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THE TRADE-OFF BETWEEN GROWTH AND REPRODUCTION IN AN ALPINE HERBACEOUS PLANT ALONG AN ELEVATION GRADIENT

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Abstract

The relationship between growth and reproduction is a fundamental aspect of the reproductive strategy for a plant. Using an allometric perspective for both vegetative and reproductive traits allows us to understand and predict the impact of environmental change on a plant species. Here, we investigated the allometric relationships in *Gentiana rigescens* Franch. ex Hemsl. individuals at non-flowering and flowering stages along an elevation gradient in southwest China. We found that the mean values of the metrics were significantly higher in *G. rigescens* plants at reproductive stage than those at vegetative stage. However, allometric analysis showed that the plants in vegetative stage had higher root and stem biomass than those in reproductive stage at a given size, while leaf biomass showed fixed allometric trajectory. The height of *G. rigescens* was higher in flowering individuals than that in non-flowering individuals at small size, while the contrary was obtained at large size. Analysis of covariance showed that the root biomass was not affected by elevation, whereas the stem biomass, leaf biomass, and total biomass increased with increasing elevation. In conclusion, allocating biomass to roots and stems in *G. rigescens* individuals reduced when flowering occurred, but the resource investment in leaves was not changed. As the total biomass increased with increasing elevation, the effects of elevation on leave and stem biomass of *G. rigescens* could be partly size-dependent.

Key words: Alpine, *Gentiana rigescens*, Gentianaceae

Introduction

The relationship between growth and reproduction is a fundamental aspect of the reproductive strategy for a plant (Sun *et al*., 2014). In many perennial species, present reproduction can result decreased probabilities of future survival and fecundity (Doust, 1989; Obeso, 1993). When both vegetative and reproductive structures have the same energy available for investment, an increase in reproductive effort inevitably results in both an increase in current reproduction and a decrease in growth (Obeso, 2002; Reekie & Avila-Sakar, 2005). The allocation pattern of a plant is an important factor in understanding the plant distribution and adaptation (Bazzaz *et al*., 1987). A study showed that the relative reduction in vegetative growth was approximately 24% in *Arum italicum* plants at reproductive stage, compared to the growth in the plants in vegetative stage (Méndez & Obeso, 1993).

Allometry is a powerful quantitative tool to study the relationship between growth and allocation (Weiner, 2004). Using an allometric perspective for both vegetative and reproductive traits could reveal functional responses to resource availability and to maximize fitness across a range of environments (Bonser & Aarssen, 2003; Obeso, 2004), which allows us to understand and predict the impact of environmental change on a plant species (Zhang *et al*., 2015).

The objectives of this study were to: (1) compare biomass allocation between different plant growing stages and (2) assess the effect of elevation on biomass allocation of the plants at different growing stages. Here, we investigated the allometric relationships in *Gentiana rigescens* individuals at non-flowering and flowering stages from the same populations along an elevation gradient. The wide distribution of *G. rigescens* individuals at vegetative and reproductive stages in a large range of elevations provides a good chance to understand the effects of growing stage and elevation on the plant biomass allocation. We hypothesize that (1) allocating biomass to each vegetative part in *G. rigescens* individuals would reduce when flowering occurred and (2) the allometric relationships in both flowering and non-flowering *G. rigescens* individuals could change along an elevation gradient.

Material and Methods

Study sites and sampling methods: *Gentiana rigescens* Franch. ex Hemsl. (family Gentianaceae) is a perennial plant distributed in southwest China and Myanmar (Flora of China Editorial Committee, 1988). Our investigations were conducted in in Guizhou, Sichuan, and Yunnan provinces in southwest China. The sampling area is very close to the Qinghai–Tibet Plateau which is considered to be a geographical source area for genus *Gentiana* (Favre *et al*., 2016). From December 2012 to February 2013 and October to November, 2013, we collected 1116 individuals (621 non-flowering individuals and 495 flowering individuals) of *G. rigescens* from 24 wild populations in the elevation range of 1550-2726 m a.s.l. (Table 1).

In each population, we randomly collected 11-44 individuals (26 individuals on average) at vegetative stage and 9-29 individuals (21 individuals on average) at flowering stage. Whole plants were carefully taken from the soil and brought to the laboratory. The roots were thoroughly washed with tap water. Each individual was divided into roots, stems, leaves, and flowers (if it had). Samples were dried to constant mass at 60^{o}C and weighted to determine the biomass for each part. Stem length was recorded as plant height.

Table 1. Sampling information of *Gentiana rigescens* populations.

Population code	Number of samples at flowering stage	Number of samples at vegetative stage	Elevation (m)	Latitude (°N)	Longitude (°E)	Site
1	24	17	1963	24.98247222	98.4885	Baoshan, Yunnan
2	22	23	1770	24.90577778	99.38138889	Baoshan, Yunnan
3	11	44	2256	24.63822222	104.1519167	Qujing, Yunnan
4	26	20	2158	25.16141667	104.8400833	Xingyi, Guizhou
5	27	25	1954	25.41797222	104.4287778	Qujing, Yunnan
6	26	14	2180	25.3483	102.7867722	Kunming, Yunnan
7	20	14	2164	25.55626111	102.8392417	Kunming, Yunnan
8	23	27	2726	24.76126111	102.9052444	Yuxi, Yunnan
9	25	30	1615	23.71311111	104.2485833	Wenshan, Yunnan
10	17	38	2024	23.32283333	103.1470833	Honghe, Yunnan
11	21	34	2013	25.70241667	102.4854167	Kunming, Yunnan
12	21	34	2111	25.07	101.4136944	Chuxiong, Yunnan
13	18	36	2105	25.31109167	101.2709444	Chuxiong, Yunnan
14	9	24	2370	25.64241667	101.1059	Chuxiong, Yunnan
15	16	38	1969	25.63069444	101.4818861	Chuxiong, Yunnan
16	18	34	2203	25.46186111	102.8704167	Kunming, Yunnan
17	29	25	2531	27.05783333	102.9744444	Zhaotong, Yunnan
18	23	25	2085	25.21358333	103.0960278	Kunming, Yunnan
19	20	11	2102	25.846675	100.1012361	Dali, Yunnan
20	19	20	2017	25.58471944	100.3049361	Dali, Yunnan
21	12	18	2348	26.77430556	101.5225556	Panzhihua, Sichuan
22	28	27	2487	25.94461389	100.8412333	Dali, Yunnan
23	20	27	2480	26.6075	103.9366389	Bijie, Guizhou
24	20	16	1550	26.56944444	107.3649722	Qiannan, Guizhou

Statistical analyses: Data were log transformed before analyses. Linear regression models of the form log $y = a$ log x + log b were used for the allometric relationships defined as log y and log x, where a is the slope and log b is the intercept. The different of slopes represents the different developmental trajectories of a plant trait, while the different of intercepts indicates that, at a given size, the plant in different environments (or different treatments) have different traits (Xie *et al*., 2012). The slopes and intercepts of the allometric relationships were estimated by Standardized Major Axis regression, using the R software package 'smatr' version 3.4 (R Core Team, 2017; Warton *et al*., 2012). To compare the allometric relationships in *G. rigescens* individuals between vegetative and reproductive stages, we used R package 'smatr' to run a test of heterogeneity in slopes between different growing stages. If the slopes were not different, we tested for differences in intercept or shift along main axis with Wald statistics (Warton *et al*., 2006). To examine the effect of growing stage and elevation on the biomass and height, an analysis of covariance (ANCOVA) was conducted using SPSS Statistics 22(IBM Corporation), with growing stage as a fixed factor and elevation as a random factor. Graphs for the relationships of biomass and height to elevation were produced by JMP 13.2.1 (SAS Institute).

Results

The histograms show different frequency distributions for metrics we determined between different growing stages (Fig. 1). The mean values of the root biomass, stem biomass, leaf biomass, total biomass, and height were higher in plants at reproductive stage than those at vegetative stage (t-tests, p<0.001) (Table 2).

Both of the individuals at vegetative and reproductive stages showed allometric regressions in root biomass, stem biomass, leaf biomass, and height to total biomass relationships (Fig. 2, Table 3). Individuals in vegetative stage and reproductive stage shared a common slope in root biomass vs. total biomass, stem biomass vs. total biomass, and leaf biomass vs. total biomass relationships, respectively (Table 4). Slopes for height vs. total biomass relationship were different between different growing stages (Table 4). Between the regressions of different growing stages, intercepts were different and there were shifts along the main axes in root biomass vs. total biomass and stem biomass vs. total biomass relationships (Table 4), which indicates that, at a given plant size, the root biomass and the stem biomass were larger in non-flowering plants than those in flowering plants, respectively. For leaf biomass vs. total biomass relationship, intercepts were equal but there was a shift along the main axis (Table 4). In height vs. total biomass relationships, the slopes were significantly different between flowering and non-flowering plants (Table 4).

ANCOVA shows that growing stage had significant effect on root biomass, but elevation didn't (Table 5). Stem biomass, leaf biomass, total biomass, and plant height had been influenced by growing stage and elevation, but there was no interaction effect for elevation and growing stage (Table 5). Stem biomass, leaf biomass, and total biomass increased with increasing elevation, while plant height decreased with increasing elevation (Fig. 3).

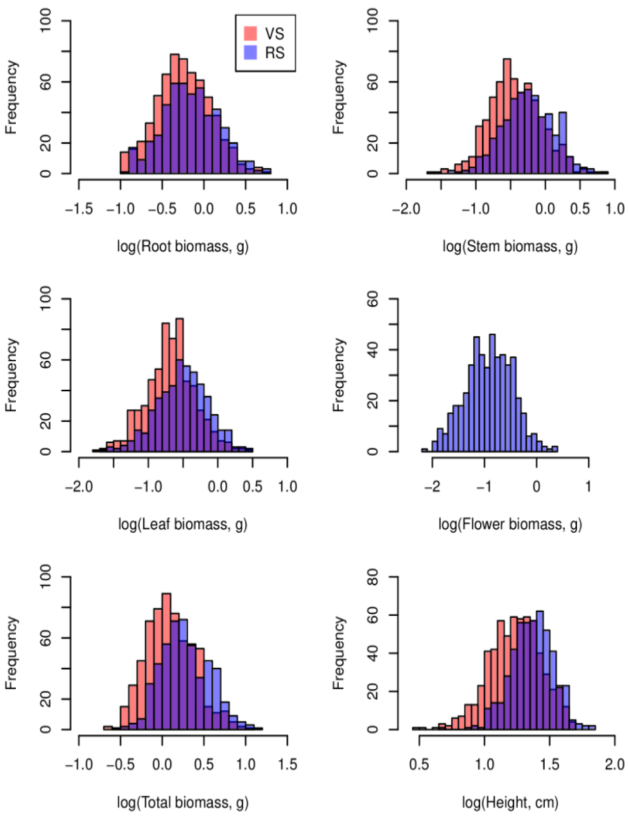

Fig. 1. Histogram of biomass and plant height of *Gentiana rigescens* at different growing stages.
VS: vegetative stage; RS: reproductive stage.

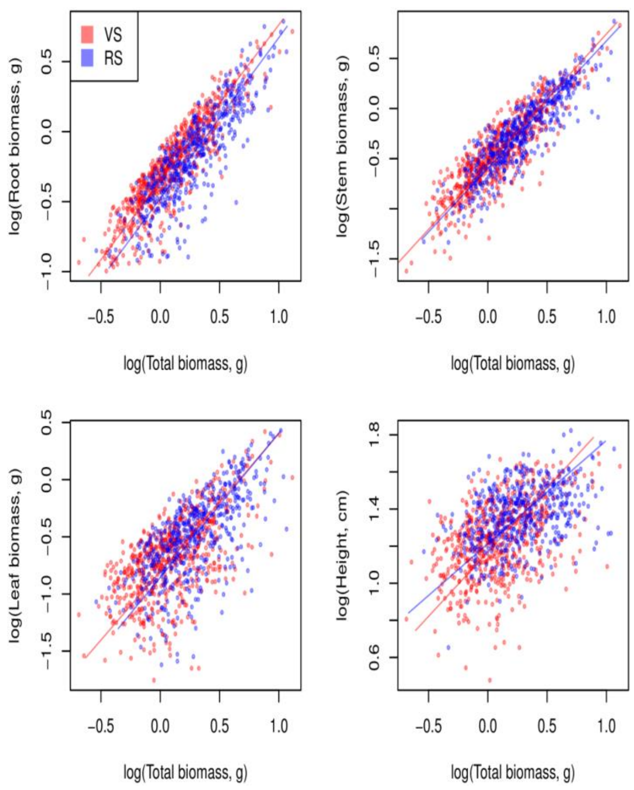

Fig. 2. Relationships of root biomass, stem biomass, leaf biomass, and height to total biomass for *Gentiana rigescens* individuals at different growing stages.
VS: vegetative stage; RS: reproductive stage.

Table 2. Comparison of biomass and height between *Gentiana rigescens* individuals at different growing stages.

	VS			RS		
	Mean ± SD	**Min.**	**Max.**	**Mean ± SD**	**Min.**	**Max.**
Root biomass (g)	0.755 ± 0.657a	0.101	5.193	0.914 ± 0.793b	0.121	6.135
Stem biomass (g)	0.552 ± 0.623a	0.024	6.770	0.791 ± 0.748b	0.046	7.421
Leaf biomass (g)	0.288 ± 0.286a	0.018	2.632	0.428 ± 0.379b	0.024	2.691
Flower biomass (g)	ND	ND	ND	0.206 ± 0.261b	0.020	9.880
Total biomass (g)	1.594 ± 1.346a	0.206	13.006	2.338 ± 1.730b	0.289	11.609
Height (cm)	19.1 ± 8.6a	3.0	50.0	24.7 ± 9.1b	4.5	66.6

Data were log transformed before analysis and are presented as non-log-transformed values. Different letters indicate significant differences by *t* test at $p<0.001$, d.f.=1114. VS: vegetative stage; RS: reproductive stage

Table 3. Regression parameters of log-log relationships in *Gentiana rigescens* individuals at different growing stages, estimated by the standard major axis regression.

	VS				RS			
	Slope	**Intercept**	R^2	**CI of slope**	**Slope**	**Intercept**	R^2	**CI of slope**
logR vs. logT	1.12	-0.36	0.80	1.08-1.16	1.15	-0.48	0.73	1.10-1.20
logS vs. logT	1.30	-0.56	0.76	1.25-1.35	1.27	-0.60	0.79	1.22-1.32
logL vs. logT	1.20	-0.80	0.37	1.13-1.28	1.26	-0.86	0.45	1.18-1.35
logH vs. logT	0.69	1.17	0.19	0.65-0.74	0.56	1.21	0.16	0.51-0.60

logR: log (root biomass); logT: log (total biomass); logS: log (stem biomass); logL: log (leaf biomass); logH: log (height). VS: vegetative stage; RS: reproductive stage

Table 4. Tests for heterogeneity of slope and shift in intercept or in location along the common slope for log-log relationships between *Gentiana rigescens* at different growing stages.

	If slopes are equal		If intercepts are equal		If no shift along the axis	
	Likelihood ratio statistic	***P***	**Wald statistic**	***P***	**Wald statistic:**	***P***
logR vs. logT	0.8557	0.3549	124.6	<0.0001	52.16	<0.0001
logS vs. logT	0.6196	0.4312	15.97	<0.0001	84.74	<0.0001
logL vs. logT	1.096	0.2952	5.077	0.0242	96.03	<0.0001
logH vs. logT	15.8	<0.0001				

logR: log (root biomass); logT: log (total biomass); logS: log (stem biomass); logL: log (leaf biomass); logH: log (height). $p<0.01$

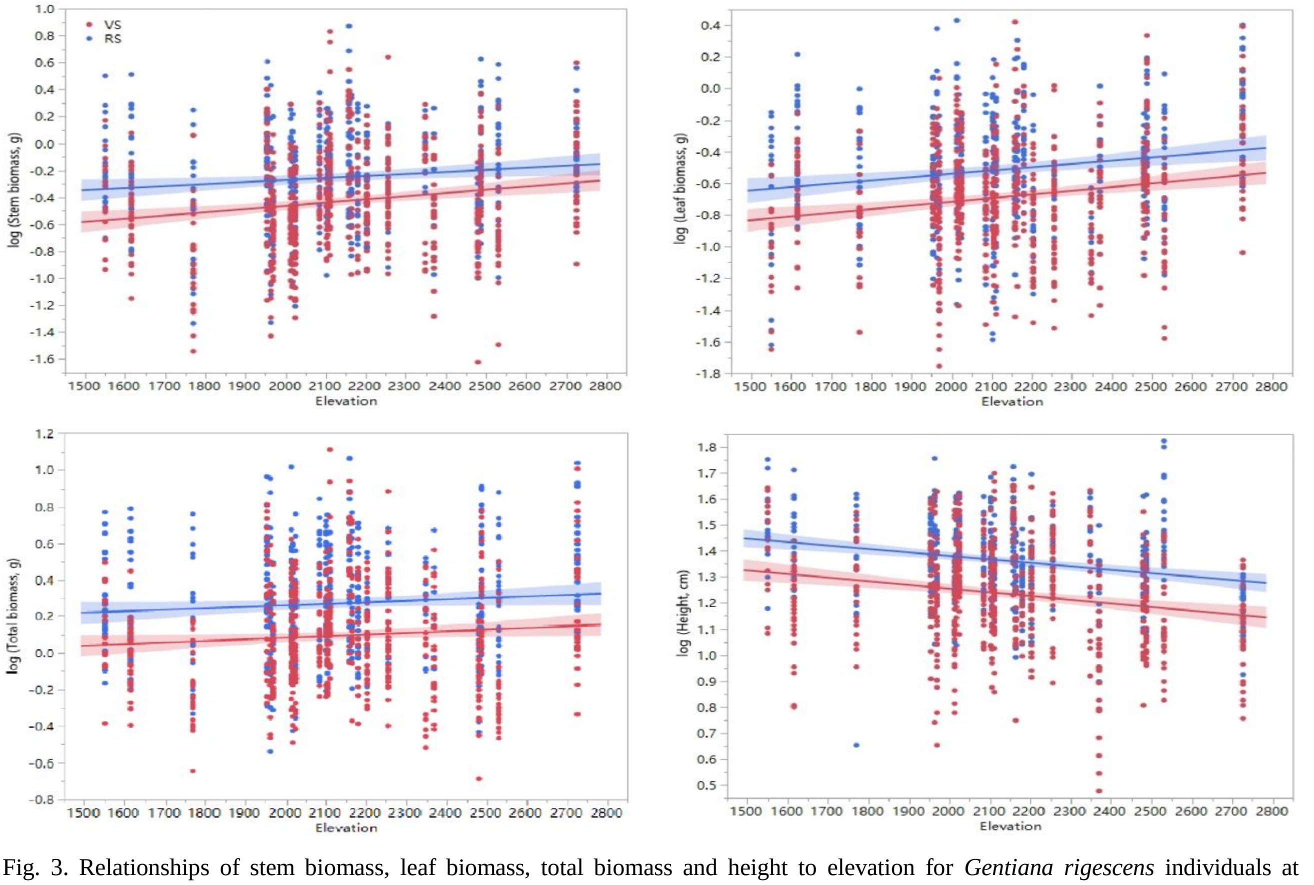

Fig. 3. Relationships of stem biomass, leaf biomass, total biomass and height to elevation for *Gentiana rigescens* individuals at different growing stages
VS: vegetative stage; RS: reproductive stage

Table 5. ANCOVA to test the effects of growing stage and elevation on biomass and height of *Gentiana rigescens*.

	d.f.	Root biomass			Stem biomass			Leaf biomass			Total biomass			Height		
		Sum of squares	F ratio	*P*	Sum of squares	F ratio	*P*	Sum of squares	F ratio	*P*	Sum of squares	F ratio	*P*	Sum of squares	F ratio	*P*
Growing stage	1	1.23	13.81	**<0.001**	6.66	61.43	**<0.001**	5.64	56.41	**<0.001**	6.30	91.12	**<0.001**	3.72	150.63	**<0.001**
Elevation	23	21.10	10.30	0.006	34.19	13.72	**<0.001**	32.07	13.95	**<0.001**	17.04	10.72	**<0.001**	9.39	16.54	**<0.001**
Growing stage × Elevation	23	3.16	1.54	0.049	4.03	1.62	0.033	2.12	0.92	0.567	2.80	1.76	0.015	1.20	2.11	0.002
Model	47	26.30	6.28	**<0.001**	47.98	9.42	**<0.001**	42.82	9.11	**<0.001**	28.01	8.63	**<0.001**	16.16	13.93	**<0.001**
Error	1068	95.17			115.73			106.77			73.78			26.38		
Total	1116	170.87			300.92			561.65			135.81			1906.66		

Boldfaced P-values are statistically significant at the $p<0.05$ level

Discussion

Plant traits at different growing stages: The mean values of the metrics were higher in *G. rigescens* plants at reproductive stage than those at vegetative stage. The reason could be that part of the non-flowering individuals that had not yet reached the minimum size for reproduction, while all flowering *G. rigescens* had reached the minimum size (Bell, 1980; Weiner, 2004). Moreover, it indicates that the biomass of each vegetative part (roots, stems, and leaves) was continually increasing at reproductive stage. To increase their reproductive output, plants can allocate their resources to reproduction and grow more to increase their potential reproductive output (Jongejans & de Kroon H, 2006; Weiner *et al.*, 2009). The responses to investment in reproduction are variable due to different factors, such as plant architecture and resource availability (Obeso, 2002). Realized physiological cost of reproduction in *G. rigescens* plant should be considered.

Allometric relationships between different growing stages: In this study all of the log-log relationships yield the linear regressions and, at a given size, the plants in vegetative stage had higher root and stem biomass than those in reproductive stage. It indicates that resources diverted to flowers rather than roots and stems in *G. rigescens*. Interestingly, the leaf biomass showed fixed allometric trajectory which meant that the plant's strategy to invest resources in leaves didn't change when flowering (Weiner, 2004). As plants allocate biomass to different parts to reduce any imbalance between soil resource acquisition by roots and carbon fixation by leaves, the degree of plasticity in changing these allometric allocations should be related to the temporal variability in resource supply rates in nature (Shipley & Meziane, 2002). The height of *G. rigescens* was higher in flowering individuals than that in non-flowering individuals at small size, while the contrary was obtained at large size. Increasing plant size produced a lesser increase in height in flowering plants than that in non-flowering plants.

Effect of elevation on plant traits: As the plant size (total biomass) increased with increasing elevation, the effects of elevation on leave and stem biomass of *G. rigescens* could be partly size-dependent. Meanwhile, the plant height decreased with increasing elevation. This reduction at high elevations can decouple plant's climate from the ambient, which may have a positive effect on the reproduction (Fabbro & Körner, 2004). Size-dependent variation in reproductive effort had been observed in six *Gentiana* species (Liang *et al.*, 2008). He *et al.*, (2017) found that the reproductive allocation of *G. hexaphylla* increased with elevation.

Conclusion

Allocating biomass to roots and stems in *G. rigescens* individuals reduced when flowering occurred, while the resource investment in leaves was not changed. The stem and leaf biomass in both non-flowering and flowering individuals increased with increasing elevation. Further studies are needed of the effects of the factors on the specific functional traits of plants under controlled experimental conditions.

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