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Effects of soil substrate heterogeneity and moisture on interspecific competition between *Alternanthera philoxeroides* and four native species

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Abstract

Aims

Clonal plant species have the potential for high relative performance in heterogeneous environments, and this might increase the competitive ability and invasiveness of introduced clonal plant species. It was hypothesized that clonal species whose performance responds more to heterogeneity of a resource have higher competitive ability in habitats where this resource is more heterogeneous and that this relationship is stronger when other resources are less limiting.

Methods

To test these hypotheses, the perennial clonal herb *Alternanthera philoxeroides*, which is invasive in China, was grown alone or with each of four clonal perennial, co-occurring herbs native to China, i.e. *Alternanthera sessilis*, *Cynodon dactylon*, *Hemarthria altissima* and *Wedelia chinensis*. Plants were given homogeneous or heterogeneous soil substrate crossed with low and high levels of soil moisture.

Important Findings

Effects of heterogeneity on the accumulation of mass and ramets and on competitive effect and response of *A. philoxeroides* differed between native species and interacted with effects of soil moisture. *A. philoxeroides* reduced the final total mass or ramet number of the native species except *A. sessilis*, and the negative competitive effects on *H. altissima* and *C. dactylon* were more pronounced in heterogeneous than in homogeneous soil. Competitive response of *A. philoxeroides* was more negative to *A. sessilis* than to the other native species. Across native species, the competitive response of *A. philoxeroides* was more negative in heterogeneous than in homogeneous soils at low moisture level, but the reverse was true at high moisture level. Results do not consistently support either hypothesis, but do suggest that competitive ability can be partly explained by individual species traits such as size, and that some competitive effects and responses are emergent properties of interspecific interactions.

Keywords: alligator weed, clonal plant, competitive effect, competitive response, soil heterogeneity, soil moisture, foraging behavior.

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INTRODUCTION

Sessile plants have considerable ability to integrate fine-scale environmental heterogeneity by locating organs such as roots or leaves where levels of resources such as soil nutrients or light are high and by redistributing resources within the plant (de Kroon *et al.* 2005, 2009; Hutchings and John 2004; Hutchings *et al.* 2003). Plants with clonal growth, i.e. those that produce vegetative offspring (ramets) along stems or roots, can enhance this ability by locating offspring where resource availability is high and by translocating resources between connected ramets within a clone (Dong *et al.* 2015a, 2015b; He *et al.* 2011; Keser *et al.* 2014; Roiloa *et al.* 2014). The capacity to integrate resource patchiness in this manner, often referred to as foraging ability, differs between species, such that some plant species have higher foraging ability than others (Einsmann *et al.* 1999; Kembel and Cahill 2005; Keser *et al.* 2014; Wijesinghe *et al.* 2001).

The degree of heterogeneity of resources such as soil nutrients can affect the outcome of interspecific competition (Bliss *et al.* 2002; Day *et al.* 2003; Fransen *et al.* 2001; Mommer *et al.* 2011, 2012), and one consequence of high foraging ability could be high competitive ability in heterogeneous habitats. Although traits of individual species do not always predict relative competitive ability (Bellingham *et al.* 2004; Burns and Winn 2006; Goldberg 1996), pair-wise competitive interactions can be modeled from species traits in at least some systems (Gaudet and Keddy 1988; Susko and Cavers 2008; Yu *et al.* 2012). This suggests the hypothesis that clonal species that accumulate more mass or ramets in response to greater fine-scale environmental heterogeneity will have more negative competitive effects on other species and less negative competitive responses to other species in more heterogeneous habitats.

The effect of heterogeneity in availability of one resource is likely to interact with levels of other resources (García-Palacios *et al.* 2012; Maestre and Reynolds 2006, 2007). In particular, since intensity of competition for a resource in plants generally depends upon the degree to which the resource is limiting (Grover 1997), heterogeneity in one resource is more likely to affect competition between species if other resource levels are high. For example, low soil moisture might reduce ability to forage for nutrients (Hodge 2010; Neatrour *et al.* 2007). This suggests the additional hypothesis that the positive effect of resource heterogeneity on the competitive effect and response of clonal species that respond more positively to heterogeneity environments will be greater when other resource levels are higher.

These two hypotheses are of special interest in relation to introduced, invasive clonal species. Both competition and facilitation between introduced and native plants species can be important in biological invasions (Fridley *et al.* 2007; Mitchell *et al.* 2006). Some introduced clonal species become extremely abundant and widespread (Lu *et al.* 2013; Richards *et al.* 2012; Zhang *et al.* 2010), suggesting that they successfully outcompete native species. However, there is still only limited direct evidence for the role of competitive ability in invasions by introduced clonal plants, or for mechanisms that might underlie high competitive ability in invasive clonal plants.

A greenhouse experiment was therefore conducted to test these hypotheses using a well-studied, highly invasive, clonal species in China and a set of native clonal species with similar stature but with a range of growth forms and ecological distributions. The invasive species was *Alternanthera philoxeroides* (Mart.) Griseb., a perennial, amphibious herb in the Amaranthaceae native to South America and also one of the most invasive plant species in the world (Holm *et al.* 1977; Julien *et al.* 2012). *A. philoxeroides* produces creeping stems that root at the nodes, which thus function as ramets, occurs in wetlands, riparian habitats, grasslands and agricultural fields (Dong *et al.* 2012, 2015b; Julien *et al.* 2012; Xu *et al.* 2010), and exhibits high tolerance of disturbances such as herbivory, mowing and flooding (Geng *et al.* 2007; Lu *et al.* 2013; Xu *et al.* 2003). In southern China, *A. philoxeroides* has extremely low genetic diversity, and mainly relies on asexual reproduction; it spreads by means of stem or root fragments, and establishes extensive networks of connected ramets (Dong *et al.* 2015b; Gao *et al.* 2010; Xu *et al.* 2003).

It was specifically predicted that: (1) species would differ in the degree to which soil heterogeneity in substrate, especially in the availability of nutrients, promotes accumulation of mass and of ramets in the absence of competition; (2) when soil substrate was heterogeneous, the invasive species would have more negative competitive effects and less negative competitive responses to species that show less positive responses to heterogeneity and (3) relationships between soil substrate heterogeneity and growth or competitive ability would be more pronounced at high than at low soil moisture.

MATERIALS AND METHODS

The four native species selected were *Alternanthera sessilis* (L.) DC. (Amaranthaceae, with habit and ecological range similar to *A. philoxeroides*; Geng *et al.* 2006; Wu and Raven 2003), *Cynodon dactylon* (Linn.) Pers. (Poaceae, with both stolons and rhizomes, widespread in open habitats including disturbed or moderately dry areas; Dong and de Kroon 1994); *Hemarthria altissima* (Poir.) Stapf et C. E. Hubb. (Poaceae, with both stolons and rhizomes, found in riparian but also dry habitats; Luo *et al.* 2009); and *Wedelia chinensis* (Osbeck.) Merr. (Asteraceae, with ascending stolons; Wu and Raven 2011).

C. dactylon, *H. altissima* and *W. chinensis* are perennial (Dong and de Kroon 1994; Luo *et al.* 2009; Wu and Raven 2011). *A. sessilis* is mostly annual, but also biannual or perennial in some areas in southern China (Wu and Raven 2003). All four native species can produce viable seeds in the summer and autumn, and are widespread in provinces of southern China such as Zhejiang, Fujian, Guangdong, Sichuan and Yunnan. Distribution maps of the species are available at http://www.floraofchina.org.

A. philoxeroides was collected in Zhejiang Province in May 2011, *A. sessilis* and *W. chinensis* in Guangdong Province in the summer of 2009, and *C. dactylon* and *H. ltissima* in Sichuan Province in May 2011. All species were propagated vegetatively in a greenhouse at Forest Science Co., Ltd., of Beijing Forestry University in Beijing, China. Stem fragments of 15 cm long were cut from stock plants for use in the experiment. The initial dry mass (mg) of stolon fragments, determined by drying and weighing eight similar, additional fragments per species was (mean [SE]): *A. philoxeroides*—112 (14), *A. sessilis*—136 (8), *C. dactylon*—42 (2), *H. altissima*—70 (4) and *W. chinensis*—90 (9).

Each of the four native species was subjected to two levels of competition (without or with *A. philoxeroides*) crossed with two levels of soil substrate (heterogeneous or homogeneous) and with two levels of soil moisture (low and high), to give eight treatment combinations per species. In addition, *A. philoxeroides* was grown without competition at each of the four soil substrate and moisture treatment combinations. There were eight replicates of each treatment combination.

For the treatments without competition, a single stem fragment was planted in the center of a circular plastic pot that was 16 cm in diameter at the top, 12 cm in diameter at the bottom and 15 cm tall, and divided with plastic partitions into four equal quadrants. For the treatments with competition, one fragment of one of the native species and one of *A. philoxeroides* were planted in the center of the same pot at a distance of 1 cm from each other. In the heterogeneous soil treatment, two opposite quadrants of each pot were respectively filled with 400 ml of a 9:1 mixture of quartz sand (0.5–1 mm particle diameter) and commercial potting soil (Meishimei Bio-Tech Co. Ltd, Beijing, China), and the other two with 400 ml of a 1:9 mixture of quartz and potting soil; nutrient content of the mixtures is reported in Dong *et al.* (2015a). The partitions dividing quadrants were removed after the pot had been filled. In the homogeneous soil treatments, each pot was filled in the same way, but the soil was then thoroughly mixed after removing the partitions. Total amounts of soil nutrients and soil substrate per pot were thus the same in both soil substrate treatments.

For the high soil moisture treatment, pots were kept at field capacity, or 40% volumetric water content (i.e. volume fraction of soil water). For the low soil moisture treatment, pots were kept at one half of field capacity, or 20%. Field capacity was defined as water content of soil that is saturated and then allowed to drain by gravity (Kirkham 2014). Soil moisture level was measured on the basis of soil moisture velocity (TZS-1, Zhejiang Top Instrument Co. Ltd., China) and adjusted as needed by adding tap water.

A randomized block design was used in the experiment. Fragments of each species were ordered by size and assigned to blocks such that the first block contained the largest fragments, the second block was the second largest and so on. Each block contained one replicate of each species by competition by heterogeneity by moisture treatment. Blocks were arranged randomly in a single array in the greenhouse and left in the same position throughout the experiment.

The experiment began on 3 September 2014 and ended after 10 weeks, on 16 November 2014. During the experiment, the mean temperature in the greenhouse was 18.1 ± 0.5°C (mean [SE]) (iButton DS1923; Maxim Integrated Products, Sunnyvale, CA, USA). Temperature during the experiment was unlikely to have been optimal for growth of all the species, but was well above the minimal temperatures for stem and leaf growth (Zhang *et al.* 2006). Another caveat is that the duration of the experiment was only designed to show the short-term effects of water availability and nutrient heterogeneity on competitive ability of *A. philoxeroides*.

At harvest, each fragment was measured for number of ramets, total stolon length and total leaf area (WinFOLIA Pro2004a, Regent Instruments, Québec, Canada), and then divided into roots, stems and leaves, dried at 70°C for 48 h, and weighed. Competitive effect and response were measured as log response ratios, LnRR = Ln (P_w/ P_o), where P_w is total dry mass or number of ramets of a species per pot with competition and P_o is mass or ramets without competition; replicates were generated using blocks (Armas *et al.* 2004; Hedges 2008). The distribution of LnRR is symmetrical around zero, with negative values indicating competition and positive values indicating facilitation (Armas *et al.* 2004; Hedges 2008). Log response ratio was also used to measure response of each species based on total mass or ramet number to soil substrate heterogeneity in the absence of competition, LnRR = Ln (value in the heterogeneous treatment/value in the homogeneous treatment).

ANOVAs were used to test for effects of species, soil heterogeneity, and water capacity (fixed effects) plus a block effect on the competitive effect and response of *A. philoxeroides* and on response to soil substrate heterogeneity in the absence of competition as measured by total dry final mass or number of ramets (Quinn and Keough 2002). Similar ANOVAs were used to test effects on final total dry mass and number of ramets of four native species. Differences between individual means were tested with linear contrasts. Differences of individual means from zero were tested with *t*-tests. All analyses were conducted with SPSS 22.0 (SPSS, Chicago, IL, USA).

RESULTS

In the absence of competition, responses to soil heterogeneity differed between species, as measured both by final total dry mass and by final number of ramets (Fig. 1, Table 1). *H. altissima* showed a positive response to heterogeneity at low soil moisture and, as measured by number of ramets, at high soil moisture. *A. sessilis* responded positively to heterogeneity at high but not at low soil moisture. Other species showed no consistent pattern of either positive or negative response to heterogeneity. Soil moisture had no overall effect on responses to heterogeneity.

A. philoxeroides had negative competitive effects on all of the native species, that is, reduced their final total mass or ramet number, except *A. sessilis* (Fig. 2, Table 2). Effects on some but not all species were more negative in heterogeneous than in homogeneous soils. This was true for the effect on *H. altissima* and *C. dactylon* at high soil moisture but not for the effect on *W. chinensis*.

Competitive response of *A. philoxeroides* was more negative to *A. sessilis* than to the other native species (Fig. 3, Table 3). This mirrored the pattern of competitive effect, which was less negative on *A. sessilis* than on other species (Fig. 2). Other patterns of competitive response showed little relation to

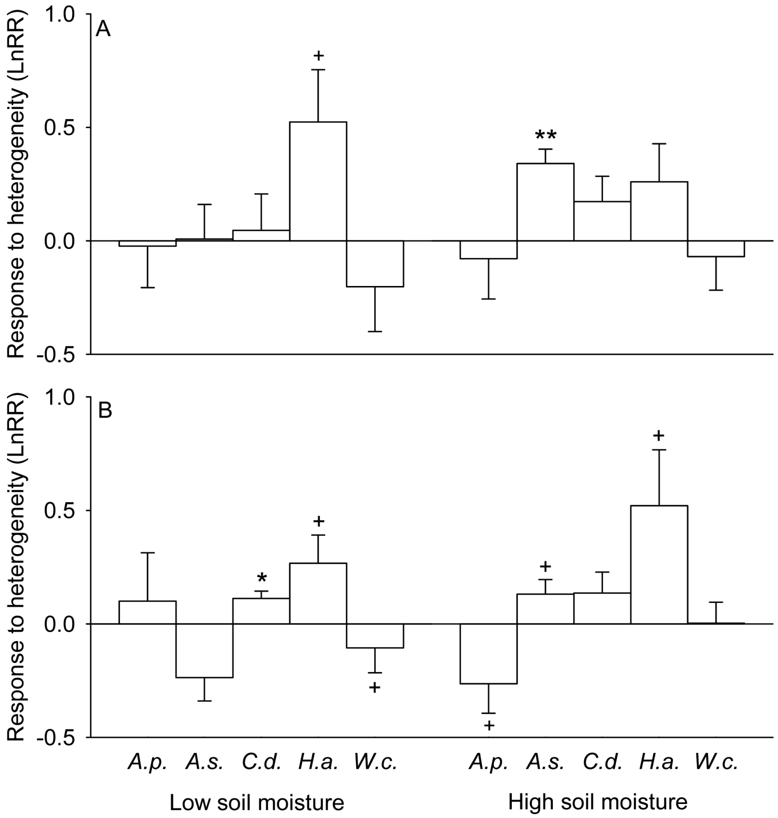

Figure 1: response of study species to soil heterogeneity at two levels of soil moisture in the absence of competition. Bars show mean log response ratio (+ SE) of final (**A**) total dry mass and (**B**) number of ramets in heterogeneous and homogeneous treatments; positive values indicate greater growth in heterogeneous than in homogeneous soil. Symbols show probability that ratio did not differ from zero: (no symbol) > 0.1; + 0.05–0.1; * 0.01–0.05; ** 0.001–0.01. Species are: *A.p.* - *Alternanthera philoxeroides*; *A.s.* - *A. sessilis*; *C.d.* - *Cynodon dactylon*; *H.a.* - *Hemarthria altissima*; *W.c.* - *Wedelia chinensis*. See Table 1 for ANOVAs.

Table 1: ANOVAs for effects of species and soil moisture on response to soil heterogeneity in the absence of competition as measured by log response ratio of final total dry mass or number of ramets

		Biomass		Number of ramets	
	df	*F*	*P*	*F*	*P*
Block	7,63	0.87	0.53	1.13	0.36
Species (S)	4,63	**3.07**	**0.023**	**4.44**	**0.003**
Moisture (M)	1,63	0.27	0.61	0.84	0.36
S × M	4,63	0.91	0.46	2.17	0.083

Values where $P < 0.05$ are in bold.

competitive effect. For instance, as measured by final number of ramets but not by final total dry mass, competitive response was more negative at high than at low soil moisture. At high soil moisture, overall competitive response of *A. philoxeroides* across native species was more negative in homogeneous than in heterogeneous soils. At low soil moisture, the reverse was true and competitive response was even positive in some instances in homogeneous soils.

Competitive response of *A. philoxeroides* was not predicted by its growth in the absence of competition (Fig. 4, Table 4). When grown alone, *A. philoxeroides* accumulated more mass and ramets at high than at low soil moisture. However, competitive response in terms of ramet number was more negative at higher soil moisture (Fig. 3, Table 3). When grown alone at high moisture, *A. philoxeroides* produced more ramets in homogeneous than in heterogeneous soil (Fig. 4, Table 4). At high soil moisture, competitive response was still more negative in homogeneous than in heterogeneous soil (Fig. 3, Table 3).

Competitive effect of *A. philoxeroides* was partly predicted by the growth of the native species in the absence of competition (Fig. 5). *A. sessilis*, the only native species that showed no negative competitive effect of *A. philoxeroides*, also accumulated the most final dry mass in the absence of competition, about 1.3 g per pot across water and heterogeneity treatments. *C. dactylon* accumulated the least mass of any species in the absence of competition, about 0.2 g. However, *C. dactylon* did not show more negative competitive effects than *H. altissima*, which accumulated about 0.7 g final dry mass in the absence of competition, or *W. chinensis*, which accumulated about 0.8 g.

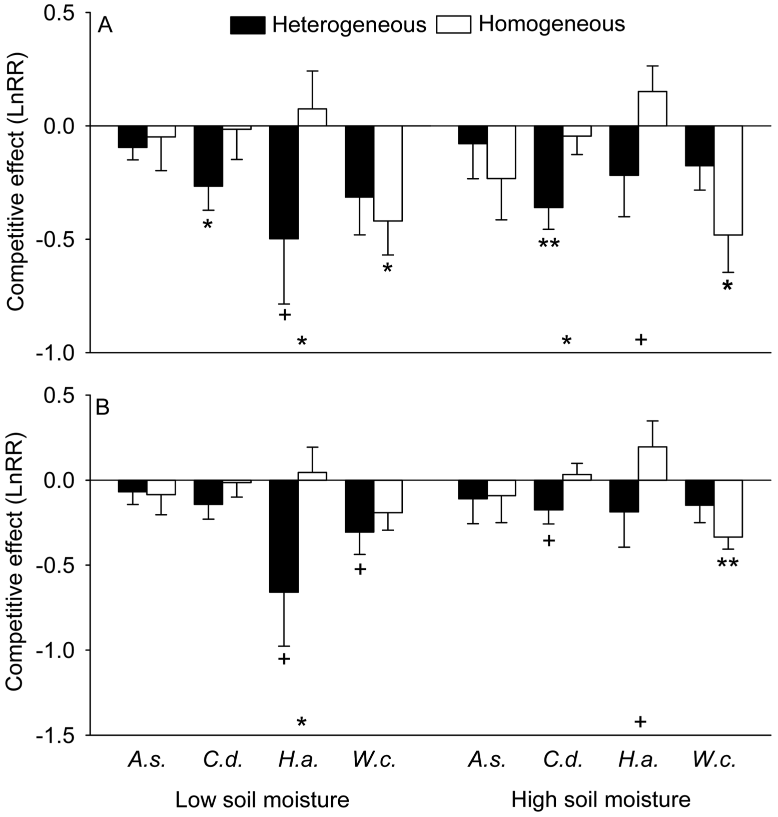

Figure 2 : competitive effect (log response ratio, mean + SE) of *Alternanthera philoxeroides* on four native species in heterogeneous or homogeneous soils at two levels of soil moisture based on final (**A**) total dry mass and (**B**) number of ramets; negative values indicate lower growth in the presence than in the absence of *A. philoxeroides*. Symbols by individual bars show probability that effect did not differ from zero: (no symbol) > 0.1; + 0.05–0.1; * 0.01–0.05; ** 0.001–0.01. Symbols below pairs of pairs show probability that effect did not differ between heterogeneous and homogeneous soils. Species are: *A.s.* - *Alternanthera sessilis*; *C.d.* - *Cynodon dactylon*; *H.a.* - *Hemarthria altissima*; *W.c.* - *Wedelia chinensis*. See Table 2 for ANOVAs.

Table 2: ANOVAs for effects of species, soil moisture and soil substrate heterogeneity on competitive effect of *Alternanthera philoxeroides* on four native species

		Biomass		Number of ramets	
	df	*F*	*P*	*F*	*P*
Block	7,104	**3.83**	**0.001**	1.70	0.12
Species (S)	3,104	2.69	0.05	1.13	0.34
Moisture (M)	1,104	0.23	0.63	0.86	0.36
Heterogeneity (H)	1,104	2.18	0.14	**6.73**	**0.011**
S × M	3,104	1.14	0.34	0.90	0.44
S × H	3,104	**3.94**	**0.01**	**4.12**	**0.008**
M × H	1,104	1.45	0.23	1.09	0.30
S × M × H	3,104	0.36	0.78	0.75	0.53

Values where $P < 0.05$ are in bold. See Fig. 2 for data.

Final mass and number of ramets of individual native species showed some effects of soil heterogeneity and moisture across competition treatments (Fig. 5, Table 5). *A. sessilis* accumulated more mass and ramets at higher soil moisture if soil nutrients were heterogeneous. *W. chinensis* also showed a larger response of ramet production to soil moisture in heterogeneous than in homogeneous soils, and accumulated more mass and ramets at higher soil moisture in both homogeneous and heterogeneous soils.

DISCUSSION

As expected, species differed in the degree to which their performance increased with greater soil nutrient heterogeneity (Hodge 2010; Johnson and Biondini 2001; Kembel and Cahill 2005). In addition, the competitive effect of *A. philoxeroides* on some native species was greater in heterogeneous than in homogeneous soils. However, there was no evident relationship between the response to heterogeneity in the absence of competition and the interaction between heterogeneity and competitive effect or response (Robinson *et al.* 1999). Two native species (*A. sessilis* and *H. altissima*) produced more mass or ramets in heterogeneous than in homogeneous soils. *A. philoxeroides* had little competitive effect on *A. sessilis*, and its competitive effect on *H. altissima* was greater rather than smaller in heterogeneous than in homogeneous

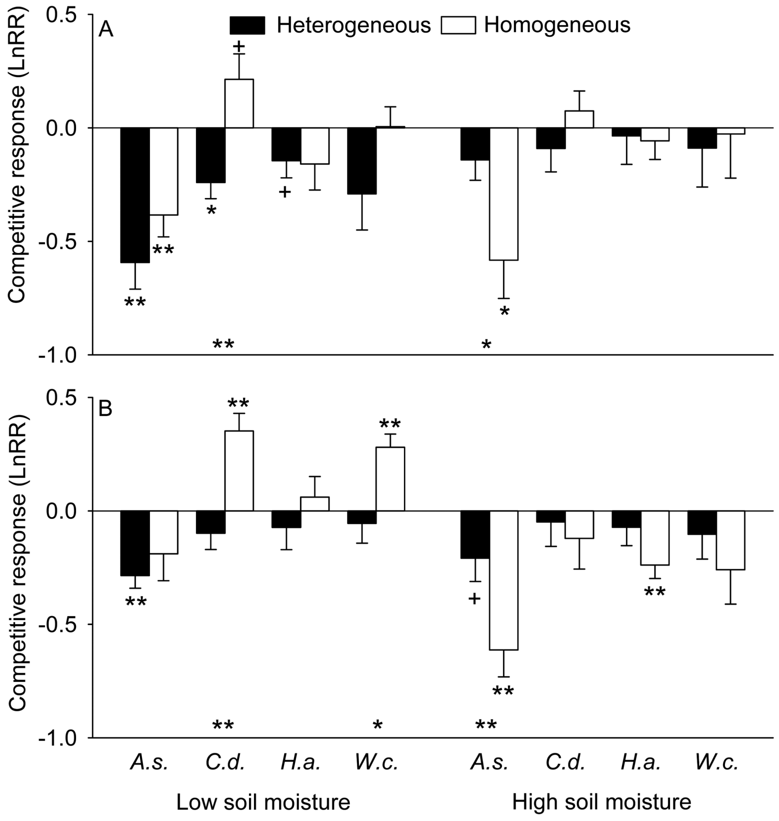

Figure 3: competitive response (log response ratio, mean + SE) of *Alternanthera philoxeroides* to four native species in heterogeneous or homogeneous soils at two levels of soil moisture based on final (**A**) total dry mass and (**B**) number of ramets; negative values indicate lower growth in the presence than in the absence of *A. philoxeroides*. Symbols by individual bars show probability that effect did not differ from zero: (no symbol) > 0.1; + 0.05–0.1; * 0.01–0.05; ** 0.001–0.01. Symbols below pairs of pairs show probability that effect did not differ between heterogeneous and homogeneous soils. Species are: *A.s.* - *Alternanthera sessilis*; *C.d.* - *Cynodon dactylon*; *H.a.* - *Hemarthria altissima*; *W.c.* - *Wedelia chinensis*. See Table 3 for ANOVAs.

Table 3: ANOVAs for effects of species, soil moisture and soil substrate heterogeneity on competitive response of ***Alternanthera philoxeroides*** **to four native species**

		Biomass		Number of ramets	
	df	*F*	*P*	*F*	*P*
Block	7,104	**3.27**	**0.004**	**4.30**	**<0.001**
Species (S)	3,104	**10.58**	**<0.001**	**11.88**	**<0.001**
Moisture (M)	1,104	2.13	0.15	**20.42**	**<0.001**
Heterogeneity (H)	1,104	2.57	0.11	0.50	0.48
S × M	3,104	0.23	0.88	0.37	0.78
S × H	3,104	**2.95**	**0.036**	**2.84**	**0.042**
M × H	1,104	**6.68**	**0.011**	**24.62**	**<0.001**
S × M × H	3,104	1.42	0.24	0.32	0.81

Values where $P < 0.05$ are in bold. See Fig. 3 for data.

soil. Competitive responses of *A. philoxeroides* to *A. sessilis* and *H. altissima* were similar or less negative, rather than more negative, in heterogeneous than in homogeneous soil. Results thus did not support the hypothesis that clonal species that accumulate more mass or ramets in response to greater fine-scale environmental heterogeneity will have more negative competitive effects on other species and less negative competitive responses to other species in more heterogeneous habitats (Bliss *et al.* 2002; Mommer *et al.* 2012; Robinson *et al.* 1999).

Some relationships between soil heterogeneity and plant growth or competitive ability were more pronounced at high than at low soil moisture. In the absence of competition, final mass and ramet number of *A. sessilis* were higher and ramet number of *A. philoxeroides* was lower in heterogeneous than in homogeneous soil at high but not at low soil moisture. However, the competitive effects of *A. philoxeroides* on the four native clonal species showed no overall interactive effect of heterogeneity and moisture. Results thus did not clearly support the hypothesis that the positive effect of resource heterogeneity on the competitive effect and response of clonal species that respond more positive to heterogeneity environments will be greater when other resource levels are higher (García-Palacios *et al.* 2012; Maestre and Reynolds 2006, 2007).

The competitive responses of *A. philoxeroides* to the four native clonal species showed an unexpected interactive effect

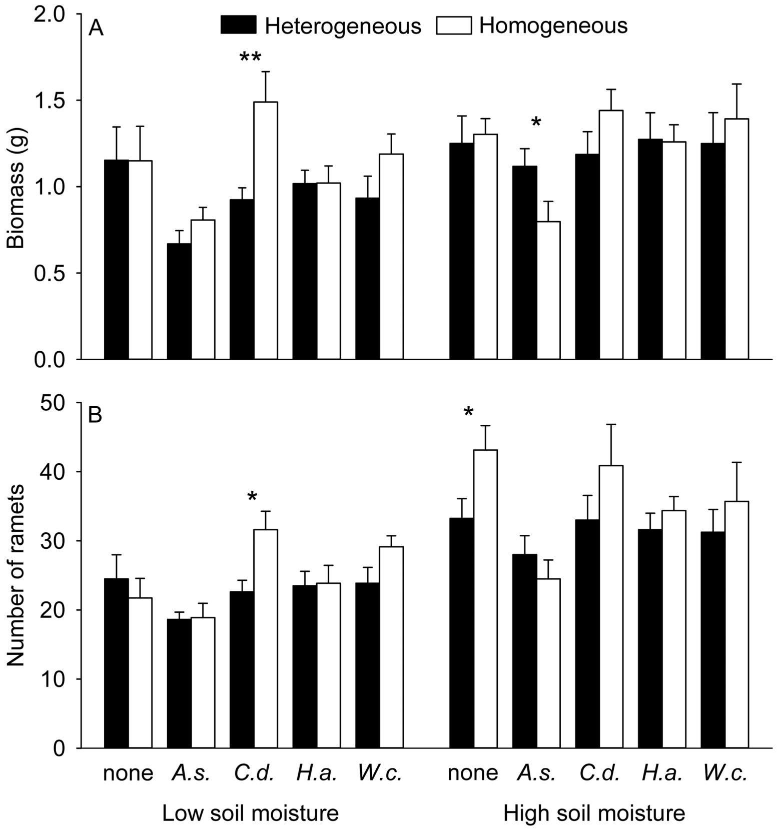

Figure 4: effects of soil heterogeneity, soil moisture and competition with native species on mean (A) final total dry mass and (**B**) number of ramets of *Alternanthera philoxeroides*. Error bars show SE. Symbols show probability that means did not differ between heterogeneity treatments: (no symbol) > 0.1; + 0.05–0.1; * 0.01–0.05; ** 0.001–0.01.

Table 4: ANOVA for effects of soil moisture, soil heterogeneity and competition (without, or with each of four native species) on final mass and number of ramets of *Alternanthera philoxeroides*.

		Biomass		Number of ramets	
	df	*F*	*P*	*F*	*P*
Block	7,132	4.47	<0.001	4.38	<0.001
Moisture (M)	1,132	**11.99**	**0.001**	**60.99**	**<0.001**
Heterogeneity (H)	1,132	3.77	0.054	**7.57**	**0.007**
Competition (C)	4,132	**7.04**	**<0.001**	**7.08**	**<0.001**
M × H	1,132	2.32	0.13	0.68	0.41
M × C	4,132	0.33	0.86	1.21	0.31
H × C	4,132	**2.60**	**0.039**	1.84	0.13
M × H × C	4,132	0.74	0.56	1.26	0.29

Values where $P < 0.05$ are in bold. See Fig. 4 for data.

of soil heterogeneity and moisture: competitive response across native species was more negative in heterogeneous than in homogeneous soil at low soil moisture and more negative in homogeneous than in heterogeneous soil at high soil moisture. This did not correspond to the effects of heterogeneity and moisture on growth of *A. philoxeroides* in the absence of competition, where heterogeneity had little effect at low soil moisture and a marginally negative effect at high soil moisture. It does show that the response to heterogeneity of one resource can depend upon and even be reversed by the level of availability of a different resource and may be an example of an emergent property of species interactions (García-Palacios *et al.* 2012), where the effects of environmental factors on competition cannot be predicted from their effects on the growth of species individual (Fransen *et al.* 2001; Mommer *et al.* 2012).

Performance of species in the absence of competition did predict competitive effect or response in some cases (Yu *et al.* 2012). For example, the native species with the largest initial dry mass and the largest final dry mass and ramet number (*A. sessilis*) was the only species to show little negative competitive effect of *A. philoxeroides* and also the species to which *A. philoxeroides* showed the most negative competitive response. Relative size is often if not always a strong predictor of the relative competitive ability of species, at least when species have similar growth form (Gaudet and Keddy 1988; Susko and Cavers 2008). In this case, the apparent competitive superiority of *A. sessilis* to *A. philoxeroides* does not match their relative abundances in China, since *A. philoxeroides* is much more widespread and locally abundant (Geng *et al.* 2006, 2007; Pan *et al.* 2006).

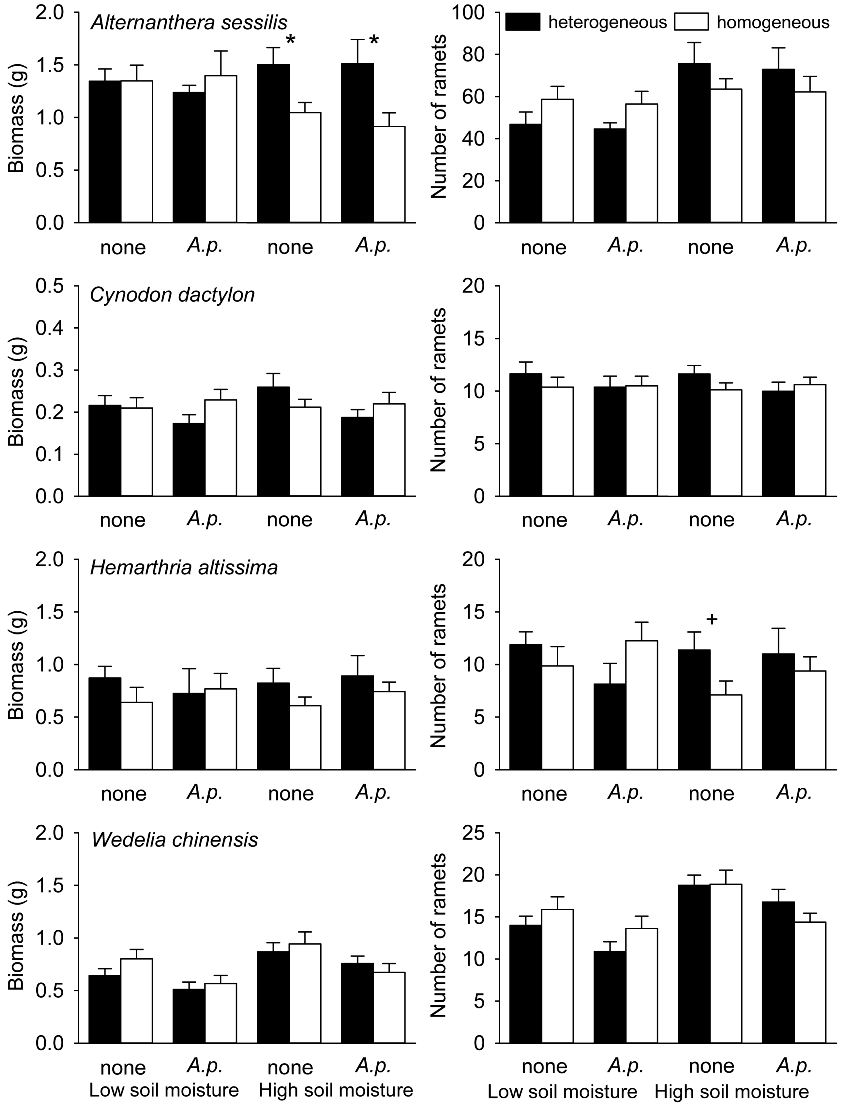

Figure 5: effects of soil heterogeneity, soil moisture and competition with *Alternanthera philoxeroides* on mean final total dry mass and number of ramets of native species. Error bars show SE. Symbols show probability that means did not differ between heterogeneity treatments: (no symbol) > 0.1; + 0.05–0.1; * 0.01–0.05. 'None' indicates that the target species was grown alone; '*A.p.*' indicates that the target species was grown with *A. philoxeroides*.

Previous studies have attempted to correlate plant attributes with the invasive success of *A. philoxeroides* in the introduced region (Dong *et al.* 2015b; Geng *et al.* 2007; Gao *et al.* 2010; Schooler *et al.* 2010). For example, unlike *A. sessilis*, *A. philoxeroides* is perennial throughout its range and possesses more rapid sprouting of clonal fragments after disturbances such as flooding and after winter frost (Chen *et al.* 2013; Liu *et al.* 2009). High phenotypic plasticity may also favor *A. philoxeroides* (Geng *et al.* 2007), e.g. *A. philoxeroides* increases specific leaf area under shaded conditions, elongates internodes in anoxic aquatic environments (Chen *et al.* 2013), and allocates more biomass to storage roots in response to aboveground disturbance (Geng *et al.* 2007; Jia *et al.* 2009). Over longer periods than tested in this study, such traits may compensate for the short-term competitive disadvantage found here, thereby leading to the invasion success in a wide range of habitats.

In sum, our results provide additional evidence for variation between clonal plant species in response to environmental heterogeneity (Hutchings *et al.* 2003; Keser *et al.* 2014) and new evidence that effects of heterogeneity can interact with other environmental factors in unexpected ways (García-Palacios *et al.* 2012; Maestre and Reynolds 2006, 2007). Results also strengthen the conclusion that some outcomes of competition can be predicted from the traits of individual species (Yu *et al.* 2012) but that other outcomes depend upon traits that emerge from interactions between species (Day *et al.* 2003; Fransen *et al.* 2001; Mommer *et al.* 2012).

Table 5: ANOVAs for effects of soil moisture, soil heterogeneity and competition with *Alternanthera philoxeroides* on final mass and ramets of four native species

		Biomass		Number of ramets	
	df	*F*	*P*	*F*	*P*
Alternanthera sessilis					
Block	7,49	2.95	0.012	**6.90**	**<0.001**
Moisture (M)	1,49	2.09	0.154	**17.16**	**<0.001**
Heterogeneity (H)	1,49	**6.29**	**0.016**	0.37	0.545
Competition (C)	1,49	0.81	0.372	0.45	0.506
M × H	1,49	**7.55**	**0.008**	**7.91**	**0.007**
M × C	1,49	0.19	0.666	0.04	0.838
H × C	1,49	0.14	0.715	0.04	0.844
M × H × C	1,49	0.51	0.480	<0.01	0.993
Cynodon dactylon					
Block	7,49	1.61	0.155	0.83	0.572
Moisture (M)	1,49	0.86	0.357	0.01	0.960
Heterogeneity (H)	1,49	0.15	0.699	0.53	0.470
Competition (C)	1,49	2.93	0.093	0.91	0.346
M × H	1,49	0.63	0.430	0.02	0.888
M × C	1,49	0.22	0.643	<0.01	0.972
H × C	1,49	3.48	0.068	2.19	0.146
M × H × C	1,49	0.02	0.956	0.12	0.729
Hemarthria altissima					
Block	7,49	**8.69**	**<0.001**	**3.13**	**0.008**
Moisture (M)	1,49	0.93	0.339	0.33	0.568
Heterogeneity (H)	1,49	1.85	0.180	0.25	0.618
Competition (C)	1,49	0.22	0.640	0.01	0.913
M × H	1,49	0.03	0.870	3.38	0.072
M × C	1,49	0.66	0.421	1.40	0.242
H × C	1,49	**4.91**	**0.031**	**6.45**	**0.014**
M × H × C	1,49	1.86	0.179	0.74	0.394
Wedelia chinensis					
Block	7,49	1.94	0.083	**4.50**	**0.001**
Moisture (M)	1,49	**9.37**	**0.004**	**19.22**	**<0.001**
Heterogeneity (H)	1,49	0.43	0.515	0.81	0.374
Competition (C)	1,49	**10.04**	**0.003**	**13.27**	**0.001**
M × H	1,49	1.26	0.267	**4.56**	**0.038**
M × C	1,49	0.13	0.724	0.04	0.847
H × C	1,49	0.73	0.397	<0.01	0.998
M × H × C	1,49	0.15	0.701	1.39	0.244

Values were log-transformed before analysis. Values where $P < 0.05$ are in bold.

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