Diversity of hydraulic traits in nine *Cordia* species growing in tropical forests with contrasting precipitation

Brendan Choat[1,3], Lawren Sack[2] and N. Michele Holbrook[1]

[1]Department of Organismic and Evolutionary Biology, Harvard University. Cambridge, MA 02138, USA; [2]Department of Botany, University of Hawaii, 3190 Maile Way, Honolulu, HI 96822, USA; [3]Present address: Department of Viticulture and Enology, University of California, Wickson Hall, Davis, CA 95161, USA

Summary

Author for correspondence:
Brendan Choat
Tel: +1 530 7527185
Fax: +1 530 7520382
Email: bchoat@ucdavis.edu

• Inter- and intraspecific variation in hydraulic traits was investigated in nine *Cordia* (Boraginaceae) species growing in three tropical rainforests differing in mean annual precipitation (MAP).
• Interspecific variation was examined for the different *Cordia* species found at each site, and intraspecific variation was studied in populations of the widespread species *Cordia alliodora* across the three sites.
• Strong intra- and interspecific variation were observed in vulnerability to drought-induced embolism. Species growing at drier sites were more resistant to embolism than those growing at moister sites; the same pattern was observed for populations of *C. alliodora*. By contrast, traits related to hydraulic capacity, including stem xylem vessel diameter, sapwood specific conductivity (K_s) and leaf specific conductivity (K_L), varied strongly but independently of MAP. For *C. alliodora*, xylem anatomy, K_s, K_L and Huber value varied little across sites, with K_s and K_L being consistently high relative to other *Cordia* species.
• A constitutively high hydraulic capacity coupled with plastic or genotypic adjustment in vulnerability to embolism and leaf water relations would contribute to the ability of *C. alliodora* to establish and compete across a wide precipitation gradient.

Key words: *Cordia alliodora*, drought, embolism, hydraulic conductivity, plasticity, precipitation.

Introduction

In tropical environments, the amount and seasonality of rainfall have a defining influence on forest structure and productivity (Gentry, 1988; Clark *et al.*, 2001; Engelbrecht *et al.*, 2006). It has long been known that water availability exerts strong control over xylem anatomy, such that the structure of xylem conduits differs markedly between species occurring in wet and dry environments (Carlquist, 1977). Because a plant's hydraulic architecture influences the rate at which water can be transported from the roots to the canopy, differences in xylem conduit structure have the potential to affect leaf water status and consequently to limit photosynthesis and growth (Sperry & Saliendra, 1994; Brodribb & Feild, 2000; Santiago *et al.*, 2004). Thus, the interaction of water

availability and hydraulic architecture can strongly influence the distribution of plant species (Pockman & Sperry, 2000).

The majority of studies documenting variation in xylem structure in relation to changes in water availability have been based on diverse groups of distantly related taxa (Carlquist, 1977; Barajas-Morales, 1985; Wheeler & Baas, 1991). In moist tropical climates, species generally have wood with wide xylem vessels, whereas areas that are extremely dry or cold are dominated by species with a high frequency (per cross-sectional area) of narrow vessels (Dickison, 2000; Carlquist, 2001). The difference in xylem structure between wet and dry climates is thought to reflect the competing requirements of the water transport system. Specifically, the need to transport water to the canopy at a high rate, so as to maximize stomatal conductance and photosynthesis, is thought to be balanced by the necessity

to minimize the induction and propagation of embolism through the vascular system (Sperry, 2003). Embolism reduces the ability of plants to move water to the canopy and, under severe conditions, can lead to desiccation and death of the plant (Tyree & Sperry, 1989; Rood *et al.*, 2000). Although the diameter of xylem vessels is not strongly correlated with vulnerability to drought-induced embolism across species (Tyree & Ewers, 1996), plants with greater redundancy in their vascular system (many small vessels) are inherently 'safer' than those which rely on a small number of large vessel to fulfil their transport requirements, because redundant conduits provide flow pathways around embolized conduits (Tyree & Zimmermann, 2002).

Species that occur across wide moisture gradients provide an alternative system for understanding how precipitation patterns influence xylem structure and leaf physiological traits. Differences in water availability can drive intraspecific trait variation through genetic (ecotypic) differentiation and/ or phenotypic plasticity. Previous studies indicate that the response of hydraulic traits to water availability varies among species. For instance, maximum xylem vessel diameter decreased with precipitation in two evergreen oak species (Villar-Salvador *et al.*, 1997). However, a co-occurring deciduous oak species showed no change in vessel diameter, indicating that the response of hydraulic traits to changes in water availability may depend on a species' leaf phenology. Manipulative experiments have shown that xylem vessel diameters increase with greater water availability in grapevine (Lovisolo & Schubert, 1998) and in cactus species (Stevenson & Mauseth, 2004).

A commonly observed response in plants exposed to hotter or drier environments is an increased ratio of sapwood cross-sectional area to leaf area (Huber value, HV) (Shumway *et al.*, 1991; Schultz & Matthews, 1993; Maherali & DeLucia, 2000; Cornwell *et al.*, 2005), which increases the capacity of the vascular system to supply water to the leaves (leaf specific conductivity, K_L). One important consequence of this adjustment is a reduction in the water potential gradient for a given transpiration rate. Higher K_L may thus assist in maintaining xylem water potentials above the level that would trigger drought-induced embolism during high evaporative demand or low water availability. Additionally, plants growing in hotter or drier environments may develop more embolism-resistant xylem, allowing stomata to remain open despite increasing water stress. Intraspecific variation in vulnerability to drought-induced embolism has been observed in response to changing water availability in some species (Alder *et al.*, 1996; Pockman & Sperry, 2000) but not in others (Maherali *et al.*, 2002; Cornwell *et al.*, 2005). Thus, general patterns in the response of hydraulic traits to changing water availability remain elusive.

Previous studies have focused on the plasticity of hydraulic traits in single species, or across distantly related taxa. In this study, variation was simultaneously examined in a widespread species, and in eight congeners from the genus *Cordia*
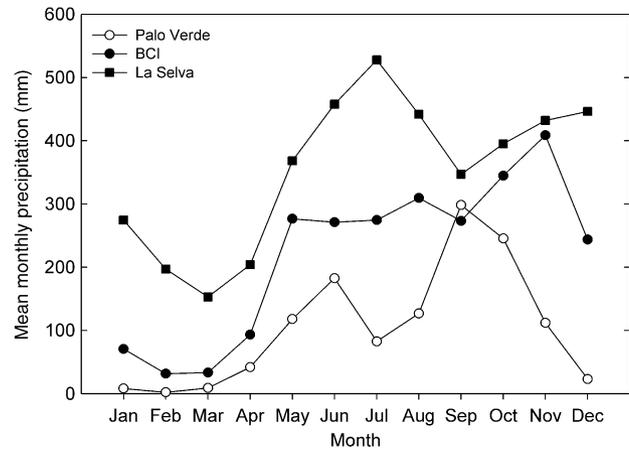

Fig. 1 Mean monthly precipitation for three neotropical forests of contrasting mean annual rainfall. Data are from monthly averages collected at Palo Verde (1996–2006), Barro Colorado Island (1924–2004) and La Selva (1957–2004).

(Boraginaceae). *Cordia* comprises 350 species with a pantropical distribution; in the neotropics, *Cordia* species are most common in seasonally dry areas but also occur in mesic environments including cloud forests and lowland rainforests (Gottschling *et al.*, 2005). *Cordia alliodora* has the widest distribution of the genus, growing in both wet and dry sites with a native range extending from central Mexico to northern Argentina (*c.* 25°N to 25°S). The distribution of *Cordia* species offers an ideal system in which to test the following hypotheses: that species within a genus will vary in hydraulic traits according to differing precipitation regime; and that adjustment in hydraulic traits contributes to the ability of *C. alliodora* to establish and compete in a wide range of habitats. Here, we documented intraspecific variation in hydraulic traits of *C. alliodora* occurring in three tropical forests differing in mean annual precipitation and investigated the interspecific variation in a number of congenerics occurring in the same forests.

Materials and Methods

Field sites

Field measurements were made between December 2003 and March 2004 at three sites with differing mean annual precipitation (MAP) in Central America (Fig. 1). The driest site was located within the seasonally dry forest of Palo Verde National Park in the Pacific northwest of Costa Rica (10°21′N, 85°21′W). MAP at this site is 1460 mm although this has declined to 1250 mm in the last 10 yr. Rainfall is seasonal at Palo Verde, with 80% of precipitation occurring from June to November and a pronounced dry season between December and May. The intermediate site was located in the tropical moist forest of Barro Colorado Island (BCI), Panama (9°09′N, 79°51′W) with a MAP of 2600 mm. Rainfall is also

Table 1 Growth habit, average height range and xylem anatomy of *Cordia* species growing at three sites of contrasting precipitation

Species	Height[a]	Habit	D_h (µm)	VD (mm^{-2})	Ψ_{pd} (MPa)	Ψ_{min} (MPa)
Palo Verde			47.6 (1.02) A	41 (4) A	−1.2 (0.2) A	−1.8 (0.3) A
C. alliodora	10–15 m	Tree	50.6 (2.1) bc	62 (13) ab	−2.1 (0.2) a	−3.2 (0.1) a
C. collococca	6–8 m	Tree	55.7 (2.4) ab	39 (4) ab	−0.9 (0.1) c	−1.9 (0.1) c
C. dentata	5–7 m	Shrub	55.7 (2.1) ab	21 (5) b	−1.2 (0.1) b	−2.1 (0.1) b
C. inermis	2–3 m	Understorey tree	36.2 (2.4) d	41 (5) ab		−1.1 (0.1) e
C. pringle	1–2 m	Shrub	39.6 (2.4) cd	41 (5) ab	−1.3 (0.1) b	−1.8 (0.1) c
Barro Colorado Island			53.1 (1.27) B	52 (5) A	−0.4 (0.2) B	−1.5 (0.1) B
C. alliodora	15–20 m	Tree	49.7 (2.1) bc	70 (9) a	−0.6 (0.1) cd	−1.6 (0.1) d
C. lasiocalyx	4–6 m	Understorey tree	47.8 (2.4) bcd	37 (1) ab	−0.5 (0.2) cde	−1.0 (0.1) e
C. panamensis	8–10 m	Tree	61.8 (2.1) a	50 (7) ab	−0.2 (0.1) ef	−1.8 (0.1) cd
La Selva			53.26 (1.33) B	44 (5) A	−0.2 (0.1) C	
C. alliodora	20–30 m	Tree	53.1 (2.4) ab	60 (13) ab	−0.1 (0.1) f	
C. cymosa	8–10 m	Understorey tree	55.1 (2.1) ab	47 (9) ab	−0.2 (0.1) def	
C. lucidula	4–6 m	Tree	51.5 (2.4) abc	23 (2) b	−0.3 (0.1) def	

D_h, hydraulically weighted mean vessel diameter; VD, vessel density per mm^2; Ψ_{pd}, predawn leaf water potential; Ψ_{min}, midday leaf water potential.
[a]Average height ranges for each species are taken from observations in each forest and from literature values (Croat, 1978).
Mean (SE) values are given for individual species (*n* = 3–5) and pooled for species at each site (*n* = 3) with one standard error given in parentheses. Within a column, different lower case letters indicate a significant difference (*P* < 0.05, HSD) and different upper case letters indicate a significant difference (*P* < 0.05, HSD) between sites.

seasonal at BCI, with 80% of rain falling between June and December. The wettest site was located in the tropical rainforest around the La Selva research station on the Caribbean slopes of Costa Rica (10°25′N, 84°00′W), with a MAP of 4200 mm. In contrast to Palo Verde and BCI, La Selva generally receives significant rainfall in all months of the year. At the time of sampling, conditions varied between each forest. Sampling at Palo Verde occurred in December 2003, a relatively dry period; only 4 mm of rain fell during that month. Sampling at BCI occurred in January 2004; only 13 mm of rain fell during that month, although 287 mm fell the previous month. Sampling at La Selva occurred in February 2004, during which 302 mm of rain fell during storms, such that the soil was continuously wet.

Study species

At each site, three to five species of trees or shrubs in the genus *Cordia* were selected for study. *Cordia alliodora* (Ruiz & Pav.) Oken occurred at all of the sites, while other species usually occurred at only one of the sites. The following species were studied at each site: at Palo Verde, *C. alliodora*, *C. collococca* L., *C. dentate* Poir., *C. inermis* (Mill) I.M. Johnst. and *C. pringle* Robins.; at BCI, *C. alliodora*, *C. lasiocalyx* Pittier., and *C. panamensis* Riley.; and at La Selva, *C. alliodora*, *C. cymosa* (Donn. Sm.) Standl. and *C. lucidula* I.M. Johnst. Although other *Cordia* species occurred in each forest, the focal species were selected based on commonness and proximity to the laboratory. The majority of species selected occurred in open areas in full sunlight or as canopy emergents, but two species

occurred in understorey environments (Table 1). At each site, three mature individuals were located for each of the target species.

The leaf phenology of species included in this study is not well known but based on the observations of Miller (1985) these species are classified as evergreen (*C. cymosa*, *C. panamensis*, *C. lasiocalyx*, *C. lucidula*), semideciduous (*C. dentata*) and deciduous (*C. alliodora*, *C. colloacocca*, *C. inermis*, *C. pringle*). Thus, species selected at wetter sites are primarily evergreen and those selected at Palo Verde are deciduous. Detailed information for leaf phenology is available only for *C. alliodora*. The phenological behavior of *C. alliodora* is curious, classified as wet season deciduous. At BCI, trees shed their leaves close to the end of the dry season or early in the wet season, and remain leafless for up to 8 wk into the wet season (Croat, 1978). At La Selva, a similar phenological pattern is apparent in reproductively mature individuals (Fetcher *et al.*, 1994). In drier forests, the timing of leaf drop and flushing are slightly shifted; leaf loss occurs from February to March, well before the end of the dry season, and leaf flush occurs in June, early in the wet season (Bullock & Solis-Magallanes, 1990; Borchert, 1994).

Cordia alliodora is also an important timber and agroforestry species in Central and South America. Considerable phenotypic variation is evident in natural populations of *C. alliodora*, with those growing on the seasonally dry Pacific coast of Central America being smaller in stature those growing in the wet Atlantic watershed (Greaves & McCarter, 1990). Variation has also been observed in leaf size and other morphological characters over the natural range of the species (Miller, 1985).

The relative role of environment and genetic variation in the phenotypic differences are currently unknown; however, the available evidence suggests genetic differentiation between populations across broad geographical zones. A study of isozyme variation in populations of *C. alliodora* growing in Costa Rica indicated that there were significant genetic differences between (wet) Atlantic and (dry) Pacific populations (Chase *et al.*, 1995). Additionally, provenance trails for *C. alliodora* demonstrated that the trees of Atlantic provenance consistently grew more vigorously than Pacific provenances, although differences in performance of the two groups decreased at drier trial sites (Greaves & McCarter, 1990).

Xylem anatomy

Xylem vessel diameter and density were measured in branches of each of the 11 populations listed in Table 1. Transverse sections of xylem tissue were made with a sliding microtome from branches used in hydraulic conductivity measurements; measurements were made from one branch from each of the three individuals per species. Sections were digitally photographed under a light microscope using bright field illumination (AxioCam, Zeiss, Jena, Germany) and images were analyzed using Image J software (National Institutes of Health, Bethesda, MD, USA, http://rsb.info.nih.gov/ij/). For each transverse section, a binary image was created and the lumen area of each vessel in the conductive xylem area was automatically measured using the 'analyze particles' function. In cases where the boundary of adjacent vessels was not clear, the 'watershed' function was used to separate vessels. The lumen area of vessels was then transformed into an equivalent circular diameter for each vessel counted. The mean hydraulically weighted vessel diameter was calculated for each image as $D_h = (\Sigma D^4/N)^{1/4}$, where D is the vessel diameter and N is the number of vessels in that section. The hydraulically weighted vessel diameter is the average diameter needed for a given vessel density to result in the theoretical hydraulic conductivity for that stem (Tyree & Zimmermann, 2002). Vessel density in cross-section (VD, mm^{-2}) was also calculated for each sample. Theoretical hydraulic conductivity (K_t, kg s^{-1} m^{-1} MPa^{-1}) was calculated as $K_t = \pi D_h^4/128\eta VD$, where η is the viscosity of water (1.002×10^{-9} MPa s at 20°C).

Hydraulic conductivity

Sapwood specific hydraulic conductivity (K_s), leaf specific hydraulic conductivity (K_L) and Huber value (HV) were measured for each population of *Cordia* listed in Table 1. Measurements were made with a portable steady-state flowmeter (Feild & Holbrook, 2000). Branches of 2 m in length were collected in the early morning, sealed in plastic bags with moist paper towels and returned to the laboratory. Branch segments 5 cm in length and 3–5 mm in diameter were cut underwater, trimmed with a fresh razor blade and

connected to the flow meter. Segments were perfused with filtered, 10 mmol KCl solution. The perfusing solution was supplied from a reservoir raised above the flow meter to generate a gravity-induced pressure head of approx. 10 kPa. The pressure drop across PEEK tubing of known resistance generally resulted in a pressure difference across the stem segment of *c.* 5 kPa. The segment was perfused with solution until a steady-state flow was attained, at which point the hydraulic conductivity of the segment was calculated as $K_h = FL/\Delta P$, where F is the flow rate (kg s^{-1}) and ΔP is the pressure drop (MPa) along the stem segment of length L (m). After the initial measurement, the stem was flushed at a pressure of 100 kPa for 15 min to remove air emboli and then re-measured to obtain the maximum conductivity. Upon completion of the measurement, segments were perfused with 0.01% Safranin dye to determine conductive sapwood area. Leaf surface area distal to the stem segment was measured using a digital camera and image analysis software (Image J) or a leaf area meter (LI-Cor, Lincoln, NE, USA). Sapwood and leaf area measurements were used to calculate K_s, K_L and HV. At each site, parameters were measured for three replicate branches from each of three trees per species ($n = 3$). Values of K_s and K_L analyzed after maximum values are flushing.

The segment length of 5 cm was selected to standardize among species that vary in shoot morphology. This length was less than the maximum vessel length for all species and therefore open vessels were present in the segments used for hydraulic measurements. While these measurements provide a good basis for comparison between species in this study, the high conductance of open vessels means caution should be used when comparing values of K_s and K_L given here with values determined using different methods in other studies.

Vulnerability to embolism

Vulnerability to water stress-induced embolism was measured for three species at each site by benchtop dehydration of detached branches. Large (2 m) branches were collected from three trees of each species late in the evening or in the early morning, sealed in plastic bags and returned to the laboratory. At the drier sites (Palo Verde and BCI), branches were re-cut under water and then rehydrated over night with cut ends in water and covered with plastic bags. The following morning the water potential of branches was measured with a pressure chamber to confirm that the xylem tissue had been fully rehydrated. This procedure was unnecessary at La Selva because frequent rainfall ensured that freshly collected branches were fully hydrated. A series of measurements was then made on branch tissue using the steady-state flow meter to assess the percentage loss of hydraulic conductivity as a result of embolism (PLC). The first measurements were made on fully hydrated tissue. The xylem water potential (Ψ_x) of branch segments was assessed by measuring the water potential of two to three leaves distal to the stem segment which had been

covered with aluminum foil and plastic bags. A stem segment 2–4 cm in length was then cut under water and connected to the flow meter. Following an initial measurement of K_h, the segment was flushed at 100 kPa for *c.* 20 s to remove emboli. A second measurement was then made to assess the maximum K_h of the segment. This procedure was repeated on branches that were dried on the bench top for 1–4 d to induce water stress. For each branch, three to five segments were selected for measurement. The total number of measurements for each species was between 20 and 40. Vulnerability curves were generated for each species by fitting curves for PLC against Ψ_x (Pammenter & Vander Willigen, 1998).

Leaf water status and pressure–volume curves

Leaf water potential was measured predawn (Ψ_{pd}) and at midday (Ψ_{min}) at each site using a Scholander pressure chamber (Plant Moisture Stress, Albany, OR, USA). Measurements were made on three leaves on each of three individuals for each species ($n = 3$). Measurements of Ψ_{pd} were not made for *C. inermis* and Ψ_{min} values were not obtained at La Selva because of frequent rain and logistical constraints. It is important to note that measurements of Ψ_{pd} and Ψ_{min} do not represent seasonal minima or the greatest amounts of water stress to which each species is subject. Pressure–volume curves were generated for leaves of three species at each site using the air drying method (Koide *et al.*, 2000). Branches were collected from five trees of each species and rehydrated overnight. The following morning a leaf was cut from the branch and its water potential immediately measured with a pressure chamber. The leaf was weighed on an electronic balance and left to transpire for a short time interval on the benchtop before it was weighed and its water potential measured again. This process was repeated until the leaf showed obvious signs of tissue damage from dehydration. The dry weight of leaves was determined after 48 h at 70°C in a drying oven. Osmotic potential at full turgor (π_{ft}) and turgor loss point (Ψ_{tlp}) and relative water content at turgor loss (RWC_{tlp}) were calculated from regression analysis of plots of $1/\Psi_L$ against the relative water content of the leaf (RWC). The elastic modulus at full turgor (ε_{ft}) was calculated as ($\Delta\Psi_p/\Delta RWC_s$) using the first four points of the plot where $\Delta\Psi_p$ is the change in leaf turgor pressure and ΔRWC_s is the change in the relative water content of the symplasm. Parameters were generated from three to five leaves for each species, with each leaf from a different individual ($n = 3–5$).

Statistics

For hydraulic parameters, K_s, K_L and HV, differences among species and between the three sites were established using a general linear model with species nested within site and trait data averaged for each replicate tree ($n = 3–5$; jmp, SAS Institute, Cary, NC, USA). For xylem anatomical traits and leaf tissue water relations parameters, differences were determined with a general linear model with species nested within site. Post-hoc comparisons were conducted using Tukey HSD to test for differences between sites and species. Correlations between traits and MAP and between different traits were determined using Spearman rank correlation coefficient (r). To test for the effects of *C. alliodora* being measured at each site, general linear models were also run with *C. alliodora* excluded from the analysis. The site differences were unaltered for all of the parameters with the exception of K_s, for which there was clearer differentiation between the sites, demonstrating that the inclusion of *C. alliodora* at all sites did not bias interspecies comparisons in our analyses.

Results

Xylem anatomy

Hydraulically weighted vessel diameters were significantly narrower ($P < 0.05$) at Palo Verde than at moister sites, La Selva and BCI (Table 1), although there was no difference between the two moister sites, and the relationships between D_h and MAP, and between VD and MAP, were not significant ($r = 0.20$, $P = 0.54$ and $r = 0.08$, $P = 0.82$, respectively).

Variation between species at given sites was greater than the average variation across sites for both D_h and VD (D_h site, $P = 0.0015$, species $P < 0.0001$; VD site, $P = 0.2$, species $P = 0.006$). For example, Palo Verde species *C. collococca* and *C. dentata* had wider D_h than most species at BCI and La Selva, while *C. inermis* and *C. pringle*, also at Palo Verde, had the narrowest D_h. *Cordia alliodora* exhibited high D_h and VD relative to other *Cordia* species; there was no significant variation in D_h or VD between populations of *C. alliodora* at the three sites.

Hydraulic parameters

There was a significant negative relationship ($r = -0.72$, $P = 0.01$) between HV and MAP but not between K_s or K_L and MAP ($r = 0.42$, $P = 0.20$, $r = 0.20$, $P = 0.54$), with average K_s and K_L values being lowest at Palo Verde, but higher at BCI than at La Selva (Fig. 2b,d). Once again, the lack of strong relationships between K_s or K_L and MAP could be attributed mainly to the high within-site variation in these parameters. In general, a greater percentage of variation in hydraulic parameters was accounted for by differences between species within a site than by differences between sites.

Contrary to expectations, there was no significant difference ($P > 0.05$) in K_s, K_L or HV between populations of *C. alliodora* growing at the three sites (Fig. 2). However, *C. alliodora* was conspicuous in having higher values of K_s and K_L than other species at each site. This was most obvious at Palo Verde, where the K_s and K_L values of *C. alliodora* were more than twice that of co-occurring *Cordia* species.
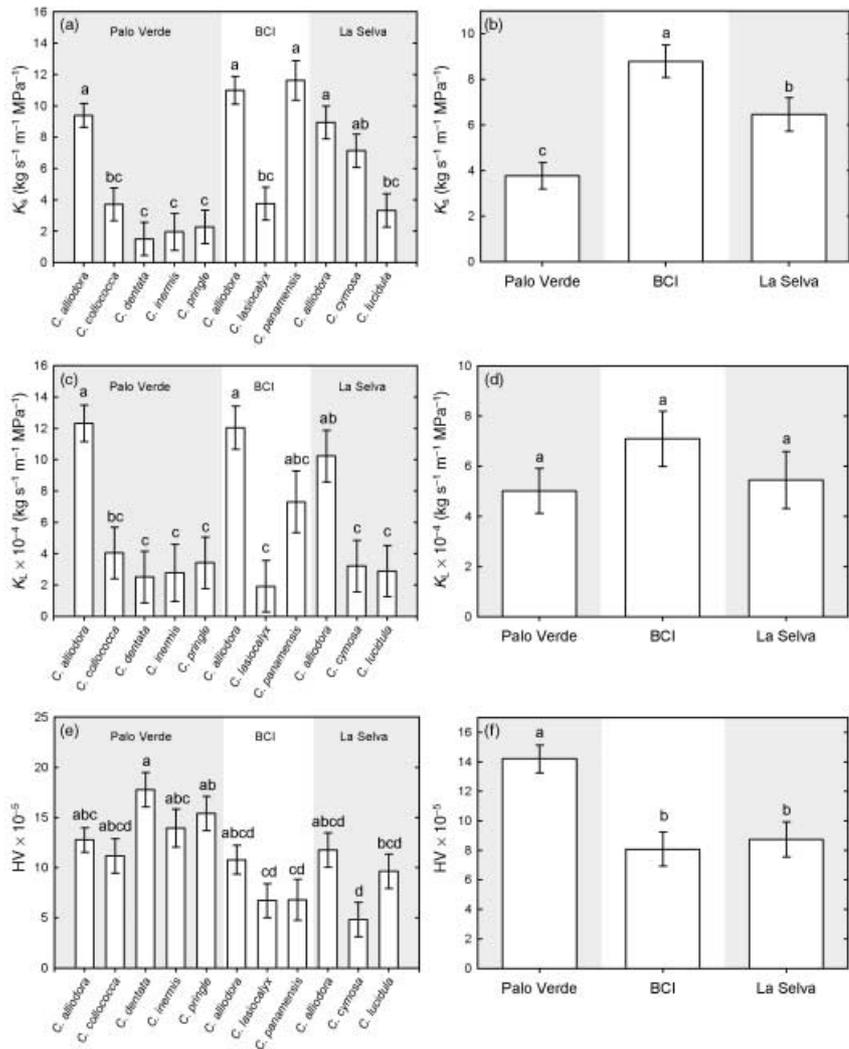
Fig. 2 Individual and site-averaged stem hydraulic traits for *Cordia* species growing at sites of differing mean annual precipitation: Palo Verde (1460 mm), Barro Colorado Island (2600 mm) and La Selva (4200 mm). Values are shown for sapwood specific conductivity (K_s) (a, b), leaf specific conductivity (K_L) (c, d), and Huber value (HV, sapwood area/leaf area) (e, f). Values are means of three replicate branches from each of three trees ($n = 3$) with bars showing standard error of the mean. For each graph, different lower case letters represent significant differences ($P < 0.05$, HSD).

Vulnerability to embolism

Species occurring in the driest forest, Palo Verde, were less vulnerable to embolism than species at BCI and La Selva (Fig. 3). There was a significant relationship ($r = 0.84$, $P = 0.004$) between the xylem water potential at which a 50% loss of conductivity occurred (P50) and MAP, with P50 values least negative at La Selva, the wettest site. Intraspecific variation in populations of *C. alliodora* mirrored interspecific variation, with populations occurring at the wetter sites less resistant to embolism than species occurring at the drier sites.

Leaf water status and pressure–volume curves

There was a significant difference ($P < 0.05$, HSD) between the sites in both Ψ_{pd} and Ψ_{min}, although there was also variation between species within each site (Table 1). In general, species from Palo Verde has lower Ψ_{pd} and Ψ_{min} than species from the two wetter sites. Across species, π_{ft}, Ψ_{tlp} and RWC_{tlp} were

correlated with MAP ($r = 0.90$, 0.84, and 0.95, respectively, $P < 0.05$). Mean osmotic pressures at full hydration and turgor loss point were significantly higher at BCI and La Selva than at Palo Verde (Table 2). Thus, leaves of species occurring at the moister sites had lower osmotic concentrations, and lost turgor at higher water potentials and at higher relative water contents than those at drier sites. There was no trend of ε_{ft} with MAP. Intraspecific variation between sites was also observed in populations of *C. alliodora* with π_{ft}, Ψ_{tlp} and RWC_{tlp} being highest in populations at La Selva and lowest at Palo Verde.

Relationships between traits

There was only a weak positive relationship ($r = 0.23$, $P = 0.50$) between K_s and D_h but a strong correlation between K_s and K_t ($r = 0.86$, $P < 0.01$), as K_t incorporates both D_h and VD (Fig. 4a,b). To determine whether HV or K_s was responsible for driving overall variation in K_L, intercorrelations between these three variables were tested. K_L and K_s were significantly
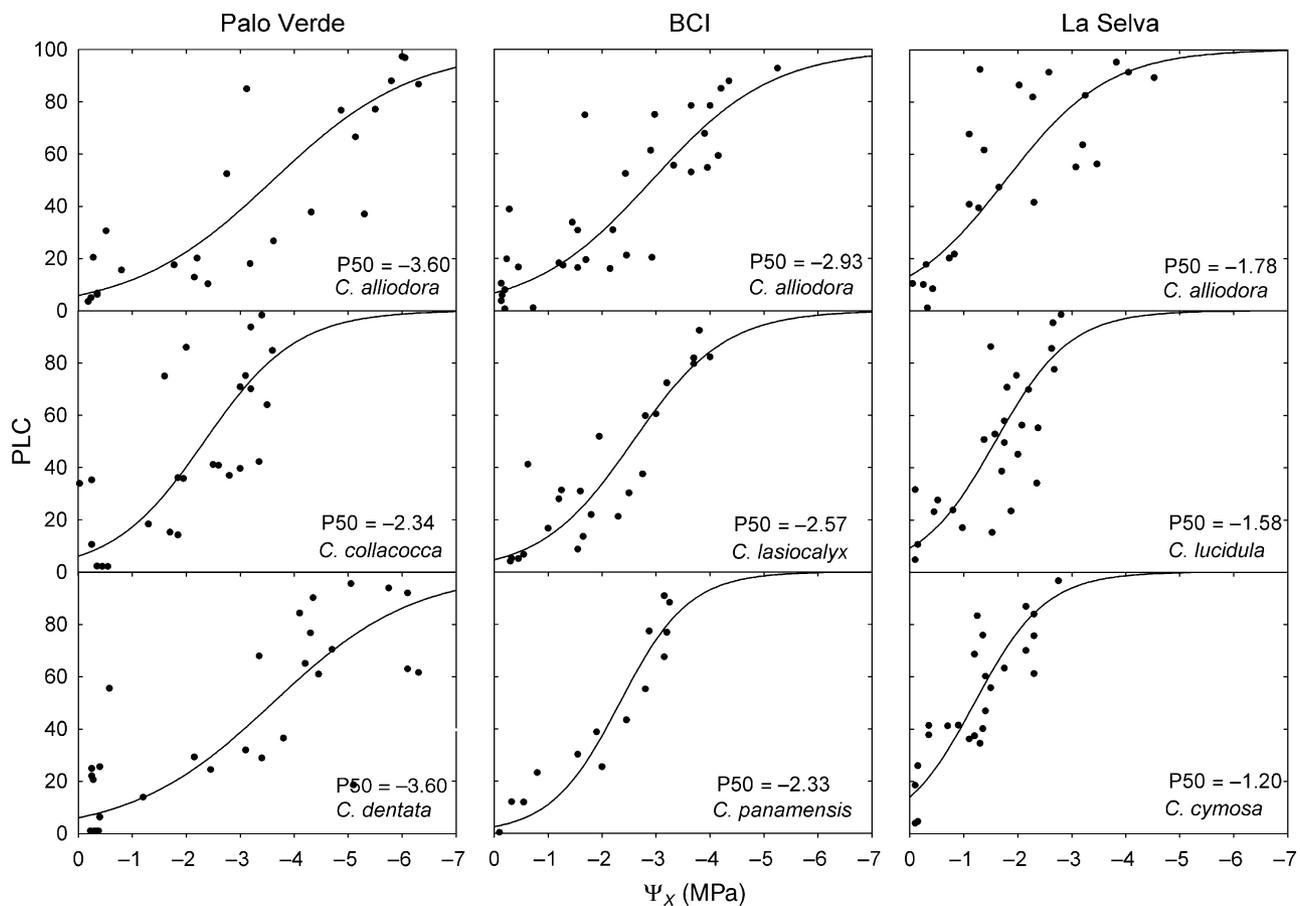
Fig. 3 Vulnerability to drought-induced embolism in *Cordia* species growing at three sites of contrasting mean annual precipitation. Percentage loss of conductivity (PLC) is plotted against xylem water potential (Ψ_x) for each species. Data are shown for three species at each site, with *C. alliodora* occurring at all sites. Each point represents one measurement and lines were fitted using $PLC = 100/(1 + \exp(a(\Psi_x - b)))$, where *a* is the slope of the line and *b* is the xylem water potential at which 50% loss of conductivity occurs (P50).

Table 2 Leaf tissue water relations of *Cordia* species growing at three sites of contrasting moisture availability

Site/species	π_{ft} (MPa)	Ψ_{tlp} (MPa)	RWC_{tlp}	ε_{ft} (MPa)
Palo Verde	−1.87 (0.03) A	−2.13 (0.03) A	0.88 (0.01) A	11.24 (0.84) A
C. alliodora	−1.93 (0.06) c	−2.16 (0.07) c	0.89 (0.02) ab	12.84 (0.41) a
C. dentata	−1.88 (0.02) c	−2.14 (0.04) c	0.89 (0.01) b	11.86 (0.73) a
C. collococca	−1.80 (0.04) c	−2.09 (0.04) c	0.86 (0.01) ab	9.01 (0.67) a
BCI	−1.66 (0.03) B	−1.84 (0.03) B	0.91 (0.01) B	12.85 (0.82) A
C. alliodora	−1.71 (0.06) bc	−1.89 (0.08) bc	0.92 (0.01) ab	14.16 (1.64) a
C. lasiocalyx	−1.48 (0.04) ab	−1.63 (0.04) ab	0.91 (0.01) ab	11.96 (1.52) a
C. panamensis	−1.79 (0.09) c	−2.00 (0.08) c	0.90 (0.01) ab	12.46 (1.74) a
La Selva	−1.42 (0.03) C	−1.59 (0.03) C	0.93 (0.01) B	11.25 (0.82) A
C. alliodora	−1.64 (0.02) bc	−1.86 (0.05) bc	0.93 (0.01) a	12.16 (1.13) a
C. cymosa	−1.34 (0.02) a	−1.50 (0.03) a	0.93 (0.01) a	11.13 (0.61) a
C. lucidula	−1.29 (0.03) a	−1.40 (0.02) a	0.92 (0.01) a	10.46 (1.62) a

π_{ft}, osmotic potential at full turgor; Ψ_{tlp}, water potential at the turgor loss point; RWC_{tlp}, relative water content and turgor loss; ε_{ft}, elastic modulus estimated above the turgor loss point.
Mean (SE) values are given for individual species ($n = 3$–5) and pooled for species at each site ($n = 3$) with one standard error given in parentheses. Within a column, different lower case letters indicate a significant difference ($P < 0.05$, HSD) and different upper case letters indicate a significant difference ($P < 0.05$, HSD) between sites.
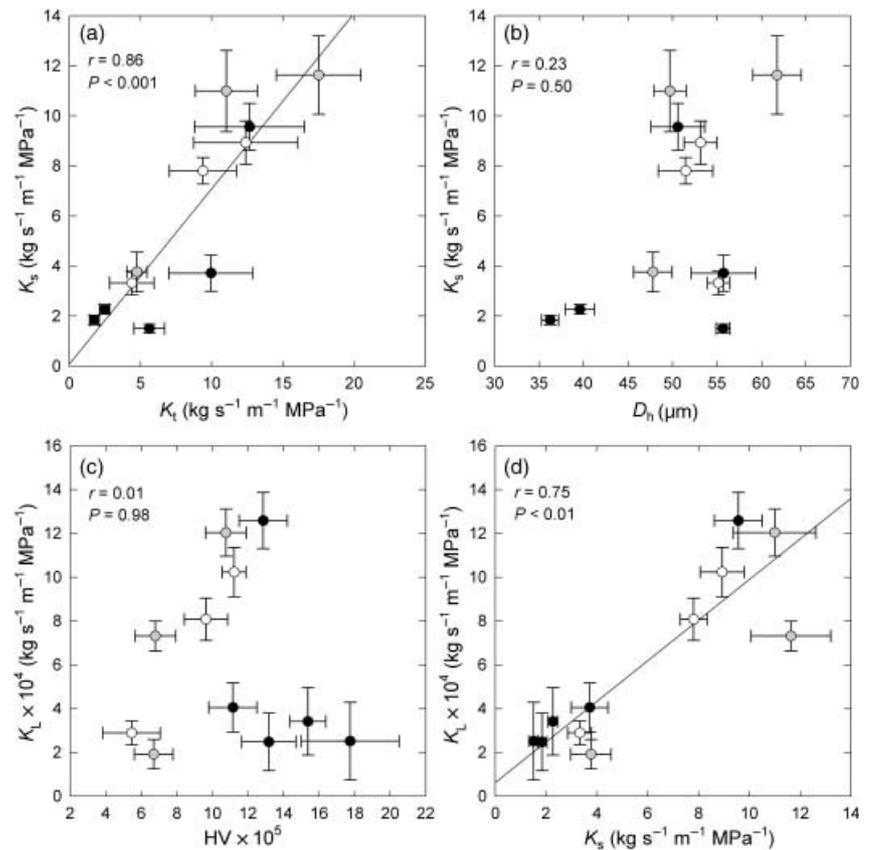
Fig. 4 Correlations between hydraulic traits of *Cordia* species growing in three sites of contrasting mean annual precipitation. (a) Sapwood specific conductivity (K_s) vs theoretical hydraulic conductivity (K_t); (b) K_s vs hydraulically weighted mean vessel diameter (D_h); (c) leaf specific conductivity (K_L) vs Huber value (HV); (d) K_L vs K_s. Symbols represent different sites: black circles, Palo Verde; grey circles, Barro Colorado Island; white circles, La Selva. Correlations between traits were assessed using Spearman rank correlation coefficients (r).

correlated ($r = 0.75$, $P < 0.01$) but K_L and HV were independent ($r = 0.01$, $P = 0.98$; Fig. 4c,d). Thus, species differences in K_L were driven more by changes in xylem anatomy and hydraulic supply than by adjustment in leaf area. Neither D_h nor K_s was significantly correlated with P50 across the *Cordia* species surveyed ($r = 0.25$ and -0.07, $P = 0.52$ and 0.86, respectively) (Fig. 5a,b). K_s and K_L were also not significantly related to leaf tissue water relations parameters, although there was a strong correlation between P50 and Ψ_{pd} ($r = 0.79$, $P = 0.01$), π_{ft} ($r = 0.75$, $P = 0.02$), Ψ_{tlp} ($r = 0.68$, $P = 0.04$) and RWC_{tlp} ($r = 0.78$, $P = 0.03$) (Fig. 5c,d).

Discussion

Interspecific variation in traits

Hydraulic function varied substantially in *Cordia* species distributed in tropical forests across a precipitation gradient. *Cordia* species in drier habitats were more resistant to drought-induced embolism and lost turgor at lower leaf water potentials than those in wetter habitats. Surprisingly, there was not a significant relationship between MAP and other hydraulic traits such as vessel diameter, K_s and K_L. These findings indicate that increased drought tolerance does not necessarily require a trade-off in hydraulic capacity.

In general, a greater proportion of variation in hydraulic traits was accounted for by differences between species within a site than differences across sites. This finding suggests that *Cordia* species may have diversified in hydraulic behavior, corresponding to different niches within each given forest, or else that they previously adapted to diverse conditions, and have recently come to coexist at given sites (Cavender-Bares *et al.*, 2004). Strong within-site variation among species in key functional traits eclipsing the average differences across sites has been reported in studies of diverse species sets examining traits such as leaf mass per area, foliar nutrient concentrations, and seed mass (Wright *et al.*, 2001; Grubb, 2002; Moles *et al.*, 2005). Our data are the first, to our knowledge, to show this pattern in hydraulic traits for species within a wide-ranging genus.

Studies of general trends in xylem anatomy have demonstrated that vessel diameters are, on average, larger in wet habitats than in dry habitats (Dickison, 2000), including for wet vs dry tropical forest taxa (Barajas-Morales, 1985). This trend was also apparent in the larger average vessel diameters at the two moister sites than at Palo Verde. However, the relationship between vessel diameter and precipitation is complex (Baas, 1986) and general trends can mask differences in hydraulic function that occur within a site. We observed a range of vessel diameters within each site, with the greatest range
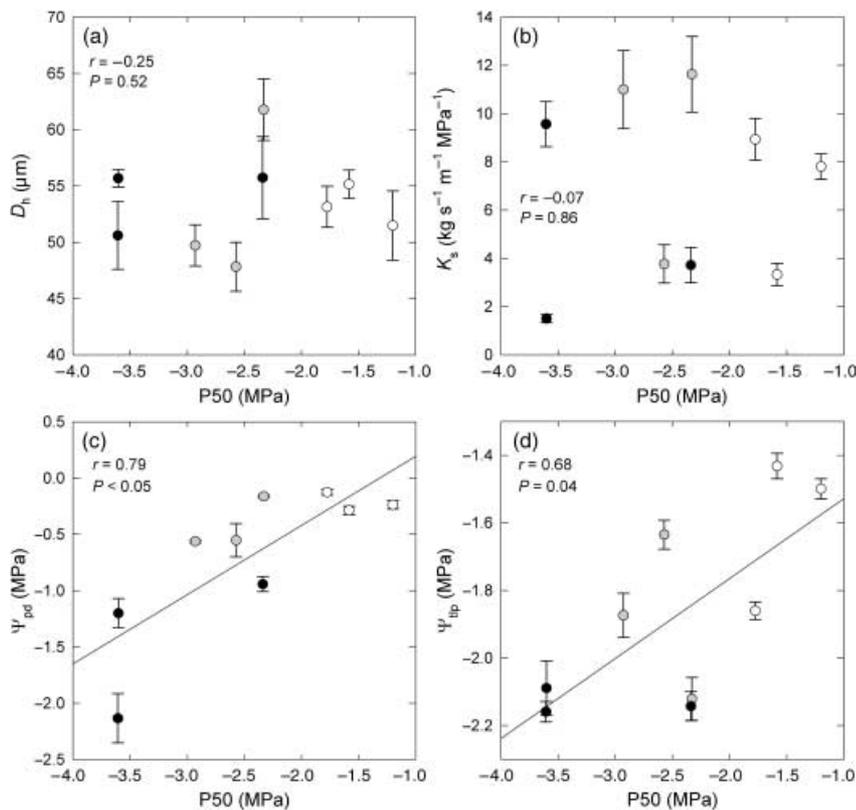
Fig. 5 Correlations between hydraulic traits of *Cordia* species growing in three sites of contrasting mean annual precipitation. (a) Xylem water potential at which 50% loss of conductivity occurs (P50) vs hydraulically weighted mean vessel diameter (D_h); (b) P50 vs sapwood specific conductivity (K_s); (c) P50 vs predawn leaf water potential (Ψ_{pd}); (d) P50 vs osmotic potential at turgor loss point (Ψ_{tlp}). Symbols represents different sites: black circles, Palo Verde; grey circles, Barro Colorado Island; white circles, La Selva. Correlations between traits were assessed using Spearman rank correlation coefficients (r).

occurring at the driest site. Hydraulic function is influenced by the frequency of vessels in cross-sections as well as vessel diameter. At Palo Verde, species with wider vessels (*C. collacocca* and *C. dentata*) had lower VD than species with narrow vessels (*C. inermis* and *C. pringle*), resulting in similar K_s values for these species. The exception to this trend was *C. alliodora*, in which the combination of wide vessels and high VD resulted in a K_s three times higher than other species at Palo Verde. It is possible that some of this variation in vessel anatomy is correlated with seasonal patterns of leaf phenology (Sobrado, 1993; Choat *et al.*, 2005a), but investigation of this relationship will require further detailed comparative observations of leaf shedding in these *Cordia* species.

There were significant differences in K_s and HV between *Cordia* species at Palo Verde and at the two wetter forests. However, K_s and K_L were highest at the intermediate site (BCI) and there was no relationship between MAP and these hydraulic traits. This may be partly because of the role other environmental factors have played in shaping hydraulic traits. At the wetter sites, it was apparent that light regime also influenced hydraulic parameters, and thus the variation of hydraulic traits is associated with the occurrence of *Cordia* species in a range of environments in each forest. On BCI, the understorey species *C. lasiocalyx* had significantly lower K_s than *C. alliodora* and *C. panamensis*, which both favor disturbed areas with high light and high evaporative demand. Lower K_s

and K_L for shade-establishing relative to light-demanding tropical woody species parallels trends for leaf hydraulic conductance (Sack *et al.*, 2005).

The higher HV in Palo Verde species compared with species at wetter sites is consistent with previously observed increases in HV as a genetic or plastic adjustment to increasing evaporative demand and declining soil moisture availability (Shumway *et al.*, 1993; Magnani *et al.*, 2002). However, the bulk of the variation in K_L was driven by variation in K_s, indicating that shifts in wood xylem traits are responsible for the diversity of hydraulic capacity, rather than shifts in shoot leaf : sapwood allocation. This contrasts with the relationship observed in *Pereskia* species occurring across a rainfall gradient, for which K_L was strongly related to HV (Edwards, 2006). For *Cordia* species at Palo Verde (except for *C. alliodora*), differences in HV were not great enough to compensate for low K_s. As such, K_L was lower for the Palo Verde species, meaning that they would generate a greater xylem pressure gradient (more negative Ψ_x) at a given transpiration rate. Thus, *Cordia* species from Palo Verde do not rely on high K_L to reduce water potential gradients generated by transpiration but rather depend upon greater resistance to embolism to tolerate increasingly negative Ψ_x as the dry season progresses.

The results of our study are consistent with previous research showing that species occurring in mesic environments are generally less vulnerable to drought-induced embolism than

species in xeric environments (Pockman & Sperry, 2000; Maherali *et al.*, 2004). Our findings confirm this pattern among species within a diverse genus. *Cordia* species occurring at Palo Verde had the most negative P50, and species at La Selva had the least negative P50. The fact that vulnerability to embolism was more tightly correlated with MAP than other hydraulic traits illustrates its importance in determining drought tolerance and is consistent with the strong relationship between P50 and Ψ_{pd} observed for *Cordia* species. Studies of chaparral species have shown that P50 is tightly correlated with the seasonal minimum of predawn water potential, indicating that this parameter is finely tuned to variations in water availability (Pratt *et al.*, 2007). Further, other studies have shown variation in vulnerability to embolism for groups of closely related species growing across precipitation gradients, suggesting that this trait is frequently important for the radiation of a lineage into different moisture regimes (Willson & Jackson, 2006; T. E. Dawson, unpublished).

The differences found across species may reflect the combination of plasticity across environments as well as genetic differences. The available data provide strong circumstantial evidence that variation observed in vulnerability to embolism and leaf tissue water relations parameters may partially arise from adaptation to contrasting moisture regimes. The current phylogeny shows that three species measured at Palo Verde, the driest forest – *C. alliodora*, *C. collococca*, and *C. dentata* – are more distantly related to one another than to at least one species at the intermediate site (Gottschling *et al.*, 2005). Thus, it would appear that the consistently high resistance to embolism observed at Palo Verde is not a result of shared ancestry and the variation is far more likely to be adaptive in nature. Beyond this finding, unfortunately, it is currently not possible to place the variation in functional traits observed for *Cordia* species within a phylogenetic context, as the most recent *Cordia* phylogeny incorporates molecular data for only four of the species used in our study (Gottschling *et al.*, 2005). We note that a phylogeographic understanding of trait diversification in these species would be complicated by the fact that much of their evolution may not have taken place in these forests. Given the relatively recent uplift of Panama and Costa Rica, the species examined in this study may have evolved elsewhere and moved into forest habitats that suited their trait combinations, in which case ecological sorting would have played a larger role than adaptation in driving the observed relationships between hydraulic traits and MAP.

Leaf tissue water relations parameters derived from pressure–volume curves differed between species at the three sites. The lower π_{ft}, Ψ_{tlp} and RWC_{tlp} of species growing at Palo Verde are typical of drought-tolerant species, allowing them to maintain positive turgor as leaf water potential and RWC decline during drought (Sobrado, 1986; Fanjul & Barradas, 1987; Holbrook *et al.*, 1995). We observed a strong correlation between P50 and Ψ_{tlp}, suggesting an integration of stem and leaf hydraulic traits conferring drought tolerance in *Cordia* species across the

precipitation gradient. This finding is similar to the correlation of stem cavitation threshold and stomatal closure observed by Brodribb *et al.* (2003) in a phenologically and taxonomically diverse group of species co-occurring in one dry tropical forest. It is now becoming clear that stem and leaf traits are integrated across species at a number of levels, including flow capacity (Edwards, 2006; Sack & Holbrook, 2006), the coordination of hydraulic and photosynthetic capacity (Brodribb & Feild, 2000; Brodribb *et al.*, 2002; Santiago *et al.*, 2004), and, as shown here, drought tolerance.

In *Cordia* species at Palo Verde, there was a much larger safety margin between the water potentials at which turgor loss occurred and P50 values, suggesting that water loss from leaves would be reduced by declining stomatal conductance well before water potentials reached dangerous levels in the stems. At the wetter sites, particularly La Selva, lower safety margins may be more acceptable because water stress is less severe and opportunities for mitigation of water stress and refilling of embolized vessels are more frequent.

Intraspecific variation in hydraulic traits for *C. alliodora*

With the exception of drought-induced embolism, there was a striking lack of variation in hydraulic traits between populations of *C. alliodora* growing across a broad precipitation gradient. This suggests that plasticity and ecotypic divergence in traits conferring high wood hydraulic capacity are not key requirements for its extensive distribution. Rather, *C. alliodora* may owe its success to an ability to maintain high K_s and K_L across a wide gradient in water availability while vulnerability to embolism and leaf-tissue parameters vary according to site water availability. This pattern is consistent with previous studies that have correlated the high stem and leaf hydraulic capacity of *C. alliodora* with high rates of photosynthesis (Santiago *et al.*, 2004), high leaf vein density, and large stomatal pore area (Sack *et al.*, 2005; Sack & Frole, 2006). These traits would contribute to the well documented success of *C. alliodora* as a fast-growing early successional species in wet and dry environments (Huante *et al.*, 1995; Kapp *et al.*, 1997; Hiremath *et al.*, 2002).

Several studies have reported a correlation between vulnerability to embolism and water availability within a species (Franks *et al.*, 1995; Alder *et al.*, 1996; Mencuccini & Comstock, 1997; Sparks & Black, 1999). Generally, these studies have demonstrated that populations from drier environments are less vulnerable than those from wetter environments. This is consistent with the results of our study, with populations of *C. alliodora* at the wetter sites having higher P50 than those at drier sites. At Palo Verde, the high embolism resistance of *C. alliodora* is consistent with its ability to tolerate greater xylem tensions (daily $\Psi_{min} = -3.1$ MPa). Borchert (1994) observed that *C. alliodora* growing at a nearby site in the Guanacaste province (Hacienda La Pacifica) desiccated strongly (stem $\Psi_{min} < -4.0$ MPa) in the dry season and maintained

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leaves for longer than many co-occurring deciduous species. Resistance to embolism found in the BCI population (P50 = –2.9 MPa) was high relative to other tree species at this site (Machado & Tyree, 1994; Meinzer *et al.*, 2003; Lopez *et al.*, 2005). This may be linked with unusual leaf phenology of *C. alliodora* on BCI; the high resistance to embolism would allow for the maintenance of a canopy during the dry season. A similar leaf phenology is apparent in individuals growing at La Selva, although the P50 of this population was only –1.8 MPa. The fact that this phenology remains viable at La Selva despite higher P50 probably relates to the mild dry seasons and low frequency of drought experienced at this site.

There did not appear to be a trade-off between hydraulic efficiency and vulnerability to embolism across populations of *C. alliodora*. Indeed, the combination of higher efficiency and lower vulnerability to embolism in the Palo Verde population is unusual. However, the absence of a strong relationship between D_h or K_s and vulnerability to embolism is consistent with the air seeding hypothesis, which relates vulnerability to drought-induced embolism to the porosity of pit membranes rather than the diameter of xylem conduits (Tyree & Zimmermann, 2002). It is likely that observed differences in vulnerability to embolism are related to pit membrane structure and contact area between vessels (Choat *et al.*, 2003, 2005b; Wheeler *et al.*, 2005). However, the measurements of K_s in the present study included open vessels and it is possible that hydraulic limitations resulting from pit membrane resistance were not fully taken into account, masking a trade-off in hydraulic safety and efficiency across populations of *C. alliodora*.

Future common-garden experiments are needed to determine the degree to which the variation of hydraulic traits observed across populations of *C. alliodora*, and across *Cordia* species, are the result of ecotypic differentiation or phenotypic plasticity. Although previous studies have provided evidence that Atlantic and Pacific populations of *C. alliodora* are genetically distinct (Greaves & McCarter, 1990; Chase *et al.*, 1995), this does not confirm that differences in vulnerability to embolism are genetically driven. Within other species, common-garden experiments demonstrate that differences in vulnerability to embolism are often maintained when water availability is held constant (Neufeld *et al.*, 1992; Franks *et al.*, 1995; Sparks & Black, 1999, T. E. Dawson, unpublished) indicating that variation in vulnerability to embolism is more likely to be under genetic control than the result of phenotypic plasticity. This view is consistent with experiments showing that P50 differed between four *Eucalyptus* clones, but that within each clone, there was no difference in P50 between populations growing at mesic and xeric sites (Pammenter & Vander Willigen, 1998). Future study of the possible genetic basis for diversification of hydraulic traits will help to explain not just the evolution of variation in plant function, but also the ability of related species to establish in given moisture regimes, and, thereby, potentially to elucidate both their biogeographical distribution and their ability to coexist within species-rich tropical communities (Harms *et al.*, 2001; Engelbrecht *et al.*, 2006).

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