

Original Research

Differences in Leaf Functional Traits between Simple and Compound Leaves of *Canavalia maritima*

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Abstract

The response of leaf functional traits to the shift in environmental variables can raise plant adaptiveness in a wide variety of habitats and subsequently broaden their ecological niche. This study aims to determine the differences in leaf functional traits between simple and compound leaves of *Canavalia maritima* to illuminate the mechanisms underlying the ecological strategy of plant species with different leaf forms. Single-leaf wet weight of compound leaves of *C. maritima* was significantly lower than that of simple leaves of *C. maritima*. Thus, compound leaves of *C. maritima* possess higher resource capture ability as well as higher relative growth rate than simple leaves of *C. maritima*. The petiole length of compound leaves of *C. maritima* was significantly higher than that of simple leaves of *C. maritima*. Thus, the biomass allocation to petiole for compound leaves of *C. maritima* was significantly higher than that of simple leaves of *C. maritima*. Meanwhile, the higher range of phenotypic plasticity of SLA of compound leaves of *C. maritima* may enhance the advantage in resource (especially sunlight) capture and use efficiency by shifting the material investment per unit area and per lamina.

Keywords: *Canavalia maritima*, leaf form, leaf functional traits, simple leaf, compound leaf

Introduction

Leaves can enable plant species absorb sunlight, which is perhaps one of the most critical environmental factors that affect plant growth and survival [1-2]. In particular, leaves often exposed to a multivariate habitat and thereby the response of leaf functional traits to the shift in environmental variables can raise plant adaptiveness in a wide variety of habitats and

subsequently broaden their ecological niche [3-7]. As one of the most fundamental leaf functional traits, specific leaf area (SLA) is used as a proxy for the resource-use strategy of plants [3, 8-10]. Specific leaf area is defined as the investment of sunlight capture surface per unit area of leaf [3, 8-10]. Generally, leaves with high SLA values are typically associated with higher resource acquisition and use efficiency, faster growth rates, more rapid turnover of leaf material, and lower investment in leaf construction and protective tissues than leaves with low SLA [3, 8-10]. In addition, petiole length (indicative of the material investment on the support

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of lamina structures), leaf size (indicated by leaf length and leaf width; indicative of leaf photosynthetic area), leaf shape index (calculated as the ratio of leaf length to leaf width; indicative of leaf shape and variation), leaf chlorophyll and nitrogen (N) concentrations (indicative of leaf photosynthetic capacity), and single-leaf wet weight (indicative of the material investment on lamina structures) are also crucial indices of leaf functional traits because those indices are also used as powerful indicators of the resource-use strategy of plants [3, 4-8, 11-13].

Normally, leaf functional traits may vary by leaf forms because leaf forms vary in their biomass allocation strategy and the environmental selection pressures [14]. Accordingly, the differences in the leaf functional traits with different leaf forms can characterize their ecological strategy. Malhado et al. [15] found that trees with compound leaves in Amazonia grow faster than those with simple leaves. Meanwhile, the results of Warman et al. [14] revealed that the leaf N concentration of compound leaves was higher than that of simple leaves. Consequently, determining the differences in leaf functional trait with different leaf forms is important for illuminating the mechanisms underlying the ecological strategy of plant species with different leaf forms.

This study aims to determine the differences in leaf functional traits between simple and compound leaves of *Canavalia maritima* to illuminate the mechanisms underlying the ecological strategy of plant species with different leaf forms. *C. maritima* is an annual herbaceous vine. The leaf form of the first leaves of *C. maritima* is simple with opposite phyllotaxis and the leaf form of subsequent leaves of *C. maritima* is ternate palmate-compound with alternate phyllotaxis. In this study, leaf functional traits (i.e., petiole length, leaf size, leaf shape index, leaf chlorophyll and nitrogen concentrations, single-leaf wet weight, and SLA) of *C. maritima* with different leaf form were determined to gain insight into its growth mechanisms.

This study tests the following hypotheses. First, the SLA of compound leaves of *C. maritima* may be higher than that of simple leaves of *C. maritima* because compound leaves often arrange the small leaflets along the rachis to maximize sunlight interception [16]. Second, the biomass allocation to petiole for compound leaves of *C. maritima* may be higher than that of simple leaves of *C. maritima* because petiole mass disproportionately increased with increasing lamina mass and twig mass [16, 17].

Materials and Methods

Experimental Design

C. maritima was selected as the experimental plant species. Its seeds were bought from a local vegetable market in Zhenjiang, China (32.20°N, 119.53°E) which

has a subtropical humid climate. The annual mean temperature of the area is approximately 15.9°C, and its monthly mean temperature reaches a maximum of 28°C in July and decreases to a minimum of 2.9°C in January. The annual precipitation is approximately 1101.4 mm, and monthly mean precipitation reaches a maximum of approximately 205.6 mm in July and decreases to a minimum of approximately 33.4 mm in December. The site climate summaries are derived from the local yearbook [18].

Experiments were performed by using the pot cultivation experiment. Nine seeds of *C. maritima* were planted in garden pots that contained humus soil. The diameter of each pot was approximately 12 cm. The samples were incubated at room temperature for approximately one month. Deionized water was supplied according to soil moisture during incubation. Sixteen fully expanded and intact leaf samples both of simple and compound leaves of *C. maritima* were collected randomly to determine the functional traits.

Determining Leaf Functional Traits

Petiole length was determined by ruler measurement [4, 13, 19].

Leaf shape index was calculated as the ratio of leaf length to the corresponding leaf width [20, 21]. Leaf length is the maximum value along the midrib, while the width is the maximum value perpendicular to the midrib [21]. Leaf length and leaf width were measured using a ruler [4-6, 12, 13, 19].

The relative chlorophyll and N concentrations in the leaves were estimated with a hand-held plant nutrient meter (TYS-3N, China). YYS-3N was used to calculate the index in "SPAD units" based on absorbance at 650 nm and 940 nm [5, 6, 12, 13].

Single-leaf wet weight was determined using an electronic balance with an accuracy of 0.001 g [4-6].

SLA was computed using the ratio of the leaf area to the corresponding leaf dry weight (cm² g⁻¹), according to previous studies [4-6, 8].

Plasticity index – the index ranged from zero (no plasticity) to one (maximum plasticity) – of leaf functional traits of both simple and compound leaves of *C. maritima* were calculated with the following equation [22, 23]:

$$\text{Plasticity index} = \frac{\text{Maximum mean} - \text{minimum mean}}{\text{Maximum mean}}$$

Statistical Analyses

Data were verified to determine the deviations from normality and homogeneity of the variances before data analysis using the Shapiro-Wilk normality test. One-way ANOVA was performed to evaluate the differences in leaf functional traits of simple and compound leaves of *C. maritima*. Correlation analysis was performed using

Table 1. Differences in leaf functional traits between simple and compound leaves of *C. maritima*.

Leaf form	PL	LL	LW	LSI	LCC	LNC	SLWW	SLA
Simple	5.175± 0.264b	12.000± 0.606ns	13.419± 0.676a	0.900± 0.028b	41.138± 1.934ns	3.431± 0.136ns	2.363± 0.217a	512.604± 23.061ns
Compound	8.344± 0.555a	13.177± 0.507ns	7.392± 0.291b	1.794± 0.047a	43.240± 1.051ns	3.579± 0.070ns	1.084± 0.079b	508.390± 31.145ns

Data (mean with standard error) with different letters in a vertical row indicate a significant difference ($P < 0.05$). "ns" means no significant difference ($P > 0.05$). Abbreviations: PL, petiole length (cm); LL, leaf length (cm); LW, leaf width (cm); LSI, leaf shape index; LCC, leaf chlorophyll concentration (SPAD); LNC, leaf nitrogen concentration (mg g^{-1}); SLWW, single-leaf wet weight (g); SLA, specific leaf area ($\text{cm}^2 \text{g}^{-1}$).

the Pearson product-moment correlation coefficient to determine the patterns among various dependent variables. All statistical analyses were performed using IBM SPSS Statistics (version 22.0; IBM Corp., Armonk, NY, USA). Then a Mantel test [24] was performed using

TFPGA (version 1.3) to determine the relationships given in the correlation matrix between leaf functional traits of simple leaves of *C. maritima* and those of compound leaves of *C. maritima*. Statistical significance was set at P values equal to or lower than 0.05.

Table 2. ANOVA of the effects of leaf form on leaf functional traits of *C. maritima*.

		Sum of Squares	df	Mean Square	F	P
PL	Between Groups	80.328	1	80.328	26.596	<0.001
	Within Groups	90.609	30	3.020		
	Total	170.937	31			
LL	Between Groups	10.928	1	10.928	2.188	0.150
	Within Groups	149.854	30	4.995		
	Total	160.782	31			
LW	Between Groups	291.008	1	291.008	67.155	<0.001
	Within Groups	130.002	30	4.333		
	Total	421.010	31			
ISI	Between Groups	6.406	1	6.406	264.082	<0.001
	Within Groups	0.728	30	0.024		
	Total	7.133	31			
LCC	Between Groups	35.490	1	35.490	0.916	0.346
	Within Groups	1162.337	30	38.745		
	Total	1197.827	31			
LNC	Between Groups	0.195	1	0.195	1.044	0.315
	Within Groups	5.612	30	0.187		
	Total	5.807	31			
SLWW	Between Groups	13.146	1	13.146	30.830	<0.001
	Within Groups	12.792	30	0.426		
	Total	25.938	31			
SLA	Between Groups	142.172	1	142.172	0.012	0.914
	Within Groups	360443.509	30	12014.784		
	Total	360585.681	31			

P values equal to or lower than 0.05 are in bold print. Abbreviations have the same meanings as described in Table 1.

Table 3. Differences in plasticity indices of leaf functional traits between simple and compound leaves of *C. maritima*.

Leaf form	PL	LL	LW	LSI	LCC	LNC	SLWW	SLA
Simple	0.577	0.565	0.429	0.436	0.448	0.405	0.808	0.416
Compound	0.496	0.371	0.446	0.395	0.281	0.242	0.640	0.553

Abbreviations have the same meanings as described in Table 1.

Table 4. Relationship among leaf functional traits of simple and compound leaves of *C. maritima*.

			PL	LL	LW	LSI	LCC	LNC	SLWW	SLA	
PL	Simple	r	1.000	0.812***	0.765***	0.081	0.160	0.149	0.734**	-0.594*	
		P		<0.001	<0.001	0.766	0.554	0.583	0.001	0.015	
	Compound	r	1.000	0.570*	0.358	0.167	0.177	0.251	0.735**	-0.587*	
		P		0.021	0.173	0.536	0.511	0.349	0.001	0.017	
LL	Simple	r		1.000	0.853***	0.288	0.132	0.118	0.756***	-0.667**	
		P			<0.001	0.280	0.627	0.662	<0.001	0.005	
	Compound	r		1.000	0.711**	0.335	-0.051	-0.012	0.883***	-0.070	
		P			0.002	0.204	0.850	0.963	<0.001	0.797	
LW	Simple	r			1.000	-0.249	-0.083	-0.102	0.894***	-0.731**	
		P				0.353	0.760	0.706	<0.001	0.001	
	Compound	r			1.000	-0.412	0.015	0.026	0.745***	-0.192	
		P				0.113	0.955	0.924	<0.001	0.476	
LSI	Simple	r				1.000	0.406	0.419	-0.216	0.127	
		P					0.119	0.106	0.421	0.640	
	Compound	r				1.000	-0.152	-0.103	0.126	0.218	
		P					0.574	0.704	0.643	0.418	
LCC	Simple	r					1.000	0.998***	-0.218	0.014	
		P						<0.001	0.417	0.959	
	Compound	r					1.000	0.960***	0.095	-0.579*	
		P						<0.001	0.727	0.019	
LNC	Simple	r						1.000	-0.242	0.033	
		P							0.367	0.903	
	Compound	r							1.000	-0.683**	
		P								0.493	0.004
SLWW	Simple	r							1.000	-0.740**	
		P								0.001	
	Compound	r								1.000	-0.429
		P									0.098
SLA	Simple	r								1.000	
		P									
	Compound	r									1.000
		P									

*, **, and *** indicate significant differences at 0.05, 0.01, and 0.001 probability level, respectively. *P* values equal to or lower than 0.05 are in bold print. Abbreviations have the same meanings as described in Table 1.

Results

Petiole length and leaf shape index of compound leaves of *C. maritima* were significantly higher than those of simple leaves of *C. maritima* (Tables 1 and 2, $P < 0.001$). By contrast, leaf width and single-leaf wet weight of compound leaves of *C. maritima* were significantly lower than those of simple leaves of *C. maritima* (Tables 1 and 2, $P < 0.001$). No significant difference was observed in leaf length, leaf chlorophyll and nitrogen concentrations, and SLA between simple and compound leaves of *C. maritima* (Tables 1 and 2, $P > 0.05$).

Plasticity index of SLA of compound leaves of *C. maritima* was obviously higher than that of simple leaves of *C. maritima* (Table 3), while plasticity indices of leaf length, leaf chlorophyll, and nitrogen concentrations, and single-leaf wet weight of compound leaves of *C. maritima* were obviously lower than those of simple leaves of *C. maritima* (Table 3). There was no significant difference in plasticity indices of petiole length, leaf width, and leaf shape index between simple and compound leaves of *C. maritima* (Table 3).

Many significant correlations were revealed among leaf functional traits for each leaf form of *C. maritima* (Table 4). In particular, petiole length was positively correlated with leaf size and single-leaf wet weight for simple leaves of *C. maritima* (Table 4, $P < 0.01$) and with leaf length and single-leaf wet weight for compound leaves of *C. maritima* (Table 4, $P < 0.05$). Meanwhile, petiole length was negatively correlated with SLA for both simple and compound leaves of *C. maritima* (Table 4, $P < 0.05$). Leaf length was positively correlated with leaf width and single-leaf wet weight for both simple and compound leaves of *C. maritima* (Table 4, $P < 0.01$). Meanwhile, leaf length was negatively correlated with SLA for simple leaves of *C. maritima* (Table 4, $P < 0.01$). Leaf width was positively correlated with single-leaf wet weight for both simple and compound leaves of *C. maritima* (Table 4, $P < 0.001$). Meanwhile, leaf width was negatively correlated with SLA for simple leaves of *C. maritima* (Table 4, $P < 0.01$). Leaf chlorophyll concentration was positively correlated with leaf nitrogen concentration for both simple and compound leaves of *C. maritima* (Table 4, $P < 0.001$). Meanwhile, leaf chlorophyll and nitrogen concentrations were negatively correlated with SLA for compound leaves of *C. maritima* (Table 4, $P < 0.05$). Single-leaf wet weight was negatively correlated with SLA for simple leaves of *C. maritima* (Table 4, $P < 0.01$).

Discussion

Plants attempt to develop an optimal and successful ecological strategy of the trade-off between various morphological characteristics to maximize resources and exhibit fitness advantage in the multivariate

environments [4, 19]. Generally, compound leaves often arrange the small leaflets along the rachis to maximize sunlight interception [16]. Accordingly, compound leaves may be an important adaptive feature contributing to minimizing branching and to rapid height gain, particularly in sunlight-demanding plant species [16, 25]. Meanwhile, low leaf construction costs are closely related to efficient energy use, which consequently facilitates plant growth [26, 27]. It was therefore expected that compound leaves can display high SLA characterized by high resource acquisition and use efficiency with low leaf construction cost in order to obtain a higher relative growth rate, especially under the condition with overlapping sunlight. However, this study rejected the first hypothesis by showing that no significant difference was observed in SLA between simple and compound leaves of *C. maritima*. Accordingly, there are no differences in the material investment per unit area and per lamina between simple and compound leaves of *C. maritima*. Hence, SLA may not necessarily contribute to successful ecological strategy of compound leaves of *C. maritima* in this study. However, single-leaf wet weight of compound leaves of *C. maritima* was significantly lower than that of simple leaves of *C. maritima*. To some extent, this indicated that compound leaves of *C. maritima* possess higher resource capture ability as well as higher relative growth rate than simple leaves of *C. maritima*, suggesting that single-leaf wet weight rather than SLA may play an important role during the process of successful ecological strategy of simple and compound leaves of *C. maritima*. Meanwhile, the higher leaf shape index and the lower leaf width of compound leaves of *C. maritima* than simple leaves of *C. maritima* can improve the efficiency of resource capture (especially sunlight capture) via adjustments to leaf shape and size [7] for compound leaves of *C. maritima* to maximize reducing the negative effects of overlapping sunlight on leaf growth.

A previous study found that the petiole mass disproportionately increased with increasing lamina mass and twig mass, and the costs of supporting the lamina increased with increasing twig size due to the allometric relationship between petiole mass and twig mass [4, 17, 19, 28]. Consequently, the biomass allocation to petiole for compound leaves may be significantly higher than those for simple leaves. The result of this study revealed that the petiole length of compound leaves of *C. maritima* was significantly higher than that of simple leaves of *C. maritima*. This indicated that the biomass allocation to petiole for compound leaves of *C. maritima* was significantly higher than that of simple leaves of *C. maritima*. This was consistent with the study's second hypothesis. Previous studies also found that lamina support of plant species with compound leaves was significantly higher than that of plant species with simple leaves [16, 19]. The higher biomass allocation to petiole of compound leaves than simple leaves can contribute to its advantages of lamina support [16, 19].

In particular, leaf petiole exhibited a raised robustness to enable leaves to adapt to the updated pattern of resource allocation [4]. This study also found that petiole length shows a strongly positive correlation with leaf size as well as single-leaf wet weight. Thus to a certain extent, branching is expensive in terms of gaining height for resource capture (especially sunlight capture) [19].

The phenotypic plasticity of leaf functional traits of plant species can enable plants to occupy a wide variety of environmental conditions and then enhance their competitive advantage [3, 22, 23, 29]. In particular, the higher range of phenotypic plasticity of plants for any functional traits may play a key role in their successful strategy [3, 22, 23, 29]. This study showed that the plasticity index of SLA of compound leaves of *C. maritima* was obviously higher than that of simple leaves of *C. maritima*. The higher range of phenotypic plasticity of SLA of compound leaves of *C. maritima* may enhance the advantage in resource (especially sunlight) capture and use efficiency by shifting the material investment per unit area and per lamina.

Generally, leaf size was positively correlated with SLA because leaves with a high SLA payment low biomass into leaf structures and leaves with low SLA allocate more structural investment [3, 9-11]. However, unlike these previous studies, SLA shows a negative correlation with leaf size for simple leaves of *C. maritima*. The negative relationship between SLA and leaf size may be ascribed to that species with larger leaves having diminishing returns on the biomass they invest in sunlight capture and run-away selection for species with smaller leaves [30]. Thus, leaves with larger size did not always invest low resource allocation on leaf construction and possess low SLA [6]. In addition, SLA did not have a significant relationship with leaf size for compound leaves of *C. maritima* in this study. Conflicting results for the correlations between leaf size and SLA also arrived by previous studies, including positive [6, 31], negative [4, 30], or unrelated [5, 19, 32]. Accordingly, the relationship between leaf size and SLA varies by species as well as leaf forms. Based on the results of the Mantel test, there were significant positive correlation patterns between leaf functional traits of simple leaves of *C. maritima* and those of compound leaves of *C. maritima*. Hence, the correlation patterns between leaf functional traits of simple leaves of *C. maritima* and those of compound leaves of *C. maritima* are similar. Consequently, the main factor affecting the successful ecological strategy of simple and compound leaves of *C. maritima* may be ascribed to the differences in leaf functional traits between simple and compound leaves of *C. maritima* rather than the differences in the correlation patterns among leaf functional traits between simple and compound leaves of *C. maritima*.

Conclusions

The purpose of this study was to evaluate differences in leaf functional traits between simple and compound leaves of *C. maritima* to illuminate the mechanisms underlying the ecological strategy of plant species with different leaf forms. No significant difference was observed in SLA between simple and compound leaves of *C. maritima*. However, single-leaf wet weight of compound leaves of *C. maritima* was significantly lower than that of simple leaves of *C. maritima*. Thus, compound leaves of *C. maritima* possess higher resource capture ability as well as higher relative growth rate than simple leaves of *C. maritima*, suggesting that single-leaf wet weight rather than SLA may play an important role during the process of successful ecological strategy of simple and compound leaves of *C. maritima*. The petiole length of compound leaves of *C. maritima* was significantly higher than that of simple leaves of *C. maritima*. Thus, the biomass allocation to petiole for compound leaves of *C. maritima* was significantly higher than that of simple leaves of *C. maritima*. SLA shows a negative correlation with leaf size for simple leaves of *C. maritima*, while SLA did not have a significant relationship with leaf size for compound leaves of *C. maritima*. Thus, the relationship between leaf size and SLA may vary by leaf forms. The plasticity index of SLA of compound leaves of *C. maritima* was obviously higher than that of simple leaves of *C. maritima*. The higher range of phenotypic plasticity of SLA of compound leaves of *C. maritima* may enhance the advantage in resource (especially sunlight) capture and use efficiency by shifting the material investment per unit area and per lamina. Meanwhile, the main factor affecting the successful ecological strategy of simple and compound leaves of *C. maritima* may be ascribed to the differences in leaf functional traits between simple and compound leaves of *C. maritima* rather than the differences in the correlation patterns among leaf functional traits between simple and compound leaves of *C. maritima*.

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Conflict of Interest

The authors declare no conflict of interest.

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