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The effects of intervessel pit characteristics on xylem hydraulic efficiency and photosynthesis in hemiepiphytic and non-hemiepiphytic *Ficus* species

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Xylem vulnerability to cavitation and hydraulic efficiency are directly linked to fine-scale bordered pit features in water-conducting cells of vascular plants. However, it is unclear how pit characteristics influence water transport and carbon economy in tropical species. The primary aim of this study was to evaluate functional implications of changes in pit characteristics for water relations and photosynthetic traits in tropical *Ficus* species with different growth forms (i.e. hemiepiphytic and non-hemiepiphytic) grown under common conditions. Intervessel pit characteristics were measured using scanning electron microscopy in five hemiepiphytic and five non-hemiepiphytic *Ficus* species to determine whether these traits were related to hydraulics, leaf photosynthesis, stomatal conductance and wood density. *Ficus* species varied greatly in intervessel pit structure, hydraulic conductivity and leaf physiology, and clear differences were observed between the two growth forms. The area and diameter of pit aperture were negatively correlated with sapwood-specific hydraulic conductivity, mass-based net assimilation rate, stomatal conductance (g_s), intercellular CO_2 concentration (C_i) and the petiole vessel lumen diameters (D_v), but positively correlated with wood density. Pit morphology was only negatively correlated with sapwood- and leaf-specific hydraulic conductivity and D_v. Pit density was positively correlated with g_s, C_i and D_v, but negatively with intrinsic leaf water-use efficiency. Pit and pit aperture shape were not significantly correlated with any of the physiological traits. These findings indicate a significant role of pit characteristics in xylem water transport, carbon assimilation and ecophysiological adaptation of *Ficus* species in tropical rain forests.

Abbreviations – C_i, intercellular; CO_2, concentration; D_{PAL}, diameter of the outer pit aperture along the longer axis; D_{PAS}, diameter of the outer pit aperture along the shorter axis; D_{PITL}, diameter of the outer pit membrane measured along the longer axis; D_{PITS}, diameter of the outer pit membrane measured along the shorter axis; D_v, petiole vessel lumen diameters; F_{AP}, proportion of pit aperture area per pit membrane area; F_{AV}, proportion of pit aperture area per vessel area; F_{PV}, proportion of pit membrane area per vessel area; g_s, stomatal conductance; N_P, pit density; R_{PA}, ratio of the longer axis of outer pit aperture to the shorter axis (pit aperture shape); R_{PIT}, ratio of the longer axis of outer pit membrane to the shorter axis (pit membraneshape); SEM, scanning electron microscope; S_{PIT}, intervessel pit surface area; S_{PA}, pit aperture surface area; WUE, water-use efficiency.

Introduction

Xylem water transport from the root to the canopy against the force of gravity occurs under negative tension, which renders the xylem elements susceptible to cavitation and embolism due to gassing out of the air dissolved in the transpiration stream (Dixon and Joly 1895, Tyree and Zimmermann 2002). Xylem cavitation and embolism are thought to be the major constraint on plant growth and survival in water-limited environments (Rood et al. 2000, Davis et al. 2002, McDowell et al. 2008, Brodribb and Cochard 2009, Brodribb et al. 2010, Lens et al. 2013). It has long been recognized that intervessel pits, in particular pit membranes, play a crucial role in limiting the spread of air bubbles and pathogens while allowing the movement of water and nutrients from one conduit to an adjacent conduit and thus maintaining the integrity of the water-transport system in plants (Zimmermann and Brown 1971, Crombie et al. 1985, Tyree and Sperry 1989, Holbrook and Zwieniecki 1999, Tyree and Zimmermann 2002, Choat et al. 2008, Li et al. 2016). Maintenance of active water transport is crucial for plant photosynthetic performance and there is ample evidence demonstrating strong positive correlations between leaf (Aasamaa et al. 2002, 2005, Brodribb et al. 2007) and stem (Brodribb and Feild 2000) hydraulic conductance and leaf photosynthetic capacity.

Yet, depending on pit membrane ultrastructure and density, pit membranes can be responsible for 50% or more of the total hydraulic resistance in the xylem (Pittermann et al. 2005, Sperry et al. 2005, Wheeler et al. 2005, Choat et al. 2006, Hacke et al. 2006), leading to xylem safety vs hydraulic efficiency trade-offs (Pittermann et al. 2005, 2010, Hacke et al. 2006, Choat et al. 2008, Jansen et al. 2009, Lens et al. 2011). In particular, the porosity of pit membranes is related to the vulnerability of xylem to water stress-induced embolism and refilling of embolized vessels from adjacent functioning conduits (Tyree and Sperry 1989, Holbrook and Zwieniecki 1999, Choat et al. 2003, 2008, Sperry and Hacke 2004). Thus, pit membrane thickness and porosity strongly influence the total hydraulic resistance of plants. Small intervessel pit surface area increases cavitation resistance of the water transport system (Orians et al. 2004, Choat et al. 2005, Wheeler et al. 2005, Ellmore et al. 2006, Hacke et al. 2006), while larger pit membrane area, larger aperture, higher aperture fraction (aperture area per pit membrane area) and/or lower pit density have been found to increase sapwood hydraulic conductivity in angiosperms (Lens et al. 2011, Jacobsen et al. 2016). Pit aperture shape is also correlated with embolism resistance, with more cavitation-resistant species exhibiting narrower and more elliptical pit apertures (Lens et al. 2011, Scholz et al. 2013). Furthermore, increasing wood density was strongly correlated with enhanced resistance to cavitation (Hacke et al. 2001, Lachenbruch and McCulloh 2014), which may reflect differences in vessel size and intervessel connectivity as well as correlated changes with pit characteristics and vessel length. Despite the importance of pit traits, there are few comprehensive studies, especially in the tropics, that have examined the relationships between pit anatomical characteristics, wood anatomy and leaf photosynthetic performance across species with different pit structure.

Comparative studies have revealed a wide range of intra- and interspecific variation in intervessel pit morphology and anatomy, including pit and pit aperture size, shape, density and ratio of total pit aperture area to vessel wall area, which reflect differences in environmental adaptation and ecological distribution as driven by plastic and genetic components of variability (Orians et al. 2004, Ellmore et al. 2006, Schmitz et al. 2007, Lens et al. 2011, Jacobsen et al. 2016, Zhang et al. 2017). For example, polyploid birch species (*Betula*) typically have more but smaller pits, indicating greater ability to withstand harsh climate conditions relative to their diploid counterparts (Zhang et al. 2017). Compared with non-burned plants, chaparral shrubs resprouting after fire exhibited significantly lower pit density but no changes in pit membrane area, leading to a decrease in pit membrane surface area per conduit contact area, and resulting in resprouting plants being more vulnerable to water stress (Jacobsen et al. 2016). Additionally, mangrove species growing at different salinity levels have been shown to differ slightly in intervessel pit characteristics, suggesting that ecological adaptability in response to soil water salinity is also linked to pit anatomy (Schmitz et al. 2007).

Although significant variation in pit characteristics has been demonstrated across species and across environmental gradients, no attention has been paid to the variation in pit characteristics between different growth forms, e.g. hemiepiphytic and non-hemiepiphytic species, which, due to different positions in the community and life history strategies, might also differ in water use characteristics. Here, we studied pit characteristics among hemiepiphytic and non-hemiepiphytic *Ficus* species. The genus *Ficus*, the largest genus of the family Moraceae, contains more than 800 species and is one of the most important components of lowland tropical rainforests worldwide (Berg and Corner 2005, Harrison 2005). Within *Ficus*, there are about 500 species exhibiting a hemiepiphytic habit, i.e.

growing as epiphytes until the roots reach the soil (Berg and Corner 2005). Water availability is thought to be the major factor limiting growth and development for hemiepiphytic *Ficus* species due to the limited rooting volume and substrate during their epiphytic growth stage. Previous studies on hemiepiphytic and non-hemiepiphytic *Ficus* species have focused on leaf and stem anatomical and functional traits such as hydraulic conductivity and photosynthesis, which are strongly related to the evolutionary and ecophysiological adaptation to shade or drought stress (Holbrook and Putz 1996a, b, Hao et al. 2010, 2011a, 2011b, 2013). Indeed, previous studies have demonstrated that hemiepiphytes, compared with non-hemiepiphytes, exhibit drought-tolerant traits such as substantially smaller leaf size, higher leaf mass per area and smaller xylem vessel lumen diameters (Hao et al. 2011a, 2013), stronger stomatal control, lower rates of epidermal water loss and lower stem hydraulic conductivity (Patiño et al. 1995, Holbrook and Putz 1996a, b, Hao et al. 2011a). Apart from differences in stem hydraulic conductance, hemiepiphytes had significantly lower leaf hydraulic conductivity but greater water use efficiency than non-hemiepiphytes, further suggesting that hemiepiphytes were more drought tolerant (Hao et al. 2011a, b, 2013). Given the differences in morphological and physiological traits between these two contrasting growth forms occupying different ecological niches, divergence in structural adaptations at the pit level was hypothesized. We predicted functional differentiation of pit traits between hemiepiphytic and non-hemiepiphytic species.

In the present study, we examined intervessel pit characteristics and their correlation with hydraulic safety, as indicated by wood density and efficiency in five hemiepiphytic and five non-hemiepiphytic *Ficus* species. We studied *Ficus* growing in a common garden to determine trait differences arising from species and growth form rather than due to plastic variation across natural habitats (Patiño et al. 1995, Monson 1996, Hao et al. 2011a, Niinemets 2015). The aim of this study is to evaluate functional implications of changes in pit characteristics for water relations and photosynthetic traits among hemiepiphytic and non-hemiepiphytic *Ficus* species. By combining anatomical, hydraulic and photosynthetic measurements with scanning electron microscopy imaging of pits, we addressed three questions: (1) how do hemiepiphytic and non-hemiepiphytic *Ficus* species differ in fine-scale intervessel pit characteristics? (2) Are differences aligned with ecological strategies, adaptation and distribution of these two growth forms? (3) How are pit characteristics correlated with other anatomical and functional traits, such as hydraulic conductivity, photosynthetic characteristics and wood density across *Ficus* species and life forms?

Materials and methods

Study site and plant material

Six to eight mature individuals of each of the five hemiepiphytic (*Ficus altissima, Ficus benjamina, Ficus concinna, Ficus curtipes* and *Ficus virens*) and of the five non-hemiepiphytic (*Ficus callosa, Ficus esquiroliana, Ficus fistulosa, Ficus hispida* and *Ficus semicordata*) species were selected for this study. The plants were growing at the Xishuangbanna Tropical Botanical Garden (XTBG) of the Chinese Academy of Sciences in southern Yunnan, China (21°41′N, 101°25′E, and elevation 570 m). This region is at the northern margin of the Asian tropics, with a mean annual temperature of 21.7°C and a mean annual precipitation of 1560 mm, of which about 85% occurs during the wet season from May to October. However, there is heavy fog from midnight to noon almost every day in the first 4 months of the dry season, maintaining high soil moisture.

Mature trees selected for the study were growing in relatively open habitats and homogeneous soil. Mature, high light exposed branches and leaves from the outer canopy were selected for this study. Branch samples for pit characteristics measurement were collected during the wet season of 2012. The data from Hao et al. (2011a, b, 2013) were measured during the wet season of 2008. For all the measurements, branch samples were from different tree individuals growing in the common garden.

Estimation of pit characteristics by scanning electron microscopy

After cutting, branch samples were placed in 70% ethanol and transported to the lab at the University of Technology Dresden, Germany, where they were kept in 90% ethanol at room temperature of ~25°C. The samples were re-cut to remove both ends and dehydrated in an ascending series of ethanol solutions, and then critical-point-dried in carbon dioxide in a critical-point-dryer (Model CPD 030, BAL-TEC AG). Samples were then fixed to aluminum sample holders (Plano GmbH) using a carbon adhesive tape (Leit-Tabs; Plano GmbH), sputter-coated with a 20-nm-thick gold layer under an argon atmosphere using the sputter-coater Emitech K550 (Emitech Ltd.), and viewed and imaged using a LEO 420 scanning electron microscope (SEM, Leo Electron Microscopy Ltd.) at an acceleration voltage of 5 kV. Image analysis software (IMAGE J, National

Institutes of Health) was used to determine the following pit characteristics: pit aperture surface area (S_{PA}), intervessel pit surface area or intervessel pit membrane area (S_{PIT}), proportion of pit aperture area per pit membrane area (F_{AP}), proportion of pit aperture area per vessel area (F_{AV}), proportion of pit membrane area per vessel area (F_{PV}), diameter of the outer pit aperture along the longer axis (D_{PAL}), diameter of the outer pit aperture along the shorter axis (D_{PAS}), ratio of the longer axis of outer pit aperture to the shorter axis (pit aperture shape, R_{PA}), diameter of the outer pit membrane measured along the longer axis (D_{PITL}), diameter of the outer pit membrane measured along the shorter axis (D_{PITS}), ratio of the longer axis of outer pit membrane to the shorter axis (pit membrane shape, R_{PIT}) and pit density (N_P) (Table 1).

Data on wood density, petiole vessel lumen diameters, gas exchange and hydraulic conductivity

The data on wood density, petiole vessel lumen diameters, gas exchange and hydraulic conductivity measured in the same experiment have been published in Hao et al. (2011a,b, 2013) and are compiled in Table S1, Supporting Information.

Statistical analysis

The differences in pit structural characteristics among the two growth forms were tested with one-way ANOVA followed by the Tukey's post hoc test using SPSS 16.0 (SPSS). We analyzed the relationships between pit traits and wood density, xylem hydraulic conductivity, petiole characteristics, and leaf gas exchange traits using linear or nonlinear regressions depending on which functional form best approximated the data. All statistical tests were considered significant at $P < 0.05$.

Results

Variation in structure and morphology of intervessel pits in hemiepiphytic and non-hemiepiphytic Ficus

SEM pictures were used to examine intervessel pits in hemiepiphytic (Fig. 1A–C) and non-hemiepiphytic *Ficus* (Fig. 1D–F). Pit apertures were generally oval to elliptical in shape, sealed with a pit membrane (Fig. 1). Hemiepiphytic *Ficus* species had significantly greater pit aperture surface area (S_{PA}), intervessel pit surface area (S_{PIT}), diameter of the outer pit aperture as measured along both the longest and shortest axis (D_{PAL} and D_{PAS}, respectively) and diameter of the outer pit membrane

Table 1. Pit characteristics of five hemiepiphytic (H) and five non-hemiepiphytic (NH) *Ficus* species measured from SEM micrographs. S_{PA}, pit aperture surface area; S_{PIT}, intervessel pit surface area or intervessel pit membrane area; F_{AP}, proportion of pit aperture area per pit membrane area; F_{AV}, proportion of pit aperture area per vessel area; F_{PV}, proportion of pit membrane area per vessel area; D_{PAL}, diameter of the outer pit aperture along the longer axis; D_{PAS}, diameter of the outer pit aperture along the shorter axis; R_{PA}, pit aperture shape, ratio of the longer axis of outer pit aperture to the shorter axis; D_{PITL}, diameter of the outer pit membrane measured along the longer axis; D_{PITS}, diameter of the outer pit membrane measured along the shorter axis; R_{PIT}, pit membrane shape, ratio of the longer axis of outer pit membrane to the shorter axis; N_P, pit density; Data are mean ± SE (n = 6). Statistical differences between H and NH growth forms are denoted $^{**}P < 0.01$; $^{*}P < 0.05$, ^{NS} indicates non-significant differences ($P > 0.05$; one-way ANOVA).

Growth form	Species	$S_{PA}{}^{*}$ (μm^2)	$S_{PIT}{}^{**}$ (μm^2)	$F_{AP}{}^{NS}$ (%)	$F_{AV}{}^{NS}$ (%)	$F_{PV}{}^{NS}$ (%)	$D_{PAL}{}^{**}$ (μm)	$D_{PAS}{}^{*}$ (μm)	$R_{PA}{}^{NS}$	$D_{PITL}{}^{**}$ (μm)	$D_{PITS}{}^{NS}$ (μm)	$R_{PIT}{}^{NS}$	$N_P{}^{*}$ (no. μm^{-2})
H	*Ficus altissima*	6.37 ± 0.38	41.1 ± 2.1	15.77 ± 0.95	12.93 ± 0.39	85.5 ± 1.7	4.03 ± 0.17	1.91 ± 0.05	2.12 ± 0.08	7.89 ± 0.23	6.23 ± 0.23	1.28 ± 0.06	0.020 ± 0.0014
H	*Ficus benjamina*	7.44 ± 0.29	50.3 ± 0.1	14.65 ± 0.60	11.20 ± 0.36	75.0 ± 3.6	4.96 ± 0.2	1.75 ± 0.06	2.94 ± 0.19	8.48 ± 0.13	6.98 ± 0.13	1.25 ± 0.03	0.015 ± 0.0007
H	*Ficus concinna*	3.12 ± 0.27	28.7 ± 3.0	11.23 ± 1.23	8.78 ± 0.54	80.6 ± 4.9	2.62 ± 0.13	1.40 ± 0.08	1.92 ± 0.20	6.05 ± 0.26	4.78 ± 0.22	1.27 ± 0.06	0.028 ± 0.0017
H	*Ficus curtipes*	3.32 ± 0.12	45.1 ± 0.8	7.38 ± 0.27	5.17 ± 0.22	68.0 ± 2.4	2.56 ± 0.07	1.60 ± 0.04	1.61 ± 0.06	8.13 ± 0.16	7.03 ± 0.10	1.17 ± 0.03	0.015 ± 0.0007
H	*Ficus virens*	5.47 ± 0.6	29.8 ± 3.2	18.43 ± 1.11	11.53 ± 0.18	62.8 ± 1.0	4.46 ± 0.52	1.92 ± 0.13	2.34 ± 0.23	7.23 ± 0.63	4.96 ± 0.38	1.72 ± 0.33	0.021 ± 0.0003
	H mean	5.15 ± 0.8	39.0 ± 4.3	13.49 ± 1.92	9.92 ± 1.36	74.4 ± 4.1	3.73 ± 0.49	1.72 ± 0.10	2.19 ± 0.22	7.55 ± 0.43	6.00 ± 0.48	1.34 ± 0.10	0.020 ± 0.0024
NH	*Ficus callosa*	2.02 ± 0.19	17.7 ± 1.4	11.56 ± 0.25	7.04 ± 0.25	61.5 ± 2.7	2.92 ± 2.20	0.83 ± 0.03	3.55 ± 0.24	5.42 ± 0.13	3.81 ± 0.53	1.54 ± 0.29	0.035 ± 0.0004
NH	*Ficus esquiroliana*	1.97 ± 0.07	27.2 ± 0.8	7.36 ± 0.31	6.49 ± 0.14	88.8 ± 4.0	2.37 ± 0.05	1.12 ± 0.03	2.14 ± 0.05	6.37 ± 0.12	5.20 ± 0.07	1.23 ± 0.02	0.033 ± 0.0004
NH	*Ficus fistulosa*	1.88 ± 0.08	21.1 ± 0.8	9.06 ± 0.53	7.28 ± 0.34	83.0 ± 3.1	2.16 ± 0.06	1.04 ± 0.03	2.09 ± 0.07	5.49 ± 0.11	4.83 ± 0.13	1.14 ± 0.03	0.039 ± 0.0016
NH	*Ficus hispida*	2.04 ± 0.16	17.6 ± 0.5	11.33 ± 0.59	11.41 ± 1.21	88.3 ± 5.1	2.72 ± 0.11	0.87 ± 0.05	3.34 ± 0.24	5.32 ± 0.15	4.12 ± 0.07	1.30 ± 0.04	0.047 ± 0.0026
NH	*Ficus semicordata*	2.08 ± 0.12	32.4 ± 1.5	8.21 ± 2.01	4.96 ± 0.34	81.9 ± 2.7	2.09 ± 0.07	1.24 ± 0.04	1.71 ± 0.05	6.96 ± 0.19	5.89 ± 0.12	1.21 ± 0.03	0.027 ± 0.0012
	NH mean	2.00 ± 0.03	23.2 ± 2.99	9.51 ± 0.84	7.44 ± 1.07	80.7 ± 5.0	2.45 ± 0.16	1.02 ± 0.08	2.57 ± 0.37	5.91 ± 0.32	4.77 ± 0.37	1.28 ± 0.07	0.036 ± 0.0034

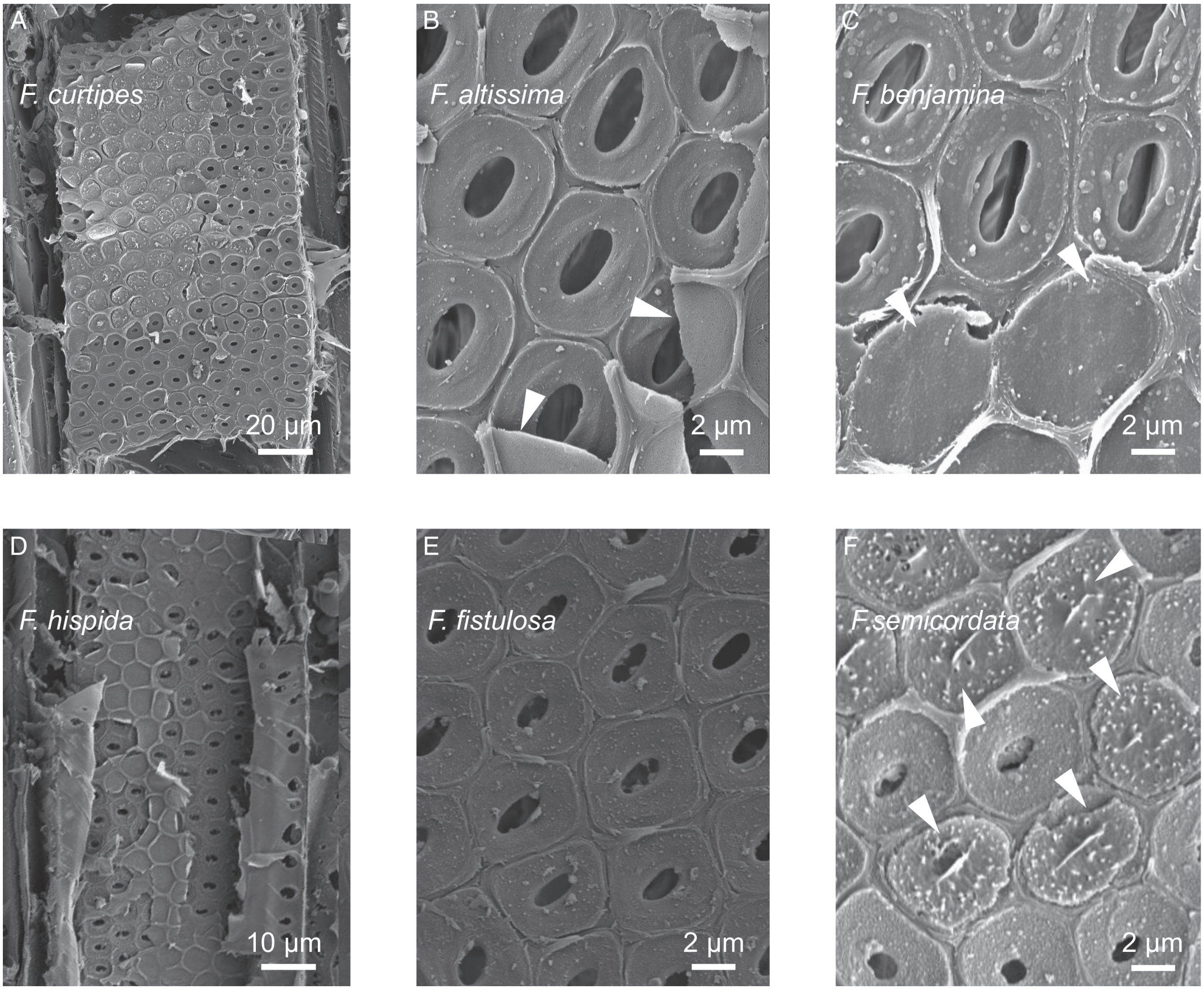

Fig. 1. Scanning electron micrographs of intervessel pits of hemiepiphyte (A, *Ficus curtipes*; B, *Ficus altissima*; C, *Ficus benjamina*) and non-hemiepiphyte species of *Ficus* (D, *Ficus hispida*; E, *Ficus fistulosa*; F, *Ficus semicordata*) in surface view. Vessel elements of *F. curtipes* (A) and *F. hispida* (D) showing alternate intervessel pitting and a simple perforation plate. Arrowheads indicate pits with pit membranes.

as measured along both axes (D_{PITL} and D_{PITS}, respectively), but substantially lower pit membrane density (N_{P}) than their congeneric non-hemiepiphytic species (Table 1). The proportion of pit aperture area per pit membrane area (F_{AP}), proportion of pit aperture and pit membrane area per vessel area (F_{AV} and F_{PV}, respectively) and pit aperture and membrane shape (R_{PA} and R_{PIT} ratio, respectively) did not differ between the growth forms (Table 1).

The magnitude of variation was generally larger for pit aperture characteristics in hemiepiphytic than in non-hemiepiphytic *Ficus* species (Table 1). S_{PA} varied about 2.4-fold in hemiepiphytic species (from $3.12 \pm 0.27\,\mu\mathrm{m}^2$ in *F. concinna* to $7.44 \pm 0.29\,\mu\mathrm{m}^2$ in *F. benjamina*), while 1.1-fold in non-hemiepiphytic *Ficus* species (from $1.88 \pm 0.08\,\mu\mathrm{m}^2$ in *F. fistulosa* to $2.08 \pm 0.12\,\mu\mathrm{m}^2$ in *F. semicordata*). F_{AP} varied 2.5-fold in hemiepiphytic species (from $7.38 \pm 0.27\%$ in *F. curtipes* to $18.4 \pm 1.1\%$ in *F. virens*) and 1.6-fold in non-hemiepiphytic species (from $7.36 \pm 0.31\%$ in *F. esquiroliana* to $11.56 \pm 0.25\%$ in *F. callosa*). D_{PAL} varied 1.9- and 1.4-fold, respectively. However, there were no differences in the variability in S_{PIT} (1.7- vs 1.8-fold), F_{AV} (2.5- vs 2.3-fold), F_{PV} (1.4- vs 1.4-fold), D_{PAS} (1.4- vs 1.5-fold), R_{PA} (1.8- vs 2.1-fold), D_{PITL} (1.4- vs 1.3-fold), D_{PITS} (1.4- vs 1.6-fold), R_{PIT} (1.5- vs 1.4-fold) and N_{P} (1.9- vs 1.7-fold) between hemiepiphytic and non-hemiepiphytic *Ficus* species. S_{PA}, S_{PIT}, D_{PAL}, D_{PITL}, D_{PAS} and D_{PITS} were negatively related with N_{P} (Fig. 2). However, stronger relationships between N_{p} and pit dimensions than between N_{P} and pit aperture traits were found (Fig. 2).

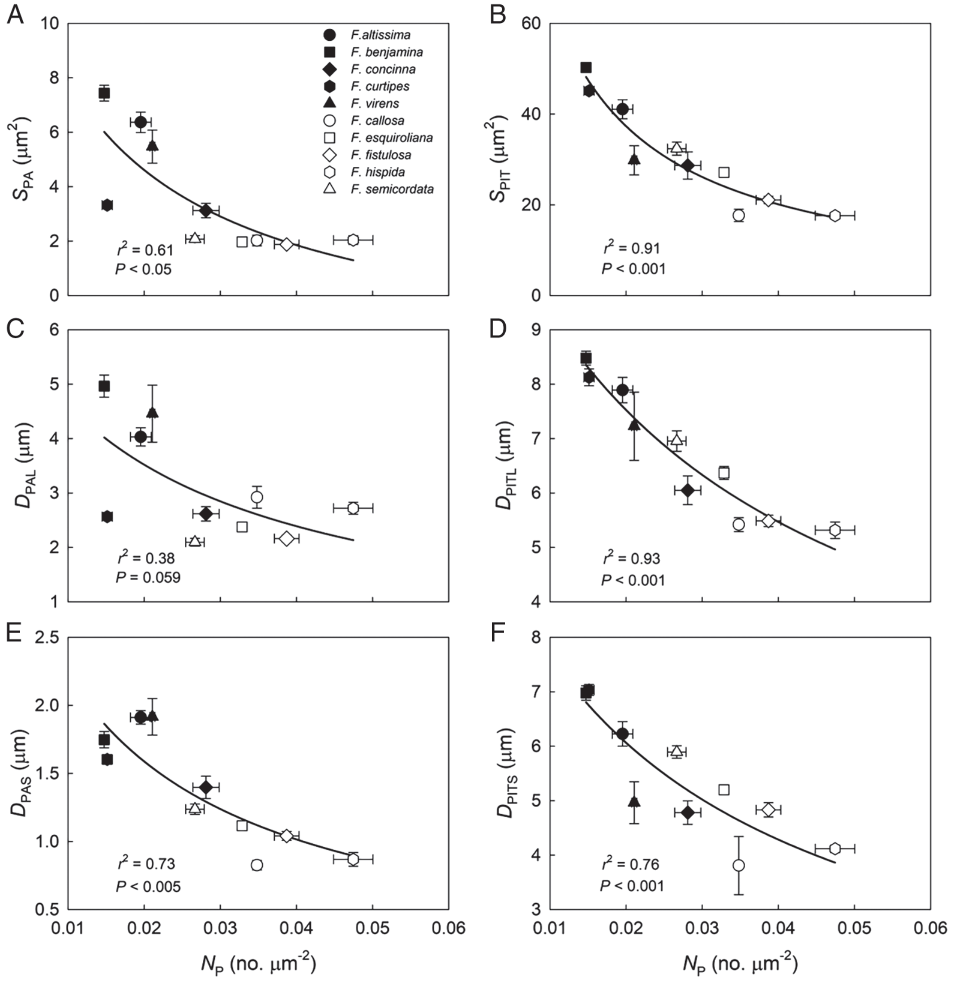

Fig. 2. Pit aperture and inter-vessel pit surface area (S_{PA} and S_{PIT}, respectively), diameter of the outer pit aperture and pit membrane measured along the longer and shorter axes (D_{PAL}, D_{PITL}, D_{PAS}, D_{PITS}) in relation to pit density (N_p) in the studied *Ficus* species. Data were fitted by a hyperbolic regression. Error bars indicate ± SE (n=6). Hemiepiphytic and non-hemiepiphytic species are distinguished by solid and open symbols, respectively; each species has a different symbol as defined in (A).

Correlations between pit characteristics and hydraulic conductivity

Hemiepiphytic *Ficus* species showed significantly lower mean sapwood-specific hydraulic conductivity (K_s) and leaf area-specific hydraulic conductivity (K_l) compared with non-hemiepiphytic *Ficus* species (Table S1). Briefly, K_s varied about 2.1- and 2.5-fold in hemiepiphytic and non-hemiepiphytic *Ficus* species, respectively. K_l varied 3.2-fold in hemiepiphytic species (from $1.11 \pm 0.30 \times 10^{-4}$ kg m^{-1} s^{-1} MPa^{-1} in *F. concinna* to $3.52 \pm 0.97 \times 10^{-4}$ kg m^{-1} s^{-1} MPa^{-1} in *F. altissima*) and 1.7-fold in non-hemiepiphytic species (from $5.78 \pm 1.13 \times 10^{-4}$ kg m^{-1} s^{-1} MPa^{-1} in *F. hispida* to $9.85 \pm 2.01 \times 10^{-4}$ kg m^{-1} s^{-1} MPa^{-1} in *F. semicordata*). Across species, K_s was negatively correlated with S_{PA}, S_{PIT}, D_{PAL}, D_{PAS}, D_{PITL} and D_{PITS} (Fig. 3; in Fig. 3B-F, *F. semicordata* was not included in these correlations because it had much greater K_s than other species), although the correlation between K_s and D_{PAL} was only marginally significant (Fig. 3C). K_l was only negatively correlated with S_{PIT} (excluding the outlier *F. semicordata*; Fig. S1).

Relationships between pit and photosynthetic characteristics

Hemiepiphytic *Ficus* species had significantly lower mass-based net assimilation rate (A_m), stomatal conductance to water vapor per unit leaf area (g_s) and intercellular CO_2 concentration (C_i) than non-hemiepiphytic *Ficus* species, but greater leaf intrinsic water-use efficiency (WUE$_i$; Table S1). However, net CO_2 assimilation rate per unit leaf area (A_a) was not statistically different between the two functional groups (Table S1). There were no significant differences in variability in A_a (1.5- vs 1.1-fold), A_m (1.6- vs 1.8-fold), g_s (1.34- vs 1.26-fold), C_i (1.03- vs 1.04-fold) and WUE$_i$ (1.1- vs 1.3-fold) between hemiepiphytic and non-hemiepiphytic *Ficus* species.

A_a was negatively correlated only with F_{AP} (data not shown). A_m was negatively correlated with S_{PA},

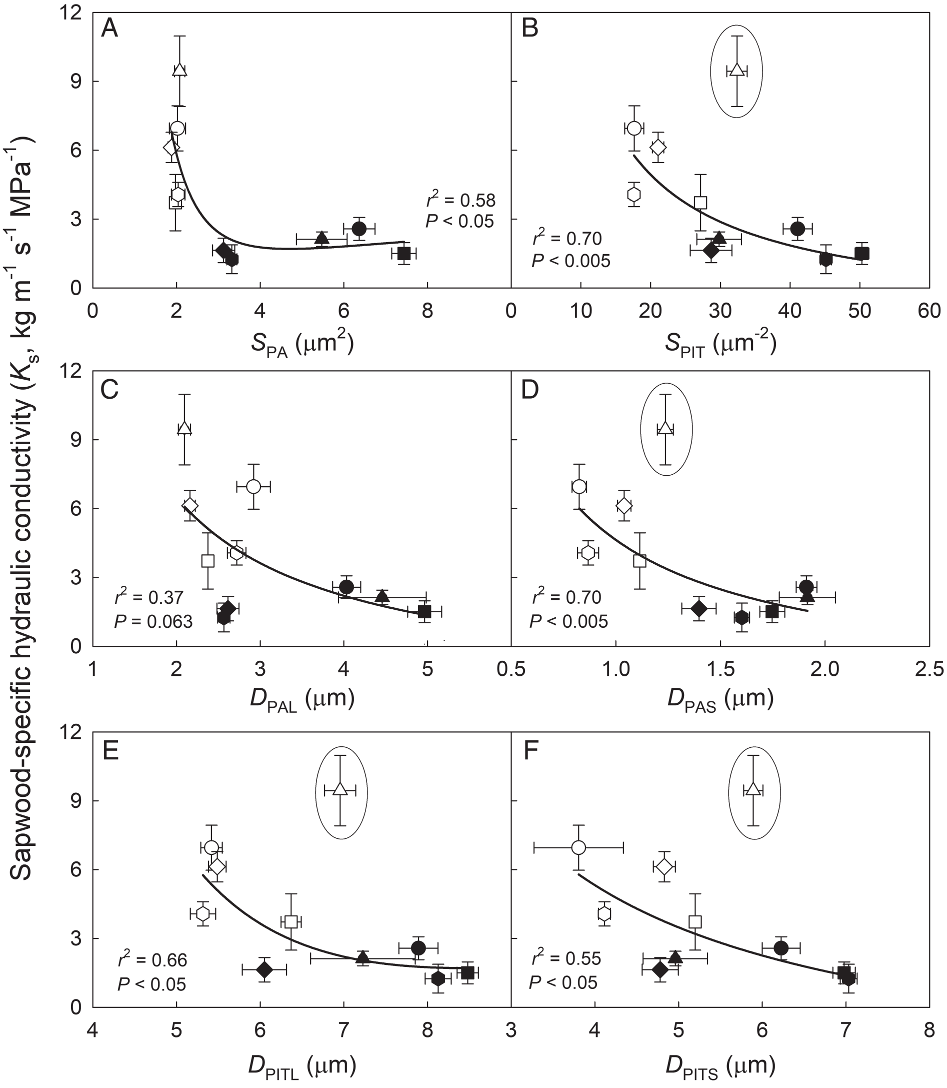

Fig. 3. Sapwood-specific hydraulic conductivity (K_s) in relation to pit aperture surface area (S_{PA}; A), intervessel pit surface area (S_{PIT}; B), diameter of the outer pit aperture measured along the longer axis (D_{PAL}; C), diameter of the outer pit aperture measured along the shorter axis (D_{PAS}; D), diameter of the outer pit membrane measured along the longer axis (D_{PITL}; E) and diameter of the outer pit membrane measured along the shorter axis (D_{PITS}; F) in the studied *Ficus* species. Polynomial regressions were fitted to the data. The regressions in (B), (D), (E) and (F) do not include *Ficus semicordata* (the circled open triangles facing up). Error bars indicate ± SE (n = 6~8). Symbols are as defined in Fig. 2A.

F_{AP}, D_{PAL} and D_{PAS} (Fig. 4), although the correlation between A_m and D_{PAL} was only marginally significant (Fig. 4C). No other correlations were found between A_m and other pit traits across the species studied (data not shown). Stomatal conductance to water vapor, g_s, depended strongly on pit aperture characteristics (Fig. 5A–F). Importantly, g_s scaled negatively with S_{PA}, F_{AP}, F_{AV}, D_{PAL}, D_{PAS} (Fig. 5A–E), but positively with N_P (Fig. 5F). The negative correlation between g_s and F_{AV} was marginally significant (Fig. 5C). A negative linear relationship was found between C_i vs D_{PAS} (Fig. 6A), whereas pit density was positively correlated with C_i (Fig. 6B). The intrinsic water use efficiency (WUE$_i$) varied ca. 1.6-fold across species (Table S1). WUE$_i$ was negatively correlated with N_P (Fig. 6C).

Correlations between pit properties and wood anatomy

Although there were significant differences in wood density between the two growth forms (0.542 ± 0.006 g cm^{-3} for hemiepiphytic species vs 0.455 ± 0.024 g cm^{-3} for non-hemiepiphytic species; Table S1), the difference in variability within hemiepiphytic and non-hemiepiphytic *Ficus* species was minor (1.1- vs 1.3-fold; Table S1). Wood density scaled positively with S_{PA} and D_{PAS} (Fig. 7A,B). Stronger negative correlations between petiole vessel lumen diameters (D_v) and S_{PA} and between D_v and D_{PAS} were observed (Fig. S2A,C), and D_v also scaled negatively with S_{PIT} and positively with N_P, although the correlations were only marginally significant (Fig. S2B,D).

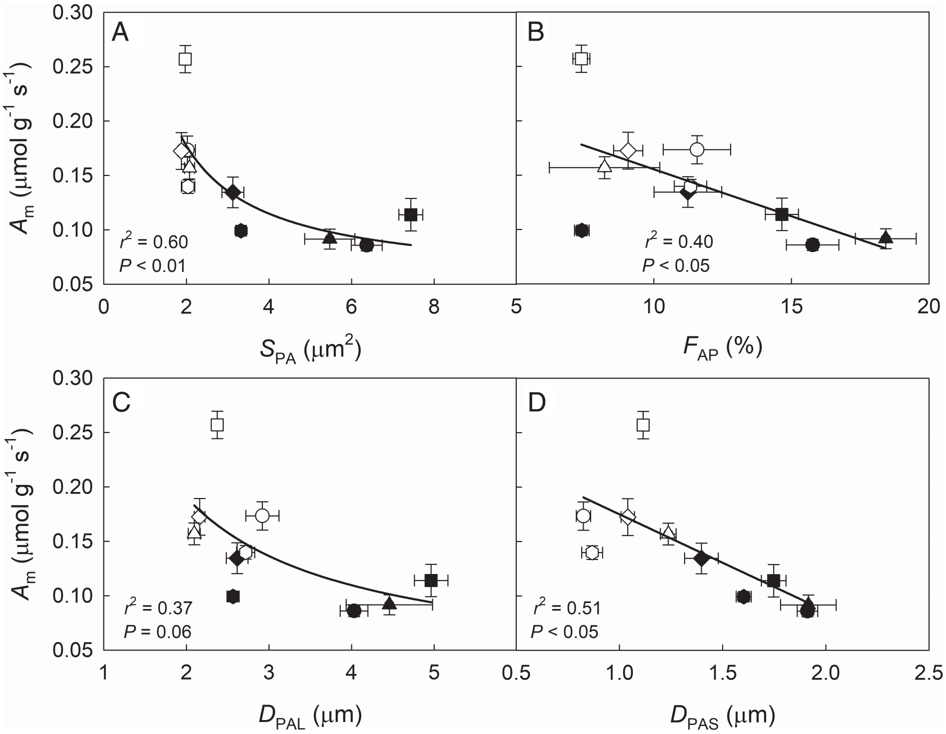

Fig. 4. Leaf mass based photosynthetic CO_2 assimilation rate (A_m) in relation to pit aperture surface area (S_{PA}; A), proportion of pit aperture area per pit membrane area (F_{AP}; B), diameter of the outer pit aperture measured along the longer axis (D_{PAL}; C) and diameter of the outer pit aperture measured along the shorter axis (D_{PAS}; D). Data were fitted by an inverse polynomial (A and C) and linear regression (B and D). Error bars indicate ± SE (n = 4~6). Symbols are as defined in Fig. 2A.

Discussion

Remarkable variation in intervessel pit characteristics across species

Knowledge of how plant growth forms respond to variations in environment is highly relevant for understanding the performance of plant communities. As for many tropical trees, there is a lack of data on quantitative pit characteristics even for widespread genera such as *Ficus*. As far as we know, this is the first study where pit characteristics have been quantitatively evaluated and compared between different growth forms of *Ficus*. There was wide variation in the pit characteristics of the 10 species examined, especially in pit and pit aperture sizes (Table 1, Fig. 1). This variation is consistent with previous studies that have observed significant inter- and intraspecific variation in the pit structure of angiosperms, suggesting that pit morphology could be an important factor influencing the trade-off between hydraulic safety and efficiency and thereby contribute to plant survival and distribution in different environments (Schmitz et al. 2007, Jansen et al. 2009, Lens et al. 2011, 2013, Jacobsen et al. 2016, Zhang et al. 2017, Pfautsch et al. 2018).

Large differences in pit characteristics found between hemiepiphytic and non-hemiepiphytic *Ficus* species within a common garden point to genetic differences across congeneric species native to different environments (Monson 1996). In general, trends in pit morphology with canopy height have been used to estimate the maximum height to which trees can grow. For example, pit aperture diameter decreased significantly with increasing height in Douglas fir (*Pseudotsuga menziesii*), suggesting a height growth limitation as a consequence of trade-offs between xylem water transport efficiency and water column safety (Domec et al. 2006, 2008). The variation in pit characteristics across different habitats can be used to elucidate ecophysiological adaptations. Structural differences in the pit micromorphology among species could be interpreted as alternative solutions to cope with environmental stresses such as salinity and drought conditions (Schmitz et al. 2007, Zhang et al. 2017). In our study, despite the relatively large variation within each growth form, hemiepiphytic species had xylem with significantly larger pit and pit aperture sizes and lower pit densities than non-hemiepiphytic species (Table 1). These findings support the hypothesis that intervessel pit morphology is a key factor in determining the adaptation to water supply in different life forms.

Relationship between pit characteristics and hydraulic conductance

Previous studies in *Acer* tree and shrub species have suggested that larger pit membrane areas and larger pit apertures allow for increased flow, contributing to increased sapwood hydraulic conductivity, but

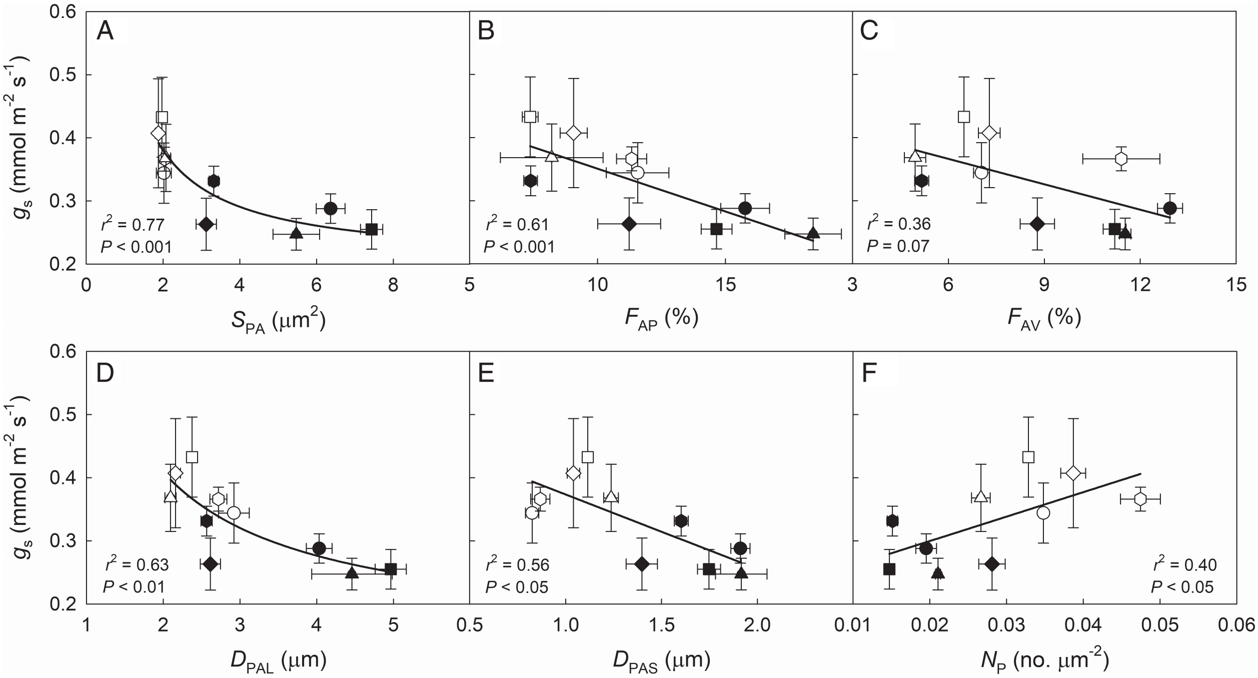

Fig. 5. Maximum stomatal conductance (g_s) in relation to pit aperture surface area (S_{PA}; A), proportion of pit aperture area per pit membrane area (F_{AP}; B), proportion of pit aperture area per vessel area (F_{AV}; C), diameter of the outer pit aperture measured along the longer axis (D_{PAL}; D), diameter of the outer pit aperture measured along the shorter axis (D_{PAS}; E) and pit density (N_P; F). Polynomial (A and D) or linear (B, C, E and F) regressions were fitted to the data. Error bars indicate ± SE (n = 4∼6). Symbols are as defined in Fig. 2A.

decreased resistance to air seeding (Lens et al. 2011, Jacobsen et al. 2016). In contrast, in our study, hemiepiphytic *Ficus* species that are facing drought conditions more frequently in their habitats had greater pits, and there were negative correlations between S_{PA} and K_s and between S_{PIT} and K_s (Fig. 3A, B). On the other hand, there was a trade-off between pit size and density (Fig. 2). Thus, across *Ficus* species, more drought tolerant species had fewer pits and thus, overall less water flow, while less drought tolerant species had smaller pit membrane and/or aperture area and higher pit density to facilitate water transport in the xylem (Fig. 3). Thus, there are numerous potential arrangements and alterations in xylem structures that can influence the coordination between hydraulic efficiency and safety among species of different growth forms. Although we found a correlation between S_{PA} and leaf-specific hydraulic conductivity (K_l) in only 9 of the 10 species included in this study (Fig. S1), we argue that such correlation is indicative of the important role of pits in the hydraulic supply to leaves.

Due to limited rooting volume in the epiphytic stage, juvenile hemiepiphytic *Ficus* species frequently experience water limitation. As an adaptation, hemiepiphytic species exhibited lower sapwood- and leaf-specific hydraulic conductivity than non-hemiepiphytic *Ficus* species (Patiño et al. 1995, Hao et al. 2011a). Non-hemiepiphytic *Ficus* tend to have greater vulnerability to drought-induced cavitation but higher water transport efficiency, resulting in greater rates of gas exchange (Santiago et al. 2004, Hao et al. 2011a). In addition, leaves represent a major bottleneck in the whole plant water flow pathway and are a key determinant of plant hydraulic responses and water relations (Sack et al. 2003, Sack and Holbrook 2006, Brodribb and Cochard 2009). Therefore, pit characters must influence the water transport significantly in the xylem of both branches and leaves.

Plants must maintain a delicate balance between maximizing water transport and limiting the risk of embolism and loss of hydraulic conductance. Although the properties of intervessel pits are very important in controlling hydraulic efficiency (Domec et al. 2006, Lens et al. 2011, Jacobsen et al. 2016), the apparent negative relationships between pit membrane and/or aperture size and sapwood- and leaf-specific hydraulic conductivity in the hemiepiphytic and non-hemiepiphytic *Ficus* species suggest that hydraulic conductivity of stems cannot simply be predicted from intervessel pit characteristics.

Apart from the effects of pit traits on maximum water flow rate, differences in pit aperture size, shape and

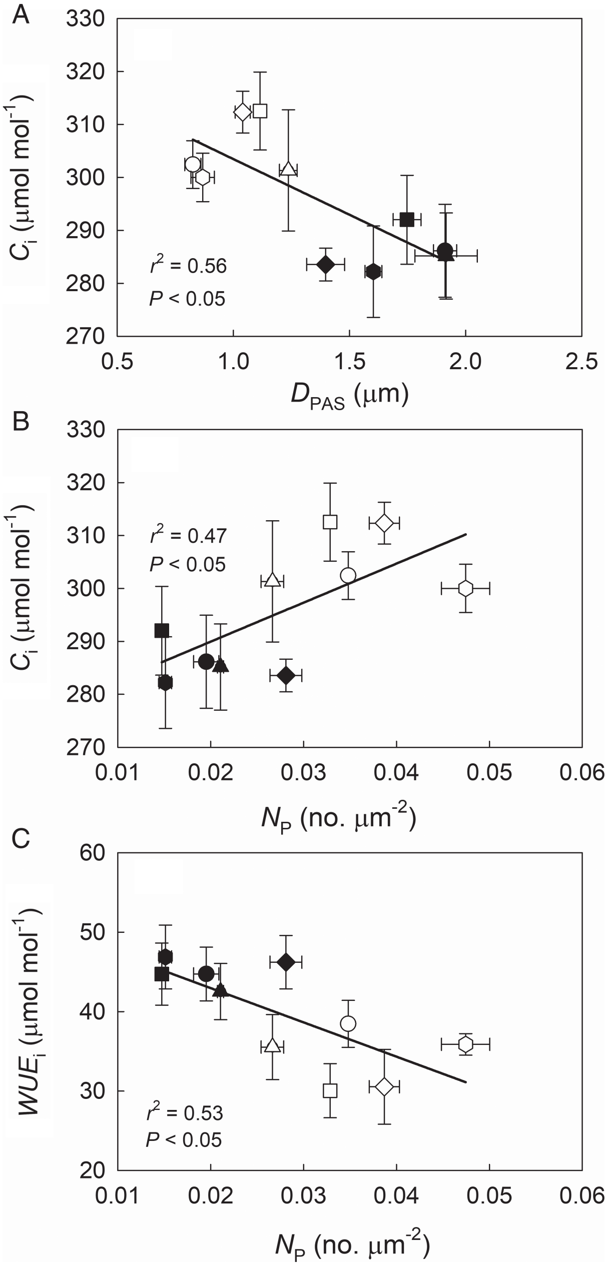

Fig. 6. Correlations of the intercellular CO_2 concentration (C_i) with (A) diameter of the outer pit aperture measured along the shorter axis (D_{PAS}) and (B) pit density (N_P) and the correlation between (C) intrinsic leaf water use efficiency (WUE_i) and pit density (N_P) in the studied *Ficus* species. Linear regressions were fitted to the data. Error bars indicate ± se (n = 4~6). Symbols are as defined in Fig. 2A.

density are associated with differences in water flow between vessels and unavoidably alter their ability to resist air seeding through inter-conduit pits and hence drought-induced xylem cavitation and embolism. This compromise between the ability to cope with drought and to grow rapidly under favorable water conditions might explain the contradictory correlation with respect to the strategy of drought-tolerant species from mesic and humid habitats. Overall, our data suggest that hydraulic efficiency is more crucial than hydraulic safety for hemiepiphytic species in adapting to water-limited conditions during their epiphytic early growth stage in the canopy, while hydraulic safety is more important for non-hemiepiphytic species in adapting to greater competition given higher water supply in their terrestrial early growth stage.

Correlations between pit and photosynthetic traits

The coordination between hydraulics and photosynthesis across distantly related species is well known (Brodribb and Feild 2000, Brodribb et al. 2002, 2007, Santiago et al. 2004, Franks 2006). However, the correlation between xylem anatomy and photosynthetic characteristics has not been evaluated experimentally. Hemiepiphytic *Ficus* species have lower CO_2 assimilation rates when expressed on per unit leaf biomass, lower stomatal conductance and lower intercellular CO_2 concentration, but greater water use efficiency, indicating that these species that tend to have greater drought tolerance have high rates of gas exchange when water is available (Table S1) (Hallik et al. 2009; Hao et al. 2011a). In fact, hemiepiphytic *Ficus* species tend to be more successful than non-hemiepiphytic *Ficus* species in terms of species richness and total biomass throughout humid tropical forests of the world. This is because hemiepiphytic *Ficus* species colonize the canopy of dense rain forests, a widespread microhabitat with high light availability, while the pioneers of non-hemiepiphytic *Ficus* species are dependent on canopy gaps for regeneration and directly compete with a large number of other rain forest tree species (Harrison et al. 2003, Harrison 2005, Harrison and Shanahan 2005).

The relationships between pit and photosynthetic characteristics showed similar trends as the correlations between pit structure and hydraulic conductivity, providing evidence for the positive coordination between hydraulics and photosynthesis across a variety of terrestrial habitats and suggesting the importance of stem xylem anatomy in enabling rapid carbon assimilation and water transpiration in leaves. As discussed above, more numerous but smaller intervessel pits are correlated with higher hydraulic conductivity and higher photosynthetic rates. In *Ficus* species, seedlings of more drought resistant hemiepiphytic species had lower conductivity, and despite lower photosynthetic rate and stomatal conductance, they had greater water use efficiency (Fig. 6C). These findings could parsimoniously explain the strategies of hemiepiphytic *Ficus* species adapted to

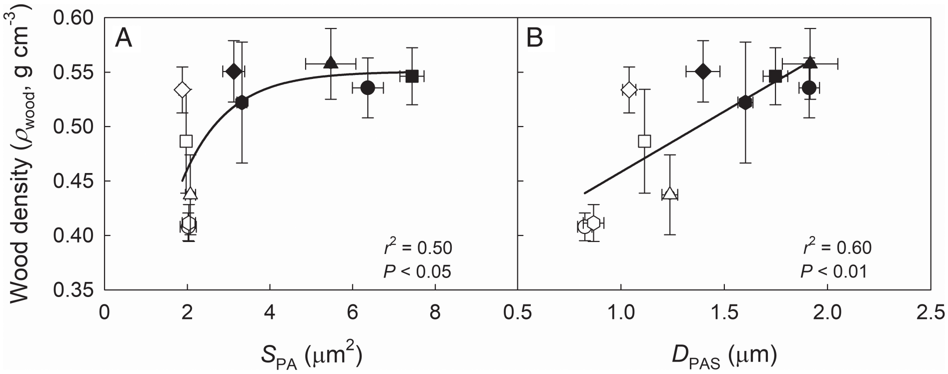

Fig. 7. Relationships between wood density (ρ_{wood}) and pit aperture surface area (S_{PA}; A), and between ρ_{wood} and diameter of the outer pit aperture measured along the shorter axis (D_{PAS}; B). Exponential (A) or linear (B) regressions were fitted to the data. Error bars indicate ± SE (n = 6~8). Symbols are as defined in Fig. 2A.

drought and non-hemiepiphytic *Ficus* species adapted to wet condition during early stages of growth. In particular, the strategy differences are strongly linked to differences in xylem structure and function, consequently leading to the trade-offs between carbon assimilation and water transport. However, this evidence suggests that xylem-mediated ecophysiological trade-offs between the two growth forms in *Ficus* are contrary to general expectations in trees or shrubs (Lens et al. 2011, Jacobsen et al. 2016, Zhang et al. 2017).

Wood and petiole characteristics strongly scale with pit aperture

Much is known about the influence of xylem properties such as the density and diameter of xylem conduits (Tyree et al. 1994, Wheeler et al. 2005), and wood density (Hacke et al. 2001, Roderick and Berry 2001, Barbour and Whitehead 2003, Chave et al. 2009) on xylem hydraulic conductivity. However, relatively little is known about the influence of variations in pit characteristics on stem and leaf anatomy. Our data provide a first empirical test of the importance of intervessel pits on wood density and vessel lumen diameter in leaf petioles (Figs 7 and S2). In general, species with low wood density have greater xylem hydraulic conductivity and thus growth rates, whereas greater wood density represents an increased cost of wood growth per volume (Roderick and Berry 2001, Barbour and Whitehead 2003, Chave et al. 2009, Zanne et al. 2010). Because pit aperture was negatively correlated with hydraulic conductivity in our study, the positive correlation between pit aperture and wood density suggests coordination of anatomy and function of xylem in plant water transport. Furthermore, drought-adapted species often have smaller vessels, resulting in lower hydraulic conductivity (Tyree et al. 1994, Martínez-Vilalta et al. 2002, Wheeler et al. 2005, Hao et al. 2011a). The negative relationship between pit aperture size and vessel lumen diameter (Fig. S2) also suggests that the trade-offs between hydraulic efficiency and safety are very important in allowing *Ficus* species to adapt to their growth conditions.

Physiological and ecological implications of variation in pit structure

The large variation in pit and physiological characteristics observed in this study are expected to have a significant effect on the ecological adaptation of hemiepiphytic and non-hemiepiphytic *Ficus*. Given that, on average, pit resistance is estimated to account for half of total xylem resistance (Pittermann et al. 2005, Sperry et al. 2005, Wheeler et al. 2005, Choat et al. 2006, Hacke et al. 2006), this variation could significantly influence hydraulic efficiency of the xylem and gas exchange of the leaf. Across a range of *Ficus* species, there were significant negative correlations between traits characterizing pit size and xylem hydraulic conductivity (Fig. 3). Previous studies have shown that species with larger intervessel pits with greater hydraulic conductivity, were more vulnerable to embolism (Orians et al. 2004, Choat et al. 2005, Wheeler et al. 2005, Ellmore et al. 2006, Hacke et al. 2006, Lens et al. 2011, Jacobsen et al. 2016). However, we found a negative relationship between pit size and K_s, which seemed to contradict previous studies. Species growth forms and environmental conditions may provide an explanation for this result. Hemiepiphytic *Ficus* species are adapted to drought conditions when young, whereas non-hemiepiphytic *Ficus* species are adapted for greater competition with higher water supply. In this situation, the changes of pit characteristics mediate the trade-offs between hydraulic efficiency and safety occurring with plant growth from juvenile to adult stages.

In light of the new evidence from the present study demonstrating large variation in pit characteristics and correlations with hydraulics across species, it seems that pit structure might play a negligible role in this trade-off. Notably, hemiepiphytic *Ficus* species preserve their epiphytic habit and structure even in the adult terrestrially rooted stage where plants at this stage have good water supply and undergo dramatic ontogenetic changes in structure and physiology during the transition from epiphyte to rooted phase (Holbrook and Putz 1996a,b). Therefore, we would expect that the variation in vulnerability to embolism between species with different pit size and density should be consistent with the strategies of plant adaptation. Such structural variation and functional correlations suggest that intervessel pits play an important role in adaptation to their environments in *Ficus*, consistent with substantial differences in ecological performance including xylem hydraulic conductivity, leaf water use and carbon economy (Hao et al. 2011a).

Conclusions

This study provides a comprehensive comparative analysis of pit anatomy and its functional implications on the relationship between hydraulics and photosynthesis within *Ficus*. This study conclusively demonstrates that there is remarkable variation in pit characteristics between hemiepiphytic and non-hemiepiphytic *Ficus* species, i.e. hemiepiphytic species have greater pit aperture and a greater pit aperture area to vessel wall area, but lower pit density compared to non-hemiepiphytic species. In addition, this study reveals strong correlations between pit characteristics and hydraulic conductivity, photosynthetic traits and wood density across both hemiepiphytic and non-hemiepiphytic *Ficus* species. Surprisingly, pit membrane and aperture area were negatively correlated with sapwood hydraulic conductivity, and pit aperture shape showed no coordination with either hydraulic conductivity or photosynthetic traits, which contradicts previous studies (Lens et al. 2011, Scholz et al. 2013, Jacobsen et al. 2016). Notably, photosynthetic characteristics showed similar correlations with pit variables. In other words, smaller pit membrane areas, smaller apertures and higher pit densities were correlated with increases in sapwood and leaf hydraulic conductivity and potentially increase net CO_2 assimilation rate and stomatal conductance. Furthermore, larger pit aperture can contribute to the increase in wood density, but decrease in vessel lumen diameter in leaf petioles.

We argue that these variations and correlations have important implications for the ecological success of different groups of *Ficus* and can explain the distribution and niche differentiation in this super-diverse genus in tropical rainforests. Overall, the present results indicate that pit characteristics and their relationships to other traits are notably different even among different growth forms within a single plant genus. Further work is needed to gain an insight into the role of pit characteristics including pit membrane porosity and thickness in xylem water transport, carbon assimilation and ecophysiological adaptation across other species coexisting with *Ficus* in tropical forests and into how these traits affect plant survival, distribution and evolution under climate change.

Author contributions

S.L. designed the study; S.L. and G.-Y.H. performed the measurements; S.L. performed the statistical analysis; S.L., G.-Y.H., Ü.N., P.C.H., S.W., F.L., Y.-J.Z. and K.-F.C. contributed to the interpretation of results; S.L. wrote the first version of the manuscript, which was reviewed and revised by all the authors.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Fig. S1. Leaf-specific hydraulic conductivity in relation to intervessel pit surface area in the studied *Ficus* species.

Fig. S2. Vessel lumen diameter of leaf petiole in relation to pit aperture surface area, intervessel pit surface area, diameter of the outer pit aperture measured along the shorter axis and pit density in the studied *Ficus* species.

Table S1. Hydraulic conductivity, photosynthesis and wood anatomical traits of five hemiepiphytic and five non-hemiepiphytic *Ficus* species.

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