

Ecological differentiation in xylem cavitation resistance is associated with stem and leaf structural traits

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ABSTRACT

Cavitation resistance is a critical determinant of drought tolerance in tropical tree species, but little is known of its association with life history strategies, particularly for seasonal dry forests, a system critically driven by variation in water availability. We analysed vulnerability curves for saplings of 13 tropical dry forest tree species differing in life history and leaf phenology. We examined how vulnerability to cavitation (P_{50}) related to dry season leaf water potentials and stem and leaf traits. P_{50} -values ranged from -0.8 to -6.2 MPa, with pioneers on average 38% more vulnerable to cavitation than shade-tolerants. Vulnerability to cavitation was related to structural traits conferring tissue stress vulnerability, being negatively correlated with wood density, and surprisingly maximum vessel length. Vulnerability to cavitation was negatively related to the Huber-value and leaf dry matter content, and positively with leaf size. It was not related to SLA. We found a strong trade-off between cavitation resistance and hydraulic efficiency. Most species in the field were operating at leaf water potentials well above their P_{50} , but pioneers and deciduous species had smaller hydraulic safety margins than shade-tolerants and evergreens. A trade-off between hydraulic safety and efficiency underlies ecological differentiation across these tropical dry forest tree species.

Key-words: Bolivia, cavitation, deciduousness, functional traits, hydraulic conductivity, leaf water potential, shade-tolerance, tropical dry deciduous forest, wood density.

INTRODUCTION

Water is transported through the xylem of woody plants under negative pressure (Tyree 1997). When drought occurs, soil water potentials drop, the pressure gradient in the xylem increases and vessels are more likely to cavitate and lose their hydraulic conductivity. For trees from seasonally dry forests, it is thus advantageous for their growth

and survival to protect their vascular system against excessive cavitation and secure hydraulic conductivity in dry periods (Brodribb *et al.* 2003; Engelbrecht & Kursar 2003; Tyree *et al.* 2003; Choat *et al.* 2007). The aim of this study was to explain ecological performance of coexisting tree species in the field in relation to some basic mechanisms of their hydraulic architecture. We determined how functional types of tropical dry forest tree species vary in vulnerability to cavitation and identified mechanisms responsible for these differences.

The extent to which species can conduct water and resist cavitation in their stem xylem is determined by the adaptation of the vessels. Wide vessels have the advantage of a greater water transport capacity or hydraulic efficiency, as the Hagen-Poiseuille law predicts that hydraulic efficiency of a vessel increases with the fourth power of its diameter (Tyree & Zimmermann 2002). About 50% of the resistance in the hydraulic pathway arises at the pit membranes that connect separate vessels (cf. Zimmermann 1983; Wheeler *et al.* 2005; Choat *et al.* 2006), and all else being equal, a hydraulic pathway build up of longer vessels will be more efficient in transporting water than a pathway made up of short vessels. Consequently, evolution has driven plants towards wider and longer vessels, but within limits (Tyree, Davis & Cochard 1994).

As is the case with many adaptive traits, there are costs involved (Givnish 1986). Long, wide vessels are more efficient in water transport than narrow, short vessels, but may also be more vulnerable to drought-induced cavitation. Cavitation occurs due to air being sucked into the xylem, resulting in emboli (Tyree & Sperry 1989) and takes place when the pressure in the vessels becomes negative enough to break the hydrogen bonds in the meniscus of the largest pit pores and air is sucked into the vessel ('air-seeding': Zimmermann 1983; Sperry & Tyree 1988). Vulnerability to air-seeding is both related to the pitted area of contact between vessels – a bigger area implies an increased probability of having large pores – (Hacke *et al.* 2006) and pit characteristics such as porosity and thickness (Jansen, Choat & Pletsers 2009). The extent to which tissue level and pit level characteristics influence vulnerability to air-seeding depends on the

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data set used (Hacke *et al.* 2006; Christman, Sperry & Adler 2009). Vulnerability to air-seeding of the vessel may, therefore, relate geometrically to vessel length (Tyree *et al.* 1994; Sperry, Hacke & Wheeler 2005).

The xylem pressure at 50% loss of hydraulic conductivity (P_{50} ; in MPa) is the most widely used measure of vulnerability to cavitation and varies enormously among taxa. The most vulnerable species are found in wet tropical forest, where 50% loss of conductivity is reached at values as high as -0.18 MPa, while P_{50} values as low as -14.1 MPa occur in the most resistant dry forest species (reviewed in Maherali, Pockman & Jackson 2004). Across a global data set, there was a large overlap in P_{50} values between major lineages and life form groups, with conifers on average less vulnerable to cavitation than angiosperms and shrubs less than trees (Maherali *et al.* 2004). One of our goals was thus to compare evergreen and deciduous tree species in a given diverse tropical dry forest community. One might expect evergreen species that tolerate seasonal drought to be less vulnerable than deciduous species that shed their leaves in the dry season. Surprisingly, this pattern did not hold up in a global meta-analysis, as both groups had similar P_{50} values (Maherali *et al.* 2004). Yet, in this meta analysis, evergreen species were mostly compared with temperate winter deciduous species, while tropical drought deciduous species were underrepresented (Maherali *et al.* 2004); one of the recommendations of this study was therefore to do make future comparisons within climate types, especially for coexisting evergreen and deciduous tree species from dry ecosystems.

Tropical dry forests are characterized by relatively low annual rainfall and pronounced seasonality of rainfall distribution, which has pronounced effects on the ecosystem structure and function (Murphy & Lugo 1986). As the risk of cavitation would be greatest during seasonal drought, we expected dry forest tree species to have low vulnerability to cavitation at the cost of a reduced hydraulic efficiency (Zimmermann 1983; Tyree *et al.* 1994). Such a trade-off would have pronounced effects on the ecological performance of dry forest tree species and could underlie functional type differentiation. However, few studies have made the link between cavitation resistance, species traits and species' life history or ecological performance in the field.

Many trees in tropical dry forests shed their leaves in the dry season, such that across species, deciduousness is the most successful strategy to survive prolonged drought (Poorter & Markesteijn 2008). As deciduous species are drought-avoiding they were expected to be more vulnerable to cavitation than coexisting evergreens. Nonetheless, water is not the only limiting resource in tropical dry forests. In the wet growth season, the forest canopy is closed, vegetation is dense and species compete for light in the forest understory. Light-demanding pioneer species tend to realize high growth rates in part by reducing costs involved with the construction of well-protected tissues (Van Gelder, Poorter & Sterck 2006; Kitajima & Poorter 2010). Pioneers are thus expected to be more vulnerable to cavitation than shade-tolerant species.

In addition to adaptations in wood anatomy, species are expected to control stomatal conductance to keep water potentials above the critical point at which cavitation is induced (Jones & Sutherland 1991; Nardini & Salleo 2000), thus avoiding excessive cavitation or 'runaway embolism' (Tyree & Sperry 1988). In this way, hydraulic conductivity could be maintained at high efficiency, securing plant survival, but the disadvantage is a reduction of photosynthetic rate, growth and productivity. An alternative strategy would be to maximize short-term productivity at the expense of reduced survival, and thus to allow cavitation to occur (Jones & Sutherland 1991). In the context of the growth-survival trade-off found between pioneers and shade-tolerant species (Kitajima 1994; Wright *et al.* 2003; Gilbert *et al.* 2006; Poorter & Bongers 2006), we hypothesized that shade-tolerant species would be conservative with safer xylem, while pioneers would take greater risks and operate closer to the point of hydraulic failure. The same differentiation would be found between evergreen and deciduous species (Sobrado 1993).

We examined the cavitation resistance of 13 tropical dry forest tree species. We also assessed how stem and leaf traits were associated with vulnerability to cavitation and how vulnerability to cavitation was related to the minimum leaf water potential that species tolerates in the dry season. We hypothesized that: (1) pioneer species would be more vulnerable to cavitation than shade-tolerant species and that deciduous species would be more vulnerable than evergreens; (2) vulnerability to cavitation would relate negatively to wood density (WD) and positively to vessel length; (3) vulnerability to cavitation and hydraulic conductivity would be negatively associated, reflecting a trade-off between hydraulic safety and efficiency; and (4) vulnerability to cavitation would relate positively to the leaf water potential that species tolerate in the dry season, and that pioneers and deciduous species would operate closer to the point of hydraulic failure than shade-tolerant and evergreen species, respectively.

METHODS

Study area and species

Fieldwork was carried out in a tropical dry forest in the eastern lowlands of Bolivia, near 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 in the south (Killeen *et al.* 1998). The forest is private property of a certified timber company (INPA Parket Ltda., Concepción, Bolivia) and one of the long-term research sites of the Instituto Boliviano de Investigación Forestal (IBIF) (Villegas *et al.* 2009).

The study site ($16^{\circ}07'S$, $61^{\circ}43'W$) has been classified as a tropical lowland dry deciduous forest, with a mean annual temperature of $24.3^{\circ}C$, a mean annual precipitation of 1160 mm (meteorological data from 1943–2005 from

Table 1. Vulnerability to cavitation of 13 tropical dry forest tree species

Species	Family	Leaf habit	Slope (% MPa ⁻¹)	P ₂₀ (MPa)	P ₅₀ (MPa)	P ₈₀ (MPa)
Pioneer species:						
<i>Astronium urundeuva</i>	Anacardiaceae	D	6.0	-0.5	-1.8	-4.2
<i>Bougainvillea modesta</i>	Nyctaginaceae	E	11.2	-2.4	-3.7	-4.9
<i>Cecropia concolor</i>	Urticaceae	E	57.7	-0.5	-0.8	-1.0
<i>Ceiba speciosa</i>	Malvaceae	D	23.3	-0.3	-1.4	-3.5
<i>Centrolobium microchaete</i>	Fabaceae	D	12.1	-0.1	-1.2	-2.4
<i>Solanum riparium</i>	Solanaceae	E	17.4	-1.3	-2.1	-2.9
Shade-tolerant species:						
<i>Acosmium cardenasii</i>	Fabaceae	E	6.2	-4.0	-6.2	-8.5
<i>Anadenanthera colubrina</i>	Fabaceae	E	11.4	-4.2	-5.7	-6.6
<i>Aspidosperma cylindrocarpon</i>	Apocynaceae	D	13.7	-1.9	-2.9	-3.9
<i>Aspidosperma tomentosum</i>	Apocynaceae	E	9.1	-3.2	-4.7	-6.2
<i>Casearia gossypiosperma</i>	Salicaceae	D	9.0	-3.0	-4.6	-6.1
<i>Copaifera chodatiana</i>	Fabaceae	E	6.9	-3.7	-5.7	-7.7
<i>Trichilia elegans</i>	Meliaceae	E	14.0	-2.5	-3.5	-4.5

Species are grouped as pioneers and shade-tolerant species. Leaf habit (D, Deciduous; E, Evergreen), the slope of the vulnerability curves (% MPa⁻¹) and the xylem pressure at 20, 50 and 80% loss of hydraulic conductivity (P₂₀, P₅₀ and P₈₀) are given. Nomenclature follows the database of the Missouri Botanical Garden (W³Tropicos); <http://www.tropicos.org>

AASANA for Concepción at 40 km) and a dry period of 3 months (June–September) in which the potential evapotranspiration exceeds precipitation. The study area has a mean altitude of about 458 m with 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. The most dominant species in the area are *Acosmium cardenasii* H.S. Irwin & Arroyo (Fabaceae), *Casearia gossypiosperma* Briquet (Salicaceae) and *Caesalpinia pluviosa* DC (Fabaceae).

We studied vulnerability to cavitation for 13 tree species from 9 angiosperm families (Table 1). Species were selected to range strongly in shade-tolerance, based on field distribution patterns (Justiniano *et al.* 2004; Poorter & Kitajima 2007) and were grouped as seven shade-tolerant species and six pioneers. Furthermore, species differed in leaf habit; five species were drought-deciduous and eight species were evergreen.

Hydraulic conductivity

Sapwood-specific and leaf-specific hydraulic conductivity (K_s and K_l, respectively) were determined for five saplings of each species. Selected saplings were 150–200 cm tall, and located along roads, exposed to full or partial overhead light. We expected these saplings to experience the greatest vapour pressure deficits and water stress; this design also allowed sampling from similar light habitat, as pioneers are rarely found under canopy shade, while shade-tolerant species are frequently found under exposed conditions.

The aboveground shoots of saplings were harvested and transported to a field laboratory for further processing. Lateral branches and leaves were cut from the main stem and wounds were sealed with instant adhesive glue. The stems were re-cut under distilled water, and distal ends were trimmed with a razorblade to clear any accidentally blocked vessels and bark was removed from about 1 cm of the shoot ends. While submerged, the shaved basal 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-ethene 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 mM solution of KCl in degassed and filtered (0.2 μm) distilled water. Stems were flushed for at least 30 min to remove emboli and connected to a second manifold attached to a hydraulic apparatus (Sperry, Donnelly & Tyree 1988), supplying the flow solution to the stems at ~5 kPa for 10 min before measuring. Three repeated measurements were taken to assure that water flow had reached a steady state. Solution injection always followed the direction of natural water flow in the plant, from base to top.

For all stems, we estimated the sapwood area as the stem cross-sectional area after bark removal, minus the area of pith, and calculated sapwood specific conductivity (K_s; mol m⁻¹ s⁻¹ MPa⁻¹) by dividing the measured conductivity by the sapwood area and multiplying by 18.02 (the molar mass of water). Sapwood area of the stem segments ranged from 6.0 to 27.6 mm² (mean ± se = 15.2 ± 0.8) across species. Additionally we determined total leaf area above the measured stem segment. Leaf specific conductivity (K_l; mmol m⁻¹ s⁻¹ MPa⁻¹) was calculated as the measured

conductivity divided by the total leaf area and multiplied by the molar mass of water.

Vulnerability to cavitation

For three saplings per species cavitation resistance was determined by estimating the xylem pressure at 20%, 50% and 80% loss of hydraulic conductivity (P_{20} , P_{50} , P_{80}) using the bench drying technique (Sperry *et al.* 1988; Tyree & Sperry 1989). Saplings were harvested in the beginning of June, early in the morning around sunrise (6.00 h) to avoid excessive cavitation. Cut saplings were put into a bucket of water, transported to the field station and hung upside-down in the sun to dehydrate. Segments of five branches per sapling were measured in sequence of increasing dehydration. Two a-priori selected leaves per branch were bagged and covered in shade cloth and xylem pressure was estimated with a pressure chamber (SKPM 1405, Skye instruments Ltd. Powys, UK). Branches were re-cut under water into smaller segments with a mean length (\pm se) of 131.6 mm (\pm 4.3) (range; 105.6–158.6 mm) across species. The mean diameter of the sections was 8.1 mm (\pm 0.5) (range; 5.9–8.0 mm). By first measuring the native conductance and secondly the maximum conductance after flushing, the percentage loss of hydraulic conductivity (PLC) was calculated (Tyree & Sperry 1989). Paired PLC measurements and mean xylem pressure were plotted to determine vulnerability curves for each of the 13 species (Fig. 1), fitting an exponential sigmoid function (Pammenter & Vander Willigen 1998):

$$PLC = \frac{100}{1 + e^{a(\Psi - b)}} \quad (1)$$

where Ψ is the measured xylem pressure, a is the maximum slope of the curve and b is the xylem pressure at 50% loss of hydraulic conductivity. Curve parameters a and b were estimated with the non-linear regression procedure in SPSS 15.0 (SPSS Inc., Chicago, IL, USA).

Stem and leaf traits

For a sample taken from the distal end of each stem we estimated the fresh volume without the bark and pith using the water displacement method (Ilic *et al.* 2000). Samples were oven-dried for 48 h at 75 °C, their dry mass was measured and WD (g cm^{-3}) was calculated as dry mass divided by fresh volume.

Maximum vessel length (VL; cm) was determined by air injection (Ewers & Fisher 1989) for five saplings per species. It has to be emphasized that the vessel length determined with this method represents that of the longest continuous conduit only. Maximum vessel length is therefore a rather rough estimator of vessel size that is not necessarily related to the mean vessel length of the species.

For each sapling the Huber-value (Hv; $\text{cm}^2 \text{cm}^{-2} \times 10^{-6}$) was calculated as the cross-sectional sapwood area of the upper end of the stem divided by the total supported leaf

area. Subsamples of the leaf material collected to estimate the total leaf area were saturated overnight in moist paper towels in a refrigerator after which their fresh mass and average leaf size (LS; cm^2) were determined. Samples were then 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 the leaf dry mass divided by the fresh mass. The specific leaf area (SLA; $\text{cm}^2 \text{g}^{-1}$) was calculated as the leaf area divided by the dry mass.

Dry season leaf water potential

In the dry season of 2008, the midday leaf water potential (ψ_l) of one leaf per sapling and five saplings per species was measured, from plants of the same habitat as those measured for xylem vulnerability. The ψ_l measurements were made 2 months after the onset of the dry season (June) and before drought in this forest was at its peak (August–September; Markesteijn *et al.* 2010). As such, comparative measurements of evergreen and drought-deciduous species were still possible, before the latter shed their leaves. Fully expanded and exposed healthy leaves, without signs of herbivory were selected. Between 1400 and 1700 h, leaves were cut from the saplings and immediately sealed into plastic bags that had been exhaled into. Leaves were bagged for transportation purposes and never longer than 5 min. Measurements were made with a pressure chamber (Model SKPM 1405, Skye Instruments Ltd., Powys, UK).

Data analysis

Differences between pioneers and shade-tolerant species and deciduous and evergreen species were analysed with independent samples *t*-tests. Linear regression analyses were used to determine the relationship between P_{50} and stem structural traits (e.g. WD and maximum vessel length) and to the dry season leaf water potential. A backward multiple regression analysis was used to evaluate which species traits best explained P_{50} . Pearson correlation analyses were used to examine the associations between P_{50} and hydraulic and leaf traits across species. All analyses were performed by using SPSS 15.0 (SPSS Inc.).

RESULTS

Vulnerability to cavitation of tropical dry forest tree species

Vulnerability curves varied substantially among species (Fig. 1). Species can be compared in the maximum slopes of their curves, which indicates how quickly species lose hydraulic conductivity in response to desiccation, or they can be compared using the water potential at which species lose 20%, 50% and 80% in hydraulic conductivity (P_{20} , P_{50} and P_{80} , respectively), where lower potentials indicate higher resistance to cavitation. The mean maximum slope was 15% MPa^{-1} (\pm 14) and varied almost 10-fold among

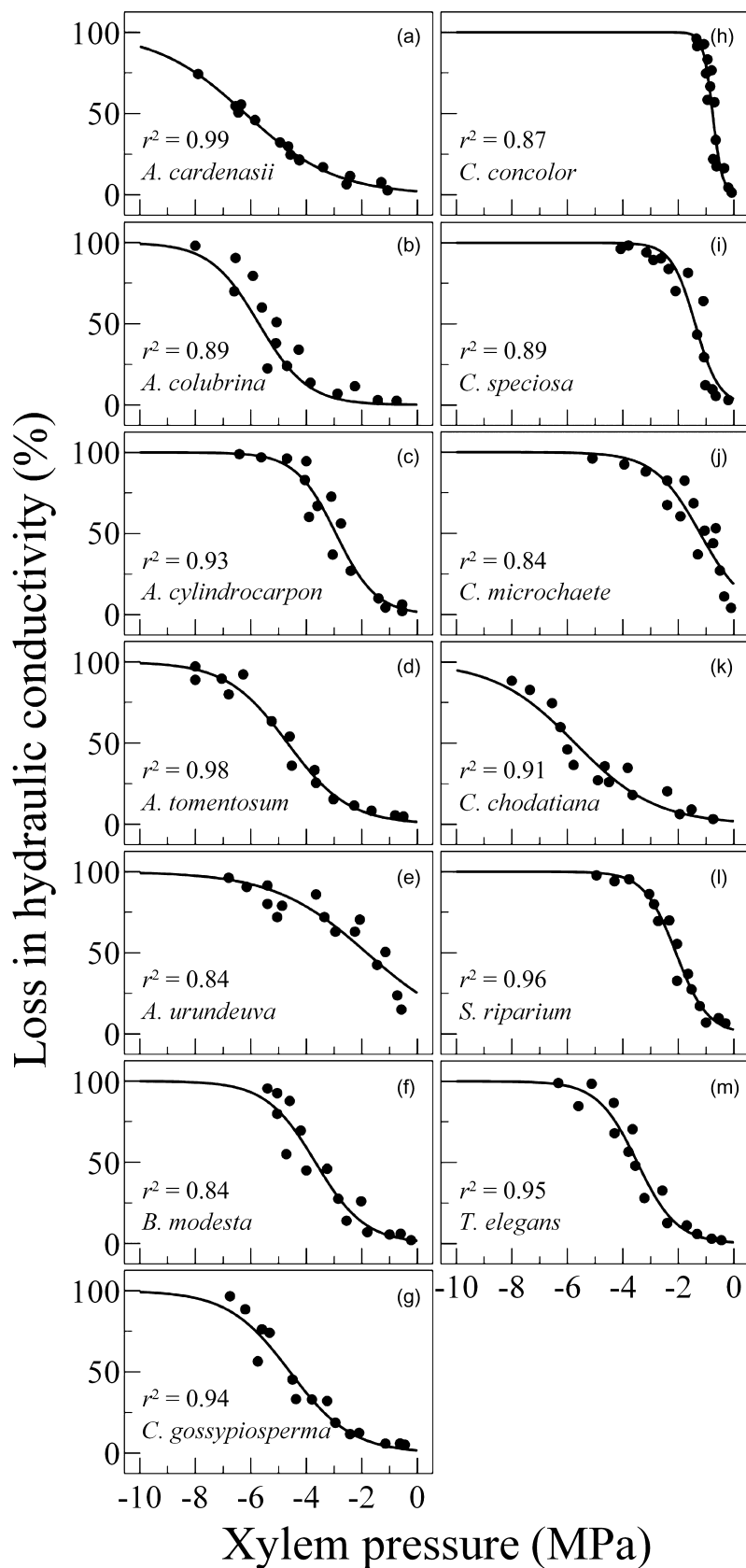


Figure 1. Relations between percentage loss of hydraulic conductivity and xylem pressure for 13 tropical dry forest tree species. Vulnerability curves were estimated from 15 samples per species. Figures represent the different species studied, alphabetically organized.

Table 2. Differences in mean vulnerability to cavitation between pioneers ($n = 6$) and shade-tolerant species ($n = 7$) and deciduous ($n = 5$) and evergreen species ($n = 8$)

	Pioneer	Shade-tolerant	<i>t</i> -test		Deciduous	Evergreen	<i>t</i> -test	
	Mean \pm SE	Mean \pm SE	<i>t</i>	<i>P</i>	Mean \pm SE	Mean \pm SE	<i>t</i>	<i>P</i>
Slope	21.3 \pm 7.7	10.0 \pm 1.2	1.57	ns	12.8 \pm 2.9	16.7 \pm 6.0	-0.48	ns
P ₂₀	-0.86 \pm 0.36	-3.20 \pm 0.31	-5.03	***	-1.17 \pm 0.57	-2.71 \pm 0.46	-2.10	ns
P ₅₀	-1.83 \pm 0.41	-4.76 \pm 0.46	-4.66	***	-2.39 \pm 0.63	-4.04 \pm 0.68	-1.66	ns
P ₈₀	-3.13 \pm 0.56	-6.22 \pm 0.61	-3.67	**	-4.01 \pm 0.62	-5.28 \pm 0.88	-1.03	ns
Safety margin (P ₅₀ - ψ_l)	-1.12 \pm 0.41	-2.07 \pm 0.32	-1.86	ns	-0.94 \pm 0.33	-2.07 \pm 0.33	-2.27	*

Mean slopes of the vulnerability curves, xylem pressures at 20, 50 and 80% loss of hydraulic conductivity (P₂₀, P₅₀ and P₈₀) and the hydraulic safety margin (P₅₀ - ψ_l) (\pm standard error; SE) are given with the *t*-test statistics of differences between functional groups.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

ns, non-significant.

species, ranging from very gentle (6% MPa⁻¹) for *Astرونium urundeuva* (Fig. 1e) to very steep (58% MPa⁻¹) for *Cecropia concolor* (Fig. 1h). Mean P₅₀ was -3.41 MPa (± 1.9) and varied 8-fold across species, ranging from -6.2 MPa for *A. cardenasii* to -0.8 MPa for *Cecropia concolor* (Table 1). Species ranked similarly in P₂₀, P₅₀ and P₈₀.

On average, the maximum slopes of the vulnerability curves did not differ significantly between functional groups (Table 2). However, pioneer species were more vulnerable to cavitation with substantially higher (less negative) P₂₀, P₅₀ and P₈₀ values than the shade-tolerant species (Table 2). Deciduous species tended to have higher P₂₀, P₅₀ and P₈₀ values than evergreen species, although the differences were not significant (Table 2). Species hardly showed any cross-overs in the ranking of P₂₀, P₅₀ and P₈₀. Between P₅₀ and P₈₀, for instance, only four species shifted in rank (data not shown), but never more than two ranks, suggesting that the species ranking is maintained at different intensities of drought.

Vulnerability to cavitation in relation to hydraulic traits

The P₅₀ was positively associated with K_s and K₁ (Fig. 2), which confirms that the often found trade-off between hydraulic safety and efficiency is also found across species in a tropical dry forest. Further, the P₅₀ was positively correlated with ψ_l across species (Fig. 3). We analysed the implication of this coordination for safety margins of the study species. At the 1:1 line in Fig. 3 (the dotted line), the ψ_l equals P₅₀. The distance between the 1:1 line and the regression thus represents the hydraulic safety margin, that is, the distance these species operate from their hydraulic limit. We found that species with more negative P₅₀ values had larger safety margins than species with less negative P₅₀ values. On average, shade-tolerant species tended to have larger safety margins than pioneers (although the difference was marginal, Table 2, *t*-test, $P = 0.09$) and evergreen species had significantly larger safety margins than deciduous species (Table 2, Fig. 3).

Vulnerability to cavitation in relation to stem and leaf traits

A backward multiple regression analysis showed that P₅₀ was negatively related to WD ($\beta = -1.5$, $P < 0.01$), which explained 70% of the variation in P₅₀, and negatively related to VL ($\beta = -0.40$, $P < 0.05$) explained an additional 12% of the variation. By itself, VL was not related to P₅₀ (Fig. 4b).

P₅₀ was negatively associated with the Hv and LDMC, and positively with leaf size (Fig. 5). Species with lower allocation to sapwood per unit leaf area, and with small and dense leaves were most resistant to drought-induced cavitation; Notably, P₅₀ was not associated with SLA (Fig. 5d).

DISCUSSION

Pioneer and shade-tolerant species differed more in vulnerability to cavitation than deciduous and evergreen species

The 13 species in this study varied substantially in cavitation resistance (Fig. 1, Table 1). This variability among species may be an important mechanism underlying species coexistence in this seasonally dry forest. Among species P₅₀ values ranged from -0.8 to -6.2 MPa (median value of -3.5 MPa) and fall well within the range of P₅₀ values for tropical dry forests (reviewed in Maherali *et al.* 2004), though our median P₅₀ value was almost 1 MPa lower than the overall median of tropical dry forests. As predicted by our hypothesis, pioneer species were more vulnerable to cavitation than shade-tolerant species. Pioneers are geared for fast growth with a high photosynthetic capacity that involves high transpiration rates and thus greater hydraulic demand (Poorter & Bongers 2006). Among 40 species in this forest, we found that pioneers typically had a high maximum hydraulic conductivity compared to shade-tolerant species (Markesteijn 2010). Such high hydraulic supply involves a cost in reduced drought-induced cavitation resistance, as reported for diverse

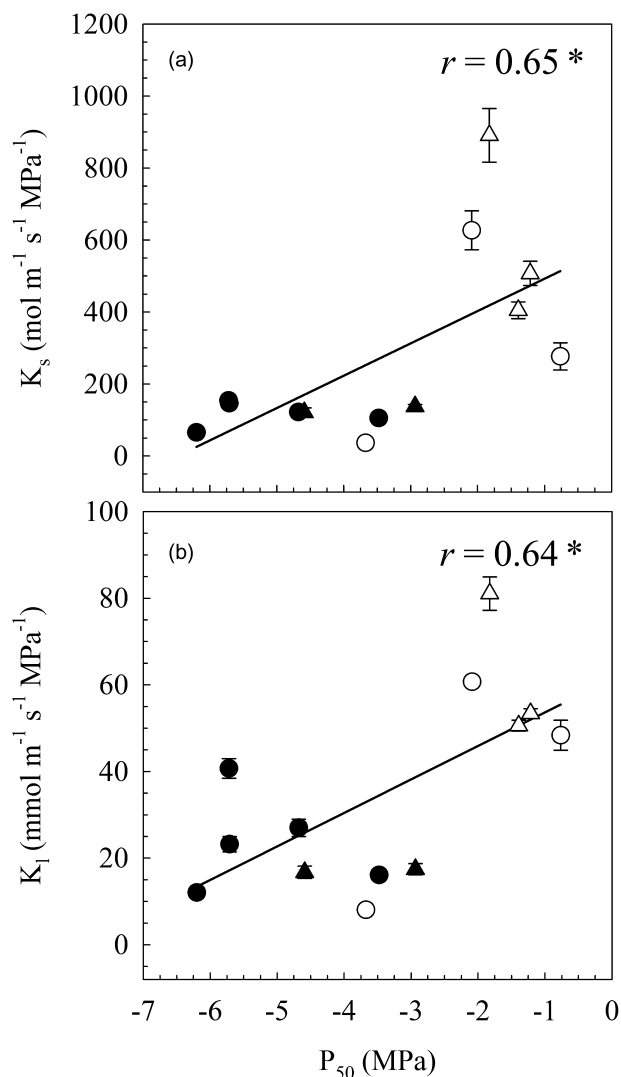


Figure 2. Relations between stem hydraulic conductivity (K_s) (a), leaf hydraulic conductivity (K_l) (b) and vulnerability to cavitation (P_{50}) of tropical dry forest species. Different symbols represent evergreen (triangles) versus deciduous (dots) and shade-tolerant (closed) versus pioneer species (open). Pearson correlation coefficients and their level of significance are given. $*P < 0.05$.

species sets (Sobrado 1993; Tyree *et al.* 1994; Martínez-Vilalta *et al.* 2002; Hacke *et al.* 2006).

In contrast to some studies (Maherali *et al.* 2004; Choat *et al.* 2005; Chen, Zhang & Cao 2009), evergreen and deciduous species did not show this clear difference in P_{50} . Still, other studies also showed a substantial overlap in hydraulic traits between both groups in tropical dry forests (Sobrado 1997; Brodribb *et al.* 2003; Ishida *et al.* 2010). The large variation in P_{50} may partly be explained by variation in leaf lifespan. While we separated species into two distinct groups, they are most likely part of a continuum of strategies, as found for Costa Rican dry forest tree species (Borchert 1994). Williams, Bunyavejchewin & Baker (2008) stretched, therefore, that leaf phenology should be treated

as a continuous variable. Traditionally most (eco)physiological dry forest studies focused on the contrast between evergreen and deciduous species while our study suggests that other strategy axes, such as shade tolerance, might be even more important (Table 1).

Strong association of vulnerability to cavitation with hydraulic traits

The positive relation between P_{50} and K_s (Fig. 2) represents a key ecological trade-off between hydraulic safety and efficiency (Zimmermann 1983; Tyree *et al.* 1994). WD was the best predictor of both P_{50} (this study) and of K_s and K_l across species (Markesteyn 2010). In their meta-analysis Maherali *et al.* (2004) found little evidence for evolutionary coordination of P_{50} and K_s . Possibly, the trade-off between cavitation resistance and hydraulic efficiency is uncoupled when species from different communities are pooled together, while among species within naturally assembled communities the trade-off is stronger. The findings of the current study corroborate with several other studies that also found a trade-off between hydraulic safety and efficiency (Pockman & Sperry 2000; Martínez-Vilalta *et al.* 2002; Hacke *et al.* 2006; Sperry, Meinzer & McCulloh 2008; Zhu & Cao 2009). P_{50} depends on structural wood anatomical adaptations and principally on pit membranes, which are

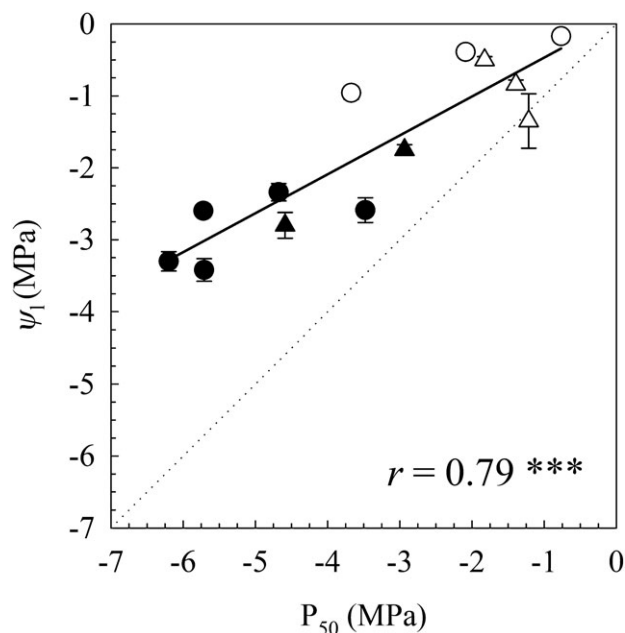


Figure 3. Regression between the dry season leaf water potential (ψ_l) and vulnerability to cavitation (P_{50}) of 13 dry forest tree species. The regression coefficient and its level of significance is given. $***P < 0.001$. The dotted line represents the theoretical point of hydraulic failure, where ψ_l equals P_{50} . The difference between the regression line and this 1:1 relationship was defined as the hydraulic safety margin, i.e. how close species were operating to the point of hydraulic failure in the field. Different symbols represent evergreen (triangles) versus deciduous (dots) and shade-tolerant (closed) versus pioneer species (open).

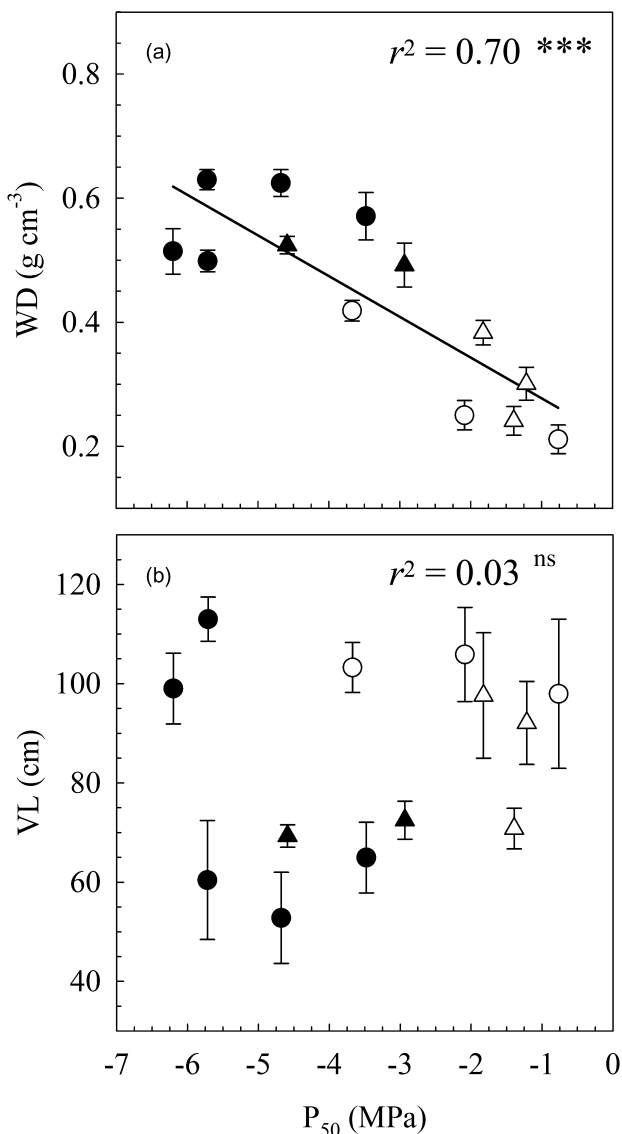


Figure 4. Regressions between vulnerability to cavitation (P_{50}) and WD (a) and maximum VL (b) of 13 dry forest species. Regression coefficients (r^2) and their level of significance are given. ns, non-significant; * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$. Different symbols represent evergreen (triangles) versus deciduous (dots) and shade-tolerant (closed) versus pioneer species (open).

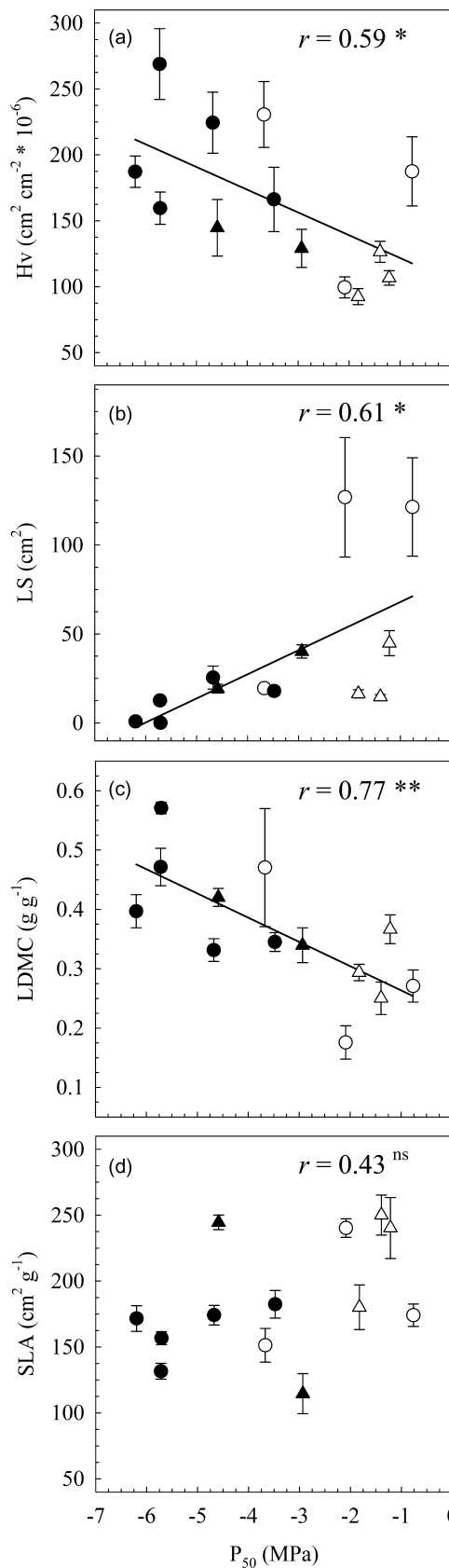


Figure 5. Associations between leaf traits and vulnerability to cavitation (P_{50}) of 13 dry forest species. Hv, Huber-value; LS, leaf size; LDMC, leaf dry matter content; and SLA, specific leaf area. Pearson correlation coefficients (r) and their level of significance are given. ns, non-significant; * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$. Different symbols represent evergreen (triangles) versus deciduous (dots) and shade-tolerant (closed) versus pioneer species (open).

the loci for air-seeding. Smaller pit membrane pores would tend to increase resistance in the flow pathway, and thus constrain hydraulic efficiency (Jarbeau, Ewers & Davis 1995). The importance of vessel dimensions for cavitation resistance remains a subject of debate, especially because pit membrane structure may vary independently from vessel size or length (Hacke & Sperry 2001).

In line with our hypotheses, we found that species with a high WD were more resistant to cavitation than species with a low WD (Fig. 4a). This finding provides additional evidence for WD being a strong correlate of drought-tolerance. A wealth of studies show that WD integrates various wood properties and is closely linked to mechanical support, water transport and (stem) storage capacity and, consequently, WD is a 'key functional trait' that plays a central role in species life history strategy (Muller-Landau 2004; Santiago *et al.* 2004; Chave *et al.* 2006; Van Gelder *et al.* 2006). Species with a low WD often realize high diameter and height growth rates (Roderick 2000; Poorter 2008; Chave *et al.* 2009), while species with a high WD have slow growth rates, but may survive drought (Poorter & Markesteijn 2008) and shade (Alvarez-Clare & Kitajima 2007) better.

In addition to WD, vessel length (VL) significantly explained 12% of the variation in P_{50} . In contrast to the hypotheses, our results suggested that longer vessels could lead to a higher cavitation resistance. This unconventional result should be interpreted with care, as we measured the length of the longest unobstructed conduit only (i.e. the maximum vessel length) and it does not necessarily relate well to the mean vessel length. Earlier studies, that actually did take mean vessel length into account, found that long vessels lead to a lower cavitation resistance (Ewers 1985); longer vessels have a greater connection area with adjacent vessels, and are thus likely to contain more pit pores, increasing the probability of air-seeding from neighbouring embolized vessels (Hargrave *et al.* 1994; Tyree *et al.* 1994; Sperry *et al.* 2005; Hacke *et al.* 2006; Zanne *et al.* 2006; Choat, Cobb & Jansen 2008). The negative relation between VL and P_{50} found in this study arose mainly from two species, *A. cardenasii* and *Anadenanthera colubrine*, which were least vulnerable to cavitation and combined a high WD with large VL. These species are also among the most abundant trees in this dry forest, together accounting for more than 40% of the stems over 10 cm in diameter at breast height. Probably these species are both well protected against drought-induced cavitation, while still relatively efficient in conducting stem water, which could contribute to their dominant presence in this tropical dry forest.

How is vulnerability to cavitation associated with leaf traits?

We found clear relationships between leaf traits with stem hydraulic traits, indicating the coordination of traits associated with drought-tolerance in dry forest tree species. The P_{50} was negatively associated with the Hv and LDMC, and positively with leaf size (LS) (Fig. 5). Hv and WD were positively associated (Pearson $r = 0.56$, $P = 0.04$). Hence, the

cross-sectional sapwood area of more vulnerable species was relatively small as it probably consists of fewer, larger diameter vessels that are more vulnerable to cavitation and, according to the Hagen-Poiseuille law, more efficient in water transport (Jacobsen *et al.* 2007). Across 40 dry forest tree species, low Hv species had a high stem hydraulic conductivity (K_s) (Markesteijn 2010), which was also found among Australian rainforest species (Brodribb & Feild 2000).

LS was positively associated with P_{50} (Fig. 5b), indicating that drought-tolerant species with low P_{50} had small leaves. Small leaves are characteristic of species of arid environments (McDonald *et al.* 2003) and have a smaller boundary layer resistance, which facilitates convective cooling and regulation of temperature close to the optimal for photosynthesis (Parkhurst & Loucks 1972). Still, the thinner boundary layer may at the same time come at the expense of an increased transpiration, which enhances water loss in an arid environments (Parkhurst & Loucks 1972; Nicotra *et al.* 2008; Yates *et al.* 2010). The advantage of small leaves to drought-tolerance is that they are less expansive to shed than large ones as a final means to reduce transpiration. Further, many small leaved species have (bi)pinnate compound leaves which they may fold at times of high evaporative demand, thus reducing light interception and heat load.

Across species, LDMC was negatively related to P_{50} (Fig. 5c). LDMC is related to the leaf's modulus of elasticity, or stiffness, as leaves with higher LDMC tend to have thicker and more rigid cell walls, which enable the maintenance of turgor at a lower leaf water potential (Cheung, Tyree & Dainty 1975; Zimmermann 1978; Monson & Smith 1982) and minimize damage to the cell under severe drought (Bowman & Roberts 1985; Engelbrecht & Kursar 2003; Tyree *et al.* 2003). In Panama, Kursar *et al.* (2009) found that LDMC was closely related to the minimum seasonal leaf water potential species could tolerate, and that it predicted species' drought performance and distribution across a gradient in dry season length.

Surprisingly, we did not find a clear relation between SLA and P_{50} , though SLA has been considered a key trait that modulates leaf and whole plant function. Numerous studies have shown SLA to decrease with drought tolerance across species (e.g. Skarpe 1996; Cunningham, Summerhayes & Westoby 1999; Fonseca *et al.* 2000), and as a plastic response to drought within species (Poorter *et al.* 2009). Notably, a low SLA can result from a higher leaf density and/or a thicker leaf. A low SLA that results from an increased leaf density will be well related to P_{50} , as it is related to a lower modulus of elasticity. In this dry forest it was LDMC and not SLA that was associated with species drought tolerance (Markesteijn 2010).

Does vulnerability to cavitation influence the leaf water potential that species can tolerate in the dry season?

P_{50} was strongly associated with the dry season midday leaf water potential (ψ_l) across species (Fig. 3). Xylem cavitation

resistance is, therefore, related to the tensions experienced during the dry season, and similar findings were obtained from dry Mexican (Bhaskar, Valiente-Banuet & Ackerly 2007) and Mediterranean Chaparral vegetation (Jacobsen *et al.* 2007), Sonoran desert vegetation (Pockman & Sperry 2000) and a tropical dry forest (Brodribb *et al.* 2003).

Most species were operating well above the point of xylem failure (Fig. 3 and 1:1 line) and their ψ_l corresponded to about 20% loss of hydraulic conductivity. Both theory and models have indicated that to maximize stomatal conductance and carbon gain, species should operate as close as possible to their hydraulic limit, the threshold for complete cavitation (Jones & Sutherland 1991; Sperry *et al.* 1998; Nardini & Salleo 2000). However, operating close to the hydraulic limit would be very risky and not likely for all species in this forest community. Pioneer species were marginally operating closer to their hydraulic limit than shade-tolerant species, taking greater risks, but the strongest differences in safety margins were found between deciduous and evergreen species. To compensate for a shorter growth season deciduous species typically have a higher resource use efficiency than evergreen species (Sobrado 1991; Eamus & Prior 2001), and maximize photosynthesis and carbon intake in the wet season (Eamus 1999; Ishida *et al.* 2006) and therefore need more efficient water transport (Sobrado 1997). Deciduous species would thus assume a greater risk of hydraulic failure to maximize short-term productivity, similar to pioneer species (cf. Jones & Sutherland 1991), although the question is whether they are in daily life exposed to such risk, given the fact that they are deciduous in the dry period. Drought- and shade-tolerant species, therefore, have a more conservative resource strategy with stricter constraints on carbon intake, and would operate at safe distance from hydraulic failure as long as possible, as recovering from losing branches will be very expensive. Although field screenings of seedlings showed that pioneer species have more shallow root systems than shade-tolerant species (Paz 2003; Markesteijn & Poorter 2009), further studies are needed to investigate if saplings of pioneer and deciduous species could actually have deeper rooting. If so, pioneers and deciduous species could secure water supply, reduce the risk of strong xylem tensions, and obviate the need for more resistant xylem. Another possibility is that pioneers and deciduous species, with their lower wood densities, actually have greater water storage capacity. Future work should establish relationships between the cavitation resistance of root, stem and leaf and their association with overall security of water supply to allow a complete resolution of the hydraulic basis for comparative responses among tree species that face seasonal drought.

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