

Leaf morphology correlates with water and light availability: What consequences for simple and compound leaves?

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Abstract

Leaves are organs sensitive to environmental changes in the process of evolution and may exhibit phenotypic plasticity as a response to abiotic stress. However, affirmation of leaf morphological plasticity and its regulations in different environments are still unclear. We performed a simulated experiment to study the variations of leaf morphology in different gradients of water and light availability. Considering different types of leaves and venation, we chose pinnate-veined simple leaves of *Quercus acutissima* and compound leaves of *Robinia pseudoacacia* as the study objects. The morphological parameters we investigated include leaf size, shape and venation pattern which can be easily measured in the field. Significant variations occurred in many parameters due to the effects of the environment and/or allometry. There were broadly consistent trends for leaf morphological variations along the gradients. The leaf size became smaller with a short supply of resources. Leaf elongation and fractions of the lamina area altered to enhance resources acquisition and conservation. Trade-offs between investments in support and functional structures optimized the venation pattern of major and minor veins. Leaflets partially played a role such as leaf teeth, for they are not only individual units, but also a part of the compound leaf. We suggest that more or less the same trends in morphological variations may be an important explanation for coexisting species to adapt to similar habitats and form the niche differentiation.

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Keywords: Environmental correlation; Leaf morphological trait; Leaf type; Venation pattern; *Quercus acutissima*; *Robinia pseudoacacia*

1. Introduction

Under abiotic stress, plants alter their physiology, morphology and development in response to environmental changes. These repertoires make the ecological breadth of plant species wider for each habitat type [1,2]. Leaves are important organs for photosynthesis and play an important role in survival and growth of a plant. The leaf shape and structure are defined mainly in a brief period of primary morphogenesis based on the possible role of reaction–diffusion systems and can be altered by the

allometric expansion [3,4]. Phenotypic plasticity also occurred to produce a range of leaf traits that are environmentally affected [5,6].

Many previous studies have revealed that variations in leaf traits are the result of adapting to growth habitats [7,8]. Recent studies in plant traits have found that some relationships between specific leaf traits are globally repeated despite large variations in the values of the traits across individual species with very diverse phylogenetic, biogeographical and environmental affinities [9,10]. Leaf traits can thus provide a link between various environmental factors and leaf functions [11]. They have been widely used in functional–structural plant models [12,13] and have become the proxies for reconstructing paleoclimates or predicting global warming [14,15].

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The correlation of visible leaf traits such as size, dimension, margin and venation characteristics to climate still need to be further understood. Meanwhile, defining such leaf traits to environmental changes will only be a useful management tool if the key traits are easily recognizable in the field. Leaf physiognomy can be regarded as an excellent tool for ecological studies [16]. The geometric measurement of leaf morphology should receive much attention in future because of its ease of measurement and interpretation.

There are so many types of leaves in nature, from blades to needles. Differences in leaf size can significantly alter whole-lamina- and whole-leaf-integrated chemical and structural characteristics and thereby modify general scaling relationships between plant structure, chemistry and function [17]. Theoretical studies suggest that, for a common biomass investment in major veins, palmate- and parallel-veined leaves are hydraulically and mechanically more efficient than pinnate-veined leaves due to a more uniform distribution of major veins in parallel/palmate-veined leaves [18]. So, the minor veins play a more important part in leaf support and will be more sensitive to environmental variations. Flowering plants can have either simple or compound leaves. Leaflets originate on compound leaves in a manner very similar to that of leaf lobes initiation in simple leaves [19]. Whitfield suggested that perhaps the most striking aspect to be investigated further was the different ‘decisions’ made by different plants with different leaves in the same places [15].

In this study, we chose leaves from *Quercus acutissima* Carr. and *Robinia pseudoacacia* L. for the research of leaf morphological variations. The two plant species usually form the mixed forests in north China. The former species belongs to the family Fagaceae, and its leaf type is the simple leaf. The latter species belongs to the family Leguminosae, and its leaf type is the compound leaf. The venation patterns are both pinnate. The objective of this study was (1) to investigate whether leaf morphological differences would occur; (2) to find out which reaction norms would underlie variations of leaf shape and venation pattern and (3) to distinguish the possible different responses among different leaf type species by comparing the simple leaf with the compound leaf in different gradients of water and light availability.

2. Materials and methods

2.1. Study site

The study was conducted at the Fanggan Research Station of Shandong University, Shandong Province, China (36°26′N, 117°27′E). The site is characterized by a warm temperate monsoon climate, with a mean annual temperature of 13±1 °C and an average annual precipitation of ca. 600–850 mm, mostly during the summer. The soil type of this area is yellow cinnamon soil, and the parent material is limestone [20].

Sawtooth oak (*Q. acutissima*) and black locust (*R. pseudoacacia*) are the predominant deciduous broadleaf species in this area [21]. The canopy of the mixed forest has a dominant layer reaching 14 m and crown lower limits at about 9 m. The leaf area index (LAI) was 5.12 when the trees were flourishing in August. In the shrub layer of the understory, *Vitex negundo* L. var. *heterophylla* (Franch) Rehd. and *Zizyphus jujuba* Mill. var. *spinosa* (Bge.) Hu ex H.F. Chow are abundant.

2.2. Plant materials

Acorns of *Q. acutissima* and seeds of *R. pseudoacacia* were collected from a hill near the research station in early spring and planted in plastic pots (9 l volume, 32 cm × 29 cm, height × diameter). The soil contained a 64:22:14 (v/v/v) mixture of humic soil, sand and loam. Its saturated water content was 36% by mass, the largest volumetric water content was 28%, and the porosity was 68%. The pH was 4.4, and the major chemical components included 88.4 g of organic matter, 3.7 g of total nitrogen and 42.3 mg of available phosphorus per kilogram. All of the pots were irrigated regularly and subjected to weed control before the beginning of the experiment.

2.3. Experimental design

The experiment was carried out during July and September 2007. The seedlings were submitted to water and light-control experiments. Water was withheld from the drought groups until the soil moisture reached 50%, 30% and 10% of field capacity, while the well-watered groups received daily irrigation to maintain soil water content between 70% and 80% of field capacity. All of the pots were moved into a rainout shelter in order to avoid the disturbance of precipitation. The soil water content was controlled by a gravimetric probe, and the pots were weighed daily to maintain the four different water contents.

The light-control treatment was conducted in shade shelters covered by plastic films or woven black nylon nets. The frame of the shelter was 5.0 × 2.5 × 3.0 m (length × width × height) and built replicated to avoid pseudoreplication. The microclimate was monitored using a micro-quantum sensor and temperature sensor of Mini-PAM (Walz GmbH, Effeltrich, Germany). The average photosynthetic active radiations (PAR) measured from 07:00 to 16:00 (local time) were 544 ± 71, 361 ± 17 and 56 ± 6.7 μmol m⁻² s⁻¹ in the open field, under plastic films and nylon nets, respectively. The light transmission ratios were 66% and 10% under the stress condition compared to the control. There was no significant difference ($P = 0.534$) in air temperature between the three light gradients (32.8 ± 0.46, 32.4 ± 0.40, and 32.1 ± 0.39 °C) as determined by analysis of variance.

In order to quantify the gradients of water and light availability, we chose relative water content (RWC) and relative light intensity (RLI) as the standards. RWC was

calculated by averaging the diurnal soil water content of the sampled seedlings. The average light intensity of sampled seedlings was obtained by measuring PAR in four directions where the seedlings were located. RLI was then calculated by dividing average light intensity with the maximal value. Ten pots were randomly assigned to each treatment of water and light availability. After a 2-month treatment period, 15 simple leaves and 20 leaflets from four compound leaves per treatment were taken for morphological measurements.

2.4. Morphological measurements

Leaf area was measured with a CI-203 laser area meter (CID Inc., Washington, USA). The linear measurement was taken using a digital caliper. Leaf dry mass was measured after oven drying at 80 °C for 48 h. Detailed information of morphological parameters measurements and definitions is shown in Fig. 1 and Table 1.

2.5. Statistical analysis

Analysis of covariance (ANCOVA) was used to test for differences between the gradients of water and light avail-

ability in morphological parameters in relation to the leaf area was used as the covariate [22]. We used linear and non-linear regression analyses in the form $y = a + bx$ and $y = a + b_1x + b_2x^2$ to test for statistical relationships between leaf morphological variables and different gradients of water and light availability. Regression fits and associated r^2 and P values were given in each panel. All regressions were considered significant at $P < 0.05$. All statistical analyses were done with the SPSS 13.0 software package (SPSS Inc., Chicago, USA). Plots were drawn using the Origin 7.5 software (OriginLab Co., Massachusetts, USA).

3. Results

The results of the one-way ANCOVA are given in Tables 2 and 3 for effects of different gradients of water and light availability on leaf morphological parameters by distinguishing the effect of allometry under different treatments. SLA and LL/LPL showed significant differences due to the main effects under both treatments for *Q. acutissima*. The water effect on LMF was also significantly different. The main effects on *R. pseudoacacia*, LWD, NLT and MDV were significantly different in the

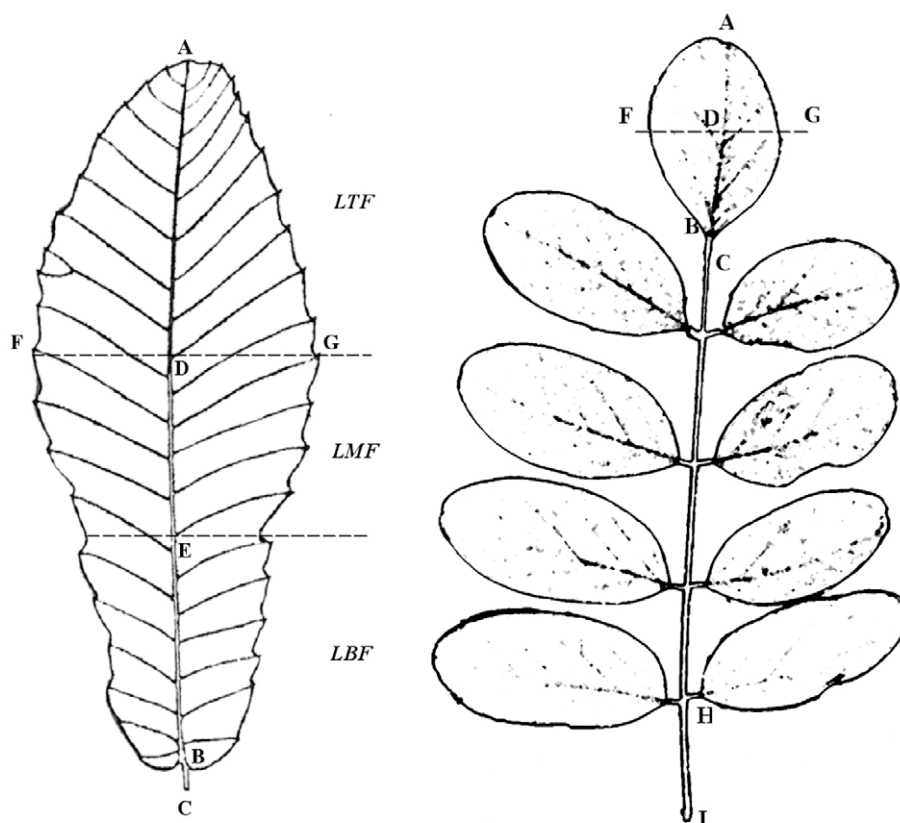


Fig. 1. Illustrated diagram of leaf morphology measurements in *Q. acutissima* (left) and *R. pseudoacacia* (right). The dashed lines perpendicular to the midrib indicate the widest (above) and bulgy (below) part of the leaf lamina. The two lines are determined by the angles between the midrib and the edge of the lamina. The positions where the angle is the smallest and the largest represent the widest and bulgy part of the leaf lamina, respectively. The leaf is divided into three fractions by these two lines. Only the widest division is measured in the leaflet of *R. pseudoacacia*. The capital letters along the lines represent the positions located at the midrib, leaf axis or the edge of the lamina. See Table 1 for more details.

Table 1
Leaf morphological parameters and their definitions.

Variable	Definition
LA (cm ²)	Leaf area
LLA (cm ²)	Leaflet area (for <i>R. pseudoacacia</i>)
CLA [§] (cm ²)	Compound leaf area (for <i>R. pseudoacacia</i>)
LDM (g)	Leaf dry mass
CLDM [§] (g)	Compound leaf dry mass (for <i>R. pseudoacacia</i>)
SLA [§] (cm ² g ⁻¹)	Specific leaf area (ratio of leaf area to leaf dry mass)
LL (cm)	Leaf length = <i>AB</i>
LW (cm)	Leaf width = <i>FG</i>
LPL (cm)	Leaf petiole length = <i>BC</i>
CLPL [§] (cm)	Compound leaf petiole length = <i>HI</i> (for <i>R. pseudoacacia</i>)
LE	Leaf elongation (ratio of leaf length to leaf width)
LL/LPL	Leaf length to petiole length ratio
LAX/CLPL [§]	Leaf rachis to petiole length ratio = <i>CH/HI</i> (for <i>R. pseudoacacia</i>)
LWD	Leaf widest division = <i>AD/BD</i>
LBD	Leaf bulgy division = <i>AE/BE</i> (for <i>Q. acutissima</i>)
LTF (%)	Leaf top fraction = <i>AD/AB</i> (for <i>Q. acutissima</i>)
LMF (%)	Leaf middle fraction = <i>DE/AB</i> (for <i>Q. acutissima</i>)
LBF (%)	Leaf bottom fraction = <i>BE/AB</i> (for <i>Q. acutissima</i>)
NLT [§]	Number of leaf teeth (for <i>Q. acutissima</i>)
	Number of leaflets (for <i>R. pseudoacacia</i>)
MDV [§] (cm)	Mean distance between veins = <i>2AB/(NLT + 1)</i> (for <i>Q. acutissima</i>)
	Mean distance between leaflets = <i>2CI/(NLT + 1)</i> (for <i>R. pseudoacacia</i>)

Special variables for the species are emphasized. Variables, which are calculated for compound leaf measurements, are marked with [§]. The two capital letters in the definition demonstrate the linear distance between the corresponding two points located in Fig. 1.

gradients of water availability, whereas only LW, CLPL and MDV were not different in the gradients of light availability.

The differences of LL and LW were derived from the differences of leaf area in spite of water and light treatments, both for *Q. acutissima* and *R. pseudoacacia*. The significant difference of MDV disappeared at a common leaf area in spite of water and light treatments for *Q. acutissima*. The allometric relationships between leaflet area and LDM, LPL and LE were also significantly observed in the gradients of water availability for *R. pseudoacacia*. LDM and LPL of *Q. acutissima* were affected by both treatments and allometry. Effects of leaf area on LDM, LPL, LL/LPL, LAX/CLPL and LWD concurred in the gradients of light availability for *R. pseudoacacia*.

LA linearly increased with water availability for *Q. acutissima* (Fig. 2, $r^2 = 0.43$, $P < 0.00$). On the contrary, there was not a significant linear relationship between LA and RWC for *R. pseudoacacia* ($r^2 = 0.02$, $P = 0.65$). LDM ($r^2 = 0.45$, $P < 0.00$), SLA ($r^2 = 0.30$, $P < 0.00$), LL ($r^2 = 0.34$, $P < 0.00$), LW ($r^2 = 0.36$, $P < 0.00$) and LPL ($r^2 = 0.55$, $P < 0.00$) were positively correlated with water availability for *Q. acutissima*, but not for *R. pseudoacacia* ($r^2 < 0.03$, $P > 0.14$) because of the size-dependent responses to treatments.

Neither LE ($r^2 < 0.01$, $P > 0.29$) nor LWD ($r^2 < 0.03$, $P > 0.23$) was correlated with water availability for both *Q. acutissima* and *R. pseudoacacia* (Fig. 2). LPL was negatively ($r^2 = 0.33$, $P < 0.00$) and MDV was positively

Table 2
One-way ANCOVAs of the effects of different gradients of water availability on leaf morphological parameters of *Q. acutissima* and *R. pseudoacacia* with leaf area and leaflet or compound leaf area as the covariates.

Variable	<i>Q. acutissima</i>				<i>R. pseudoacacia</i>			
	Water effect		Covariate		Water effect		Covariate	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
LDM (g)	3.84	0.014 [*]	55.36	0.000 ^{***}	0.84	0.501 ^{ns}	55.76	0.000 ^{***}
SLA (cm ² g ⁻¹)	5.98	0.001 ^{***}	0.97	0.329 ^{ns}	0.68	0.580 ^{ns}	0.01	0.954 ^{ns}
LL (cm)	2.47	0.072 ^{ns}	204.42	0.000 ^{***}	0.16	0.922 ^{ns}	207.35	0.000 ^{***}
LW (cm)	1.01	0.397 ^{ns}	154.39	0.000 ^{***}	0.67	0.575 ^{ns}	343.73	0.000 ^{***}
LPL (cm)	7.65	0.000 ^{***}	12.93	0.001 ^{***}	1.50	0.223 ^{ns}	14.77	0.000 ^{***}
CLPL (cm)	—	—	—	—	1.37	0.303 ^{ns}	0.20	0.667 ^{ns}
LE	1.46	0.235 ^{ns}	0.13	0.722 ^{ns}	0.29	0.831 ^{ns}	4.92	0.030 [*]
LL/LPL	8.21	0.000 ^{***}	1.34	0.252 ^{ns}	1.84	0.146 ^{ns}	3.79	0.055 ^{ns}
LAX/CLPL	—	—	—	—	1.09	0.395 ^{ns}	0.09	0.769 ^{ns}
LWD	0.65	0.589 ^{ns}	0.14	0.708 ^{ns}	6.39	0.001 ^{***}	2.38	0.127 ^{ns}
LBD	2.30	0.088 ^{ns}	0.04	0.840 ^{ns}	—	—	—	—
LTF (%)	1.59	0.201 ^{ns}	0.02	0.880 ^{ns}	—	—	—	—
LMF (%)	3.63	0.018 [*]	0.08	0.777 ^{ns}	—	—	—	—
LBF (%)	0.56	0.646 ^{ns}	0.15	0.700 ^{ns}	—	—	—	—
NLT	0.21	0.893 ^{ns}	0.61	0.439 ^{ns}	5.59	0.014 [*]	0.44	0.520 ^{ns}
MDV (cm)	0.21	0.887 ^{ns}	12.26	0.001 ^{***}	4.59	0.026 [*]	4.49	0.058 ^{ns}

$n = 60$ for variables of *Q. acutissima*. $n = 16$ for variables of the compound leaf and $n = 80$ for variables of the leaflet of *R. pseudoacacia*.

Significance level:

^{ns} $P > 0.05$.

^{*} $P < 0.05$.

^{***} $P < 0.001$.

Table 3

One-way ANCOVAs of the effects of different gradients of light availability on leaf morphological parameters of *Q. acutissima* and *R. pseudoacacia* with leaf area and leaflet or compound leaf area as the covariates.

Variable	<i>Q. acutissima</i>				<i>R. pseudoacacia</i>			
	Light effect		Covariate		Light effect		Covariate	
	F	P	F	P	F	P	F	P
LDM (g)	17.72	0.000***	33.02	0.000***	4.42	0.050*	101.39	0.000***
SLA (cm ² g ⁻¹)	12.87	0.000***	0.59	0.448 ^{ns}	16.81	0.002**	0.28	0.613 ^{ns}
LL (cm)	1.06	0.357 ^{ns}	86.91	0.000***	4.98	0.010**	187.59	0.000***
LW (cm)	3.44	0.042*	74.22	0.000***	2.73	0.074 ^{ns}	308.47	0.000***
LPL (cm)	6.09	0.005**	5.80	0.021*	20.04	0.000***	26.57	0.000***
CLPL (cm)	—	—	—	—	2.13	0.181 ^{ns}	0.59	0.464 ^{ns}
LE	2.13	0.132 ^{ns}	0.034	0.854 ^{ns}	4.03	0.021*	1.83	0.181 ^{ns}
LL/LPL	8.45	0.001***	3.54	0.067 ^{ns}	10.37	0.000***	9.05	0.004**
LAX/CLPL	—	—	—	—	31.79	0.000***	9.22	0.016*
LWD	1.59	0.216 ^{ns}	0.24	0.627 ^{ns}	10.81	0.000***	12.61	0.001***
LBD	0.46	0.634 ^{ns}	0.01	0.952 ^{ns}	—	—	—	—
LTF (%)	0.45	0.641 ^{ns}	0.01	0.932 ^{ns}	—	—	—	—
LMF (%)	0.60	0.553 ^{ns}	0.21	0.650 ^{ns}	—	—	—	—
LBF (%)	1.66	0.202 ^{ns}	0.22	0.646 ^{ns}	—	—	—	—
NLT	1.43	0.251 ^{ns}	0.50	0.484 ^{ns}	14.98	0.002**	0.56	0.476 ^{ns}
MDV (cm)	2.52	0.093 ^{ns}	12.4	0.001***	0.90	0.445 ^{ns}	2.10	0.186 ^{ns}

$n = 45$ for variables of *Q. acutissima*, $n = 12$ for variables of the compound leaf and $n = 60$ for variables of the leaflet of *R. pseudoacacia*.

Significance level:

^{ns} $P > 0.05$.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

($r^2 = 0.08$, $P = 0.03$) correlated with water availability, but these relationships were significant only for *Q. acutissima*. On the contrary, NLT scaled positively with water availability ($r^2 = 0.48$, $P < 0.00$) only for *R. pseudoacacia*. As for the special variables, the relationship of LBD with RWC was not significant ($r^2 = 0.00$, $P = 0.92$), but LAX/CLPL was positively correlated with water availability ($r^2 = 0.39$, $P = 0.02$).

LA was positively correlated with light availability, both for *Q. acutissima* (Fig. 3, $r^2 = 0.42$, $P < 0.00$) and for *R. pseudoacacia* ($r^2 = 0.43$, $P = 0.02$). Correspondingly, LDM, LL, LW and LPL significantly increased at increasing light availability in these two species ($r^2 > 0.17$, $P < 0.00$). On the contrary, SLA significantly decreased at increasing light availability ($r^2 > 0.48$, $P < 0.00$). The slopes of these variables were larger in *Q. acutissima* than in *R. pseudoacacia*.

At the increasing gradients of light availability, LE significantly decreased for *Q. acutissima* (Fig. 3, $r^2 = 0.16$, $P < 0.00$), but it significantly increased for *R. pseudoacacia* ($r^2 = 0.08$, $P = 0.03$). LL/LPL was negatively correlated with light availability only for *Q. acutissima* ($r^2 = 0.14$, $P = 0.01$). LWD and LBD were also negatively correlated with light availability for *Q. acutissima*, but these relationships were not significantly different ($r^2 < 0.07$, $P > 0.08$). NLT were fewer at increasing light availability for *Q. acutissima*, and the relationship was significantly linear ($r^2 = 0.11$, $P = 0.03$). On the contrary, the variable LAX/CLPL and NLT for *R. pseudoacacia* generated a non-linear relationship of which the maximum values occurred in

medium light conditions. A converse non-linear trend appeared when considering LWD at increasing light availability for *R. pseudoacacia*. MDV increased at increasing light availability, and it was only significantly different for *R. pseudoacacia* ($r^2 = 0.37$, $P = 0.04$).

Three leaf fractions of *Q. acutissima* showed a weak linear relationship in the different gradients of water and light availability (Fig. 4). LMF and LTF became smaller at decreasing water availability, and the rate of LBF accordingly became larger. The trends of these leaf fractions were just converse at decreasing light availability, and the relationship between LBF and RLI was significant ($r^2 = 0.13$, $P = 0.02$).

4. Discussion

4.1. Scaling of leaf size with environmental gradients

Our study highlighted that leaf size was obviously restricted with a short supply of water and light by considering leaf area and dry mass. Reduction in leaf size in stressful environments has been explained on the basis of leaf boundary-layer conductance for heat and gaseous transport. So, variations in leaf size along climatic gradients may result from greater evaporative demand of larger leaves due to enhanced thickness of the boundary layer for energy and gaseous exchange [14]. However, leaf size may also decline due to overall resources limitation in stressful environments, making the construction of large leaves with extensive vascular and cell-wall fractions overly expensive

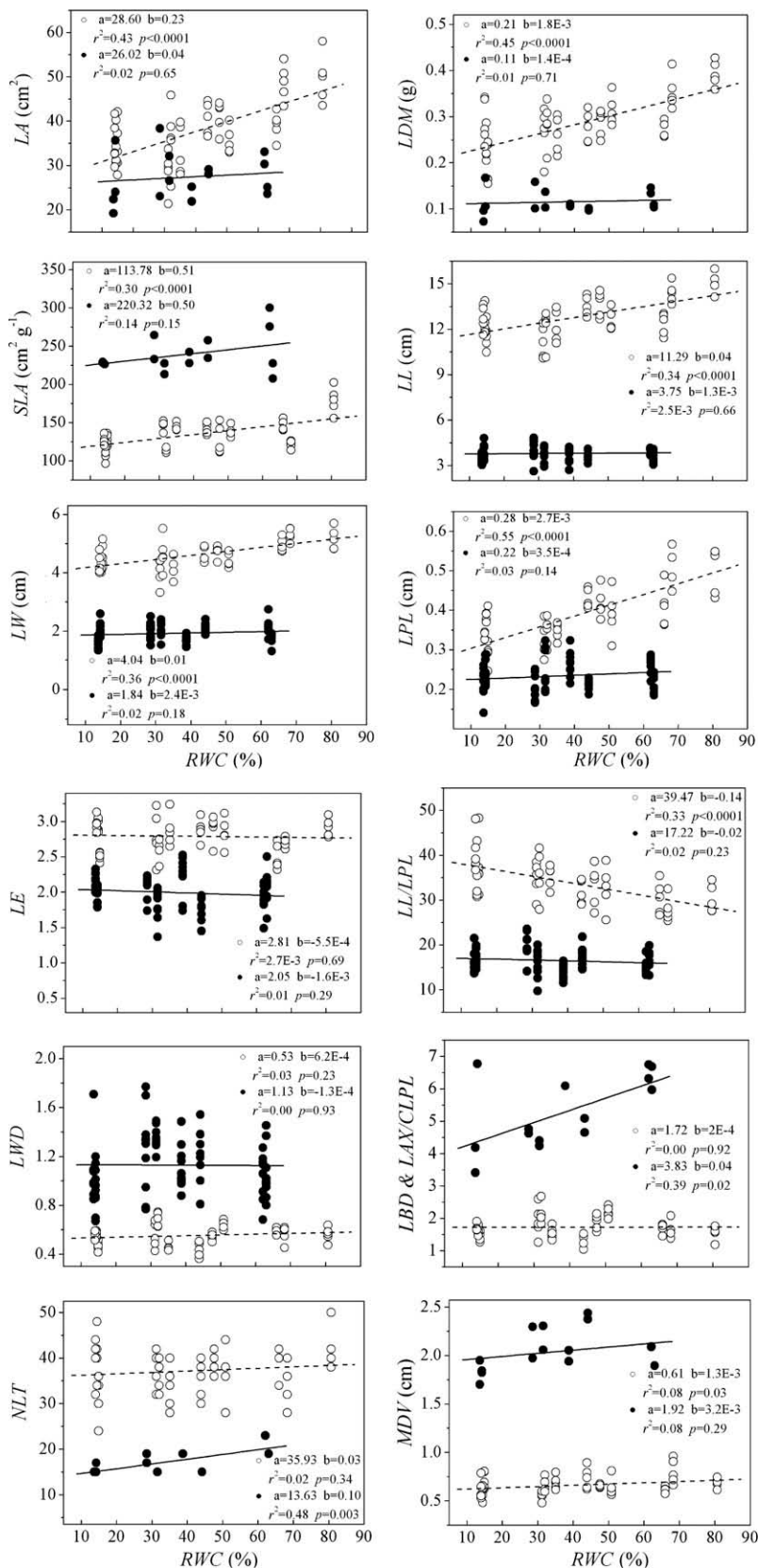


Fig. 2. Leaf morphological variables of *Q. acutissima* and *R. pseudoacacia* in the different gradients of water availability. Open and solid circles refer to variables of *Q. acutissima* and *R. pseudoacacia*, respectively. The coefficients a and b are the intercept and the slope of the regression lines. $n = 60$ for variables of *Q. acutissima*. $n = 16$ for variables of the compound leaf, and $n = 80$ for variables of the leaflet of *R. pseudoacacia*.

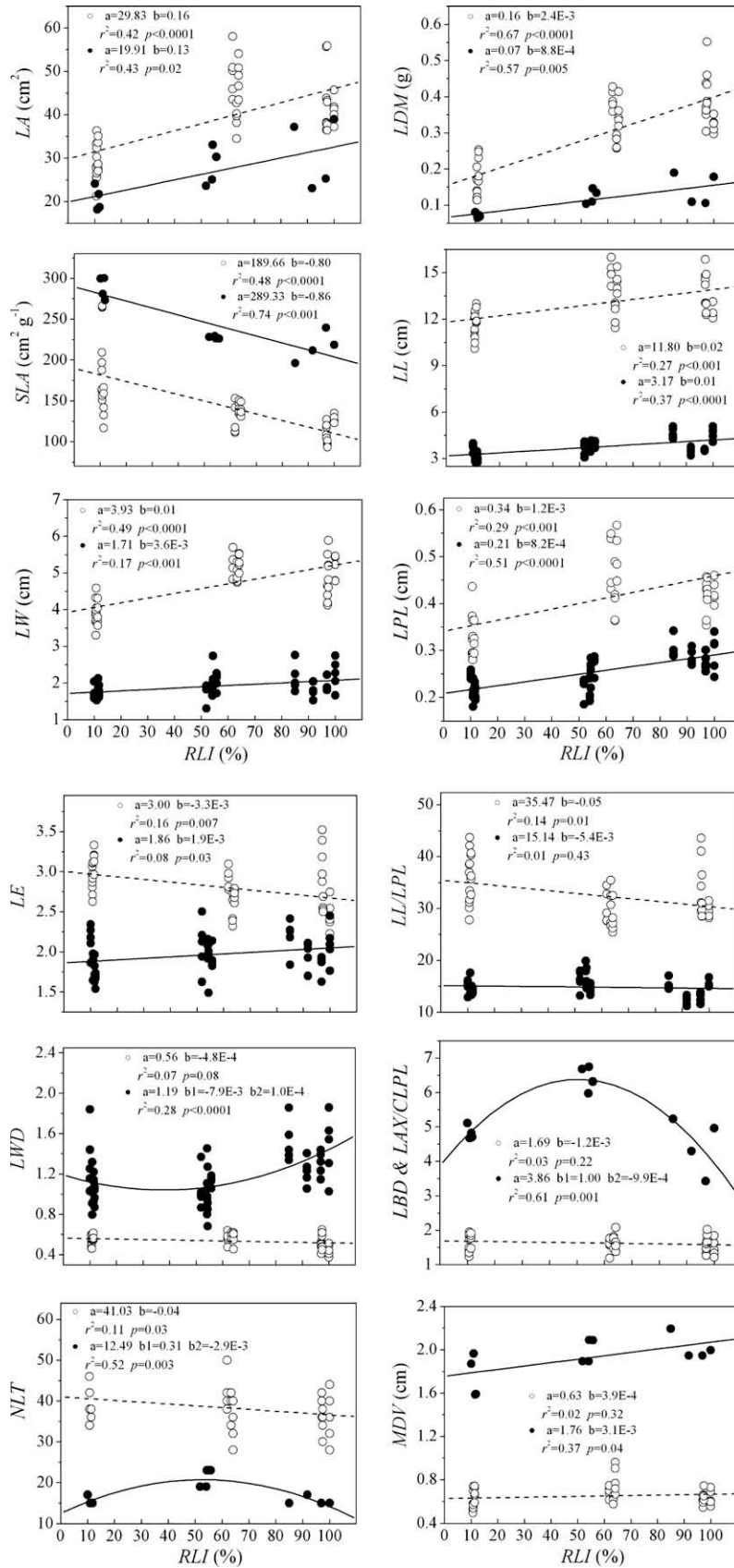


Fig. 3. Leaf morphological variables of *Q. acutissima* and *R. pseudoacacia* in the different gradients of light availability. Open and solid circles refer to variables of *Q. acutissima* and *R. pseudoacacia*, respectively. The coefficients a and b are the intercept and the slope of the regression lines. Some variables are fitted using the quadratic model, where a , b_1 and b_2 are the coefficients of the function $y = a + b_1x + b_2x^2$. $n = 45$ for variables of *Q. acutissima*. $n = 12$ for variables of the compound leaf and $n = 60$ for variables of the leaflet of *R. pseudoacacia*.

[17]. More significant effects were observed in simple leaves than in compound leaves. Compound leaves may act as highly dissected leaves to improve heat transfer efficiency in a plant by allowing better air exchange over the leaf surface [23]. In this regard, the advantages of small leaves may be offset. Leaves of *R. pseudoacacia* are short-lived and cheap to manufacture, while leaves of *Q. acutissima* are expensive but make up for that in durability according to the ‘worldwide leaf economics spectrum’ [9]. Fewer resources are needed for leaf formation and maintenance in compound leaves, so the restriction in leaf size should be weaker in compound leaves than in simple leaves.

Specific leaf area (SLA) is an integration of leaf area and dry mass. It is an important parameter of growth rate because the larger the SLA, the larger the area for capturing light per unit of previously captured mass. There is empirical evidence, which is consistent with our results, that SLA often shows no relationship with leaf size across many species and community types [24]. It reflects the important meanings of environmental effects on SLA. SLA is negatively correlated with leaf lifespan and positively correlated with mass-based nitrogen content, photosynthetic capacity, transpiration rate and respiration rate [9,25]. To achieve different ameliorative aims, variations along the gradients of water and light availability showed divergent trends in our study. In water-limited environments, the cell walls of lamina are thicker and often strongly lignified. On one side, this structure can enhance the epidermal resistance of water vapor through cuticles to reduce water loss. On the other side, self-support of lamina can significantly rely on lamina cells (non-specific support) in addition to vasculature [26]. Higher dry mass per area in drought-stress leaves also enables the prolongation of the leaf lifespan to compensate for fewer units and lower activity of the photosynthetic apparatus. Sun and shade environments are likely to be selected for different leaf constitutions, that is, differing investment in structural and symplastic components [27]. The intensity of visible and UV light is positively correlated with cuticle thickness and integration of protective flavonoid compounds in the cuticle. Plants grown in high light generally have thick leaves caused by extra layers of palisade mesophyll or longer palisade cells to protect them from

high-light damage [28]. However, the production of leaves with a more symplastic component should be advantageous in the shade by reducing both construction and maintenance costs [29]. The larger SLA is also accommodated to decrease self-shading of chloroplasts in the abaxial surface of leaves [30].

4.2. Variations of leaf dimension in resources acquisition and conservation

Leaf elongation characterizes the overall slenderness of the leaves. It reflects the integrated changes of leaf major and minor axes [31]. Leaf length and width increased along with the expansion of leaf area. The dominant allometric effects in the gradient of water availability made leaf elongation relatively stable despite the various leaf areas. However, the leaf dimension is represented by not only the leaf elongation, but also the distribution of leaf area fractions in our research also included more information about leaf shape. Drought caused the leaf bottom fraction, which represents the narrow part of the leaf, to increase in proportion to the whole-leaf lamina. Actually, the leaves became narrower and were thought to be an adaptation to xeric environments, for narrow leaves could reduce the transpiration by reducing the size of the boundary layer.

The effect of light availability was more significant on leaf dimension than that of water availability in our study. In simple leaves, not only did the leaf elongation increase, but also lamina areas located close to the leaf apex increased in the low light available condition. By this means, leaves can maximize light capture areas and reduce self-shading [32]. The effects of shade on leaf fractions were just contrary to that of drought. Xeromorphic features often serve multiple functions such as water-repellence, defense and protection from excess light [33,34]. So, sun leaves will also display increased xeromorphy in comparison to shade leaves. In compound leaves, variations of leaflet dimension should take the whole compound leaf into account. The leaflets became wider to compensate for the shade-induced decreasing quantity in the rachis. A larger fraction of lamina was located close to the leaf base to efficiently keep more investments in the functional tissues.

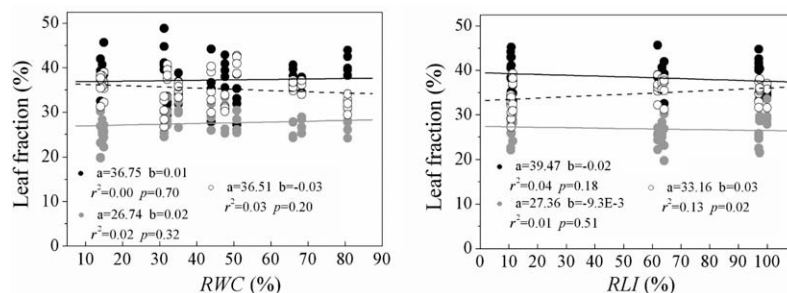


Fig. 4. Changes of the three leaf fractions of *Q. acutissima* in the different gradients of water and light availability. ○, ● and ● refer to variables of LBF, LMF, and LTF, respectively. The coefficients a and b are the intercept and the slope of the regression lines. $n = 60$ for variables in water gradients and $n = 45$ for variables in light gradients.

Elongation of the leaf and petiole also shows a trade-off between resource acquisition and resource-conservative stress tolerance [35]. In our study, changes of petiole length were consistent with changes of leaf area and dry mass, which indicated that there was a positive relationship between leaf petiole length and leaf size. Due to the economics of light interception and biomechanical requirements, increases in leaf size are often bound to enhanced biomass investment in the petiole [36]. The elongation of petioles will achieve optimal leaf display to deal with the denseness of the canopy, but it may not be the major way to reduce self-shading, as the plants face a trade-off between the need for increasing interception areas and support structures. Increasing the investment in petioles needs to synthesize more xylogens, and longer petioles will lead the leaf to bend [37].

4.3. Leaf venation pattern in support and function

The investments in leaf venation have important implications for leaf physiological activity and hydraulic and light-utilization efficiency. For example, as larger leaves have effectively longer lever arms, biomechanical considerations for leaf self-support suggest that larger leaves should have a relatively larger fraction of investment in the midrib [31]. Increased distances of leaf margins from the midrib need a larger vein network to carry resources to and away from cells. Large networks supply cells more slowly and will cause large leaves to photosynthesize more slowly [13]. Investments in support will also cost the biomass invested into functional leaf activity.

In our study, there was a weak increased trend of vein density under drought stress to avoid leaf dehydration. Enhanced vein density (lower values of MDV) can provide an important compensatory way to reduce water potential gradients along the lamina, for strong positive correlations have been observed between vein density and leaf hydraulic conductance [38]. Relatively broader and thinner leaves in the low light available condition showed higher vein density to prevent leaf margins drooping, for the centroid was far away from the leaf base which increased the overall bending moment. These data indicate that a significant variation in vein density has important implications for leaf hydraulic efficiency and mechanical support.

4.4. Serrations in simple leaves vs. leaflets in compound leaves

Vegetative leaves come mainly in two basic arrangements: simple and compound. The evolution of leaf types has as yet not been clearly researched by phylogenetic methods [39]. Theoretically, it could occur by progressive elaboration of a simple leaf to form a compound leaf or by progressive simplification of a compound leaf to form a simple leaf. Leaflets in a compound leaf play a role as lobes or teeth in a simple leaf [19]. The relationship between leaf teeth and climate has been revealed in woody

and herbaceous species [40,41]. Leaves with teeth are more active with respect to photosynthesis and transpiration than leaves without teeth [40]. Also, the number of teeth, teeth area and degree of blade dissection correlate with climate [14]. This can explain why the leaves in the present experiments had more teeth or leaflets in the shade treatments. But leaf teeth, which can enhance rates of sap flow and water loss, are disadvantageous for plants in drought environments. It was also observed in our results that fewer leaf teeth or leaflets existed under drought treatments.

There was the inflexion in the compound leaves when considering the light effect on the number of leaflets in our study. The results suggested that adding leaflets might not be a beneficial way in compound leaves when light resources were devoid. It has been proved that teeth area correlate negatively with leaf mass per area [14]. The compound leaf can be considered pinnatisect, and the lobes area is bigger than the teeth area in the simple leaf. The overall investments distributed to maintain the quality of leaflets will restrict the quantity of leaflets.

5. Conclusions and future research

The relationships between leaf morphology and climate are broadly consistent, but do differ in some respects with different leaf types. We have also shown in previous research that simulated experiments can achieve similar effects to those in wild habitats [42]. The leaf can be considered as a microcopy of the plant, and the variations of leaf morphology can reflect the plant capacity to acquire, use and conserve resources. Our research may suggest that the resolution of taxonomy would require the consideration of heterogeneity within the same species based on leaf allometry and phenotypic plasticity [43] and may provide evidence of adaptation and niche differentiation of coexisting species. However, we recognize that the limited geographical and phylogenetic scope in our research allows only a preliminary assessment of this expectation.

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