Cross-species patterns in the coordination between leaf and stem traits, and their implications for plant hydraulics

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Through identifying and understanding ecologically important dimensions of plant trait variation we gain insight into why particular trait combinations are favoured and into the implications of trait differences among species. Here, we describe relationships among several poorly understood leaf and stem traits across species from several Australian vegetation types. Species with lower wood density (WD) consistently deployed more leaf area per unit shoot mass (LA/SM), as did the larger-leaved species within forested sites. Higher LA/SM is likely to lead to faster growth rates, implying a previously unrecognized implication to interspecific variation in leaf size and WD. Leaf : sapwood area ratio is one of several important traits contributing to a plant's water-use strategy, yet, we still only poorly understand how plants vary in the extent to which hydraulic properties and traits such as leaf size, WD and LM/SM are coordinated, and what the implications of this variation may be.

Introduction

When two or more ecologically important plant traits are consistently correlated among species, they may be thought of as forming a strategic 'dimension' (or spectrum, or axis) of trait variation. Through identifying and understanding such trait-dimensions, we can begin to make sense of functional diversity among plants (Grime et al. 1997, Reich et al. 1999, Westoby et al. 2002, Ackerly 2004, Diaz et al. 2004). Questions that may be asked during this process include: (1) Is a greater proportion of the variation in the underlying traits found among species, rather than within species?; (2) How is trait variation patterned phylogenetically, and are the traits correlated similarly in different clades? and (3) What does a species' position along a trait-dimension tell us about its ecological 'strategy'? (e.g. where it is most competitive, or how it uses resources). The extent to which different trait-dimensions are orthogonal (unrelated) is of particular interest, because unrelated dimensions convey independent information about the ecological strategies of plants (Ackerly 2004). Some trait-dimensions are reasonably well understood. For example, the 'seed size – seed output' dimension is underpinned by a clear trade-off between better seedling survival in the face of hazards and the number of seeds produced per square metre of canopy (Moles and Westoby 2004), while the 'leaf economics spectrum' (Wright et al. 2004) runs from species with high specific leaf area (SLA), high leaf N and P concentrations, fast rates of gas exchange, but short leaf life-span (e.g. many herbs, grasses and deciduous trees), to species with the opposite set of traits (e.g. many evergreen shrubs and trees).

Abbreviations – A_{area}, photosynthetic rate per unit leaf area; Ks, sapwood conductivity; LA/SA, ratio of leaf area to stem cross-sectional area; LAR, leaf area ratio; LA/SM, total leaf area per stem dry mass; LM/SM, ratio of leaf dry mass to stem dry mass; NAR, net assimilation rate; RGR, relative growth rate; SLA, specific leaf area; WD, wood density

In this study, we focused on variation in traits that are less well understood: wood density (WD) (dry mass per fresh volume), leaf size (average one-sided surface area of individual leaves) and the proportional deployment of leaf vs stem tissues. We quantified relationships among these traits across species from several sites in eastern Australia that vary widely in rainfall (390–2800 mm year^{-1}). Our focus was on interpreting trait relationships in terms of their implications for plant growth and in relation to the hydraulic properties of stems. Our aim was to bridge between approaches and literatures that have tended to remain restricted to either comparative plant ecology or plant physiology.

WD is related to several somewhat distinct aspects of plant ecological strategy. Lower WD tends to be associated with faster stem diameter and volumetric growth (Enquist et al. 1999, Roderick 2000, Muller-Landau 2004, King et al. 2005), but high WD also has advantages, for example, in increasing the mechanical strength of stems and the resistance of stem material to pathogens (Loehle 1988, Givnish 1995). WD is also related to hydraulic properties of plants. For example, with increasing WD, the resistance to xylem cavitation tends to increase among species, whereas sapwood conductivity (Ks) and stem water storage tend to decrease (Stratton et al. 2000, Meinzer 2003, Ackerly 2004, Bucci et al. 2004, Santiago et al. 2004, Hacke et al. 2005). The conductive capacity of stems needs to be coordinated with the amount of leaf deployed and with the hydraulic properties of leaves (Sack et al. 2003, Martinez-Vilalta et al. 2004). Many species adjust leaf deployment over time in response to seasons and rainfall (Bucci et al. 2005), but differences across species along environmental gradients have also been reported (Whitehead 1998, Cavender-Bares and Holbrook 2001, Preston and Ackerly 2003). On the basis of the premise that Ks would be generally higher in low-WD species, our working hypothesis was that WD would be negatively correlated with total leaf area per unit stem (or sapwood) cross-sectional area, LA/SA (Ackerly 2004, Cavender-Bares et al. 2004).

Species with thicker stems tend to deploy more total leaf area per stem. This makes sense for both mechanical and hydraulic reasons (White 1983, Tyree and Zimmerman 2002, Preston and Ackerly 2003). Although, in principle, the larger total leaf area of thicker-stemmed species could result either from having more leaves per stem or, instead, from individual leaves being larger, it seems that the second of these explanations is more generally true (Westoby et al. 2002). Why should this be, what are the implications of this relationship and, more generally, what are the implications of variation among species in leaf size? Leaf size varies 10^5

to 10^6-fold among species, yet, the costs and benefits of this variation are relatively unclear. In theory, larger leaves have thicker boundary layers and thus overheat more easily than smaller leaves, leading to higher respiration and transpiration costs in larger-leaved species (Givnish 1978). This effect may help explain why community-mean leaf size tends to decrease with increasing site aridity or irradiance (Givnish 1978, Fonseca et al. 2000). However, 10^3-fold variation in leaf size is commonly seen among sets of co-occurring species (Fonseca et al. 2000), suggesting that other types of costs and benefits must also vary with leaf size. Among Australian evergreen species, for example, herbivory levels may increase with increasing leaf size (Moles and Westoby 2000), while the degree of self-shading may decrease (Falster and Westoby 2003). Of particular relevance to this study, leaf size has now been shown to be negatively correlated with WD in a number of different vegetation types (Ackerly 2004, Cavender-Bares et al. 2004, Pickup et al. 2005, Rossetto and Kooyman 2005), but for unknown reasons.

Until recently, the dry-mass costs of deploying leaf area as few, large leaves vs. many, small leaves had been little investigated. In classical seedling growth analysis (equation 1), relative growth rate (RGR) is decomposed into the product of net assimilation rate (NAR; rate of dry mass acquisition per unit leaf area) and leaf area ratio (LAR; ratio of total leaf area to total plant dry mass). LAR can itself be decomposed into the product of leaf mass fraction (LMF; ratio of leaf to plant dry mass) and SLA (average leaf area per unit leaf dry mass).

$$RGR = NAR \cdot LAR = NAR \cdot LMF \cdot SLA \qquad (1)$$

By definition, a doubling in any of NAR, LAR, LMF or SLA would translate directly into a doubling of RGR unless there were correlated changes in other components. Pickup et al. (2005) partitioned the rate of dry mass acquisition by a shoot (RGR$_{shoot}$) into its components in an analogous fashion (equation A1 in Supplementary Material), relativizing leaf area and mass deployment to the dry mass of shoots rather than to that of whole plants (i.e. leaf area per shoot mass LA/SM and leaf mass per shoot mass LM/SM). Importantly, they noted that LA/SM, LM/SM and SLA can be measured and compared across species, even in the absence of data about the whole plant, or dry mass gain over time. In that study, LA/SM increased in concert with leaf size across 70 species from four sites in eastern Australia, implying a potential growth advantage (RGR$_{shoot}$) associated with being larger-leaved. However, LA/SM and leaf size were positively correlated at only one of four individual sites, suggesting that any such advantage may not be generally true.

Table 1. Site details. Climate data are long-term averages from the nearest weather station [for tropical rainforest (TRF) values are means from the two subsites]. MAT: mean annual temperature. Sampling points refer to 250 mm distance from the branch tip, 10 mm² sapwood or stem cross-sectional area (sapwood at GHP, GLP, RHM and RHW, stem, after removal of bark, at Ash, Myall and TRF) and whole terminal twigs

Site and site abbreviation	Vegetation type	Soil P (ppm)	Latitude, longitude	Rainfall (mm year⁻¹)	MAT (°C)	Sampling points	References, number of species sampled
Tropical rainforest (subsites: Cape Tribulation, Mt Lamington) (TRF)	Rainforest (complex mesophyll vine forest)		16°06′ S, 145°27′ E; 17°07′ S, 145°39′ E	2800	24	10 mm², 250 mm	Falster and Westoby (2005a, unpublished) 45
Mountain ash (*Eucalyptus regnans*) forest (Ash)	Tall closed forest		37°23′ S, 145°14′ E	1400	11.0	10 mm², 250 mm	Falster & Westoby (unpublished) 21
Myall Lakes National Park (Myall)	Low open sclerophyll forest		32°30′ S, 152°20′ E	1350	17.0	10 mm², 250 mm	Falster and Westoby (2005b) 12
Gosford, high soil P (GHP)	Closed forest	335	33°23′ S, 151°19′ E	1300	17.5	10 mm²	Pickup et al. (2005) 20
Gosford, low soil P (GLP)	Open woodland	98	33°22′ E, 151°19′ S	1300	17.5	10 mm², 250 mm	Pickup et al. (2005, and unpublished) 20
Kuringai Chase National Park (KCNP)	Open woodland	94	33°42′ S, 151°09′ E	1220	17.5	Terminal twigs	Westoby and Wright (2003) 33
Round Hill Nature Reserve, low soil P (RHM)	Open mallee woodland	250	33°23′ S, 151°19′ E	390	17.6	10 mm², terminal twigs	Pickup et al. (2005), Westoby and Wright (2003) 22
Round Hill Nature Reserve, high soil P (RHW)	*Eucalyptus/Callitris* woodland	132	33°23′ S, 151°19′ E	390	17.6	10 mm², terminal twigs	Pickup et al. (2005), Westoby and Wright (2003) 17

In this study, we combined data from Pickup et al. (2005) with other published and unpublished data from our studies of leaf and stem deployment in eastern Australia, the combined dataset covering 175 species from eight sites (Table 1). First, we extended the analyses of Pickup et al. (2005) to assess whether there was any apparent growth advantage associated with being larger-leaved across this broader sample of species and sites (i.e. whether leaf size and components of RGR_{shoot} such as LA/SM were correlated). Second, we quantified relationships between leaf size, LA/SA and WD. Finally, we assessed whether there was any apparent growth advantage associated with variation in WD (in particular, whether LA/SM and WD were correlated).

Methods

Site and species selection

All study sites (Table 1) were dominated by evergreen woody perennials and located in nature reserves. 'Site' is used relatively loosely here. Several patches of nearby, similar vegetation with different times since the last fire were sampled at Myall (Falster and Westoby 2005b); two patches of similar vegetation with different times since the last fire were sampled at Ash (Falster and Westoby, unpublished); the tropical rainforest (TRF) 'site' actually consisted of two geographically separated subsites. As in the original study (Falster and Westoby 2005a), these were treated as one site because many species were common to the two subsites and the vegetation at both is similar complex mesophyll vine forest (Webb 1968). Mean annual rainfall and temperature varied considerably among the eight sites (Table 1). Seasonality of rainfall also varied, TRF (to the north) receiving most rain over the warmer months, Ash (to the south) over the colder months and the other sites showing weak seasonality in rainfall, where any. All species sampled were locally common evergreen trees or shrubs, except for four herbaceous species (two at Ash, two at Myall). The dataset represented 175 different species from 39 families and 21 orders (higher delineations from Angiosperm Phylogeny Group; http://www.mobot.org/MOBOT/research/APweb/; accessed May 2005). The most strongly represented families were Myrtaceae, Proteaceae and Fabaceae (*sensu lato*), together contributing 93 species.

Measuring leaf and stem deployment

No single best point exists to compare traits such as LM/SM, LA/SM and LA/SA when considering a set of species

that varies widely in canopy architecture and typical maximum height (here, approximately 20 cm to 85 m). We have used several approaches (Table 1). In one study, we made measurements on the terminal twigs of each species, i.e. on a relatively standard developmental unit (Westoby and Wright 2003). For species at Ash, GLP, Myall and TRF, traits were measured at each of several different distances back down the stem from the branch tip (Falster and Westoby 2005a, 2005b and unpublished, Pickup et al. 2005). At GHP, RHM and RHW, traits were measured at a standard sapwood cross-sectional area (10 mm^2; Pickup et al. 2005). For the present re-analysis, we took the raw data from the previous studies and, for every species possible, calculated patterns of leaf and stem deployment at two standard points: at 250 mm distance from the branch tip (Ash, GLP, Myall and TRF) and at 10 mm^2 stem (Ash, Myall, TRF) or sapwood (GHP, GLP, RHM, RHW) cross-sectional area (250 mm or 10 mm^2 formulation denoted as subscript in trait abbreviations). This was done as follows. For each individual plant, total leaf and stem dry mass at 250 mm distance was estimated by straight-line interpolation from values measured at the nearest sampling points on either side of this distance. As the dry mass data tended to display non-linear (power) relationships with distance from the branch tip, the interpolated values were calculated from log_{10}-log_{10}-transformed data, then back-transformed to the original scale. The same approach was used for interpolating data to the standard stem (or sapwood) cross-sectional area. For individuals where measurements had not been made on either side of the desired point but the nearest measurement had been made within 25 mm of 250 mm or 1 mm^2 of 10 mm^2 cross-section (i.e. within 10% of the desired point), we extrapolated (rather than interpolated) the measured data to the standard point. This allowed us to include a number of individuals and species for which interpolation was not possible. Still, several large-leaved, large-stemmed species from the TRF site could not be included in the 10-mm^2 cross-section dataset. No unusual tendencies in analyses, including the extrapolated data, were seen in comparison to analyses including interpolated data only (details not shown). To illustrate how species' morphology varied at the two standard sampling points, species-mean stem cross-sectional area varied between 1.2 and 258 mm^2 at 250 mm distance from the branch tip, while the distance from the branch tip at which stem cross-sectional area reached 10 mm^2 varied from 64 to 995 mm.

All traits were measured on outer canopy branches only. For compound-leaved species, leaf size refers to the average size of leaflets, and the mass of the rachis

was included in stem mass. Four to five fully expanded leaves were sampled from each individual plant to calculate average leaf size and SLA values (leaf area measured on a flatbed scanner); these were then averaged to calculate species-mean values (in total 15–20 leaves were sampled per species). At the two standard sampling points we then calculated LM/SM, total leaf area (leaf dry mass × SLA), LA/SM (LM/SM × SLA) and LA/SA. Rather than measuring sapwood cross-sectional area, Falster and Westoby measured stem cross-sectional area following removal of the bark (thus, any pith, if present, was included in the measured area). Visual inspection suggested little heartwood formation at the 250 mm and $10 \, mm^2$ sampling points. WD was measured at 250-mm distance by Falster and Westoby. Pickup et al. measured WD at $10 \, mm^2$ sapwood cross-sectional area for all species, but WD could also be interpolated to 250 mm distance for species at the GLP site. WD was measured on stem segments 40–70 mm in length, following standard methods (Pickup et al. 2005).

Treatment and analysis of data

Variance components analyses (ANOVA) indicated that 70–80% of the total variation in each trait occurred among rather than within species. Consequently, species-mean trait values were used in all analyses. Leaf size was log_{10}-transformed because its distribution was strongly right-skewed. The other traits showed approximately normal distributions and were left untransformed. Trait relationships across the species at each site were quantified using linear regression. The generality across sites of each relationship was assessed using analysis of covariance (ANCOVA). That is, slope heterogeneity was indicated by a significant site–trait interaction term; when the interaction term was non-significant ($P > 0.05$), a regression model with main effects only was run, from which a common regression slope was obtained. In some cases, we also report trait correlations calculated across all species considered together (i.e. ignoring site structure). Site rainfall was strongly right-skewed across the seven sites and so was log_{10}-transformed for Pearson correlation analyses involving the measured traits and annual rainfall, considered across all species. Similarly, LA/SM and LA/SA showed right-skewed distributions across all species considered together. Consequently, these traits were log_{10}-transformed for the rainfall-related correlation analysis, as was LA/SM for all species regressions concerning WD. Kolmogorov–Smirnov tests indicated that all other traits were distributed in a manner not significantly different from a normal distribution and thus required no transformation.

Results

Trends in leaf area per shoot mass (LA/SM) with leaf size

Across all species, leaf size and $LA/SM_{10 \, mm^2}$ showed a broken (two-phase) relationship (Fig. 1A). For example, dividing species at a leaf size of $1000 \, mm^2$, we found that the traits were unrelated across the smaller-leaved group ($P = 0.775$) but clearly correlated across the larger-leaved species ($r^2 = 0.52$, $P < 0.001$; n = 57). Indeed, on average, $LA/SM_{10 \, mm^2}$ increased from 4.9 to $10.7 \, mm^2 \, mg^{-1}$ (approximately 2.2-fold) as leaf size increased from 1000 to $1000 \, mm^2$. Differences in trait relationships among individual sites clearly lay beneath this two-phase relationship. Leaf size and $LA/SM_{10 \, mm^2}$
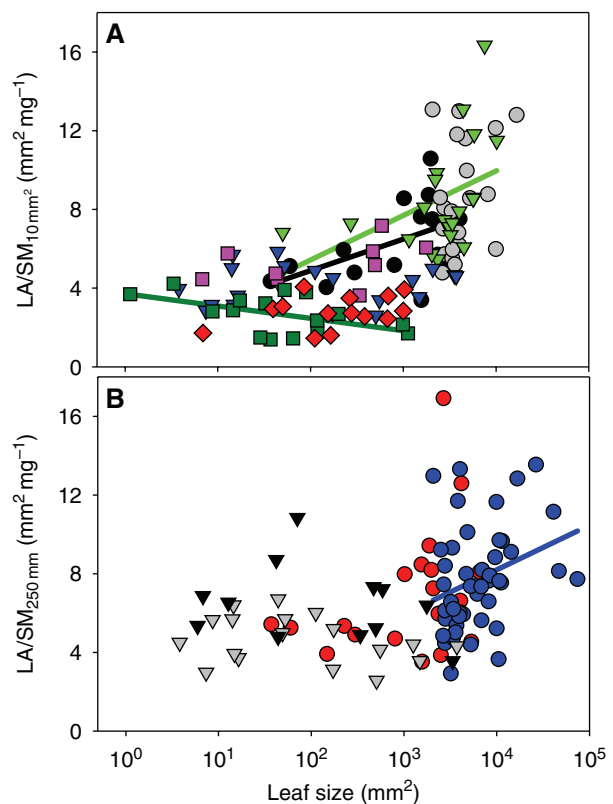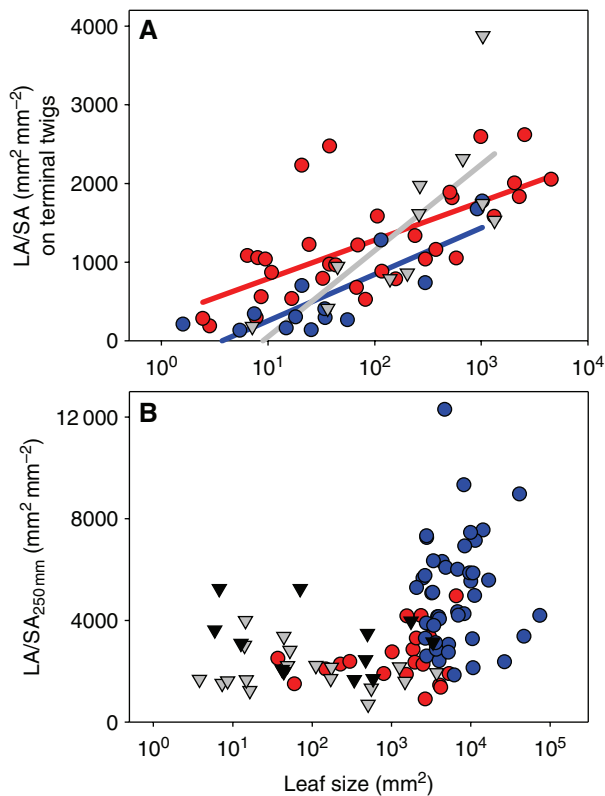

Fig. 1. Relationships between log_{10} leaf size and total leaf area per shoot dry mass (LA/SM). Regression lines are shown for significant within-site relationships only. (A) $LA/SM_{10 \, mm^2}$ and leaf size were positively correlated at GHP and Ash ($r^2 = 0.18$ and 0.25, respectively, both $P = 0.60$), negatively correlated at RHM ($r^2 = 0.27$, $P = 0.039$) and elsewhere unrelated (all $P > 0.130$). Data from seven sites (see Table 1). Symbols: Ash, black circles; TRF, grey circles; GHP, light green triangles; GLP, blue triangles; Myall, pink squares; RHM, dark green squares; RHW, red diamonds. (B) $LA/SM_{250 \, mm}$ and leaf size were positively correlated at TRF ($r^2 = 0.09$, $P = 0.041$) but elsewhere unrelated (all $P > 0.14$). Symbols: Ash, red circles; TRF, blue circles; GLP, grey triangles; Myall, black triangles.

were positively correlated at two of the seven sites (GHP and Ash), negatively correlated at one (RHM) and elsewhere unrelated (Fig. 1A). Qualitatively similar results were seen when $LA/SM_{250 mm}$ was considered rather than $LA/SM_{10 mm^2}$ (Fig. 1B). That is, the traits were unrelated among smaller-leaved species and positively correlated among those with larger leaves, reflecting the positive relationship at the TRF site and a lack of relationship at the other three sites. Relationships between leaf size and the underlying components of LA/SM (LM/SM and SLA) are reported in the Supplementary Material.

Larger-leaved species deployed more total leaf area per stem but not necessarily per stem cross-section

On their terminal twigs, larger-leaved species deployed more total leaf area than smaller-leaved species (three sites, $r^2 = 0.79–0.89$, all $P < 0.001$), as well as more total leaf area per stem cross-sectional area (LA/SA; all three sites, Fig. 2A). At 250 mm distance, leaf size and total leaf area were again correlated (four sites,

$r^2 = 0.33–0.48$, all $P < 0.015$), but in this case, leaf size and LA/SA were unrelated (four of four sites, all $P > 0.370$; Fig. 2B). This reflected the fact that, on average, larger-leaved species had thicker stems at this standard distance (stem cross-section vs leaf size: positive correlation at all four sites; $r^2 = 0.34–0.62$, all $P < 0.008$). At 10 mm^2 stem or sapwood cross-sectional area, LA/SA and leaf size were unrelated at six of seven sites (all $P > 0.16$) and only marginally correlated at the seventh (RHW: $r^2 = 0.21$, $P = 0.096$).

Do species with lower WD have larger leaves and deploy more leaf area per stem cross-sectional area?

In general, species with lower WD were larger-leaved. $WD_{250 mm}$ and leaf size were negatively correlated at all four sites (Fig. 3A). These individual slopes were heterogeneous ($P = 0.001$), although the TRF and Ash slopes
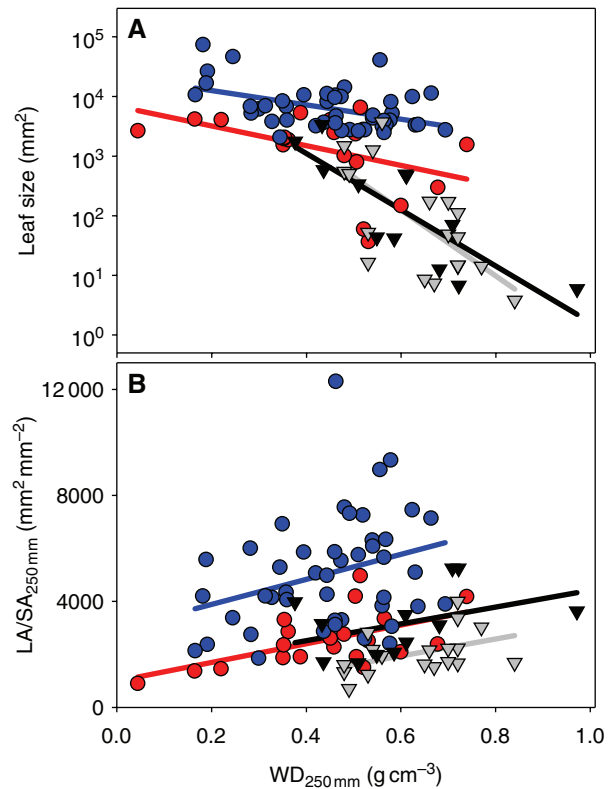

Fig. 2. Relationships between leaf area per unit stem cross-section (LA/SA) and leaf size. (A) Considering terminal twigs, the traits were correlated at all three sites ($r^2 = 0.45–071$, all $P < 0.008$). Symbols: KCNP, red circles; RHM, blue circles; RHW, grey triangles. (B) $LA/SA_{250 mm}$ and leaf size were unrelated at all four sites (all $P > 0.370$). Symbols as for Fig. 1B.

Fig. 3. Relationships between wood density, LA/SA (both measured at 250 mm) and leaf size. Symbols as for Fig. 1B. (A) Leaf size and $WD_{250 mm}$ were negatively correlated at all four sites ($r^2 = 0.21–0.65$, all $P < 0.02$) as well as across all species ($r^2 = 0.43$, $P < 0.001$). (b) $LA/SA_{250 mm}$ and $WD_{250 mm}$ were positively correlated at three of four sites, at least marginally ($r^2 = 0.09–0.32$, $0.009 < P < 0.072$). At Myall the traits were associated with similar strength as elsewhere ($r^2 = 0.17$), but this was clearly non-significant ($P = 0.185$, n = 12). All four regression slopes are shown. Common fitted slope across all sites = 3978 (mm^2 mm^{-2})/(g cm^{-3}).

did not differ from another ($P = 0.150$; common log-linear slope of -1.7, indicating 47% increase in leaf size for each 0.1 decrease in $WD_{250\,mm}$) and neither did the slopes fitted to the GLP and Myall sites ($P = 0.678$; common log-linear slope of -5.1, indicating 3.2-fold increase in leaf size for each 0.1 decrease in $WD_{250\,mm}$). The within-site relationships were less consistent when comparing $WD_{10\,mm^2}$ and leaf size, being significantly negative at two of four sites (GHP, GLP; $r^2 = 0.38, 0.44$, both $P < 0.012$), but weaker at the other two ($r^2 = 0.15$, 0.21; both $0.095 < P < 0.140$). Still, the slopes did not differ from one another ($P = 0.421$), with the common slope (-4.5) indicating that leaf size increased 2.8-fold for each 0.1 decrease in $WD_{10\,mm^2}$.

Our working hypothesis was that LA/SA and WD would be negatively correlated. However, $WD_{250\,mm}$ and $LA/SA_{250\,mm}$ were in fact *positively* correlated at three of four sites, at least marginally (Fig. 3B). There was no difference in regression slopes among sites ($P = 0.949$), with the common slope indicating that for a 0.1 increase in WD, on average, approximately 400 mm^2 more leaf area was deployed per square millimetre stem cross-sectional area. Considered at 10 mm^2 sapwood cross-section, LA/SA and WD were unrelated at each of the four sites (all $P > 0.3$).

A general tendency for LA/SM to increase as WD decreased

$LA/SM_{250\,mm}$ and $WD_{250\,mm}$ were negatively correlated at two sites (Ash and TRF), positively related at one and unrelated at one (Fig. 4A), with the individual slopes deemed significantly heterogeneous ($P < 0.001$). However, fitting a single regression line across all species, $\log_{10}LA/SM_{250\,mm}$ and $WD_{250\,mm}$ were negatively correlated, with LA/SM increasing on average by 11% for every 0.1 g cm^{-3} decrease in WD ($r^2 = 0.20$, $P < 0.001$). $LA/SM_{10\,mm^2}$ and $WD_{10\,mm^2}$ were negatively correlated at only one of four sites (GHP; Fig. 4B). Again, the individual slopes were heterogeneous ($P < 0.001$); however, fitting a single regression line across all species, $\log_{10}LA/SM_{10\,mm^2}$ increased sharply with decreasing $WD_{10\,mm^2}$, with LA/SM increasing by 30% for every 0.1 g cm^{-3} decrease in WD ($r^2 = 0.53$, $P < 0.001$). Relationships between WD and the underlying components of LA/SM (i.e. LM/SM and SLA) are reported in the Supplementary Material.

Patterning of trait relationships by site and by site properties

Considerable trait variation was patterned according to site, with this patterning itself associated with differences
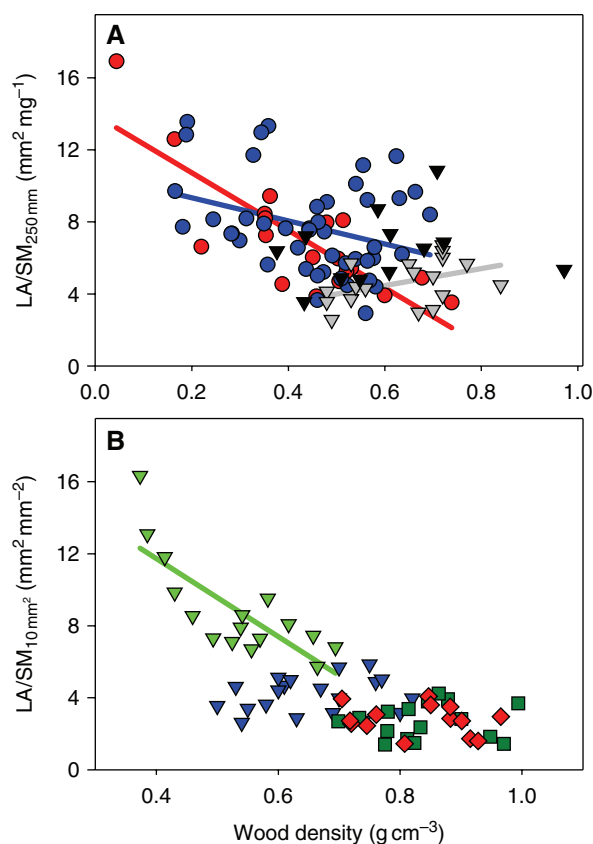
Fig. 4. Relationships between wood density (WD) and LA/SM. Regression lines are shown for significant within-site relationships only. (A) $WD_{250\,mm}$ and $LA/SM_{250\,mm}$ were negatively correlated at Ash and TRF ($r^2 = 0.67, 0.11$), marginally positively correlated at GLP ($r^2 = 0.18$, $P = 0.080$), and unrelated at Myall ($P = 0.536$). Across all species, $\log_{10}$ ($LA/SM_{250\,mm}$) increased as $WD_{250\,mm}$ decreased ($P < 0.001$, $r^2 = 0.20$). (B) A negative relationship was observed between $WD_{10\,mm^2}$ and $LA/SM_{10\,mm^2}$ at the GHP site ($r^2 = 0.61$) and across all species ($r^2 = 0.55$, $P < 0.001$); elsewhere the traits were unrelated (all $P > 0.44$).

in vegetation type and/or annual rainfall among sites. For example, species at the TRF, GHP (and less so) the Ash sites (all closed forests) tended to have larger leaves, lower WD and higher SLA, LA/SM and LA/SA than species from other sites (Figs 1–4, Figs S1 and S2). There was also more variation in traits such as LA/SM and LA/SA among species at these sites. These were also the three sites where LA/SM and leaf size tended to be positively correlated, and LA/SM and WD were negatively correlated. Considered across all species, leaf size, LA/SM, LM/SM and SLA increased as site rainfall increased, while WD and rainfall were negatively correlated (Table 2). On average, species at higher rainfall sites had higher $LA/SA_{250\,mm}$, but there were no relationships between $LA/SM_{10\,mm^2}$ and rainfall.

Table 2. Relationships among site rainfall and the measured traits. Data for seven sites (all but KCNP) except for LA/SA$_{250\ mm}$, for which there were data for four sites only. Correlation r-values are reported, followed by the corresponding P-values and sample sizes (number of species)

	Leaf size	LA/SM$_{10\ mm^2}$	LA/SM$_{250\ mm}$	LA/SM$_{10\ mm^2}$	LA/SM$_{250\ mm}$	WD$_{10\ mm^2}$	WD$_{250\ mm}$	LA/SM$_{10\ mm^2}$	LA/SM$_{250\ mm}$	SLA
Rainfall										
r	0.62	0.74	0.37	0.08	0.65	−0.76	−0.34	0.49	0.43	0.48
P	<0.001	<0.001	<0.001	0.426	<0.001	<0.001	0.001	<0.001	<0.001	<0.001
n	150	116	96	116	96	66	97	116	96	150

Discussion

Is there a growth advantage associated with being larger-leaved?

LA/SM increased with increasing leaf size among species from the three forest sites (Ash, GHP and TRF). At least for these species then, our results suggest a potential growth advantage associated with being larger-leaved: unless there was a countervailing trend in NAR$_{shoot}$, RGR$_{shoot}$ should increase in direct proportion to any increase in LA/SM. For the example given, in which LA/SM increased 2.2-fold as leaf size increased 10-fold, NAR$_{shoot}$ would have to simultaneously decrease by at least 54% for there *not* to be any increase in RGR$_{shoot}$.

There is no obvious reason why NAR$_{shoot}$ would be sufficiently lower in larger-leaved species so as to counteract the potential RGR advantage implied by their higher LA/SM. Although NAR$_{shoot}$ was not measured as part of this study, this possibility can still be assessed, at least indirectly. Assuming that variation in NAR$_{shoot}$ is largely driven by variation in photosynthetic rate (A$_{area}$), as is variation in seedling NAR (Poorter and van der Werf 1998), we can then ask whether A$_{area}$ is generally lower in species with larger leaves. While this was indeed the case among the 19 chaparral species studied by Ackerly (2004), more generally, it seems not to be: elsewhere, A$_{area}$ and leaf size have either been positively correlated or have shown no relationship (Hogan et al. 1995, Ackerly and Reich 1999, Reich et al. 1999, Wright et al. 2001, Prior et al. 2003, Cavender-Bares et al. 2004).

All species sampled at TRF and GHP had leaf size >1000 mm^2, as did 15 of the 21 species sampled at the Ash site, whereas very few species from other sites had leaves this large. Why should it be that LA/SM increased with leaf size at forest sites only? One possibility is that it has something to do with differences in site properties between forest and non-forest sites. For example, forests tend to have more severe light attenuation from the top of the plant canopy down to the ground. If larger-leaved species generally grew in lower-light microsites within sites than smaller-leaved species, or if they experienced a higher degree of self-shading, it is possible that they would have generally lower A$_{area}$, and thus NAR. Indeed, leaf size was negatively correlated with microsite light level in a study made nearby to the Kuringai Chase National Park site (in an open woodland), although this was true only when the comparisons were made at a given plant height (Bragg and Westoby 2002). On the contrary, the possibility that larger-leaved species experience higher degrees of self-shading appears unlikely; in fact, the opposite may be more true, if anything (Falster and Westoby 2003).

In conclusion, there is little evidence to suggest that species with larger leaves may have lower NAR$_{shoot}$. Thus, their higher LA/SM appears likely to translate into a growth advantage via higher RGR$_{shoot}$.

Low WD, LA/SM and a possible growth advantage

Lower WD tended to be associated with higher LA/SM, not only at the three forest sites but also in regressions fitted across all species. Again, this suggests that species with lower WD (especially in forests) may have obtained a growth advantage via RGR$_{shoot}$, provided the trend is not counteracted by a trend of NAR$_{shoot}$ in the lower WD species. As for leaf size, this possibility can be explored via indirect evidence. However, using A$_{area}$ again as a proxy for NAR, the opposite appears to be true, if anything, with A$_{area}$ and WD either negatively correlated (Santiago et al. 2004, Aiba and Nakashizuka 2005) or unrelated elsewhere (Ackerly 2004). Another possibility to evaluate is whether lower WD species typically grow in lower light microsites and thus tend to have lower NAR$_{shoot}$. Again, the opposite is more likely to be true, especially in the tropical forests, where lower WD species are often fast-growing, light-demanding pioneers (Muller-Landau 2004).

In conclusion, it appears likely that low WD species have a growth advantage via higher LA/SM, at least in forests, if not generally. This accords with the common observation that species with low WD have generally faster stem-diameter and volumetric growth rates (see *Introduction*) and provides a prospective explanation for this trend.

Linking leaf/stem deployment to WD and plant hydraulics

Leaf and stem deployment can be linked with plant water use as follows (Martinez-Vilalta et al. 2004):

$$LA \cdot g \cdot V = Ks \cdot SA \cdot \Delta\Psi, \qquad (1)$$

where g is conductance of water vapour between leaves and air, V is vapour pressure deficit of the atmosphere, Ks is sapwood hydraulic conductivity, $\Delta\Psi$ the water potential gradient through the system, and LA and SA are leaf area and sapwood area, respectively. Transpiration rate is given by g·V; hence, the equation describes the steady-state condition at which water flow through the xylem matches water loss from leaves. Although we expected that species with lower WD might support a larger total leaf area per stem cross-section (LA/SA), we tended to find either no relationship or the opposite trend to that predicted. Inspection of equation 2 helps explain why relationships among traits such as LA/SA and WD may vary, both among species and among sites: plant water use (assuming soil water is available) is determined by several, presumably coordinated plant properties, as well as by the humidity of the air surrounding leaves. Even for a given set of coexisting species (for which V might be considered more or less constant), equation 2 suggests that LA/SA should increase as either Ks or $\Delta\Psi$ increase, or as g decreases. Variation in WD is likely to be negatively related to Ks but positively related to $\Delta\Psi$, Ks often being lower in species with high WD (Stratton et al. 2000, Bucci et al. 2004, Gartner and Meinzer 2005) although not always (Gartner et al. 1990). Ks could be lower in species with high WD because vessel lumens make up a smaller proportion of stem cross-sections or because the average size of individual vessels is smaller, conductivity scaling to the fourth power of vessel diameter (the Hagen–Poiseuille law). On the other hand, resistance to vessel implosion under very negative pressures (higher $\Delta\Psi$) tends to increase with WD. This may largely reflect that fact that implosion resistance increases as the thickness-to-diameter ratio of vessels increases, which, itself, increases in concert with WD (Hacke and Sperry 2001, Hacke et al. 2005). Thus, the nature of the relationship between WD and LA/SA among a given set of species should, in principle, depend on the relative strength of the relationships between WD and each of Ks and $\Delta\Psi$, and on how leaf-to-air conductance (g) varies with these other traits. In other words, a variety of hydraulic and leaf/stem deployment traits need measuring to understand the implications of results such as ours.

Several recent studies illustrate this point nicely. Both among six tree species in Brazil (Bucci et al. 2004) and 12 conifers (Martinez-Vilalta et al. 2004), species with higher Ks (and lower WD, where measured) deployed less LA/SA, were more vulnerable to cavitation and/or developed less negative minimum midday water potentials (Ψmin). All else being equal, deploying a larger LA/SA would lead to a higher $\Delta\Psi$ and thus greater cavitation risk. Consequently, in the conifer study, the lower Ks associated with higher LA/SA was thought to represent trait coordination acting to lower this risk. In line with our prediction, but in contrast to the Brazilian and conifer studies, two other recent studies reported *negative* WD – LA/SA and positive Ks (or D_H)–LA/SA relationships (Ackerly 2004, Cavender-Bares et al. 2004). However, just as in the Bucci et al. and Martinez-Vilalta et al. studies, the higher Ks (or D_H)/lower WD species exhibited less negative Ψmin, or showed a greater proportional loss of conductivity (PLC), comparing field to maximum (fully flushed) values. Thus, without having yet measured the relevant traits for our species, it is difficult to interpret the hydraulic implications of the positive WD–LA/SA relationship that we observed.

Another interesting aspect to our study was that, besides LA/SA being positively correlated with $WD_{250\,mm}$, it was unrelated to traits such as leaf size, SLA or to $WD_{10\,mm^2}$. This suggests that LA/SA, which must surely be coordinated with other hydraulic traits, not only showed mixed relationships with WD (which is related not only to hydraulics but to several other aspects of plant strategy; see *Introduction*), but furthermore varied independently from the trait-dimension represented by leaf size and from the leaf economics spectrum (Wright et al. 2004), here represented by SLA.

Why do species with lower WD tend to have larger leaves?

Leaf size and WD were found here to be negatively related, both at most individual sites and in the common ANCOVA relationships. This accords with several recent reports (Ackerly 2004, Cavender-Bares et al. 2004, Rossetto and Kooyman 2005), although no prospective explanations have yet been offered. Our tentative interpretation invokes an indirect correlation via plant hydraulics: (1) If, on average, species with lower WD have higher Ks (all else being equal), this would allow a larger total leaf area to be deployed per stem; (2) Variation in individual leaf size seems to drive variation in total leaf area per branch more so than variation in leaf number (*Results*; see also Westoby and Wright 2003). Hence, species with larger leaves tend also to have lower WD. Still, our results and those from studies cited above show that this prospective pathway is certainly not guaranteed. WD has not

always been negatively correlated with Ks; Ks and LA/SA show different relationships in different studies, WD and LA/SA also.

Shifts in plant traits with site properties

Several traits were correlated with site rainfall. On average, $LA/SA_{250\ mm}$, leaf size, LM/SM, LA/SM and SLA were higher at wetter sites, while WD was lower. These trends were not entirely unexpected. For example, lower whole-plant LAR (the analogue of LA/SM) in low rainfall species has been reported for seedlings in eastern Australia (Wright and Westoby 1999). In adult plants, generally lower SLA in species from low rainfall sites has also been reported, and smaller mean leaf size also (see review by Westoby et al. 2002). The trend in LA/SA was also not unexpected, with similar patterns observed previously among oaks in Florida (Cavender-Bares and Holbrook 2001, Cavender-Bares et al. 2004) and within several genera in California (Preston and Ackerly 2003). The shift towards higher WD at lower rainfall in our data most probably indicates that these species can run to lower stem water potentials without risk of vessel implosion (and also have a higher degree of cavitation protection). Presumably, where water is more limiting, the disadvantages of vessel implosion or cavitation are greater and the potential for refilling vessels following cavitation lower; where water is less limiting, plants can employ a higher risk strategy (e.g. higher LA/SA).

Considering $LA/SM_{10\ mm^2}$ – $WD_{10\ mm^2}$ relationships, not only was there a distinct separation in trait values according to site rainfall (Fig. 4D) but, in addition, among the high rainfall species, LA/SM tended to be higher and WD lower for species growing at the higher fertility site (i.e. GHP, compared with GLP). Higher LAR in species from higher nutrient soils has been observed before, for seedlings (Wright and Westoby 1999), and, in general, species on richer soils would be expected to have faster growth rates, at least partly due to higher LAR. Lower mean WD has been seen on higher fertility soils also, at least in the Neotropics (Muller-Landau 2004), although no such trend was seen among species in tropical Guyana (ter Steege and Hammond 2001).

Conclusions

Our aims were to explore the ecological implications of variation among species in the size of their leaves, in the density of their wood and in their patterns of leaf and stem deployment. Two key findings from this study were that, via higher LA/SM, there appear to be growth

(RGR_{shoot}) advantages to being larger-leaved (at least for forest species) or to having lower WD. We provided further evidence of the increasingly reported, and poorly understood, negative relationship between leaf size and WD. The questions we addressed focused on understanding trait differences between species, but to understand the ecological implications of trait differences we need to know about the underlying mechanisms. Ideally, hydraulic traits should be measured in conjunction with those describing leaf and stem deployment (e.g. Bucci et al. 2004, Cavender-Bares et al. 2004). Thus, these questions bridge across comparative ecology to detailed physiology, which, naturally, is more typically concerned with elucidating mechanisms in smaller numbers of species at a time. To measure hydraulic traits on large numbers of species would be especially informative but would take vast effort; thus this is not normally achievable in any one study. However, if measurements made by different researchers are made in comparable ways, but would take vast effort; thus this is not normally achievable this could open the way for synthesis across many studies (e.g. Maherali et al. 2004) and also to a more comprehensive understanding of functional diversity among plant species.

Supplementary material

The following material is available from www.blackwell-synergy.com/loi/ppl

Appendix S1: Supplementary analyses

References

Ackerly DD (2004) Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. Ecol Monogr 74: 25–44

Ackerly DD, Reich PB (1999) Convergence and correlations among leaf size and function in seed plants: a comparative test using independent contrasts. Am J Bot 86: 1272–1281

Aiba M, Nakashizuka T (2005) Sapling structure and regeneration strategy in 18 *Shorea* species co-occurring in a tropical rainforest. Ann Bot 96: 313–321

Bragg JG, Westoby M (2002) Leaf size and foraging for light in a sclerophyll woodland. Funct Ecol 16: 633–639

Bucci SJ, Goldstein G, Meinzer FC, Scholz FG, Franco AC, Bustamante M (2004) Functional convergence in hydraulic

architecture and water relations of tropical savanna trees: from leaf to whole plant. Tree Physiol 24: 891–899

Bucci SJ, Goldstein G, Meinzer FC, Franco AC, Campanello P, Scholz FG (2005) Mechanisms contributing to seasonal homeostasis of minimum leaf water potential and predawn disequilibrium between soil and plant water potential in neotropical savanna trees. Trees-Struct Funct 19: 296–304

Cavender-Bares J, Holbrook NM (2001) Hydraulic properties and freezing-induced cavitation in sympatric evergreen and deciduous oaks with contrasting habitats. Plant Cell Environ 24: 1243–1256

Cavender-Bares J, Kitajima K, Bazzaz FA (2004) Multiple trait associations in relation to habitat differentiation among 17 Floridian oak species. Ecol Monogr 74: 635–662

Diaz S, Hodgson JG, Thompson K, Cabido M, Cornelissen JHC, Jalili A, Montserrat-Marti G, Grime JP, Zarrinkamar F, Asri Y, Band SR, Basconcelo S, Castro-Diez P, Funes G, Hamzehee B, Khoshnevi M, Perez-Harguindeguy N, Perez-Rontome MC, Shirvany FA, Vendramini F, Yazdani S, Abbas-Azimi R, Bogaard A, Boustani S, Charles M, Dehghan M, de Torres-Espuny L, Falczuk V, Guerrero-Campo J, Hynd A, Jones G, Kowsary E, Kazemi-Saeed F, Maestro-Martinez M, Romo-Diez A, Shaw S, Siavash B, Villar-Salvador P, Zak MR (2004) The plant traits that drive ecosystems: Evidence from three continents. J Veg Sci 15: 295–304

Enquist BJ, West GB, Charnov EL, Brown JH (1999) Allometric scaling of production and life-history variation in vascular plants. Nature 401: 907–911

Falster DS, Westoby M (2003) Leaf size and angle vary widely across species: what consequences for light interception? New Phytol 158: 509–525

Falster DS, Westoby M (2005a) Alternative height strategies among 45 dicot rain forest species from tropical Queensland, Australia. J Ecol 93: 521–535

Falster DS, Westoby M (2005b) Tradeoffs between height growth rate, stem persistence and maximum height among plant species in a post-fire succession. Oikos 111: 57–66

Fonseca CR, Overton JM, Collins B, Westoby M (2000) Shifts in trait combinations along rainfall and phosphorus gradients. J Ecol 88: 964–977

Gartner BL, Meinzer FC (2005) Structure-function relationships in sapwood water transport and storage. In: Zwieniecki MA, Holbrook NM (eds) Vascular Transport in Plants. Elsevier/Academic Press, Oxford, pp 307–331

Gartner BL, Bullock SH, Mooney HA, Brown VB, Whitbeck JL (1990) Water transport properties of vine and tree stems in a tropical deciduous forest. Am J Bot 77: 742–749

Givnish TJ (1978) Ecological aspects of plant morphology: leaf form in relation to environment. In: Sattler R (ed) Theoretical Plant Morphology. Leiden University Press, Leiden, pp 83–142

Givnish TJ (1995) Plant stems: biomechanical adaptation for energy capture and influence on species distributions. In: Gartner B (ed) Plant Stems: Physiology and Functional Morphology. Academic Press, San Diego, pp 3–49

Grime JP, Thompson K, Hunt R, Hodgson JG, Cornelissen JHC, Rorison IH, Hendry GAF, Ashenden TW, Askew AP, Band SR, Booth RE, Bossard CC, Campbell BD, Cooper JEL, Davison AW, Gupta PL, Hall W, Hand DW, Hannah MA, Hillier SH, Hodkinson DJ, Jalili A, Liu Z, Mackey JML, Matthews N, Mowforth MA, Meal AM, Reader RJ, Reiling K, Ross-Fraser W, Sutton F, Tasker DE, Thorpe PC, Whitehouse J (1997) Integrated screening validates primary axes of specialisation in plants. Oikos 79: 259–281

Hacke UG, Sperry JS (2001) Functional and ecological xylem anatomy. Perspect Plant Ecol Evol Syst 4: 97–115

Hacke UG, Sperry JS, Pittermann J (2005) Efficiency versus safety tradeoffs for water conduction in angiosperm vessels versus gymnosperm tracheids. In: Holbrook NM, Zwieniecki MA (eds) Vascular Transport in Plants. Elsevier/Academic Press, Oxford, pp 333–353

Hogan KP, Smith AP, Samaniego M (1995) Gas exchange in six tropical semi-deciduous forest canopy tree species during the wet and dry seasons. Biotropica 27: 324–333

King DA, Davies SJ, Nur Supardi MN, Tan S (2005) Tree growth is related to light interception and wood density in two mixed dipterocarp forests of Malaysia. Funct Ecol 19: 445–453

Loehle C (1988) Tree life history strategies: the role of defences. Can J for Res 18: 209–222

Maherali H, Pockman WT, Jackson RB (2004) Adaptive variation in the vulnerability of woody plants to xylem cavitation. Ecology 85: 2184–2199

Martinez-Vilalta J, Sala A, Pinol J (2004) The hydraulic architecture of Pinaceae – a review. Plant Ecol 171: 3–13

Meinzer FC (2003) Functional convergence in plant responses to the environment. Oecologia 134: 1–11

Moles A, Westoby M (2000) Do small leaves expand faster than large leaves, and do shorter expansion times reduce herbivore damage? Oikos 90: 517–526

Moles AT, Westoby M (2004) Seedling survival and seed size: a synthesis of the literature. J Ecol 92: 372–383

Muller-Landau HC (2004) Interspecific and inter-site variation in wood specific gravity of tropical trees. Biotropica 36: 20–32

Pickup M, Westoby M, Basden A (2005) Dry mass costs of deploying leaf area in relation to leaf size. Funct Ecol 19: 88–97

Poorter H, van der Werf A (1998) Is inherent variation in RGR determined by LAR at low irradiance and by NAR at high irradiance? A review of herbaceous species. In: Lambers H, Poorter H, Van Vuuren MMI (eds) Inherent Variation in Plant Growth. Physiological Mechanisms and

Ecological Consequences. Backhuys Publishers, Leiden, pp 309–336

Preston KA, Ackerly DD (2003) Hydraulic architecture and the evolution of shoot allometry in contrasting climates. Am J Bot 90: 1502–1512

Prior LD, Eamus D, Bowman DMJS (2003) Leaf attributes in the seasonally dry tropics: a comparison of four habitats in northern Australia. Funct Ecol 17: 504–515

Reich PB, Ellsworth DS, Walters MB, Vose JM, Gresham C, Volin JC, Bowman WD (1999) Generality of leaf trait relationships: a test across six biomes. Ecology 80: 1955–1969

Roderick ML (2000) On the measurement of growth with applications to the modelling and analysis of plant growth. Funct Ecol 14: 244–251

Rossetto M, Kooyman RM (2005) The tension between dispersal and persistence regulates the current distribution of rare palaeo-endemic rain forest flora: a case study. J Ecol 93: 906–917

Sack L, Cowan PD, Jaikumar N, Holbrook NM (2003) The 'hydrology' of leaves: coordination of structure and function in temperate woody species. Plant Cell Environ 26: 1343–1356

Santiago LS, Goldstein G, Meinzer FC, Fisher JB, Machado K, Woodruff D, Jones T (2004) Leaf photosynthetic traits scale with hydraulic conductivity and wood density in Panamanian forest canopy trees. Oecology 140: 543–550

ter Steege H, Hammond DS (2001) Character convergence, diversity, and disturbance in tropical rain forest in Guyana. Ecology 82: 3197–3212

Stratton L, Goldstein G, Meinzer FC (2000) Stem water storage capacity and efficiency of water transport: their functional significance in a Hawaiian dry forest. Plant Cell Environ 23: 99–106

Tyree MT, Zimmerman HM (2002) Xylem Structure and the Ascent of Sap. Springer, Berlin.

Webb LJ (1968) Environment relationships of the structural types of Australian rain forest vegetation. Ecology 49: 296–311

Westoby M, Falster DS, Moles AT, Vesk PA, Wright IJ (2002) Plant ecological strategies: some leading dimensions of variation between species. Ann Rev Ecol Syst 33: 125–159

Westoby M, Wright IJ (2003) The leaf size-twig size spectrum and its relationship to other important spectra of variation among species. Oecologia 135: 621–628

White PS (1983) Evidence that temperate east north American evergreen woody plants follow Corner's Rules. New Phytol 95: 139–145

Whitehead D (1998) Regulation of stomatal conductance and transpiration in forest canopies. Tree Physiol 18: 633–644

Wright IJ, Westoby M (1999) Differences in seedling growth behaviour among species: trait correlations across species, and trait shifts along nutrient compared to rainfall gradients. J Ecol 87: 85–97

Wright IJ, Reich PB, Westoby M (2001) Strategy-shifts in leaf physiology, structure and nutrient content between species of high and low rainfall, and high and low nutrient habitats. Funct Ecol 15: 423–434

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin FS, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas M-L, Niinemets Ü, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas EJ, Villar R (2004) The world-wide leaf economics spectrum. Nature 428: 821–827

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