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ORIGINAL RESEARCH

Allometric Effects of *Agriophyllum squarrosum* in Response to Soil Nutrients, Water, and Population Density in the Horqin Sandy Land of China

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Abstract We monitored the allometric effects for greenhouse-grown *Agriophyllum squarrosum* plants in response to variations in population density and the availability of soil nutrients and water. Biomass allocations were size-dependent. The plasticity of roots, stems, leaves, and reproductive effort was "true" in response to changes in nutrient content. At a low level of soil minerals, plants allocated more resources to the development of roots and reproductive organs than to leaves, but data for stem allocations were consistent for tradeoffs between the effects of nutrients and plant size. The plasticities of leaf allocation and reproductive effort were "true" whereas those of root and stem allocations were "apparent" in response to fluctuations in soil water, being a function of plant size. Decreasing soil water content was associated with higher leaf allocation and lower reproductive effort. Except for this "apparent" plasticity of leaf allocation, none was detected with population density on biomass allocation. Architectural traits were determinants of the latter. For roots, the determining trait was the ratio of plant height to total biomass; for stems and reproduction, plant height; and for leaves, the ratio of branch numbers to plant height.

Keywords *Agriophyllum squarrosum* · Allometry · "Apparent" plasticity · Architectural traits · Biomass allocation · "True" plasticity

The capacity for a plant to capture resources and allocate biomass to different organs depends on biotic or abiotic variables, such as soil nutrients, water content, and population density. The plant response to environmental fluctuations is an important ecological question. The optimal allocation theory of Bloom et al. (1985) states that plants should allocate resources to the organ that acquires the most limiting resource. This theory has been applied in many studies (Thomas 1996; McConnaughay and Coleman 1999). For example, plants distribute more biomass to leaves under low light (Shipley and Meziane 2002) or to root systems when levels of soil nutrients or water are reduced (Mony et al. 2007; Gonzáles et al. 2008). However, the theory itself has been questioned (Coleman et al. 1994; McCarthy and Enquist 2007) because, although it regards plant allocation as being size-independent, almost all such patterns are in fact size-dependent (Pino et al. 2002; Ogawa 2003). Moreover, the ratio of biomass allocation changes not only with environmental conditions but also with plant size. Therefore, if the optimal allocation theory is applied, it is unclear whether variations in that ratio are driven by environmental conditions or by the allocation pattern in different-sized plants.

In contrast, the allometric theory is useful for resolving increasingly contentious debates concerning biomass allocation (Solow 2005; Niklas 2006). Allometric analysis can

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incorporate plant size into computations of plant biomass to help minimize bias when comparing allocation patterns (Wang et al. 2006; Allen et al. 2008). Many species show allometric relationships among the biomasses of different organs (Naumburg et al. 2001; Bernacchi et al. 2007). Examples include the above- and belowground biomasses in four white pine species (Peichl and Arain 2007) and in *Larrea tridentata* (Allen et al. 2008). These relationships are affected by environmental conditions (Shipley and Meziane 2002; Allen et al. 2008), and plasticity is a response mechanism for modifying growth and development (Bradshaw 1965; Bazzaz et al. 1987; Strand and Weisner 2004). This plasticity of biomass allocation may be either related to growth rates ("apparent" plasticity) or a result of varying environmental conditions ("true" plasticity) (McConnaughay and Coleman 1999; Weiner 2004; Geng et al. 2007). Growth rates fluctuate with plant size, but differences in plasticity due to environmental factors disappear when plants of equivalent size are compared. The phenomenon of "apparent" plasticity indicates no difference in allocation patterns (i.e., allometric relationships between different biomasses). According to allometric analysis, "apparent" plasticity exists in many plants (Wang et al. 2006; Geng et al. 2007). Nevertheless, it is difficult to distinguish between "apparent" and "true" plasticity without applying careful allometric study (McConnaughay and Coleman 1999; Wang et al. 2006).

Architectural traits are important for regulating biomass allocations in response to environmental conditions (Duffy et al. 1999; Suzuki and Ohnishi 2006; Wang et al. 2006; Yoon et al. 2007). For instance, reproductive effort is affected by branch length (Wang et al. 2006), and branched plants produce significantly more seeds than do unbranched plants (Lortie and Aarssen 2000).

Agriophyllum squarrosum (Chenopodiaceae) is a pioneer annual found on sand dunes in the arid regions of Central Asia (Li et al. 2005; Liu et al. 2006). Its habitat is extremely unstable because the surface substrate frequently shifts, the availability of soil nutrients and water fluctuates widely, and site conditions do not permit the growth of any other plant species (Memoto and Lu 1992; Zhang et al. 2005). Populations vary from individuals only to many plants crowded within a small space. Therefore, this species should reveal patterns that vary in response to environmental conditions.

We conducted greenhouse experiments with *A. squarrosum* under controlled parameters for nutrients, water, and plant density. Four questions were addressed: (1) do allometric relationships exist among the biomasses of different organs; (2) if so, do these relationships vary according to environment; (3) is the plasticity of biomass allocation "apparent" or "true"; and (4) do architectural traits significantly affect these allocations?

Materials and Methods

Study Area

The study area was located in Naiman County (lat 42°55′ N, long 120°42′ E, 345 m a.s.l.) in the central region of the Horqin Sandy Land in the eastern part of Inner Mongolia. The climate is temperate continental semiarid monsoon. Annual mean precipitation is 366 mm, and the mean annual potential evaporation is 1,935 mm. The annual frost-free period is approximately 130 to 150 days. Average annual wind speed is 3.4 m s^{-1}, but 4.3 m s^{-1} in the springtime. Dunes alternate with gently undulating lowland (Li et al. 2004; Zhao et al. 2007).

Experimental Design

On 9 May 2007, seeds were sown in plastic plates containing sandy soil collected from 17 plants within that severely degraded site. The sandy soil was taken from 1-m-deep underground severely degraded sandy land. At the two-leaf stage (i.e., 2 weeks after emergence), the seedlings were transplanted into 27.6 cm×26.5 cm plastic pots containing the same soil type. Three treatments (soil nutrients, soil water, and population density) were chosen to reflect both stressed and unstressed habitats. Soil-nutrient and population-density treatments were applied after the seedlings had been transferred to pots whereas the soil-water treatment was applied at 4 weeks after emergence. Each factor had two levels: *N*+ (high nutrients), in which 20 g of slow-release fertilizer Osmocote NPK (14:14:14) was added per pot; *N*− (low nutrients), with no additional supplements (total N content of the original sandy soil was 49 to 53 mg kg^{-1}); *W*+ (high water), where the equivalent of 400 mm of rainfall during the growing season was applied as 530 ml of water every 3 days; *W*− (low water), with 265 ml of water applied every 3 days (approximately equal to 200 mm of rainfall during the growing season); *D*+ (high population density), in which six plants per pot were arranged in an equilateral hexagonal pattern (=100 plants m^{-2}); and *D*− (low density), with three plants per pot in an equilateral triangle (=50 m^{-2}). We constructed a full-factorial design (816 total plants, 102 per treatment) for these eight possible combinations of high/low nutrients, water, and density. All pots were placed in an unheated greenhouse with natural sunlight plus ventilation to ensure that the difference in temperature was no more than 5°C between inside and outside. To avoid edge effects, the pots for each treatment were placed together, and their positions were altered every 2 weeks.

Measurements

On 15 September 2007, 15 to 20 intact plants were randomly harvested from each treatment. They were separated into roots, stems, leaves, and reproductive organs (i.e., rachis, utricles, seeds, perianth segments, and bracts). Roots were washed of soil, and the dry masses for all components were determined after oven-drying them to a constant weight at 80°C. The following traits were recorded for each individual: absolute height (H); numbers of primary branches (NP), secondary branches (NS), and tertiary branches (NT); biomasses of roots (BRO), stems (BS), leaves (BL), reproductive organs (BRE), and shoots (BSH); vegetative biomass (BV=BRO+BS+BL); total biomass (BT); root:shoot ratio [RSR=BRO/(BS+BL+BRE)]; relative biomasses of stems (RS=BS/BT) and leaves (RL=BL/BT); reproductive effort (RE=BRE/BV); NP, NS, and NT per gram of stem biomass (NP/BS, NS/BS, and NT/BS); the ratio of plant height to total biomass (H/BT); and the ratio of primary-branch count to plant height (NP/H).

Statistical Analysis

Data were analyzed with SPSS statistical software (version 11.5; SPSS Inc., Chicago, IL, USA). A three-way analysis of variance (ANOVA) was performed to test the effects of nutrients, water, and density on biomass allocations and architectural traits.

To identify the primary determinants of allocation among traits, multiple stepwise regressions were calculated. The $\log_{10}(x+1)$-transformed regression independent variables—H, NP, NS, NT, NP/BS, NS/BS, NT/BS, H/BT, and NP/H—were entered into the completed model while the dependent RSR, RS, RL, and RE variables were entered separately.

Regressions of BRO (*Y*) on BSH (*X*), BS (*Y*) on BT (*X*), BL (*Y*) on BT (*X*), and BRE (*Y*) on BV (*X*) were conducted to characterize the allometric effect of biomass allocations to different environmental conditions. The allometric relationship between *X* and *Y* was $Y=bX^a$, where *a* was the scaling exponent (slope) and *b* was the allometric coefficient or "scaling factor" (*Y* intercept). Model Type II (reduced major axis, RMA) regression analysis was used to determine the scaling exponents: $a_{\mathrm{RMA}}=a_{\mathrm{OLS}}/r$, where a_{OLS} was the ordinary least squares scaling exponent and *r* was the ordinary least squares correlation coefficient. This regression procedure is recommended when the variables of interest are biologically interdependent and subject to unknown measurement errors (Niklas 1994). The variation in allometric exponent (*a*) in response to environmental treatment was evaluated using ANCOVA to test for interactions between the covariate (*X*) and environmental factors (Müller et al. 2000; Brown and Eckert 2005; Wang et al. 2006).

Results

Relationships between Biomass Allocation Traits and Environmental Factors

Except for RS (relative stem biomass) with soil nutrient content, the traits of biomass allocation were significantly affected by nutrient and water contents while only RL (relative leaf biomass) was significantly influenced by population density (Table 1). Root:shoot ratios (RSRs) ranged from 0.036 to 0.354, RS from 0.240 to 0.557, RL from 0.193 to 0.600, and reproductive effort (RE) from 0.007 to 0.721. RSR significantly increased with a decrease in nutrient and water contents, and RS significantly increased with greater water availability. RL significantly rose with nutrient content and with declines in both water content and population density. Similarly, RE was signifi-

Table 1 Results from three-way ANOVA testing of the effects of environmental conditions on biomass allocations and architectural traits

Trait	Nutrients (*N*)	Water (*W*)	Density (*D*)	*N*×*W*	*N*×*D*	*W*×*D*	*N*×*W*×*D*
RSR	86.88***	7.34**	0.12	4.83*	0.99	1.42	1.43
RS	2.71	6.26*	2.99	47.1***	2.38	0.07	0.26
RL	504.35***	55.49***	8.19**	3.19	0.56	0.98	0.69
RE	103.98***	14.59***	0.05	10.24**	0.01	0.01	0.09
H	104.32***	144.77***	14.25***	73.15***	5.00*	0.02	3.41
NP	203.29***	24.46***	6.01*	19.28***	0.00	0.48	0.70
NS	101.03***	29.44***	25.54***	29.44***	25.54***	7.62**	7.62**
NT	1.23	1.23	1.23	1.23	1.23	1.23	1.23
NP/BS	33.98***	19.54***	8.24**	17.87***	6.59*	0.00	4.15*
NS/BS	110.73***	1.87	11.46***	1.87	11.46***	0.05	0.05
NT/BS	1.23	1.23	1.23	1.23	1.23	1.23	1.23
H/BT	231.09***	6.10*	9.35**	0.56	0.28	0.11	0.13
NP/H	138.47***	1.34	0.74	0.57	2.62	0.67	0.24

The residual *df* is 150 for each parameter. *F*-values and their significances are presented

$^*P<0.05$; $^{**}P<0.01$; and $^{***}P<0.001$

cantly enhanced as nutrient content dropped or water content increased (Fig. 1; Table 1). RSR, RS, and RE were significantly affected by $N \times W$ while other interactions had no significant influence on any biomass allocation trait. Except for RL, the influence of soil nutrient content was the largest source of variation among all three allocation traits (Table 1).

Changes in Allometric Relationships in Response to Environmental Factors

Similar to the allometry between root and shoot biomasses (BRO and BSH), significant relationships existed between stem and total biomasses (BS and BT), but these were significantly affected by nutrients and not by water or population density (Table 2). As with the relationships between biomasses for reproductive and vegetative organs (BRE and BV), the allometry was significant between BL and BT; being influenced by soil nutrients and water content but not by density (Table 2). All relationships for biomass allocations were positive (Fig. 2; Table 2). Values for BRO and BS increased with greater nutrient content. When equivalent plant sizes were compared, BL rose with higher nutrient content but declined with water content (Fig. 2A, B, C, D). However, the same comparison revealed elevated BRE values as both nutrient and water contents increased (Fig. 2E, F). In contrast to the effect of water content, allometric relationships of regressions between BRE and BV were lower when more soil nutrients were available. Relationships between BRO and BSH, and between BL and BS, were not so obvious (Table 2).

Relationships between Traits for Biomass Allocation and Plant Architecture

Architectural traits were significantly affected by soil nutrients, except for NT (tertiary branch number) and NT/BS (branch count in proportion to stem biomass). Soil water content had a significant effect on plant height, numbers of primary and secondary branches, and the ratios between branching or height and stem and total biomasses (H, NP, NS, NP/BS, and H/BT, respectively) while population density had a significant influence on H, NP, NS, NP/BS, NS/BS, and H/BT (Table 1). The stepwise regression model showed that H/BT and NP were determinants of RSR for plants undergoing different treatments, explaining 73.5% of the variance in RSR. H and NP/BS were determinants of RS, accounting for 56.7% of the

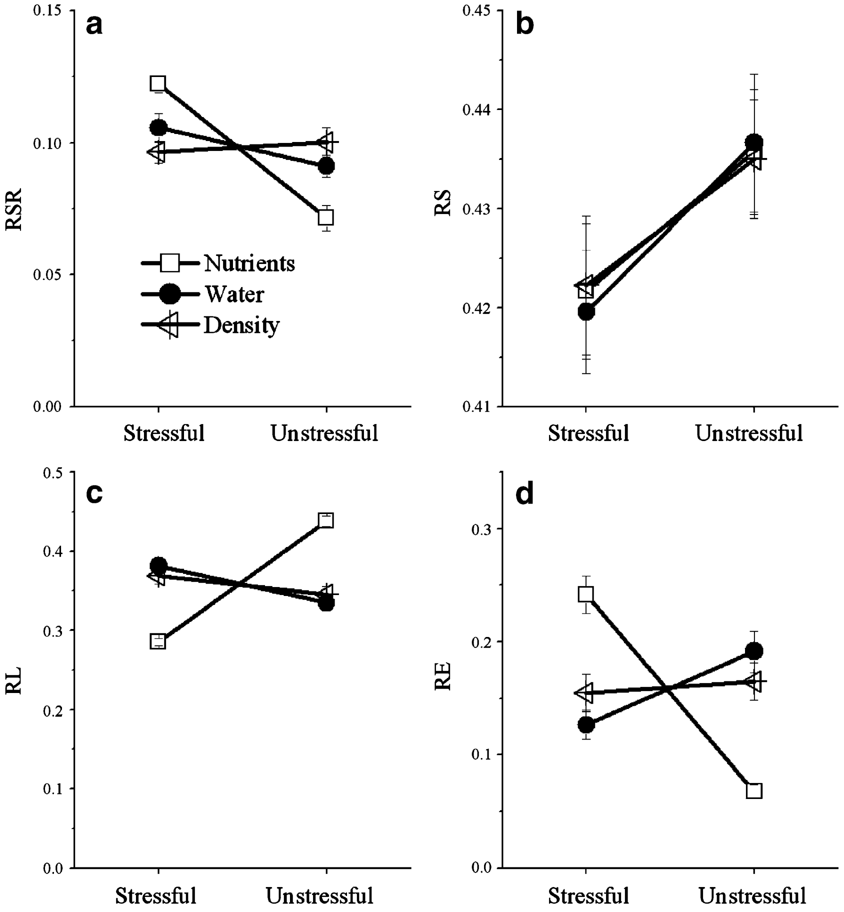

Fig. 1 Responses of biomass allocation traits to environmental factors (mean±SE). Root: shoot ratio (**a**), relative stem biomass (**b**), relative leaf biomass (**c**), and reproductive effort (**d**)

Table 2 Scaling exponents (a_{RMA}±SE) in allometric regression models ($Y=bX^{a}$) between a, shoot biomass (X) and root biomass (Y) for different treatments; b, total biomass (X) and stem biomass (Y) for different treatments; c, total biomass (X) and leaf biomass (Y) for different treatments; or d, vegetative biomass (X) and reproductive biomass (Y) for different treatments

Treatment			a			b			c			d		
			a_{RMA}±SE	r^2	Sig^{A}	a_{RMA}±SE	r^2	Sig^{A}	a_{RMA}±SE	r^2	Sig^{A}	a_{RMA}±SE	r^2	Sig^{A}
N−	*W*−	*D*+	1.202±0.226	0.611	–***	1.023±0.104	0.842	–***	1.002±0.053	0.953	–***	1.805±0.674	0.285	–*
		D−	0.864±0.060	0.919	–***	1.023±0.032	0.982	–***	0.981±0.049	0.956	–***	1.446±0.363	0.469	–***
	W+	*D*+	1.001±0.118	0.800	–***	1.250±0.056	0.965	–***	1.046±0.061	0.942	–***	0.796±0.350	0.223	–*
		D−	1.042±0.076	0.913	–***	1.149±0.062	0.951	–***	0.910±0.063	0.921	–***	1.219±0.333	0.426	–**
N+	*W*−	*D*+	0.956±0.178	0.644	–***	1.054±0.050	0.966	–***	0.917±0.044	0.965	–***	2.226±0.458	0.596	–***
		D−	1.436±0.556	0.323	–*	1.030±0.066	0.946	–***	0.970±0.116	0.834	–***	2.882±1.659	0.177	ns
	W+	*D*+	0.719±0.077	0.829	–***	1.067±0.025	0.990	–***	0.989±0.041	0.970	–***	1.650±0.548	0.335	–**
		D−	1.065±0.176	0.710	–***	1.097±0.045	0.975	–***	0.912±0.072	0.913	–***	2.239±1.043	0.235	–*
Overall			0.758±0.024	0.868	–***	1.060±0.011	0.985	–***	1.146±0.018	0.964	–***	0.929±0.117	0.296	–***
Sig^{B}														
Nutrient			–**			–***			–***			–***		
Water			ns			ns			–**			–***		
Density			ns			ns			ns			ns		

ns no significance ($P>0.05$), Sig^{A} significance of regression model in ANOVA, Sig^{B} significance of experiment×covariate in ANCOVA

*$P<0.05$; **$P<0.01$; and ***$P<0.001$

variance in RS while NP/H and NS/BS were determinants of RL, explaining 64.0% of the variance in RL. Lastly, H was a determinant of RE, for 50.0% of the variance in RE (Table 3).

RSR increased with greater H/BT. In contrast to water content and density, soil nutrients had significant effects on allometric relationships. The value for RSR also rose with decreasing nutrient content at an equivalent H/BT (Fig. 3A; Table 4). RS grew with increasing H, and that allometric relationship was significantly affected by nutrient and water contents, i.e., its value rose as nutrient and water contents declined at an equivalent H (Fig. 3B, E; Table 4). RL increased with rising NP/H, and their allometric relationship was significantly affected by all three environmental factors. That is, RL values were enhanced with decreasing nutrient content and increasing water content and density at an equivalent NP/H (Fig. 3C, F, H; Table 4). RE increased with decreasing H, that relationship being significantly influenced by nutrient and water contents. Shorter plants tended to allocate more resources to reproductive organs while taller ones distributed more to their vegetative organs. RE values rose with decreasing nutrient content and increasing water content when compared at equivalent heights. Moreover, at equivalent H values, when nutrients were less available, plants allocated more biomass to the reproductive organs than to other traits. In contrast, under low water availability and at equivalent H, more biomass was allocated to organs other than the reproductive components (Fig. 3D, G; Table 4).

Discussion

Allometric Relationships between Root and Shoot Biomasses

Our values for root:shoot ratios (RSRs) were affected by environmental conditions, which is in agreement with previous reports (Lloret et al. 1999; Hwangbo and Kwak 2001; Mony et al. 2007). Higher ratios resulted from deficiencies in soil nutrients and water content (Mony et al. 2007; Gonzáles et al. 2008). However, allometric relationships were significantly influenced by nutrients but not by water. This indicated that the plasticity of the root:shoot ratio for water treatments was "apparent" (Table 5). Patterns on root allocation were identical under different levels of moisture availability, and variations in RSR were caused by plant size and not water content. The plasticity of RSR in response to nutrient treatments was "true" (Table 5), with plants allocating more biomass to their root systems when nutrient supplies were low. Population density did not significantly affect either RSR values or the allometric relationships between root and shoot biomasses. These

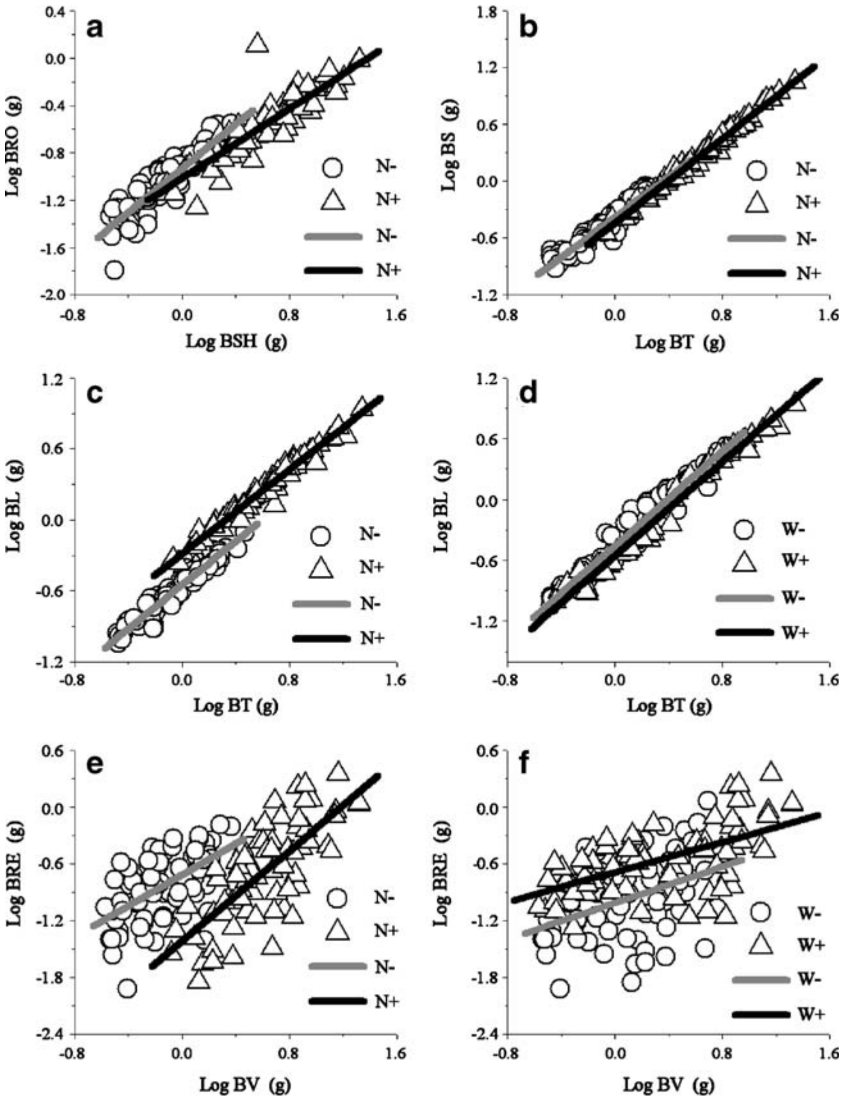

Fig. 2 Allometric relationships among organs in response to variations in environmental conditions. *BRO* root biomass, *BSH* shoot biomass, *BS* stem biomass, *BT* total biomass, *BL* leaf biomass, *BRE* reproductive biomass, *BV* vegetative biomass, *N*− low nutrient level, *N*+ high nutrient level, *W*− low water level, *W*+ high water level

results indicate that no plasticity of RSRs occurred in response to density (Table 5). Casper et al. (2008) also have shown that plants maintain consistent patterns of root allocation at different densities.

Table 3 Results of stepwise regressions showing architectural determinants of biomass allocations

Trait	Variable entered	Partial *r*	Model r^2	Significance
RSR	H/BT	0.721	0.520	–***
	NP	0.014	0.540	–***
RS	H	0.535	0.286	–***
	NP/BS	0.032	0.321	–***
RL	NP/H	0.584	0.341	–***
	NS/BS	0.056	0.420	–***
RE	H	0.500	0.250	–***

***$P<0.001$

We also found correlations between the root:shoot ratio and architectural traits. As noted earlier by Wang et al. (2006), the root allocation pattern was affected by environmental factors by way of self-regulation between architectural traits and biomass allocation. At low nutrient availability, the increase in RSR was primarily a result of greater height per gram of total biomass. Plants of *A. squarrosum* are thin and tall and, therefore, possess a relatively high ratio of height to total biomass.

Allometric Relationships between Stem and Total Biomasses

In contrast to a previous investigation (Wang et al. 2008), which suggested that plants allocate more biomass to stems when grown in soils with high nutrient contents, our current RS was unaffected by nutrient levels. The allometric relationships between stem and total biomasses were significantly

Fig. 3 Allometric relationships between biomass allocations and architectural traits under different environmental conditions. *RSR* root:shoot ratio, *RS* relative stem biomass, *RL* relative leaf biomass, *RE* reproductive effort, *H/BT* ratio of plant height to total biomass, *H* plant height, *NP/H* number of branches per cm plant height, *N*− low nutrient level, *N*+ high nutrient level, *W*− low water level, *W*+ high water level, *D*− low density level, *D*+ high density level

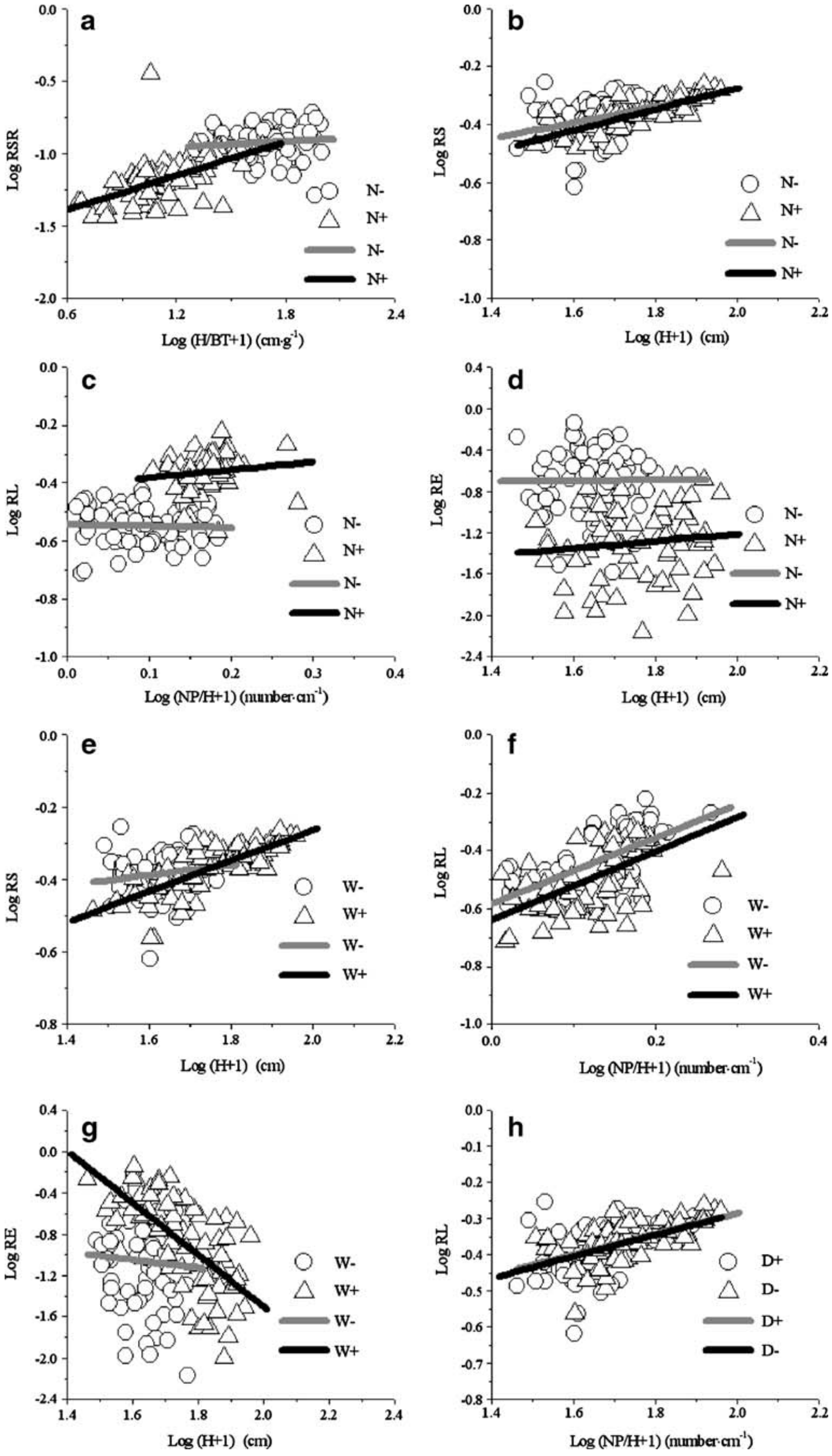

Table 4 Scaling exponents (a_{RMA}±SE) in allometric regression models ($Y = b(X+1)^a$) between biomass allocations and architectural traits

Y	*X*	a_{RMA}±SE	95% CI	r^2	Sig^A	Sig^B		
						Nutrients	Water	Density
RSR	H/BT	0.126±0.014	0.060–0.093	0.369	–***	–**	ns	ns
RS	H	0.552±0.072	0.411–0.694	0.286	–***	–**	–**	ns
RL	NP/H	2.024±0.231	1.568–2.479	0.341	–***	–***	–***	–**
RE	H	−3.847±1.12	−1.641–0.442	0.073	–***	–***	–***	ns

ns no significance ($P>0.05$), Sig^A significance of regression model in ANOVA, Sig^B significance of experiment×covariate in ANCOVA
**$P<0.01$; and ***$P<0.001$

influenced by nutrient supply, leading to "true" plasticity of stem allocation (Table 5). However, increases in RS in response to low nutrients were balanced by plant size. Those values were, therefore, not significantly affected by nutrient content whereas stem allocation patterns were.

Although Boogaard et al. (1997) have shown that RS is influenced by soil water, we did not see this in our analysis of allometric relationships. Plasticity of stem allocation was "apparent" in response to water content (Table 5). In contrast, population density had no effect on RS values or on allometric relationships between stem and total biomasses, such that no plasticity occurred for stem allocation with regard to density (Table 5).

Plant height was the primary determinant of stem allocation for architectural traits. Significant allometric relationships existed between those two, and were also affected by nutrients and water level, with taller plants distributing more biomass to their stems. Similar to the overall effect that plant size had on allometric stimulus, height was also balanced by nutrient and water availabilities.

Table 5 Plasticity of biomass allocations for different environmental factors

Parameter	Environment factor	Plasticity[a]
Root:shoot ratio (RSR)	Nutrients	True
	Water	Apparent
	Density	Nonexistent
Relative stem biomass (RS)	Nutrients	True
	Water	Apparent
	Density	Nonexistent
Relative leaf biomass (RL)	Nutrients	True
	Water	True
	Density	Apparent
Reproductive effort (RE)	Nutrients	True
	Water	True
	Density	Nonexistent

[a] Plasticity is "true" if allometric relationships are significantly affected by environmental conditions; "apparent" if relationships are significantly unaffected by environmental conditions while the value of biomass allocation is affected; or "nonexistent" if allometric relationships and the value of biomass allocation are both significantly unaffected by environmental conditions

Allometric Relationships between Leaf and Total Biomasses

Our experiments clearly demonstrated that leaf allocation was significantly affected by all three environmental factors. When the nutrient supply is deficient, plants distribute more biomass to other organs than to the leaves (Gindaba et al. 2005; Wang et al. 2008). Here, allometric relationships between leaf and total biomasses were affected by nutrients and water, making the plasticity of RL "apparent" in response to density (Table 5). That is, plant spacing influenced size but not leaf allocation patterns. However, the plasticity of RL was "true" in response to nutrient and water contents (Table 5).

NP/H was the primary determinant of leaf allocation, with a higher distribution being correlated with a greater number of branches per centimeter of plant height. Nutrient and water contents affected allometric relationships between RL and NP/H, and the former parameter also fluctuated with changes in nutrient and water contents at an equivalent NP/H.

Allometric Relationships between Reproductive and Vegetative Biomasses

Reproductive efforts vary according to environmental factors (van Kleunen et al. 2001), for example, either increasing (Hickman 1977) or decreasing (Snell and Burch 1975) in response to greater population density. Here, spacing did not have a significant effect on the allometric relationships of BRE and BV, suggesting no plasticity between RE and D (Table 5). However, both reproductive effort and the allometric relationships of BRE and BV were significantly influenced by nutrient and water contents, indicating that RE plasticity was "true" (Table 5). Results have been similar for *Atriplex sagittata* (Mandak and Pysek 1999), *Rumex obtusifolius* (Pino et al. 2002), and *Plantago major* (Reekie 1998).

Plants either increase their reproduction in response to environmental stress (Hickman 1977; Wu and Jain 1979; Li et al. 2001) or else maintain similar, modest levels of reproductive output in resource-poor environments. This demonstrates the ability of plants to maintain fecundity under less desirable conditions or, as previously stated, to "make the best of a bad job" (Sultan, 2001). Our current results support the positions that (1) a subtraction of nutrients can increase reproductive efforts, (2) additional water can improve RE, and (3) altered density may impose no effect on reproductive efforts or the allometric influence of reproductive biomass.

Architectural traits also play an important role in reproduction (Cheplick 2002; Wang et al. 2006). Here, height, though negatively correlated, was the determinant of reproductive effort, and the availability of nutrients and water had a significant effect on this correlation. In contrast to water level, nutrient content was negatively related to the allometric relationships between RE and H.

In conclusion, significant relationships were found among the biomasses of different organs, and were affected by environmental conditions. In response to nutrient content, the plasticity of all biomass allocations was "true". At lower nutrient levels, plants tended to allocate more biomass to the roots, stems, and reproductive organs. Although values for BRO and RE were higher, those for BS were constant because of the tradeoff between the effects of plant size and nutrient content. In response to water content, plasticity was "true" for relative leaf biomass and reproductive effort. At a low water content, *A. squarrosum* allocated more biomass to leaves than to reproductive organs. Plasticity was "apparent" for root and stem allocations; in response to density, the plasticity of leaf allocation also was "apparent", while that of other biomass allocations was "nonexistent". Allometric relationships were significant between biomass allocation and architectural traits, with patterns for the former being affected by environmental conditions via self-regulation.

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