

COORDINATION OF FOLIAR AND WOOD ANATOMICAL TRAITS CONTRIBUTES TO TROPICAL TREE DISTRIBUTIONS AND PRODUCTIVITY ALONG THE MALAY-THAI PENINSULA¹

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Drought is a critical factor in plant species distributions. Much research points to its relevance even in moist tropical regions. Recent studies have begun to elucidate mechanisms underlying the distributions of tropical tree species with respect to drought; however, how such desiccation tolerance mechanisms correspond with the coordination of hydraulic and photosynthetic traits in determining species distributions with respect to rainfall seasonality deserves attention. In the present study, we used a common garden approach to quantify inherent differences in wood anatomical and foliar physiological traits in 21 tropical tree species with either widespread (occupying both seasonal and aseasonal climates) or southern (restricted to aseasonal forests) distributions with respect to rainfall seasonality. Use of congeneric species pairs and phylogenetically independent contrast analyses allowed examination of this question in a phylogenetic framework. Widespread species opted for wood traits that provide biomechanical support and prevent xylem cavitation and showed associated reductions in canopy productivity and consequently growth rates compared with southern species. These data support the hypothesis that species having broader distributions with respect to climatic variability will be characterized by traits conducive to abiotic stress tolerance. This study highlights the importance of the well-established performance vs. stress tolerance trade-off as a contributor to species distributions at larger scales.

Key words: abiotic stress; climatic variability; gas exchange; geographic range size; Malaysia; Thailand; tropical forest dynamics; wood anatomy.

The connection between plant traits and environmental conditions has long been recognized (e.g., Cowles, 1899) and continues to be an active area of research contributing substantially to our understanding of species distributional patterns at local, regional, and global scales (Wright et al., 2006; Ackerly and Cornwell, 2007; Cornwell and Ackerly, 2009). Much recent work has emphasized trade-offs between performance and stress tolerance with respect to foliar and wood traits (Reich et al., 2003; Wright et al., 2004; Hacke et al., 2006; Chave et al., 2009) as well as whole-plant measures such as growth and mortality (Russo et al., 2005, 2008). Furthermore, there is functional coordination among these traits with limits as to the trait combinations and values possible

(Wright et al., 2004; Chave et al., 2009). Generally speaking, we expect that a species will be characterized by a suite of functional traits that provide some adaptive advantage in terms of growth and/or survival in its native habitat but may have negative consequences for competitive ability or survival in another habitat (Ackerly, 2003).

Species range sizes vary by orders of magnitude, and with increasing range, species encounter greater variability with respect to environmental conditions. It is predicted that species having the capacity to span broader environmental gradients will necessarily be more tolerant of abiotic stress (Morin and Chuine, 2006). Recent work examining the distribution of tropical tree species with respect to a rainfall seasonality gradient provided evidence of this trade-off in that widespread species occupying both aseasonal and seasonal forests had lower growth rates and sensitivity to local habitat variability when compared with species restricted to the aseasonal forests (Baltzer et al., 2007). The basis of such differences presumably lies in trade-offs occurring among the functional traits that are best suited for the resource availability encountered by each distributional grouping. If seasonal drought is contributing to these distributional limits then we would expect to see more conservative functional traits that enhance drought tolerance in the widespread species. Lethal water potential (i.e., the lowest water potential at which a plant can maintain living tissue) and the corresponding minimum relative water content have been shown to correspond well with tree species' distributions along rainfall and seasonality gradients in the equatorial tropics (Engelbrecht and Kursar, 2003; Baltzer et al., 2008). However, the mechanistic basis of differential lethal

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water potentials presumably lies in the ability to prevent or minimize cavitation and resulting xylem dysfunction during drought, thereby maintaining water flow through the plant and supporting living tissues. There should thus be an important contribution of wood anatomical traits (either via contribution to cavitation avoidance or tolerance) with implications for potential canopy productivity due to the inherent coordination of these traits. In the present study, we attempt to quantify such functional coordination of foliar and wood anatomical traits and its role in tropical tree distributions with respect to rainfall seasonality.

It is well known that canopy photosynthesis is largely under the control of hydraulic architecture as stomatal response is critical to avoidance of hydraulic limitations (Meinzer et al., 1995; Nardini and Salleo, 2000; Sperry, 2000). Furthermore, hydraulic and xylem anatomical traits form the basis of species' resistance to loss of xylem function via cavitation (the spontaneous transition of water from liquid to gas when under excessive tension). It is well accepted that an important mechanism affording drought tolerance is a "safe" hydraulic system but that the traits providing such safety may compromise the hydraulic efficiency via increased resistance to water transport (Baas et al., 2004; Hacke et al., 2006; Pratt et al., 2007). In this way, safety from embolism limits canopy productivity and should result in lower growth rates. Thus, one would anticipate that the leaf and wood economics spectra will also be correlated, with stress tolerant species having both conservative foliar and safe wood traits. Indeed, there is a growing body of theoretical and empirical evidence of the coordination between the plant hydraulic system and foliar photosynthetic traits (Brodribb and Feild, 2000; Brodribb et al., 2002; Katul et al., 2003; Bucci et al., 2004; Santiago et al., 2004; Ishida et al., 2008).

Poleward from the equator, a strong gradient in rainfall seasonality impacts forest structure, diversity, and productivity (Gentry, 1988; Clark et al., 2001; Engelbrecht et al., 2006). Water availability exerts a strong influence over wood anatomical structure and clear patterns of differentiation in the conduit structure have long been recognized between dry and wet climates (e.g., Carlquist, 1977). Furthermore, global examinations of hydraulic traits as a function of climate have demonstrated a significant correlation between resistance to cavitation and mean annual precipitation in evergreen angiosperms (Maherali et al., 2004). In the present study, we quantified a range of wood anatomical features and foliar physiological traits in tree species occurring along the Malay-Thai Peninsula having widespread (occurring in both aseasonal and seasonally dry forests) or southern (restricted to aseasonal forests) distributions. We predicted that wood anatomical and leaf trait coordination should be evident such that "safer" wood anatomical features that contribute to cavitation resistance during drought will come at the cost of lower canopy productivity. Therefore, we would expect more conservative leaf traits in those species capable of occupying seasonally dry forests. Baltzer et al. (2007) previously demonstrated performance differences along this same gradient, and we anticipate that coordination of the hydraulic system and photosynthetic traits underlies these performance-related differences.

MATERIALS AND METHODS

Study area—The Kangar-Pattani Line (hereafter the KPL) is a key phyto-geographical transition that bisects the Thai-Malay Peninsula near the political

border (Van Steenis, 1950). At this transition, over 500 genera of vascular plants meet their distributional limits. Because there is presently no geophysical barrier at the KPL, two mechanisms have been proposed as potential explanations for this floristic transition. The first is historical in nature and hypothesizes that during the Miocene and Pliocene eras seaways bisected the Thai-Malay Peninsula at both the KPL and the Isthmus of Kra (Fig. 1) (Woodruff, 2003). A second, environmentally derived mechanism has also been invoked for explaining distributional patterns at the KPL. Specifically, the KPL coincides with a major climatic transition that occurs along the Peninsula; forests south of the KPL are perhumid (i.e., relative humidity typically 100% or greater) and aseasonal, while those to the north are seasonally dry with a 2–3 mo drought with little or no change in total annual rainfall; such a climatic transition could presumably play a critical role in determining the distributions of plant species (Whitmore, 1984; Ashton, 1997). Forests to the north of the KPL are evergreen, seasonal forests with low incidence of drought deciduousness.

Plant material and growth conditions—The mature seeds of 21 tree species (Table 1) were collected between July and October 2005 in the Pasoh Forest Reserve, Malaysia (2°58'N, 102°18'E) and the Khao Chong Peninsular Botanical Garden, Thailand (7°34'N, 99°47'E) (hereafter Pasoh and Khao Chong; Fig. 1). Average rainfall in Pasoh is 1950 mm·y⁻¹ (0 mo of drought) and 2700 mm·y⁻¹ (2–3 mo of drought) in Khao Chong. Minimum/maximum temperatures daily temperatures in Pasoh and Khao Chong are 23/33°C and 22/34°C, respectively. Species were classified as southern or widespread based upon floristic records for the region. Primary sources were the *Tree Flora of Malaya* (Whitmore, 1972), *Flora Malesiana* (Van Steenis, 1950), and *Flora of Thailand* (Smitinand and Larsen, 1970), all of which list the states/provinces and other countries in which the species occurs. Additional range data were collected from other reliable sources (e.g., Symington, 2004; Van Welzen and Chayamarit, 2005). Species with no floristic records in the seasonally dry forests north of the KPL were classified as southern, while those whose distributions traversed the rainfall gradient were classified as widespread. For all but two species, the seeds of two or more individuals were obtained (Table 1). All seeds were germinated and seedlings grown in polybags (15.2 cm diameter × 22.9 cm height) filled with clay-rich soil collected near Pasoh. A wooden structure covered with neutral density shade cloth provided 15% full sunlight during the study. Minimum/maximum temperature, humidity, and vapor pressure deficit (VPD) within the structure were 23/31°C, 62/100%, and 0/0.23 psi, respec-

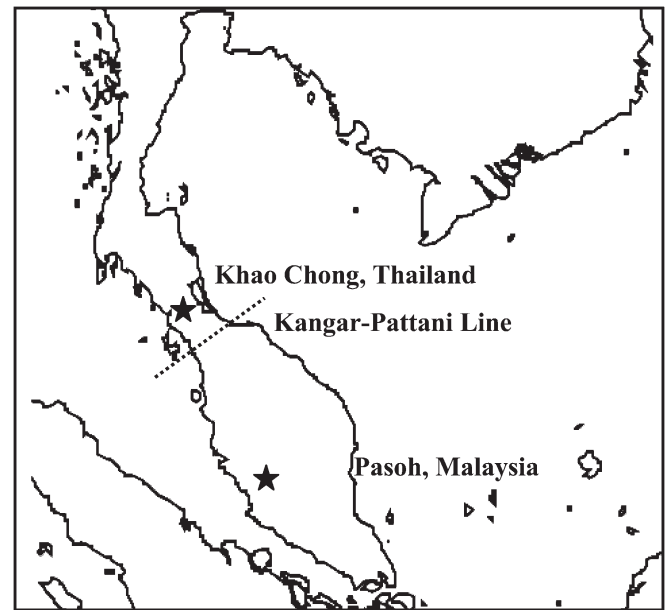


Fig. 1. Map of the locations of the Kangar-Pattani Line (KPL; dashed line), Pasoh Forest Reserve (Pasoh; Peninsular Malaysia, 2°58'N, 102°18'E) and Khao Chong Peninsular Botanical Garden (Khao Chong; Peninsular Thailand, 7°34'N, 99°47'E). North of the KPL the climate is largely seasonal while to the south rainfall is primarily aseasonal. Modified from Baltzer et al. (2008).

TABLE 1. List of study species, family and distributions (Dist; S = southern, W = widespread) in relation to the Kangar-Pattani Line. Habit indicates the location in the canopy: E, emergent; M, main canopy; U, understory. Abbreviations (Abb.) correspond to those in Figs. 2–4. Location indicates the seed collection site (P = Pasoh, KC = Khao Chong); number of seed sources is indicated in parentheses. In the Dipterocarpaceae, mast fruiting often did not allow accurate counts of seed sources; thus the numbers represent the seed collection locations. Perforation plate type and vestures are defined in Table 2.

Family	Species	Habit	Abb.	Dist.	Location	Perforation plate	Vestures
Dipterocarpaceae	<i>Parashorea stellata</i> Kurz.	Tree; E	pst	W	KC (5)	Scalariform	No
	<i>Parashorea densiflora</i> (Y.Sl.) ex Sym.	Tree; ME	pde	S	P (1)	Simple	No
	<i>Shorea guiso</i> (Blanco) Blume	Tree; E	sgu	W	P (2)	Simple	No
	<i>Shorea lepidota</i> (Korth) Blume	Tree; E	sle	S	P (>3)	Simple	Yes
	<i>Shorea macroptera</i> Dyer	Tree; E	sma	S	P (>3)	Simple	Yes
	<i>Shorea parvifolia</i> Dyer	Tree; E	spa	S	P (>3)	Simple	Yes
Euphorbiaceae	<i>Mallotus penangensis</i> Müll. Arg.	Tree; M	mpe	S	P (3)	Simple	Yes
	<i>Neoscortechinia kingii</i> Hk.f.	Tree; M	nki	S	P (2)	Simple	No
Fabaceae	<i>Millettia atropurpurea</i> (Wall.) Benth.	Tree; M	mat	W	P (2); KC (5)	Simple	Yes
	<i>Sindora coriacea</i> (Baker) Prain	Tree; E	sco	W	P (3); KC (2)	Simple	Yes
	<i>Sindora wallichii</i> Graham ex Benth	Tree; M	swa	S	P (3)	Simple	Yes
Fagaceae	<i>Lithocarpus wrayi</i> (King) A. Lamus	Tree; M	lwr	S	P (2)	Scalariform	No
	<i>Quercus semiserrata</i> Roxb.	Tree; M	qse	W	KC (2)	Simple	No
Phyllanthaceae	<i>Aporosa globifera</i> Hook f.	Tree; U	agl	S	P (2)	Scalariform	No
	<i>Aporosa microstachya</i> Hook f.	Tree; U	ami	W	P (5)	Simple	No
	<i>Aporosa symplacoides</i> (Hook f.) paqx	Tree; U	asy	S	P (3)	Scalariform	No
Polygalaceae	<i>Xanthophyllum affine</i> Korth.	Tree; M	xaf	W	P (1)	Simple	Yes
Sapotaceae	<i>Palaquium maingayi</i> K&G	Tree; M	pma	S	P (3)	Scalariform	No
	<i>Palaquium sumatrana</i> Burck	Tree; M	psu	W	KC (2)	Simple	No
	<i>Payena lucida</i> (Don) DC	Tree; M	plu	W	P (>3)	Simple	No
Violaceae	<i>Rinorea anguifera</i> (Lour.) OK	Tree; U	ran	W	P (8)	Simple	No

tively. Seedling locations within the nursery were randomly assigned and rotated regularly to avoid confounding effects of light and temperature gradients. Seedlings were watered daily if diurnal rainfall had been insufficient. After 1 year of growth, stems and leaves were harvested from the saplings. The stems were stored in 70% ethanol for processing at a later date.

Foliar trait measurements—Using a LI-6400 gas-exchange system (Licor, Lincoln, Nebraska, USA) we measured gas exchange on recent, fully expanded leaves of four individuals per species (and provenance where seeds of multiple provenances were collected). Measurements were made from 9 to 16 July 2006 before noon with cuvette conditions maintained at 370 ppm CO₂ and 60–80% relative humidity (RH) and leaf temperatures between 25 and 30°C. Gas-exchange measurements were made at light levels of 0 and 1500 μmol·m⁻²·s⁻¹. Stability of gas-exchange values was determined visually using graphics available in the LI-6400 programming. Maximum stomatal conductance to water (g_w) corresponding to A_{max} was used to characterize stomatal response across species and distribution. Gas-exchange leaves were harvested, measured for fresh leaf area, dried at 60°C, and weighed for calculation of leaf mass per area (LMA).

Wood anatomical trait measurements—Stem sections from three specimens of each species were used to characterize anatomical traits. Stem cross and tangential sections were made for each sample using a sliding microtome at 20 μm and 5 μm thickness, respectively. All sections were wet mounted and digital images obtained using a Carl Zeiss Photomicroscope I (Oberkochen, Germany) combined with a PixeLink PL-A662 Camera Kit (Prague, Czech Republic). Photographic scale was calibrated using a standard ocular micrometer slide. All vessels in each image (~100 vessels) were measured. The diameter and total area of every vessel in each cross-sectional image was measured, as was total xylem area. From these measurements, maximum vessel diameter and vessel fraction (vessel area/xylem area) were determined. Vessel diameter contributes directly to the upper limit on rate of flow in the vessel and correlates positively with the pore area in the perforation plates that connect adjacent xylem vessels (Chave et al., 2009). Larger vessels mean more efficient flow but correspond with larger pit area and higher probability of large pit pores. Vessels with large pores are more prone to cavitation by air seeding (Choat et al., 2003; Hacke et al., 2006). Similarly, a larger vessel fraction accommodates greater water flow to the canopy. Hydraulically weighted mean diameter was calculated as:

$$2(\sum r^5 / \sum r^4)$$

following Sperry et al. (1994). This weights the proportional importance of radii to the estimated hydraulic conductance of the conduits and corresponds

closely with hydraulic conductance (Sperry et al., 1994; Pratt et al., 2007). The double wall thickness of adjacent conduits (*t*) was quantified from the tangential sections and the maximum conduit span (*b*) estimated following Hacke et al. (2001); these two metrics allow for the calculation of conduit reinforcement as (*t/b*)². Wood density was calculated as the oven-dried mass of the wood sample divided by the green volume measured following removal of bark and pith (Hacke et al., 2000). Wood density correlates with cavitation resistance and stress tolerance because high wood density is generally associated with greater structural reinforcement of the xylem (Hacke et al., 2001). Both wood density and conduit reinforcement have been shown to be excellent predictors of the water potential at which 50% loss of hydraulic conductivity by cavitation is observed (Hacke et al., 2001; Pratt et al., 2007). Perforation plate type and vesture presence were also determined from the tangential sections. The type of perforation plates present influence the rate at which water can move up and down the vessels (hydraulic efficiency). Simple perforation plates having a single opening create less friction as water moves through them than do scalariform perforation plates (multiple elongated openings separated by ladder-like bars) (Baas, 1986; Carlquist, 2001; but see Schulte et al., 1989); however, the relative importance of this is a function of the pore size and number in the scalariform perforation plate (Schulte, 1999).

Statistical analysis—In two cases (*Millettia atropurpurea* and *Sindora coriacea*), seeds were collected from both the Pasoh and Khao Chong provenances. These samples are included in all analyses as separate data points. Sample sizes for gas-exchange and wood anatomy traits were 4 and 3, respectively. To test for the effect of distribution on wood and leaf traits, we conducted a randomized block ANOVA with distribution as the fixed variable and genus as the random variable. Dependent variables included four foliar traits (area-based photosynthetic and respiration rates [A_{max} and R_d respectively], maximum stomatal conductance [g_s], and leaf mass per area [LMA]) and five wood traits (maximum vessel diameter, mean hydraulic diameter, wood density, (*t/b*)², and vessel fraction). Trait names, abbreviations, and units of measure can be found in Table 2. Species mean trait values can be found in Appendix S1 (see Supplemental Data with the online version of this article). To meet assumptions of normality maximum vessel diameters, vessel fraction, and wood density were log-transformed prior to analysis. To assess how measured traits were associated and where the two distributional groups occurred in multivariate trait space, we conducted a principal component analysis (PCA). Due to unusually high maximum vessel diameter values in the two provenances of *Millettia atropurpurea*, this species was excluded from the PCA. LMA was not correlated with any of the significant components, so it was removed from the analysis. Perforation plate type and presence/absence of vesturing were coded with

dummy variables (0 = simple, 1 = scalariform; 0 = vestures absent, 1 = vestures present). Differences in loadings along the first two axes as a function of distribution were tested using ANOVA. These analyses were conducted using the program R (v. 2.1; R Foundation for Statistical Computing, Vienna, Austria).

To determine coordination of and potential shifts in hydraulic and photosynthetic traits as a function of distribution, we employed standardized major axis regression analysis using the SMATR program (Falster et al., 2003). For these analyses, species' mean values were used. None of the significant linear relationships showed elevational shifts in the intercept or shifts along a common slope; therefore, only pooled cross-species bivariate trait correlations are presented. To account for phylogenetic relatedness in the bivariate relationships, we conducted phylogenetically independent contrasts (PICs) (Felsenstein, 1985). We used a maximally resolved tree created in the program Phylomatic 2 (Webb and Donoghue, 2007), which employs the angiosperm phylogeny (Stevens, 2001) as the hypothesis for the phylogenetic relationships among study taxa. Phylogenetic relationships to the genus level of the broad range of taxa included in our study are well resolved. The tree was then run through the program *bladj* (Webb and Donoghue, 2007), which uses the angiosperm node ages of Wikström et al. (2001) to assign conservative branch lengths by placing the nodes evenly between dated nodes, and between dated nodes and terminals. This minimizes variance in branch length, within the constraints of dated nodes and can be a marked improvement on using the number of intervening nodes as a phylogenetic distance (Webb, 2000). Where polytomies occurred that could not be resolved by genus-specific phylogenies, we randomly split the species to force the bifurcating structure necessary for PIC. There were only two instances where this had to be done: the light-red meranti section of *Shorea* (*S. parvifolia*, *S. macroptera* and *S. lepidota*) and the genus *Aporosa*. Because of the low number of polytomies, altering the order of the branching pattern in these had little impact (data not shown). Correlation coefficients were calculated for resulting PICs on a pairwise basis.

RESULTS

Does distribution with respect to seasonality predict leaf and wood traits?—Distribution with respect to rainfall seasonality affected all wood traits examined with the exception of maximum vessel diameter and mean hydraulic diameter (Fig. 2). Vessel fraction was significantly lower in widespread species while both $(t/b)^2$ and wood density were significantly higher in species having widespread distributions with respect to rainfall seasonality (Fig. 2). Foliar traits similarly showed systematic shifts with respect to species' distributions with the exception of leaf mass per area (Fig. 3). Area-based photosynthetic and respiration rates and maximum stomatal conductance were all significantly higher in southern-distributed species though the difference in stomatal conductance was only marginally significant (Fig. 3).

There were four significant components in the PCA explaining 84% of the variation across species; the first two components explained 55% of the total variation. The two distributional categories separated significantly along the first axis ($F_{1,19} = 8.12$, $P = 0.0102$); widespread species tended to be located in the right quadrats, while southern species were located in the left quadrats (Fig. 4). All traits with the exception of perforation plate type and g_s loaded quite strongly onto the first axis (Fig. 4). This axis essentially corresponds with the safety–efficiency trade-off with widespread species located largely to the right of the axis with high wood density and conduit reinforcement and southern species to the left with high physiological rates, large maximum vessel diameters and hydraulic means, and high vessel fractions. Along the second axis, there seems to be a bit of a breakdown in terms of the trait coordination with physiological traits and perforation plate type (0 = simple, 1 = scalariform) loading positively and wood anatomical traits, with the exception of the vessel fraction, loading negatively. Distributional grouping (S vs. W) did not separate significantly along the second axis ($F_{1,19} = 1.26$, $P = 0.2752$); however, it should be noted with the exception of perforation plate type (axis 1) and R_d (axis 2), all traits loaded significantly onto both axes (Fig. 4A). In general, species having widespread distributions were characterized as having conservative, stress tolerant traits, while southern species tended to have traits associated with faster growth.

Coordination of anatomical and photosynthetic traits—

There were several hydraulic–photosynthetic trait pairs that showed coordination within our cross-species analysis (Table 3A).

Both A_{\max} and g_s showed a significant, positive relationship with LMA and correlated positively with one another (Table 3A). R_d showed significant positive correlations with maximum vessel diameter and mean hydraulic diameter (Table 3A). LMA did not correlate with any of the wood anatomical traits measured. Vessel fraction was positively correlated with both maximum vessel diameter and hydraulic mean, which showed the strongest correlation of all pairs, and correlated negatively with wood density. There was a moderate positive correlation between wood density and $(t/b)^2$ (Table 3A).

Most of the same relationships existed when phylogenetically independent contrasts were used for the correlation analysis, and for the most part, these relationships were strengthened

TABLE 2. Symbols, units of measurement, and definitions for all traits measured in the study.

Trait	Symbol	Units	Definition
Photosynthetic capacity	A_{\max}	$\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$	Area-based carbon assimilation at saturating light conditions
Dark respiration rate	R_d	$\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$	Area-based carbon loss in the dark
Maximum stomatal conductance	g_s	$\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$	Resistance for diffusion of water vapor through the stomata
Leaf mass per area	LMA	$\text{g}\cdot\text{cm}^{-2}$	Leaf mass expressed per unit leaf area
Maximum vessel diameter	Max vessel	μm	Upper fifth percentile of all cross-sectional vessel diameters
Vessel fraction	Vessel fraction	—	Ratio of cross-sectional area occupied by vessels to that occupied by all xylem tissue
Wood density	Density	$\text{g}\cdot\text{cm}^{-3}$	Mass of oven-dried wood per green volume
Conduit reinforcement	$(t/b)^2$	—	Double wall thickness (t) relative to the maximum span of the vessel (b) (see Hacke et al., 2001)
Mean hydraulic diameter	Hydraulic mean	μm	Hydraulically weighted mean diameter that weights the importance of radii in proportion to estimated hydraulic conductance of the conduits (Sperry et al., 1994)
Perforation plate type	Perforation	—	Openings in end wall of vessel elements where primary wall and middle lamella have been hydrolyzed allowing free water flow between vessels
Vestures	Vestures	—	Bordered pits where pit chamber or outer pit aperture is wholly or partially lined with projections from secondary cell wall (see Jansen et al., 2004)

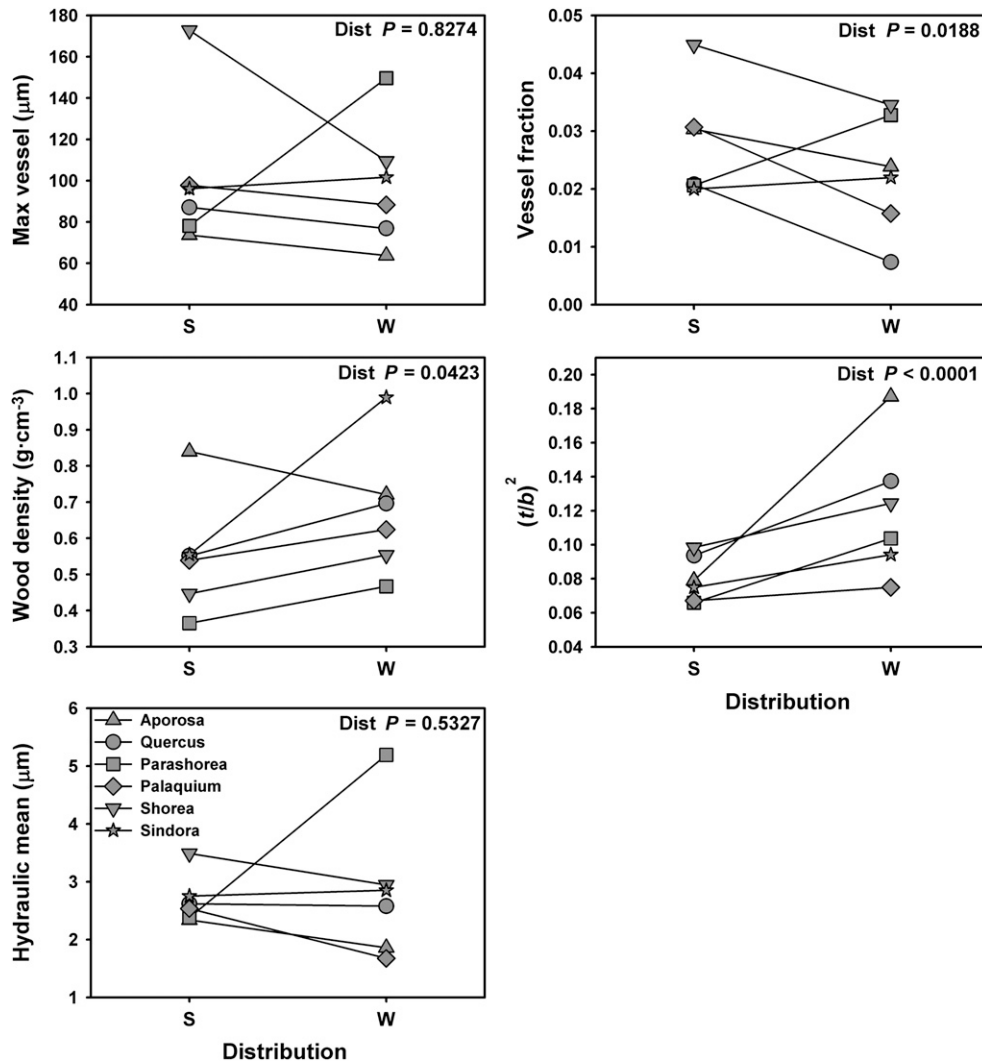


Fig. 2. Congeneric species pair mean values for wood traits divided based upon distribution in relation to the Kangar-Pattani Line (KPL). Error bars have been excluded for clarity but species mean (\pm SE) values can be found in the online Appendix S1. Southern (S) species are those with distributions restricted to the aseasonal forests south of the KPL, while widespread (W) species have distributions including the seasonally dry forests north of the KPL. Trait names and definitions corresponding to abbreviations can be found in Table 2. Randomized block ANOVA (random blocking term: genus; fixed treatment term: distribution, Dist) P -values for each trait are provided for the distribution term. Maximum vessel diameter, wood density, and vessel fraction analyses were conducted on log-transformed variables.

substantially (Table 3). Two relationships were no longer significant when phylogeny was accounted for: g_s vs. LMA, and vessel fraction vs. wood density (Table 3B). However, a number of new relationships were detected using this method and overall, the coordination of foliar and wood traits became more apparent. There was a significant, positive correlation between A_{max} and R_d and negative relationships of A_{max} with both wood density and $(t/b)^2$ (Table 3B). Stomatal conductance also correlated negatively with $(t/b)^2$.

DISCUSSION

As a consequence of the necessarily broader climatic variability associated with larger range sizes, greater tolerance of abiotic stress has been invoked as a determinant of species' geographical extents (Morin and Chuine, 2006). Baltzer et al.

(2007) demonstrated performance differences in keeping with greater abiotic stress tolerance in widespread compared with southern species in adult trees. These differences included slower growth and lower responsiveness to variation in edaphic conditions in widespread tropical tree species occupying both seasonally dry and aseasonal climates. As growth rates were calculated for one forest only, differences could be attributable to a number of factors, either biotic or abiotic, systematically negatively influencing widespread species. We suggested, however, that these differences were a consequence of the capacity of the widespread species to tolerate seasonal drought and that this stress tolerance was trading off against performance and competitive ability (Baltzer et al., 2007).

This prediction was supported in our phylogenetically controlled, distribution-based differences in mean trait values: widespread species capable of occurring in seasonally dry for-

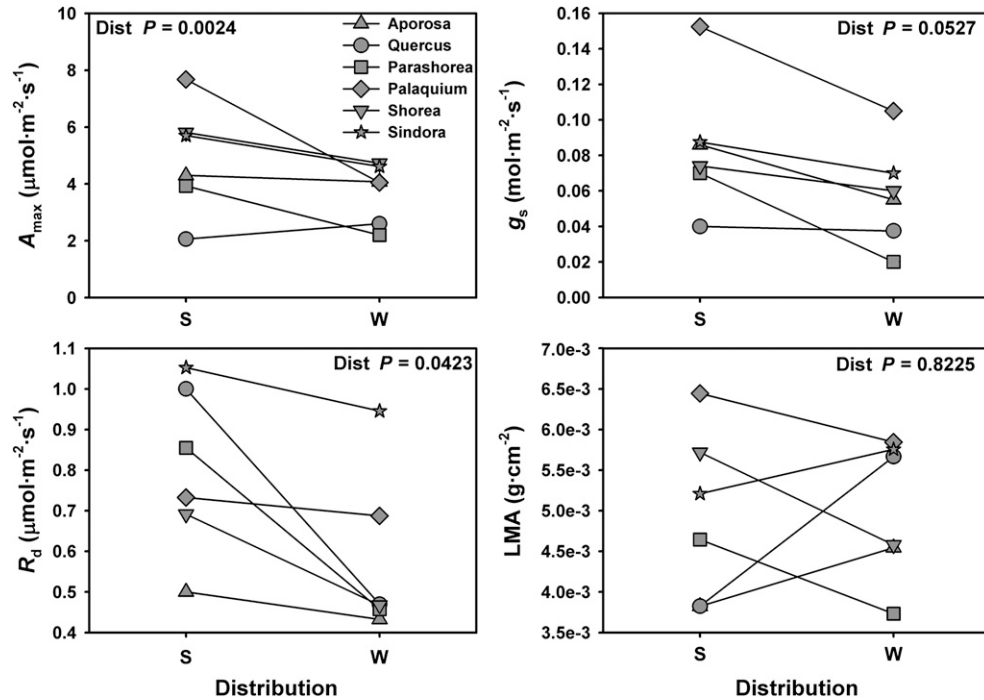


Fig. 3. Mean foliar gas-exchange values for congeneric species pairs divided based upon distribution in relation to the Kangar-Pattani Line (KPL). Error bars have been excluded for clarity, but species means (\pm SE) can be found in the online Appendix S1. Classification for southern vs. widespread species and abbreviations follows Fig. 2. Trait names and definitions corresponding the abbreviations can be found in Table 2. Analytical description follows Fig. 2.

ests were characterized by denser wood, greater conduit reinforcement, and lower vessel fraction. These traits provide increased resistance to xylem cavitation and increased biomechanical support (Hacke et al., 2001), features that should enable tolerance of lower soil water potentials. Previous work using the same set of species in fact demonstrated that the widespread species are able to maintain living tissue at lower leaf water potentials and relative water contents than are species restricted to the aseasonal forests of Malaysia (Baltzer et al., 2008). Engelbrecht et al. (2007) found similar patterns in saplings of neotropical tree species and found a strong connection between desiccation tolerance and both local and regional distributional patterns. Foliar traits tracked wood traits reasonably closely and widespread species tended to have lower physiological rates. These differences resulted in separation of widespread and southern species along a productivity–stress tolerance gradient with safety and efficiency/productivity traits loading onto opposite ends of the primary PCA axis (Fig. 4). This trade-off appears to form the mechanistic basis for performance differences observed between widespread and southern species in this region and may have important consequences for forest productivity and species distributions along this seasonality gradient. Our results should be interpreted with the following caveats. First, the results are based on a well-watered, common garden study but that both wood anatomical and foliar traits can show plastic responses to water availability (Bauerle et al., 2003; Corcuera et al., 2004; Fisher et al., 2007; Slot and Poorter, 2007). The differences that we have demonstrated should correspond with inherent physiological and anatomical trait differences, but there is the distinct possibility that differential trait plasticity among species could occur under conditions of drought that might either strengthen or obscure the

results. Further work should assess the degree of plasticity of drought tolerance and performance traits across seasonality gradients to determine the contribution of the plasticity of these traits to species distributions. Second, many morphological, physiological, and anatomical traits change through ontogeny in trees, therefore caution must be exercised when extrapolating findings based on juvenile traits to adult tree performance.

An additional qualitative feature of widespread species was the nearly exclusive use of simple perforation plates (Table 1). Simple perforation plates provide a single, low resistance opening to water flow between vessel elements without compromising hydraulic safety from drought induced cavitation events (Schulte, 1999; Jansen et al., 2004; but see Schulte et al., 1989). In contrast, scalariform plates have several elongated openings with ladder-like bars between them, essentially creating a larger resistance. Scalariformity is considered the ancestral trait in many lineages (Baas et al., 2000; Jansen et al., 2004); therefore, the consistent appearance of simple plates in the widespread species sampled is suggestive from the perspective of adaptation to seasonally dry environments though this trait did not load onto axis 1 where separation of distributional groupings occurred. Jansen et al. (2004) provided strong evidence that woody species in seasonal tropical forests tend to have both low incidences of scalariform perforation plates as well as having a higher proportion of genera with vestured pits. Vestures are thought to provide mechanical support of the pit membrane when pressure differentials among vessels are great thereby reducing the likelihood of air seeding (Choat et al., 2008). Although vesturing loaded onto axis 1 in our PCA analysis, the direction of the trait was such that southern species tended to have greater incidence of vesturing (Fig. 4; 42% and 30% in southern and widespread, re-

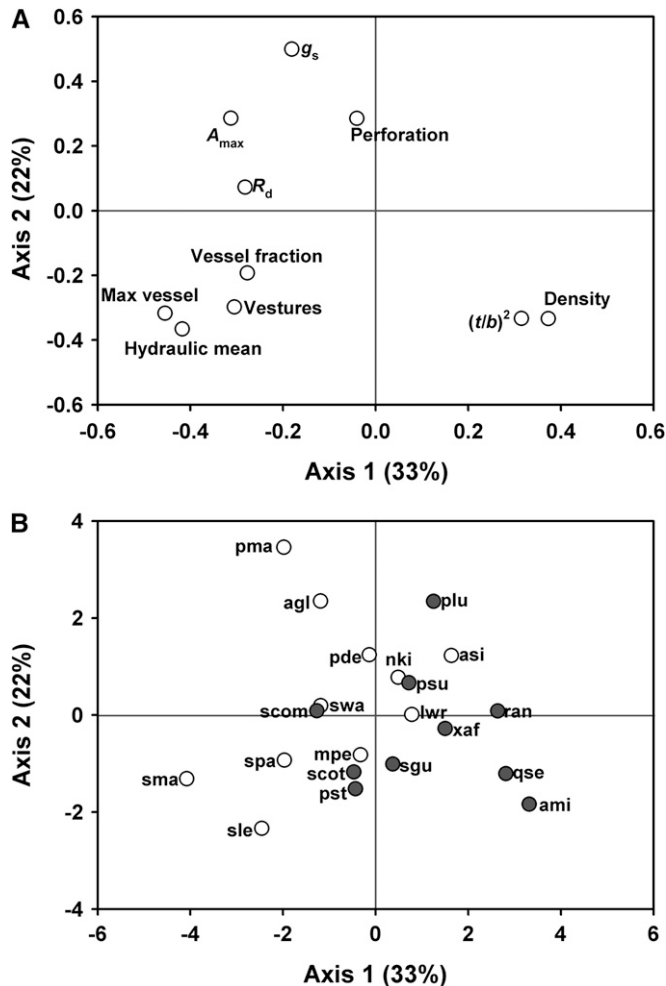


Fig. 4. Principal component analysis of 10 seedling traits of 21 tropical tree species. (A) Loading plot for the first two components; (B) species loadings on the first two axes. Species abbreviations are given in Table 1. Species restricted to aseasonal forests south of the KPL (southern) are denoted by open circles; species whose distributions include seasonally dry forests to the north of the KPL (widespread) are indicated with closed circles. Trait abbreviations, definitions and units can be found in Table 2.

spectively; Table 1). Undoubtedly, this pattern was in part a function of the much smaller sampling of species in the current study and potential phylogenetic biases (e.g., the Fabaceae have a very high incidence of vesturing; Table 1 and Jansen et al., 2004).

Coordination of foliar and wood anatomical traits—A well-documented trade-off exists between traits conducive to cavitation resistance and those that facilitate rapid water transport: the safety vs. efficiency trade-off (Baas et al., 2004; Hacke et al., 2006). One premise of this trade-off is that canopy productivity should be reduced in woody plants having “safe” features. Such coordination between hydraulic and photosynthetic traits has been demonstrated repeatedly (Sperry et al., 1993; Brodrribb and Feild, 2000; Brodrribb et al., 2002; Santiago et al., 2004). Some evidence for such coordination was found in the present study with the predicted relationships existing between certain wood anatomical or biomechanical traits and the performance-related physiological parameters. When phylogeny was ac-

counted for, both area-based photosynthetic rates and maximum stomatal conductance showed negative correlations with conduit reinforcement and A_{\max} also correlated negatively with wood density (Table 3B). Wood density has been suggested to be a good predictor of a species’ placement along the gradient of performance vs. stress tolerance (e.g., Wright et al., 2003), and greater wood density and conduit reinforcement help in the prevention of implosion of xylem vessels during drought stress (Hacke et al., 2001). Our data support this idea as species with lighter wood tended to have higher rates of photosynthesis and stomatal conductance, and consequently, higher canopy productivity. Both greater wood density and conduit reinforcement presumably also result in more space taken by structural components within the stem, less space available for water transport or storage, and corresponding reductions in physiological and growth rates (Roderick, 2000). Thus, the coordination between physiological and biomechanical traits seems to support the safety-efficiency trade-off hypothesis.

It is interesting to note, however, that neither wood density nor $(tlb)^2$ correlated with mean hydraulic diameter, maximum vessel diameter, or vessel fraction, which correspond with hydraulic efficiency (e.g., Pratt et al., 2007). Chave et al. (2009) review available wood economics data and suggest that vulnerability to cavitation and hydraulic efficiency may in fact be largely independent axes of the wood economics spectrum. Maherali et al. (2004) demonstrated in a phylogenetic framework that the relationship between hydraulic conductivity and Ψ_{50} was largely driven by structural differences between conifers and angiosperms and disappeared when the groups were separated. Further to this, results demonstrating the relationship between wood density and water transport efficiency are somewhat ambiguous (Preston et al., 2006; Pratt et al., 2007). The lack of coordination of safety- (wood density and conduit reinforcement) vs. efficiency- (vessel diameter, hydraulic mean, vessel fraction) related anatomical traits in either cross-species or PIC correlations would suggest that this was the case in our data despite trade-offs between biomechanical safety and canopy productivity. Area-based respiration rates, on the other hand, showed strong positive PIC (but not cross-species) correlations with both maximum vessel diameter and hydraulic mean but did not correspond with biomechanical wood traits (Table 3B).

Foliar traits showed a surprising lack of coordination. Typically, strong positive relationships exist among A_{\max} , g_s , and R_d , and all three show negative relationships with LMA (e.g., Wright et al., 2004). The expected A_{\max} - g_s relationship was observed; however, the remainder of anticipated relationships were not evident in cross-species correlation analysis, and both A_{\max} and g_s were found to have positive relationships with LMA (Table 3). In the PIC correlation, the anticipated relationship between R_d and A_{\max} was detected. A couple of factors may have been contributing to the unusual leaf trait coordination patterns. First, there was a fairly narrow range in terms of functional groups: all species were trees, and most if not all the species tended toward the shade tolerant end of the spectrum. As a consequence, the range of trait values was narrower than that of studies incorporating species ranging widely in shade tolerance (e.g., Davies, 1998) or those sampled across broad climatic gradients (e.g., Wright et al., 2004). The strength of the relationships may therefore be expected to be weaker, and the direction of relationships may be affected (e.g., LMA- A_{\max} relationship) due to the proportionally greater variation in bivariate trait pairs within a narrow range of the leaf economics spectrum (Diemer

TABLE 3. Spearman's rho values for (A) cross-species and (B) phylogenetically independent contrast (PIC) analyses of all wood and leaf traits measured.

Trait	A_{\max}	R_d	g_s	LMA	Max vessel	Vessel fraction	Density	$(t/b)^2$
A) Cross-species								
R_d	0.31	—	—	—	—	—	—	—
g_s	0.68**	0.05	—	—	—	—	—	—
LMA	0.61*	0.16	0.40	—	—	—	—	—
Max vessel	0.19	0.52*	-0.13	-0.13	—	—	—	—
Vessel fraction	0.24	0.01	-0.14	-0.23	0.60*	—	—	—
Density	-0.33	-0.16	-0.12	0.17	-0.30	-0.39	—	—
$(t/b)^2$	-0.19	-0.31	-0.19	-0.09	-0.02	0.04	0.45*	—
Hydraulic mean	0.14	0.52**	-0.19	-0.13	0.98***	0.54**	-0.27	-0.05
B) PIC								
R_d	0.45*	—	—	—	—	—	—	—
g_s	0.70**	0.14	—	—	—	—	—	—
LMA	0.59**	0.40	0.24	—	—	—	—	—
Max vessel	0.21	0.79***	-0.04	-0.05	—	—	—	—
Vessel fraction	0.23	0.28	0.15	-0.10	0.53*	—	—	—
Density	-0.43*	0.05	-0.22	-0.14	0.19	-0.05	—	—
$(t/b)^2$	-0.69**	-0.16	-0.62**	-0.32	0.08	-0.10	0.46*	—
Hydraulic mean	0.14	0.76***	-0.11	-0.05	0.99***	0.50*	0.19	0.12

Notes: Significant relationships are in boldface: bolded with no asterisk, $P < 0.1$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.0001$. Trait abbreviations, units, and definitions can be found in Table 2. The phylogeny used for analysis can be found in Appendix S2.

et al., 1992; Reich, 1993). Second, no differences in LMA were detected as a function of distribution, while all three gas-exchange traits were significantly higher in southern species, suggestive of a potential decoupling of trait relationships as a function of distribution at this scale.

Conclusions—The present data provide evidence of systematic, distribution-related differences in anatomical correlates of hydraulic conductivity and resistance to cavitation and the corresponding canopy physiological traits. Widespread species demonstrated safer, more stress-tolerant wood and leaf traits corresponding with lower growth rates and greater desiccation tolerance in this group (Baltzer et al., 2007, 2008). The data presented here further strengthen the notion that the climatic transition that exists near the Kangar-Pattani Line is contributing to the maintenance of species distributions in this region. Such systematic differences have important implications both from the perspective of understanding present day forest dynamics and species distributions as well as predicting potential responses to future changes in precipitation and soil water availability in this region.

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