantage of sectoriality might be minimized if leaves are arranged to capture resources independently, with minimal self-shading or, if during periods of high resource supply, the plants have sufficient water and nutrients to supply all leaves optimally.

A comparative study across species with diverse ecological tolerances would shed light on the adaptive advantages and disadvantages of differential sectoriality. Further, an emerging area of important research is the potential correlation to whole plant sectoriality, and its consequences for whole plant performance. For example, work is needed to determine the correlation of leaf-to-leaf and root-to-leaf hydraulic sectoriality. Previous results for root-to-leaf connectivity across species show similarities with the patterns in this study; for instance, *Betula* is highly integrated in terms of nitrogen and water transport (Fort *et al.*, 1998; Orians *et al.*, 2004), while *Acer* and *Quercus* are more sectored (Orians *et al.*, 2004; CM Orians, unpublished data). There are many potential implications. Integrated transport coupled with patchy resource availability both above and below-ground (*sensu* Jackson and Caldwell, 1993) may allow for relatively even distribution of resources in a plant and may enhance the ability of plants to respond to patchy resources (*sensu* van Vuuren *et al.*, 2003). Sectoriality, on the other hand, would have no disadvantage if adequate resources supply all leaves and it may play a role in limiting the spread of embolism. Differences among species in sectoriality are thus expected to scale up to differences in whole-plant performance and ecology.

Acknowledgements

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