





Article

Overlapping Water and Nutrient Use Efficiencies and Carbon Assimilation between Coexisting Simple- and Compound-Leaved Trees from a Valley Savanna

Yang-Si-Ding Wang ^{1,2,3,†}, Da Yang ^{1,2,†} , Huai-Dong Wu ¹, Yun-Bing Zhang ^{1,2,3},
Shu-Bin Zhang ^{1,4} , Yong-Jiang Zhang ⁵  and Jiao-Lin Zhang ^{1,2,*} 

- ¹ CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla 666303, China; wangyangsiding@xtbg.ac.cn (Y.-S.-D.W.); yangda@xtbg.ac.cn (D.Y.); 1129594125qq@163.com (H.-D.W.); zhangyib@xtbg.org.cn (Y.-B.Z.); zhangshubin@xtbg.ac.cn (S.-B.Z.)
- ² Center of Plant Ecology, Core Botanical Gardens, Chinese Academy of Sciences, Mengla 666303, China
- ³ University of Chinese Academy of Sciences, Beijing 100049, China
- ⁴ Yuanjiang Savanna Ecosystem Research Station, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Yuanjiang 653300, China
- ⁵ School of Biology and Ecology, University of Maine, Orono, ME 04469, USA; yongjiang.zhang@maine.edu
- * Correspondence: zjl@xtbg.org.cn; Tel.: +86-691-871-3046; Fax: +86-691-871-5070
- † Equal contribution.

Received: 6 October 2020; Accepted: 26 October 2020; Published: 29 October 2020



Abstract: Identifying differences in ecophysiology between simple and compound leaves can help understand the adaptive significance of the compound leaf form and its response to climate change. However, we still know surprisingly little about differences in water and nutrient use, and photosynthetic capacity between co-occurring compound-leaved and simple-leaved tree species, especially in savanna ecosystems with dry-hot climate conditions. From July to September in 2015, we investigated 16 functional traits associated with water use, nutrients, and photosynthesis of six deciduous tree species (three simple-leaved and three compound-leaved species) coexisting in a valley-savanna in Southwest China. Our major objective was to test the variation in these functional traits between these two leaf forms. Overall, overlapping leaf mass per area (LMA), photosynthesis, as well as leaf nitrogen and phosphorus concentrations were found between these coexisting valley-savanna simple- and compound-leaved tree species. We didn't find significant differences in water and photosynthetic nitrogen or phosphorus use efficiency between simple and compound leaves. Across these simple- and compound-leaved tree species, photosynthetic phosphorus use efficiencies were positively related to LMA and negatively correlated with phosphorus concentration per mass or area. Water use efficiency (intrinsic water use efficiency or stable carbon isotopic composition) was independent of all leaf traits. Similar ecophysiology strategies among these coexisting valley-savanna simple- and compound-leaved species suggested a convergence in ecological adaptation to the hot and dry environment. The overlap in traits related to water use, carbon assimilation, and stress tolerance (e.g., LMA) also suggests a similar response of these two leaf forms to a hotter and drier future due to the climate change.

Keywords: compound leaves; functional traits; leaf form; nutrient use efficiency; photosynthesis; water use strategy

1. Introduction

Plant leaves can be classified into two categories: a simple leaf with a single lamina and single rachis, and a compound leaf with multiple leaflets that occur in various arrangements along the rachis [1–3]. Previous researchers have been investigating the similarities and differences between simple and compound leaf development for decades [3], and have clearly identified several important key genes for the regulation and development of compound versus simple leaf forms [2,4,5]. Leaves as the main CO₂-fixation organs, the diversity of leaf forms also reflects the plant morphological and physiological adaptation [6]. An intact compound leaf may require larger within-leaf support for mechanical stability compared with a simple leaf [7,8], and the differences in leaf and stem properties between simple- and compound-leaved species may result in co-variation of morphology, physiology, and growth. However, we still know very little about the differences in eco-physiological adaptation between simple and compound leaf forms. Such knowledge will be useful to predict the comparative responses of these two leaf forms to rainfall patterns related to climate change.

There has been a long-held hypothesis that compound leaves are associated with rapid growth during favorable light conditions [7,9,10]. Malhado et al. (2010) have found evidence for supporting the fast growth hypothesis of compound-leaved species by measuring the radial growth rates of the Amazon rainforest trees [2]. The main mechanism is that compound leaf structure, as a cheap ‘throwaway’ twig, decreases the construction cost in woody structures and thus promotes rapid growth [2,7,9]. There has been evidence that compound-leaved species tend to have high hydraulic conductance and photosynthetic capacity associated with fast growth in a temperate forest of Northeast China [11], which provides a physiological explanation of the fast growth of compound-leaved species. In addition, midday stomatal conductance in compound-leaved species decreases at higher percentages than that of simple-leaved trees [12]. However, few investigations have yet been conducted to test the difference in photosynthetic physiology in relation to adaptive significance across simple- and compound leaves from different vegetation types [2,13–15].

Savanna ecosystems are an important terrestrial vegetation type with high species richness and endemism covering nearly 1/3 of the world’s land surface [16–18]. Valley-savanna ecosystems in Southwest China have a dry-hot climate and a six-month dry season, with the co-existence of diverse simple- and compound-leaved species [19]. Although a previous study has shown that compound leaves tend to have higher photosynthetic rates than simple leaves in a temperate forest [11], such a pattern remains untested in hot and dry ecosystems. In dry habitats, compound leaves may have an adaptive advantage to seasonal drought [13,20], because compound-leaved plants can minimize water loss by dropping the rachises as well as leaves during dry periods [9], which may mitigate the influence of drought on photosynthetic carbon assimilation and growth. However, quantitative data on testing the variation in traits across coexisting valley-savanna simple- and compound-leaved plant species are still lacking.

In savannas, water availability is the main factor limiting plant photosynthesis and growth, especially in the dry season [21]. Water deficits can cause stomatal and non-stomatal limitations to photosynthesis [22,23], while water and nutrient use efficiencies are important drivers for liana diversity in a Chinese valley savanna [24]. In addition, temperate compound-leaved trees have lower water use efficiency than coexisting simple-leaved species [11]. However, a surprising knowledge gap still exists about the comparison of water and nutrient use advantages between these two leaf forms in dry and hot habitats.

Here, we investigated 16 functional traits associated with leaf water use, nutrient economy, and carbon assimilation of six common deciduous woody species (three simple-leaved and three compound-leaved species) coexisting in a valley-savanna ecosystem with a dry-hot environment in Southwest China. This ecosystem is dominated by deciduous woody species, with some evergreen woody species co-occurring [19]. Our objectives were to test: (1) whether leaf photosynthetic rate and stomatal conductance were higher in compound-leaved species than in simple-leaved species, and (2) how simple- and compound-leaved species differ in water and nutrient use efficiencies.

We expected that compound leaves exhibit higher photosynthetic capacity and nutrient use efficiency, but lower water use efficiency than simple leaves.

2. Materials and Methods

2.1. Study Site

The present study was carried out in Yuanjiang Savanna Ecosystem Research Station (YSERS; 23°28' N, 102°10' E, 481 m a.s.l.) of Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, southwestern China. According to YSERS (2012–2019), the mean annual temperature is 24.9 °C, the extremely maximum temperature is 45.0 °C (including 35 °C for more than 100 days during a year), the extremely minimum temperature is 3.6 °C, the maximum ground temperature is 77.8 °C, the minimum ground temperature is 2.1 °C, the air humidity is 67%, the mean annual precipitation is 732.8 mm (the rainy season from May to October, accounting for 77.9% of the precipitation), the potential evaporation is 1750 mm, and the sunshine hours are 2350 h. The soil is a ferralic cambisol with a soil profile of pH 6.63–7.75, 0.196–0.427% nitrogen, 0.055–0.12% phosphorus and 1.601–1.737% potassium at 0–20 cm depth. The station area possesses typical well-preserved hot-dry valley savanna vegetation.

We chose the 6 most common deciduous tree species around YSERS, including 3 compound-leaved species *Bischofia polycarpa*, *Cipadessa baccifera*, *Campylotropis delavayi* and 3 simple-leaved species *Bauhinia brachycarpa*, *Strophoblachia fimbricalyx*, *Trigonostemon tuberculatus* for the study (Table 1). All measurements were made of canopy leaves from 3–5 individuals per species during July to September in 2015.

Table 1. A list of compound-leaved (CL) and simple-leaved (SL) species studied.

Species	Family	Leaf Type
<i>Bauhinia brachycarpa</i>	Leguminosae	SL
<i>Strophoblachia fimbricalyx</i>	Euphorbiaceae	SL
<i>Trigonostemon tuberculatus</i>	Euphorbiaceae	SL
<i>Bischofia polycarpa</i>	Euphorbiaceae	CL
<i>Cipadessa baccifera</i>	Meliaceae	CL
<i>Campylotropis delavayi</i>	Leguminosae	CL

2.2. Leaf Mass Per Area

We chose 4–5 leaves or leaflets per species and used a portable scanner (CanoScan 9000F Mark II, CANON, Tokyo, Japan) to scan leaves at 300 dpi resolution. Leaf area was measured by the ImageJ software (National Institutes of Health, Bethesda, MD, USA). We then oven-dried leaf samples at 80 °C for at least 48 h to get the leaf dry mass. Leaf mass per area (LMA, g m^{−2}) was calculated as leaf dry mass divided by leaf area.

2.3. Leaf Gas Exchange

Area-based maximum photosynthetic rate (A_a , $\mu\text{mol m}^{-2} \text{s}^{-1}$) and stomatal conductance (g_s , $\text{mol m}^{-2} \text{s}^{-1}$) were measured between solar time 08:00 and 11:00 a.m. using a portable photosynthesis measurement system (Li-6400XT, LI-COR, Lincoln, NE, USA) with a 6400-02B light source that included both red and blue LEDs. Six sun-exposed mature leaves of three individuals (two leaves per individual) of each species were chosen. During measurement, reference CO₂ was maintained at 400 $\mu\text{mol mol}^{-1}$ via a 6400-01 CO₂ injector System and light intensity was set at 1200 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Air temperatures and relative humidity during the measurements were around 31 °C and 60%, respectively. Mass-based maximum photosynthetic rate (A_m , $\text{nmol g}^{-1} \text{s}^{-1}$) was calculated as A_a/LMA .

2.4. Leaf Nutrients

Mature leaf samples with petioles and main veins removed were used to analyze leaf carbon, nitrogen and phosphorus concentrations. Fresh leaf samples were first wiped clean, oven-dried at 80 °C for 48 h, crushed, and ground to pass a 60-mesh sieve (pore size is 0.25 mm). Carbon (C, mg g⁻¹) and nitrogen concentrations per mass (N, mg g⁻¹) were measured by a C-N analyzer (Vario MAX CN, Elementar Analysensysteme GmbH, Hanau, Germany). Phosphorus concentration per mass (P, mg g⁻¹) was measured by an inductively coupled plasma atomic-emission spectrometer (iCAP6300, Thermo Fisher Scientific, Cambridge, UK). Leaf carbon to nitrogen concentration ratio (C/N) and nitrogen to phosphorus concentration ratio (N/P) were then calculated. We used LMA to calculate area-based carbon (C_a , mg m⁻²), nitrogen (N_a , mg m⁻²) and phosphorus concentrations (P_a , mg m⁻²).

2.5. Leaf Water and Nutrient Use Efficiencies

Other leaf samples were passed through a 100-mesh sieve for measurement of stable carbon isotopic composition ($\delta^{13}\text{C}$) using an isotope ratio mass spectrometer (IsoPrime100, Isoprime Ltd., Cheshire, Manchester, UK), using Pee Dee Belemnite (PDB) as a standard. $\delta^{13}\text{C}$ was calculated as:

$$\delta^{13}\text{C} (\text{‰}) = [(R_{\text{sample}})/(R_{\text{standard}}) - 1] \times 1000 \quad (1)$$

where R_{sample} and R_{standard} are the ratios of $^{13}\text{C}/^{12}\text{C}$ in the sample and in the PDB standard, respectively. Leaf $\delta^{13}\text{C}$ is used as an indicator of long-term water use efficiency integrated over the lifetime of a leaf [25]. Plants with less negative $\delta^{13}\text{C}$ values generally possess higher time-integrated water use efficiency [25].

Intrinsic water use efficiency (WUE_i) was calculated as A_a/g_s . Photosynthetic nitrogen use efficiency (PNUE) and photosynthetic phosphorus use efficiency (PPUE) were calculated as $A_m \times 14/N$ and $A_m \times 31/P$, respectively.

2.6. Data Analysis

All trait values of each species were averaged and then log₁₀-transformed to improve the normality. During analysis, we converted $\delta^{13}\text{C}$ from negative to positive by multiplying -1 for further analysis. The independent-samples *t*-test was used to test for the differences in 16 leaf traits between two leaf forms through the 't.test' function in the 'stats' package in R. Pearson's correlation was used to test for the relationships between pair of traits via 'corr.test' function in 'psych' package in R. All analyses were performed in R v.4.0.0 (R Core Team, 2020).

3. Results

There was no significant difference in LMA between compound- and simple-leaved species (Figure 1a, Table 2, $p = 0.76$). Compound-leaved (CL) species didn't have significantly higher leaf stomatal conductance (g_s) and photosynthetic rate (A_a , A_m) than co-occurring simple-leaved (SL) species (Figure 1b–d, $p = 0.88$, 0.94 and 0.64 , respectively). Compound- and simple-leaved species showed comparable water use efficiency (both WUE_i and $\delta^{13}\text{C}$) (Figure 2, Table 2, $p = 0.72$ and 0.94 , respectively).

Table 2. Differences in leaf traits between compound-leaved species (CL) and simple-leaved species (SL).

Trait Name	Abbreviation	Unit	CL	SL	<i>t</i> -Values	<i>p</i> -Values
			Mean \pm SE	Mean \pm SE		
Leaf mass per area	LMA	g m ⁻²	89.23 \pm 20.66	76.90 \pm 12.90	0.34	0.76
Maximum photosynthetic rate per mass	A_m	nmol g ⁻¹ s ⁻¹	173.17 \pm 16.04	162.26 \pm 11.47	0.50	0.64
Maximum photosynthetic rate per area	A_a	$\mu\text{mol m}^{-2} \text{s}^{-1}$	13.35 \pm 3.71	12.5 \pm 2.35	0.09	0.94
Stomatal conductance per area	g_s	mol m ⁻² s ⁻¹	0.21 \pm 0.05	0.25 \pm 0.10	-0.17	0.88
Intrinsic water use efficiency	WUE_i	$\mu\text{mol mol}^{-1}$	62.09 \pm 5.78	58.73 \pm 13.84	0.40	0.72
Stable carbon isotopic composition	$\delta^{13}\text{C}$	‰	26.93 \pm 0.48	27.01 \pm 0.65	-0.09	0.94

Table 2. Cont.

Trait Name	Abbreviation	Unit	CL	SL	<i>t</i> -Values	<i>p</i> -Values
			Mean \pm SE	Mean \pm SE		
Leaf carbon concentration per mass	C	mg g ⁻¹	467.56 \pm 7.35	453.44 \pm 6.01	1.50	0.21
Leaf nitrogen concentration per mass	N	mg g ⁻¹	19.90 \pm 2.75	25.06 \pm 4.02	-1.12	0.33
Leaf phosphorus concentration per mass	P	mg g ⁻¹	1.29 \pm 0.46	1.81 \pm 0.35	-1.01	0.38
Photosynthetic N use efficiency	PNUE	μ mol mol ⁻¹ s ⁻¹	124.72 \pm 15.16	96.66 \pm 18.99	1.13	0.34
Photosynthetic P use efficiency	PPUE	mmol mol ⁻¹ s ⁻¹	5.20 \pm 1.73	3.08 \pm 0.80	1.12	0.33
Leaf carbon to nitrogen ratio	C/N		24.23 \pm 2.66	18.97 \pm 2.75	1.30	0.27
Leaf nitrogen to phosphorus ratio	N/P		17.90 \pm 3.91	14.86 \pm 3.01	0.58	0.60
Leaf carbon concentration per area	C _a	mg m ⁻²	41,432.06 \pm 9167.82	35,019.26 \pm 6373.80	0.44	0.69
Leaf nitrogen concentration per area	N _a	mg m ⁻²	1662.08 \pm 221.70	1893.22 \pm 314.62	-0.50	0.65
Leaf phosphorus concentration per area	P _a	mg m ⁻²	96.91 \pm 10.57	129.83 \pm 8.03	-2.27	0.11

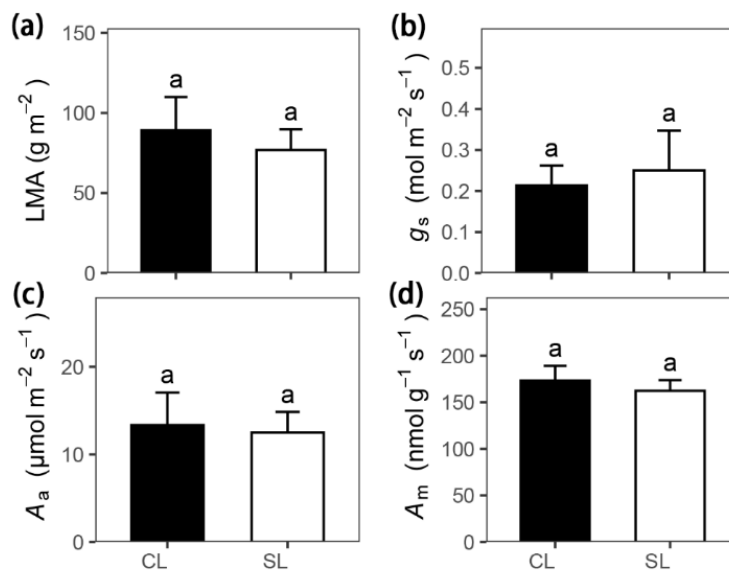


Figure 1. Average values of (a) leaf mass per area (LMA), (b) stomatal conductance (g_s), (c) area-based maximum photosynthetic rate (A_a), and (d) mass-based maximum photosynthetic rate (A_m) in compound-leaved (CL, black bar) and simple-leaved (SL, open bar) species. Bars are means + standard errors.

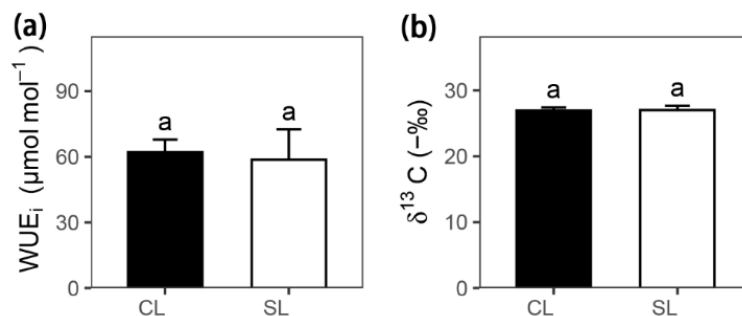


Figure 2. Average values of (a) intrinsic water use efficiency (WUE_i) and (b) stable carbon isotopic composition ($\delta^{13}C$) in compound-leaved (CL, black bar) and simple-leaved (SL, open bar) species. Bars are means + standard errors.

In addition, there was no significant differences in leaf carbon, nitrogen and phosphorus concentrations per mass (C, N, P) or per area (C_a , N_a , P_a) between simple- and compound-leaved species (Figure 3a–f, Table 2, $p = 0.21$, 0.33 , 0.38 , 0.69 , 0.65 and 0.11 , respectively). We found no significant differences in C/N, N/P, PNUE and PPUE between simple- and compound-leaved species as well (Figure 3g,h, $p = 0.27$ and 0.60 , and Figure 4, $p = 0.34$ and 0.33 , respectively, Table 2).

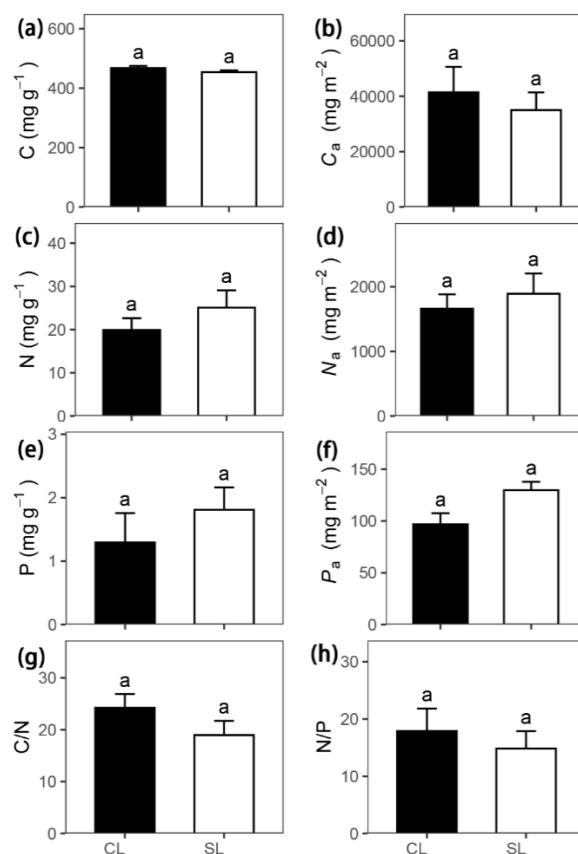


Figure 3. Average values of (a) carbon concentration per mass (C) and (b) per area (C_a), (c) nitrogen concentration per mass (N) and (d) per area (N_a), (e) phosphorus concentration per mass (P) and (f) per area (P_a), (g) leaf carbon concentration to nitrogen concentration ratio (C/N) and (h) leaf nitrogen concentration to phosphorus concentration ratio (N/P) in compound-leaved (CL, black bar) and simple-leaved (SL, open bar) species. Bars are means + standard errors.

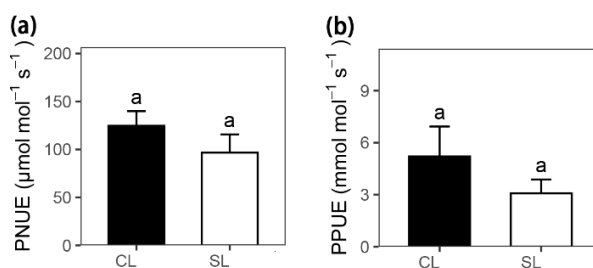


Figure 4. Average values of (a) photosynthetic nitrogen use efficiency (PNUE) and (b) photosynthetic phosphorus use efficiency (PPUE) in compound-leaved (CL, black bar) and simple-leaved (SL, open bar) species. Bars are means + standard errors.

Across these simple- and compound-leaved species, PNUE was significantly negatively related to P and P_a (Figure 5a,b, $p = 0.002$ and 0.024 , respectively), and significantly positively related to LMA (Figure 5c, $p = 0.048$). P was significantly negatively correlated with LMA (Figure 5d, $p = 0.009$). Across all six species, both LMA and g_s were significantly positively related to C_a (Figure 6a,b, $p < 0.001$ and 0.049 , respectively). A_a was significantly positively correlated with g_s (Figure 6d, $p = 0.046$), but not with LMA (Figure 6c, $p = 0.127$). Leaf N was less related to other leaf traits than leaf P; water use efficiency was not related to all other leaf traits (Table 3).

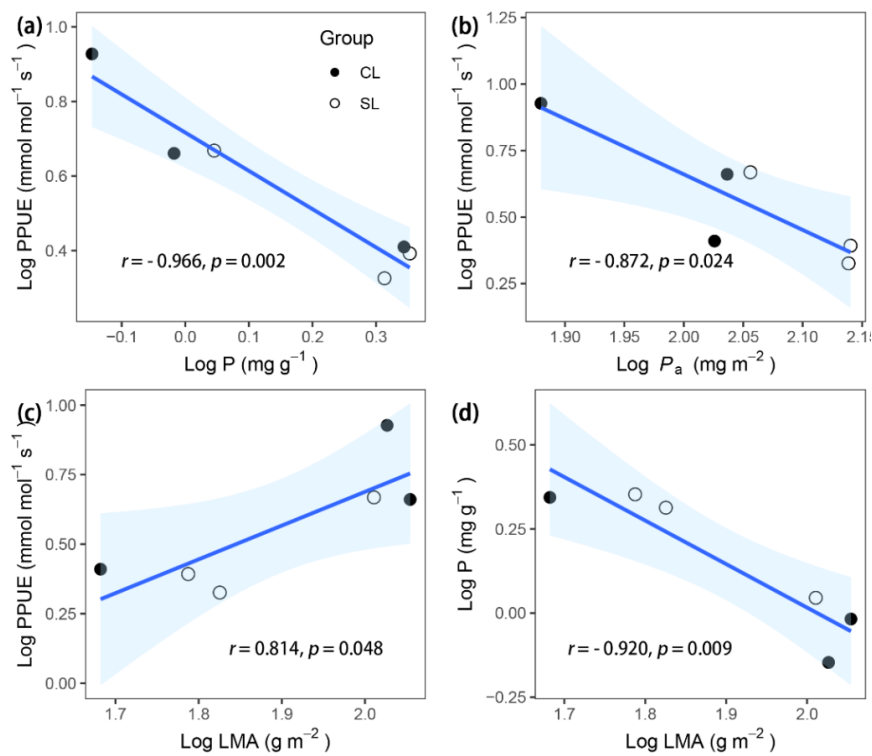


Figure 5. Log-log relationships of photosynthetic phosphorus use efficiency (PPUE) with (a) phosphorus concentration per mass (P), (b) phosphorus concentration per area (P_a), and (c) leaf mass per area (LMA), P concentration per mass with (d) LMA across six species studied. All data were log₁₀-transformed.

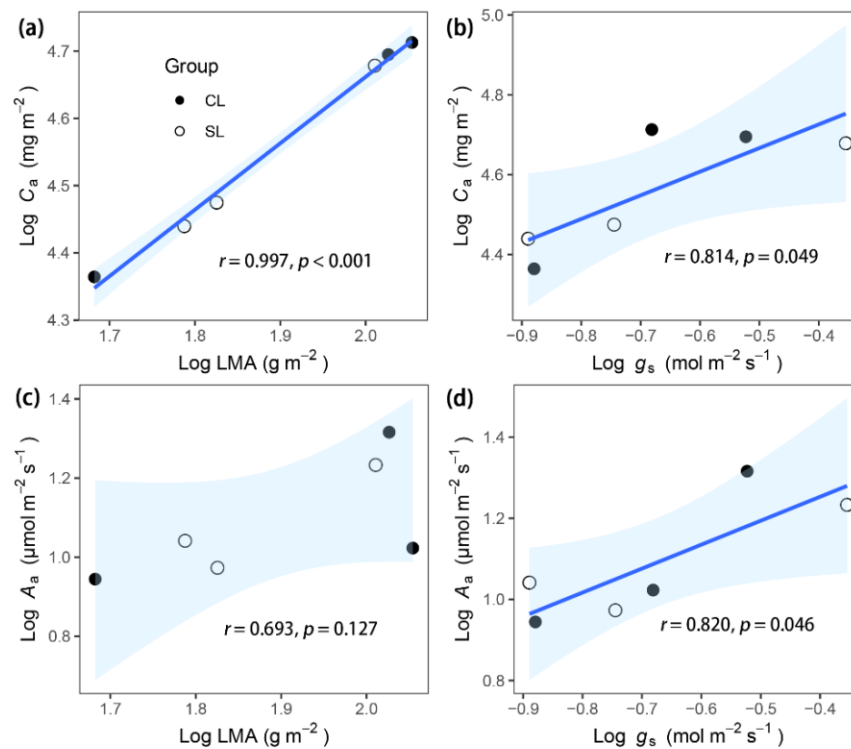


Figure 6. Log-log relationships of carbon concentration per area (C_a) with (a) leaf mass per area (LMA) and (b) leaf stomatal conductance (g_s), area-based maximum photosynthetic rate (A_a) with (c) LMA and (d) g_s across six species studied. All data were log₁₀-transformed.

Table 3. Coefficients of Pearson's correlation among leaf traits across six species.

	LMA	A _m	A _a	g _s	WUE _i	δ ¹³ C	C	N	P	PNUE	PPUE	C/N	N/P	C _a	N _a
A _m	−0.200														
A _a	0.693	0.475													
g _s	0.796	0.014	0.820*												
WUE _i	−0.511	0.565	−0.172	−0.705											
δ ¹³ C	−0.051	0.520	0.409	0.490	−0.338										
C	−0.150	0.585	0.167	0.135	−0.026	0.743									
N	−0.659	−0.279	−0.512	−0.309	−0.102	0.060	−0.142								
P	−0.920 **	−0.095	−0.789	−0.764	0.338	−0.091	−0.158	0.714							
PNUE	0.435	0.650	0.609	0.251	0.323	0.176	0.364	−0.911 *	−0.605						
PPUE	0.814*	0.349	0.866 *	0.723	−0.171	0.220	0.300	−0.744	−0.966 **	0.739					
C/N	0.629	0.337	0.519	0.318	0.097	0.022	0.248	−0.994 ***	−0.716	0.931 **	0.761				
N/P	0.802	−0.063	0.724	0.831 *	−0.533	0.166	0.117	−0.282	−0.874 *	0.196	0.806	0.289			
C _a	0.997 ***	−0.155	0.712	0.814 *	−0.518	0.008	−0.072	−0.676	−0.941 **	0.468	0.846 *	0.654	0.819 *		
N _a	0.703	−0.529	0.435	0.763	−0.774	−0.011	−0.334	0.071	−0.546	−0.284	0.377	−0.106	0.797	0.683	
P _a	−0.471	−0.536	−0.667	−0.446	−0.058	−0.287	−0.597	0.551	0.778	−0.666	−0.872 *	−0.605	−0.683	−0.523	−0.103

Notes: See Table 2 and text for trait abbreviations. Data were log₁₀-transformed before analysis. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

4. Discussion

Different from previous studies showing high photosynthetic rates and low water use efficiencies in compound-leaved species [11,26], we found overlaps in photosynthesis and water use efficiency between compound and simple-leaved trees in a savanna ecosystem in Southwest China. Our results suggest a convergence in leaf functional traits toward high water use efficiencies in dry and hot ecosystems. The overlap in functional traits related to water and nutrient use, carbon assimilation, and stress tolerance (e.g., LMA) between these two leaf forms may also suggest a similar response to a drier and hotter future in this region, as predicted by climate change models [27].

4.1. Comparable Photosynthetic Capacity between Simple- and Compound-Leaved Species

Previous studies have suggested that compound leaf form with multiple leaf laminas growing on one rachis has a potentially high photosynthetic capacity and growth rates [26]. Our results for savanna plants do not support this hypothesis. No differences in area- or mass-based maximum photosynthetic rates were found between simple- and compound-leaved species in this valley savanna. The simple and compound leaves also had similar maximum stomatal conductance and LMA. Consistent with our results, no significant differences in A_a and g_s were found between compound- and simple-leaved leguminous trees from a tropical seasonal rain forest with pronounced dry seasons [11]. However, a previous study in temperate forests has shown that, compared with co-occurring simple-leaved trees, compound-leaved species tend to have lower LMA and higher area-based maximum photosynthetic rates, which potentially contribute to their fast growth rates [11]. Malhado et al. (2010) also found that compound leaves are associated with faster diameter growth rates, constituting adaptive strategies that promote the rapid growth of the Amazon rain forest trees [2]. These findings together suggest that the differences between compound- and simple-leaved species in water use and carbon assimilation are site-specific, which may depend on the selecting forces working in a specific ecosystem [11,28]. For dry and hot savannas and other ecosystems with pronounced dry seasons, water deficits could be a significant environmental factor shaping the development of leaf functional traits. This selecting force imposed by water deficits and high transpiration demand may confer compound-leaved species conservative water use rather than high photosynthetic carbon assimilation [21].

4.2. Convergence in Photosynthetic Nutrient Use Strategy across Simple- and Compound-Leaved Species

Photosynthetic capacity is widely regarded to be limited by leaf nutrient contents, particularly by N [29,30]. For instance, in West African and Australia savannas, the photosynthetic capacity of plant species was limited by leaf N due to low soil N availability in local sites. However, we did not find significant N_a - A_a or N - A_m relationships across six savanna species. Other studies have also shown a varied or no relationship between leaf N and photosynthetic capacity [31–33]. In agreement with this, the drier the climate condition is, the weaker the relationship between photosynthetic capacity and leaf N becomes [34]. This lack of the relationship between leaf N and photosynthetic capacity may also be due to differences in N allocation to light capture, photosynthetic machinery within leaves or a proportionally greater leaf structural N investment associated with high LMA [31,35]. Plants with high LMA can allocate more N to the structure to increase major vein or mesophyll cell layers [36,37]. However, we found that compound- and simple-leaved species had comparable LMA in the dry-hot valley savanna, although some temperate compound-leaved species have significantly lower LMA than simple-leaved species [11]. High LMA in tropical savanna compound-leaved species is a characteristic of the dry and hot regions, probably because denser leaves associated with high LMA have lower water requirements to avoid wilting under water deficits and adapt to intermittent water availability [33,38], rather than contribute to growth [39]. Compound-leaved species tend to shed their leaves in facing water limitation (9,13). There is evidence that during the severe drought period, compound-leaved species have larger hydraulic safety margins in stems than in compound leaf petioles allowing plants to minimize the risk of hydraulic failure in the stem conduit network by sacrificing leaves [40].

Furthermore, there is evidence that leaf P has a stronger impact on leaf photosynthetic capacity than N in ecosystems with limited P availability [30,33,41,42]. In the present study, we found that leaf P was more strongly related to other leaf traits than leaf N. This is probably because of the low P availability of valley savanna soils [21,39]. The valley-savanna species have higher photosynthetic P use efficiency (PPUE) compared to rainforest tree species, which means a more economic utilization of limited resources, and high PPUE of valley-savanna species could be a long-term adaptation to dry and hot stresses in the savannas [39]. The valley-savanna species had consistently higher photosynthetic capacity and PPUE at a given stomatal conductance or leaf nutrients (N, P), which can lead to a convergence in photosynthetic and nutrient use strategies between simple- and compound-leaved species. We did find overlapping nutrient concentrations (N, P), nutrient use efficiency, and photosynthetic capacity between these two leaf forms. This may suggest that the compound leaves of valley-savanna plants have no advantages in photosynthetic physiology and nutrient use than simple leaf form.

4.3. Water Use Efficiency across Simple- and Compound-Leaved Species

Our previous results have shown that simple leaves present higher intrinsic water use efficiency (WUE_i) than compound leaves in temperate forest trees [11]. In this study, we found that there were no significant differences in WUE_i and long-term water use efficiency ($\delta^{13}\text{C}$ [25]) between simple- and compound-leaved groups. In the present study area, previous results also found that six plant species with different leaf phenology have similar long-term water use efficiency ($\delta^{13}\text{C}$) [21]. Additionally, these valley-savanna plants have higher leaf $\delta^{13}\text{C}$ than tropical rainforest tree species in the same region [39,43]. These results indicate that plants in the dry and hot habitats have a consistently higher water use efficiency than rainforest plants and tend to employ a more conservative water use strategy no matter what leaf form or phenology is. Interestingly, we found that water use efficiency is independent of other leaf traits. As an example, we found no relationship between leaf N- and water use efficiency in the present site with relatively high soil N availability, although additional N can lead to higher water use efficiency [39,44]. This is probably the reason why water use strategy overlaps between simple- and compound-leaved woody species in the dry-hot habitats. However, previous studies have shown that compound-leaved species have a higher leaf or the whole shoot hydraulic conductance than coexisting simple-leaved species, suggesting contrasting hydraulic efficiency between these two leaf forms (11,12). Further studies on plant hydraulic architecture are needed to explore variation and co-variation of hydraulic and photosynthetic capacity across more simple- and compound-leaved species.

5. Conclusions

Our study did not find significant differences in water- and nutrient-use strategy between deciduous simple- and compound-leaved species. Nor did we find significant differences in photosynthetic capacity between these two leaf forms. The ecophysiological advantages of being compound versus simple leaves seem to be weak in savannas, at least in the studied valley savanna with a dry and hot climate. Our results did not support the hypothesis of the advantage of compound leaves (e.g., fast growth hypothesis) over simple leaves [2,11]. Due to the overlap in photosynthetic water and nutrient use efficiencies between these two leaf forms, and the high selecting force for high water use efficiencies in savannas, a predicted drier future in this region will probably not change the relative abundance of the compound- and simple-leaved species. Ultimately, we suggest testing these long-held hypotheses about the compound and simple leaf form across a wider range of vegetation types and climate regions.

Author Contributions: H.-D.W. and J.-L.Z. conceived and designed the experiment. H.-D.W. and J.-L.Z. collected data. Y.-S.-D.W. and D.Y. analyzed the data. Y.-S.-D.W. and D.Y. wrote the manuscript. Y.-S.-D.W., D.Y., Y.-B.Z., S.-B.Z., Y.-J.Z., and J.-L.Z. revised this manuscript. All authors have read and agreed to the published version of the manuscript.

Funding: This work was supported by the Light of West China of the Chinese Academy of Sciences (2020000021), the National Natural Science Foundation of China (31870385, 31901285), and CAS 135 program (2017XTBG-F01).

Acknowledgments: The Public Technology Service Center, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences analyzed the foliar nutrient concentrations. Yuanjiang Savanna Ecosystem Research Station provided the climate and soil data.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Hareven, D.; Gutfinger, T.; Parnis, A.; Eshed, Y.; Lifschitz, E. The making of a compound leaf: Genetic manipulation of leaf architecture in tomato. *Cell* **1996**, *84*, 735–744. [\[CrossRef\]](#)
2. Malhado, A.C.M.; Whittaker, R.J.; Malhi, Y.; Ladle, R.J.; Ter Steege, H.; Phillips, O.; Aragao, L.E.O.C.; Baker, T.R.; Arroyo, L.; Almeida, S.; et al. Are compound leaves an adaptation to seasonal drought or to rapid growth? Evidence from the Amazon rain forest. *Glob. Ecol. Biogeogr.* **2010**, *19*, 852–862. [\[CrossRef\]](#)
3. Ogden, M.S.; Lacroix, C.R. Comparative development of simple and compound leaves in the genus *Cecropia*. *Botany* **2017**, *95*, 185–193. [\[CrossRef\]](#)
4. Bharathan, G.; Goliber, T.E.; Moore, C.; Kessler, S.; Pham, T.; Sinha, N.R. Homologies in leaf form inferred from *KNOX* gene expression during development. *Science* **2002**, *296*, 1858–1860. [\[CrossRef\]](#) [\[PubMed\]](#)
5. Nicotra, A.B.; Leigh, A.; Boyce, C.K.; Jones, C.S.; Niklas, K.J.; Royer, D.L.; Tsukaya, H. The evolution and functional significance of leaf shape in the angiosperms. *Funct. Plant Biol.* **2011**, *38*, 535–552. [\[CrossRef\]](#) [\[PubMed\]](#)
6. Wang, Y.; Jiao, Y.L. Keeping leaves in shape. *Nat. Plants* **2020**, *6*, 436–437. [\[CrossRef\]](#) [\[PubMed\]](#)
7. Niinemets, U. Are compound-leaved woody species inherently shade-intolerant? An analysis of species ecological requirements and foliar support costs. *Plant Ecol.* **1998**, *134*, 1–11. [\[CrossRef\]](#)
8. Niinemets, U.; Portsmuth, A.; Tobias, M. Leaf size modifies support biomass distribution among stems, petioles and mid-ribs in temperate plants. *New Phytol.* **2006**, *171*, 91–104. [\[CrossRef\]](#)
9. Givnish, T. Ecological aspects of plant morphology: Leaf form in relation to environment. *Acta Biotheor.* **1978**, *27*, 83–142.
10. Givnish, T.J. Leaf and canopy adaptations in tropical forests. In *Physiological Ecology of Plants of the Wet Tropics*, 1st ed.; Medina, E., Mooney, H.A., Vázquez-Yanes, C., Eds.; Springer: Dordrecht, The Netherlands, 1984; Volume 12, pp. 51–84. [\[CrossRef\]](#)
11. Yang, D.; Zhang, Y.J.; Song, J.; Niu, C.Y.; Hao, G.Y. Compound leaves are associated with high hydraulic conductance and photosynthetic capacity: Evidence from trees in Northeast China. *Tree Physiol.* **2019**, *39*, 729–739. [\[CrossRef\]](#)
12. Zhao, W.L.; Zhang, J.L.; Zhang, Y.J.; Cao, K.F. Analysis of photosynthesis–water relationship between simple- and compound-leaved leguminous trees. *Plant Sci. J.* **2019**, *37*, 628–636, (In Chinese with English Abstract). [\[CrossRef\]](#)
13. Stowe, L.G.; Brown, J.L. A geographic perspective on the ecology of compound leaves. *Evolution* **1981**, *35*, 818–821. [\[CrossRef\]](#) [\[PubMed\]](#)
14. Wright, I.J.; Falster, D.S.; Pickup, M.; Westoby, M. Cross-species patterns in the coordination between leaf and stem traits, and their implications for plant hydraulics. *Physiol. Plant.* **2006**, *127*, 445–456. [\[CrossRef\]](#)
15. Niinemets, Ü.; Portsmuth, A.; Tena, D.; Tobias, M.; Matesanz, S.; Valladares, F. Do we underestimate the importance of leaf size in plant economics? Disproportional scaling of support costs within the spectrum of leaf physiognomy. *Ann. Bot.* **2007**, *100*, 283–303. [\[CrossRef\]](#)
16. Huntley, B.J.; Walker, B.H. *Ecology of Tropical Savannas*, 1st ed.; Springer: Berlin/Heidelberg, Germany, 1982.
17. Silva, J.M.C.; Bates, J.M. Biogeographic patterns and conservation in the South American Cerrado: A tropical savanna hotspot. *BioScience* **2002**, *52*, 225–234. [\[CrossRef\]](#)
18. Furley, P. Tropical savannas. *Prog. Phys. Geogr.* **2006**, *30*, 105–121. [\[CrossRef\]](#)
19. Jin, Z.Z.; Ou, X.K. *Yuanjiang, Nuijiang, Jinshajiang, Lancangjiang: Vegetation of Dry–Hot Valley*, 1st ed.; Yunnan University Press & Yunnan Science and Technology Press: Kunming, China, 2000. (In Chinese)
20. Gates, D.M.; Schmerl, R.B. *Perspectives of Biophysical Ecology*, 1st ed.; Springer: Berlin/Heidelberg, Germany, 1980; p. 611.

21. Zhang, J.L.; Zhu, J.J.; Cao, K.F. Seasonal variation in photosynthesis in six woody species with different leaf phenology in a valley savanna in southwestern China. *Trees* **2007**, *21*, 631–643. [\[CrossRef\]](#)
22. Tezara, W.; Mitchell, V.J.; Driscoll, S.D.; Lawlor, D.W. Water stress inhibits plant photosynthesis by decreasing coupling factor and ATP. *Nature* **1999**, *401*, 914–917. [\[CrossRef\]](#)
23. Lawlor, D.W.; Cornic, G. Photosynthetic carbon assimilation and associated metabolism in relation to water deficits in higher plants. *Plant Cell Environ.* **2002**, *25*, 275–294. [\[CrossRef\]](#)
24. Zhang, Y.B.; Wu, H.D.; Yang, J.; Song, X.Y.; Yang, D.; He, F.L.; Zhang, J.L. Environmental filtering and spatial processes shape the beta diversity of liana communities in a valley savanna in southwest China. *Appl. Veg. Sci.* **2020**. (Early View). [\[CrossRef\]](#)
25. Farquhar, G.D.; Ehleringer, J.R.; Hubick, K.T. Carbon isotope discrimination and photosynthesis. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* **1989**, *40*, 503–537. [\[CrossRef\]](#)
26. Royer, D.L.; Wilf, P. Why do toothed leaves correlate with cold climates? Gas exchange at leaf margins provides new insights into a classic paleotemperature proxy. *Int. J. Plant Sci.* **2006**, *167*, 11–18. [\[CrossRef\]](#)
27. Zomer, R.J.; Xu, J.C.; Wang, M.C.; Trabucco, A.; Li, Z.Q. Projected impact of climate change on the effectiveness of the existing protected area network for biodiversity conservation within Yunnan Province, China. *Biol. Conserv.* **2015**, *184*, 335–345. [\[CrossRef\]](#)
28. Song, J.; Yang, D.; Niu, C.Y.; Zhang, W.W.; Wang, M.; Hao, G.Y. Correlation between leaf size and hydraulic architecture in five compound-leaved tree species of a temperate forest in NE China. *For. Ecol. Manag.* **2018**, *418*, 63–72. [\[CrossRef\]](#)
29. Bahar, N.H.A.; Ishida, F.Y.; Weerasinghe, L.K.; Guerrieri, R.; O’Sullivan, O.S.; Bloomfield, K.J.; Asner, G.P.; Martin, R.E.; Lloyd, J.; Malhi, Y.; et al. Leaf-level photosynthetic capacity in lowland Amazonian and high-elevation Andean tropical moist forests of Peru. *New Phytol.* **2017**, *214*, 1002–1018. [\[CrossRef\]](#)
30. Norby, R.J.; Gu, L.H.; Haworth, I.C.; Jensen, A.M.; Turner, B.L.; Walker, A.P.; Warren, J.M.; Weston, D.J.; Xu, C.G.; Winter, K. Informing models through empirical relationships between foliar phosphorus, nitrogen and photosynthesis across diverse woody species in tropical forests of Panama. *New Phytol.* **2017**, *215*, 1425–1437. [\[CrossRef\]](#) [\[PubMed\]](#)
31. Coste, S.; Roggy, J.C.; Imbert, P.; Born, C.; Bonal, D.; Dreyer, E. Leaf photosynthetic traits of 14 tropical rain forest species in relation to leaf nitrogen concentration and shade tolerance. *Tree Physiol.* **2005**, *25*, 1127–1137. [\[CrossRef\]](#) [\[PubMed\]](#)
32. Domingues, T.F.; Ishida, F.Y.; Feldpausch, T.R.; Grace, J.; Meir, P.; Saiz, G.; Sene, O.; Schrod, F.; Sonke, B.; Taedoumg, H.; et al. Biome-specific effects of nitrogen and phosphorus on the photosynthetic characteristics of trees at a forest-savanna boundary in Cameroon. *Oecologia* **2015**, *178*, 659–672. [\[CrossRef\]](#) [\[PubMed\]](#)
33. Gvozdevaite, A.; Oliveras, I.; Domingues, T.F.; Peprah, T.; Boakye, M.; Afriyie, L.; Peixoto, K.D.; de Farias, J.; de Oliveira, E.A.; Farias, C.C.A.; et al. Leaf-level photosynthetic capacity dynamics in relation to soil and foliar nutrients along forest-savanna boundaries in Ghana and Brazil. *Tree Physiol.* **2018**, *38*, 1912–1925. [\[CrossRef\]](#) [\[PubMed\]](#)
34. Prentice, I.C.; Dong, N.; Gleason, S.M.; Maire, V.; Wright, I.J. Balancing the costs of carbon gain and water transport: Testing a new theoretical framework for plant functional ecology. *Ecol. Lett.* **2014**, *17*, 82–91. [\[CrossRef\]](#)
35. Dusenage, M.E.; Wallin, G.; Gardesten, J.; Niyonzima, F.; Adolfsson, L.; Nsabimana, D.; Uddling, J. Photosynthetic capacity of tropical montane tree species in relation to leaf nutrients, successional strategy and growth temperature. *Oecologia* **2015**, *177*, 1183–1194. [\[CrossRef\]](#) [\[PubMed\]](#)
36. Milla-Moreno, E.A.; McKown, A.D.; Guy, R.D.; Soolanayakanahally, R.Y. Leaf mass per area predicts palisade structural properties linked to mesophyll conductance in balsam poplar (*Populus balsamifera* L.). *Botany* **2016**, *94*, 225–239. [\[CrossRef\]](#)
37. John, G.P.; Scoffoni, C.; Buckley, T.N.; Villar, R.; Poorter, H.; Sack, L. The anatomical and compositional basis of leaf mass per area. *Ecol. Lett.* **2017**, *20*, 412–425. [\[CrossRef\]](#) [\[PubMed\]](#)
38. Poorter, H.; Niinemets, U.; Poorter, L.; Wright, I.J.; Villar, R. Causes and consequences of variation in leaf mass per area (LMA): A meta-analysis. *New Phytol.* **2009**, *182*, 565–588. [\[CrossRef\]](#)
39. Zhang, J.L.; Poorter, L.; Cao, K.F. Productive leaf functional traits of Chinese savanna species. *Plant Ecol.* **2012**, *213*, 1449–1460. [\[CrossRef\]](#)

40. Liu, Y.Y.; Song, J.; Wang, M.; Li, N.; Niu, C.Y.; Hao, G.Y. Coordination of xylem hydraulics and stomatal regulation in keeping the integrity of xylem water transport in shoots of two compound-leaved tree species. *Tree Physiol.* **2015**, *35*, 1333–1342. [[CrossRef](#)]
41. Domingues, T.F.; Meir, P.; Feldpausch, T.R.; Saiz, G.; Veenendaal, E.M.; Schrod, F.; Bird, M.; Djabbley, G.; Hien, F.; Compaore, H.; et al. Co-limitation of photosynthetic capacity by nitrogen and phosphorus in West Africa woodlands. *Plant Cell Environ.* **2010**, *33*, 959–980. [[CrossRef](#)]
42. Walker, A.P.; Quai, T.; Van Bodegom, P.M.; De Kauwe, M.G.; Keenan, T.F.; Joiner, J.; Lomas, M.R.; MacBean, N.; Xu, C.G.; Yang, X.J.; et al. The impact of alternative trait-scaling hypotheses for the maximum photosynthetic carboxylation rate (V_{cmax}) on global gross primary production. *New Phytol.* **2017**, *215*, 1370–1386. [[CrossRef](#)]
43. Qu, C.M.; Han, X.G.; Su, B.; Huang, J.H.; Jiang, G.M. The characteristics of foliar $\delta^{13}\text{C}$ values of plants and plant water use efficiency indicated by $\delta^{13}\text{C}$ values in two fragmented rainforests in Xishuangbanna, Yunnan. *Acta. Bot. Sin.* **2001**, *43*, 186–192, (In Chinese with English Abstract). [[CrossRef](#)]
44. Adams, M.A.; Turnbull, T.L.; Sprent, J.I.; Buchmann, N. Legumes are different: Leaf nitrogen, photosynthesis, and water use efficiency. *Proc. Natl. Acad. Sci. USA* **2016**, *113*, 4098–4103. [[CrossRef](#)]

Publisher's Note: MDPI stays neutral with regard to jurisdictional claims in published maps and institutional affiliations.



© 2020 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<http://creativecommons.org/licenses/by/4.0/>).