

# Insights into the differences in leaf functional traits of heterophyllous *Syringa oblata* under different light intensities

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**Abstract** Many plants exhibit heterophylly; the spatially and temporally remarkable ontogenetic differences in leaf morphology may play an adaptative role in their success under diverse habitats. Thus, this study aimed to gain insights into differences in leaf functional traits of heterophyllous *Syringa oblata* Lindl., which has been widely used as an ornamental tree around the world under different light intensities in East China. No significant differences existed in specific leaf area (SLA) between lanceolate- and heart-shaped leaves. Differences in the investment per unit of light capture surface area deployed between lanceolate- and heart-shaped leaves may be

not obvious. This may be attributing to the fact that single leaf wet and dry weight of heart-shaped leaves were significantly higher than those of lanceolate leaves but leaf length and leaf thickness of heart-shaped leaves were significantly lower than those of lanceolate leaves. The SLA of shade trees was significantly higher than that of sun trees. The investment per unit of light capture surface of shade trees was lower than that of sun trees, making it possible to increase light capture and use efficiency in low-light environments. The phenotypic plasticity of most leaf functional traits of lanceolate leaves was higher than those of heart-shaped leaves because the former is the juvenile and the latter is the adult leaf shape during the process of phylogenetic development of *S. oblata*. The higher range of phenotypic plasticity of leaf thickness and leaf moisture for sun trees may be beneficial to obtain a more efficient control of water loss and nutrient deprivation in high-light environments, and the lower range of phenotypic plasticity of single leaf wet and dry weight, and SLA for shade trees may gain an advantage to increase resource (especially light) capture and use efficiency in low-light environments. In brief, the successfully ecological strategy of plants is to find an optimal mode for the trade-off between various functional traits to obtain more living resources and achieve more fitness advantage as much as possible in the multivariate environment.

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## Introduction

Since leaves are exposed to and sensitive to environmental changes, the response of leaf functional traits to changes in environmental factors could enable plants to occupy a wide

variety of environmental conditions and thereby reflect the successful ecological strategy of plants during their life cycle (Poorter et al. 2009; Campitelli and Stinchcombe 2013).

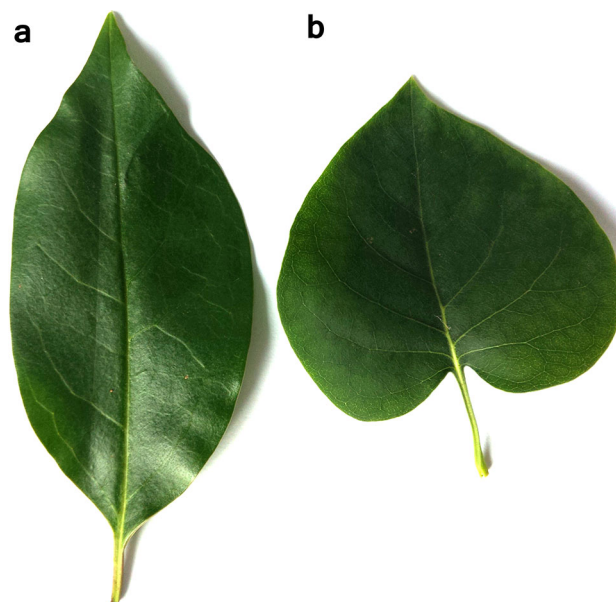
Many plants exhibit heterophylly, which refers to the leaf component of heteroblasty, i.e., variations in the size and shape of leaves produced along the axis of an individual plant during their life cycle (Pardos et al. 2009; Tanaka-Oda et al. 2010; Leigh et al. 2011; Momokawa et al. 2011). The spatially and temporally remarkable ontogenetic differences in leaf morphology may play an adaptative role in their success under diverse habitats (Pardos et al. 2009; Tanaka-Oda et al. 2010; Leigh et al. 2011; Momokawa et al. 2011) because their leaf morphology could trigger pronounced effects on leaf functions (Pardos et al. 2009; Leigh et al. 2011; Momokawa et al. 2011).

Given that leaf functional traits and the heterophyllous phenomenon may be all affected by environment factors (especially light intensity) (Burns and Beaumont 2009; Momokawa et al. 2011; Yang et al. 2014), understanding the differences in leaf functional traits of heterophylly of plants under different light intensities is necessary to elucidate the mechanism underlying their successful ontogenetic strategies. Unfortunately, existing studies on heterophyllous plants mainly focus on hydrophyte but often ignore terrestrial species (except for the gymnospermous species *Ginkgo biloba* L.).

This study was conducted using cross-site comparisons to elucidate the differences in leaf functional traits of heterophylly (two leaf forms: lanceolate and heart-shaped leaves, Fig. 1) *Syringa oblata* Lindl. (abbreviated as *S. oblata* hereafter) under different light intensities (i.e. low and high light). *S. oblata* has been widely used as an ornamental tree around the world. The leaf functional traits [i.e., leaf size, leaf thickness, the ratio of leaf length to petiole length, leaf shape index, single leaf wet and dry weight, leaf moisture, specific leaf area (SLA)] of the two leaf forms of *S. oblata* were assessed to provide insights into the ontogenetic strategy of heterophyllous *S. oblata* under different light intensities.

The following hypotheses were presented:

- (1) SLA of lanceolate leaves (juvenile) was higher than that of heart-shaped leaves (adult), but leaf thickness, and the single leaf wet and dry weight of lanceolate leaves was conspicuously lower than those of heart-shaped leaves because SLA decreased and leaf thickness increased during leaf development (Mediavilla and Escudero 2009; Battie-Laclau et al. 2014).



**Fig. 1** The two leaf forms of heterophyllous *Syringa oblata*. Legend: **a** lanceolate leaves, **b** heart-shaped leaves

- (2) Leaf thickness, and single leaf wet and dry weight of sun trees (under high light intensity) were significantly higher than those of shade trees (under low light intensity). By contrast, leaf size, leaf moisture, and SLA of sun trees were obviously lower than those of shade trees because sun trees have greater quantities of material investment per unit area in order to obtain a more efficient control of water loss and nutrient deprivation in high-light environments. Shade trees also have less material investment per unit area in order to increase resource (especially light) capture and use efficiency in low-light environments (Burns and Beaumont 2009; McIntyre and Strauss 2014; Yang et al. 2014); and
- (3) Leaf thickness, and single leaf wet and dry weight were negatively correlated with SLA, while leaf size and leaf moisture were positively correlated with SLA because the leaves with high SLAs provide low structural investment, but leaves with low SLAs likely invest great biomass on leaf structures (Poorter et al. 2009; Pietsch et al. 2014).

## Materials and methods

### Experimental design

In June 2014, samples of heterophyllous plant *S. oblata* were obtained from two sites in Zhenjiang, People's

Republic of China [the samples under high and low light were collected from open areas (32°20'N, 119°51'E) and shaded areas (32°20'N, 119°52'E), respectively]. A total of 14 plant samples from each site were collected to determine plant characteristics. In one plant sample, five adult and intact leaves of each leaf shape of one plant sample were selected randomly. The physiochemical properties of soil samples from each planting site were also determined. Sampling was completed in 2 days.

### Determination of plant characteristics and soil physiochemical properties

The characteristics related to plant performance and fitness were determined. Crown diameter, breast diameter, petiole diameter, and leaf thickness were calculated using a Vernier caliper with an accuracy of 0.01 mm.

Leaf shape index was calculated as the ratio of leaf length to the corresponding leaf width (Jeong et al. 2011; Wang and Zhang 2012). Leaf length is the maximum value along the midrib, and width is the maximum value perpendicular to the midrib (Wang and Zhang 2012). Leaf length and leaf width were measured using a ruler.

The ratio of leaf length to petiole length was determined using the ratio of the leaf length to the corresponding petiole length.

Leaf moisture was calculated by subtracting dry leaf weight from leaf wet weight; the difference was then divided by wet leaf weight. Single wet leaf weight was determined using an electronic balance. Single dry leaf weight was obtained by initially drying the samples to in an oven set at 60 °C for 24 h to achieve a constant weight; the final single dry leaf weight was then determined using an electronic balance with an accuracy of 0.001 g.

To estimate SLA, ten leaf discs with a definite area per leaf shape were cut from adult and intact leaves by using a borer with a definite diameter. The main leaf veins were carefully avoided during coring to reduce sample variation. The collected leaf discs were stored in small parchment bags, transported to the laboratory 12 h, and oven-dried at 60 °C for 24 h to obtain a constant weight determined using an electronic balance with an accuracy of 0.001 g. SLA was calculated by dividing leaf area by the corresponding leaf dry weight ( $\text{cm}^2 \text{g}^{-1}$ ) (Kardel et al. 2010; Scheepens et al. 2010).

The plasticity index and relative distance plasticity index [the two indices ranged from zero (no plasticity) to one (maximum plasticity)] of functional traits of heterophyllous *S. oblata* under different light intensities were calculated according to the previously described methods in Valladares et al. (2006), Chen et al. (2013), and Lamarque et al. (2013).

Soil pH values and moisture levels were all measured using a soil acidity-moisture meter [ZD instrument (ZD-06), People's Republic of China].

### Statistical analysis

Data were evaluated to determine deviations from normality and homogeneity of variance before data analysis. Differences among various dependent variables were assessed using analysis of variance. Two-way ANOVAs was applied to evaluate the effects of leaf shape and light intensity on leaf functional traits and soil physiochemical properties of *S. oblata*. Statistically significant differences were set at *P* values equal to or lower than 0.05. Patterns between various dependent variables were performed by correlation analysis using SPSS (version 17.0).

## Results

### Leaf functional traits and soil physiochemical properties of heterophyllous *S. oblata*

For heart-shaped leaves, petiole diameter, leaf length, leaf thickness, the ratio of leaf length to petiole length, and leaf shape index were all significantly lower than those of lanceolate leaves (Table 1, *P* < 0.05) but the opposite was true for petiole length, leaf width, and single leaf wet and dry weight (Table 1, *P* < 0.05). Other indices were not significantly different between lanceolate and heart-shaped leaves (Table 1, *P* > 0.05).

### Leaf functional traits and soil physiochemical properties of *S. oblata* under the two light intensities

Leaf thickness and single-leaf dry weight of sun trees were higher than those of shade trees (Table 2, *P* < 0.05). By contrast, ground diameter, breast diameter, petiole length, leaf moisture, SLA, and soil moisture of shade trees were higher than those of sun trees (Table 2, *P* < 0.05). There was no significant difference in other indices between of sun and shade trees (Table 2, *P* > 0.05).

### The effects of leaf shape and light intensity on leaf functional traits and soil physiochemical properties of *S. oblata*

ANOVA results revealed that leaf shape significantly affected petiole diameter, petiole length, leaf length, leaf width, leaf thickness, the ratio of leaf length to petiole length, leaf shape index, and single leaf wet and dry weight (Table 3, *P* < 0.001). However, leaf shape did not pose obvious effects on other indices (Table 3, *P* > 0.05). Light intensity significantly affected ground diameter, breast diameter, petiole length, leaf thickness, single leaf dry weight, leaf moisture, SLA, and soil moisture (Table 3, *P* < 0.05) but not other indices (Table 3, *P* > 0.05). The

**Table 1** Differences in leaf functional traits and soil physiochemical properties of heterophyllous *Syringa oblata*

Leaf shape	GD	BD	PD	PL	LL	LW	LT	
Heart-shaped	122.99 ± 15.15a	111.02 ± 13.86a	1.07 ± 0.04b	2.07 ± 0.06a	6.36 ± 0.29b	6.36 ± 0.17a	0.25 ± 0.01b	
Lanceolate	122.99 ± 15.15a	111.02 ± 13.86a	1.69 ± 0.03a	1.02 ± 0.09b	7.59 ± 0.28a	3.45 ± 0.17b	0.31 ± 0.02a	
Leaf shape	LL/PL	LSI	SLWW	SLDW	LM	SLA	pH	SM
Heart-shaped	3.07 ± 0.09b	1.00 ± 0.03b	0.60 ± 0.05a	0.20 ± 0.02a	0.68 ± 0.01a	189.13 ± 16.13a	6.25 ± 0.07a	0.67 ± 0.04a
Lanceolate	7.94 ± 0.49a	2.23 ± 0.06a	0.35 ± 0.03b	0.12 ± 0.01b	0.66 ± 0.03a	189.64 ± 11.41a	6.25 ± 0.07a	0.67 ± 0.04a

Data with different letters in a vertical row indicate a significant difference ( $P < 0.05$ )

GD ground diameter (mm), BD breast diameter (mm), PD petiole diameter (mm), PL petiole length (cm), LL leaf length (cm), LW leaf width (cm), LT leaf thickness (mm), LL/PL the ratio of leaf length to petiole length, LSI leaf shape index, SLWW single leaf wet weight (g), SLDW single leaf dry weight (g), LM leaf moisture (%), SLA specific leaf area (cm<sup>2</sup>/g), pH soil pH, SM soil moisture

**Table 2** Differences in leaf functional traits and soil physiochemical properties of *Syringa oblata* under different light intensities

Light intensity	GD	BD	PD	PL	LL	LW	LT	LL/PL
Low	173.16 ± 5.30a	156.28 ± 4.68a	1.35 ± 0.10a	1.67 ± 0.16a	7.32 ± 0.27a	5.10 ± 0.48a	0.25 ± 0.01b	5.12 ± 0.61a
High	72.83 ± 6.62b	65.76 ± 6.85b	1.41 ± 0.08a	1.42 ± 0.16b	6.63 ± 0.36a	4.71 ± 0.39a	0.31 ± 0.02a	5.89 ± 0.88a
Light intensity	LSI	SLWW	SLDW	LM	SLA	pH	SM	
Low	1.63 ± 0.16a	0.44 ± 0.04a	0.13 ± 0.02b	0.71 ± 0.01a	234.43 ± 8.34a	6.34 ± 0.08a	0.76 ± 0.02a	
High	1.60 ± 0.19a	0.50 ± 0.06a	0.19 ± 0.02a	0.62 ± 0.02b	144.34 ± 2.94b	6.16 ± 0.04a	0.57 ± 0.04b	

Data with different letters in a vertical row indicate a significant difference ( $P < 0.05$ )

Abbreviations have the same meanings as described above (Table 1). See Table 1 for meanings of abbreviations

interactions of leaf shape and light intensity have significant effects on leaf thickness and the ratio of leaf length to petiole length only (Table 3,  $P < 0.05$ ).

#### Plasticity index and relative distance plasticity index of leaf functional traits of heterophyllous *S. oblata* under different light intensity

The plasticity index of SLA of heart-shaped leaves was obviously higher than that of lanceolate leaves (Table 4). In specific, the plasticity index of petiole diameter, petiole length, leaf width, leaf thickness, the ratio of leaf length to petiole length, single leaf wet and dry weight, and leaf moisture of lanceolate leaves were obviously higher than those of heart-shaped leaves (Table 4). The difference in plasticity index of leaf length and leaf shape index between lanceolate and heart-shaped leaves was not obvious (Table 4). The plasticity index of leaf thickness and leaf moisture of sun trees were certainly higher than those of shade trees but the opposite for petiole diameter, single leaf wet and dry weight, and SLA (Table 4). There was no significant difference in the plasticity index of other indices

between of sun and shade trees (Table 4). Relative distance in the plasticity index of petiole diameter, petiole length, leaf width, the ratio of leaf length to petiole length, leaf shape index, and single leaf wet weight for different leaf-shape environments were obviously lower than those for the different light intensity but the opposite for SLA (Table 5). The difference in the relative distance plasticity index (of other indices) between different leaf shapes and light intensities was not obvious (Table 5).

#### Relationship between leaf functional traits and soil physiochemical properties of *S. oblata*

Correlation patterns between leaf functional traits and soil physiochemical properties of heterophyllous *S. oblata* were observed. In particular, ground diameter was positively correlated with breast diameter, SLA, and soil moisture (Table 6,  $P < 0.01$ ) but negatively correlated with leaf thickness (Table 6,  $P < 0.01$ ). Likewise, breast diameter was positively correlated with leaf width, SLA, and soil moisture (Table 6,  $P < 0.05$ ) but negatively correlated with leaf thickness and single leaf dry weight (Table 6,

**Table 3** Two-way ANOVAs on the effects of leaf shape and light intensity on leaf functional traits and soil physiochemical properties of *Syringa oblata*

	GD	BD	PD	PL	LL	LW	LT	LL/PL	
Leaf shape									
F	0.00	0.00	155.34	105.60	11.37	158.66	16.30	128.08	
P	1.000	1.000	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	
Light intensity									
F	129.07	109.81	1.63	6.09	3.49	2.90	14.42	3.20	
P	<b>&lt;0.001</b>	<b>&lt;0.001</b>	0.214	<b>0.021</b>	0.074	0.102	<b>&lt;0.001</b>	0.087	
Leaf shape × light intensity									
F	0.00	0.00	3.76	0.09	4.02	2.07	4.86	7.07	
P	1.000	1.000	0.064	0.769	0.056	0.163	<b>0.037</b>	<b>0.014</b>	
			LSI	SLWW	SLDW	LM	SLA	pH	SM
Leaf shape									
			379.84	21.32	20.05	0.47	0.00	0.00	0.00
			<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	0.500	0.950	1.000	1.000
Light intensity									
			0.24	1.19	11.76	11.66	106.62	3.95	18.61
			0.630	0.285	<b>0.002</b>	<b>0.002</b>	<b>&lt;0.001</b>	0.059	<b>&lt;0.001</b>
Leaf shape × light intensity									
			1.56	0.48	0.02	1.77	2.69	0.00	0.00
			0.224	0.497	0.883	0.196	0.114	1.000	1.000

See Table 1 for meanings of abbreviations. P values equal to or lower than 0.05 are in bold face print. Abbreviations have the same meanings as described above (Table 1)

**Table 4** Plasticity index of leaf functional traits of heterophyllous *Syringa oblata* under different light intensities

		PD	PL	LL	LW	LT	LL/PL	LSI	SLWW	SLDW	LM	SLA
Leaf shape	Heart-shaped	0.36	0.31	0.42	0.32	0.42	0.33	0.32	0.58	0.60	0.20	0.58
	Lanceolate	0.67	0.69	0.37	0.49	0.52	0.56	0.31	0.78	0.80	0.50	0.45
Light intensity	High	0.36	0.76	0.44	0.67	0.53	0.77	0.70	0.72	0.72	0.46	0.22
	Low	0.54	0.75	0.37	0.67	0.32	0.71	0.62	0.87	0.83	0.27	0.36

See Table 1 for meanings of abbreviations

$P < 0.05$ ); petiole diameter was positively correlated with leaf length, leaf thickness, the ratio of leaf length to petiole length, and leaf shape index (Table 6,  $P < 0.01$ ) but negatively correlated with petiole length, leaf width, and single leaf wet weight (Table 6,  $P < 0.01$ ); petiole length was positively correlated with leaf width, and single leaf wet and dry weight (Table 6,  $P < 0.01$ ) but negatively correlated with leaf thickness, the ratio of leaf length to petiole length, and leaf shape index (Table 6,  $P < 0.01$ ). Leaf length was positively correlated with the ratio of leaf length

to petiole length and leaf shape index (Table 6,  $P < 0.05$ ); leaf width was positively correlated with single leaf wet and dry weight (Table 6,  $P < 0.001$ ) but negatively correlated with leaf thickness, the ratio of leaf length to petiole length, and leaf shape index (Table 6,  $P < 0.05$ ). Leaf thickness was positively correlated with the ratio of leaf length to petiole length and leaf shape index (Table 6,  $P < 0.05$ ) but negatively correlated with SLA (Table 6,  $P < 0.05$ ); the ratio of leaf length to petiole length was positively correlated with leaf shape index (Table 6,

**Table 5** Relative distance plasticity index of leaf functional traits of heterophyllous *Syringa oblata* under different light intensities

	PD	PL	LL	LW	LT	LL/PL	LSI	SLWW	SLDW	LM	SLA
Leaf shape	0.22	0.34	0.09	0.30	0.11	0.44	0.38	0.27	0.26	0.01	0.00
Light intensity	0.02	0.08	0.05	0.04	0.10	0.07	0.01	0.06	0.20	0.07	0.24

See Table 1 for meanings of abbreviations

**Table 6** Relationship among leaf functional traits and soil physicochemical properties of *Syringa oblata*

	GD	BD	PD	PL	LL	LW	LT	LL/PL	LSI	SLWW	SLDW	LM	SLA	pH	SM
GD	r	1.00	<b>0.98**</b>	-0.07	0.19	0.26	0.10	-0.12	0.03	-0.26	-0.46*	0.35	<b>0.86**</b>	0.23	<b>0.54**</b>
	P	<0.001	0.719	0.337	0.188	0.609	0.003	0.556	0.872	0.176	0.015	0.071	<0.001	0.242	0.003
BD	r	1.00	-0.08	0.19	0.28	0.11	-0.56**	-0.12	0.03	-0.22	-0.42*	<b>0.38*</b>	<b>0.81**</b>	0.23	<b>0.58**</b>
	P	0.687	1.00	0.330	0.148	0.583	0.002	0.532	0.863	0.266	0.026	0.046	<0.001	0.249	0.001
PD	r	<b>-0.82**</b>	<b>0.48*</b>	-0.81**	<b>0.50**</b>	<b>0.82**</b>	-0.49**	<b>0.86**</b>	<0.001	0.008	0.053	0.249	0.492	0.655	0.706
	P	<0.001	1.00	<0.001	0.007	0.007	0.007	<0.001	<b>0.66**</b>	<b>0.54**</b>	0.19	0.20	0.20	0.10	0.21
PL	r	1.00	<b>0.92**</b>	-0.56**	-0.93**	<0.001	<0.001	<0.001	<0.001	0.003	0.329	0.297	0.297	0.600	0.273
	P	0.385	<0.001	0.002	0.002	0.29	0.29	<b>0.40*</b>	<b>0.50**</b>	-0.15	0.00	0.32	0.32	0.12	0.28
LL	r	1.00	-0.19	0.322	0.035	<b>0.93**</b>	-0.43*	0.023	1.00	0.023	0.023	0.023	0.023	0.023	0.145
	P	0.322	1.00	0.023	0.023	0.023	0.023	0.023	0.023	0.023	0.023	0.023	0.023	0.023	0.12
LW	r	1.00	<b>0.45*</b>	0.016	<b>0.90**</b>	-0.61**	-0.52**	-0.13	0.320	0.046	0.227	0.074	-0.38*	-0.24	-0.34
	P	0.016	0.751	0.871	0.871	0.871	0.871	0.871	0.871	0.871	0.871	0.871	0.871	0.871	0.871
LL/PL	r	1.00	<b>0.62**</b>	<0.001	1.00	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	P	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
LSI	r	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	P	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
SLWW	r	1.00	<b>0.88**</b>	0.17	-0.26	0.185	-0.53**	-0.13	0.912	0.912	0.912	0.912	0.912	0.912	0.912
	P	0.17	<0.001	0.382	0.382	0.382	0.382	0.382	0.382	0.382	0.382	0.382	0.382	0.382	0.382
SLDW	r	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	P	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
LM	r	1.00	0.004	0.496	0.377	0.377	0.377	0.377	0.377	0.377	0.377	0.377	0.377	0.377	0.377
	P	0.004	0.496	0.377	0.377	0.377	0.377	0.377	0.377	0.377	0.377	0.377	0.377	0.377	0.377
SLA	r	1.00	0.007	0.118	0.152	0.152	0.152	0.152	0.152	0.152	0.152	0.152	0.152	0.152	0.152
	P	0.007	0.118	0.152	0.152	0.152	0.152	0.152	0.152	0.152	0.152	0.152	0.152	0.152	0.152
pH	r	1.00	0.27	0.169	0.003	0.05	0.783	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	P	0.27	0.169	0.003	0.05	0.783	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
SM	r	1.00	0.05	0.783	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	P	0.05	0.783	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

\* and \*\* indicates significant differences at the 0.05 and 0.01 probability level, respectively. P values equal to or lower than 0.05 are in bold face print. Abbreviations have the same meanings as described in Table 1)

$P < 0.001$ ) but negatively correlated with single leaf wet and dry weight (Table 6,  $P < 0.01$ ); leaf shape index was negatively correlated with single leaf wet and dry weight (Table 6,  $P < 0.001$ ); single leaf wet weight was positively correlated with single leaf dry weight (Table 6,  $P < 0.001$ ); single leaf dry weight was negatively correlated with SLA (Table 6,  $P < 0.01$ ) but leaf moisture was positively correlated with SLA (Table 6,  $P < 0.01$ ); and SLA was positively correlated with soil moisture (Table 6,  $P < 0.01$ ).

## Discussion

Previous studies found an obvious difference in the leaf functional traits between different leaf shapes of heterophyllous species. For example, the northern temperate gymnosperm *G. biloba* has two leaf types borne on different kinds of shoots (short-shoots leaves and long-shoot leaves) and short-shoot leaves were thinner and had higher vein density, lower stomatal pore index, smaller bundle sheath extensions and lower hydraulic conductance than long-shoot leaves (Leigh et al. 2011). Meanwhile, *Sabina vulgaris* is a heterophyllous tree with two leaf forms: needle leaves and scale leaves, and scale leaves had a larger leaf mass area, higher leaf area-based photosynthetic rate, higher water-use efficiency, and stronger tolerance of photoinhibition compared to needle leaves (Tanaka-Oda et al. 2010). The differences in leaf morphology may play a key role in their successful survival (Pardos et al. 2009; Tanaka-Oda et al. 2010; Leigh et al. 2011; Momokawa et al. 2011). Because SLA decreased and leaf thickness increased during leaf development (Mediavilla and Escudero 2009; Battie-Laclau et al. 2014), the SLA of lanceolate leaves may be higher than that of heart-shaped leaves, but opposite for leaf thickness. The result of this study indicates that the difference in the investment per unit of light capture surface deployed between lanceolate and heart-shaped leaves may be not obvious. This result is inconsistent with our first hypothesis. This phenomenon may be attributing to the fact that single leaf wet and dry weight of heart-shaped leaves were significantly higher than those of lanceolate leaves but leaf length and leaf thickness of heart-shaped leaves were significantly lower than those of lanceolate leaves.

Meanwhile, petiole diameter, leaf length, leaf thickness, the ratio of leaf length to petiole length, and leaf shape index of heart-shaped leaves were significantly lower than those of lanceolate leaves, but opposite for petiole length, leaf width, and single leaf wet and dry weight. This means lanceolate leaves differ morphologically from heart-shaped leaves. This result may be attributed to the difference in growth stage of the two leaf shapes because the former is

the juvenile and the latter is the adult. The reason may also be as a result of the difference in survival environment, i.e., the location of the former is lower than that of the latter and thus receives relatively less acceptable light. For example, the higher the ratio of leaf length to petiole length of lanceolate leaves than that of heart-shaped leaves may indicate that juvenile lanceolate leaves may invest more biomass on lamina structures rather than petiole to capture light with a maximum efficiency.

Light is one of the most important ecological factors that affect plant establishment, growth, and survival, particularly for understory species (Liu et al. 2010; Meng et al. 2014). Thus, shade trees may pay less material investment per unit area so as to increase light capture and use efficiency in low-light environments (Burns and Beaumont 2009; McIntyre and Strauss 2014; Yang et al. 2014). Shade trees also may make an utmost effort in order to increase light capture efficiency by producing thin, high area, and less tough leaves with high SLAs (Rozendaal et al. 2006). Clearly, the material investment per unit area (SLA) and per lamina (single leaf dry weight) of shade trees were significantly lower than that of sun trees. Meanwhile, the petiole length and leaf moisture of shade trees was also significantly lower than those of sun trees but opposite for leaf thickness. In addition, leaf size (leaf length and leaf width as the indicator) of shade trees was higher than that of sun trees and single leaf wet weight of shade trees was lower than sun trees although not substantially. This may be due to that larger leaf size allows the plants to gain height more rapidly because fewer woody branches and lower twig biomass are required to support the larger smaller leaves (Sun et al. 2006); that said, longer petioles are needed to avoid self-shading (Pearcy et al. 2005).

Increases in leaf size are often bound to enhanced biomass investment in the petiole, and may also bring about larger fractional biomass allocation in the midrib (Ninemets and Sack 2006). Results obtained in this study thereby are only partly consistent with the second hypothesis. Generally, shade trees may possess many functional traits, such as less leaf thickness, high petiole length, high leaf moisture, and high SLAs, which can allows shade trees to gain a competitive advantage in low-light environments according to the results of this study and also previous studies (Rozendaal et al. 2006; Liu et al. 2010; Meng et al. 2014).

Since any functional traits that contribute a fitness advantage to a species in its environment will be under selection pressure and may thus evolve, phenotypic plasticity should be a potential target for selection (Poorter et al. 2009; McIntyre and Strauss 2014). The enhanced phenotypic plasticity of plants for any functional traits may play a key role in their successful survival (Poorter et al. 2009; McIntyre and Strauss 2014). The result of this study

means that the range of phenotypic plasticity of most functional traits of lanceolate leaves may be higher than those of heart-shaped leaves. The reason may be due to the fact that lanceolate leaves are the juvenile and heart-shaped leaves are the adult leaf shape during the process of phylogenetic development of heterophyllous *S. oblate*. Meanwhile, plasticity index of leaf thickness and leaf moisture of sun trees was markedly higher than that of shade trees but opposite for petiole diameter, single leaf wet and dry weight, and SLA. We think that the higher range of phenotypic plasticity of leaf thickness and leaf moisture may help to obtain a more efficient control of water loss and nutrient deprivation in high-light environments and the lower range of phenotypic plasticity of single leaf wet and dry weight, and SLA may gain an advantage in increasing resource (especially light) capture and use efficiency in low-light environments (Burns and Beaumont 2009; McIntyre and Strauss 2014; Yang et al. 2014). The range of the relative distance plasticity index of SLA for different light intensities was obviously higher than that for different leaf-shape environments. This means that SLA may play an important role in resource (especially light) capture and use efficiency under different light intensities.

Generally, leaves with higher SLAs, which could invest less biomass into leaf construction in order to achieve a high resource acquisitive and use efficiency, show lower leaf thickness, and single-leaf wet and dry weight but higher leaf size and leaf moisture (Poorter et al. 2009; McIntyre and Strauss 2014; Pietsch et al. 2014; Yang et al. 2014). We found that SLA was positively correlated with leaf moisture but negatively correlated with leaf thickness and single-leaf dry weight. Unfortunately, SLA and leaf size (leaf length and leaf width as the characterization) did not show a significant relationship. Empirical studies also achieve conflicting results, with observed correlations between leaf size and SLA that are positive (Ackerly et al. 2002; Burns and Beaumont 2009), negative (Milla and Reich 2007; Niklas et al. 2007), unrelated (Wright et al. 2007), or variable amongst habitats (Pickup et al. 2005). What this suggests is that there is species specificity for the relationship among leaf functional traits. Consequently, results obtained in this study are only partly consistent with the third hypothesis.

Previous studies founded that leaf size and SLA decline along gradients of decreasing moisture (Fonseca et al. 2000; Ackerly et al. 2002). Thus, we suppose that soil moisture is positively correlated with leaf size and SLA, but not exactly the same as we found an inconsistent result, i.e., soil moisture was only significant correlated with SLA but not leaf size. The positive relationship between SLA and soil moisture may be due to the fact that plants which growth in the more humid soil subsystems have a relatively

high growth rate and lead to a decrease in the amount of biomass invested in leaf construction and then induced a high SLA (Fonseca et al. 2000; Ackerly et al. 2002). This paper also confirmed this point, that soil moisture in a shade environment was significantly higher than that in sun environment and the SLA of shade trees was also significantly higher than that sun trees.

## Conclusion

The purpose of this study was to gain insights into the differences in leaf functional traits of the heterophyllous plant *S. oblata* under different light intensities. Results showed that petiole diameter, leaf length, leaf thickness, the ratio of leaf length to petiole length, and leaf-shape index of heart-shaped leaves were significantly lower than those of lanceolate leaves but opposite for petiole length, leaf width, and single-leaf wet and dry weight. However, there was no significant difference in SLA between lanceolate and heart-shaped leaves. Thus, the difference in the investment per unit of light-capture surface deployed between lanceolate and heart-shaped leaves may be not obvious. Leaf thickness and single-leaf dry weight of sun trees were higher than those of shade trees but the opposite for petiole length, leaf moisture, and SLA. Therefore, the material investment per unit area and per lamina of shade trees was significantly lower than that of sun trees to enhance light capture and use efficiency in low-light environments. The plasticity index of petiole diameter, petiole length, leaf width, leaf thickness, the ratio of leaf length to petiole length, single-leaf wet and dry weight, and leaf moisture of lanceolate leaves were obviously higher than those of heart-shaped leaves but opposite for SLA. Thus, the phenotypic plasticity of most functional traits of lanceolate leaves was higher than those of heart-shaped leaves. This may be due to the fact that lanceolate leaves are the juvenile and heart-shaped leaves are the adult leaf shape during the process of phylogenetic development of heterophyllous *S. oblate*.

The plasticity index of leaf thickness and leaf moisture of sun trees were obviously higher than those of shade trees but opposite for petiole diameter, single-leaf wet and dry weight, and SLA. The higher range of phenotypic plasticity of leaf thickness and leaf moisture may be beneficial to obtain a more efficient control of water loss and nutrient deprivation in high-light environments, and the lower range of phenotypic plasticity of single-leaf wet and dry weight, and SLA may gain an advantage in order to increase resource (especially light) capture and use efficiency in low-light environments. All in all, the successfully ecological strategy of plants is to find an optimal mode for the trade-off between various functional traits to obtain more



living resources and achieve greater fitness advantages in the survival environment.

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