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Size dependent associations between tree diameter growth rates and functional traits in an Asian tropical seasonal rainforest

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Abstract. Many studies focus on the relationships between plant functional traits and tree growth performances. However, little is known about the ontogenetic shifts of the relationships between functional traits and tree growth. This study examined associations between stem and leaf functional traits and growth rates and their ontogenetic shifts across 20 tropical tree species in a tropical seasonal rainforest in Xishuangbanna, south-west China. For each species, physiological active branches of individual trees belonged to three size classes (i.e. small, diameter at breast height (DBH) 5–10 cm; middle, DBH 10–20 cm; big, DBH >20 cm) were sampled respectively. We measured 18 morphological and structural traits, which characterised plant hydraulic properties or leaf economic spectrum. Associations between diameter growth rates and functional traits were analysed across three size classes. Our results revealed that diameter growth rates of big-sized trees were mainly related to traits related to plant hydraulic efficiency (i.e. theoretical hydraulic conductivity (K_{theo}) and leaf vein density (D_{vein})), which suggests that the growth of large trees is limited mainly by their xylem water transport capacity. For middle-sized trees, growth rates were significantly related to traits representing leaf economic spectrum (i.e. specific leaf area (SLA), individual leaf mass (ILM), palisade thickness (PT) and spongy thickness (SP)). Diameter growth rates of small-sized trees were not correlated with hydraulic or leaf economic traits. Thus, the associations between tree growth rates and functional traits are size dependent. Our results suggest ontogenetic shift of functional traits which could potential contribute to different growth response to climate change.

Keywords: functional trait, growth rate, hydraulic conductivity, leaf economic spectrum, palisade thickness, size dependent, specific leaf area, stomatal size, theoretical hydraulic conductivity, tree growth, tropical rainforest, vessel density.

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Introduction

Plant functional traits can directly reflect plants performance under environmental change, and thus may contribute to a better understanding of the influence of global change on the demographic rates and species composition (McGill *et al.* 2006; Mouillot *et al.* 2013). The leaf and wood economic spectrum (Wright *et al.* 2004; Chave *et al.* 2009) have been linked to their functional impacts on plant performance over larger phylogenetic and spatial scales (Poorter and Bongers 2006; Kattge *et al.* 2011). For example, higher specific leaf area (SLA), higher leaf nutrient concentration and lower wood density (WD) relate to higher ability of resource acquisition and resource use efficiency, and thus contribute to faster growth of tree species, whereas lower SLA and higher WD are associated with high survival but lower growth rate (Poorter and Bongers 2006; Rüger *et al.* 2012). Many studies have explored the linkages between plant growth performance and their morphological and physiological features (Wright *et al.* 2004; Poorter *et al.* 2008, 2017; Yang *et al.* 2020). However, previous studies often showed weak linkages between tree growth rates and those easily measured traits (i.e. WD, SLA) (Poorter *et al.* 2017; Yang *et al.* 2018).

Recent studies reported that the trait-demography relationships are size-dependent, which could be a result of the effects of developmental and environmental changes with increasing tree size (Iida *et al*. 2014*b*). From the understory to the canopy, there is an increase in irradiance, temperature, wind speed and atmospheric water stress (Niinemets and Valladares 2004). Thus, traits that can enhance light capture, photosynthetic carbon gain and shade tolerance (e.g. wider crowns and higher SLA) may increase growth rates for small or understory trees (Sterck *et al*. 2003; Iida *et al*. 2014*a*), whereas traits that increase species capacity to transport water (e.g. higher vein density and hydraulic conductivity) should enhance growth rates for large or canopy trees (Koch *et al*. 2004).

Few studies have shown how trait-growth relationships change with tree size from saplings to large trees. Iida *et al*. (2014*b*) reported that relationships between functional traits and demographic rates varied with tree size, possibly due to the effects of developmental and environmental changes with increasing tree size. In eight dry forests at south-eastern Brazil, traits that enhance light capture lead to higher growth and lower mortality rates for small sized trees, whereas traits that enhance drought tolerance lead to lower mortality rates of big sized trees (Jamir *et al*. 2016). As trees are exposed to a strong vertical gradient of abiotic conditions, size-dependent approach is needed when linking functional traits to tree growth performances (Wright *et al*. 2010). To date, size-dependent variations of functional traits and their contributions to trait-demography relationships are still largely unexplored.

We measured stem and leaf traits for 181 individuals of 20 tree species across three size classes (small, diameter at breast height (DBH) 5–10 cm; middle, DBH 10–20 cm; big, DBH >20 cm) in a tropical seasonal forest in Xishuangbanna, south-west China. We evaluated the associations between hydraulic traits, leaf economic traits and growth performance. We asked: (1) which functional traits (or their combinations) can predict tree growth rates in a tropical rainforest? And (2), are the associations between functional traits and growth rates size dependent?

Materials and methods

Study site and species

The study was conducted at a 1-ha permanent forest plot, located in Xishuangbanna Nature Reserve (21°55′39″N, 101°15′55″E, 750 m above sea level), Yunnan Province, south-west China. The region has a typical tropical monsoon climate with a distinct dry season from November to next April. The mean precipitation is 1492 mm, of which ~80% falls during the rainy season from May to October. Mean annual temperature is 21°C with a monthly mean temperature of 16°C during the coldest month (December) and 25.7°C during the warmest month (June).

An 1-ha permanent forest plot was established since 1994, with all free-standing woody trees (totally 730 trees belong to 152 species, 96 genera and 46 families) with a diameter at breast height (DBH) $\geq$ 5 cm were mapped, tagged, and identified. The maximum DBH is 150 cm, and maximum tree height is 45 m. The forest age is ~200 years (Cao *et al*. 1997). Since 1999, all trees with a DBH $\geq$ 2 cm were tagged. The DBH measurement was conducted annually from 1999 to 2010, and then changed to 5-year interval. In this study, we used data from the 2000–2015 censuses.

We selected 20 tree species belonging to 20 genera and 15 families, according to the degree of dominance, important values (important value = relative density (RD) + relative frequency (RF) + relative dominance (RA)), diameter and height ranges of species (see Table S1, available as Supplementary Material to this paper). In the 1-ha plot, the 20 studied species represented 22% of total tree numbers (DBH $\geq$ 2 cm), 36% of all-species important values and 45% of the total basal area, respectively. For each species, we sampled trees belong to three size classes, i.e. small size class with DBH range from 5 to 10 cm, middle size class with DBH range from 10 to 20 cm (middle size), and big size class with DBH >20 cm (Table S1). According to the distribution of stem diameter and height from all individuals in the 1-ha plot, small size class (DBH 5–10 cm) represent juvenile trees below 10 m height in the forest understory, middle size class (DBH 10–20 cm) represent trees with height below 15 m at the sublayer, big size class (DBH >20 cm) represent the canopy trees (see Fig. S1, available as Supplementary Material to this paper). We chose 3–5 healthy trees for each size class of each species and sampled a branch of 50 cm in length from the outer canopy of each tree. We totally sampled 181 individuals belong to three size classes of 20 tree species. Samples were collected during the rainy season (October) of 2016 when seasonal shoot growth and leaf expansion had been completed.

Functional trait measurements

We measured 18 stem and leaf traits across three size classes for each of the 20 studied tree species. For each sampled branch, we cut a segment of 3–5 cm in length for measuring stem relative water content (RWC_s) and sapwood density (WD). After removing the bark and pith with a blade, the fresh weight (FW) of sapwood was weighed with an electronic balance and sapwood fresh volume was measured by the water-replace method. Sapwood was then soaked in pure water for 24 h, and its saturated weight (SW) was determined. Wood samples were then oven-dried at 70°C to a constant weight for at least 48 h to determine the dry weight (DW). Sapwood relative water content (RWCs) was calculated as: RWCs = (FW – DW)/(SW – DW) × 100%. Sapwood density (WD, g cm^{-3}) was calculated by dividing the dry mass by the sapwood volume.

Wood anatomy

Another segment (~5 cm in length) from the same branch was cut and fixed in FAA (70% alcohol 95%, acetic acid 5% and formaldehyde 5%). Before sectioning, samples were embedded with paraffin. Transvers sections of ~8–10μm were made on a rotary microtome (DM2245, Leica). Cross-sections were stained with safranin, dehydrated and fixed with Canada balsam, and then imaged at 200× magnification with a digital camera mounted on a microscope (DM2500, Leica). Four pictures were taken at different locations of each section. We measured vessel diameters for their major and minor axes using ImageJ software (ver. 1.50, http://rsb.info.nih.gov/ij/, accessed 10 May 2018). Due to the elliptical shape of the vessel, the vessel diameter was calculated as $D = (32(ab)^3/(a^2 + b^2))^{1/4}$, where a and b are the major and the minor axis respectively. Hydraulic weighted vessel lumen diameter (D_h) is calculated as $D_h = \sum D^5/\sum D^4$. Vessel density (VD, no. mm^{-2}) was calculated as the number of vessels per unit sapwood area. We calculate theoretical hydraulic conductivity (K_{theo}) according to the Hagen-Poiseuille equation: $K_{theo} = \pi\rho/(128\eta A_s)(\sum D^4)$, where ρ is the water density (998.2 kg m^{-3} at 20°C) and η is the water viscosity (1.002×10^{-9} MPa s^{-1} at 20°C), where A_s is the sapwood area.

Leaf area, specific leaf area and relative water content

For each sampled branch, we selected 10 fully expanded sun-exposed leaves and measured their leaf area (LA) with an area meter (Li-3000A; Li-COR Biosciences). After measuring leaf fresh mass (FW), leaves were immersed into pure water and soaked for 24 h, and leaf saturation weight (SW) was determined. Leaves were oven-dried at 80°C for 48 h to determine dry mass (DW). Leaf relative water content (RWC_l) were calculated as (FW – DW)/(SW – DW) × 100%. Individual leaf mass (ILM) were determined as the ratio of total mass to leaf numbers. Specific leaf area (SLA, mm^2 g^{-1}) was calculated as leaf area per unit of dry mass.

Leaf anatomy

We selected additional five full-expanded leaves the same branch, and immersed in the FAA solution for 48 h. Leaf sections without major veins from the middle of leaves were cut and embedded them with paraffin. Transverse cross-sections with 8–12 μm thickness were made with a rotary microtome (DM2245, Leica) and mounted on glass slides. All cross-sections were stained with safranin solution. After dehydration (70–85–95–100% ethanol), the sections were fixed with Canada Balsam. Leaf cross-sections were examined with a light microscope (DM 2250, Leica) and photographed at 200× magnifications with a digital camera (DFC295, Leica). Total leaf thickness (LT, μm), palisade thickness (PT, μm), spongy thickness (ST, μm), lower epidermis thickness (LET, μm) were measured by using the ImageJ software (ver. 1.50, http://rsb.info.nih.gov/ij/, accessed 10 May 2018).

Leaf stomatal size (SS, μm) was represented as the guard cell length, and stomatal density (SD, no mm^{-2}) were calculated as the number per unit of area. Transparent leaves were prepared by boiling for 5–10 min and then immersed in a 1 : 1 solution of glacial acetic acid and hydrogen peroxide in a water bath at 70°C for 8–10 h. Then epidermis was separated from the mesophyll cells. The transparent leaves were stained with safranin and leaf veins were photographed under a microscope. Leaf vein density (D_{vein}, mm mm^{-2}) were calculated as the total length of veins per area.

Leaf mineral nutrient concentration

Oven-dried leaves were grounded to powder for nutrient analysis. Leaf mass-based nitrogen concentrations (N, mg g^{-1}) were measured using a C-N analyser (Elemental Analyser, Vario MAX CN). Leaf mass-based phosphorus (P, mg g^{-1}) and potassium (K, mg g^{-1}) concentrations were measured using atomic-emission spectrometer (IRIS Advantage-ER, Thermo Fisher Scientific).

Tree diameter growth rate

By using the community survey data, we calculated the relative density (RA), relative frequency (RF), and relative dominance (RD) of each selected tree species (Table S1). For 20 species, based on the census data in the year of 2000, 2374 individuals belong to 154 genera and 55 families with DBH ≥ 2 cm were recorded in the 1-ha plot of tropical seasonal rainforest. We totally sampled 181 healthy trees belong to three size classes (DBH 5–10 cm, 10–20 cm, >20 cm) of the 20 tree species. For each tree, the DBH at consecutive censuses was regressed against the corresponding measurement date by using linear function. The corresponding slope was used to obtain an annual diameter growth rate (GR, mm $year^{-1}$). Trees included in this analysis had 12 DBH measurements. Trees with negative or anomalous growth which were assumed to be caused by measurement error were excluded from the analyses.

Statistical analyses

We calculated the median, 5th and 95th percentile and coefficient of variation of all 18 measured traits. We did an ANOVA analysis to evaluate trait variation among species and among individuals of the same species and the variance of measurement error. We calculated arithmetical means of growth and trait data for each species. Original growth rate and trait data were log-transformed to fit the normality of distributions (Kerkhoff and Enquist 2009). To evaluate associations among functional traits, we calculated Pearson's correlations for all pairwise combinations of traits. We performed principal components analysis (PCA) on the traits of individuals by using the FactoMineR package (Lê *et al*. 2008). We calculated the partial Pearson's correlation between growth rate and functional traits by holding the influence of tree size (DBH). Linear regressions were used to evaluate the relationships between subset of functional traits and growth rate. All analyses were conducted using R ver. 3.5.1 statistical software (R Core Team 2018).

Results

Trait variation

Trait values varied substantially across size class and tree species in this tropical rainforest community. For example, when the 5th and the 95th percentiles of the trait values are compared, theoretical hydraulic conductivity (K_{theo}) varied 8.8-fold, wood density (WD) varied 2.1-fold, vessel diameter (D_h) varied 2.1-fold, leaf relative water content (RWC_l) varied 15-fold, leaf species area (SLA) varied 2.3-fold, leaf thickness (LT) varied 2.5-fold, total nitrogen concentration (TN) varied 2.7-fold (Table 1). Traits showed a median coefficient of variation of 41% (range 21–82%). For the 18 traits, ANOVA analysis indicated that species explained

Table 1. Overview of traits included, the type of traits, traits abbreviation units, median, range and 5th percentiles, 95th percentiles and coefficient of variation (CV) of stem and leaf functional traits of 20 tree species in an Asian tropical rainforest

Trait	Abbreviation	Units	Median	5th Percentile	95th Percentile	CV (%)
Diameter breast height	DBH	cm	11.80	5.37	31.52	82
Sapwood density	WD	g mm^{-3}	0.51	0.32	0.67	22
Stem relative water content	RWC_s	%	0.12	0.02	0.30	63
Leaf relative water content	RWC_l	%	0.11	0.04	0.25	54
Vessel lumen diameter	D_h	m	39.80	28.98	62.13	25
Vessel density	VD	no. cm^{-2}	148.08	58.29	292.22	47
Theoretical hydraulic conductivity	K_{theo}	kg m^{-1} K Pa^{-1} s^{-1}	12.97	4.44	38.93	73
Vein density	D_{vein}	μm $μm^{-2}$	11.39	8.05	19.18	29
Stomatal size	SS	μm	21.58	15.37	31.03	21
Stomatal density	SD	No. $μm^{-2}$	492.92	189.58	1281.60	67
Individual leaf mass	ILM	g	0.25	0.06	0.75	63
Specific leaf area	SLA	mm^2 g^{-1}	165.73	109.92	248.81	25
Leaf thickness	LT	μm	145.83	101.40	258.51	30
Palisade thickness	PT	μm	31.10	19.19	58.62	36
Spongy thickness	SP	μm	95.25	46.59	172.56	41
Lower epidermis thickness	LET	μm	10.08	5.70	19.58	36
Total nitrogen concentration	TN	g kg^{-1}	25.96	15.01	40.43	28
Total phosphorus concentration	TP	g kg^{-1}	1.36	0.84	3.22	45
Total potassium concentration	TK	g kg^{-1}	12.76	4.14	24.03	51

69% of the trait variation on average, ranging from 51% for specific leaf area to 90% for stomatal size (Fig. 1), while size class explained 9.3% of the trait variation. The remainder of the trait variation was due to variation among individuals and measurement error.

Correlations among functional traits

The wood density (WD) was correlated positively with vessel density and stomatal size and negatively with vessel lumen diameter and theoretical hydraulic conductivity (Table S2). For the hydraulic traits, theoretical hydraulic conductivity correlated positively with vessel lumen diameter and negatively with vessel density. Leaf vein density was negatively correlated with stomatal size and positively with stomatal density, stem and leaf relative water content (Table S2), indicating a coordinative effect on water transport and utilisation. Leaf vein density (D_{vein}) was positively correlated with leaf relative water content (RWC_l) and theoretical hydraulic conductivity (K_{theo}). In term of leaf economic spectrum, the specific leaf area (SLA) correlated positively with leaf nutrient concentration (TN, TK, and TP) and negatively with the leaf thickness, tissue thickness of the leaves (PT, SP; Table S2).

Results of the principal component analysis (PCA) showed that the first axis of PCA explained for 26.6% of the total variance among the 18 traits, which mainly loaded the hydraulic architecture traits (Fig. 2). The positive loads of PC#1 mainly represented vessel diameter (D_h), theoretical hydraulic conductivity (K_{theo}), stem and leaf relative water content (RWC_s and RWC_l), vein density (D_{vein}) and stomatal density (SD). PC#1 negatively loaded variations of wood density (WD), vessel density (VD), stomatal size (SS) and leaf lower epidermis thickness (LET). The second axis of PCA explained 20.1% of the total variance, which mainly represented the leaf economic spectrum (Fig. 2). In other words, species with higher specific leaf area (SLA) and higher leaf mass-based nutrient concentration (TN, TK, TP), thus more efficient for light and nutrient capturing, were less thick in their leaf (LT) and tissue thickness (PT, SP). Species with higher SLA had lower individual leaf mass (ILM).

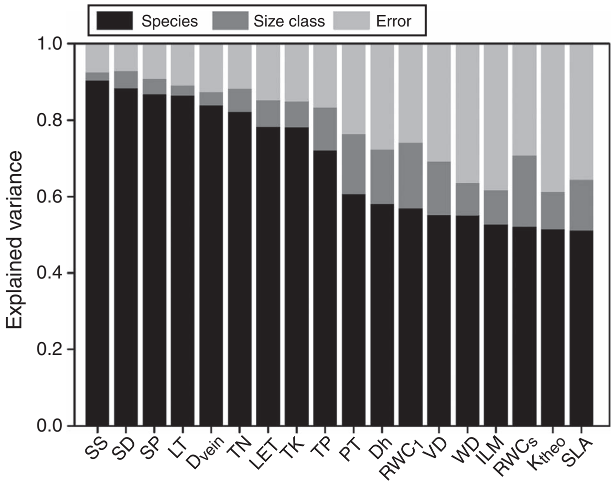

Fig. 1. Variance in trait values explained by species (black) and size class (grey) and measurement error (light grey). Stacked bars are shown for functional traits. Abbreviations are the same as in Table 1. The traits are ranked according to explained variance by species (n = 20).

Relationships between functional traits and diameter growth rate

Stem diameter growth rates correlated positively with the first PC scores but negatively with the second PC scores (Fig. 3), indicating that high hydraulic efficiency and high ability of

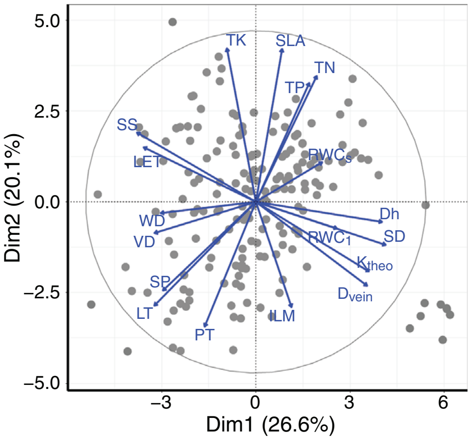

Fig. 2. Principal component analyses (PCA) of 18 functional traits for 181 individuals in an Asian tropical rainforest. Grey dots represent species scores of the PCA. Abbreviations are the same as in Table 1.

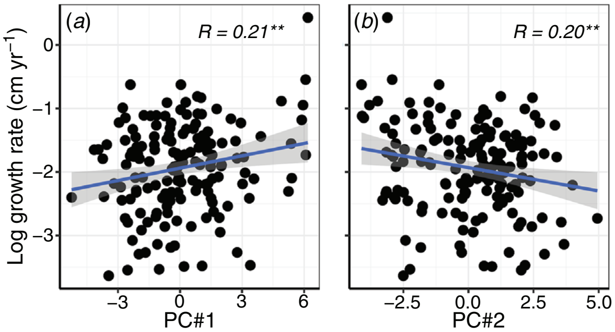

Fig. 3. Relationships between stem diameter growth rates and the first (*a*) and second (*b*) principal component of 18 traits of 20 studied tree species in an Asian tropical rainforest. Note that the growth data are log-transformed. Pearson's correlation and significance are shown: **, $P < 0.01$.

resource acquisition result in high growth rate across species and individuals. Separate PCA analyses showed similar factor loadings of traits for three size classes (Fig. 4*a, d, g*). However, tree growth rate are significantly associated with the first PC (representing hydraulic efficiency) within the big sized tree group (DBH >20 cm) (Fig. 4*h*), whereas correlation between growth rates and the second PC (representing leaf economic spectrum) was significant for the middle sized tree group (DBH 10–20 cm) (Fig. 4*f*). For small sized tree group (DBH 5–10 cm), growth rates were neither correlated with the first PC nor with the second PC (Fig. 4*b, c*).

Partial correlation analysis by controlling tree size (DBH) showed that traits relating to hydraulic architectures (i.e. K_{theo}, D_{vein}) correlated significantly with diameter growth rate for big sized trees (DBH >20 cm) (Table 2; Fig. 5), but this correlation became non-significant for the middle (DBH 10–20 cm) and small (DBH 5–10 cm) sized trees. Traits relating to leaf economic spectrum (i.e. SLA, ILM, LT, PT, SP) correlated significantly with diameter growth rate for middle sized trees (DBH 10–20 cm) (Table 2; Fig. 6). For small-sized trees (DBH 5–10 cm) size trees, growth rate did not show any correlations with measured functional traits (Table 2).

Discussion

Our results indicate that the relationships between functional traits and diameter growth rates varied among size classes in an Asian tropical seasonal rainforest. Growth rates of the big sized trees were related most strongly to hydraulic traits, while growth rates of middle sized trees were related to leaf economic traits. This suggests that different traits have different predict ability on tree growth rate across different size classes.

We found that tree diameter growth rates were positively correlated with the first principal component which representing stem and leaf hydraulic efficiency (Fig. 3).

This result are in line with previous findings which showed that stem hydraulic conductivity traits are better predictor of tree growth rate than wood density in tropical rainforest (Fan *et al*. 2012; Hoeber *et al*. 2014). It is well known that coordination between stem and leaf hydraulic traits maintain water consumption and supply (Wright *et al*. 2006). Wood traits evolve in a coordinated way and trees adjust their hydraulic capacity to meet the requirements of water supply, hence photosynthetic rates, thus fuelling growth (Chave *et al*. 2009). The high growth rates are attained through a greater photosynthetic capacity and leaf area allocation (Poorter and Bongers 2006), which results in higher transpiration rates and greater leaf-level water demand. Terminal vein density is an important index reflecting the plant leaves water supply capacity, while higher vein density generally has greater ability to transpiration (Boyce *et al*. 2009; Beerling and Franks 2010; Brodribb and Feild 2010; McKown *et al*. 2010). High leaf vein density can support a faster delivery of water and ultimately support faster photosynthetic and growth rates (Brodribb *et al*. 2007).

Xylem theoretical hydraulic conductivity (K_{theo}) and leaf vein density (D_{vein}) were positively correlated with growth rates in big-sized trees (Table 2; Figs 4, 5). Trees adjust wood structure across ontogenetic stages to meet the hydraulic and mechanical requirements, via radial changes of wood density, vessel area and specific hydraulic conductivity (Hietz *et al*. 2017). Larger trees normally have bigger vessels and thus higher hydraulic conductance (Sperry *et al*. 2006), which facilitating higher stomatal conductance and more photosynthetic carbon gain (Santiago *et al*. 2004). In contrast, large trees have to transport water along longer path along with greater resistance as they attain the canopy and experience greater exposure to direct sunlight and wind (Ryan *et al*. 2006). Thus, taller or fast-growing trees can produce wider conduits and show high hydraulic conductivity but also have higher vulnerability to drought induced xylem embolism (Voltas *et al*. 2013; De Micco *et al*. 2019). Previous studies showed that drought tends to have a greater impact on the growth and mortality of large trees than small trees in tropical forests (Phillips *et al*. 2010; Bennett *et al*. 2015). Due to the limitations of hydraulic structures, large trees are more severely affected by water stress and show higher mortality than younger trees (Rowland *et al*. 2015). Tall

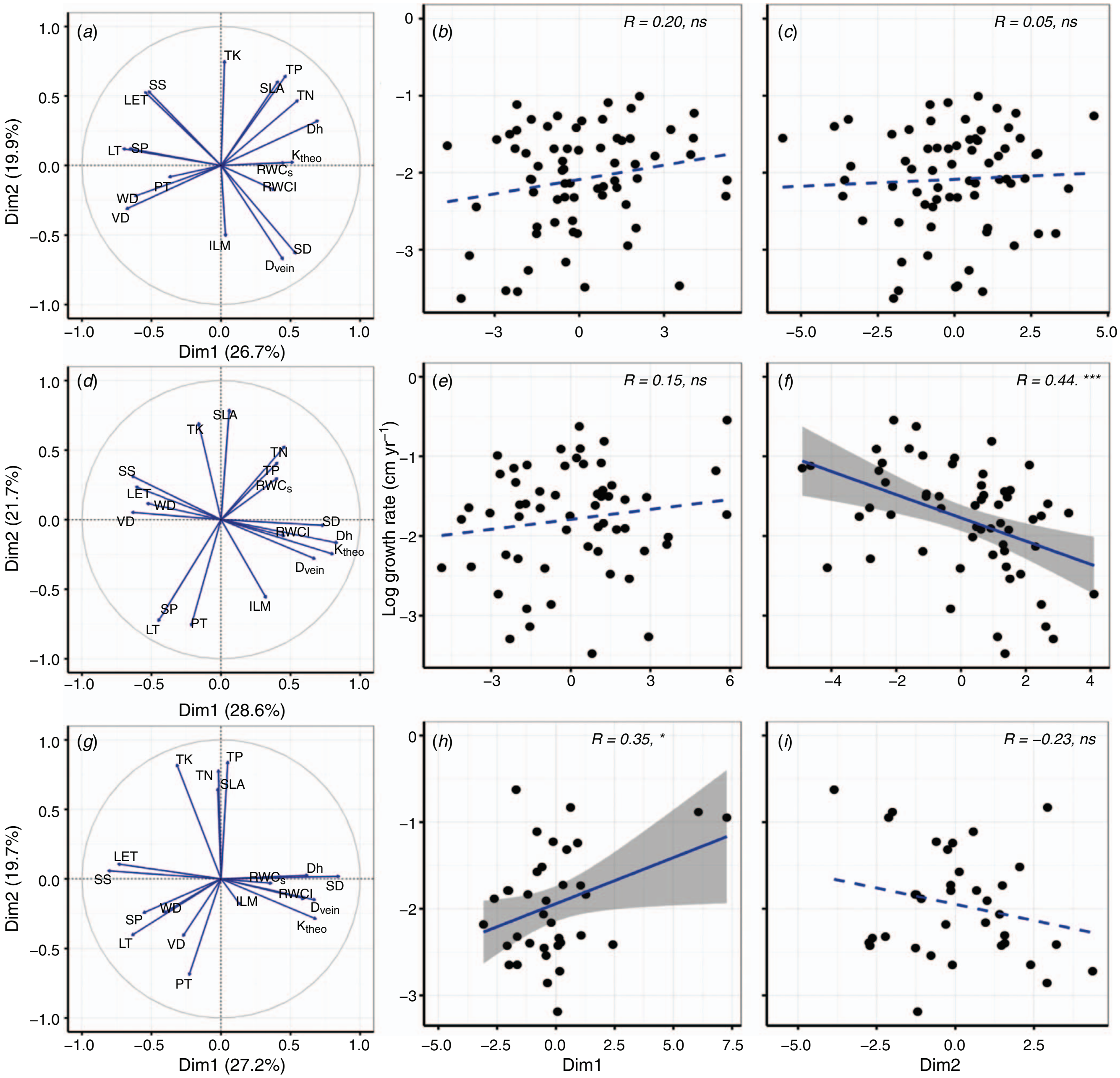

Fig. 4. Biplots of principal component analyses (PCA) (*a*, *d*, *g*), the relationships between stem diameter growth rates and the first (*b*, *e*, *h*) and second (*c*, *f*, *i*) principal components. PCs were performs for 18 functional traits of three size classes (*a*–*c*, 5–10 cm; *d*–*f*: 10–20 cm; *g*–*i*, >20 cm) of 20 tree species in an Asian tropical rainforest. Values in parentheses in the axis labels are percentages explained by the first and second components, respectively. Abbreviations are the same as in Table 1.

trees are thus hydraulically highly efficient and able to comply with the increased water demand for photosynthesis and fast growth, but this comes at a cost, as their xylem is less protected against drought-induced cavitation (Markesteijn *et al*. 2011).

Our result found that leaf economic traits were associated with diameter growth rates for middle-sized trees, but not for larger and smaller trees (Figs 4, 6). Leaf structural characteristics have a great influence on leaf gas exchange, photosynthesis, transpiration, plant growth (Kattge *et al*. 2011). Many studies have shown that leaf traits can predict the plant growth performance (Falster and Westoby 2003; Reich *et al*. 2003). Leaf economic spectrum traits play an important role in light and nutrients acquisition and plant growth and survives (Iida *et al*. 2014*a*). Studies in multiple forest sites have found that specific leaf area is correlated with growth, mortality and shade tolerance of tropical seedlings or saplings (Poorter and Bongers 2006; Baltzer and Thomas

Table 2. Partial correlations (*R* and *P*-values) between diameter growth rate and each of the 18 traits holding the influence of tree size (diameter at breast height, DBH) constant

Partial correlations were calculated for three size classes (DBH 5–10 cm, 10–20 cm, >20 cm) of 20 tree species in an Asian tropical rainforest. Significant correlations are indicated: *, $P < 0.05$; **, $P < 0.01$. Trait abbreviations are the same as in Table 1

Trait	5–10 cm		10–20 cm		>20 cm	
	R	*P*-value	*R*	*P*-value	*R*	*P*-value
WD	–0.187	0.139	–0.196	0.151	0.306	0.074
RWC_s	0.364*	0.005**	0.016	0.91	0.075	0.673
RWC_l	0.134	0.304	–0.028	0.842	–0.28	0.103
D_h	0.02	0.891	0.078	0.608	0.101	0.588
VD	0.019	0.894	0.034	0.821	0.085	0.649
K_{theo}	–0.082	0.577	0.166	0.269	0.191	0.303
D_{vein}	0.009	0.95	0.189	0.243	0.434*	0.015*
SS	–0.07	0.635	–0.241	0.124	0.256	0.189
SD	0.11	0.451	0.124	0.433	–0.141	0.474
ILM	0.07	0.601	0.346*	0.012*	0.119	0.547
SLA	0.053	0.686	–0.278*	0.044*	–0.194	0.272
LT	–0.09	0.513	0.306*	0.034*	–0.309	0.076
PT	0.062	0.653	0.288*	0.047*	0.284	0.104
SP	–0.078	0.57	0.303*	0.036*	–0.518*	0.002**
LET	–0.191	0.164	–0.028	0.848	0.077	0.666
TN	0.132	0.344	–0.087	0.57	–0.125	0.481
TP	0.17	0.223	–0.025	0.871	–0.187	0.29
TK	0.235	0.09	–0.231	0.126	–0.089	0.618

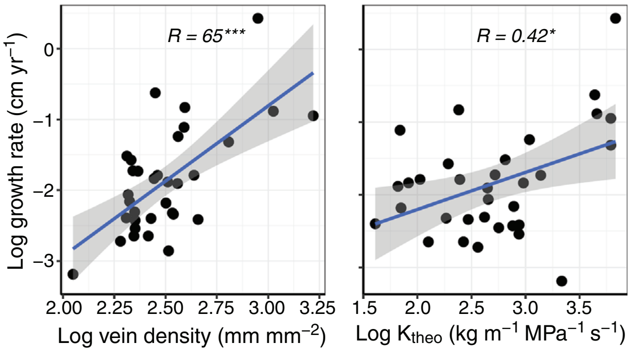

Fig. 5. Relationships between stem diameter growth rate and leaf vein density (D_{vein}) and theoretical hydraulic conductivity (K_{theo}) for big sized trees (DBH > 20 cm) of 20 tree species in an Asian tropical seasonal rainforest. Note that the growth data are log-transformed. Shading areas represent 95% confidence intervals of linear regression. Pearson's correlation and significance are shown: ***, $P < 0.001$; *, $P < 0.05$.

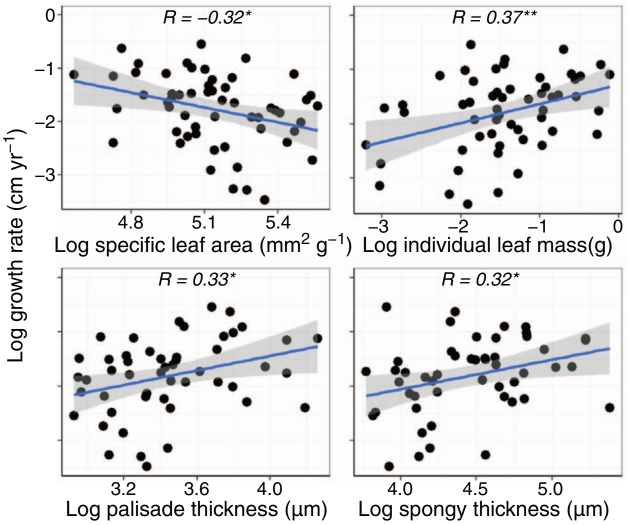

Fig. 6. Relationships between stem diameter growth rate and specific leaf area (SLA), individual leaf mass (ILM), palisade thickness (PT) and spongy thickness (SP) for middle sized trees (DBH = 10–20 cm) of 20 tree species in an Asian tropical seasonal rainforest. Note that the growth data are log-transformed. Shading areas represent 95% confidence intervals of linear regression. Pearson's correlation and significance are shown: **, $P < 0.01$; *, $P < 0.05$.

2007). SLA has repeatedly been found to be a strong predictor of relative growth rate, regardless of vegetation type or growth form (Lambers and Poorter 1992; Reich *et al*. 1992; Grime *et al*. 1997; Wright and Westoby 1999). Species with a high SLA and short-lived leaves are assumed to gain a quick return on leaf investments, by investing in cheap leaves to pre-empt resources and achieve faster growth (Poorter and Bongers 2006).

We found a significant negative relationship between growth and SLA in middle-sized tress (DBH 10–20 cm), but non-significantly for large-sized trees (DBH >20 cm), probably because that smaller trees need high SLA to capture more light in the light-limited environment. This results are also found by previous studies, which showed that the relationship between growth and SLA becomes notably weaker (Poorter *et al*. 2008) or non-existent (Wright *et al*. 2010) when larger trees are analysed. The correlation between relative growth rate and SLA shifted from strongly positive at seedling stage to not significant at adult stage (Anaïs *et al*. 2016). Poorter *et al*. (2008) found that SLA is weakly or not related to the growth of larger-sized trees, possibly because leaf area and light interception of large trees are rarely determined by the number of active meristems (Sterck and Bongers 2001). Leaf thickness (LT), palisade thickness (PT) and spongy thickness (SP) were negatively correlated with SLA (Table S2). The relationship between growth rate and LT, PT and SP also varied with tree size, with significant correlations were found between growth rates and leaf tissue thickness (LT, PT, SP) (Table 2). A possible explanation for this shift is the change of light and water conditions along a vertical profile in a forest (Yoda 1974). Previous studies showed that leaf traits were important drivers of seeding growth rates may be not important drivers of adult growth (Paine *et al*. 2015; Wright *et al*. 2019). Large trees are located in light-exposed canopy where interspecific differences in leaf tissue thickness are expected to reflect differentiation in topographic habitat preference. Growth rates were strongly related to SLA and leaf tissue thickness in saplings, growth in larger trees is likely to be more strongly related to total leaf number (Poorter 2009), or integration of leaf level traits into a whole-plant allocation context (Yang *et al*. 2018). Leaf economic traits are possibly linked with growth rates of large-sized trees, but this linkage may only be demonstrated when integrating the trait values across the entire crown deployed by the individual (Enquist *et al*. 2007).

A growing body of research suggests traits and growth relationships may vary systematically with plant size (Wright *et al*. 2010; Iida *et al*. 2014*b*; Gilbert *et al*. 2016; Visser *et al*. 2016). Most tree species decrease growth rates along with the increasing of age and size, as large trees face more water stress due to longer hydraulic pathways (Koch *et al*. 2004), or shifting allocation from growth to reproduction or senescence (Thomas 2011). When plants grow larger, a greater amount of energy and biomass are devoted into the building and maintaining of non-photosynthetic tissues (Givnish 1995; King 2011). Size-dependent changes in growth rates are expected to be driven by differences in species traits, such as tissue properties, leaf physiology, plant architecture, and reproductive performance (Iida *et al*. 2014*b*).

Conclusions

This study showed that stem diameter growth rates correlated significantly with leaf economic spectrum traits for middle-sized trees, but for large trees hydraulic efficiency traits play a more important role on growth. Thus, the association between diameter growth rates and functional traits is size dependent, which may relate to the differences of environmental stresses shift from light limitation for small trees to water limitation for big trees. Large trees release from light limitations when they reach a position in the canopy, however, other resource limitation such as water stress become more crucial for their growth and survival (Iida *et al*. 2014*a*, 2014*b*). Our results highlight that tropical larger trees may be particularly challenged to maintain functional hydraulic pathways under future climates which are projected to be more water limiting.

Conflicts of interest

The authors declare no conflicts of interest.

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