

**BIOMASS ALLOCATION TO VEGETATIVE AND REPRODUCTIVE ORGANS
OF *CHENOPODIUM ACUMINATUM* WILLD. UNDER SOIL NUTRIENT
AND WATER STRESS**

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Abstract

Biomass allocation was size-dependent. Under soil nutrient, the plasticity of the leaf and reproductive allocation was “true” plasticity, the plasticity of stem allocation was “apparent” plasticity, which is dependent on plant size, but there was no plasticity in root allocation. Under soil water stress, the plasticity of root, leaf and reproductive allocation was “true”. In response to population density, the plasticity of stem allocation is “true” plasticity, while the value of the stem allocation is consistent because of the trade off between the effects of plant size and population density. The biomass allocation strategy increases reproductive allocation but decrease leaf allocation with the decrease of soil nutrient, when compared at the same plant size. At lower soil water, the plant allocated more biomass to the root and leaf rather than to reproductive organ.

Introduction

In plants, allocation of the biomass to different organs depends on biotic or abiotic environmental variables, such as soil nutrient, water and population density. According to the optimal allocation theory (Bloom *et al.* 1985), plant should allocate resources to the organ that acquires the most resource, and often limits the growth. Optimal allocation theory has been applied in many studies (McConnaughay and Coleman 1999). For example, plant allocated more biomass to leaf under low light intensity (Shiple and Meziane 2002), and more biomass to root under low soil nutrient or water (González *et al.* 2008, Mony *et al.* 2007). However, the optimal allocation theory has also been questioned (Coleman *et al.* 1994, Huang *et al.* 2009b, Weiner 2004). The optimal allocation theory suggested that plant allocation is size-independent (Bloom *et al.* 1985). But Pino *et al.* (2002) and Ogawa (2003) found that almost all plant allocation patterns are size-dependent. This indicated that the biomass allocation to different organs varied not only with the environments, but also with plant size.

Plants can modify the growth and development in response to changes in environmental conditions (Strand and Weisner 2004). This ability is called plasticity. Many researchers showed that allometric relationships are affected by environment (Allen *et al.* 2008, Bernacchi *et al.* 2007, Shiple and Meziane 2002, Wang *et al.* 2006). The environment may only affect the plant size, but does not change the allometric relationships between different biomass. Thus the difference of plasticity between different environmental factors would disappear when compared at the same plant size. This phenomenon is called “apparent” plasticity. However, the growth ratio of plant may vary with the plant size and plant may change the pattern of biomass allocation themselves in

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response to variable environments (Geng *et al.* 2007, McConnaughay and Coleman 1999, Weiner 2004) which is so-called “true” plasticity. The “apparent” plasticity exists in many plants (Geng *et al.* 2007, Wang *et al.* 2006). It is difficult to distinguish between “apparent” and “true” plasticity without a careful study of allometry (McConnaughay and Coleman 1999, Wang *et al.* 2006). There are allometric relationships among biomass of different organs in many plants (Bernacchi *et al.* 2007, Huang *et al.* 2009a, Komiyama *et al.* 2007, Naumburg *et al.* 2001). For instance, Peichl and Arain (2007) found allometric relationships between above- and below-ground biomass in 4 age-sequences of white pine (*Pinus strobus* L.).

Chenopodium acuminatum (Chenopodiaceae) is a weed species in cropland, which is commonly found in the abandoned habitats (Zhao *et al.* 2005), often in inter-dune lowland and cropland (Peng *et al.* 2005), which plays an important role in the restoration succession in the degraded sandy land in Horqin Sandland of China. This species shows high phenotypic plasticity and occupies a range of habitats differing degree of degraded sandy land and differing land uses (sandy dune, grassland and cropland). Therefore, this species is expected to reveal the strategy of plant in response to variable environments.

The objectives of this study are to answer the following three questions, whether (1) the biomass allocation of *C. acuminatum* is size-dependent, (2) the plasticity of biomass allocation is “apparent” or “true”, and (3) what is the biomass allocation strategy under different environment stress?

Materials and Methods

Chenopodium acuminatum seeds were collected from a severely degraded sandy site at Naiman County (42°55' N, 120°42' E, 345 m MSL) in the centre of Horqin Sandland in the eastern part of Inner Mongolia.

On 9 May 2007, seeds were sown in plastic plates with the sandy soil obtained from the same location where seeds were collected. The soil contained 49 to 53 mg/kg total nitrogen. At the two-leaf stage (about 2 weeks), the seedlings were transplanted to plastic pots (13.8 cm diameter × 26.5 cm deep) containing the same soil. Treatments were applied 2 weeks after transplanting.

There were three treatment factors (soil nutrient, soil moisture and plant density) with a 2 × 2 × 2 factorial design with 17 or 34 replicates, respectively for high and low plant density (816 total plants, 102 plants per treatment). There were two soil nutrient levels. Each pot was applied 0 (N-) or 20 g (N+) (equivalent to 500 kg nitrogen per ha) of slow-release fertilizer (Osmocote, containing N 14%, P 14% and K 14% and microelements) at the beginning of experiment. For the soil moisture, each pot was watered every 3 days with total amount of 265 (W-) or 530 ml of water (W+) during experimental period, which was equivalent to 200 or 400 mm of rainfall during the growing season. There were two plant densities. At high density level, 6 plants in each pot arranged in an equilateral hexagonal fashion pattern (equivalent to 100 plants/m²) and at low density level, 3 plants in each pot arranged in an equilateral triangular pattern (which was equal to 50 plants/m²).

All pots were placed in a greenhouse, which had been ventilated to reduce differences between inside and outside of the greenhouse. In order to avoid edge effect, the pots of each treatment were placed together. The position of pots of each treatment was changed every two weeks.

The plants were harvested on 13 September. A total of 12 - 20 intact plants from each treatment were selected at random for measurement. Each plant was separated into the root, stem, leaf, and reproductive organs (including the rachis, utricles, seeds, perianth segments and bracts). The roots were washed free of soil. Dry weight was determined after oven-drying to a constant

mass at 80°C. The following biomass traits were recorded for each individual plant: total biomass, root biomass, stem biomass, leaf biomass, reproductive biomass, shoot biomass (total biomass - root biomass), non-stem biomass (total biomass - stem biomass), non-leaf biomass (total biomass - leaf biomass), and vegetative biomass (total biomass - reproductive biomass). Biomass allocation traits were calculated as follows: root : shoot ratio (root biomass/shoot biomass), stem : non-stem ratio (stem biomass/non-stem biomass); leaf : non-leaf ratio (leaf biomass/non-leaf biomass) and reproductive effort (reproductive biomass/vegetative biomass).

Data were analyzed with SPSS statistical software (version 11.5) (SPSS Inc., Chicago, Illinois). A three-way analysis of variance was performed to test the main effects of nutrient (N), water (W) and density (D) on biomass allocation and architectural and their interactions.

Regression analysis was conducted to characterize the allometric relationships between root biomass (y) on shoot biomass (x); stem biomass (y) on non-stem biomass (x); leaf biomass (y) on non-leaf biomass (x); and reproductive biomass (y) on vegetative biomass (x). The allometric relationship can be described by $y = bx^a$, where a is the scaling exponent (slope) and b is the allometric coefficient or “scaling factor” (y intercept). Differences in shifting along the slope and in elevation of regression slopes (y intercept) were assessed using standardized major axis regression (SMA, also known as reduced major axis, RMA) using the R software package (SMATR; Falster *et al.* 2006, Warton *et al.* 2006).

Results and Discussion

The biomass allocation traits were significantly affected by soil nutrient content and water content, while population density had no effect on any traits (Table 1). Root : shoot ratio ranged from 0.036 to 0.224, stem : non-stem ratio from 0.222 to 0.960, leaf : non-leaf ratio from 0.002 - 0.457, and reproductive effort from 0.264 to 2.224. Root : shoot ratio was high at low soil water, and stem : non-stem ratio was significantly higher at high soil nutrient. Leaf : non-leaf ratio was significantly high at high soil nutrient or low soil water and reproductive effort was significant high at low soil nutrient or high soil water (Table 1, Fig. 1). There was significant interactions between soil nutrient and soil water for leaf:non-leaf ratio ($p < 0.001$) and reproductive effort

Table 1. Analysis of variance for the main effects of nutrient, water and plant density, and their interactions on the biomass allocation traits and morphological traits.

Source	df	Root : shoot ratio	Stem : non-stem ratio	Leaf : non-leaf ratio	Reproductive effort
Nutrient	1	3.49 ^{ns}	9.52**	119.27***	50.95***
Water	1	7.09**	1.06 ^{ns}	55.57***	8.41**
Density	1	3.10 ^{ns}	2.05 ^{ns}	0.07 ^{ns}	3.36 ^{ns}
Nutrient × water	1	3.65 ^{ns}	2.33 ^{ns}	7.95**	4.52*
Nutrient × density	1	0.02 ^{ns}	3.06 ^{ns}	0.12 ^{ns}	1.71 ^{ns}
Water × density	1	3.12 ^{ns}	0.00 ^{ns}	0.00 ^{ns}	0.32 ^{ns}
Nutrient × water × density	1	1.92 ^{ns}	4.78*	2.67 ^{ns}	1.35 ^{ns}

^{ns}not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. The residual df = 139.

($p < 0.05$). There was significant 3-way interactions between soil nutrient, soil water and population density for stem : non-stem ratio ($p < 0.05$). With the exception of root : shoot ratio, the effect of soil nutrient was the largest source of variation in all three biomass allocation traits (Table 1).

There were significant allometric relationships between root biomass and shoot biomass. The regression slope shifted along common slope and shifted in elevation between soil water treatments (Fig. 2), whereas the regression slope shifted along common slope between soil nutrient treatments or population density treatments (Fig. 2).

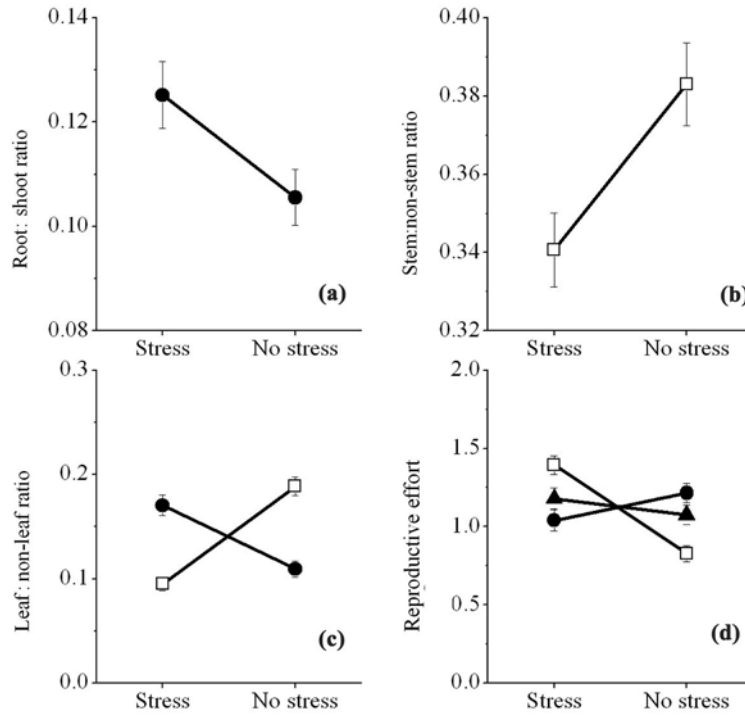


Fig. 1. Biomass allocation traits in response to different stress (mean \pm SE). (a) Root : shoot ratio; (b) relative stem biomass, (c) relative leaf biomass and (d) reproductive effort. \square nutrient, \bullet water, \blacktriangle density.

There were significant allometric relationships between stem biomass and non-stem biomass. The regression slope significantly shifted along common slope for soil nutrient or water treatments. However, the regression slope was different between population density treatments (Table 2, Fig. 2).

In all shift along common slope and shift in elevation, the line of increased water was above in root biomass vs. shoot biomass, the line of increasing soil nutrient, and decreasing soil water was above in leaf biomass vs. non-leaf biomass, and the line of increasing soil nutrient, and decreasing soil water was under in reproductive vs. vegetative biomass (Fig. 2).

When the relationships between different organs do not shift or only shift along the common slope, the plasticity is “apparent”, which means that the biomass allocation holds the consistent patterns in different environments (Wang *et al.* 2006, Weiner 2004). These results indicated that root : shoot ratio did not have plasticity in response to soil nutrient. The plants hold the consistent patterns of root allocation in different soil nutrient (Casper *et al.* 1998).

Table 2. Scaling exponents (slope) in allometric regression models ($y = bx^a$) between different organs for different treatments.

Treatment	Shoot biomass (x) and root biomass (y)			Non-stem biomass (x) and stem biomass (y)			Non-leaf biomass (x) and leaf biomass (y)			Vegetative biomass (x) and reproductive biomass (y)		
	Slope	95% CI	R ²	Slope	95% CI	R ²	Slope	95% CI	R ²	Slope	95% CI	R ²
N- D+	1.285	1.027-1.608	0.804***	1.208	0.991-1.472	0.848***	1.167	0.881-1.546	0.690***	0.828	0.672-1.021	0.830***
D-	1.09	0.897-1.325	0.853***	0.976	0.865-1.103	0.943***	1.375	1.151-1.642	0.878***	0.899	0.748-1.081	0.870***
W+ D+	1.018	0.847-1.223	0.870***	1.128	0.987-1.288	0.932***	1.759	1.277-2.424	0.594***	0.865	0.743-1.007	0.911***
D-	1.131	0.894-1.432	0.799***	1.2	0.894-1.610	0.683***	2.307	1.468-3.627	0.221**	0.871	0.596-1.272	0.464***
N+ D+	1.153	0.949-1.400	0.874***	1.44	1.255-1.653	0.937***	0.923	0.688-1.239	0.705***	0.805	0.569-1.137	0.590***
D-	1.259	1.074-1.476	0.949***	1.274	1.093-1.484	0.953***	1.18	0.939-1.483	0.893***	0.632	0.462-0.865	0.796***
W+ D+	1.471	1.156-1.872	0.759***	1.238	0.910-1.685	0.601***	1.865	1.469-2.369	0.763***	0.647	0.452-0.927	0.451***
D-	0.973	0.739-1.281	0.763***	1.049	0.833-1.321	0.835***	1.273	1.005-1.612	0.827***	0.971	0.763-1.235	0.820***
Overall	1.095	1.035-1.157	0.891***	1.142	1.091-1.195	0.927***	1.336	1.210-1.475	0.651***	0.859	0.799-0.923	0.818***
Nutrient	Shift along common slope			Shift along common slope			Shift along common slope and shift in elevation			Shift along common slope and shift in elevation		
Water	Shift along common slope and shift in elevation			Shift along common slope			Shift along common slope and shift in elevation			Shift along common slope and shift in elevation		
Density	Shift along common slope			Difference in slope			Shift along common slope			Shift along common slope		

** p < 0.01, *** p < 0.001.

Root biomass increased with increases in soil water. Deficiencies of soil water resulted in high root : shoot ratio. Relatively, more biomass was allocated to the root than to the shoot, and plant allocated more resource to the belowground growth. The allocation also had been observed in other plants (González *et al.* 2008, Mony *et al.* 2007).

These results indicated that the plasticity of root : shoot ratio in population density treatments was the “apparent” plasticity. So the population density had no effect on the strategy of aboveground and belowground allocation. The population density only affected the plant size. The root : shoot ratio varied with plant size.

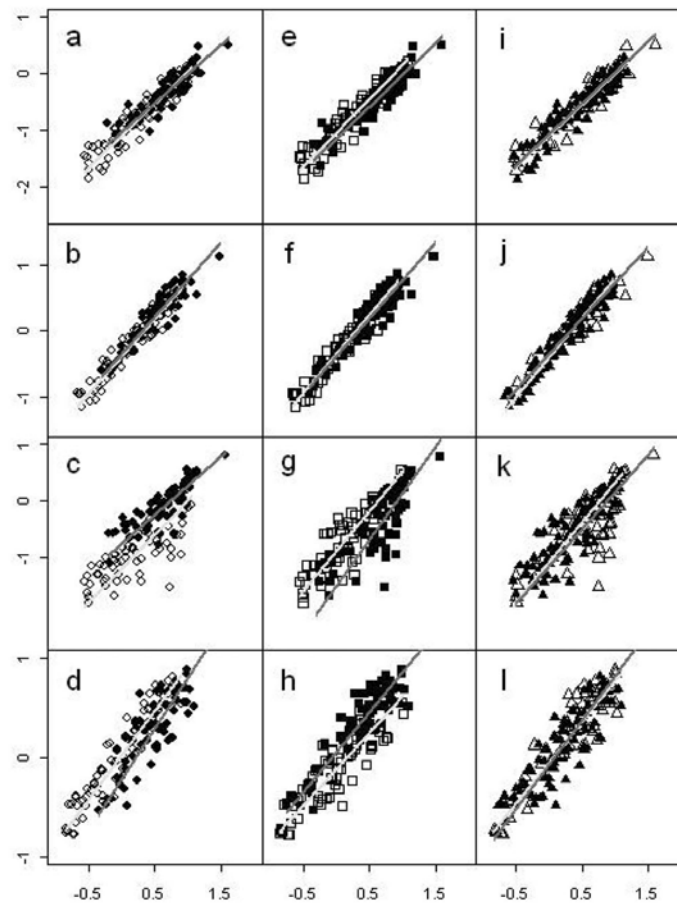


Fig. 2. Log-log plots between organs in response to variation in environment. (a, e, i), Between root (Y) and shoot (X). (b, f, j), Between stem (Y) and non-stem (X). (c, g, k), Between leaf (Y) and non-leaf (X). (d, h, l), Between reproductive (Y) and vegetative biomass (X). Eight treatments include low nutrient level (\circ), high nutrient level (\bullet), low water level (\square), high water level (\blacksquare), low density level (\triangle), high density level (\blacktriangle). The grey and white lines are the reduced major axis regression (RMA) curves for the low level and high level environment, respectively.

The plasticity of stem : non-stem ratio in soil nutrient treatments was the “apparent” plasticity, and stem : non-stem ratio did not have plasticity in response to soil water. The allometric exponent varied with population density, the plasticity of stem : non-stem ratio in population density

treatments was the “true” plasticity. However, because of the tradeoff between the effects of plant size and soil water content, the stem : non-stem ratio was not varied with soil water.

Present result clearly demonstrated that the leaf allocation was significantly affected by soil nutrient. At fertile soil or deficiencies of soil water, plant allocated more biomass to the leaf (Gindaba *et al.* 2005, Wang *et al.* 2008). The allometric relationship between biomass of the leaf and total biomass was affected by soil nutrient and water. The plasticity of leaf : non-leaf ratio to soil nutrient was the “true” plasticity. Both the leaf allocation and the allometric relationship between leaf biomass and non-leaf biomass were not affected by population density. The plant did not have plasticity in response to population density.

Reproductive effort varied with different environmental factors (van Kleunen *et al.* 2001). For instance, it can either increase (Hickman 1977) or decrease (Snell and Burch 1975) in response to increase in population density. In the present study, density did not have a significant effect on reproductive effort and the allometric relationship between vegetative biomass and reproductive biomass. The plant produced similar reproductive biomass allocation ratios at all densities, which suggested that reproductive effort did not have plasticity in response to population density.

Similar results had been found in such as *Atriplex sagittata* (Mandak and Pysek 1999), *Rumex obtusifolius* (Pino *et al.* 2002) and *Plantago major* (Reekie 1998). The result supports that subtraction of nutrient can increase reproductive effort, addition of water can increase reproductive effort, and altered density may impose no effect on reproductive effort or the allometry of reproductive biomass.

In conclusion, at lower soil water, the strategy of plant is to allocate more biomass to the root and leaf rather than to reproductive organ. Root, leaf and reproductive allocation did not have plasticity in response to population density. The plasticity of stem allocation is the “true” plasticity, while the value of the stem allocation is consistent because of the tradeoff between the effects of plant size and population density.

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