Hydraulics and life history of tropical dry forest tree species: coordination of species' drought and shade tolerance

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Summary

- Plant hydraulic architecture has been studied extensively, yet we know little about how hydraulic properties relate to species' life history strategies, such as drought and shade tolerance. The prevailing theories seem contradictory.
- We measured the sapwood (K_s) and leaf (K_l) hydraulic conductivities of 40 coexisting tree species in a Bolivian dry forest, and examined associations with functional stem and leaf traits and indices of species' drought (dry-season leaf water potential) and shade (juvenile crown exposure) tolerance.
- Hydraulic properties varied across species and between life-history groups (pioneers vs shade-tolerant, and deciduous vs evergreen species). In addition to the expected negative correlation of K_l with drought tolerance, we found a strong, negative correlation between K_l and species' shade tolerance. Across species, K_s and K_l were negatively correlated with wood density and positively with maximum vessel length. Consequently, drought and shade tolerance scaled similarly with hydraulic properties, wood density and leaf dry matter content. We found that deciduous species also had traits conferring efficient water transport relative to evergreen species.
- Hydraulic properties varied across species, corresponding to the classical trade-off between hydraulic efficiency and safety, which for these dry forest trees resulted in coordinated drought and shade tolerance across species rather than the frequently hypothesized trade-off.

Introduction

Several theories have been developed to explain the high biodiversity of tropical forests, including a balance among dispersal, speciation, immigration and extinction (reviewed in Wright, 2002), and one of the most persistent theories, the niche differentiation theory. This theory postulates that different plant species can coexist by partitioning gradients in resource availability (Grubb, 1977; Hutchinson, 1978; cf. Tilman, 1982) and by diverging in traits associated with high performance in particular niches (Westoby *et al.*, 2002; Poorter, 2007). Traditionally, niche partitioning

studies have mainly focused on light availability as the key factor determining species coexistence (e.g. Denslow, 1987; Swaine & Whitmore, 1988; Popma & Bongers, 1991), partly because most of these studies were conducted in wet tropical forests, where light is more limiting than in open dry forests (Coomes & Grubb, 2000; Asner *et al.*, 2003; Lebrija-Trejos, 2009). Tree species in wet tropical forest occupy similar light niches in the adult stage, but may show large continuous variation in their light niches in the regeneration stage, related to physiological and morphological adaptations (cf. Grubb, 1977; Poorter, 2007; Markesteijn & Poorter, 2009).

More recently, attention has shifted towards the role of water availability as a factor in species coexistence. All tropical tree species have to cope with periodic water shortage at some point, and even in the wet tropics short dry spells can affect survival in the field (Engelbrecht *et al.*, 2006). On a coarse scale, tree species distribution varies with precipitation (Bongers *et al.*, 2004; Engelbrecht *et al.*, 2007; Maharjan *et al.*, in press), while at finer scales species performance and distribution vary along topographical gradients of soil water availability (Borchert, 1994; Clark, 1999; Valencia *et al.*, 2004; Comita & Engelbrecht, 2009). Species partitioning along gradients in water availability will to a great extent be determined by the ability of species to compete for water and tolerate drought. Species hydraulic architecture should thus be one of the major drivers of species partitioning in tropical forests.

All land plants potentially face the same fundamental trade-off to efficiently acquire water and maintain hydraulic conductivity to secure photosynthesis, while running the risk of drought-induced cavitation, which can lead to dysfunctional vessels, stomatal closure, and eventually to the abscission of leaves, shoots, and branches, and finally to plant death (Tyree & Sperry, 1988; Davis *et al.*, 2002; Engelbrecht *et al.*, 2005). A trade-off between stem hydraulic safety and efficiency has indeed been found across many species sets (Zimmermann, 1983; Tyree *et al.*, 1994) and can be explained by structural adaptations. Examples of such adaptations are narrower and shorter vessels, with thicker cell walls, and smaller pit pores, all of which can limit hydraulic efficiency and increase resistance to drought-induced cavitation and the spread of embolism (Hacke *et al.*, 2001; Jacobsen *et al.*, 2005, 2007). Although the basic mechanisms of plant hydraulic architecture are fairly well understood, we still know little about how hydraulic properties are related to species' life-history strategies, such as drought and shade tolerance (Tyree & Ewers, 1991; but see Tyree *et al.*, 1998; Preston *et al.*, 2006; Kursar *et al.*, 2009). If there is such a trade-off between hydraulic efficiency and hydraulic safety, it would be expected that species with high hydraulic conductivity would occur in habitats with high water availability, while species with lower conductivity would occur mainly in habitats with low water availability (Carlquist, 1975; Tyree & Zimmermann, 2002).

Light-demanding species tend to regenerate in high-light habitats, and have high inherent relative growth rates compared with shade-tolerant species. These high relative growth rates are attained through a greater photosynthetic capacity and leaf area allocation (Poorter & Bongers, 2006), and, as a consequence, result in higher transpiration rates and greater leaf-level water demand. These factors necessitate an increased water supply to the leaf and thus an increased stem- and leaf-specific hydraulic conductivity. Indeed, earlier studies on small species sets have suggested

that light-demanding species tend to possess a high hydraulic conductivity (Tyree *et al.*, 1998; Choat *et al.*, 2005; Sack *et al.*, 2005; Markesteijn *et al.*, 2011), although to our knowledge no study has compared coexisting light-demanding and shade-tolerant species within a community in terms of their stem hydraulic conductivity.

Similarly, one would expect hydraulic properties to differ between drought-deciduous and evergreen species. Drought-deciduous species tend to have high photosynthetic rates to maximize carbon gain in their shorter growing season, at the expense of water use efficiency (Goldstein *et al.*, 1989; Sobrado, 1993; Eamus, 1999). To supply their leaves with sufficient water, deciduous species tend to have relatively high stem hydraulic conductivity compared with evergreens (Sobrado, 1993; Choat *et al.*, 2005). By contrast, evergreen species tend to face a greater risk of hydraulic failure through cavitation in the dry season and to protect water transport they have a higher cavitation resistance (Chen *et al.*, 2009).

There are three alternative predictions for the association between shade and drought tolerances, the contribution of hydraulic architecture to these tolerances, and the potential consequences for species niche partitioning. (1) If there is a trade-off between hydraulic efficiency and safety, then the ecological consequence would be that light-demanding species with high hydraulic efficiency would be less drought tolerant, and thus confined to relatively wet habitats. Light-demanding species would thus be confined to wet microsites, or rely on allocation to deeper rooting systems to acquire water in the dry season, or be limited in their growth to the wet season. Conversely, shade-tolerant species, with lower hydraulic efficiency, should be more drought tolerant and able to persist at drier sites, where they would have higher survival rates and prevail over species that are more vulnerable to drought-induced cavitation. Such a pattern would contrast with a prediction formulated by Smith & Huston (1989), who argued for (2) a trade-off between drought and shade tolerances based primarily on a trade-off in carbon allocation to water vs light acquisition, that is, to roots vs shoots. In this case, light-demanding pioneers, which have the capacity to efficiently supply water to leaves, would sustain growth and outcompete shade-tolerant species in drier habitats. Notably, recent studies suggested an alternative pattern, that (3) there is not necessarily an intrinsic trade-off between hydraulic safety and hydraulic efficiency. Depending on the set of species or the type of community assessed, hydraulic safety and efficiency can vary independently (Maherali *et al.*, 2004; Jacobsen *et al.*, 2005; Choat *et al.*, 2007). Such independence would be consistent with an uncoupling of drought and shade tolerances across species and explain why they can vary independently of each other (Holmgren, 2000; Sack & Grubb, 2002; Sack, 2004; Markesteijn & Poorter, 2009). In this case, both light-demanders and shade-tolerant

species could occupy a diverse array of positions along moisture gradients.

In this study, we evaluated, for 40 tropical dry forest species, how hydraulic properties are related to shade and drought tolerance and whether hydraulic architecture may underlie niche partitioning of tree species. We used two independent indices as proxies of the variation in shade and drought tolerance among species, that is, the juvenile crown exposure index (CE_{juv}) and the dry season midday leaf water potential (ψ_l). At any given time, ψ_l expresses the leaf water deficit that species tolerate and integrates the dryness of the soil in which they are rooting and/or the degree to which they maintain stomatal conductivity and transpiration in that soil. In earlier work, we showed a strong relationship between ψ_l and cavitation resistance (P_{50}) – the least ambiguous measure of drought tolerance – among evergreen and deciduous species ($r = 0.79$, $P < 0.001$; Markesteijn et al., 2011), which justifies the use of ψ_l as a proxy for drought tolerance. Still, a word of caution is needed as, because of their deciduous leaf habit at the height of the dry season, the degree to which deciduous species actually 'tolerate' this ψ_l remains unclear.

The following three questions and hypotheses were addressed. (1) How do stem hydraulic properties differ among tropical dry forest species, and between life-history strategies? We expected a large variation in hydraulic properties, with pioneer species and deciduous species having higher hydraulic efficiency than shade-tolerant and evergreen species, respectively. (2) How is stem hydraulic conductivity related to key stem and leaf traits? We expected that stem hydraulic conductivity would be negatively associated with wood density and positively with maximum vessel length (MVL), reflecting a trade-off between hydraulic safety and efficiency. (3) How are hydraulic properties related to species' drought and shade tolerances? As a result of the trade-off between hydraulic safety and efficiency, we expected that stem hydraulic conductivity would be negatively associated with both the shade and drought tolerances of the species, because light-demanding pioneers have higher photosynthetic capacity, and increased transpiration and leaf water demand, and thus would be expected to have greater hydraulic efficiency and greater sensitivity to cavitation than shade-tolerant species.

Materials and Methods

Study area

Fieldwork was carried out in a deciduous tropical dry forest in the eastern lowlands of Bolivia, near the town of Concepción, Santa Cruz. The forest site is part of the Chiquitano dry forest formation, situated on the Precambrian Brazilian shield (Cochrane, 1973) at the transition of the Amazonian tropical lowland evergreen rain forest in the north and the thorn-shrub formations of the Gran Chaco region in the south (Killeen et al., 1998; Jardim et al., 2003). The forest is the private property of a certified timber company (INPA Parket Ltda., Bergen op Zoom, the Netherlands) and one of the long-term research sites of the Instituto Boliviano de Investigación Forestal (IBIF).

The study site (16°07′S, 61°43′W; mean elevation of c. 458 m) has been classified as a tropical lowland dry deciduous forest, with a mean annual temperature of 24.3°C, a mean annual precipitation of 1160 mm (meteorological data from 1943–2005 from Bolivia's national airports administrator (AASANA) for Concepción at 40 km from the study site) and a dry period of 3 months (June–September) in which the potential evapotranspiration exceeds precipitation. The study area has generally poor oxisol soils (Navarro & Maldonado, 2002). The forest has a mean stem density of 420 trees ha⁻¹, a basal area of 18.3 m² ha⁻¹, and a species richness of 34 ha⁻¹ (trees ≥ 10 cm diameter at breast height; M. Peña-Claros et al., unpublished). Average canopy height is 20 m and virtually all canopy trees shed their leaves in the dry season. Some species in this forest are facultatively deciduous or show ontogenetic changes in leaf lifespan; that is, evergreen as juveniles and deciduous as adults. The most dominant species in the area are *Acosmium cardenasii* H.S. Irwin & Arroyo (Fabaceae), *Casearia gossypiosperma* Briquet (Salicaceae), and *Caesalpinia pluviosa* DC (Fabaceae). Nomenclature follows Stevens (2010).

Species and sapling selection

We studied the hydraulic properties of 40 tree species belonging to 37 different genera, 21 families and 12 orders (Stevens, 2010). The 40 selected species included some of the most abundant in this type of forest, and together they represented > 75% of species with stems over 10 cm dbh (IBIF, unpublished) (Table 2). We sampled 10 species from the Fabaceae, because of their dominance in this forest.

Species' drought and shade tolerance indices

To express species drought and shade tolerances, we used two independent indices: the dry season midday leaf water potential (ψ_l) and the juvenile crown exposure (CE_{juv}) of the species, where a low CE indicates a shade-tolerant species. These are qualitative and integrative indices, representing the stress tolerance of the plant (and of the leaf tissues in the case of ψ_l) in its natural habitat. These indices of experienced resource availability are thus of higher resolution than, but similar in information content to, the rankings used to describe shade or drought tolerance by Ellenberg et al. (1991), or those compiled for temperate trees and shrubs by Niinemets & Valladares (2006), based on subjective assessments of natural species occurrences.

The ψ_l was measured in the dry season of 2008 for five individual saplings per species, one leaf per sapling. Saplings were selected from exposed locations along the road. Midday leaf water potential was measured with a pressure chamber (Model SKPM 1405; Skye Instruments Ltd, Powys, UK). We selected fully expanded and exposed healthy leaves, without signs of herbivory. Between 14:00 and 17:00 h, leaves were collected and immediately sealed into plastic bags into which breath was exhaled. The ψ_l was taken as an indicator of the leaf water deficit that different species could tolerate and at midday integrates the dryness of the soil in which they are rooting and/or the degree to which they maintain stomatal conductance and transpiration in that soil. The ψ_l was measured in June, 2 months after the onset of the dry season but before the drought in this forest was at its peak (August–September; Markesteijn *et al.*, 2010). In this way we were able to compare drought-tolerant evergreens and also drought-avoiding deciduous species, which are a large component of the species pool. The necessity of measuring ψ_l before the actual peak in drought, precluded using the minimum seasonal leaf water potential (ψ_{min}) as an index for drought tolerance, although the ψ_{min} has been found to be a good indicator for species distribution along water availability gradients (Pockman & Sperry, 2000; Ackerly, 2004; Bhaskar & Ackerly, 2006; Jacobsen *et al.*, 2007; Kursar *et al.*, 2009). Other studies in seasonally dry tropical forests have shown cross-species correlations between dry season midday leaf water potential and other indices of physiological drought tolerance, such as leaf water potential at 50% loss of stem conductivity, turgor loss point, and leaf water potential at 50% stomatal closure (Brodribb *et al.*, 2002, 2003; Baltzer *et al.*, 2008). In a separate study we showed, for a subset of these species, that ψ_l was also strongly correlated with P_{50} (stem cavitation vulnerability) (Pearson $r = 0.79$, $P \leq 0.001$, $n = 13$; Markesteijn *et al.*, 2011), which further justified its use as a proxy for physiological drought tolerance. The ψ_l values were multiplied by -1 such that species' values were positive and represented a range from drought intolerant (low ψ_l) to drought tolerant (high ψ_l).

We used an independent, objective and continuous measure of species' regeneration light requirements, the average population-level crown exposure at a standard height of 2 m (CE_{juv}; Poorter & Kitajima, 2007). Values of CE vary from 1 to 5, indicating that the tree receives (1) no direct light, (2) lateral light only, (3) overhead light on 10–90% of the vertical projection of the crown surface, (4) overhead light on > 90% of the vertical projection of the crown, and (5) overhead light over the whole crown (emergent crown). Although individual trees of similar size can occur under a variety of light conditions, species with a low CE_{juv} mainly regenerate in the shaded forest understory (shade-tolerant species), whereas species with a high CE_{juv} mainly regenerate in high-light gaps (light-demanding pioneer species). To scale species from shade intolerant to shade tolerant we used $5 - CE_{juv}$ as a proxy for shade tolerance.

Hydraulic conductivity

In the first 2 months after the onset of the dry season, sapwood-specific and leaf-specific hydraulic conductivities were determined for five saplings of each of the 40 species. We collected saplings, 1.5–2 m tall, that were located along logging roads and exposed to full or partial overhead light. Entire shoots of saplings were harvested and transported to the field station for measurements of maximum hydraulic conductivity. Stems were recut under distilled water to avoid the introduction of new embolisms. Distal ends were trimmed with a razor blade to clear any accidentally blocked vessels and *c.* 1 cm of the bark at each side of the branch was removed. While submerged, the shaved end of the branch was wrapped in Parafilm (Pechiney Plastic Packaging, Chicago, IL, USA) and connected to a manifold of hysteresis-resistant poly-tetra-fluor-etheen (PTFE) tubing, which held up to five stems simultaneously. With all stems in place, the manifold was attached to a pressurized reservoir (150 kPa) filled with a flow solution of 10 mmol KCl dissolved in degassed and filtered (0.2 μm) distilled water. The stems were flushed for *c.* 30 min to remove emboli and connected to a second manifold attached to a hydraulic flow apparatus (Sperry *et al.*, 1988). An elevated water reservoir supplied the same flow solution to the stems, with the height quantified for each conductivity measurement to allow determination of pressure (*c.* 5 kPa). To hamper microbial growth in the reservoir and tubing, the flow meter was frequently flushed with a 10% bleach solution and rinsed. Water flow through the stems was left to equilibrate for *c.* 10 min, after which flow rates were determined volumetrically with serological pipettes connected to the upper end of the stem. We measured the flow rates as the time (s) to fill 0.1 or 0.01 ml (in the case of low flow) of pipette volume. Hydraulic conductance (K_h; in kg s^{-1} MPa^{-1} m) was calculated as:

$$K_h = \frac{\Delta V}{(\Delta P / \Delta X)} \qquad \text{Eqn 1}$$

where ΔV is the mass flow rate (kg s^{-1}) and ΔP is the pressure drop (MPa) across a stem segment of length X (m). We estimated the sapwood area as the cross-sectional area of the upper distal end of the stem after bark removal, minus the cross-sectional area of pith. Sapwood-specific conductivity (K_s; mol m^{-1} s^{-1} MPa^{-1}) was calculated by dividing K_h by the cross-sectional sapwood area and multiplying by 18.02 (the molar mass of H_2O). The sapwood area of the stem segments ranged from 6.0 to 27.6 mm^2 across species (mean ± SE = 15.2 ± 0.8 mm^2).

For each sapling, we calculated the Huber value (Hv; cm^2 cm^{-2}) as the cross-sectional sapwood area of the upper distal end of the stem divided by the total supported leaf area. To determine the total supported leaf area above the upper, distal cut for the measured stems, the fresh mass of leaves was measured with a precision balance (± 0.01 g) and the leaf area of a subsample of known fresh mass was digitized with a flatbed scanner (Canon Lide 50, Canon, UK) and analysed for leaf area using IMAGEJ software (http://imagej.nih.gov/ij/). The total supported leaf area was estimated as the leaf area per unit fresh mass of the subsample multiplied by the fresh mass of all the leaves. Leaf-specific conductivity (K_l; mmol m^{-1} s^{-1} MPa^{-1}) was calculated as K_s multiplied by Hv. Saplings of two species had lateral branches (*Actinostemon concepcionis* and *Erythroxylum daphnites*) and one arborescent liana species had leaves along the main stem (*Bourgainvilla modesta*). In these cases, branches and leaves were cut from the main stem and wounds were sealed with instant adhesive glue. The removed leaves were not taken into account in further measurements and calculations; thus, for these three species, K_l might be overestimated to some degree. However, excluding these three species from the analyses did not lead to different results or conclusions.

Stem and leaf traits

Wood density (WD; g cm^{-3}) was determined for all 40 species. For a sample of each stem measured for conductivity, we estimated the fresh volume without the bark using the water displacement method (Ilic *et al.*, 2000). Samples were then dried in an oven for 48 h at 75°C and dry mass was measured with a precision balance (± 0.0001 g) and WD was calculated as dry mass/fresh volume.

Maximum vessel length (MVL; cm) was determined by air injection (Ewers & Fisher, 1989) for five saplings per species. Saplings were selected under the same conditions and in the same area as those measured for conductivity, cut at ground level and transported to the field station. The distal ends of the stem were trimmed with a razor blade to clear blocked vessels and the proximal end was attached to an air pump delivering *c.* 100 kPa pressure. The upper end of the stem was submerged in water and cut back in 1-cm increments until air bubbles escaped. The remaining length of the stem was taken as the length of the longest continuous vessel.

Subsamples of the leaf material collected to estimate the total leaf area were saturated overnight in moist paper towels in a refrigerator, after which we measured their fresh mass and average leaf size (LS; cm^2). The samples were oven-dried at 65°C for 48 h before the determination of dry mass. Leaf dry matter content (LDMC; g g^{-1}) was calculated as dry mass/fresh mass. The specific leaf area (SLA; cm^2 g^{-1}) was calculated as leaf area/dry mass. We took care that the leaves sampled for the measurements of SLA and LDMC were representative, healthy, fully expanded leaves that did not show clear signs of mechanical or pathogen damage. All hydraulic traits included in this paper are summarized in Table 1 and the mean values per species are shown in Table 2.

Data analyses

Before analyses, species traits were ln-transformed to improve homoscedasticity and normality, with the exception that LDMC, a proportional trait, was arcsine-transformed. Among-species differences in hydraulic properties were assessed with one-way ANOVAs with species as a fixed factor. Differences in mean hydraulic properties between life-history strategies were analysed with independent-samples *t*-tests on the mean species trait values.

Pearson correlation analyses were used to determine the relationships across species of hydraulic conductivity to the stem and leaf traits and to indices of drought tolerance (ψ_l) and shade tolerance (CE_{juv}). Forward multiple regressions were used to evaluate which traits were predictors of hydraulic conductivity and which hydraulic properties best explained ψ_l and CE_{juv}.

Multivariate associations among hydraulic properties were analysed with a principal component analysis (PCA) of the mean species values for hydraulic properties and for other wood and leaf traits. The drought and shade tolerance indices (ψ_l and CE_{juv}) were not included in the initial analysis, but plotted *a posteriori* against the PCA axes. Statistical analyses were performed using SPSS 17.0 (SPSS Inc., Chicago, IL, USA).

Results

Species differences in hydraulic properties

Dry forest tree species differed markedly in all the studied hydraulic properties (Table 3). Species differences explained

Table 1 Abbreviations of measured traits with units

Abbreviation	Trait	Units
ψ_l	Midday leaf water potential	MPa
CE_{juv}	Inverse juvenile crown exposure	
K_s	Sapwood-specific hydraulic conductivity	mol m^{-1} s^{-1} MPa^{-1}
K_l	Leaf-specific hydraulic conductivity	mmol m^{-1} s^{-1} MPa^{-1}
WD	Wood density	g cm^{-3}
MVL	Maximum vessel length	cm
Hv	Huber value (sapwood area per unit leaf area)	cm^2 cm^{-2} (×10^6)
LS	Mean leaf size	cm^2
LDMC	Leaf dry matter content	g g^{-1}
SLA	Specific leaf area	cm^2 g^{-1}

Table 2 The 40 studied species of Bolivian tropical dry forest arranged into different life-history groups according to their shade tolerance (Pioneers (P) and shade tolerant (ST)) and leaf habit (deciduous (D) and evergreen (E))

Species	Family	Guild	Leaf habit	ψ_l (-MPa)	CE_{luv} (-)	K_s (mol m⁻¹ s⁻¹ MPa⁻¹)	K_l (mmol m⁻¹ s⁻¹ MPa⁻¹)	WD (g g⁻¹)	MVL (cm)	Hv (cm² cm⁻² ×10⁶)	LS (cm²)	LDMC (g g⁻¹)	SLA (cm² g⁻¹)
Acosmium cardenasii	Fabaceae	ST	E	3.3 ± 0.13	3.6	65.3 ± 4.4	12 ± 0.2	0.51 ± 0.04	99.0 ± 7.1	187 ± 12	0.8 ± 0.1	0.40 ± 0.03	172 ± 10
Actinostemon concepcionis	Euphorbiaceae	ST	E	3.3 ± 0.14	3.4	30.7 ± 2.2	7 ± 0.3	0.71 ± 0.01	61.3 ± 6.0	221 ± 8.4	1.3 ± 0.0	0.54 ± 0.03	262 ± 4.2
Ampelocera ruizii	Ulmaceae	ST	E	1.3 ± 0.02	3.4	200 ± 20	19 ± 1.0	0.55 ± 0.01	94.8 ± 2.0	99.3 ± 12	43 ± 2.4	0.34 ± 0.02	161 ± 6.5
Anadenanthera colubrina	Fabaceae	ST	E	3.4 ± 0.16	3.2	146 ± 8.9	23 ± 1.8	0.50 ± 0.02	113 ± 4.5	160 ± 12	0.0 ± 0.0	0.57 ± 0.01	157 ± 5.0
Aspidosperma cylindrocarpon	Apocynaceae	ST	D	1.8 ± 0.07	3.7	138 ± 5.7	17 ± 1.3	0.49 ± 0.04	72.5 ± 3.8	129 ± 14	40 ± 4.2	0.34 ± 0.03	115 ± 15
Aspidosperma tomentosum	Apocynaceae	ST	E	2.3 ± 0.12	3.7	122 ± 4.5	27 ± 2.0	0.62 ± 0.02	52.8 ± 9.2	224 ± 23	25 ± 7.3	0.33 ± 0.02	174 ± 7.4
Astronium urundeuva	Anacardiaceae	P	D	0.5 ± 0.04	2.6	891 ± 74	81 ± 3.8	0.38 ± 0.02	97.6 ± 13	92.4 ± 6.1	16 ± 2.6	0.29 ± 0.01	180 ± 17
Bougainvillea modesta	Nyctaginaceae	P	E	1.0 ± 0.09	2.8	36.3 ± 4.1	8 ± 0.6	0.42 ± 0.02	103 ± 5.0	231 ± 25	20 ± 1.8	0.47 ± 0.10	151 ± 13
Caesalpinia pluviosa	Fabaceae	ST	E	1.2 ± 0.11	3.2	421 ± 18	75 ± 2.2	0.61 ± 0.02	102 ± 3.4	179 ± 2.8	1.2 ± 0.4	0.47 ± 0.02	174 ± 14
Capparis prisca	Brassicaceae	ST	E	2.5 ± 0.06	3.4	35.1 ± 4.2	4 ± 0.3	0.53 ± 0.03	60.8 ± 13	140 ± 34	73 ± 11	0.34 ± 0.03	109 ± 10
Casearia gossypiosperma	Salicaceae	ST	D	2.8 ± 0.18	3.3	121 ± 12	17 ± 1.4	0.52 ± 0.01	69.3 ± 2.3	145 ± 21	19 ± 2.8	0.42 ± 0.02	245 ± 5.5
Cecropia concolor	Urticaceae	P	E	0.2 ± 0.02	2.6	277 ± 38	48 ± 3.5	0.21 ± 0.02	98.0 ± 15	187 ± 26	121 ± 31	0.27 ± 0.03	174 ± 8.5
Ceiba samaura	Malvaceae	P	D	0.9 ± 0.11	2.5	385 ± 38	43 ± 1.9	0.24 ± 0.02	82.2 ± 4.8	115 ± 9.7	13 ± 1.5	0.25 ± 0.02	232 ± 10
Ceiba speciosa	Malvaceae	P	D	0.8 ± 0.06	3.4	405 ± 23	51 ± 1.3	0.24 ± 0.02	70.8 ± 4.1	126 ± 8.0	15 ± 1.5	0.25 ± 0.03	250 ± 15
Centrolobium microchaete	Fabaceae	P	D	1.4 ± 0.38	3.1	507 ± 34	53 ± 1.1	0.30 ± 0.03	92.1 ± 8.4	107 ± 5.5	45 ± 7.9	0.37 ± 0.02	240 ± 23
Combretum leprosum	Combretaceae	P	E	1.3 ± 0.04		299 ± 21	33 ± 1.8	0.43 ± 0.03	84.6 ± 9.3	112 ± 9.0	224 ± 35	0.39 ± 0.01	139 ± 11
Copaifera chodatiana	Fabaceae	ST	E	2.6 ± 0.03	3.1	154 ± 9.4	41 ± 2.3	0.63 ± 0.02	60.4 ± 12	269 ± 27	13 ± 1.6	0.47 ± 0.03	132 ± 6.1
Erythroxylum daphnites	Erythroxylaceae	ST	E	2.0 ± 0.37	3.4	36.3 ± 4.6	11 ± 0.9	0.75 ± 0.03	53.6 ± 4.1	311 ± 49	8.2 ± 2.3	0.54 ± 0.06	152 ± 14
Gallesia integrifolia	Phytolaccaceae	ST	E	1.1 ± 0.04	3.2	139 ± 24	14 ± 1.4	0.38 ± 0.04	105 ± 9.1	113 ± 20	57 ± 8.2	0.25 ± 0.01	220 ± 36
Hymenaea courbaril	Fabaceae	ST	E	1.0 ± 0.09		350 ± 23	49 ± 2.0	0.58 ± 0.04	111 ± 5.6	145 ± 12	29 ± 4.2	0.49 ± 0.03	128 ± 4
Machaerium acutifolium	Fabaceae	ST	E	3.0 ± 0.33	3.6	126 ± 4.5	14 ± 1.2	0.62 ± 0.03	69.4 ± 2.6	119 ± 6.7	7.4 ± 1.9	0.49 ± 0.03	236 ± 10
Machaerium scleroxylon	Fabaceae	P	D	1.4 ± 0.13	3.0	204 ± 5.4	66 ± 1.3	0.49 ± 0.02	65.2 ± 0.6	325 ± 14	3.4 ± 0.2	0.48 ± 0.01	128 ± 7.2
Manihot guaranatica	Euphorbiaceae	P	D	0.8 ± 0.04	2.3	272 ± 21	65 ± 2.2	0.19 ± 0.01	107 ± 6.6	243 ± 16	106 ± 21	0.27 ± 0.01	227 ± 8.3
Myrciaria cauliflora	Myrtaceae	ST	E	3.1 ± 0.08	3.3	31.0 ± 4.8	7 ± 0.4	0.64 ± 0.03	73.2 ± 8.1	241 ± 54	2.6 ± 0.4	0.54 ± 0.03	143 ± 5.8
Neea cf. steinbachii	Nyctaginaceae	ST	E	2.5 ± 0.10	3.4	69.7 ± 3.0	10 ± 0.4	0.42 ± 0.01	71.4 ± 6.6	151 ± 10	25 ± 0.9	0.20 ± 0.01	149 ± 10
Ouratea sp.	Ochnaceae	ST	E	0.8 ± 0.05	3.2	34.3 ± 2.3	5 ± 0.2	0.52 ± 0.02	57.5 ± 4.2	137 ± 9.0	69 ± 37	0.53 ± 0.04	103 ± 0.5
Phyllanthus sp. nov.	Euphorbiaceae	ST	E	1.9 ± 0.06	3.6	59.6 ± 5.0	16 ± 1.4	0.68 ± 0.01	78.9 ± 8.6	285 ± 34	8.4 ± 0.7	0.48 ± 0.07	242 ± 8.4
Phyllostylon rhamnoides	Ulmaceae	ST	E	2.4 ± 0.43	3.5	34.5 ± 5.8	16 ± 1.0	0.62 ± 0.03	66.6 ± 7.8	530 ± 114	11 ± 0.4	0.29 ± 0.01	186 ± 1.5
Pogonopus tubulosus	Rubiaceae	ST	D	1.2 ± 0.07	3.3	110 ± 3.8	8 ± 0.5	0.29 ± 0.03	82.4 ± 4.8	70.9 ± 3.9	201 ± 26	0.24 ± 0.01	269 ± 13
Psidium sartorianum	Myrtaceae	ST	E	1.0 ± 0.09	3.8	49.5 ± 1.1	15 ± 0.5	0.56 ± 0.03	64.6 ± 3.3	308 ± 12	11 ± 0.7	0.24 ± 0.01	172 ± 2.5
Pterogyne nitens	Fabaceae	P	E	1.8 ± 0.05	3.0	356 ± 58	57 ± 5.5	0.35 ± 0.01	57.0 ± 5.9	171 ± 22	16 ± 1.5	0.32 ± 0.02	187 ± 15
Rollinia herzogii	Annonaceae	ST	E	± 0.02		169 ± 11	43 ± 3.3	0.50 ± 0.03	69.5 ± 8.2	266 ± 38	38 ± 3.7	0.45 ± 0.01	114 ± 8.5
Schinopsis brasiliensis	Anacardiaceae	P	D	1.1 ± 0.07		128 ± 6.5	18 ± 1.0	0.51 ± 0.02	66.5 ± 5.0	138 ± 8.5	2.5 ± 0.1	0.40 ± 0.00	177 ± 6.0
Simira rubescens	Rubiaceae	ST	D	2.6 ± 0.14	3.4	229 ± 24	34 ± 1.2	0.52 ± 0.02	61.0 ± 4.2	154 ± 13	60 ± 20	0.38 ± 0.02	161 ± 4.7
Solanum riparium	Solanaceae	P	E	0.4 ± 0.03	2.0	627 ± 54	61 ± 0.8	0.25 ± 0.02	106 ± 9.5	99.5 ± 8.0	127 ± 38	0.18 ± 0.03	240 ± 7.1
Spondias mombin	Anacardiaceae	P	D	0.7 ± 0.10	2.6	452 ± 46	59 ± 6.0	0.22 ± 0.02	79.8 ± 5.3	133 ± 15	35 ± 4.2	0.23 ± 0.01	215 ± 8.9
Sweetia fruticosa	Fabaceae	ST	E	1.5 ± 0.04	3.3	454 ± 23	36 ± 3.6	0.61 ± 0.03	96.8 ± 6.4	79.1 ± 7.4	6.3 ± 1.1	0.44 ± 0.04	196 ± 25

Table 2 (Continued)

Species	Family	Guild	Leaf habit	CE_{juv} (–)	ψ_l (–MPa)	K_s (mol m⁻¹ s⁻¹ MPa⁻¹)	K_l (mmol m⁻¹ s⁻¹ MPa⁻¹)	WD (g g⁻¹)	MVL (cm)	Hv (cm² cm⁻² ×10⁶)	LS (cm²)	LDMC (g g⁻¹)	SLA (cm² g⁻¹)
Tabebuia impetiginosa	Bignoniaceae	P	E	2.6	1.1 ± 0.08	147 ± 5.1	34 ± 0.4	0.43 ± 0.03	68.4 ± 4.0	235 ± 9.6	51 ± 6.2	0.35 ± 0.03	152 ± 11
Trichilia elegans	Meliaceae	ST	E	3.4	2.6 ± 0.17	105 ± 15	16 ± 0.8	0.57 ± 0.04	65.0 ± 7.1	166 ± 24	18 ± 2.9	0.35 ± 0.02	182 ± 10
Zanthoxylum monogynum	Rutaceae	ST	E	3.5	2.7 ± 0.08	200 ± 4.5	33 ± 0.6	0.55 ± 0.02	46.3 ± 3.3	167 ± 5.0	20 ± 2.5	0.31 ± 0.03	167 ± 13

Indices of species' drought tolerance (ψ_l) and shade tolerance (CE_{juv}) are given. The hydraulic properties and trait values presented are the untransformed species means (± SE) included in this study (n = 5 per species). Trait abbreviations as in Table 1.

on average 83% of the total variation in traits (range 61–98%). Of all traits, the amount of variation explained by species differences was greatest for K_s, K_l and LS, which differed 29-, 19- and > 8000-fold across species, respectively. MVL was the least variable of the study traits and differed *c.* 2-fold across species, from 46 to 118 cm. The relatively narrow variation in MVL may relate to measurements being made on saplings of similar height.

On average, pioneers had higher K_s and K_l, and lower WD than shade-tolerant species, but the two functional groups did not differ in maximum vessel length or Hv, or in any of the leaf traits (Table 4). Deciduous species had higher K_s and K_l and lower WD than evergreen species and they also had a higher SLA and a lower LDMC (Table 4).

Hydraulic conductivity vs stem and leaf traits

K_s and K_l were strongly positively correlated (Table 5). Both K_s and K_l were correlated negatively with WD and positively with maximum vessel length. Species with a large sapwood area per unit leaf area (large Hv) had lower K_s, and, as a consequence of this compensation at the shoot level, K_l (=K_s/Hv) was less variable across species than K_s (18.5- vs 29-fold, respectively; Table 3). K_s was negatively correlated with LDMC (Table 4, Fig. 1).

The forward multiple regression showed that K_s was mainly determined by WD (standardized regression coefficient, β = −0.39, P = 0.01), which explained 51% of the variation, and to a lesser extent by Hv, which explained an additional 7% of the variation (β = −0.30, P = 0.05). For K_l, only WD was selected in the multiple regression model (β = −0.48, P = 0.002). Multivariate associations among hydraulic, wood and leaf traits were analysed with a PCA. The first two principal components together explained 59% of the variation (Fig. 3). The first axis explained 42% of the variation and mainly separated species with high K_s and K_l at high axis values and species with high WD and LDMC and large leaf size at low axis values. The second axis explained an additional 17% of the total variance. Species separation along this axis was mainly determined by K_l at high axis values and leaf size at low axis values. *A posteriori* we plotted ψ_l and CE_{juv} on the PCA loading plot, based on their correlation with the two extracted axes. Both indices correlated strongly and negatively with the first PCA axis but not with the second axis (Table 5, Fig. 2a). Drought-tolerant species combined a high WD with a high LDMC and a large sapwood area per unit leaf area. Light-demanding (shade-intolerant) species combined a high hydraulic conductivity with long vessels and a high SLA. Along the first PCA axis, pioneers were significantly separated from shade-tolerant species in their mean species scores, as were deciduous species and evergreens (Table 4) The first axis showed a strong correlation with vulnerability to cavitation (P_{50}) for a subset

Table 3 Among-species variation in hydraulic properties for 40 Bolivian tropical dry forest species, indicated by one-way ANOVA results (df = 39)

	SS	MS	F	P	R^2	Mean ± SE	Min	Max	Ratio
Hydraulics									
ψ_l	22.6	0.58	44.1	***	92	1.70 ± 0.15	0.17	3.42	20.1
K_s	81.7	2.09	111	***	96	3.88 ± 0.54	0.55	16.0	29.0
K_l	115	2.94	179	***	98	31.2 ± 3.42	4.37	81.1	18.5
Stem traits									
WD	2.08	0.05	35.6	***	90	0.48 ± 0.02	0.19	0.75	3.88
MVL	11.3	0.29	6.44	***	61	78.4 ± 2.94	46.3	113	2.44
Hv	34.8	0.89	15.7	***	79	183 ± 13.9	70.9	530	7.48
Leaf traits									
LS	317	8.12	62.7	***	94	39.6 ± 8.12	0.03	224	8053
LDMC	2.78	0.07	10.8	***	73	0.37 ± 0.02	0.18	0.57	3.25
SLA	12.8	0.33	14.7	***	78	180 ± 7.22	103	269	2.61

The table shows sums of squares (SS) and mean sums of squares (MS); F and significance values (P); the amount of variation explained by among-species differences (R^2; %); overall mean trait values (± SE); minimum (Min) and maximum (Max) species mean trait values; and the ratio of the maximum : minimum value (Ratio). ***, $P < 0.001$. Trait abbreviations as in Table 1.

Table 4 Differences in mean stress tolerance indices and hydraulic and leaf traits between pioneers ($n = 14$) and shade-tolerant species ($n = 26$) and deciduous ($n = 12$) and evergreen ($n = 28$) species of Bolivian tropical dry forest

	Pioneer	Shade tolerant	t-test		Deciduous	Evergreen	t-test	
	Mean ± SE	Mean ± SE	t	P	Mean ± SE	Mean ± SE	t	P
Stress tolerance indices								
ψ_l	0.90 ± 0.09	1.90 ± 0.11	4.35	***	1.16 ± 0.13	1.69 ± 0.12	1.89	ns
CE_{juv}	2.71 ± 0.11	3.41 ± 0.04	−6.29	***	3.02 ± 0.13	3.24 ± 0.08	−1.52	ns
Hydraulics								
K_s	285 ± 10.6	103 ± 4.72	−3.86	**	246 ± 8.29	115 ± 4.24	−2.63	*
K_l	42.8 ± 1.77	18.2 ± 1.17	−3.72	***	36.7 ± 1.93	20.2 ± 0.94	−2.34	*
Stem traits								
WD	0.33 ± 0.02	0.54 ± 0.03	5.41	***	0.35 ± 0.03	0.52 ± 0.02	3.97	***
MVL	82.6 ± 1.01	74.5 ± 1.17	−1.30	ns	80.3 ± 1.01	75.7 ± 0.85	−0.72	ns
Hv	153 ± 3.18	181 ± 4.54	1.08	ns	151 ± 4.45	181 ± 2.76	1.14	ns
Leaf traits								
LS	29.7 ± 2.90	16.0 ± 2.00	−1.38	ns	28.2 ± 2.80	16.8 ± 1.49	−1.13	ns
LDMC	0.32 ± 0.03	0.39 ± 0.02	1.88	ns	0.31 ± 0.03	0.40 ± 0.02	2.29	*
SLA	188 ± 2.12	175 ± 3.14	−0.69	ns	213 ± 4.21	166 ± 1.45	−2.55	*
PCA								
Axis 1	0.85 ± 0.25	−0.46 ± 0.13	−5.06	***	0.68 ± 0.27	−0.29 ± 0.17	−3.09	**
Axis 2	0.55 ± 0.24	−0.84 ± 0.21	0.72	ns	0.0005 ± 0.38	−0.0002 ± 0.16	−0.002	ns

Mean values of the traits (± standard error; SE) are given with the t-test statistics for differences between life-history strategies; ns, nonsignificant; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. Trait abbreviations as in Table 1.

of 13 of 40 species (Pearson $r = 0.80$, $P \leq 0.001$) (P_{50} data taken from Markesteijn *et al.*, 2011). A trade-off between hydraulic safety (high WD and LDMC, and low P_{50}) and hydraulic efficiency (high K_s and K_l) thus seems to underlie species ranking in drought and shade tolerance (Fig. 2a).

Hydraulics relate to drought and shade tolerance

We found that leaf and stem traits showed qualitatively similar relationships with both ψ_l and CE_{juv}. Both proxies

correlated negatively with K_s and K_l, maximum vessel length and leaf size and positively with WD (Fig. 3). By contrast, LDMC was positively related to Ψ_l but independent of CE_{juv} (Table 5).

Forward multiple regression analyses showed that WD and K_l were the most important predictors of both ψ_l and CE_{juv}. For ψ_l, the analyses resulted in a model in which WD was included first ($\beta = -0.48$, $P = 0.002$), explaining 38% of the variation, and K_l ($\beta = -0.30$, $P = 0.04$) second, explaining an additional 7% of the variation. For CE_{juv} the resulting model appeared to be similar; it included WD

Table 5 Bivariate relationships between midday leaf water potential (ψ_l) (as an indicator of drought tolerance) and juvenile crown exposure (CE_{juv}) (as an indicator of shade tolerance; $n = 36$) and hydraulic properties and traits of saplings of 40 dry forest tree species

	ψ_l	CE_{juv}	K_s	K_l	WD	MVL	Hv	LS	LDMC	SLA
Stress tolerance										
ψ_l										
CE_{juv}	0.63***									
Conductivity										
K_s	−0.53***	−0.60***								
K_l	−0.52***	−0.63***	0.84***							
Wood traits										
WD	0.62***	0.70***	−0.51***	−0.48**						
MVL	−0.36*	−0.48**	0.43**	0.32*	−0.40*					
Hv	0.19ns	0.19ns	−0.45**	−0.12ns	0.40*	−0.32*				
Leaf traits										
LS	−0.38*	−0.39*	0.12ns	0.05ns	−0.49**	0.21ns	−0.32*			
LDMC	0.42**	0.32ns	−0.34*	−0.25ns	0.68***	−0.08ns	0.20ns	−0.36*		
SLA	−0.04ns	−0.18ns	0.25ns	0.10ns	−0.33*	0.18ns	−0.21ns	0.08ns	−0.33*	
PCA										
Axis 1	−0.63***	−0.69***	0.81***	0.67***	−0.86***	0.57***	−0.57***	0.48**	−0.64***	0.44**
Axis 2	−0.05ns	−0.18ns	0.49**	0.62***	0.23ns	0.23ns	0.14ns	−0.60***	0.43**	−0.20ns

The table shows Pearson correlation coefficients and their significance. ns, non-significant; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. Trait abbreviations as in Table 1.

first ($\beta = -0.51$, $P < 0.001$), explaining 49% of the variation, and K_l second ($\beta = -0.37$, $P = 0.008$), explaining an additional 10%. Notably, the similar associations between traits and ψ_l and CE_{juv} might be the consequence of a moderately strong association between the two indices (Table 5; $r = 0.63$, $P \leq 0.001$).

Discussion

How do hydraulic properties differ among tropical dry forest tree species?

We found substantial differences across species in all hydraulic properties, and species differences accounted for 61–98% of the variation in traits. We found a particularly large variation across species in hydraulic conductivity (K_s and K_l) and leaf size (Table 3), suggesting that, if this variation impacts on ecological performance, these traits may play a central role in the niche differentiation of tropical dry forest tree species. The clear differences in hydraulic properties between life-history groups indeed underlined this central importance of K_s and K_l.

By contrast with shade-tolerant species, pioneers combined high hydraulic conductivity with a low WD, and had high leaf water potentials in the dry season. Pioneers are thus hydraulically highly efficient and able to comply with the increased water demand for photosynthesis and fast growth, but this comes at a cost, as their xylem is less protected against drought-induced cavitation (Markesteijn *et al.*, 2011). Pioneers thus follow a resource strategy that favours short-term gain at the expense of long-term survival, which fits the trade-off between growth and survival often

found to hold across pioneers and shade-tolerant species (Kitajima, 1994; Wright *et al.*, 2003; Gilbert *et al.*, 2006; Poorter & Bongers, 2006).

A similar contrast was found between deciduous and evergreen species. Deciduous species were geared towards high efficiency, in terms of both water transport (high K_s and K_l) and carbon gain (high SLA). Deciduous species had low WD (Table 3), which would enable them to maximize volumetric growth in their reduced growing season (Eamus & Prior, 2001) and/or to store water in the dry season (Borchert, 1994; Myers *et al.*, 1998) to be able to flush new leaves late in the dry season or early in the wet season (Duff *et al.*, 1997). The low WD of deciduous species is often associated with reduced cavitation resistance (Hacke *et al.*, 2001) and physiological drought sensitivity (cf. Choat *et al.*, 2005).

Interestingly, deciduous species and evergreens did not significantly differ in ψ_l, our proxy for drought tolerance (Table 3). Consistent with this similarity in drought tolerance we found that, for a subset of 13 of these tropical dry forest species, evergreen and deciduous species did not differ in xylem tension at 50% loss of hydraulic conductivity (P_{50}; Markesteijn *et al.*, 2011). However, we note that, despite assumed drought sensitivity during the active season, deciduous species are very successful drought survivors, as they reduce transpiration by having a deciduous leaf habit (Poorter & Markesteijn, 2008). It is important to note that, although we treated deciduous and evergreen species as two distinct life-history groups, they probably form a continuum of variation in leaf life span, as shown for Costa Rican dry forest species (Borchert, 1994). Species' hydraulic architecture is of key importance to the ecological performance
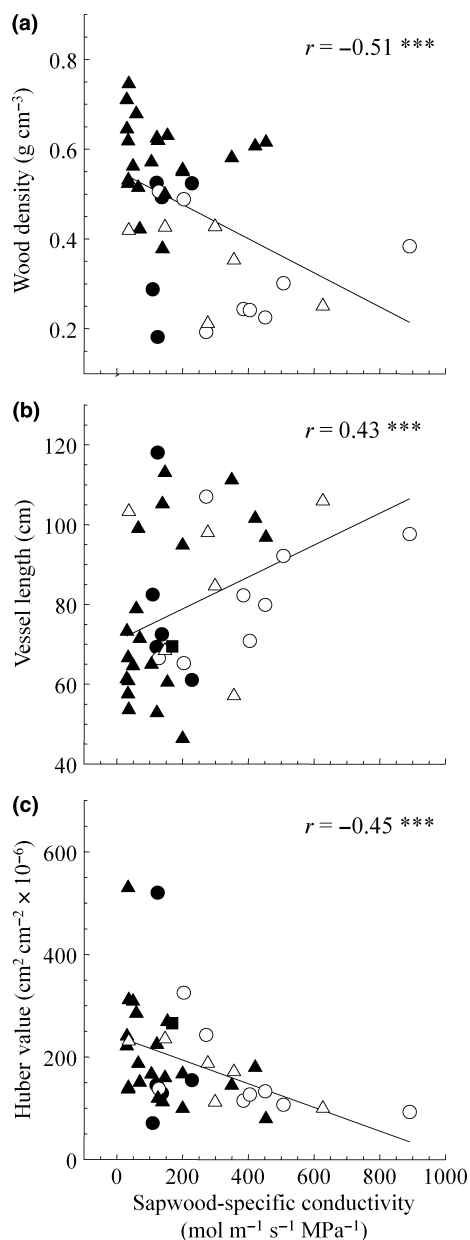
Fig. 1 Relations between stem traits and sapwood-specific hydraulic conductivity (K_s) of 40 Bolivian tropical dry forest species. Pearson correlation coefficients and their level of significance are given. ***, $P < 0.001$. Open and closed symbols, pioneer and shade-tolerant species, respectively; circles and triangles, deciduous and evergreen species, respectively.

Fig. 2 Principal component analysis (PCA) with the mean values of hydraulic properties of 40 Bolivian tropical dry forest tree species. Sub figures show the variation in trait scores (a) and species scores (b) along the first two PCA axes with the percentages of explained variation given. Indices of species' drought tolerance (ψ_l) and shade tolerance (CE_{juv}) were not included in the PCA but were plotted *a posteriori* with the two axes, as was the vulnerability to xylem cavitation (P_{50}) of a subset of 13 species (Markesteijn *et al.*, 2011). Trait abbreviations as in Table 1. Open and closed symbols in (b), pioneer and shade-tolerant species, respectively; circles and triangles, deciduous and evergreen species, respectively.

of species, in relation to both water availability and, equally importantly, light availability.

How is hydraulic conductivity related to stem and leaf traits?

We found strong correlations among functional traits (Table 5). WD emerged as an especially strong correlate of hydraulic traits. WD is an easily measured estimator provid-

ing substantial information about the hydraulic architecture of trees (Chave *et al.*, 2009). Consistent with many other hydraulic studies, we found a negative relationship between WD and hydraulic conductivity (Bucci *et al.*, 2004; Santiago *et al.*, 2004; but see Poorter *et al.*, 2010), and it was the most important predictor of both K_s and K_l.

Dense wood should imply denser cell packing, as a consequence of narrower vessel lumens, because cell wall thickness tends to be invariant with lumen diameter (Pittermann *et al.*, 2006; Zanne *et al.*, 2010). Narrower vessels thus have a higher cell wall to lumen area ratio, and a lower risk of vessel implosion when drought causes extremely negative xylem potentials (Hacke *et al.*, 2001). Notably, there is no structural necessity for a trade-off between hydraulic safety and efficiency, as lower pit air seeding pressures, a decrease in fibre lumen area or an increase in fibre wall thickness could
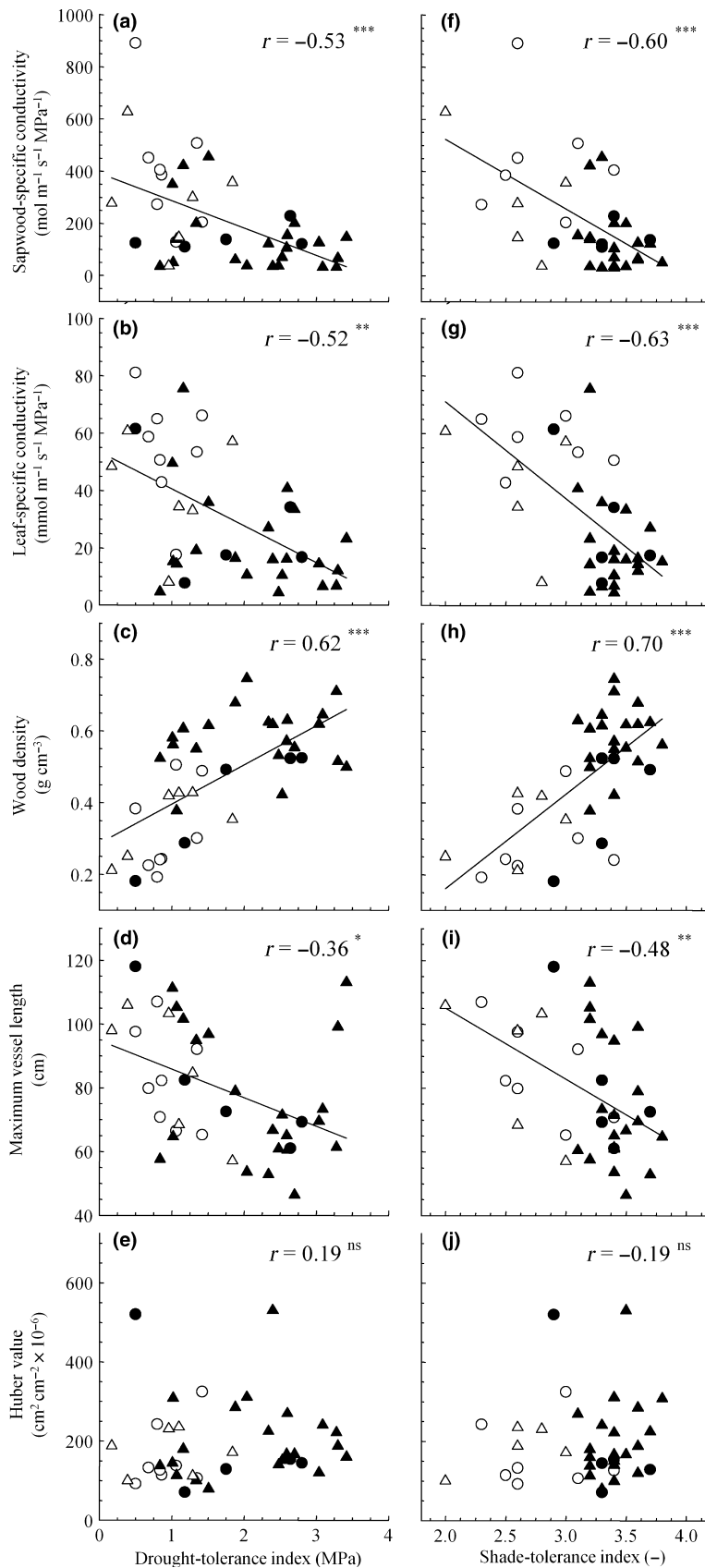
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Fig. 3 Relationships among hydraulic conductivity stem traits and indices of drought tolerance (ψ_l) and shade tolerance (CE_{juv}) for 40 Bolivian tropical dry forest species. A high ψ_l indicates a high drought tolerance and a high CE_{juv} indicates high shade tolerance. Significance of Pearson correlation coefficients: [ns], nonsignificant; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. Open and closed symbols, pioneer and shade-tolerant species, respectively; circles and triangles, deciduous and evergreen species, respectively.

protect plants against cavitation without provoking a causal decline in hydraulic conductivity (Sperry, 2000; Jacobsen *et al.*, 2005). Further, WD has other roles in the life-history variation of trees, as species with low-density wood have the potential to realize high growth rates (Roderick, 2000; Poorter, 2008; Chave *et al.*, 2009), while high wood density tends to correlate with drought and shade survival among evergreen species (Alvarez & Kitajima, 2007; Poorter & Markesteijn, 2008). However, despite these other influences, the smaller vessels associated with a high WD tend to be more resistant to cavitation than larger vessels, both within and among species (Salleo & Lo Gullo, 1989; Lo Gullo & Salleo, 1993; Hargrave *et al.*, 1994; Hacke *et al.*, 2001), but consequently have reduced conductivity.

We also found that WD related negatively to maximum vessel length. Vessel length has received relatively little attention in studies of plant hydraulics because of various technical and theoretical difficulties (Comstock & Sperry, 2000), although a reasonable estimate can be made of maximum vessel length (Ewers & Fisher, 1989). We found a positive relationship between maximum vessel length and hydraulic conductivity, especially K_s. Although the maximum and mean vessel lengths are not necessarily well correlated, this relationship may arise as a result of the resistance of the pit membranes that connect different vessel sections, which account for a major portion of stem hydraulic resistance (Hacke & Sperry, 2001; Sperry *et al.*, 2002). Thus, the more frequently water passes from one vessel to the next, the greater the pit membrane resistance and the lower the hydraulic conductivity (Hacke & Sperry, 2001). This mechanism may explain why species with greater maximum vessel length were more efficient conductors. Notably, the maximum vessel lengths in this study were very large, in several cases > 1 m. Such long vessels come at a cost, as cavitation of long vessels would lead to embolism of a greater proportion of the flow pathway. Notably, the typical vessel length frequency distribution for a given species is skewed towards shorter vessels, compensating to some degree for the higher cavitation risk of long vessels (Ewers & Fisher, 1989).

We found a lower variation in K_l than in K_s as a consequence of the apparent compensatory shoot-level relationship of xylem conductivity and leaf allocation, such that Hv was negatively related to K_s (Table 4, Fig. 2c) and not to K_l. This pattern implies that plants adjust their leaf-level water supply morphologically to modulate water supply determined by xylem properties, as was previously found among Neotropical *Cordia* (Choat *et al.*, 2005) and Australian rainforest species (Brodribb & Feild, 2000). As a consequence, species with a low Hv could still be highly conductive, because of their longer vessels which offer less hydraulic resistance (Table 4). Species may also differ in the anatomy of the pits pores in the pit membrane (Hacke & Sperry, 2001; Sperry *et al.*, 2002). At shorter timescales,

plants may be able to regulate their resistance by altering the ion concentration of the sap (Zwieniecki *et al.*, 2001).

Stem hydraulic conductivity was largely independent of leaf traits in this study (Table 4). Contrary to our expectations, we did not find a clear relationship between K_l and SLA, whereas other studies found a coordination of K_l with maximum assimilation rates, stomatal conductance and instantaneous water use efficiency (Santiago *et al.*, 2004), all of which are known to relate well to SLA for species adapted to a range of habitat irradiances. Rather than SLA, LDMC was more strongly negatively related to conductivity. High LDMC is associated with the ability to endure a low ψ_l and persist under dry conditions (Table 4, cf. Tyree *et al.*, 2002, 2003; Kursar *et al.*, 2009). LDMC was also strongly positively correlated with WD, consistent with species achieving persistence by investing simultaneously in robust leaves and stems. Such a close coordination of leaf and stem traits found in small saplings, as studied here, may thus be important during establishment, but may be decoupled when trees attain larger sizes (Baraloto *et al.*, 2010).

How are hydraulic properties related to species' drought and shade tolerance?

Drought-intolerant species typically reduce stomatal conductance to avoid dangerous reductions of leaf water potential (Markesteijn *et al.*, 2010, 2011). At a given transpiration rate, leaf water status is maintained by a high plant hydraulic conductance, which depends on high K_s and K_l (Nardini & Salleo, 2000; Bucci *et al.*, 2004). High hydraulic conductivity was associated with a low WD, a large maximum vessel length and a reduced LDMC, and WD was the best predictor of the species' drought tolerance index. Our findings are consistent with those from Panamanian forests, where drought-intolerant species had a greater stem hydraulic conductivity relative to drought-tolerant species, and where ψ_l was a good predictor of both species drought performance in the field and species distribution across a gradient in dry season length (Kursar *et al.*, 2009).

Our study extends the findings of these previous studies of the ecological preferences of tropical forest trees by indicating the hydraulic traits related to shade tolerance. Previous studies showed that light-demanding species are generally efficient, opportunistic light foragers geared to attain or maintain a dominant position in the canopy (Whitmore, 1989; Van Breugel *et al.*, 2007). Light-demanding species thus tend to have high photosynthetic rates that enhance carbon gain and boost vertical growth (Ellis *et al.*, 2000; Poorter & Bongers, 2006). A high photosynthetic capacity depends on high stomatal conductance and thus results in high transpiration rates, and has to be supported by a high water supply capacity to the leaves (Santiago *et al.*, 2004; Hernández *et al.*, 2010). A particularly novel and important finding in our study was that light-demanding

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(shade-intolerant) species had higher K_s and K_l (Table 4, Fig. 3). Our findings, with a substantial species set, extend the results previously obtained from the comparison of two light-demanders and three shade-tolerant species from a Panamanian rainforest (Tyree *et al.*, 1998) and are also consistent with the finding of a greater leaf hydraulic conductance for light-demanding as compared with shade-tolerant rainforest trees (Sack *et al.*, 2005). Light-demanding species apparently realize such a high stem hydraulic conductivity as a result of their high K_s, associated with their low WD. WD may therefore affect growth rate indirectly, through a high hydraulic conductivity, but also directly, through cheap volumetric stem construction costs. Notably, the low WD comes at the cost of less structural and mechanical support and higher mortality rates (Poorter, 2008; Chave *et al.*, 2009). We found that SLA was not related to the shade tolerance index in this tropical dry forest (Table 4), a finding that contrasts with those of studies in evergreen wet tropical forests and humid temperate forests, where shade-tolerant species are characterized by low SLA (Kitajima, 1994; Walters & Reich, 1999). By making tough, well-protected leaves with low SLA, shade-tolerant species reduce leaf herbivory, and enhance leaf longevity and hence lifetime carbon gain and plant survival in the shaded understory (Sterck *et al.*, 2006; Kitajima & Poorter, 2010). However, there would be a diversity of optimal configurations of shade tolerance and SLA in mixed deciduous–evergreen seasonal forests (Lusk & Warton, 2007) and seasonal tropical dry forests (Poorter, 2009).

We found a positive correlation between our indices of drought and shade tolerances (i.e. between midday leaf water potential in the dry season and juvenile crown exposure, respectively; Table 4), which contradicts the very weak negative correlation among qualitative shade- and drought-tolerance indices found for 806 Northern Hemisphere tree and shrub species by Niinemets & Valladares (2006) ($r^2 = 0.08$). Indeed, multiple regression analyses showed that both shade and drought tolerance indices were strongly associated with WD, followed by K_l. Given that WD is known to be a good estimator of species cavitation resistance, and was found to correlate with P_{50} in our study species (Salleo & Lo Gullo, 1989; Lo Gullo & Salleo, 1993; Hargrave *et al.*, 1994; Hacke *et al.*, 2001; Markesteijn *et al.*, 2011), and that K_l was inversely correlated with cavitation resistance (Zimmermann, 1983; Tyree *et al.*, 1994; Markesteijn *et al.*, 2011), our results indicate that the strong coordination between species' drought and shade tolerance indices in this tropical dry forest is linked to the classical trade-off between hydraulic efficiency and hydraulic safety (Zimmermann, 1983; Tyree *et al.*, 1994; Maherali *et al.*, 2004).

Light-demanding species evidently require a high hydraulic efficiency but suffer from low hydraulic safety, and are therefore restricted to habitats that have both high light and water availability. Shade-tolerant species, in contrast, have high hydraulic safety and are therefore more drought tolerant, such that they will be the better competitors in both drier and shadier habitats. Our results do not support the hypothesis of Smith & Huston (1989) that there is a trade-off between drought and shade tolerances driven by a trade-off in biomass allocation to below-ground vs above-ground plant parts. Such a trade-off would be at best weak across diverse species, given that increases in root or leaf investments may increase the plants' capacity to acquire water or light and to compete, but not necessarily the capacity to tolerate and survive scarcity (Grubb 1998; Paz, 2003; Markesteijn & Poorter, 2009). This may be especially true for tropical dry forests, where dry habitats not only compromise growth, but impose a high risk of plant death as a result of xylem cavitation. Further, there are common mechanisms for drought and shade tolerance related to reduced resource demand (Sack *et al.*, 2003), and this study indicates that low hydraulic conductivity and high WD are such key traits. By contributing to tolerance of scarcity of multiple resources, we propose that these traits are thus likely to be important in the suite of characters typical of species from low-resource environments, which include slow growth, low photosynthetic rates and low tissue turn-over (cf. Grime, 1977; Tilman, 1982, 1988; Chapin *et al.*, 1993).

Our findings support a large potential for niche differentiation across the range of light and moisture levels found in tropical dry forests, consistent with the results from growth experiments in tropical and temperate forests (Sack & Grubb, 2002; Engelbrecht & Kursar, 2003; Sack, 2004; Baltzer *et al.*, 2005; Quero *et al.*, 2006). Our findings indicate that adaptation of hydraulic capacity is integrally linked to this niche differentiation.

Acknowledgements

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