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Consistent pattern in scaling relationships of leaf dry mass versus area of woody species co-occurring in dry-hot and wet-hot habitats

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ABSTRACT

The scaling relationships between leaf dry mass (LDM) and surface area (LA) can reflect the efficiency of light harvesting and photosynthesis, as well as the ability of plants to withstand biotic and abiotic stress. However, it remains little unknown whether plants alter the scaling relationships of LDM and LA, as along with leaf mass investment per unit area in common species growing in different habitats with high temperature and contrasting water availability. This study involved measuring LA, LDM, and leaf morphological traits (e.g., leaf thickness, dry mass per unit area, and density) in 14 woody species (10 tree species, 2 shrub species, and 2 liana species) that co-occur in wet-hot (WH) and dry-hot (DH) habitats in southwest China. Our results showed that the scaling exponents (α) of LDM vs. LA were consistently greater than 1.0 (indicating the increase in LA fails to keep pace with increasing LDM) for all 14 common species at both sites, irrespective of their growth forms. Furthermore, species exhibited a higher leaf mass investment per unit area and leaf density at the DH site compared to the WH site. These results suggest that the law of "diminishing returns" applies to the scaling relationships of LDM and LA in common species inhabiting both types of habitats. Additionally, plants at the DH site increased leaf mass and density investments, potentially reflecting an essential adaptation to strong selective pressure experienced by plant species in that habitat. This study provides new insights into the scaling relationships of LDM and LA in contrasting habitats, enriching our understanding of the plant life-history strategies and adaptations in response to climate change.

1. Introduction

Plant leaves serve as the primary organ of photosynthesis; however, they exhibit high sensitivity to the surrounding environment (Tozer et al., 2015). Leaf area (LA) plays a pivotal role in light interception, carbon assimilation, and biomass allocation (Kleiman and Aarssen, 2007), thereby influencing plant growth, reproduction, and ecosystem functions (Niklas et al., 2007). Leaf dry mass (LDM) reflects the investment of biomass produced by photosynthesis, as well as water and nutrient uptake in various structures such as photosynthetic tissues, hydraulic systems, and mechanical support (Li et al., 2012; Liu et al., 2020). Leaf dry mass per unit area (LMA) represents the dry mass construction cost per unit area to sustain photosynthesis, hydraulic conductance, and resistance against herbivory, drought, and physical damage from strong winds, rainstorms, and falling branches (Wright and Westoby, 2002; Niinemets et al., 2007a; Nardini et al., 2012a, 2012b; Liu et al., 2020; Zhang et al., 2023). These functions are closely associated with plant survival and adaptation to local environments (Poorter et al., 2009). Therefore, it is crucial to understand the scaling relationships between LDM and LA.

The scaling relationship between LDM and LA can be expressed by a power-law function $LDM = \beta(LA)^{\alpha}$, where β is the normalization constant and α is the scaling exponent. When $\alpha = 1$, LA increases proportionally with increasing LDM; when $\alpha > 1$, the increase in LA fails to keep pace with increasing LDM. This phenomenon is known as the "diminishing returns" hypothesis (Niklas et al., 2007). Milla and Reich (2007) and Niklas et al. (2007) compiled data from numerous species and observed that, in general, LDM increased at a disproportionately faster rate than LA. Nonetheless, some species deviated from this "diminishing returns" pattern. Overall, a larger LA often leads to a disproportionately higher biomass investment per unit area in the LDM, constrained by the maximum LA possible.

Numerous studies have explored the scaling exponents of LDM and LA both within and among species, yet, our knowledge of these scaling

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exponents across different habitats remains uncertain. Despite this, several investigations suggest that the scaling exponent remains consistent irrespective of leaf-form, elevation, or light conditions (Li et al., 2008; Sun et al., 2017; Guo et al., 2018). For instance, Li et al. (2008) investigated 93 temperate woody species and found no significant differences in the scaling relationships of LDM and LA among leaf-forms and elevations. Similarly, the scaling relationships in bamboo species exhibit little sensitivity to light and elevation variations (Sun et al., 2017; Guo et al., 2018). However, divergent findings have been reported concerning the scaling relationship between LDM and LA, with some studies indicating that the scaling exponent is influenced by environmental factors (Pan et al., 2013; Thakur et al., 2019; Liu et al., 2020; Guo et al., 2021). As elevation increases, the scaling exponent shifts from below 1 to above 1 (Pan et al., 2013). Thakur et al. (2019) observed higher scaling exponent at higher elevations, on southern slopes, and in open habitats. Moreover, the scaling exponents of LDM and LA are influenced by other factors such as growth stage, season, and successional stage (Liu et al., 2020; Chen et al., 2021; Guo et al., 2021).

Increased drought and global warming are predicted under climate change (Dai, 2013; Dusenge et al., 2019), which may trigger widespread tree mortality and forest dieback (Allen et al., 2010; Anderegg et al., 2019; Kitudom et al., 2022). The impacts of drought and heat stress impose substantial selective pressure, fostering divergence in physiological and biochemical responses, anatomical traits, hydraulic architecture, leaf phenology, and life-history strategies (Fu et al., 2012; Hasanuzzaman et al., 2013; Kikuzawa et al., 2013; Zhang et al., 2017). When faced with drought and heat stress, plants demonstrate adaptive modifications in traits, such as reduced stomatal conductance, increased deciduousness, higher LMA, leaf thickness and density, smaller mesophyll cells with thicker walls, and a greater fraction of cell walls per leaf tissue, (Niinemets, 2001; Wright et al., 2005; Hallik et al., 2009; Greenwood et al., 2017; Pavanetto et al., 2024). Nevertheless, to date, no study has compared differences in the scaling relationships of LDM and LA for common species growing under elevated temperature and contrasting water availability. Investigating the characterization of leaf trait scaling relationships among sites with differing temperature and water availability can provide novel insights into species-level plant adaptation to high temperature and water scarcity induced by climate change (Carrijo et al., 2021).

In this study, we conducted measurements of LA, LDM, and leaf morphological traits (i.e., LMA, leaf thickness, and leaf density) of woody species co-occurring in dry-hot (Yuanjiang) and wet-hot (Xishuangbanna) habitats in Yunnan Province, southwest China. Our research aimed to address the following questions: (1) Does the law of "diminishing returns" in leaf scaling apply to common species growing in dry- and wet-hot habitats? As LA increases, plants may need more investments in construction costs to ensure coordination of leaf multiple functions (Niklas et al., 2009). We hypothesize that the scaling relationships of LDM versus LA will conform to the "diminishing returns" hypothesis in these two contrasting habitats. (2) Do the scaling exponents of LDM vs. LA differ in dry- and wet-hot habitats? Species originating from drier and hotter habitats are expected to adapt by allocating a greater leaf mass investment per unit area (Wright et al., 2004, 2005). We hypothesize that the scaling exponent of species from the dry-hot habitat will be higher than that of species from the wet-hot habitat (Fig. 1).

2. Material and methods

2.1. Study site

This study was conducted in two distinct sites in Yunnan Province, Southwest China, referred to as dry-hot site (DH) and wet-hot site (WH) for simplicity. The DH site was situated at the Yuanjiang Savanna Ecosystem Research Station, Chinese Academy of Sciences (23° 28′ N, 102° 11′ E; 481m asl.), Yuanjiang County, southwest China (Table 1). This site exhibits a dry-hot climate, with a mean annual temperature (MAT) of 25.0 °C, ranging from 16.8 °C in January to 29.9 °C in June.

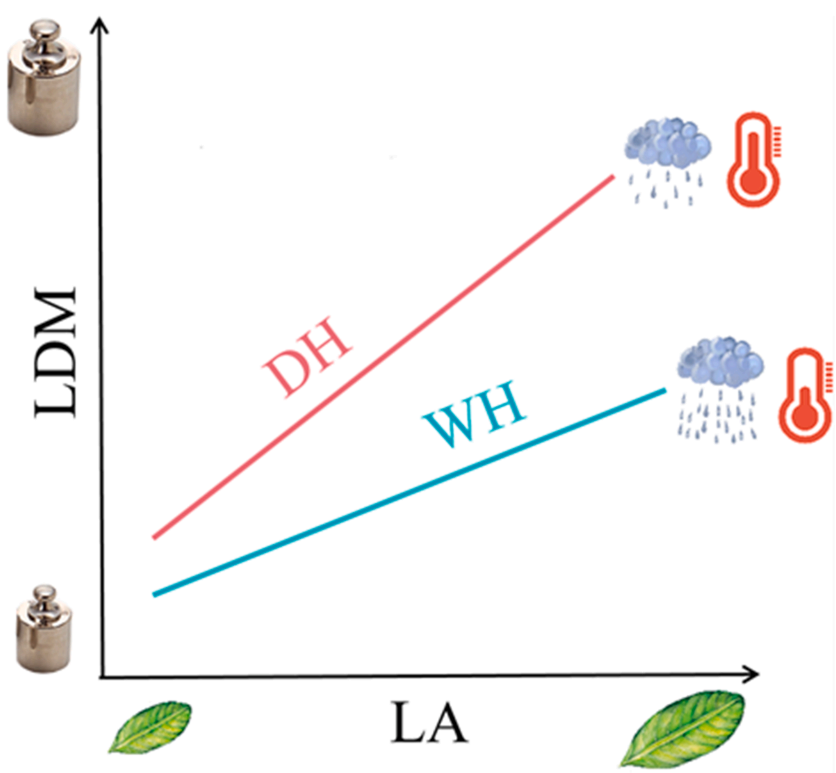

Fig. 1. Conceptual diagram for hypothesis 2. We hypothesize that the scaling exponent of LDM vs. LA in species from dry-hot (DH) habitat will be higher than from wet-hot (WH) habitat.

Table 1
Comparisons of climate and soil properties for dry-hot site (DH) and wet-hot site (WH).

Variables	DH site	WH site
Geographical location	23°28′ N, 102°11′ E	21°54′ N, 101°46′ E
Elevation	481 m	570 m
Vegetation	Savanna	Tropical Seasonal rainforest
Mean annual temperature	25.0 ℃	22.7 ℃
Mean annual precipitation	732.8 mm	1504.6 mm
Aridity index	0.33	0.96
Soil N (mg g^{-1})	3.96	3.07
Soil P (mg g^{-1})	1.30	0.69
Soil K (mg g^{-1})	12.72	10.84

The mean annual precipitation (MAP) averaged 732.8 mm. Over the period 2012–2022, rainy season (May–October) accounted for 76 % of precipitation (521.0 mm), whereas the dry season (November–April) accounted for 24 % (160.5 mm) (Fig. S1). The soil total nitrogen (N), phosphorus (P), and potassium (K) in topsoil layer (0–20 cm) were 3.96, 1.30, and 12.72 mg g^{-1}, respectively (Zhang et al., 2022). The predominant vegetation in the DH site comprises tropical savanna.

The wet-hot (WH) site is situated in the Xishuangbanna Tropical Botanical Garden (21° 54′ N, 101° 46′ E; 570m asl.), Menglun, Xishuangbanna, Yunnan Province, southwest China (Table 1). This site has a slightly lower MAT of 22.7 °C, with minimum of 16.6 °C in January and maximum of 25.6 °C in June. MAP was 1504.6 mm. Over the period 2012–2022, rainy season (May–October) accounted for 83 % of precipitation (1249.8 mm) and the dry season (November–April) accounted for 17 % (254.8 mm) (Fig. S1). In the topsoil layer (0–20 cm), the total N, P, and K were 3.07, 0.69, and 10.84 mg g^{-1}, respectively (Zhang et al., 2022). The predominant vegetation at the WH site consists of tropical seasonal rainforest. Comparatively, the DH and WH sites have aridity indices of 0.33 and 0.96, respectively (Zhang et al., 2022). The lower aridity index at the DH site signifies a significantly drier habitat in contrast to the WH site, as indicated by Nastos et al. (2013).

2.2. Plant species and leaf sampling

In this study, we selected 14 common woody species growing in both sites, comprising 10 tree species, 2 shrub species, and 2 liana species. The overview of the plant species is summarized in Table 2. For each site, we identified and sampled three mature, healthy, and similarly sized individuals per species, ensuring a minimum separation distance of 50 m between individuals for leaf sampling. Sun-exposed mature and healthy branches per individual at each site were sampled before dawn, during the rainy season (August to September 2022), corresponding to the peak growing season. The sampled branches were carefully wrapped in moist paper towels, placed in black plastic bags and sampling boxes, and then transported to the laboratory for subsequent analysis. At least 50 mature and healthy leaves or leaflets were sampled for trait measurements per species at each site.

Table 2
Plant species, family, growth form, and phenology of sampling of leaves in this study.

Species	Family	Growth form	Phenology
Psidium guajava	Myrtaceae	Tree	Evergreen
Bauhinia brachycarpa	Fabaceae	Shrub	Deciduous
Woodfordia fruticosa	Lythraceae	Shrub	Semi-deciduous
Cipadessa baccifera	Meliaceae	Tree	Deciduous
Ficus benjamina	Moraceae	Tree	Evergreen
Bischofia polycarpa	Euphorbiaceae	Tree	Semi-deciduous
Garuga forrestii	Burseraceae	Tree	Deciduous
Bombax ceiba	Bombacaceae	Tree	Deciduous
Jatropha curcas	Euphorbiaceae	Tree	Deciduous
Broussonetia papyrifera	Moraceae	Tree	Deciduous
Dregea volubilis	Asclepiadaceae	Liana	Semi-deciduous
Bridelia stipularis	Euphorbiaceae	Liana	Deciduous
Annona squamosa	Annonaceae	Tree	Semi-deciduous
Huberantha cerasoides	Annonaceae	Tree	Semi-deciduous

2.3. Measurements of leaf traits

The fresh leaves of simple-leaved species and leaflets of compound-leaved species were scanned using a 300-DPI resolution scanner (HP LaserJet Pro-MFP, USA). Subsequently, the scanned digital photographs were obtained, and leaf area (LA) was measured using ImageJ software (https://imagej.nih.gov/ij/). Leaf thickness (LT) was measured at the front, middle, and end of the leaf, excluding the leaf veins, using an electronic microcaliper (MDE-25MX, Mitutoyo Corporation, Japan) with a precision of 0.001 mm. Following this, the leaves were dried in an oven at 70 ℃ for at least 48 h to achieve a constant leaf dry mass (LDM). LDM was then determined using a precise electronic balance (ME204, Mettler Toledo Company, Greifensee, Switzerland) with a precision of 0.0001 g. Furthermore, LMA was calculated using the following formula (Wright et al., 2004):

$$\mathrm{LMA} = \frac{\mathrm{LDM}}{\mathrm{LA}}$$

Leaf density (LD) was calculated using the following formula (Witkowski and Lamont, 1991):

$$\mathrm{LD} = \frac{\mathrm{LMA}}{\mathrm{LT}}$$

2.4. Data analysis

A power-law function was employed to fit the scaling relationship between LDM and LA as follows.

$$\mathrm{LDM} = \beta(\mathrm{LA})^{\alpha}$$

where α and β represent the scaling exponent and the normalization constant, respectively. In order to stabilize the variance of leaf traits, both sides of the equation were natural-logarithm transformed (Niklas et al., 2007):

$$\ln(\mathrm{LDM}) = \ln\beta + \alpha\ln(\mathrm{LA})$$

Following log-transformation, the data demonstrated a normal distribution (Kolmogorov-Smirnov test, $P = 0.05$). The standardized major axis (SMA) method was used to examine if the slope (α) significantly deviated from 1, using the '*smatr*' package (Warton and Weber, 2002). The 95 % confidence intervals for the SMAs were calculated (Pitman, 1939). We tested whether the SMA lines of LDM and LA of common species across both sites shared a common slope using a likelihood ratio method at $P = 0.05$ (Warton and Weber, 2002). Moreover, we tested the relationships of LD–LA, LT–LA (Figs. S2, S3), LD–LMA, and LT–LMA using the same method. Furthermore, we tested the difference in leaf morphological traits between two sites using independent-samples *t*-test. All statistical analyses were performed using R software (version 4.0.2; R Development Core Team, 2020).

3. Results

All the scaling exponents (α) of LDM versus LA for 14 common species at DH and WH sites were found to exceed 1, with the lower bounds of the corresponding 95 % CIs also surpassing 1 (Table 3), regardless of growth forms (tree, shrub, and liana). These findings support the notion that the scaling relationships between LDM and LA conform to the "diminishing returns" hypothesis at both sites. The SMA slopes of LDM and LA for the common species at both sites did not exhibit significant differences ($P > 0.05$, Table 3), except for *Bombax ceiba* ($P < 0.05$). This indicates that, in general, the scaling relationship between LDM and LA remains consistent across the common species at

Table 3
SMA statistical parameters for the scaling relationships of LDM vs. LA in 14 woody species co-occurring in DH and WH habitats. P_{slope} was the significance for the test if the SMA lines share a common slope.

Species	Site	N	Equation	R^2	*P*-value	95 % CI	P_{slope}
P. guajava	WH	61	$y = 1.109x-5.173$	0.94	< 0.001	[1.037, 1.185]	0.055
	DH	70	$y = 1.227x-5.281$	0.89	< 0.001	[1.132, 1.331]	
B. brachycarpa	WH	60	$y = 1.186x-5.705$	0.83	< 0.001	[1.065, 1.320]	0.098
	DH	60	$y = 1.070x-4.980$	0.95	< 0.001	[1.010, 1.135]	
W. fruticosa	WH	70	$y = 1.144x-5.518$	0.88	< 0.001	[1.051, 1.247]	0.915
	DH	60	$y = 1.136x-5.019$	0.81	< 0.001	[1.014, 1.273]	
C. baccifera	WH	50	$y = 1.289x-6.307$	0.91	< 0.001	[1.184, 1.403]	0.566
	DH	60	$y = 1.244x-6.058$	0.88	< 0.001	[1.137, 1.360]	
F. benjamina	WH	100	$y = 1.187x-5.642$	0.78	< 0.001	[1.081, 1.303]	0.803
	DH	60	$y = 1.213x-5.560$	0.70	< 0.001	[1.052, 1.398]	
B. polycarpa	WH	100	$y = 1.246x-5.810$	0.96	< 0.001	[1.196, 1.297]	0.196
	DH	50	$y = 1.140x-5.143$	0.80	< 0.001	[1.001, 1.300]	
G. forrestii	WH	60	$y = 1.093x-5.460$	0.93	< 0.001	[1.017, 1.174]	0.353
	DH	50	$y = 1.174x-5.521$	0.78	< 0.001	[1.024, 1.346]	
B. ceiba	WH	50	$y = 1.291x-5.973$	0.93	< 0.001	[1.193, 1.394]	0.025
	DH	70	$y = 1.125x-5.111$	0.85	< 0.001	[1.023, 1.237]	
J. curcas	WH	60	$y = 1.183x-6.620$	0.90	< 0.001	[1.090, 1.284]	0.691
	DH	60	$y = 1.158x-5.858$	0.92	< 0.001	[1.074, 1.248]	
B. papyrifera	WH	80	$y = 1.081x-5.429$	0.92	< 0.001	[1.014, 1.153]	0.755
	DH	50	$y = 1.067x-4.926$	0.90	< 0.001	[1.014, 1.191]	
D. volubilis	WH	60	$y = 1.175x-6.134$	0.86	< 0.001	[1.067, 1.295]	0.352
	DH	50	$y = 1.105x-5.449$	0.88	< 0.001	[1.003, 1.213]	
B. stipularis	WH	70	$y = 1.151x-5.634$	0.81	< 0.001	[1.035, 1.280]	0.275
	DH	63	$y = 1.273x-5.739$	0.66	< 0.001	[1.097, 1.478]	
A. squamosa	WH	60	$y = 1.074x-5.527$	0.95	< 0.001	[1.011, 1.142]	0.598
	DH	60	$y = 1.100x-5.520$	0.94	< 0.001	[1.029, 1.176]	
H. cerasoides	WH	50	$y = 1.122x-5.704$	0.85	< 0.001	[1.003, 1.254]	0.374
	DH	50	$y = 1.062x-5.335$	0.97	< 0.001	[1.010, 1.117]	

DH and WH sites. However, the intercepts of SMA-fitted lines of the DH site were generally higher than those at the WH site. This indicates that the increase in LDM at the DH site was more pronounced compared to the WH site for the same given LA (Fig. 2).

At the WH site, a significantly higher LA was observed compared to the DH site in 9 out of the 14 species analyzed ($P < 0.05$, Table 4). Moreover, LMA was significantly higher at the DH site across all species ($P < 0.05$). Consistent with LMA, LD exhibited a similar pattern, with higher values at the DH site compared to the WH site ($P < 0.001$). Notably, *Cipadessa baccifera* displayed comparable LD values between the two sites ($P = 0.47$). LT was significantly higher at the WH site for 9 species ($P < 0.05$). Furthermore, the slopes of LD and LMA at both sites displayed significant differences across 8 species (Fig. 3 and Table S1), while the slopes of LT and LMA exhibited significant differences for 6 species ($P < 0.05$, Fig. 4 and Table S2).

4. Discussion

The purpose of this study was to investigate the scaling relationships of LDM and LA in 14 common woody species growing in dry-hot and

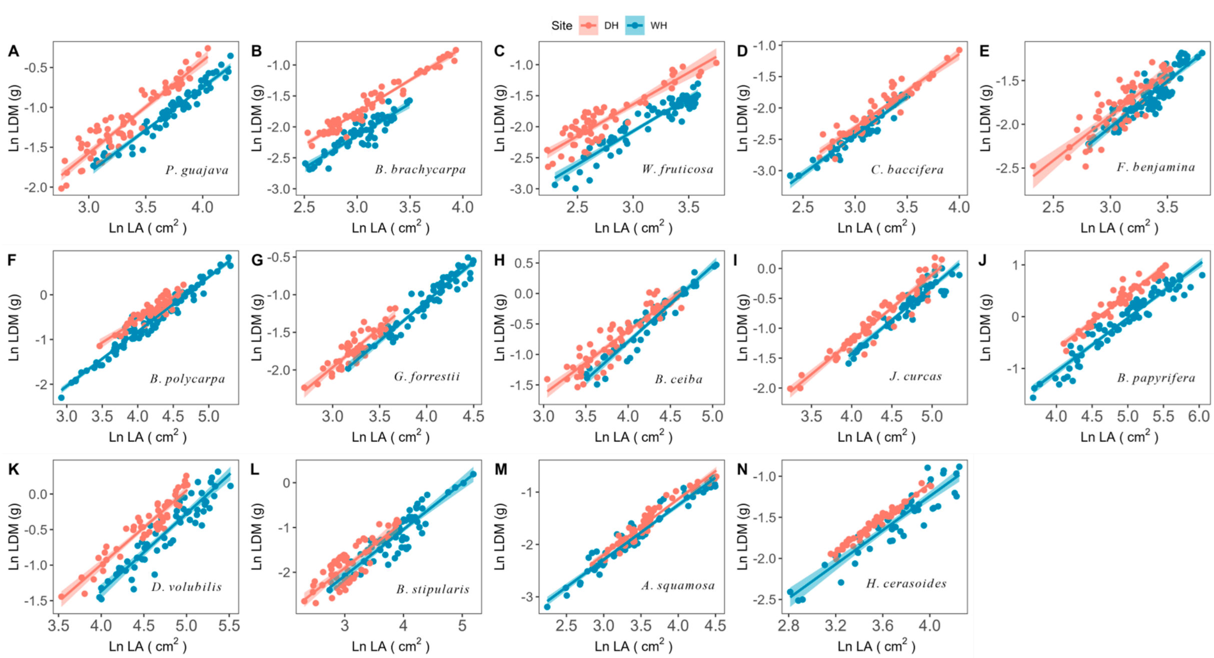

Fig. 2. Scaling relationships of LDM vs. LA in 14 woody species co-occurring in DH and WH habitats. Statistical parameters for the regression listed in Table 3.

Table 4
Comparison of leaf traits in 14 woody species co-occurring in DH and WH habitats.

Species	LA (cm^2)			LDM (g)			LMA ($g\ m^{-2}$)			LT (mm)			LD ($g\ cm^{-3}$)		
	WH	DH	*P*-value	WH	DH	*P*-value	WH	DH	*P*-value	WH	DH	*P*-value	WH	DH	*P*-value
P. guajava	43.6	30.5	<0.001	0.374	0.343	0.178	85.3	110.4	<0.001	0.289	0.257	<0.001	0.298	0.435	<0.001
B. brachycarpa	20.7	24.3	0.018	0.121	0.211	<0.001	58.5	85.9	<0.001	0.160	0.188	<0.001	0.377	0.466	<0.001
W. fruticosa	24.7	16.9	<0.001	0.158	0.165	0.579	64.0	97.6	<0.001	0.150	0.181	<0.001	0.428	0.538	<0.001
C. baccifera	21.9	26.6	<0.001	0.098	0.140	<0.001	44.3	51.9	<0.001	0.110	0.133	<0.001	0.404	0.397	0.471
F. benjamina	29.1	22.6	<0.001	0.195	0.170	0.002	66.8	75.2	<0.001	0.335	0.213	0.126	0.258	0.355	<0.001
B. polycarpa	75.7	68.6	0.104	0.679	0.727	0.343	85.4	105.9	<0.001	0.312	0.262	<0.001	0.273	0.404	<0.001
G. forrestii	58.2	26.0	<0.001	0.362	0.184	<0.001	62.0	70.8	<0.001	0.166	0.151	<0.001	0.381	0.470	<0.001
B. ceiba	80.3	54.5	<0.001	0.751	0.547	<0.001	90.7	100.0	0.001	0.345	0.280	<0.001	0.262	0.357	<0.001
J. curcas	117.1	80.6	<0.001	0.574	0.470	0.014	48.5	56.8	<0.001	0.204	0.197	0.196	0.242	0.288	<0.001
B. papyrifera	159.4	139.5	0.097	1.058	1.448	<0.001	66.4	103.3	<0.001	0.311	0.289	0.025	0.219	0.365	<0.001
D. volubilis	129.4	96.5	<0.001	0.668	0.679	0.832	50.9	69.9	<0.001	0.221	0.206	0.012	0.234	0.343	<0.001
B. stipularis	53.6	22.9	<0.001	0.356	0.178	<0.001	65.7	77.0	<0.001	0.261	0.193	<0.001	0.256	0.410	<0.001
A. squamosa	35.3	39.7	0.225	0.184	0.231	0.022	51.7	57.8	<0.001	0.177	0.137	<0.001	0.297	0.425	<0.001
H. cerasoides	42.3	34.9	0.001	0.224	0.210	0.284	52.8	60.0	<0.001	0.173	0.141	<0.001	0.305	0.427	<0.001

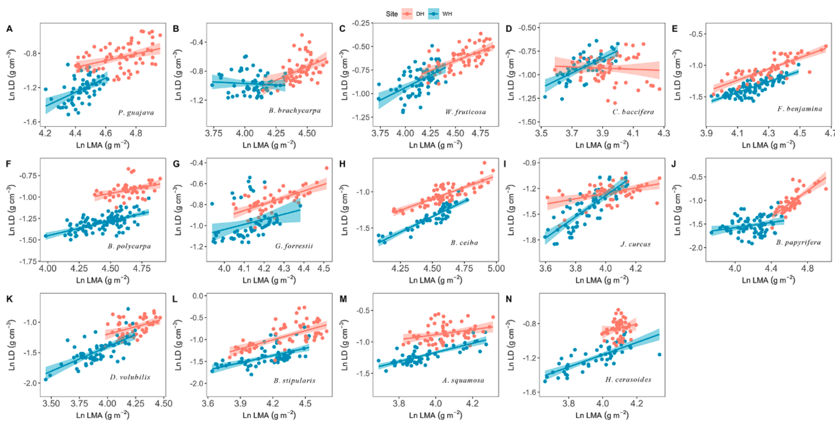

Fig. 3. Scaling relationships of LD vs. LMA in 14 woody species co-occurring in DH and WH habitats. Differences in slope were listed in Table S1.

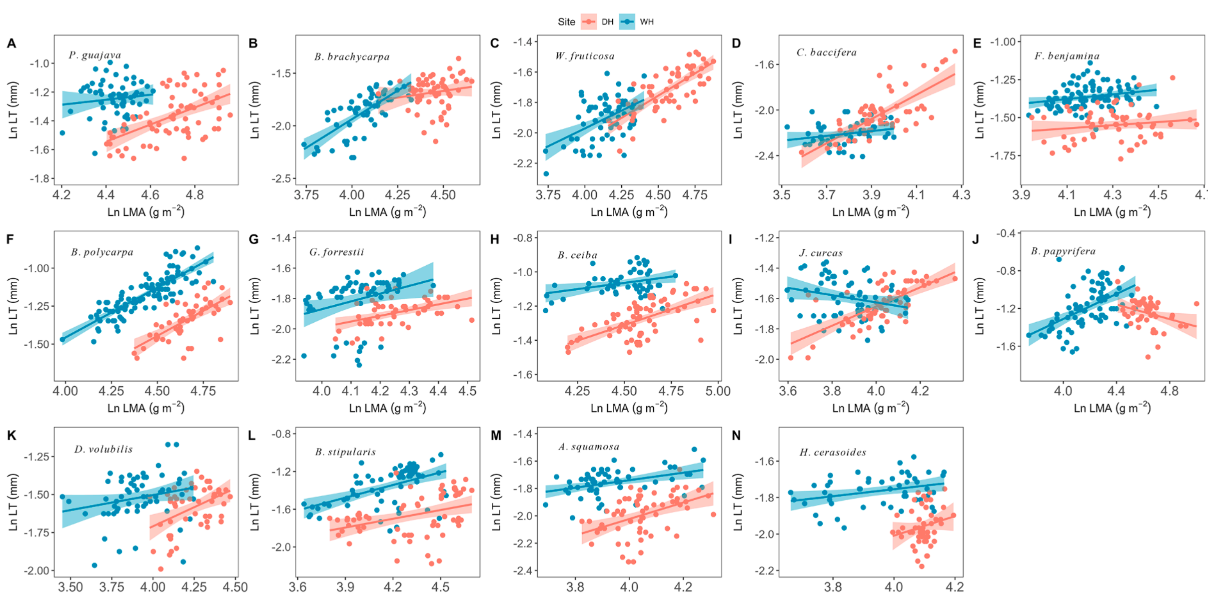

Fig. 4. Scaling relationships of LT vs. LMA in 14 woody species co-occurring in DH and WH habitats. Differences in slope were listed in Table S2.

wet-hot habitats. The data presented in this study revealed two important patterns. Firstly, the scaling exponents (α) for all common species in both habitats were greater than 1, indicating that the scaling relationships of LDM vs. LA followed the "diminishing returns" hypothesis. This consistency was observed across different growth forms (tree, shrub, and liana), confirming our initial hypothesis. Secondly, the scaling exponents did not differ between two sites, with exception of *B. ceiba,* which contradicted our second hypothesis. Overall, the investment of leaf dry mass per area or volume (LMA and LD) at the DH site surpassed that of the WH site. Below, we discuss these results within the context of the scaling relationships of LDM versus LA, as well as leaf mass investment for common species growing under elevated temperature and contrasting water availability conditions.

4.1. Scaling relationships of LDM vs. LA in DH and WH obey the "diminishing returns"

Our findings confirm that the scaling relationships of LDM vs. LA align with the "diminishing returns" hypothesis at both research sites, indicating that the increase in LA does not keep pace with the increase in LDM (Niklas et al., 2007). This finding is consistent with previous studies suggesting that leaf mass and area following the "diminishing returns" hypothesis is a widely observed phenomenon (Niklas et al., 2007; Thakur et al., 2019; Li et al., 2022; Guo et al., 2022). The scaling relationship between LDM and LA represents a tradeoff between the capacity to capture and utilize light effectively (Huang et al., 2019). Consequently, LDM and LA may impose limitations on each other. Plants optimize their growth and competitive advantage by adjusting leaf area for light capture and the allocation of leaf biomass to maintain high photosynthetic rates and carbon gains (Kleiman and Aarssen, 2007).

As LA increases, the photosynthetic area expands, requiring a proportional increase in biomass allocation to fulfill various leaf functions, including hydraulic conductance, drought resistance, biomechanical support, and defense against herbivory (Wright and Westoby, 2002; Niklas, 2004; Runions et al., 2005; Niinemets et al., 2007b; Niklas et al., 2009; Nardini et al., 2012b; Zhang et al., 2023). Leaf mass plays a crucial role not only in light harvesting and photosynthesis, but also in growth, transport of water and nutrient, storage of water and carbohydrates, defense against biotic and abiotic stresses, and other physiological processes (Enquist, 2002; Hölttä et al., 2006; Nakagawa et al., 2012). Correspondingly, leaf structures such as epidermal cells, mesophyll cells, stomata and leaf veins have evolved to accommodate the tradeoffs or synergies among multiple leaf functions (Niinemets et al., 2006; Niklas and Cobb, 2008; Niklas et al., 2009; Sack et al., 2012; Shi et al., 2022). However, when the additional costs outweigh the potential benefits of increased surface area, LA reaches its maximum value (Packard, 2014). Therefore, the tradeoffs in leaf function and structure constrain the simultaneous increase of LA with rising LDM.

The consistent scaling exponent across different habitats suggests that the influence of "diminishing returns" in differing environments may be primarily driven by mechanical constraints rather than adaptive plant responses, indicating that the scaling exponent may not accurately reflect plant adaptation to the environment. Furthermore, despite the slightly higher soil nutrient content in the DH site (Table 1), it did not have a significant effect on the scaling relationship between LDM and LA. This finding suggests that the limiting factors of temperature and precipitation may exert a more substantial influence. In the study by Thakur et al. (2019), a higher scaling exponent was observed at high elevations characterized by low temperature and precipitation (Dimri et al., 2022). However, in the current investigation, where temperature and precipitation variations were reversed, the results were consistent with those reported by Li et al. (2008). This indicates that the effects of temperature and precipitation may counterbalance each other.

Furthermore, it is essential to acknowledge the limitation of this study, which is the relatively small sample size of individual plants. This study primarily focused on comparing scaling relationships of traits at the leaf level between the DH and WH sites, emphasizing interspecific comparisons rather than exploring intraspecific trait variations. Nonetheless, intraspecific trait variation significantly influences species adaptation to diverse habitats (Liu et al., 2022). Therefore, it is crucial to expand the sample size of individual plants in future research to examine intraspecific trait variation and its role in shaping scaling relationships adapted to local environments.

4.2. Higher leaf mass investment in DH than in WH

In general, our findings indicate that LMA and LD were notably higher at the DH site compared to the WH site. This disparity in leaf mass allocation can be attributed to several factors. Firstly, the DH site exhibited significantly lower precipitation levels than the WH site (Table 1, Fig. S1), which can be attributed to the presence of the high longitudinal Himalayan mountains inducing a rain shadow effect by blocking moist air from the Bay of Bengal. Furthermore, situated in a river valley, the DH site encounters higher temperature due to downdrafts (Zhang et al., 2007; Yao et al., 2012; Li et al., 2016). The combination of seasonal drought and elevated temperature at the DH site creates a challenging environment for plant growth, imposing stronger selective pressures compared to the WH site. Consequently, plants at the DH site have adapted to these challenging conditions by enhancing leaf mass allocation, as supported by previous studies (Wright et al., 2004, 2005). Furthermore, the elevated soil nutrient levels at the DH site offer improved nutrient conditions for plant growth (Day and Ludeke, 1993). Plants utilize these essential nutrients to develop plant tissues, particularly enhancing investments in leaf structures and enabling adaptation to drought and heat stress conditions (Wright et al., 2002). Thus, the higher soil nutrient contents at the DH site also contribute to this adaptation to a drier and hotter climate.

Due to the variations in water availability and temperature between two sites, the common plant species exhibit distinct water use and life-history strategies (Zhang et al., 2017, 2022). Specifically, leaves at the DH site exhibited higher LD at same LMA (Fig. 3). This increase in LD serves as a mechanism to restrict transpiration and diminish water loss, consequently enhancing water use efficiency (Gratani and Bombelli, 2001; Zhang et al., 2012). In contrast, plants at the WH site adopt a different strategy by investing leaf mass in LT (Fig. 4). This enables them to store larger amounts of water, thereby boosting photosynthetic rates and enabling survival during the dry periods (Mitchell et al., 1999). Furthermore, thicker leaves offer short-term heat storage, serving as a protective mechanism against high temperature (Vogel, 2009; Leigh et al., 2012). Moreover, given the drier conditions DH site experiences, plants may allocate more biomass towards developing tissue structures that enhance drought resistance (Tyree et al., 2002; Zhang et al., 2007; Gibert et al., 2016). This includes reinforcing cell walls, cuticles, and increasing cell density (Niinemets, 2001; Reich et al., 2003; Wright et al., 2004). These adaptations help plants cope with water scarcity and improve their ability to withstand drought conditions. Considering the higher temperature at DH site, it is plausible that plants invest more leaf mass in the development of veins and stomata rather than LT. This allocation aims to facilitate heat transfer and maintain optimal temperature for photosynthesis (Hill et al., 2015; Lin et al., 2017). Additionally, the increased leaf mass may be directed towards the enhancement of well-developed mesophyll cells (Song and Cao, 2005; Zhang et al., 2007). This adaptation elevates diffusion resistance in intercellular spaces, increases the area of chloroplasts facing intercellular spaces, and promotes light capture, leading to the accumulation of CO_2, water, and nutrients that can be utilized by chloroplasts, ultimately favoring photosynthetic efficiency and water and nutrient utilization (Terashima et al., 2001; Evans and Vogelmann, 2003).

5. Conclusions

In this study, we investigated the scaling relationships of LDM and LA in 14 common woody species co-occurring in dry-hot and wet-hot habitats. Our findings revealed that the concept of "diminishing returns" is applicable to the scaling relationships of LDM and LA in these common species across both habitats. Specifically, species exhibited a higher investment of leaf mass per unit area and leaf density in dry-hot habitat, and leaf thickness in wet-hot habitat. These results indicate that tradeoffs between leaf structure and functions contribute to constraining the simultaneous increase of LA with rising LDM in contrasting habitats.

Nevertheless, plants demonstrate the capacity to adjust leaf mass investment in response to the long-term selective pressures from the environment. Our study provides valuable insights into the leaf-scaling relationships of LDM and LA in diverse habitats, shedding light on the understanding of plant life-history strategies in dry and hot habitats and responses to climate change in future.

Data availability

The data that support the findings and the analysis code are available on request from the corresponding author.

CRediT authorship contribution statement

Xuenan Li: Writing – original draft, Writing – review & editing, Formal analysis, Data curation. **Zhongfei Li:** Writing – original draft, Writing – review & editing, Conceptualization. **Shubin Zhang:** Writing – original draft, Writing – review & editing, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.flora.2024.152521.

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