

Research Article

Size-symmetric competition in a shade-tolerant invasive plant

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Abstract Plant responses to crowding have been investigated extensively in stands of light-demanding species, but shade-tolerant species may react differently. In the present study, we investigated the effect of density on the mortality, size inequality, and biomass allocation of *Alternanthera philoxeroides*, a shade-tolerant invasive species. Stem fragments of *A. philoxeroides* were grown at either low or high densities (6 vs. 24 plants per pot) under three light levels (10%, 34%, and 100% full sun). After 8 weeks, survival was 31% lower in pots with a higher initial density. Both high density and low light levels reduced plant size substantially. Mean plant biomass ranged from 0.23 g in high-density and low-light pots to 4.41 g in low-density and high-light pots. There were no strong or significant effects of density or light level on size inequality of survivors. Most of the variation in allocation and morphology in response to light level and crowding were due to plant size and allometric growth, with little evidence of true plasticity. There was a small but significant increase in shoot allocation, in the direction predicted by optimal allocation theory, at low light levels. Our results show that intense competition need not be size asymmetric, and suggest that tolerance to low light levels involves a reduction in phenotypic plasticity. Responses of the invasive *A. philoxeroides* to crowding may be an example of an invasive plant's success in establishing dense stands of closely related individuals that are shade tolerant, cooperative, and follow a relatively fixed allometric trajectory with low plasticity.

Key words allometry, *Alternanthera philoxeroides*, intraspecific competition, root:shoot ratio, shade tolerance, size inequality.

The effects of density on plant individuals and populations have been investigated extensively in the past (e.g., Harper, 1977; Antonovics & Levin, 1980; Keddy, 2001). Well-characterized responses to increased plant density include the reduction of mean individual biomass, increased mortality, and the development of size and reproductive inequalities among individuals (e.g. Weiner & Thomas, 1986; Schmitt et al., 1987). Competition for resources can be either size symmetric or asymmetric, and the degree of size asymmetry has major consequences for stand structure, population dynamics, and evolution. When competition is size symmetric, individuals obtain resources in proportion to their size; when competition is size asymmetric, larger individuals obtain a disproportionate share of the contested resources, growing more than smaller individuals and thus increasing size inequality among plants (Weiner et al., 1990). There is much evidence that competitive size asymmetry is due primarily to competition for light, because larger individuals shade smaller ones, but not vice versa (Schwinning & Weiner, 1998).

The modular construction of plants enables individuals to respond to crowding not only through changes in growth rates, but also through plastic changes in morphology and allocation patterns (Weiner, 2004). Many species respond to crowding with a suite of photomorphogenic changes, such as stem elongation, suppression of branching, altered biomass allocation, and accelerated flowering, commonly referred to as the “shade avoidance syndrome” (Smith, 1982). Such responses are often elicited by a change in the ratio of red to far-red light when shaded or from light reflected by neighboring plants before canopy closure, indicating that plants can detect and respond to potential future competitors before they are shaded directly (Ballaré et al., 1990). Within populations, these changes are usually dependent on an individual's ranking in a size hierarchy, with a higher relative elongation of “small suppressed” plants in relation to large “dominant” ones (Geber, 1989; Weiner et al., 1990; Berntson & Wayne, 2000).

Morphological and allocation responses to crowding have been investigated in stands of light-demanding species, but do shade-tolerant species behave in a similar way? Shade-tolerant plants generally have the ability to grow at low levels of light, so one may expect that the type of competition (e.g. symmetric vs.

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asymmetric) and the patterns of morphological and allocation responses to crowding may be different from those in light-demanding species. To our knowledge, the interplay of density, growth form, and size inequality has not yet been explored in shade-tolerant species. In addition, many exotic invasive plants can form dense, monospecific stands with high persistence (Arenas et al., 2002; Hager, 2004), where intraspecific competition for light may be generally intense. In the present study, we investigated the response patterns to crowding in the shade-tolerant invasive perennial *Alternanthera philoxeroides* (Mart.) Griseb. (alligator weed; Fig. 1). *Alternanthera philoxeroides* grows abundantly in habitats ranging from open waterways to shaded sites under dense vegetation (Longstreth & Mason, 1984; Pan, 2005). Although *A. philoxeroides* grows in open as well as shaded habitats, the claim that it is shade tolerant (Quimby & Kay, 1977; Gangstad, 1978; Longstreth et al., 1985; Timmins & Mackenzie, 1995) has been supported by substantial evidence (Pan, 2005; Shen et al., 2005; Bassetta et al., 2011).

In the present study we investigated the effects of density on the mortality, size inequality, and biomass allocation of *A. philoxeroides* under three light levels. An allometric approach is appropriate because the form and allocation patterns of most organisms change with size as they grow. Effects on biomass allocation that are solely due to size and allometric growth have been referred to as “apparent plasticity” (McConnaughay & Coleman, 1999; Weiner, 2004), whereas “true plasticity” implies a change in an allometric growth trajectory, not only the speed at which a single trajectory is followed.

We addressed three simple and fundamental questions:

1. How does size inequality within an *A. philoxeroides* population change in response to plant density under different light levels?



Fig. 1. Clonal dense population (A, B) and individual plants germinated on stem fragments (C) of *Alternanthera philoxeroides*.

2. How do allocation and morphology change in response to density under different light levels?
3. Are the changes consistent with the predictions of flexible optimal partitioning models (true plasticity) or simply size and allometric growth (apparent plasticity)?

1 Material and methods

1.1 Species

Alternanthera philoxeroides is a South American species that occurs in riparian zones and damp abandoned fields, where it often forms dense monospecific stands (Fig. 1). An individual clone can form a dense canopy up to 40–60 cm thick and 3–10 m in diameter (Pan, 2005). The ability of *A. philoxeroides* to establish and proliferate in diverse habitats is apparently related to its successful growth response under different light regimens (Longstreth & Mason, 1984; Pan, 2005).

In introduced regions, such as China, the US, and Australia, *A. philoxeroides* rarely produces viable seeds in the field and reproduces mainly through vegetative structures, such as stem and root fragments. As in the case of many aquatic and riverine plants, the stem and its fragments play important roles in the life history of *A. philoxeroides*: vegetative propagation facilitates its local dominance. Dispersal via stem fragments can contribute to long-distance dispersal along rivers and may be important in maintaining regional populations (Pan et al., 2009).

1.2 Experimental setup

The experiment was run from April to July 2004. We collected 3–5-mm diameter root fragments of *A. philoxeroides* (Fig. 1: C) in an abandoned field site in Zhuji (29.58N, 120.14E), Zhejiang, China. The roots were cut into fragments of 20 mm and germinated in the dark at 15–20 °C. After 2 weeks, we selected vigorous plantlets and transplanted them into plastic pots (20 cm diameter, 35 cm deep, ~10 L volume) containing 6.5 L of a 1:1 mixture of loamy soil and vermiculite in the greenhouse of the Faculty of Life Sciences, Fudan University, Shanghai, China. We applied 3 g/pot Peter’s Fertilizer (N:P:K = 20:20:20; Scotts Company, Marysville, OH, USA) after transplanting. The loose soil mixture compacted somewhat after repeated watering, lowering the soil surface to below half the pot height. Watering was performed by hand every other day to keep the soil mixture moist. Plants that died within the first week were replaced.

Subsequent mortality was considered an effect of the treatments.

In a factorial experiment, we assessed the effects of density (two levels) and light intensity (three levels) on the growth of *A. philoxeroides* populations. The densities were six and 24 plants per pot. These are equivalent to densities of 190 and 764 plants/m², respectively, which are typical of plants of *A. philoxeroides* growing in open habitats and riparian zones, respectively. The plants were arranged in a hexagonal pattern. Light levels were reduced from ambient with black fiberglass shade tents covered on all sides except the bottom. This type of tent was chosen in order to decrease light quantity without changing light quality. Mean (\pm SD) photon flux densities (400–700 nm) for the control (not shaded), medium (34% of control), and low (10% of control) light levels were 519 ± 310 , 175 ± 105 , and 54 ± 39 $\mu\text{mol}/\text{m}^2 \cdot \text{per s}$, respectively. The low light level was above the instantaneous light compensation point for photosynthesis of *A. philoxeroides* (Pan, 2005). There were three replicate pots for all treatments, giving a total of 260 individuals in 18 pots.

After 56 days growth, individual plants were harvested from each of the pots and the number of surviving plants per pot and the number of nodes per plant were counted. We used the node number per plant as a measure of the potential clonal reproductive output of *A. philoxeroides* (Dong et al., 2010). The length of the main stem (from the soil surface to the tip of the apical meristem) was also measured. Each plant was separated into three parts: leaves, stems, and roots. The leaf area of each plant was determined using an electronic planimeter (LI 3100; Li-Cor, Lincoln, NE, USA). In all cases, the dry mass of the three biomass compartments was oven dried at 70 °C for 48 h and weighed. We quantified size (plant dry weight and main stem length) inequalities among individuals by calculating the Gini coefficient (G) for each pot (Weiner & Solbrig, 1984), which is a measure of inequality with a minimum value of 0 when all individuals are equal and a theoretical maximum of 1.0, the ultimate in inequality. The Gini coefficient, G , is equal to half the relative mean difference; that is, the arithmetic average of the absolute values of the differences between all pairs of individuals (Sen, 1973):

$$G = \frac{\sum_{i=1}^n \sum_{j=1}^n |x_i - x_j|}{2n(n-1)x}$$

where x_i and x_j are individual dry mass, and n is sample size.

1.3 Statistical analyses

The effects of treatments on survival, total biomass per individual, total biomass per pot, total node number per pot, and G of the total biomass and stem length per individual were analyzed using ANOVA. Dependent variables, such as total biomass per individual and total biomass per pot, were log-transformed when necessary to conform to assumptions of normality and homogeneity of variance. Stem length was not transformed. To investigate the effects of density and light level on the pattern of allocation and growth, linear regressions (standard least square regressions) were fitted to the relationships between: (i) log root and log shoot biomass; (ii) log leaf area and log total biomass; (iii) log leaf area and log leaf biomass; (iv) stem length and log total biomass; and (v) node number and log total biomass. We analyzed the data using general linear models.

2 Results

2.1 Survival, biomass, and size inequality

The number of plants in the pots decreased over time. After 8 weeks, survival rates averaged 69% in the high-density pots ($F_{1,12} = 8.74$; $P = 0.012$; Fig. 2: A). The initial fourfold difference between the high- and the low-density pots (i.e. 24 vs. 6 plants per pot) was reduced to 2.8-fold by the end of the experiment (14 vs. 5 plants per pot). Plant survival was not affected by light level ($F_{2,12} = 0.06$; $P = 0.943$; Fig. 2: A) or an

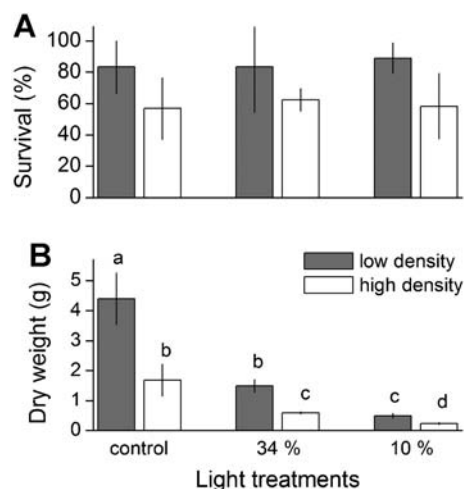


Fig. 2. Effects of density and light level on mean (\pm SE) values of (A) survival and (B) total biomass per individual of *Alternanthera philoxeroides*. Different letters indicate significant treatment differences (Tukey's HSD test).

interaction between density and light ($F_{2,12} = 0.10$; $P = 0.903$; Fig. 2: A).

Both density ($F_{1,12} = 42.04$; $P < 0.0001$) and light level ($F_{2,12} = 65.28$; $P < 0.0001$), and their interaction ($F_{2,12} = 13.84$; $P < 0.001$) had significant effects on total biomass per individual. High initial density and low light level reduced plant dry weight substantially (Fig. 2: B). Plant biomass was the lowest (0.23 g per plant) in high-density, low-light pots, and reached a maximum of 4.41 g per plant in low-density, high-light pots (Fig. 2: B).

Total biomass per pot was not affected by density ($F_{1,12} = 1.56$; $P = 0.235$; Fig. 3: A), but was reduced significantly by shading ($F_{2,12} = 339.86$; $P < 0.0001$; Fig. 3: A). The total number of nodes per pot increased at high density (+147%; $F_{1,12} = 39.14$; $P < 0.0001$; Fig. 3: B), but was not affected by shading ($F_{2,12} = 0.54$; $P = 0.596$; Fig. 3: B).

Sixty-eight percent of the variation in node number could be accounted for by variation in total biomass (Fig. 4: E). Neither density nor light level had a significant effect on the slope of the relationship. The inclusion of the two treatment factors in addition to log total biomass improved the explanatory power of the statistical model by 1.3%. Thus, the primary effects of the environment on the clonal reproductive output of *A. philoxeroides* occur via plant size.

There were no significant effects of light level or density on the Gini coefficients of stem length ($F_{1,12} = 0.31$, $P = 0.577$; and $F_{2,12} = 0.78$, $P = 0.347$, respectively) or dry weight ($F_{1,12} = 4.63$, $P = 0.069$; and $F_{2,12} = 0.06$, $P = 0.995$, respectively;

Fig. 5), but their interaction was close to significant ($F_{2,12} = 3.84$, $P = 0.067$ for stem length; $F_{2,12} = 3.92$, $P = 0.067$ for dry weight).

2.2 Allocation

Most of the variation (93%) in root biomass could be accounted for by variation in shoot biomass; Fig. 4: A). The least squares slope was significantly lower than 1 (95% confidence interval [CI] 0.78–0.88; $P < 0.01$). The effects of density and light level treatments accounted for an additional 3.4% of the variation. There was no significant difference between the low and high densities, but light treatments had a significant effect on the log root–log shoot relationship (Table 1). Plants at lower light levels allocated more biomass to shoots than those at higher light levels.

Over 96% of the variation in leaf area could be accounted for by variation in total biomass (Fig. 4: B) or leaf biomass (Fig. 4: C). The least squares slopes were significantly different from 1 (95% CI 0.85–0.91; $P < 0.01$). There were no significant effects of density or light treatments (Table 1).

Approximately 72% of the variation in stem length could be accounted for by variation in total biomass (Fig. 4: D). The effects of density and light level treatments accounted for an additional 9.5% of the variation. There were no significant effects of density or light treatments on the slope of the stem length–log total biomass relationship (Table 1).

3 Discussion

Two notable results of the present study are: (i) size inequality of *Alternanthera philoxeroides* does not increase significantly with density; and (ii) variation in allocation (root:shoot ratio, leaf area ratio [LAR], and specific leaf area [SLA]) and morphology (main stem length and node number) in response to crowding is almost solely due to allometric growth and variation in size (“apparent plasticity”).

3.1 Evidence for size-symmetric competition

Increased size inequality in populations grown at higher densities is commonly observed within plant populations (Schmitt et al., 1987) and is a result of size-asymmetric competition (Weiner & Thomas, 1986). Although plant competition is usually size asymmetric, size-symmetric competition has been observed when plants are grown for a very short time (Turner & Rabinowitz, 1983; Ramseier & Weiner, 2006), when competition occurs primarily (Stoll et al., 1994) or solely (von Wettberg & Weiner, 2003) below ground,

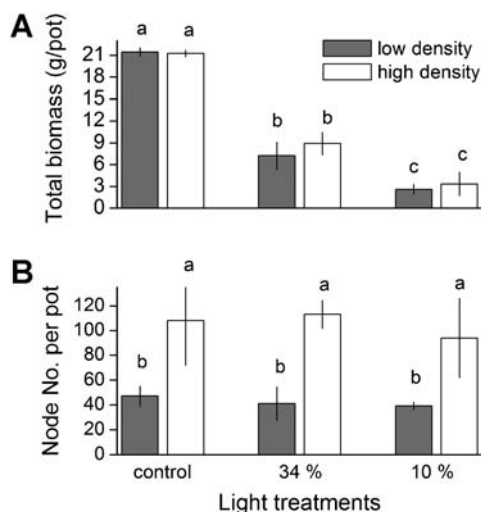


Fig. 3. Effects of density and light level on mean (\pm SE) values of (A) total biomass per pot and (B) total node numbers per pot of *Alternanthera philoxeroides*. Different letters indicate significant treatment differences (Tukey’s HSD test).

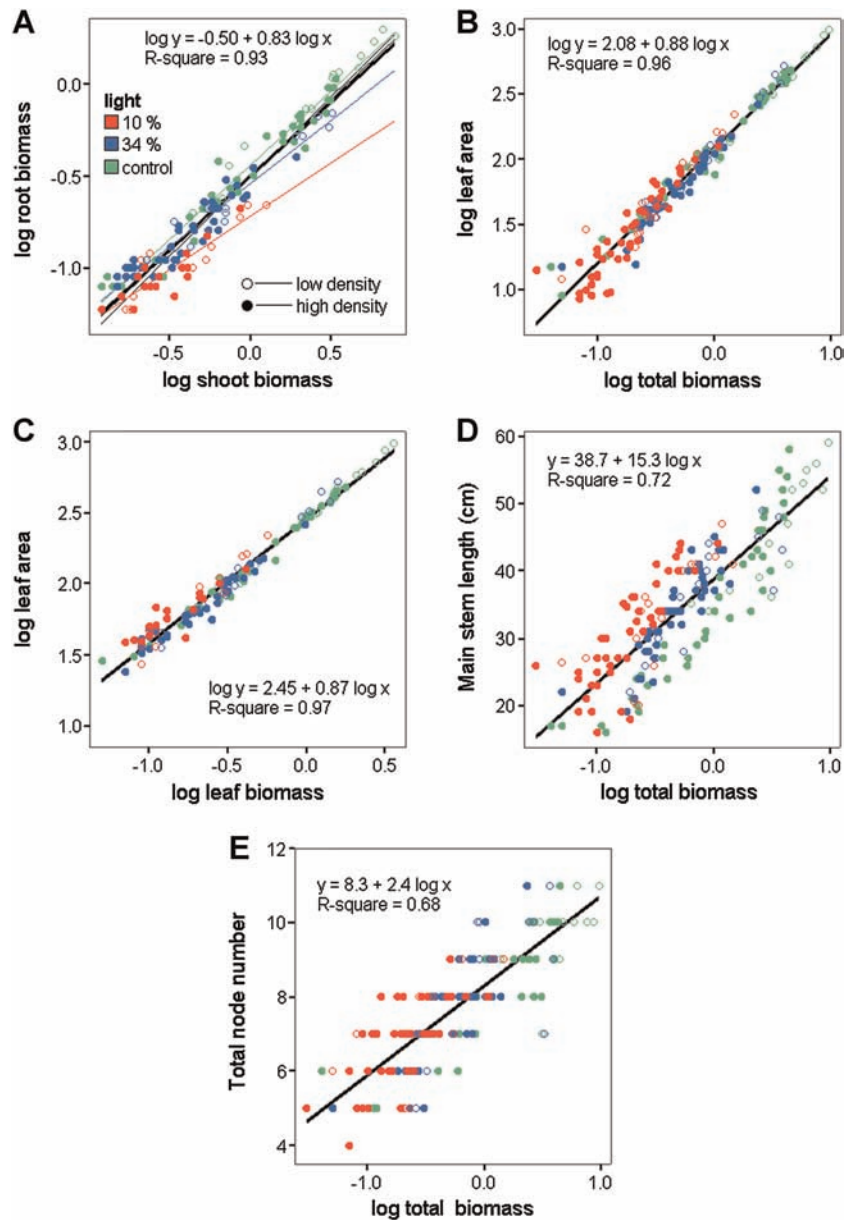


Fig. 4. Relationships between (A) root and shoot biomass, (B) leaf area and total biomass, (C) leaf area and leaf biomass, (D) main stem length and total biomass, and (E) total node number and total biomass of *Alternanthera philoxeroides* individuals grown at two density and three light levels. Least-squares regression lines for total plants are shown.

and when plants grow taller but not wider when competing (Ellison, 1987). Some of these patterns may be relevant here: (i) the experiment was relatively short and size-asymmetric competition may have developed later; (ii) the soil volume was small, so below ground competition, which is size symmetric, may have been much more important than competition for light; and (iii) crowded plant stems were able to spread out after they reached the top of the containers, thus reducing one-sided competition for light. It is also possible that the absence of evidence for size-asymmetric competi-

tion is due to a shortage of statistical power in our study or to mortality, which removed the smallest individuals, reducing inequality among survivors (Weiner & Thomas, 1986). A recent study on the effects of density and soil heterogeneity on *A. philoxeroides* also showed no increase in size variation at higher density (Zhou et al., 2012), suggesting that this result is not due to the specifics of our experimental set-up, insufficient statistical power, or mortality.

Another possible explanation for the absence of size-asymmetric competition in our experiment is kin

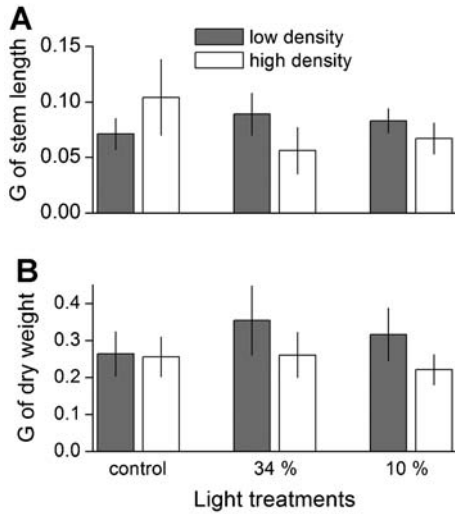


Fig. 5. Effects of density and light level on mean (\pm SE) values of the Gini coefficient, *G*, of (A) stem length and (B) total biomass per individual of *Alternanthera philoxeroides*.

selection for cooperation. *Alternanthera philoxeroides* is clonal, and it has been clearly shown that competition among ramets within a clone is controlled: clones are integrated to some degree, in part to reduce competition

among ramets (Lovett Doust, 1981; Alpert & Mooney, 1986), and this has been shown specifically for *A. philoxeroides* (Liu et al., 2008; Wang et al., 2008). Although individuals here were independent, individual ramets within a container may be behaving as if they are part of a single clone (Fig. 1). This could occur via kin selection in this clonal species if selection has favored individuals that “assume” that neighbors are close relatives or can recognize their own genotype (Biernaskie, 2011). An additional explanation for the absence of evidence for size-asymmetric competition in *A. philoxeroides* is that part of the stems that grew out of the pots under the less-crowded conditions (near pot edges) could support the growth of the stem parts grown under crowded conditions in the pots (i.e. in the pot center). This could reduce the effects of competition on the size variation of the plants. These hypotheses require testing in the future.

3.2 Plasticity versus allometric growth

In this shade-tolerant species, most of the variation in allocation (root:shoot ratio, LAR, and SLA) and morphology (main stem length and node number) resulting from differences in light level and crowding could be explained in terms of allometric growth and

Table 1 Results of general linear models for effects of density and light level on allometric relationships in *Alternanthera philoxeroides* populations grown at two densities and three light levels

Dependent variable	Source	d.f.	<i>F</i>	<i>P</i>	<i>r</i> ²
Log (root biomass)	D	1	2.18	0.142	0.933
	L	2	44.16	<0.001	
Covariate: log (shoot biomass)	D × L	2	0.46	0.636	
	D × log shoot	1	0.27	0.605	
	L × log shoot	2	7.30	0.001	
	D × L × log shoot	2	0.08	0.928	
	D	1	0.01	0.922	0.958
	L	2	0.78	0.459	
Log (leaf area)	D × L	2	1.39	0.251	
	D × log total	1	0.58	0.448	
	L × log total	2	0.09	0.917	
	D × L × log total	2	1.75	0.178	
	D	1	0.84	0.065	0.973
	L	2	0.44	0.643	
Covariate: log (leaf biomass)	D × L	2	1.06	0.072	
	D × log leaf	1	1.84	0.117	
	L × log leaf	2	0.91	0.404	
	D × L × log leaf	2	1.35	0.093	
	D	1	5.90	0.016	0.723
	L	2	13.83	< 0.001	
Main stem length	D × L	2	0.43	0.648	
	D × log total	1	1.59	0.209	
	L × log total	2	0.80	0.451	
	D × L × log total	2	0.78	0.462	
	D	1	0.12	0.726	0.685
	L	2	2.74	0.067	
Node number	D × L	2	0.04	0.965	
	D × log total	1	0.92	0.338	
	L × log total	2	1.78	0.171	
	D × L × log total	2	0.04	0.960	

Significant effects on slopes are shown in bold. D, density; L, light.

variation in size. In addition to these size-mediated effects, there were small (<4%) but significant additive effects of the light level on the partitioning of biomass between shoots and roots, and these were consistent with optimal partitioning models; that is, plants growing at lower light levels allocated more to shoots and less to roots than plants of the same size growing at higher light levels (Fig. 4: A). A previous study on root allocation in *A. philoxeroides* also showed that the growth rate of individuals was reduced at low light levels (30% full sun), but the ontogenetic trajectory remained unchanged (Geng et al., 2007), a phenomenon called “apparent plasticity” (McConnaughay & Coleman, 1999; Weiner, 2004). Similarly, density and soil heterogeneity affected size but not allocation patterns in *A. philoxeroides* (Zhou et al., 2012). We hypothesize that low plasticity may be advantageous or unavoidable for shade-tolerant species. Just as species that tolerate low nutrient conditions show little plasticity in growth rate (Chapin, 1980), so species that tolerate low light levels may show little plasticity in allometry in response to light. Shade avoidance (stem elongation in response to light quality; Ballaré & Scopel, 1997) and shade tolerance appear to be alternative strategies. Responses of the invasive *A. philoxeroides* to crowding may be an example of a shade-tolerant invasive plant’s success in establishing dense stands of closely related individuals that are cooperative and follow a relatively fixed allometric trajectory. Reduced plasticity may play a role in the success of shade tolerant invaders.

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