

POLISH JOURNAL OF ECOLOGY (Pol. J. Ecol.)	60	3	545–557	2012
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Regular research paper

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## LIFE HISTORY STRATEGY INFLUENCES BIOMASS ALLOCATION IN RESPONSE TO LIMITING NUTRIENTS AND WATER IN AN ARID SYSTEM

**ABSTRACT:** The optimal partitioning theory (OPT) predicts that a plant should allocate relatively more biomass to the organs that acquire the most limiting resource. However, variation in biomass allocation among plant parts can also occur as a plant grows in size. As an alternative approach, allometric biomass partitioning theory (APT) asserts that plants should trade off their biomass between roots, stems and leaves, and this approach can minimize bias when comparing biomass allocation patterns by accounting for plant size in the analysis.

We analyzed the biomass allocation strategy of the two species: annual *Setaria viridis* (L.) Beauv and perennial *Pennisetum centrasiatium* Tzvel from the Horqin Sandy Land of northern China by treating them with different availabilities of soil nutrient and water (added in summer and winter), and hypothesized that the two species have different patterns of biomass allocation strategy in response to different soil water content and soil nitrogen content.

After taking plant size into account, the biomass allocation strategy of *S. viridis* and *P. centrasiatium* differed in response to nitrogen and water; leaves and root:shoot ratio (RTS) of *S. viridis* were “true” in response to various soil nitrogen contents. The plasticity of roots was also “true” in response to fluctuation in soil water content. However, *P. centrasiatium* showed a different pattern with no shift of biomass allocation strategy in response to nitrogen and water. Adjustment

in organs biomass allocation pattern of *S. viridis* in response to nitrogen and water limitation was dramatic, this suggested that *S. viridis* support optimal partitioning theory (OPT). *P. centrasiatium* has better tolerance to varied environments and more likely support the allometric biomass partitioning theory (APT), this characteristic may allow *P. centrasiatium* to keep dominance in fragile habitats.

**KEY WORDS:** arid system, allometric scaling, biomass allocation, *Setaria viridis*, *Pennisetum centrasiatium*

### 1. INTRODUCTION

The strategies of biomass allocation in plants is a central question in plant ecology (McConnaughay and Coleman 1999). Understanding the biomass allocation strategies across environments can explain plant distribution and abundance patterns. There are several competing hypotheses about the mechanisms that control biomass allocation in plants (McCarthy and Enquist 2007, Kobe *et al.* 2010). The optimal partitioning theory (OPT) predicts that a plant should allocate relatively more biomass to the organs that acquire the most limiting resource (Bloom *et al.* 1985). For instance, under low

light conditions, OPT predicts that a plant allocates proportionally more biomass to leaves (Shipley and Meziane 2002), while under low soil nitrogen conditions proportionally more biomass should be allocated toward the roots (Linkohr *et al.* 2002, Mony *et al.* 2007).

However, variation in biomass allocation among plant parts can also occur as a plant grows in size (Müller *et al.* 2000, Bonser and Aarssen 2009). This could make it difficult to distinguish between variation in biomass allocation patterns due to resource limitations in the environment (“true” if allometric relationships or intercepts are affected by environmental conditions significantly) versus size-dependent allometric driven patterns (‘apparent’ plasticity; “apparent” if relationships are not affected by environmental conditions significantly) (Zhang and Jiang 2002, Weiner 2004, McCarthy and Enquist 2007). While apparent plasticity has been demonstrated in many species, distinguishing between apparent and true plasticity requires a cautious allometric analysis.

In contrast to the optimal partitioning theory, the allometric biomass partitioning theory (APT) predicts that plants must trade off allocating biomass proportionally between roots, stems and leaves (Enquist and Niklas 2002, Yang and Luo 2011). Under this hypothesis, the allometric relationships that exist among different organs of plants are consistent regardless of variation in the environment. APT is useful because it minimizes bias when comparing biomass allocation patterns by accounting for plant size in the analysis (McCarthy and Enquist 2007). According to APT, the variability in biomass due simply to the size of a plant is removed prior to analysis (McConnaughay and Coleman 1999, Yang and Luo 2011).

*Setaria viridis* (L.) Beauv is a common annual grass that inhabits degraded arid grasslands in northern China (Zhao *et al.* 2007). It is one of the dominant species in the desertified grasslands of northern China. This species exhibits high phenotypic plasticity across different habitats in response to varying environmental conditions (He *et al.* 2008). For instance, in stabilized mid-successional dunes, the root:shoot ratio (RSR) of *S. viridis* is 49% higher than in the more degraded mo-

bile dunes (He *et al.* 2008), suggesting that the biomass of *S. viridis* supports the OPT.

The perennial grass *Pennisetum centrasiaticum* Tzvel also allocates relatively more biomass to roots in low water conditions (Guo and Li 2008) suggesting that *P. centrasiaticum* also supports OPT. However, those previous studies have not considered the effect of plant size on biomass allocation pattern (Liu *et al.* 1999, Chen *et al.* 2002). If plant size is taken into account, it is not clear that the two species would still support the OPT.

In Horqin Sandy Land of northern China, desertification due to land use and climate has resulted in the conversion of 71884 km<sup>2</sup> of former arid and semi-arid grassland into shrublands and open sandy dunes (Zhao *et al.* 2004). This land degradation has significantly altered the nitrogen and water content of the soil (Li *et al.* 2009). Nitrogen and water are the two important limiting factors for plants in arid regions (Huang *et al.* 2009b). Thus there is the potential for plants to exhibit varied biomass allocation strategies in response to resource limitations across the succession gradient. For instance, at early succession stages when soil nutrient content is very low, in order to survive plants to survive would allocate more biomass to root rather than leaves in response to nutrient limitation (Huang *et al.* 2009a).

We performed a controlled manipulative experiment in the field with *S. viridis* and *P. centrasiaticum* to answer three questions: (1) Do the biomass allocation patterns of annual *S. viridis* and perennial *P. centrasiaticum* grasses differ in response to changes in environmental conditions? (2) Do the biomass allocation strategies of the two species represent “apparent” or “true” plasticity? (3) After taking the effect of plant size into account, do these two species still support the Optimal Partitioning Theory? We hypothesize that: (1) the biomass allocation strategy of *S. viridis* and *P. centrasiaticum* differs in response to changes in availability of limiting resources. We predict that *S. viridis* will allocate proportionally more biomass to root and stem at nitrogen control treatment in comparison to the nitrogen addition treatment, and it will allocate more biomass to roots at water control treatment in comparison to

the water addition treatment, while *P. centrasiaticum* will not alter biomass allocation strategies in varied nitrogen and water levels after take plant size into account. (2) We also predict that the allocation strategy of *S. viridis* will support the OPT, but *P. centrasiaticum* will not because the allometric relationships among different organs of *P. centrasiaticum* will keep constant at different nitrogen and water treatment.

## 2. STUDY SITE

The experiment was established in the central region of the Horqin Sandy Land in the eastern part of Inner Mongolia, China (42°55'N, 120°42'E, 345 m a.s.l.). The soils are very infertile and sandy with light yellow color, coarse texture and loose structure. The soil total nitrogen content is around 0.057–0.199 g kg<sup>-1</sup> and the soil bulk density is 1.29–1.59 g cm<sup>-3</sup> in the layer of soil 0–30 cm depth. The research area is covered with *P. centrasiaticum* community and is equal to 2.02 ha. The local climate is temperate continental semiarid monsoon, with a mean annual temperature of 6.8°C and annual precipitation 366 mm, and the mean annual potential evaporation equals to 1,935 mm. The annual frost-free period lasts approximately 130 to 150 days.

Dunes are alternately distributed within a gently undulating lowland (Li *et al.* 2005). Vegetation is characterized by the shrublands of *Artemisia halodendron* Lam with scattered trees and wind break tree belt of *Populus* spp. Plant canopy covers between 15 and 60% of the soil and presents a random patchy structure. The dominant plant species include *A. halodendron*, *P. centrasiaticum*, *Caragana microphylla* Turcz ex Bess and *S. viridis*.

This study was performed in a slight degraded sandy grassland. *S. viridis* is a common annual grass and has been proposed as a model to study C4 photosynthesis and related bioenergy grasses. Perennial herb *P. centrasiaticum* is a C4 plant, culms solitary or clump growth season lasts from April to October; it is a key early succession species in the desertified grasslands in northern China (Liu *et al.* 1999) due to its RSR values being higher than those of *S. viridis* and of many other species of arid northern China (Liu *et al.* 1999,

Guo and Li 2008). *P. centrasiaticum* has been shown to exhibit some apparent plasticity, *i.e.* the RR of *P. centrasiaticum* increased at arid environments in comparison with the moist environments (Chen *et al.* 2002).

## 3. METHODS

### 3.1. Experimental design

On October 5, 2009, 30 cm × 40 cm plastic pots, total number is 36, were planted in slight degraded sandy grassland, where there was a community dominated by *P. centrasiaticum* and with *S. viridis* as its accompanying species. The *P. centrasiaticum* and *S. viridis* were natural growth forms that covered the undisturbed soil. Two nutrient treatments were chosen to reflect both nutrient-stressed and nutrient-unstressed habitat conditions in May 2010. N addition includes two treatments: one is N unstressed (N<sub>+</sub>), under which 2.02 g of NH<sub>4</sub>NO<sub>3</sub> were added on June 8; and another is control (N<sub>0</sub>: stressed and the total nitrogen content is 34 mg kg<sup>-1</sup> in the layer of soil 0–40 cm deep). The soil nitrogen content in N<sub>+</sub> treatment was equal to the soil nitrogen level in the restored sandy land (Su *et al.* 2004).

There were two water treatments (summer and winter additions) and one control. W<sub>s+</sub>: High snow level (add snow in winter), amount of water equivalent to 100 mm rainfall applied during the winter (approximately equal to 30% of local average precipitation during growth season of local site in the recent 20 years); W<sub>w+</sub>: High water level (add water in summer), amount of water equivalent to 100 mm precipitation during the growing season applied as 1000 ml of water every 2 weeks; W<sub>0</sub>: low water/snow level, in which no water was added. A full-factorial design of the six possible combinations of high/low level of nitrogen and high/low level of water/snow was constructed:

N<sub>0</sub> + W<sub>0</sub> = full control;

N<sub>0</sub> + W<sub>s+</sub> = N control, Water summer addition;

N<sub>0</sub> + W<sub>wi</sub> = N control, Water winter addition;

N + W<sub>0</sub> = N addition, Water control;

N + W<sub>s+</sub> = N addition, Water summer addition;

$N+W_{wi} = N$  addition, Water winter addition.

There were 6 replicate pots in every treatment, and 36 pots in total. In each pot *P. centrasiaticum* and *S. viridis* coexisted. In each pot, there were three to eight *P. centrasiaticum* and *S. viridis* plants. Relative values in the analysis were used to minimize the effect of density. In this *P. centrasiaticum* community, *P. centrasiaticum* and *S. viridis* coexisted in undisturbed soil, and the plant interaction in all pots was similar. In addition, the effect of plant interaction was weak when compared to the effect caused by nitrogen and water treatments (Huang *et al.* 2009a). Therefore, we did not consider the effect of plant interaction on biomass allocation strategy of *P. centrasiaticum* in the study.

### 3.2. Measurements

The plants were harvested in mid-September 2010. We took out the plants and soil out of the pots carefully, and then washed the roots with tap water to remove the plants from the soil. After the plants were gently submerged in water we separated the roots of each species according to the aboveground part. Six pots from each treatment were selected for measurement of biomass traits. All individuals were numbered, and each individual was separated into leaves, stems, roots, and reproductive organs. Most individuals of *P. centrasiaticum* had not produced sufficient reproductive organs for analysis at that time, so we included any reproductive biomass in total biomass. The following traits were recorded for each individual plant: biomass of roots (BRO), biomass of stems (BS), biomass of leaves (BL), reproductive biomass (BRE), and total biomass (BT). We used those measurements to calculate the following:

Root:Shoot Ratio (RSR) =  $BRO / (BS+BL+BRE)$ ;

Relative biomass of stems (RS) =  $BS/BT$ ;

Relative biomass of leaves (RL) =  $BL/BT$ ;

Relative biomass of roots (RR) =  $BRO/BT$ .

### 3.3. Statistical analysis

All biomass traits data were log<sub>10</sub>-transformed. The data were then tested normality using the Kolmogorov-Smirnov test

(K-S test). All *P*-values of K-S test were larger than 0.05. Therefore the biomass traits data were lognormal. A two-way analysis of variance (ANOVA) was performed to test the effects of nitrogen and water on biomass allocation traits and to test for differences between the two species. Data were analyzed with SPSS statistical software (version 17.0; SPSS Inc., Chicago, IL, USA).

We tested for changes in allometric relationships between traits within each species via standardized major axis regressions and by fitting trait values to the following allometric equation:

$$\log Y = a \log X + \log b \quad \text{Eq. (1)}$$

Where *a* is the scaling exponent (slope) and *b* is the allometric coefficient of "scaling factor" (*Y* intercept). All variables (biomass traits) were log transformed. If *a* changed, the allometric relationship also changed, which indicated that at given *X* the value of *Y* will change (Warton *et al.* 2006). On log-log axes, standardized major axis regression (Esmaili *et al.* 2009) describes the best-fit scaling relationships between pairs of traits. Slopes on log-log axes, or 'scaling exponents', indicate the proportionality of pairwise trait relationships (Wright *et al.* 2004). Heterogeneity between SMA slopes is tested via a permutation (Warton *et al.* 2006) and the test for differences in SMA intercept via the SMA analogue of stand ANCOVA (Wright *et al.* 2002). Intercept homogeneity comparisons were performed only when slopes were homogeneous. The slopes and intercepts of every water and nitrogen treatment combination were calculated using the 'smart' package for R (R Development Core 2009).

## 4. RESULTS

### 4.1. Plasticity of biomass traits and allocation

The allocation of biomass among traits varied significantly between the two species and among treatments (Fig. 1). Nitrogen level significantly affected total biomass (BT) and relative biomass of leaves (RL) of *S. viridis*. Total biomass of *S. viridis* was 2.4 times higher in the nitrogen addition treatment than under ambient nitrogen conditions (Fig. 1) (*P* < 0.01). RL was 1.3 times higher in high

Table 1. Results of a two-way ANOVA testing the effects of nitrogen and water additions on biomass allocation between different plant traits. Total (total biomass per species), Root:Shoot Ratio (RSR), Relative biomass of stems (RS), Relative biomass of leaves (RL), Relative biomass of roots (RR).

Factor	df	Total	RSR	RR	RS	RL
<i>Setaria viridis</i>						
Nitrogen (N)	1	16.31***	1.18	1.91	0.58	4.88*
Water (W)	2	1.93	2.79	3.61	0.12	3.49
N × W	2	0.32	0.24	0.12	2.69	1.15
<i>Pennisetum centrasiatricum</i>						
Nitrogen (N)	1	0.375	1.264	1.857	0.016	3.17
Water (W)	2	8.89***	9.26***	8.85***	4.64**	8.39***
N × W	2	2.18	4.74*	4.00*	2.96	4.32*

F-values and their significance are presented. Dates were log transformed before analysis. The residual df is 56 for each parameter. Asterisks denote significance at  $P < 0.05$  (\*) and  $P < 0.001$  (\*\*\*)

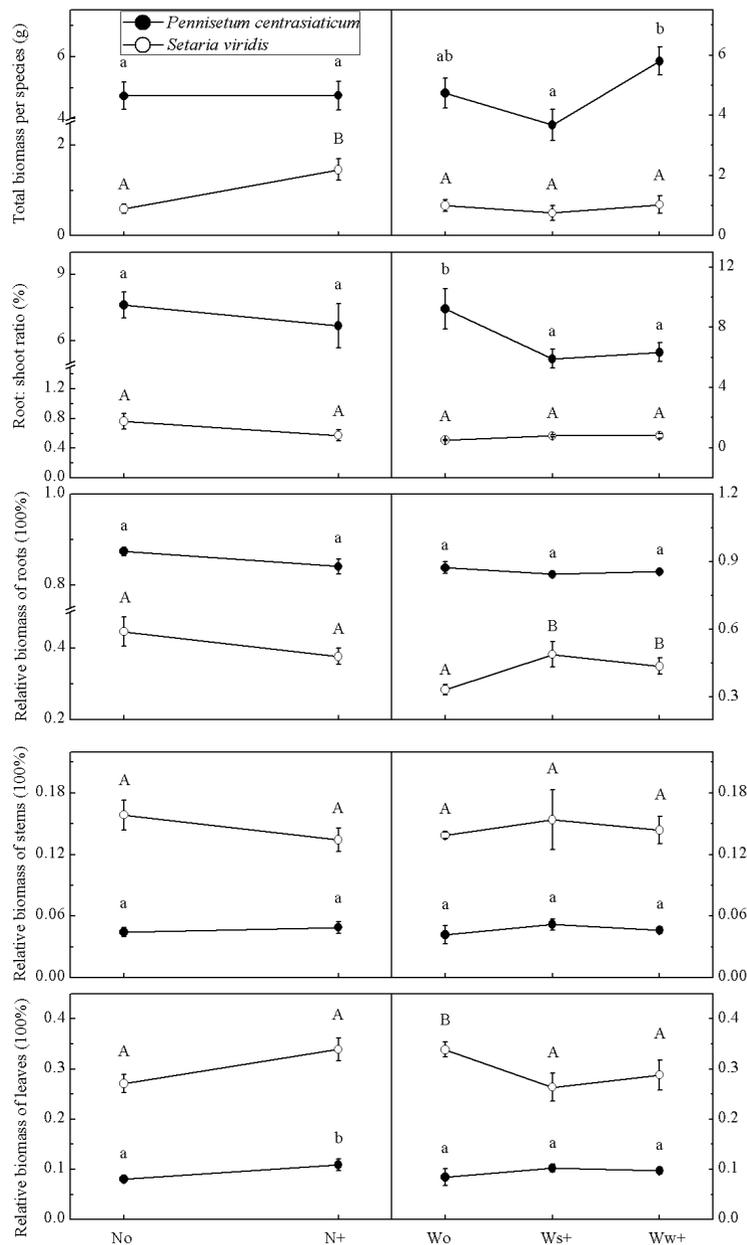


Fig. 1. Effect of nitrogen (N) and water (W) on: relative biomass of roots – RR, relative biomass of stems – RS, relative biomass of leaves – RL and root:shoot biomass ratio – RSR in *Setaria viridis* and *Pennisetum centrasiatricum*.  $N_o$  = nitrogen control;  $N_+$  = N addition;  $W_o$  = water control;  $W_{s+}$  = water summer addition;  $W_{w+}$  = water winter addition. Different letters indicate significant difference among treatments of same species ( $P < 0.05$ ). Data are the means  $\pm$  SE and are averaged across treatments.

nitrogen treatment ( $P < 0.05$ ). Root:shoot ratio (RSR) of *S. viridis* did not differ significantly between nitrogen levels, although leaf biomass increased with increasing nitrogen level. Water level and the interaction of nitrogen and water only affected the relative biomass of roots and relative biomass of leaves; RR increased and RL decreased (Table 1, 2, Fig. 1).

In contrast, nitrogen addition did not significantly alter biomass allocation in *P. centrasiaticum*. However, all of the measured trait values were significantly affected by water additions. The interaction of water level and nitrogen level influenced the RR, RL and RSR significantly. Water addition (both summer and winter) decreased the RSR. Snow added in winter increased the total biomass of *P. centrasiaticum*.

#### 4.2. Allometric relationships among biomass allocation traits

All relationships for pairwise comparisons of biomass allocations were significantly positive (Table 3, Fig. 2). For *S. viridis*, except the allometric relationships ( $a$ ) between stem

biomass and total biomass, nitrogen level altered all other pairwise allometric relationships significantly ( $P < 0.05$ ; Fig. 2); the  $a$  decreased as the nitrogen level increased.

Water did not alter the allometric relationship of biomass traits of *S. viridis*, but water supply (adding snow or water) decreased the intercept (allometric coefficient) of root biomass and total biomass and root biomass and shoot biomass, compared to low water treatment. For *P. centrasiaticum*, water and nitrogen level did not change any allometric relationship of bivariate biomass traits significantly, only alter the intercept of root biomass and total biomass; nitrogen supply increased the intercept of root biomass and total biomass but water supply decreased the intercept ( $P < 0.01$ ).

#### 5. DISCUSSION AND CONCLUSION

*S. viridis* and *P. centrasiaticum* exhibited different biomass allocation strategies in response to soil nitrogen and water. At ambient nitrogen levels, *S. viridis* tended to allocated proportionally more biomass to the roots and stems but less to leaves, compared to the nitro-

Table 2. Mean biomass traits for the two species in response to six treatments: two levels each of the factor nitrogen (N) and water (W). Total biomass (total biomass per species), Root:Shoot Ratio (RSR), Relative biomass of stems (RS), Relative biomass of leaves (RL), Relative biomass of roots (RR).

		Total number	Plot number	Total biomass	RSR	RR	RS	RL
<i>Setaria viridis</i>								
N <sub>0</sub>	W <sub>0</sub>	8	3	0.66±0.13	0.54±0.10	0.35±0.04	0.13±0.01	0.32±0.01
	W <sub>w+</sub>	4	3	1.35±0.22	0.47±0.08	0.32±0.03	0.14±0.01	0.36±0.02
	W <sub>s+</sub>	14	6	0.76±0.24	0.79±0.06	0.49±0.06	0.16±0.03	0.27±0.03
N <sub>+</sub>	W <sub>0</sub>	8	3	0.97±0.21	0.63±0.14	0.38±0.05	0.17±0.03	0.29±0.04
	W <sub>w+</sub>	7	3	0.40±0.13	1.26±0.20	0.55±0.04	0.12±0.01	0.23±0.03
	W <sub>s+</sub>	10	3	2.05±0.76	0.48±0.18	0.39±0.07	0.15±0.02	0.34±0.07
<i>Pennisetum centrasiaticum</i>								
N <sub>0</sub>	W <sub>0</sub>	36	6	4.46±0.41	8.26±1.08	0.88±0.01	0.04±0.01	0.08±0.01
	W <sub>w+</sub>	56	6	5.01±0.93	11.90±2.30	0.86±0.05	0.04±0.02	0.10±0.03
	W <sub>s+</sub>	30	6	3.21±0.34	7.02±1.08	0.86±0.02	0.05±0.01	0.09±0.01
N <sub>+</sub>	W <sub>0</sub>	31	6	4.15±0.99	4.78±0.21	0.83±0.01	0.05±0.01	0.12±0.01
	W <sub>w+</sub>	43	6	6.52±0.75	7.58±1.01	0.88±0.01	0.04±0.01	0.08±0.01
	W <sub>s+</sub>	67	6	5.07±0.42	5.09±0.23	0.84±0.01	0.05±0.02	0.12±0.01

gen addition treatment. In response to water content, only plasticity of the root:shoot ratio (RSR) was “true” (“true” if allometric relationships or intercept are affected by environmental conditions significantly). At low water contents, *S. viridis* allocated more biomass to roots than to shoots. Adjustment in root biomass allocation pattern of *S. viridis* in response to nutrient limitation was more dramatic than *P. centrasiatum*, and, coupled with rapid stem growth, enables *S. viridis* to colonize rapidly the degraded, nutrient poor sites.

In contrast, most of the plasticity in biomass allocation for *P. centrasiatum* is not “true”. Biomass allocation did not respond to variation in water level and nitrogen levels with the exception of root biomass. This indicates that *P. centrasiatum* may be more tolerant of variation in water and nitrogen. This flexibility may be the factor which enables the perennial grass to be dominant over *S. viridis* in variable habitat of arid grassland.

#### 5.1. Differential in allometric relationships between root and total biomass of the two species

The allometric relationships between root and total biomasses of *S. viridis* were significantly affected by nitrogen supply (Table 3, Fig. 2); this indicates that *S. viridis* exhibits “true” plasticity of root allocation. These results were similarly with a previous study (Hermans *et al.* 2006): a lack of nitrogen causes an accumulation of carbohydrate in the leaves and higher levels of carbon invested to the root, resulting in a shift of biomass allocation from leaves to roots (Linkohr *et al.* 2002). Therefore, at low nitrogen levels, the slope of the allometric relations between roots and total biomass will increase.

Water did not affect the overall allometric relationships between root and total biomass (slope remained the same; Fig. 3), but the intercept of root and total biomass did change with increasing water, which means at a given total biomass, the proportion of biomass invested into roots increases. Therefore, the relative biomass of root of *S. viridis* was “true” in response to water. At low water level, water uptake per unit root mass will be decreased, and nutrients uptake will also be

reduced; these would hamper the delivery of nutrients by mass flow in dry soil (Poorter and Nagel 2000).

For *P. centrasiatum*, nitrogen did not affect the RR values and allometric relationship of root and total biomass, which suggested that nitrogen has no plasticity on RR. *P. centrasiatum* is a kind of rhizome grass, spreading vegetatively with small but numerous ramet, and has highly developed rhizomes in the layer 0–20 cm of the soil (Guo and Li 2008). At high nitrogen levels, *P. centrasiatum* increases the numbers of ramet (data not shown) (Chen *et al.* 2002), but the relative biomass of the roots remains constant. Nevertheless, in tolerance range, allocation pattern on root will keep steadily regardless of soil nitrogen content. But water levels affect the intercept of root and total biomass (Table 3, Fig. 3), suggesting that at a given total biomass the proportion of biomass invested into root were changed, leading to “true” plasticity of RR to be in response to water. This is consistent with the study of Guo (Guo and Li 2008), but the results are contrary to the second hypothesis. According to APT, the allometric relationship between root and total biomass of *P. centrasiatum* should be invariant in the various environmental conditions.

#### 5.2. Differential in allometric relationships between root and shoot biomass of the two species

The root:shoot ratio (RSR) of *S. viridis* was affected by environmental conditions. *S. viridis* had higher RSR values in ambient nitrogen conditions compared to nitrogen addition treatment. This result is consistent with Huang’s study on *Agriophyllum squarrosum* (Linn) Moq., in which the RSR of *A. squarrosum* increased with soil nutrient increased (Huang *et al.* 2009b).

High RSR values under low soil nutrients has been interpreted as evidence of a plastic response by a plant in order to capture more of a limiting soil resource (Kobe *et al.* 2010). The allometric relationships of root and shoot of *S. viridis* were significantly influenced by nitrogen and water (Table 3). This indicates that *S. viridis* exhibits “true” plasticity in root:shoot ratios within this con-

Table 3. Allometric relationships between relative organs biomass for two species under study. A, root biomass (X) and shoot biomass (Y) for different treatment ; B, stem biomass (X) and total biomass (Y) for different treatment; C, leaf biomass (X) and total biomass (Y) for different treatment; D, root biomass (X) and total biomass (Y) for different treatment.

Group	Treatment	n	r <sup>2</sup>	Slope	Intercept	Common slope	P intercept	P shift
<i>Pennisetum centrasiatricum</i>								
A	N <sub>o</sub>	18	<b>0.98</b>	0.72	1.00	0.86	0.18	0.75
	N <sub>+</sub>	18	<b>0.99</b>	1.03	0.74			
B	N <sub>o</sub>	18	<b>0.50</b>	1.55	-2.17	1.20	0.65	0.84
	N <sub>+</sub>	18	<b>0.90</b>	1.02	-1.39			
C	N <sub>o</sub>	18	<b>0.73</b>	1.34	-1.59	1.20	0.074	0.58
	N <sub>+</sub>	18	<b>0.99</b>	1.04	-1.06			
D	N <sub>o</sub>	18	<b>0.95</b>	0.98	-0.03	0.98	-0.03	
	N <sub>+</sub>	18	<b>0.94</b>	0.98	-0.05			
	W <sub>o</sub>	12	<b>0.64</b>	1.43	0.74			
W <sub>s+</sub>	12	<b>0.70</b>	0.72	0.91				
W <sub>w+</sub>	12	<b>0.93</b>	0.82	0.91				
B	W <sub>o</sub>	12	<b>0.54</b>	0.81	-1.19	1.20	0.43	0.073
	W <sub>s+</sub>	12	<b>0.69</b>	1.53	-2.06			
	W <sub>w+</sub>	12	<b>0.94</b>	1.15	-1.59			
C	W <sub>o</sub>	12	<b>0.70</b>	0.80	-0.87	1.20	0.32	0.074
	W <sub>s+</sub>	12	<b>0.82</b>	1.29	-1.41			
	W <sub>w+</sub>	12	<b>0.95</b>	1.25	-1.41			
D	W <sub>o</sub>	12	<b>0.69</b>	1.0	-0.05	0.98	*	
	W <sub>s+</sub>	12	<b>0.76</b>	0.98	-0.04			
	W <sub>w+</sub>	12	<b>0.78</b>	0.96	-0.02			
<i>Setaria viridis</i>								
A	N <sub>o</sub>	12	<b>0.94</b>	0.76	-0.17	**		
	N <sub>+</sub>	9	<b>0.99</b>	1.21	-0.31			
B	N <sub>o</sub>	12	<b>0.91</b>	1.08	-0.84	1.1	0.16	0.26
	N <sub>+</sub>	9	<b>0.99</b>	1.11	-0.93			
C	N <sub>o</sub>	12	<b>0.92</b>	1.14	-0.60	*		
	N <sub>+</sub>	9	<b>0.99</b>	0.90	-0.45			
D	N <sub>o</sub>	12	<b>0.93</b>	0.87	-0.37	*		
	N <sub>+</sub>	9	<b>0.9</b>	1.15	-0.52			
	W <sub>o</sub>	6	<b>0.97</b>	1.1	-0.33			
A	W <sub>s+</sub>	6	<b>0.99</b>	0.90	-0.09			
	W <sub>w+</sub>	9	<b>0.99</b>	1.08	-0.16			
B	W <sub>o</sub>	6	<b>0.99</b>	1.03	-0.87	1.05	0.93	0.28
	W <sub>s+</sub>	6	<b>0.99</b>	1.13	-0.86			
	W <sub>w+</sub>	9	<b>0.99</b>	1.07	-0.86			
C	W <sub>o</sub>	6	<b>0.98</b>	1.04	-0.49	1.01	0.10	0.18
	W <sub>s+</sub>	6	<b>0.99</b>	1.1	-0.6			
	W <sub>w+</sub>	9	<b>0.99</b>	0.97	-0.55			
D	W <sub>o</sub>	6	<b>0.93</b>	1.09	-0.52	1.02	*	
	W <sub>s+</sub>	6	<b>0.92</b>	0.96	-0.33			
	W <sub>w+</sub>	9	<b>0.95</b>	1.09	-0.42			

Date were log transformed before analysis. Asterisks denote significance at  $P < 0.05$ (\*) and  $P < 0.01$ (\*\*).

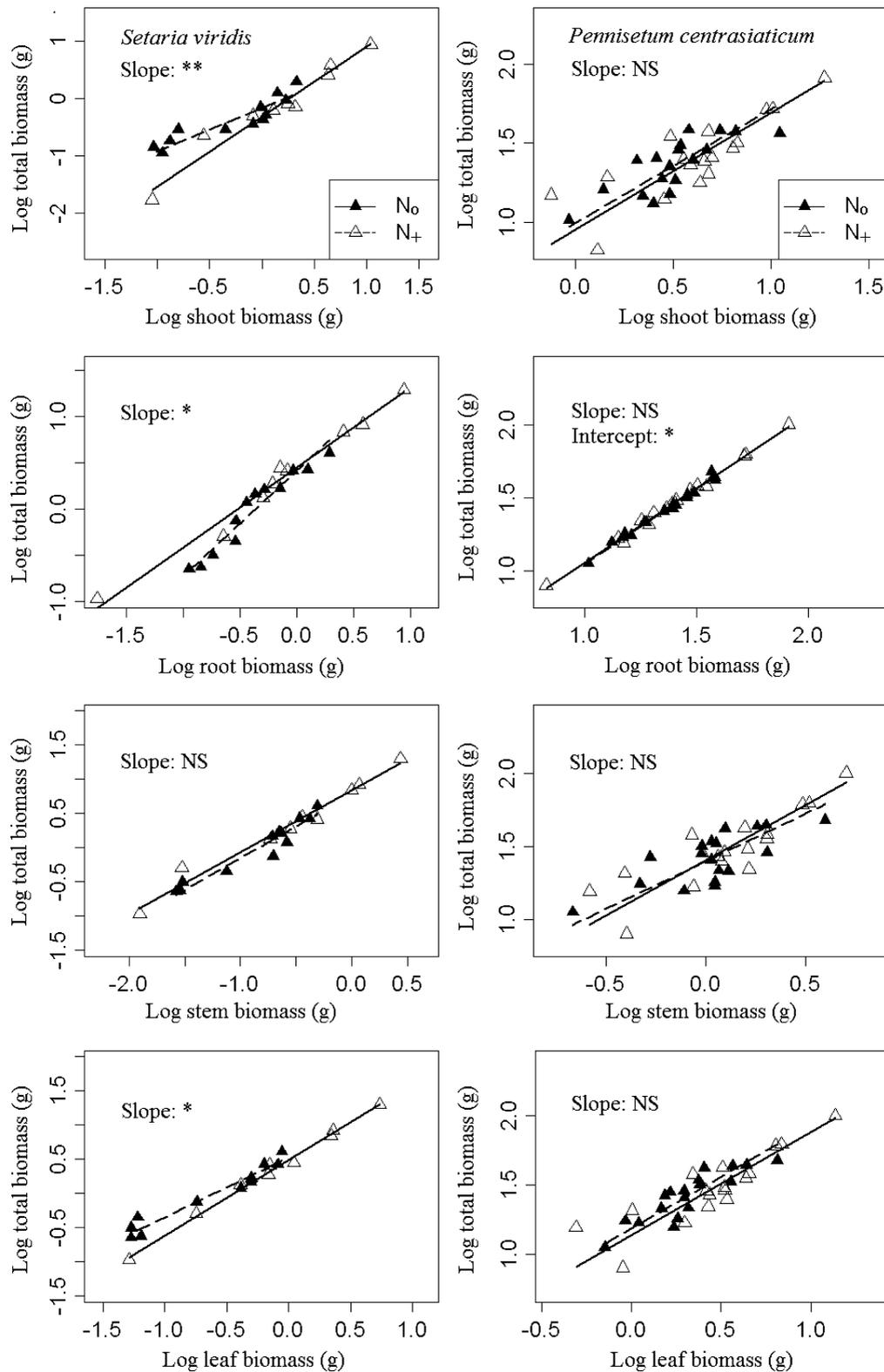


Fig. 2. Allometric relationships between biomass of leaf, stem and root and total biomass at two nitrogen supply:  $N_0$  = nitrogen control,  $N_+$  = nitrogen addition for *Setaria viridis* (left part) and *Pennisetum centrasiatricum* (right part). Asterisks denote significance at  $P < 0.05$  (\*) and  $P < 0.01$  (\*\*).

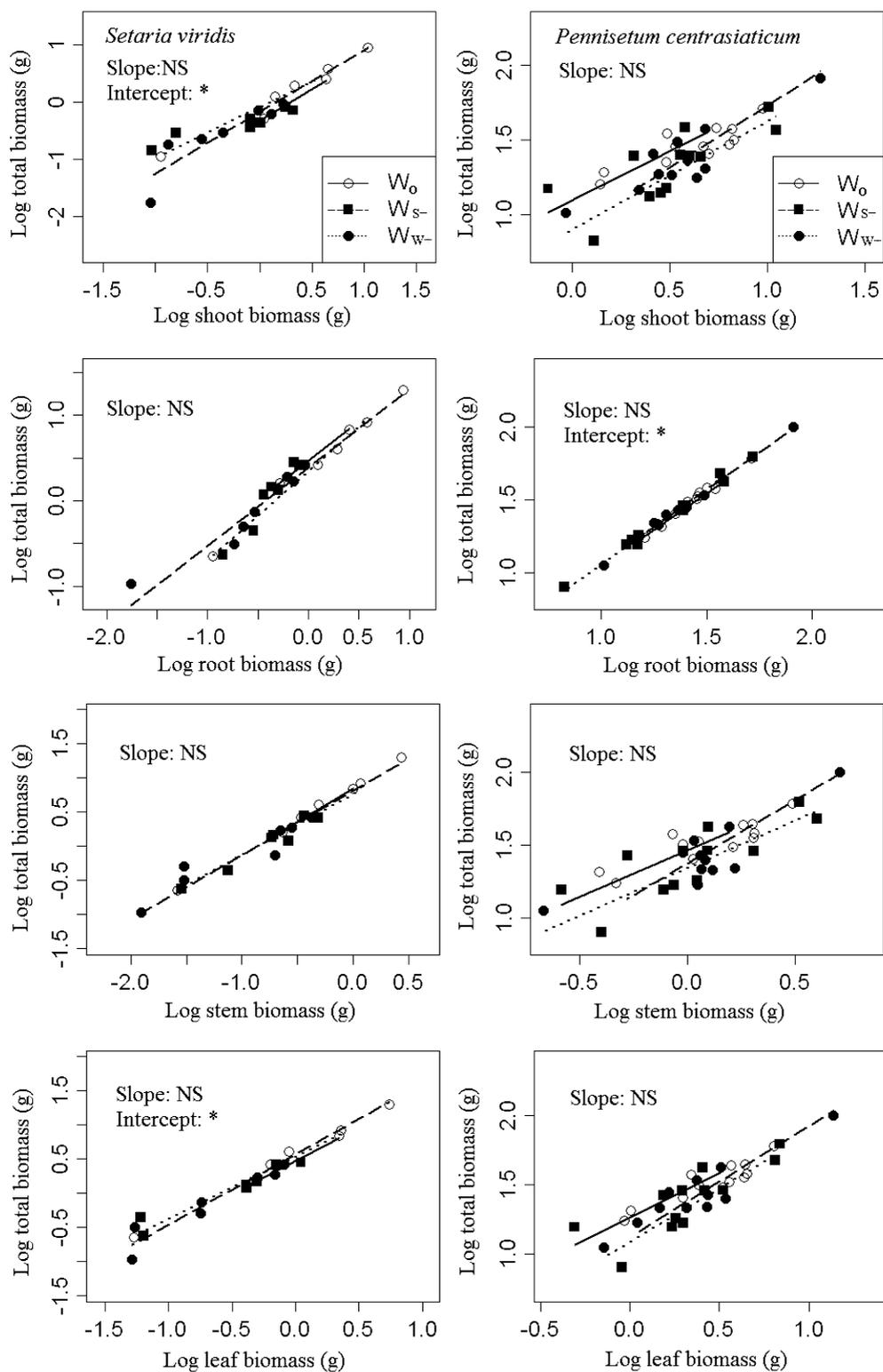


Fig. 3. Allometric relationships between biomass of leaf, stem, root and total biomass at each water supply level:  $W_0$  = water control;  $W_{s+}$  = water summer addition;  $W_{w+}$  = water winter addition for the two species: *Setaria viridis* (left part) and *Pennisetum centrasiaticum* (right part). Asterisks denote significance at  $P < 0.05$  (\*) and  $P < 0.01$  (\*\*).

text (Table 4). However, a different pattern was found in *P. centrasiatum*. Water did not alter the allometric relationships of root and shoot of *P. centrasiatum*, only affecting the RSR values of *P. centrasiatum* (Table 3), which indicates that the plasticity of RSR is “apparent” in response to water, and suggests that the variation in RSR were caused by plant size but not by water content. Nitrogen did not significantly affect either RSR values or the allometric relationships between roots and shoots biomass in *P. centrasiatum*, which suggests that no plasticity of RSR occurred in response to nitrogen. The allometric relationship of roots and shoots were not significantly affected by the combination of nitrogen and water. This contrasts with the conclusions put forward by Shipley and Meziane (2002) on 22 herbaceous species, in which nutrient supply affected the slope and the intercept of the root:shoot allometric relationships. Such a discrepancy may be due to the fact that the effect of plant size on allocation to roots and to shoots were consistent.

### 5.3. Differential in allometric relationships between stem and total biomass of the two species

The RS value, for *S. viridis*, was unaffected by nitrogen levels (Table 3). This result is inconsistent with some previous studies (Poorter and Nagel 2000), which suggests that plants allocate more biomass to stems when the soil nitrogen increases. Nitrogen levels alter the stem and total biomass allometric

relationships of *S. viridis* (Table 3, Fig. 2), leading to “true” plasticity of stem biomass allocation. This result is consistent with the conclusion reported by Müller *et al.* (2000) that the plants in low nutrient levels tended to allocate relatively more biomass to stems irrespective of plant size. Neither relative stem biomass value nor allometric relationship between stem and total biomass were altered by water, suggesting no plasticity of RS. However, the results of *P. centrasiatum* are totally different: the RS value is significantly affected by water content (Table 1), leading to an “apparent” plasticity. However, neither RS value nor allometric relationships between stem and total biomass were affected by nitrogen. This suggested that no plasticity occurred for stem biomass allocation with regard to nitrogen (Table 4). These results were inconsistent with previously stated findings (Müller *et al.* 2000). The reason is that although the availability of nitrogen was increased at high nitrogen level, *P. centrasiatum* increased the numbers of ramet to occupy resource (Chen *et al.* 2002) instead of shifting biomass allocation to stems.

### 5.4. Differential in allometric relationships between leaves and total biomass of the two species

RL (relative leaf biomass) of *S. viridis* varies according to environmental factors. Nitrogen significantly affects the RL and allometric relationship of leaf and total biomass (Table 1, 2), leading to “true” plasticity. This

Table 4. Plasticity of biomass allocations for different environmental factors\*. Root:Shoot Ratio (RSR), Relative biomass of stems (RS), Relative biomass of leaves (RL), and Relative biomass of roots (RR). \*Plasticity is “apparent” if relationships are not affected by environmental conditions significantly; “true” if allometric relationships (or intercept) are affected by environmental conditions significantly; and “nonexistent” if biomass traits and allometric relationships are both significantly unaffected by environmental conditions.

Parameter	Environment factor	Plasticity	
		<i>Pennisetum centrasiatum</i>	<i>Setaria viridis</i>
RSR	Nitrogen	Nonexistent	True
	Water	Apparent	True
RR	Nitrogen	Nonexistent	True
	Water	True	True
RL	Nitrogen	Nonexistent	True
	Water	Apparent	Nonexistent
RS	Nitrogen	Nonexistent	True
	Water	Apparent	Nonexistent

indicates that the various values of RL of *S. viridis* occurred in response to nitrogen. This is similar to Poorter's study (Poorter and Nagel 2000), which suggested that at low nutrient availability the decrease of nitrogen uptake per unit root mass will occur and usually it will reduce the transpiration per unit leaf dry mass (Hermans *et al.* 2006). Thus leaf plasticity will be altered under different nitrogen levels. By contrast, for *P. centrasiatum*, nitrogen had no effect on RL values or on allometric relationship between leaf and total biomass (Table 1, 2, Fig. 2). It means that no such plasticity occurred for leaf allocation with regard to nitrogen. RL was affected by water, leading to "apparent" plasticity of leaf biomass allocation. It indicated that water supply influenced plant size but not leaf allocation pattern.

In conclusion, our study shows that significant relationships were found among different biomass traits of the two species, and were affected by environmental conditions. But biomass allocation patterns of *S. viridis* and *P. centrasiatum* differed in response to water and nitrogen levels. The biomass allocation pattern of *S. viridis* changed in response to nutrient and water treatments, which indicates that *S. viridis* growth supports the optimal partitioning theory. Although the total biomass of root, stem and leaves of *P. centrasiatum* increased, the pattern of *P. centrasiatum* biomass allocation kept constant, suggesting that *P. centrasiatum* trade-off the biomass between roots, stems and leaves. This result indicate *P. centrasiatum* is consistent with the allometric biomass partitioning theory.

**ACKNOWLEDGMENTS:** We gratefully acknowledge the editors of the Polish Journal of Ecology for their hard work and two anonymous reviewers for their constructive comments on the manuscript. This research was funded by the National Basic Research Program of China (2009CB421102), the National Natural Science Foundation of China (41071185), the National Natural Science Foundation of China (30970471) and the Strategic priority research program (XDA05050406-4).

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Received after revision February 2012