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Shoot competition, root competition and reproductive allocation in *Chenopodium acuminatum*

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Summary

1. Root and shoot competition affect plant growth in different ways, but their effects on reproductive allocation have not been investigated. If root and shoot competition affect reproductive output in a population differently, this will influence the evolution of plant populations growing under various competitive regimes.

2. We conducted a field experiment to investigate the effects of root, shoot and full competition from naturally occurring surrounding vegetation on growth and reproduction of an annual plant, *Chenopodium acuminatum*, under low and high soil fertility. Root competition was eliminated by inserting a PVC pipe vertically into the soil around target individuals, and shoot competition was removed by installing inverted wire cones above-ground. Plants were measured after 11 weeks of growth. The relationships between reproductive (R) and vegetative (V) biomass among treatments were compared.

3. Without fertilizer, the competitive response of target plants to root competition was greater than that to shoot competition, while in the fertilized treatment, the opposite was the case. Fertilization increased target plant size under no or root competition, but did not affect mean plant size for individuals experiencing shoot or full competition. Variation in size among target plants was highest under shoot competition at high fertility.

4. The slope of log R–log V relationship under fertilized conditions was significantly higher than without fertilizer addition. The slope was higher under shoot and full competition than under root or no competition at both fertility levels. There were many more small individuals when competition was for light than for soil resources. These small individuals developed more slowly and had fewer flowering branches and lower reproductive allocation at harvest than large individuals.

5. *Synthesis.* Our results demonstrated that shoot competition affects the observed pattern of reproductive allometry among individuals in the field, and this has implications for the fitness of competing plants. The steeper log R–log V slope of populations competing above-ground may intensify the role of directional selection under light competition, making the effects of shoot competition more important than those of root competition for the evolution of weeds in fertile environments.

Key-words: above-ground competition, below-ground competition, reproductive allometry, reproductive ecology, size inequality

Introduction

The relationship between reproductive (R) and vegetative (V) mass among individuals in a population is at the core of plant life-history strategies (Ohlson 1988; Reekie 1998; Vega *et al.* 2000; Bonser & Aarssen 2009; Weiner *et al.* 2009). There is often a threshold size needed for reproduction and a linear relationship between R and V above this size (Samson & Werk 1986), or a classical allometric relationship: $R = \beta V^{\alpha}$ or $\log R = \log \beta + \alpha \log V$, where parameter α is often

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referred to as the allometric exponent and β the allometric coefficient. An α different from one indicates an allometric (i.e. non-isometric) relationship between reproductive and vegetative biomass (Bonser & Aarssen 2009; Weiner *et al.* 2009). Research on allometric relationships within populations growing under different conditions can help us understand how a species adapts to its environment over a range of conditions. It has been argued that the 'total R–V relationship', that is the cumulative R–V relationship after all individuals have senesced, is relatively fixed for a genotype and that observed changes in the R–V relationship of a genotype in different environments are due to plasticity in growth and developmental rates (Weiner *et al.* 2009). Whether changes in the R–V relationship are due to plasticity in allometric growth or in the rate of development, the actual R–V relationship in the field is what is important for the plant population's dynamics and evolution. Thus, both the total (potential) and the observed R–V relationships of plants are of interest to plant ecologists.

Competition is a ubiquitous factor in natural plant communities. Sometimes competition affects only plant size but not the R–V relationship (Grundy *et al.* 2004; Ploschuk, Slafer & Ravetta 2005; Weiner *et al.* 2009), but in some cases, both size and the R–V relationship are affected by competition (Sugiyama & Bazzaz 1998; Liu *et al.* 2008). Here, we hypothesize that the mechanism of competition (above- versus below-ground) may help explain this difference. Numerous studies have shown that root and shoot competition have different effects on plant growth (Cahill & Lamb 2007; Wang *et al.* 2010), inter- or intraspecific interactions (Cahill & Casper 1999; Lamb, Shore & Cahill 2007) and community structure (Lamb, Shore & Cahill 2007; Li *et al.* 2011; Mariotte *et al.* 2012), but we know of no studies on the differential effects of root and shoot competition on reproductive allocation. If the mechanism of competition affects reproductive allometry in the field, this might drive adaptive evolution of plant populations growing under various competitive regimes, such as stronger shoot competition in fertile environments or stronger root competition in less fertile environments.

Shoot competition may have greater effects on reproduction than root competition because reproductive structures are founded on the shoots, whereas below-ground resources may contribute primarily to plant growth rate and therefore size at any point in time. The allocation of meristems (which can be inactive or produce branches, and/or reproductive structure) is affected by competition (Bonser & Aarssen 2001, 2003). Under intense shoot competition, plants often increase height growth at the cost of lateral growth (Caton, Foin & Hill 1997; Huhta, Tuomi & Rautio 2000). One obvious outcome is a significant decrease in branch number (Zhang *et al.* 2008), which can reduce a plant's potential to produce meristems for reproduction. Similarly, if root competition changes allocation to roots versus shoots, this could also affect allocation to reproduction. Therefore, plants of the same size growing under root versus shoot competition may show different reproduction allocation, altering the actual R–V relationship among individuals (Clauss & Aarssen 1994).

In addition, shoot competition drives competitive size asymmetry (Newman 1973; Weiner 1990), so it increases size variability more than root competition does (Weiner 1986). This increased size variation in populations experiencing strong shoot competition may result in a different relationship between reproductive and vegetative biomass than populations experiencing primarily root competition.

To compare the influence of root and shoot competition on reproductive allocation, we grew individuals of the annual plant, *Chenopodium acuminatum*, with no competition, root competition, shoot competition and full competition from surrounding natural herbaceous vegetation under fertilized and unfertilized conditions. The reproductive allometric relationships among individuals experiencing different forms of competition were analysed to address four main questions: (i) What are the relative contributions of above- and below-ground competition for the size of *C. acuminatum* individuals in the field? (ii) Does competition alter the observed R–V relationship among individuals of this species? If so, (iii) are the effects similar for root and shoot competition? Finally, (iv) are the effects consistent at different soil fertility levels? We take an *in situ* field experimental approach, using the existing plant community as competitors, rather than controlling the number and species of competitors. Growing target plants in natural vegetation may result in more variation, but it better reflects the effects of competition in the field.

Materials and methods

PLANT SPECIES AND SITE

Species of the genus *Chenopodium* (Chenopodiaceae) are widely distributed throughout the world and are especially common in cultivated fields, abandoned farmland, roadsides and along riverbanks. *Chenopodium acuminatum* Willd. is an annual weed, 20–80 cm tall, with an erect stem and many branches. Its leaf blade is broad, around 2–4 cm length and 1–3 cm width. Glomerules (compact, cymose clusters of flowers) occur on upper part of branches (www.efloras.org). Flowering and seed set are indeterminate, occurring from June to September in Northeast China. *Chenopodium acuminatum* was chosen as the focal species, because it is easy to separate the reproductive organs from vegetative organs, and it shows high phenotypic plasticity (Wang 2006). Seeds used for the experiments were collected from the farmland margin nearby the research station and were air-dried and stored.

The experiments were conducted in the Pasture Ecology Research Station of Northeast Normal University, Jilin Province, China (123°44′E, 44°40′N). The typical mean temperature is 4.6–6.4 °C, and the annual precipitation 350–500 mm (Wang, Zhou & Valentine 2006). We set up the experiment in a recently abandoned farmland, which was dominated by annual and biennial weeds. The naturally occurring species competing with *C. acuminatum* in the study included *Setaria viridis* (dominant species, with cover over 50%), *C. aristatum, Ixeris denticulate, Artemisia scoparia, Xanthium strumarium* and *Chloris virgata*. The available nitrogen, phosphorous and potassium in soil were 16.23, 3.60 and 0.98 mg/kg, respectively, and the organic matter was 15.55 g/kg (P. Wang, unpubl. data).

PLOT ESTABLISHMENT

The experimental area was 6 × 50 m and was ploughed and mixed to 30 cm depth. After the soil surface was smoothed and rolled, the area was divided into 10 replicate blocks (6 × 5 m each). Within each block, 12 locations were placed in four rows and three columns. One of four competition treatments described below was randomly assigned in each position, that is three replicates for each competition treatment in each block. The distance between each position was 1 m, and the buffer zone to the edge of the block was 1.5 m wide (see Fig. S1 in Supporting Information).

COMPETITION AND FERTILIZER TREATMENTS

We imposed four competition treatments:

1. Target plants growing without roots and shoots of neighbours (no competition, NC),

2. Target plants interacting with roots but not shoots of neighbours (root competition, RC),

3. Target plants interacting with shoots but not roots of neighbours (shoot competition, SC) and

4. Target plants interacting with roots and shoots of neighbours (full competition, FC).

Root competition was eliminated by inserting a PVC pipe (9.5 cm diameter, 40 cm length) vertically into the soil. To avoid the injury to plants when pipes were inserted into soil, we set up the pipes before target plants or neighbour plants had germinated. Shoot competition was removed by installing inverted wire cones (the upper diameter is 30 cm, lower diameter is 10 cm, and the height is 40 cm), made from a wire framework surrounded with wire net (1 × 1 mm mesh). Three iron bars with thin nails inserted into soil fixed the wire cones, and the distance between nails and target plants were around 30–40 cm. The disturbance to the soil from the nails was negligible. These cones were strong enough to keep shoots of neighbours out of the cones and keep the target plant from being shaded by neighbours. These methods of isolating root and shoot competition are similar to those commonly used in other field studies (Wilson & Tilman 1993; Cahill 2003; Kiær, Weisbach & Weiner 2013).

Five blocks were fertilized by adding 15 g N/m^2 fertilizer ($CO(NH_2)_2$) with a single spray application when seedlings of target plants had two or three true leaves. The fertilized and unfertilized blocks were arranged alternatively. In total, there were 15 replicate individuals for each competition treatment under fertilized and unfertilized conditions. Since our focus was to investigate the effects of competition and soil fertility on reproductive allocation, we eliminated two other common stress factors, drought and insect herbivory, through irrigation and insecticide (pyrethrin) application as needed.

TARGET PLANTS

Five seeds of *C. acuminatum* were sown in the centre of each position (inside the pipes if present) by hand and irrigated twice per day until germination. After germination and following the emergence of the second true leaves, one seedling of average size (4–6 cm height) was kept, while others were removed manually. Any seedlings that germinated within the pipe subsequently were also removed. Wire cones were installed when shoots of target plants began to interact with neighbours. Each wire cone was checked weekly to ensure no shoots of neighbours grew within the cones.

HARVEST

After 11 weeks, which was near the end of the growing season, more than half the seeds within the infructescences were mature for most target plants. All target plants were harvested at that time to avoid seed loss due to shedding. Plant height and the number of branches >1 cm in length were recorded. Shoots were cut at the soil surface and separated into vegetative (stems, leaves) and reproductive organs (including the rachis, utricles, seeds, perianth segments and bracts) by cutting off all inflorescences at their base. Roots were removed from the soil carefully. Plants growing in pipes were easy to remove. For plants growing without pipes, we carefully removed the soil with a 40 cm depth × 30 cm diameter area centred on the target plant. The samples were hand-washed, and roots of target plants were collected. The roots were then added to the stems and leaves for our measure of vegetative biomass. Vegetative (V, including above- and below-ground parts) and reproductive biomass (R) of each individual were weighed after drying at 65 °C in an oven for 48 h.

EFFECTS OF FERTILIZATION ON THE VEGETATION

To test whether the fertilizer application increased vegetative growth, we measured canopy height (four heights randomly measured at each block), biomass (two 1 × 1 m subplots randomly harvested at each block) and light penetration rate at ground and 50 cm above-ground (measured by light metre with LI-191SA line quantum sensor during 12:00 to 14:00) at the end of the experiment.

COMPETITIVE RESPONSE

After Cahill (2002), we define competitive response as ln [(target plant biomass in the presence of competition)/(target plant biomass without competition)]. Thus, the smaller the value of the competitive response, the more competition has negatively affected the target plant.

Total competitive response = ln (FC/NC)

Above-ground competitive response = ln (SC/NC)

Below-ground competitive response: = ln (RC/NC),Where NC is the mean target plant biomass (within each block) when grown without competition (pipe and cone), SC is plant biomass when grown with the shoots, but not root competition (pipe only), RC is root, but not shoot competition (cone only), and FC is both shoot and root competition (no pipe or cone).

STATISTICAL ANALYSES

We used mixed general linear models, with fertilizer as a fixed factor, to analyse its effect on vegetation structure, including biomass, canopy height, light transpiration rate at ground and 50 cm above-ground. Block was treated as a random effect. A series of independent-sample *t*-tests were used to do mean comparisons between fertilized and unfertilized treatments. All of the data were analysed with SPSS statistical software (version 17.0; SPSS Inc., Chicago, IL, USA). To compare the differences of competitive response, total biomass, plant height and total branch number among all fertilizer and competition treatments, mixed general linear models were used to detect the effects of fertilizer, competition and their interactions on dependent variables, with block as a random effect. The mean comparisons were made using LSD. Differences reported here were significant at $P < 0.05$.

Linear regression was used to determine the relationship between plant height and branch number (both log transformed) under different competition and fertilizer treatments. We tested whether the slope among individuals within the shoot, root and full competition treatments was different from that of the no competition treatment. Standardized major axis (SMA) regression analysis was used to determine the relationship between reproductive biomass and vegetative biomass (both log transformed) at harvest under different competition and fertilizer treatments. We tested whether the slope among individuals of each treatment was different from one and whether there were significant differences in slopes among competition and fertilizer treatments (Warton *et al.* 2006). All of the SMA analyses were conducted using the software 'STANDARDIZED MAJOR AXIS TESTS and ROUTINES VERSION 2.0' (Falster, Warton & Wright 2006).

We used the coefficient of variation as a measure of inequality in total plant size and reproductive biomass for the 15 target plants under each competition–fertilizer combination. The asymptotic test statistics for coefficients of variation were conducted between values of no competition treatment with every competition treatment under each fertilizer condition, following the method of Miller (1991).

Results

Fertilization resulted in increased community biomass ($F = 123.25$, $P < 0.001$), canopy height ($F = 46.16$, $P < 0.001$) and lower light transmittance (ground surface: $F = 36.04$, $P < 0.001$; 50 cm above-ground: $F = 69.70$, $P < 0.001$, Table 1).

EFFECTS OF COMPETITION AND FERTILIZATION ON PLANT BIOMASS, HEIGHT AND BRANCH NUMBER

The total plant biomass of *C. acuminatum* was significantly affected by the mechanism of competition and its interaction with fertilizer. Though fertilization increased target plant size for individuals under no and root competition, fertilizer did not affect the plant size for individuals under shoot and full competition (Fig. 1a).

Plant height was affected by fertilization and competition (Table 2). In general, the fertilized plants were taller than the unfertilized ones, although this effect was only significant for no and root competition (Fig. 1b). Compared with individuals without competition, plant height was lower for individuals experiencing root and full competition under unfertilized condition and for individuals with shoot and full competition under fertilized conditions (Fig. 1b).

Total branch number was affected by competition, and there was a significant competition x fertilizer interaction

Table 1. Characteristics of vegetation under fertilized and unfertilized conditions. Values are means ± SE. Fertilized and unfertilized treatments were significantly different ($P < 0.01$) in every case

	Unfertilized	Fertilized
Vegetation biomass (g/m^2)	258.75 ± 10.85	423.45 ± 5.76
Canopy height (cm)	95.65 ± 2.38	115.85 ± 1.78
Light penetration rate at ground (%)	9.95 ± 0.72	3.70 ± 0.76
Light penetration rate at 50 cm above-ground (%)	72.38 ± 4.29	28.34 ± 3.07

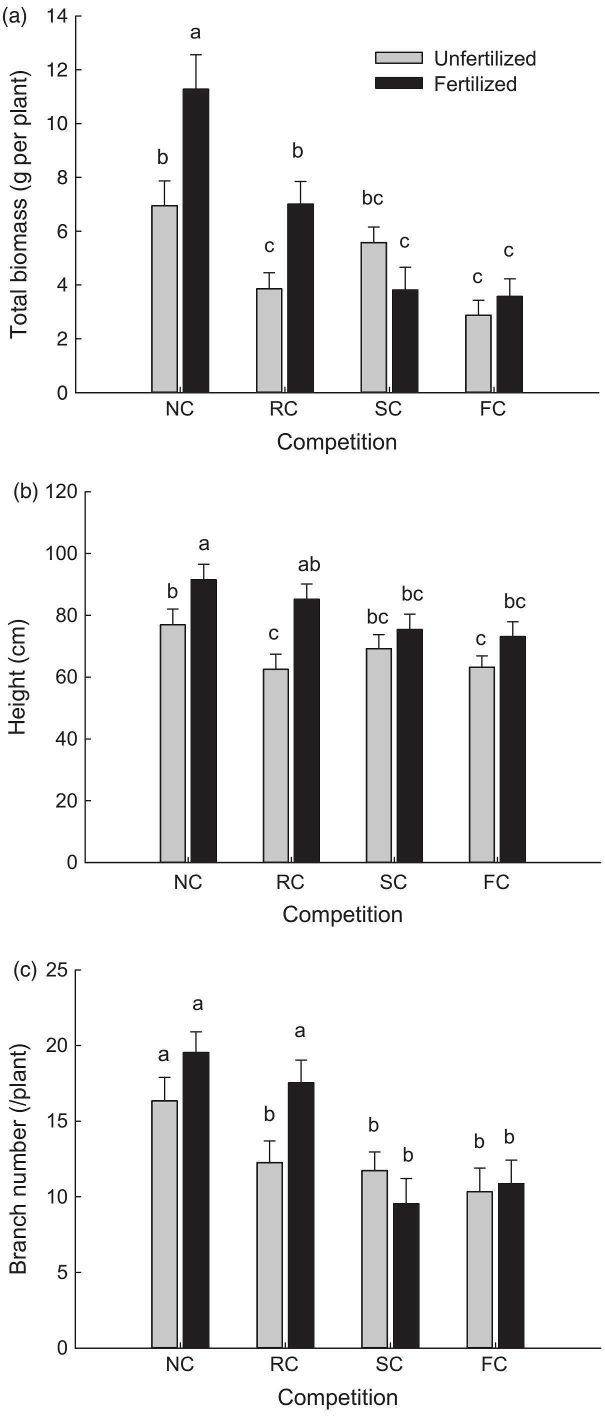

Fig. 1. Total biomass (a), height (b) and total branch number (c) of *Chenopodium acuminatum* plants in the no competition (NC), root competition (RC), shoot competition (SC) and full competition (FC) treatments under unfertilized (grey bars) and fertilized (black bars) conditions. Values are means ± SE. Values with the same letter are not significantly different among competition and fertilizer treatments at the $P < 0.05$ level.

Table 2. anova of the effects of competition (Comp), fertilizer (Fert) and their interaction on total biomass, plant height and branch number

	Total biomass		Plant height		Branch number	
Source	*F*	Sig.	*F*	Sig.	*F*	Sig.
Comp	$18.664_{3,108}$	< 0.001	$4.604_{3,108}$	0.005	$13.012_{3,108}$	< 0.001
Fert	$3.103_{1,108}$	0.081	$17.687_{1,108}$	< 0.001	$2.950_{1,108}$	0.089
Comp × Fert	$6.917_{3,108}$	< 0.001	$1.255_{3,108}$	0.294	$2.683_{3,108}$	0.05

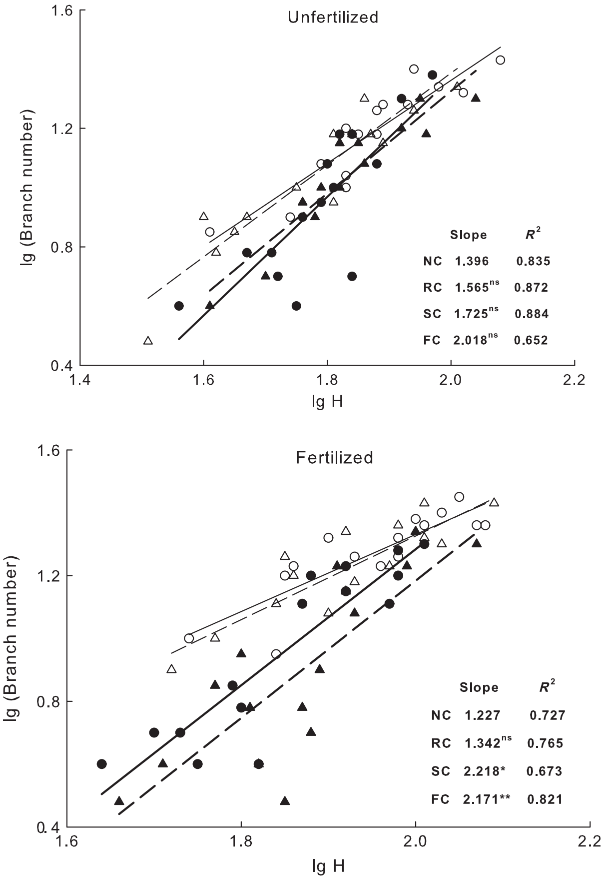

Fig. 2. The relationships between log branch number and log plant height among target individuals of *Chenopodium acuminatum* in the no competition (○, black fine solid line), root competition (Δ, black fine dotted line), shoot competition (▲, black thick dotted line) and full competition (●, black thick solid line) treatments, without and with fertilizer. The ns and asterisk on the slope represent non-significant and significant difference from the no competition (NC) treatment, respectively. All regressions are significantly different from 0 ($P < 0.001$).

(Table 2). The type of competition significantly affected the branch number under both fertilized and unfertilized conditions, with fewer branches on plants in the full and shoot competition treatments than those without competition (Fig. 1c).

There was a significant positive relationship between plant height and branch number in all cases (Fig. 2). The slopes of regression lines in shoot and full competition were not significantly different from that of no competition under unfertilized conditions, but they were different under fertilized condition.

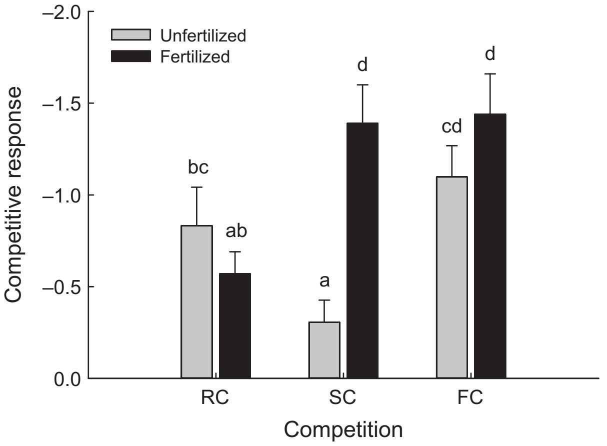

Fig. 3. The competitive response ratio of *Chenopodium acuminatum* plants experiencing root competition (RC), shoot competition (SC) and full competition (FC) under fertilized and unfertilized conditions. Values are means ± SE. Values with the same letter are not significantly different among competition and fertilizer treatments at the $P < 0.05$ level.

There were no significant differences in slope between root and no competition treatments at either soil fertility.

COMPETITIVE RESPONSE

Full competition reduced plant size more than above- or below-competition alone (Fig. 3). Without fertilizer application, the competitive response to root competition was greater than that to shoot competition, while in the fertilized treatment, the competitive response to the shoot competition was greater than that of root competition and almost equal to that of full competition (Fig. 3). The competitive response to shoot competition was much greater with than without fertilizer.

REPRODUCTIVE ALLOMETRIC RELATIONSHIPS AMONG INDIVIDUALS

There were highly significant relationships between vegetative biomass and reproductive biomass in every case (Table 3, Fig. 4). The overall slope of log R–log V relationship under fertilized conditions was significantly higher than that of unfertilized condition. The slopes of log R–log V relationship with shoot and full competition were higher than those with root and without competition under each fertilization treatment. There was no significant difference in slopes between

Table 3. Estimated slopes in allometric regression between log reproductive biomass (*Y*) and log vegetative biomass (*X*) of *Chenopodium acuminatum* in different competition treatments under unfertilized and fertilized conditions. NC: without competition; RC: with root competition; SC: with shoot competition; and FC: with root and shoot competition

	Comp.	Slope	95% CI	r^2
Unfertilized^a	NC^b	1.27*	1.00–1.61	0.84
	RC^b	1.29***	1.15–1.45	0.96
	SC^a	1.89***	1.48–2.41	0.83
	FC^a	1.71***	1.46–2.00	0.93
	Overall	1.34***	1.23–1.46	0.89
Fertilized^b	NC^b	1.12^{NS}	0.86–1.48	0.79
	RC^b	1.15^{NS}	0.95–1.40	0.90
	SC^a	1.77***	1.52–2.05	0.94
	FC^a	1.75***	1.55–1.99	0.96
	Overall	1.53***	1.43–1.64	0.93

Asterisks represent slopes that are significantly different from 1.0: *$P < 0.05$, ***$P < 0.001$, NS, not significant. Treatments within a column with different letters are significantly different at the $P < 0.05$ level.

root and no competition treatments, or between shoot and full competition treatments. Both with and without fertilizer, the log R–log V slopes under shoot and full competition treatments were all significantly different from 1. The slopes of root and no competition were significantly different from 1 under unfertilized, but not under fertilized conditions (Table 3 and Fig. 4).

INEQUALITY AMONG INDIVIDUALS

The differences of inequality in plant size and reproductive biomass were not statistically significant among competition treatments (Fig. 5). However, size inequality among target plants experiencing shoot and full competition was larger than those with root or no competition except for shoot competition without fertilizer. The inequality of reproductive biomass was larger than the inequality of total biomass among target plants experiencing light competition.

Discussion

EFFECTS OF COMPETITION ON PLANT SIZE AND SIZE INEQUALITY

Competition had major effects on plant size and reproductive output. Root competition was stronger than shoot competition without fertilizer, but with fertilizer, shoot competition alone was generally as strong as full competition (Fig. 3), as concluded in a recent review (Kiær, Weisbach & Weiner 2013).

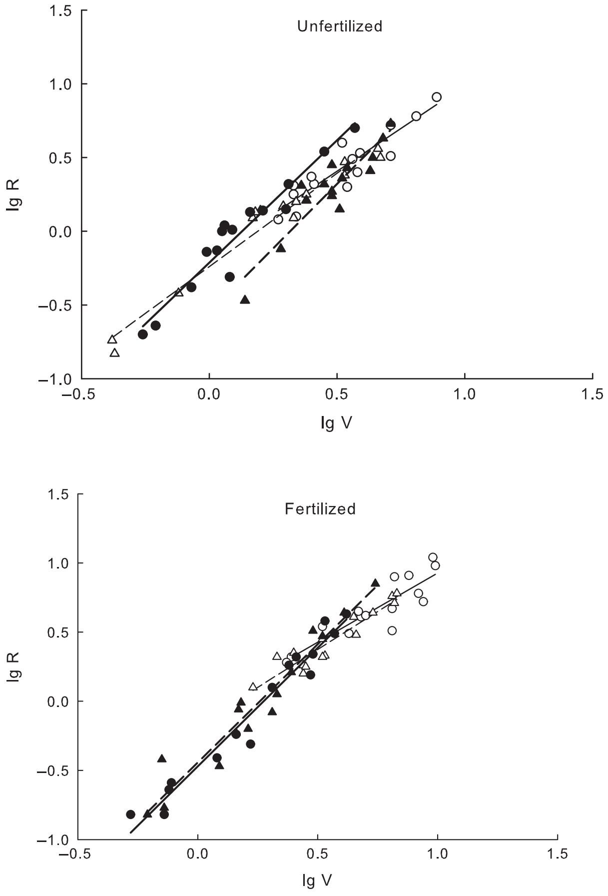

Fig. 4. The relationships between log reproductive biomass (log R) and log vegetative biomass (log V) among target individuals in no competition (○, black fine solid line), root competition (Δ, black fine dashed line), shoot competition (▲, black thick dashed line) and full competition (●, black thick solid line), without and with fertilizer, with reduced major axis regression lines for each treatment.

Addition of fertilizer reduced the effects of root competition (Fig. 3). It is to be expected that addition of a resource will reduce competition for that resource, at least in the short run. Fertilization increased average size of target plant for individuals under no and root competition, but did not affect the average size of individuals under shoot and full competition (Fig. 1). This is because fertilizer benefited the surrounding vegetation (Table 1), and asymmetric competition above-ground suppressed target plant growth such that target plants did not benefit from the fertilizer. Thus, soil fertility determined which form of competition was strongest in our experiment.

Asymmetric competition for light often drives size inequality (Newman 1973; Weiner 1990), and individuals growing with shoot competition show higher size inequality than those growing with root competition, especially at high fertility, which increases competition for light. Competition belowground, even when strong, is not highly asymmetric (Weiner 1986) and therefore does not generate large size variation. Shoot competition under high fertility generated large size variation among target individuals (Fig. 5). Some individuals were highly suppressed by the surrounding vegetation, while some individuals escaped suppression and were relatively large (Fig. 4). This emphasizes the importance of the initial size advantage when above-ground competition is strong. Species in the surrounding vegetation varied in their growth

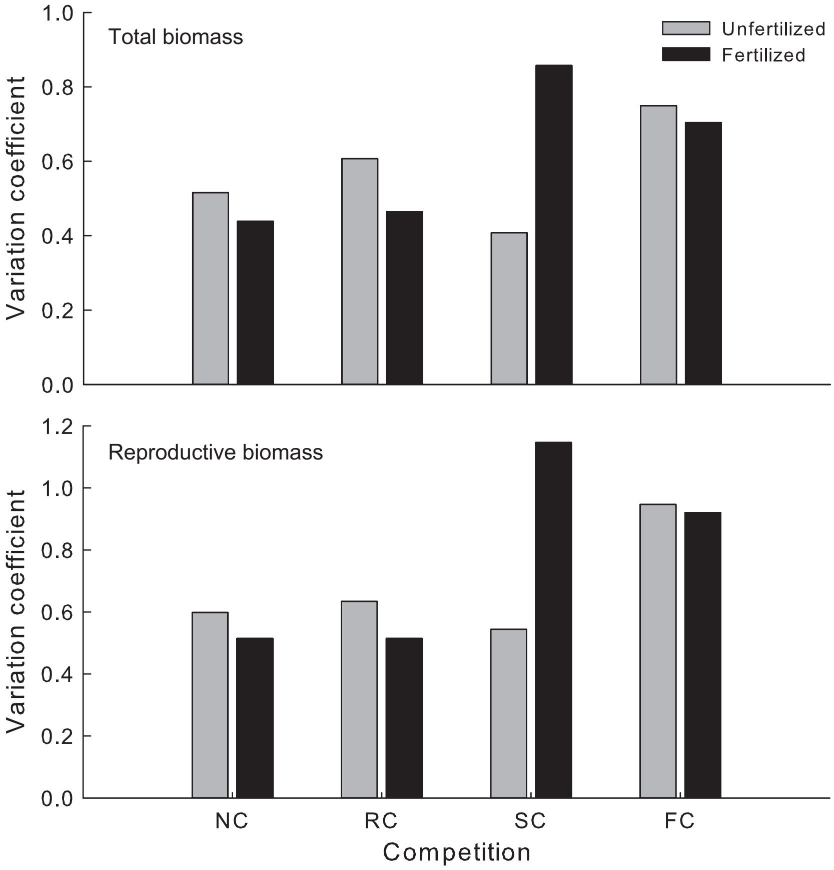

Fig. 5. The coefficient of variation of total biomass and reproductive biomass for *Chenopodium acuminatum* plants under various competition regimes (NC: without competition; RC: with root competition; SC: with shoot competition; FC: with root+shoot competition) and fertilizer treatments.

and developmental rates. When the neighbours grew relatively slowly, the target plants could acquire sufficient resources to grow fast enough to avoid being shaded by the surrounding vegetation.

SHOOT COMPETITION ALTERS OBSERVED REPRODUCTIVE ALLOMETRY

Allometry is a way at looking at the effects of size. Since reproductive allocation within a population changes with size, allometry is a useful tool in analysing the effects of different factors on reproductive allocation (Bonser & Aarssen 2009; Weiner *et al.* 2009). Competition could affect only plant size, but not the relationship between size and reproductive output. Alternatively, competition could change the log R–log V relationship as well as plant size (Sugiyama & Bazzaz 1998; Liu *et al.* 2008).

Shoot, but not root competition, affected the observed R–V relationships among *C. acuminatum* plants. The slope of the log R–log V relationship was significantly higher under full and shoot than under no or root competition (Fig. 4; Table 3). An increasing log R–log V slope within a population due to competition has been observed in some previous studies (Sugiyama & Bazzaz 1998; Grundy *et al.* 2004; Liu *et al.* 2008).

Many target plants were small when there was competition for light. Our plants grew in natural herbaceous vegetation dominated by annual and biennial weeds, and the height of vegetation was higher than the average height of target plants (Table 1 and Fig. 1). The intensive light competition in the canopy resulted in more small plants under shoot and full competition treatments, especially in the fertilized condition (Fig. 4). All *C. acuminatum* plants reproduced in this experiment. Both in unfertilized and fertilized conditions, the steeper slopes of log R–log V relationship in SC and FC indicated that the reproductive allocation of small individuals was low (Fig. 4). It appears to be primarily the small individuals that altered the R–V relationship among individuals when there was shoot competition treatments (Fig. 4).

We present three possible explanations for the effects of shoot competition on the R–V relationship:

1 Lower branch number could be the primary explanation for the low reproductive allocation of individuals that are small because of the effects of competition for light. Plants are modular, but reproductive output is related to architectural traits (Bonser & Aarssen 2003). Though offspring are the currency of natural selection, plants must first accumulate resources and build reproductive machinery (Weiner *et al.* 2009). For many annuals, the number and length of branches are likely to be important for seed production (Suzuki & Ohnishi 2006). Branching intensity usually shows plastic responses to different biotic and abiotic environments (Bonser & Aarssen 2003; Zhang *et al.* 2008; Nishimura *et al.* 2010). In favourable resource environments or in the absence of competitors, plants tend to show a higher degree of branching (Bonser & Aarssen 2001, 2003). However, competition for

light resources stimulated plants to reduce their investment in branching (lateral growth) and prioritize height growth for increasing accessibility to light (Fig. 2). The number of meristems that can potentially produce reproductive organs can be inhibited by light competition (Bonser & Aarssen 2001, 2003), negatively influencing the number of inflorescences and flowers observed. Thus, reproduction can be reduced more than vegetative size in the shaded plants (Pfitsch & Pearcy 1992). Competition makes allometric relationships among different aspects of plant size nonlinear (Weiner & Thomas 1992), and it could have a similar effect on reproductive allometry.

2 An alternative explanation is that the smaller individuals with low reproductive allocation under competition for light may simply be growing and developing more slowly, and they might reach the same log R–log V line if they had more time to develop. We cannot conclude that light competition changes the 'total R–V relationship' (cumulative at senescence), which appears to be relatively fixed (Weiner *et al.* 2009). But it is the actual R–V relationship in the field that matters for the ecology and evolution of a plant population, and the total R–V relationship is the result of natural selection acting on actual R–V patterns in the field. Often there is not enough time for small individuals to mature completely as the light and/or temperature conditions change towards the end of the growing season in temperate regions. This, both total and actual R–V relationships are of interest to the behaviour and evolution of plant populations.

3 A third possible explanation is that the relationship between log R and log V is the same for all treatments, but the relationship is not linear ('complex allometry'; Jolicoeur 1989). While the present data do not exclude this possibility, evidence from previous research argues against such an explanation. A recent review (Weiner *et al.* 2009) found little evidence for nonlinear log R–log V relationships within populations of herbaceous plants. There is evidence that non-competing plants generally show simple (i.e. linear on a log-log scale) allometric relationships (Weiner & Thomas 1992).

Although root competition had large effects on plant size, plants experiencing root and those with no competition showed similar patterns of reproduction allometry. This supports the idea that shoot competition constrains reproduction in ways that root competition does not, perhaps due to allocation of meristems or delayed developments under low light conditions. Plants competing above-ground prioritize height growth and postpone the development of inflorescences, whereas root competition affects size but not architecture and has less effect on the rate of development.

IMPLICATIONS OF ABOVE-GROUND COMPETITION FOR REPRODUCTIVE STRATEGIES AND EVOLUTION OF WEED SPECIES

Allometric (i.e. non-isometric) relationships between R and V were observed among individuals competing above-ground, and this effect was consistent for both soil fertility levels. Our results demonstrate the importance of shoot competition for reproductive allocation and have several implications for the evolution of annual plants in response to competition.

Different biotic and abiotic environments select for different reproductive strategies (Lovett Doust 1989; Wesselingh *et al.* 1997). If a reproductive strategy maximizes fitness in a given environment, this reproductive strategy will be selected. If competition is strong and ubiquitous, genotypes with higher competitive ability will leave more offspring (Aarssen & Taylor 1992; Houliston & Chapman 2004). Greater reproduction allocation means greater fitness. However, individuals allocating many resources to reproduction while competing with other plants will be at a disadvantage in competition. Therefore, the trade-off between growth and reproduction for small individuals suppressed by intense competition might be different from the trade-off experienced by large individuals experiencing less or no competition.

Shoot competition is generally size-asymmetric, while root competition is size-symmetric (Weiner 1990). Research on global patterns of plant height showed that species with a wide range of height strategies were present in cold, dry, low productivity systems (where root competition dominates), but there was a noticeable lack of very short species in wetter, warmer, more productive sites, where competition for light is very strong (Moles *et al.* 2009). This is evidence for the role of directional selection on plant height in environments where competition for light is strong. Our results support the hypothesis that shoot competition has a greater effect than root competition on plant community composition and diversity, even though competition below-ground can be as strong as above-ground (Lamb, Kembel & Cahill 2009; Kiær, Weisbach & Weiner 2013). Natural selection generated by asymmetric competition and mediated by reproductive allocation is a central process in the evolution of plant populations (Law, Marrow & Dieckmann 1997; Zu *et al.* 2008).

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References

Aarssen, L.W. & Taylor, D.R. (1992) Fecundity allocation in herbaceous plants. *Oikos*, **65**, 225–232.

Bonser, S.P. & Aarssen, L.W. (2001) Allometry and plasticity of meristem allocation throughout development in *Arabidopsis thaliana*. *Journal of Ecology*, **89**, 72–79.

Bonser, S.P. & Aarssen, L.W. (2003) Allometry and development in herbaceous plants: functional responses of meristem allocation to light and nutrient availability. *American Journal of Botany*, **90**, 404–412.

Bonser, S.P. & Aarssen, L.W. (2009) Interpreting reproductive allometry: individual strategies of allocation explain size-dependent reproduction in plant populations. *Perspectives in Plant Ecology, Evolution and Systematics*, **11**, 31–40.

Cahill, J.F. (2002) Interactions between root and shoot competition vary among species. *Oikos*, **99**, 101–112.

Cahill, J.F. (2003) Lack of relationship between below-ground competition and allocation to roots in 10 grassland species. *Journal of Ecology*, **91**, 532–540.

Cahill, J.F. & Casper, B.B. (1999) Growth consequences of soil nutrient heterogeneity for two old-field herbs, *Ambrosia artemisiifolia* and *Phytolacca americana*, grown individually and in combination. *Annals of Botany*, **83**, 471–478.

Cahill, J.F. & Lamb, E.G. (2007) Interactions between root and shoot competition and plant traits. *HortScience*, **42**, 1110–1112.

Caton, B.P., Foin, T.C. & Hill, J.E. (1997) Phenotypic plasticity of *Ammannia* spp. in competition with rice. *Weed Research*, **37**, 33–38.

Clauss, M.J. & Aarssen, L.W. (1994) Phenotypic plasticity of size-fecundity relationships in *Arabidopsis thaliana*. *Journal of Ecology*, **82**, 447–455.

Falster, D.S., Warton, D.I. & Wright, I.J. (2006) SMATR: standardised major axis tests and routines, verion 2.0 available at http://www.bio.mq.edu.au/ecology/SMATR/.

Grundy, A.C., Mead, A., Burston, S. & Overs, T. (2004) Seed production of *Chenopodium album* in competition with field vegetables. *Weed Research*, **44**, 271–281.

Houliston, G.J. & Chapman, H.M. (2004) Reproductive strategy and population variability in the facultative apomict *Hieracium pilosella* (Asteraceae). *American Journal of Botany*, **91**, 37–44.

Huhta, A.P., Tuomi, J. & Rautio, P. (2000) Cost of apical dominance in two monocarpic herbs, *Erysimum strictum* and *Rhinanthus minor*. *Canadian Journal of Botany*, **78**, 591–599.

Jolicoeur, P. (1989) A simplified model for bivariate complex allometry. *Journal of Theoretical Biology*, **140**, 41–49.

Kiær, L.P., Weisbach, A.N. & Weiner, J. (2013) Root and shoot competition: a meta-analysis. *Journal of Ecology*, **101**, 1298–1312.

Lamb, E.G., Kembel, S.W. & Cahill, J.F. (2009) Shoot, but not root, competition reduces community diversity in experimental mesocosms. *Journal of Ecology*, **97**, 155–163.

Lamb, E.G., Shore, B.H. & Cahill, J.F. (2007) Water and nitrogen addition differentially impact plant competition in a native rough fescue grassland. *Plant Ecology*, **192**, 21–33.

Law, R., Marrow, P. & Dieckmann, U. (1997) On evolution under asymmetric competition. *Evolutionary Ecology*, **11**, 485–501.

Li, W., Wen, S., Hu, W. & Du, G. (2011) Root-shoot competition interactions cause diversity loss after fertilization: a field experiment in an alpine meadow on the Tibetan Plateau. *Journal of Plant Ecology*, **4**, 138–146.

Liu, J., Wang, G.X., Wei, L. & Wang, C.M. (2008) Reproductive allocation patterns in different density populations of spring wheat. *Journal of Integrative Plant Biology*, **50**, 141–146.

Lovett Doust, L. (1989) Plant reproductive strategies and resource allocation. *Trends in Ecology & Evolution*, **4**, 230–234.

Mariotte, P., Buttler, A., Johnson, D., Thébault, A. & Vandenberghe, C. (2012) Exclusion of root competition increases competitive abilities of subordinate plant species through root-shoot interactions. *Journal of Vegetation Science*, **23**, 1148–1158.

Miller, G.E. (1991) Asymptotic test statistics for coefficients of variation. *Communications in Statistics – Theory and Methods*, **20**, 3351–3363.

Moles, A.T., Warton, D.I., Warman, L., Swenson, N.G., Laffan, S.W., Zanne, A.E., Pitman, A., Hemmings, F.A. & Leishman, M.R. (2009) Global patterns in plant height. *Journal of Ecology*, **97**, 923–932.

Newman, E.I. (1973) Competition and diversity in herbaceous vegetation. *Nature*, **244**, 310–311.

Nishimura, E., Suzaki, E., Irie, M., Nagashima, H. & Hirose, T. (2010) Architecture and growth of an annual plant *Chenopodium album* in different light climates. *Ecological Research*, **25**, 383–393.

Ohlson, M. (1988) Size-dependent reproductive effort in three populations of *Saxifraga hirculus* in Sweden. *Journal of Ecology*, **76**, 1007–1016.

Pfitsch, W.A. & Pearcy, R.W. (1992) Growth and reproductive allocation of *Adenocaulon bicolor* following experimental removal of sunflecks. *Ecology*, **73**, 2109–2117.

Ploschuk, E.L., Slafer, G.A. & Ravetta, D.A. (2005) Reproductive allocation of biomass and nitrogen in annual and perennial *Lesquerella* crops. *Annals of Botany*, **96**, 127–135.

Reekie, E.G. (1998) An explanation for size-dependent reproductive allocation in *Plantago major*. *Canadian Journal of Botany* **76**, 43–50.

Samson, D.A. & Werk, K.S. (1986) Size-dependent effects in the analysis of reproductive effort in plants. *American Naturalist*, **127**, 667–680.

Sugiyama, S. & Bazzaz, F.A. (1998) Size dependence of reproductive allocation: the influence of resource availability, competition and genetic identity. *Functional Ecology*, **12**, 280–288.

Suzuki, N. & Ohnishi, Y. (2006) Significance of the simultaneous growth of vegetative and reproductive organs in the prostrate annual *Chamaesyce maculata* (L.) Small (Euphorbiaceae). *Ecological Research*, **21**, 91–99.

Vega, C.R.C., Sadras, V.O., Andrade, F.H. & Uhart, S.A. (2000) Reproductive allometry in soybean, maize and sunflower. *Annals of Botany*, **85**, 461–468.

Wang, T.H. (2006) *The Study of Plant Phenotypic Plasticity and Life-history Strategies*. Northeast Normal University, Changchun, China.

Wang, P., Zhou, D.W. & Valentine, I. (2006) Seed maturity of harvest time affects seed quantity and quality of *Hordeum brevisubulatum*. *Seed Science and Technology*, **34**, 125–132.

Wang, P., Stieglitz, T., Zhou, D.W. & Cahill, J.F. Jr (2010) Are competitive effect and response two sides of the same coin, or fundamentally different? *Functional Ecology*, **24**, 196–207.

Warton, D.I., Wright, I.J., Falster, D.S. & Westoby, M. (2006) Bivariate line-fitting methods for allometry. *Biological Reviews*, **81**, 259–291.

Weiner, J. (1986) How competition for light and nutrients affects size variability in *Ipomoea Tricolor* populations. *Ecology*, **67**, 1425–1427.

Weiner, J. (1990) Asymmetric competition in plant populations. *Trends in Ecology & Evolution*, **5**, 360–364.

Weiner, J. & Thomas, S.C. (1992) Competition and allometry in three species of annual plants. *Ecology*, **73**, 648–656.

Weiner, J., Campbell, L.G., Pino, J. & Echarte, L. (2009) The allometry of reproduction within plant populations. *Journal of Ecology*, **97**, 1220–1233.

Wesselingh, R.A., Klinkhamer, P.G.L., De Jong, T.J. & Boorman, L.A. (1997) Threshold size for flowering in different habitats: effects of size-dependent growth and survival. *Ecology*, **78**, 2118–2132.

Wilson, S.D. & Tilman, D. (1993) Plant competition and resource availability in response to disturbance and fertilization. *Ecology*, **74**, 599–611.

Zhang, H.X., Zhou, D.W., Huang, Y.X., Japhet, W. & Sun, D.D. (2008) Plasticity and allometry of meristem allocation in response to density in three annual plants with different architectures. *Botany*, **86**, 1291–1298.

Zu, J., Wang, W., Takeuchi, Y., Zu, B. & Wang, K. (2008) On evolution under symmetric and asymmetric competitions. *Journal of Theoretical Biology*, **254**, 239–251.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Diagrammatic sketch of the block design.