

# Patterns and consequences of differential vascular sectoriality in 18 temperate tree and shrub species

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## Summary

1. Resource delivery within plants depends on supply pathways. Some species have relatively constrained (sectored) vascular connections, while others have relatively unconstrained (integrated) vascular connections.

2. In this study, patterns of vascular hydraulic sectoriality, anatomy and ecological tolerance were examined for 18 Northern Hemisphere temperate woody species growing at Arnold Arboretum, Jamaica Plain, MA, USA. A hydraulic technique was used to measure axial and tangential conductivity on branch segments. From a ratio of these values, a sectoriality index was calculated.

3. Species that were more hydraulically sectored had greater vessel size, variation in vessel area and tangential nearest-neighbour distance, as well as lower vessel density, than did integrated species.

4. Ecologically, higher tolerance to drought and wind was correlated with being sectored, while higher tolerance to flood and shade was correlated with being integrated.

5. These results suggest that sectored species should be especially prominent in xeric environments where sectoriality may reduce embolism spread by minimizing vessel-to-vessel contact and pitting, and integrated species should be especially prominent when resources are spatially patchy or heterogeneous.

*Key-words:* ecological tolerance, environmental heterogeneity, integrated, porosity, vascular anatomy

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## Introduction

Supply of water and nutrients through plants is highly dependent on the xylem pathways delivering resources from roots to leaves. Axial xylem pathways can differ considerably in their degree of interconnectedness (Orians *et al.* 2004; Orians, Babst & Zanne 2005a). Plants having relatively restricted pathways are considered sectored or sectorial, and plants having relatively unrestricted pathways are considered integrated (Watson & Casper 1984; Watson 1986; Orians & Jones 2001). Restricted pathways in sectored plants can lead to within-plant variability in tissue quality, especially when they are growing on heterogeneous or patchy resources (Watson & Casper 1984; Orians & Jones 2001; Orians, Ardon & Mohammad 2002), and differential sectoriality is likely to influence the ability of a species to establish and grow in different ecological conditions.

Studies of vascular sectoriality have focused on herbaceous and clonal species (Rinne & Langston 1960; Hay & Sackville Hamilton 1996; Marshall 1996; Price,

Hutchings & Marshall 1996; Orians *et al.* 2002), with fewer studies on woody species (Richardson 1958 as cited by Zimmermann & Brown 1971; Rudinsky & Vité 1959; Waisel, Liphshitz & Kuller 1972; Larson, Doubt & Mathes-Seares 1994). Recent studies by Orians *et al.* (2004) found that dye or <sup>15</sup>N fertilizer when applied to lateral roots of saplings showed more sectorial movement in species in *Acer* and *Populus* and more integrated movement in species in *Betula*. Orians, Smith & Sack (2005b) quantified leaf-to-leaf hydraulic sectoriality in current-year tissue across six temperate angiosperms and found varying degrees of sectored movement in all species.

Anatomical traits leading to differences in sectoriality are especially poorly known. Differences in sectoriality should be a function of xylem anatomy (Orians *et al.* 2004; see model proposed by Orians *et al.* 2005a). This model suggests that integration increases with (1) the extent of intervessel contact; and (2) the amount of vessel wall in intervessel pits and the porosity of those pits.

While it is possible to make predictions about anatomical differences contributing to variation in sectoriality, ecological selective pressures leading to these differences are unresolved. We propose that integrated species should be particularly successful in environments where resources are spatially patchy or heterogeneous

(Orians & Jones 2001), because patchy distribution of resources in the environment leads to patchy uptake by the plant. Impoverished portions of integrated plants can then draw these resources from enriched portions. On the other hand, sectored plants should have the advantage of isolating sections stressed by disease or embolism (Sprugel, Hinckley & Schaap 1991).

In this study, the degree of sectoriality within woody branches was quantified using hydraulic measurements on 18 North American and Asian temperate angiosperm tree and shrub species growing at Harvard University's Arnold Arboretum, Jamaica Plain, MA, USA. Differences in certain xylem anatomy traits (vessel size, porosity, tangential nearest-neighbour distance, density) and wood density for both springwood and summerwood were also related to differences in vascular sectoriality. After determining a suite of anatomical and physiological traits related to sectoriality, this suite was assessed relative to differences in species' ecological tolerances.

## Materials and methods

### SAMPLES

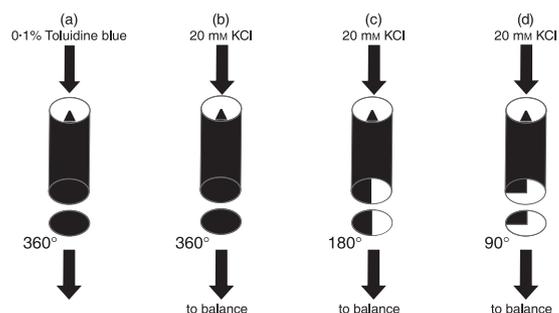
Eighteen North American and Asian temperate angiosperm tree and shrub species (see Appendix for species ranges and trait values) were sampled at Harvard University's Arnold Arboretum in Jamaica Plain, MA, USA (42°19' N, 71°5' W) with two to three species randomly selected from each of the major Angiosperm clades. Species included were *Acer pensylvanicum* L. (Sapindaceae), *Ailanthus altissima* Swingle (Simaroubaceae), *Betula populifolia* Marshall (Betulaceae), *Buckleya distichophylla* Torr. (Santalaceae), *Celtis occidentalis* L. (Celtidaceae), *Ehretia acuminata* R.Br. (Boraginaceae), *Gleditsia aquatica* Marshall (Fabaceae), *Hamamelis mollis* Oliver ex Forb. & Hemsl. (Hamamelidaceae), *Ilex opaca* [Soland.] (Aquifoliaceae), *Kalopanax septemlobus* Koidz. (Araliaceae), *Liquidambar acalycina* H.T. Chang (Altingiaceae), *Magnolia fraseri* (W. Bartram) Torr. & A. Gray (Magnoliaceae), *Nyssa aquatica* L. (Nyssaceae), *Oxydendrum arboreum* (L.) DC. (Ericaceae), *Paulownia tomentosa* Steud. (Paulowniaceae), *Picrasma quassioides* Benn. (Simaroubaceae), *Platanus occidentalis* Hook. & Arn. (Platanaceae) and *Sassafras albidum* Nees (Lauraceae).

Lower-canopy branches were collected from all 18 species using pole cutters during June and July 2003 for wood density and hydraulic measurements, and in mid-September 2003 for anatomical measurements. Hydraulics samples were kept in plastic bags and cut under water once back at Tufts University. Branch samples used for all analyses were 0.8–1.1 cm in diameter (including bark) and cut to 5 cm in length. This diameter range allowed sampling from stems >1 year old, and was chosen to control for branch length and avoid branch nodes (see below). In the hydraulic and anatomical measures, a focus was placed on vessels, as opposed to conducting tracheids, as it is assumed that vessels are moving the bulk of water.

## HYDRAULIC CONDUCTIVITY AND SECTORIALITY

Hydraulic conductivity was measured, using methods similar to those of Ellmore, Zanne & Orians 2006 based on Zwieniecki & Holbrook (1998) for two branch samples per species, except for *E. acuminata*, where only one sample was measured (this measure was similar to two other measures taken on *E. acuminata* from a separate study, A.E.Z., unpublished data), to determine both axial (direct) and tangential (indirect) conductivity. Under a microscope using a protractor reticle, the sample's proximal inflow end was sealed with a water-insoluble acrylic-based glue (Loctite Super Bonder Quick Gel 409 and Accelerator 712, Henkel Loctite Corporation, Rocky Hill, CT, USA) so that all the heartwood and all but a 60° section of the sapwood remained unsealed (Fig. 1a–d).

To map axial pathways, the inflow end of the sample was wrapped in parafilm and placed in connective tubing. A 0.1% aqueous filtered (0.22- $\mu$ m) toluidine blue stain solution was forced at 0.1 MPa (pressure was created by reducing air volume by half) with a caulking gun through the stem from a syringe (Fig. 1a). After flushing any residual stain, both cut ends of the sample were surrounded with parafilm and sealed in tubing. Then, to determine direct conductance, hydraulic measures were taken such that 0.22  $\mu$ m filtered 20-mm KCl (Zwieniecki, Melcher & Holbrook 2001) was forced through the basal end (0.1 MPa) and outflow from the distal end was sent to a balance (Denver Instrument, Denver, CO, USA) attached to a computer (Fig. 1b). To determine indirect conductance, a 180° section including half of the stained area was sealed off with glue (Fig. 1c). This step was designed to check that



**Fig. 1.** The sequence of steps used to determine axial and tangential hydraulic conductivity: white, glue; black, stain; dark grey, sapwood. Circles below the branch segments represent the distal outflow end. (a) After sealing with glue all the heartwood and all but a 60° section of the sapwood on the inflow end, axial pathways were mapped by pushing 0.1% toluidine blue stain solution (0.1 MPa) through the sample. (b) Axial conductivity ( $K_{\text{axial}}$ ) was measured by pushing 20 mM KCl through the stem (0.1 MPa). (c) After sealing with glue a 180° section of the outflow end covering half of the stained area, conductivity was remeasured to ensure that conductivity was halved from the  $K_{\text{axial}}$  value. (d) Tangential conductivity ( $K_{\text{tangential}}$ ) was measured once another 90° section covering the remaining stained area was sealed with glue.

conductance decreased by  $\approx 50\%$ ; if it did not, the sample was discarded. If conductance was reduced by  $\approx 50\%$ , an additional  $90^\circ$  section of the distal outflow end was sealed with glue (Fig. 1d), covering the rest of the stained area. Hydraulic measures were then taken as above.

Stem cross-sectional diameter including bark and pith was measured at both ends of the branch segments and averaged to determine cross-sectional area. Hydraulic conductance was divided by this cross-sectional area and multiplied by length ( $K_s$ ;  $\text{kg MPa}^{-1} \text{s}^{-1} \text{m}^{-1}$ ) for specific conductivity. Species varied greatly in axial conductivity ( $K_{\text{axial}}$ ), and this variation could influence values of tangential conductivity ( $K_{\text{tangential}}$ ). To account for this variation, each species served as its own internal control. As  $K_{\text{tangential}}$  was only measured on approximately one quarter of the cross-sectional area on the distal end, the following integration index  $= 4 \times K_{\text{tangential}}/K_{\text{axial}}$  was calculated. As species had integration indices of up to 1.18, all values were scaled such that they ranged between 0 and 1. Finally a sectoriality index  $= 1 - \text{integration index}$  was calculated, with higher values denoting greater sectoriality. Overall, this method describes the potential pathways along which resources can move, but the likelihood of these pathways being used is also dependent on a pressure gradient along the pathway (Zwieniecki *et al.* 2003).

We recognize that this hydraulic technique does not account for differences in vessel length among species. Species with shorter vessels than the sample length should encounter greater axial resistance due to end walls and thus may appear more integrated. Longer lengths, however, present their own limitations. First, nodes would have to be included and the vascular pathways would change considerably around the nodes. Second, using different lengths for different species (to standardize for vessel length) would introduce variation in frequency of vessel-to-vessel contact. We chose to avoid these confounding effects, and note that this approach provides results similar to other methods used to compare patterns of sectoriality (Orians *et al.* 2005a, 2005b).

#### XYLEM MEASURES

Vessel diameters and the distribution of vessel areas within a growth ring are key traits that may determine species-specific patterns of sectoriality. Cross-sections ( $30\text{--}40 \mu\text{m}$  thick) of each species were made with a sliding microtome, stained with Safranin-O stain and mounted on a slide in glycerol solution. Micrographs were taken with a digital camera (Olympus BX40-F) attached to a light microscope with a  $4\times$  objective using MAGNAFIRE SP software (Olympus Optical Co. Ltd, Tokyo, Japan). Second, images of three random sectors of the growth rings were taken and imported into NIH IMAGE software (ver. 1.62, <http://rsb.info.nih.gov/nih-image>, National Institute of Health, Bethesda, MD, USA) for analysis.

To measure vessel size and distribution, individual vessel area (the internal lumen) and sapwood area containing those vessels were measured. Measurements were taken from the most recent 2003 growth ring to standardize growth conditions across species. Springwood and summerwood values were treated separately, and also combined for total values. From these data, vessel density (number of vessels per sapwood area) and mean hydraulically weighted vessel diameter were determined, calculated as  $D_h = (\sum D^4/N)^{1/4}$ , where  $D$  = individual vessel diameter and  $N$  = number of vessels (Tyree & Zimmermann 2002). Coefficient of variation of individual vessel area (CV of vessel area) across the growth ring was calculated. This measure is a continuous representation of porosity, with ring-porous species having greater values than diffuse-porous species.

If two vessels are located in close proximity to one another in tangential space (around the circumference), they should be more likely to come into direct contact along the length of the stem (*sensu* Kitin *et al.* 2004) and thus share resources across their mutual pits. To determine tangential nearest-neighbour distance, three to five focal vessels were selected subjectively, radially, in both springwood and summerwood for each sector of the 2003 growth ring. For some ring-porous species, summerwood growth did not occur during 2003, so only springwood measures were available. For each focal vessel, five tangential nearest-neighbour distances were measured from vessel edge to the next closest vessel edge, and averaged.

Wood density of sapwood was measured on a 2.5-cm section taken from a branch sample of each species (adapted from Hacke, Sperry & Pittermann 2000). Wood density was determined as wood density = dry mass/wet volume ( $\text{g cm}^{-3}$ ).

#### ECOLOGICAL TOLERANCES

Ecological tolerances were determined (Flint 1997) for 16 of the 18 species. While the tolerances of Flint (1997) are based on propagating these plants in artificial settings, and do not necessarily reflect the conditions under which these species grow naturally, they do suggest the range of conditions in which the species can grow. Ecological conditions included light, wind, water and temperature. *Buckleya distichophylla* was included only in the high shade-tolerance category, as it is known to grow in the forest understorey (personal observation). All tolerances except temperature were represented as a bar showing minimum and maximum tolerances along a range. Ranges were separated into seven positions from low to high ecological tolerance (e.g. from low light to high light). Species tolerances for shade, wind, flood and drought were recorded in two categories (high and low) by dividing tolerances: low shade tolerance included positions  $<4$  along the range ( $N = 5$ ) and high shade tolerance included positions  $>5$  along the range ( $N = 12$ ); low wind tolerance included positions  $<4$  along the range ( $N = 7$ ) and

high wind tolerance included positions >5 along the range ( $N = 9$ ); low flood tolerance included positions <2 along the range ( $N = 5$ ) and high flood tolerance included positions >3 along the range ( $N = 11$ ); low drought tolerance included positions <5 along the range ( $N = 14$ ) and high drought tolerance included positions >6 along the range ( $N = 2$ ). These divisions between low and high tolerance reflect the most equal divisions between the groups. They were not divisible further, as numerous species in the middle of the range would have similar tolerance values. Drought tolerance was incorporated only in the multivariate analysis, as only two species had high tolerance. Temperature was a continuous variable describing the minimum temperature that species can tolerate in cultivation.

#### ANALYSES

To increase normality of distributions, all measures were  $\log_{10}$ -transformed except sectoriality index, which was arcsine square root-transformed because it is a ratio. As sampling was limited to one tree per species, due in part to working in an arboretum, individual species differences were not examined. Instead, patterns were investigated across species for trait associations with sectoriality. We note that work with these and other species has shown consistent rankings among species (Orians *et al.* 2005a; Ellmore *et al.* 2006; A.E.Z., unpublished data).

#### Results

Sectoriality index was significantly correlated with anatomical traits (Table 1). Species with high sectoriality index (more sectorial) had larger springwood and total  $D_h$  (hydraulically weighted vessel diameter; Fig. 2a);

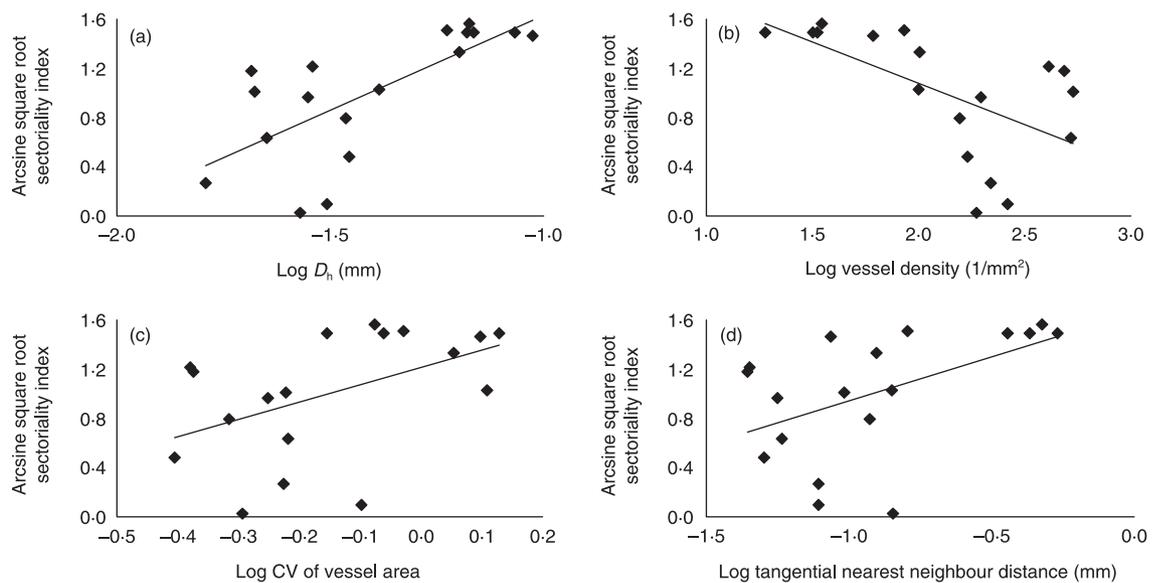
**Table 1.** Pearson's product moment correlations between sectoriality index and anatomical (hydraulically weighted vessel diameter,  $D_h$ ; wood density; vessel density; CV of vessel area; tangential nearest-neighbour distance) traits for 18 Northern Hemisphere temperate tree and shrub species from Arnold Arboretum, Jamaica Plain, MA, USA

Trait	Sectoriality index
$D_h$	
Spring	<b>0.689</b>
Summer	0.423
Total	<b>0.710</b>
Wood density	-0.230
Vessel density	
Spring	<b>-0.570</b>
Summer	<b>-0.620</b>
Total	<b>-0.584</b>
CV of vessel area	
Spring	0.414
Summer	0.286
Total	<b>0.479</b>
Tangential nearest-neighbour distance	
Spring	<b>0.555</b>
Summer	<b>0.547</b>
Total	<b>0.500</b>

Significant relationships at  $P < 0.05$  in bold,  $P < 0.1$  in italic. Sample size was  $N = 18$  for all tests, except summer anatomical measures ( $N = 15$ ).

lower vessel density (Fig. 2b); greater total CV of vessel area (Fig. 2c); and larger nearest-neighbour distances (more isolated vessels; Fig. 2d). Both CV of vessel area in summerwood and wood density were unrelated to the sectoriality index.

Species with smaller sectoriality index (more integrated) had high tolerance to shade ( $t = 3.31$ ,  $P = 0.005$ ) and flood ( $t = 5.20$ ,  $P < 0.001$ ), while no significant

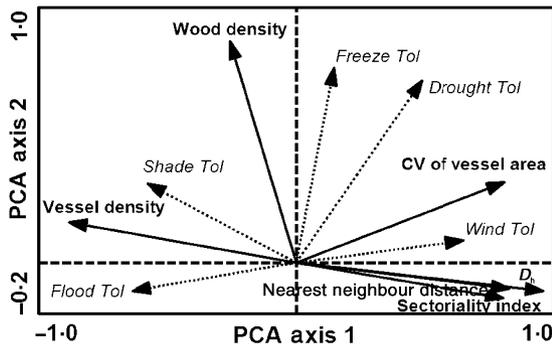


**Fig. 2.** Relationships between arcsine square root of sectoriality index vs various anatomical traits for Northern Hemisphere temperate tree and shrub species from Arnold Arboretum, Jamaica Plain, MA, USA. Lines represent best-fit linear regressions. (a) Hydraulically weighted vessel diameter,  $D_h$ ; (b) vessel density; (c) CV of vessel area; (d) tangential nearest-neighbour distance.

**Table 2.** Eigenvalues and factor loadings for hydraulic, anatomical and ecological tolerance traits for the first two axes using principal components analyses for 16 Northern Hemisphere temperate tree and shrub species from Arnold Arboretum, Jamaica Plain, MA, USA

Trait	Axis 1	Axis 2
Eigenvalue	0.47	0.19
Cumulative percentage variance	47.0	66.4
Total hydraulically weighted vessel diameter ( $D_h$ )	<b>0.960</b>	-0.111
Total vessel density	<b>-0.883</b>	0.158
Total tangential nearest-neighbour distance	<b>0.828</b>	-0.102
Total CV of vessel area	<b>0.809</b>	0.315
Sectoriality index	<b>0.805</b>	-0.140
Wind tolerance	<b>0.650</b>	0.087
Flood tolerance	<b>-0.635</b>	-0.111
Shade tolerance	<b>-0.576</b>	0.310
Drought tolerance	<b>0.488</b>	<b>0.714</b>
Wood density	-0.256	<b>0.867</b>
Freeze tolerance	0.147	<b>0.764</b>

Numbers in bold denote strong factor loadings.



**Fig. 3.** Biplot of hydraulic, anatomical and ecological tolerance traits along axes 1 and 2 using principal components analyses for 16 Northern Hemisphere temperate tree and shrub species from Arnold Arboretum, Jamaica Plain, MA, USA. For shade-, drought-, flood- and wind-tolerance traits, low values were coded as 0 and high values as 1. Vessel density; hydraulically weighted vessel diameter,  $D_h$ ; CV of vessel area; and tangential nearest-neighbour distance are total values (recorded across both seasons).

differences in the sectoriality index were found between species with low or high tolerance to wind ( $t = -1.53$ ,  $P = 0.149$ ). No significant correlations were found between freeze tolerance and sectoriality index.

When anatomical, sectoriality index and ecological tolerance values were compared together in a principal components analysis (PCA), axis 1 explained 47.0% and axis 2 explained 19.4% of the variance in the data (Table 2; Fig. 3). Axis 1 described anatomical and ecological tolerance traits related to hydraulics. As this axis increased, species had a higher sectoriality index,  $D_h$ , tangential nearest-neighbour distance (more isolated), and CV of vessel area. Moreover, these species had greater wind and drought tolerance, but lower vessel density and lower flood and shade tolerance.

Axis 2 described ecological tolerance traits related to wood density, with wood density, freeze tolerance, and drought tolerance increasing together.

## Discussion

In this study of 18 North American and Asian temperate tree and shrub species, hydraulic sectoriality showed considerable interspecific variation. This variation was strongly related to xylem anatomical traits, especially those traits associated with vessel size and distribution. Both hydraulic sectoriality and xylem anatomy were correlated with interspecific differences in species ecological tolerances, suggesting that species growing in drier environments, including those in high wind and light, tended to be more sectored; and species growing in shady or flood-prone environments tended to be more integrated.

## HYDRAULICS AND ANATOMY

While studies have documented interspecific differences in hydraulic sectoriality for a limited set of trees (Richardson 1958 as cited by Zimmermann & Brown 1971; Rudinsky & Vité 1959; Larson *et al.* 1994; Orians *et al.* 2004, 2005b), the mechanisms leading to this variation are less well known. As the water-delivery pathway consists of vessels and intervessel pits, variation in these traits is an obvious candidate; integration should increase with the frequency and length over which vessels come into contact and with the amount of wall space in and porosity of intervessel pits (Orians *et al.* 2005a). This study demonstrates that sectoriality tends to be higher in species with isolated vessels at low density and high CV in the vessel area. Thus the role of intervessel contact appears to be quite important. Further studies investigating the roles of length of vessel-to-vessel contact (Kitin *et al.* 2004) and intervessel pitting (as was done for end-wall pitting by Wheeler *et al.* 2005) in facilitating tangential water movement are logical next steps.

Additionally, the sectored species with variable vessel diameters are (by definition) the more ring-porous species. Earlier work has suggested a link between sectoriality and ring-porosity (Richardson 1958 as cited by Zimmermann & Brown 1971; Orians *et al.* 2005b). Although CV in vessel diameter (ring-porosity) is an important correlate of sectoriality in this study, it is not the only one. Our previous work demonstrates extensive variation in sectoriality among diffuse-porous temperate tree species (Orians *et al.* 2004, 2005b). Moreover, trees in wet and dry tropical forests in Costa Rica were all diffuse-porous yet vary in sectoriality (C.M.O. and A.E.Z., unpublished data). Even among conifers that lack vessels, variation in sectoriality occurs (Rudinsky & Vité 1959; Larson *et al.* 1994). Thus ecological settings and phylogenetic relations can lead to variability in the links between these hydraulic and anatomical traits.

## TRADE-OFFS – WHY BE SECTORED?

In temperate seasonal environments with highly variable temperature and moisture availability, sectored and integrated species (ring-porous and diffuse-porous, respectively) co-occur, although abundance varies among environments (e.g. mesic *vs* xeric; Guthrie 1989; see below). As hydraulic conductivity is predicted to increase to the fourth power of the diameter (Tyree & Zimmermann 2002), sectored species with large-diameter springwood vessels would be able to move much more water when it is readily available than small diameter vessels. But, as vessel diameter increases, vessels would become more vulnerable to freeze-induced embolism (Sperry *et al.* 1994; Tyree, Davis & Cochard 1994), blocking the path of water flow. While vulnerability to drought-induced embolism should be best related to porosity of the pit membrane (Hacke & Sperry 2001; Tyree & Zimmermann 2002), some evidence suggests a positive relationship between vessel diameter and propensity to embolize during drought (Hargrave *et al.* 1994; Tyree & Zimmermann 2002; Baas *et al.* 2004; Wheeler *et al.* 2005). Thus a trade-off may well be occurring. Sectored species have high hydraulic efficiency with wide, isolated vessels allowing high hydraulic conductivity while avoiding the spread of drought-induced embolism. In contrast, integrated species have high hydraulic safety with narrow vessels allowing low hydraulic conductivity, but can avoid freeze-induced embolism (Hacke & Sperry 2001). The strong links between sectoriality and porosity may well be a result of the seasonal temperate environment, where species have to persist through both drought and freezing.

ECOLOGICAL IMPLICATIONS: SPATIAL *VS*  
TEMPORAL VARIATION

Differences in ecological tolerance among these species were related to variability in sectoriality. We suggest that sectored species may do best in temporally variable environments, while integrated species may do best in spatially variable but temporally predictable environments. Sectored species could be investing in hydraulic efficiency in the spring for rapid conductivity when moisture is most available (Abrams 1990; Tyree *et al.* 1994) and safety when moisture availability declines during the summer (or during episodic droughts; Larson *et al.* 1994), while integrated species could be investing in hydraulic safety throughout the year. These differences probably contribute to differences in distribution within a forest. Sectored ring-porous species have been found to dominate xeric sites that are probably undergoing larger seasonal shifts in water availability, while integrated diffuse-porous species have been found to dominate mesic to hydric sites (Waisel *et al.* 1972; Watson & Casper 1984; Guthrie 1989), where substantial spatial variation in resource availability occurs.

The tolerance of sectored species to high light, wind and drought conditions suggests that these species do

best in environments that are patchy over time, at least for moisture, with high wind and light contributing to increased drying. They may capitalize on the ephemeral higher water availability in the spring with rapid growth, but minimize embolism spread, especially in their summerwood. The latter response may be especially directed towards isolating embolized springwood from still-functioning summerwood. Within an annual growth ring of the ring-porous *Fraxinus languinosa*, Kitin *et al.* (2004) found vessel-to-vessel contact and pitting within springwood and within summerwood, but very little contact between spring and summerwood vessels.

On the other hand, more integrated diffuse-porous species are likely to grow best in environments that are spatially patchy (Orians & Jones 2001), such as in flooded soil or low-light understorey conditions. Flooded soils decrease root access to gases such as oxygen (Kreuzwieser, Papadopoulou & Rennenberg 2004), and species growing in the low light of the forest understorey are quite dependent on ephemeral sunflecks that reach a small portion of the plant's crown (Chazdon 1988). These patchy distributions of resources will probably lead to patchy uptake by the plant. In integrated plants, impoverished sectors of the plant will be able to draw resources from enriched sectors.

Based on our findings, we suggest that studies examining the patterns of sectoriality and the consequences of differential sectoriality for a species' tolerance of temporal and spatial heterogeneity are warranted. It would be especially interesting to ascertain the generality of the pattern found here, determining whether differences hold across other seasonal or aseasonal environments. For instance, does the co-ordination of vessel size and sectoriality hold when freezing is not a limiting environmental factor (lowland tropical forests), or in drought-dominated communities where leaf phenology is important to drought avoidance (e.g. the Great Basin; Sperry & Hacke 2002)?

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### Supplementary material

The following supplementary material is available for download as part of the full-text version of the article from <http://www.blackwell-synergy.com>

**Appendix S1.** Species means for hydraulic, anatomical and ecological tolerance traits for 18 northern hemisphere temperate tree and shrub species from Arnold Arboretum, Jamaica Plain, MA.