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Shifts in growth and competitive dominance of the invasive plant *Alternanthera philoxeroides* under different nitrogen and phosphorus supply

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ABSTRACT

The availability of nitrogen and phosphorus is an important factor determining the growth and competitive dominance of invasive plants. To clarify the influence of nutrient availability on the performance of alien species, we conducted a greenhouse experiment in which the invasive plant *Alternanthera philoxeroides* was planted as a monoculture or in mixed culture with noninvasive species (*Oenanthe javanica* or *Iris pseudacorus*) under combined conditions of various nutrient level (low, medium, and high) and N/P ratio (1, 10, and 100). Nutrient level and N/P ratio both affected the growth of *A. philoxeroides* and the effects were similar in mixed culture and monoculture. Increased nutrient level significantly increased the total biomass and total stolon length of *A. philoxeroides* under all N/P ratios. At low nutrient level, N/P ratio had little influence on the total biomass and total stolon length of *A. philoxeroides*. At medium and high nutrient levels, however, increased N/P ratios inhibited the growth of *A. philoxeroides*. Nutrient level rather than N/P ratio affected the relative dominance index (RDI) of *A. philoxeroides*, with increased nutrient levels enhancing the competitive dominance of *A. philoxeroides*. Furthermore, the RDI of *A. philoxeroides* in mixed culture with *I. pseudacorus* was consistently higher than that of *A. philoxeroides* when grown with *O. javanica*. Therefore, our results indicate that nutrient enrichment (such as over-fertilization and eutrophication) would aggravate the already serious impact of biological invasions and that the identity of resident plant species might also affect the competitive dominance of exotic plants.

1. Introduction

Invasions of alien species, which have profound impacts on invaded habitats, have become severe problems in many ecosystems (Mack et al., 2000; Suding et al., 2004; Liu et al., 2006). Although ecologists have proposed several hypotheses to explain the mechanisms underlying the invasiveness of exotic species, such as the biotic resistance hypothesis (Levine and D'Antonio, 1999), the enemy release hypothesis (Keane and Crawley, 2002) and the propagule pressure hypothesis (Lockwood et al., 2005), there is still no consensus on invasion mechanisms (Jeschke, 2014). Undoubtedly, however, resource (such as nutrients) availability is an important factor that determines the invasive capacity of alien plants (González et al., 2010; Yuan et al., 2013). In this regard, increased resource availability can strengthen interspecific competition and facilitate the success of plant invasion (Blumenthal et al., 2009; Holdredge et al., 2010; Baribault and Kobe, 2011; Chisholm et al., 2015).

The availability of nitrogen (N) and phosphorus (P), in terms of both nutrient level (N and P content) and N/P ratio, not only has profound impacts on plant growth but also influences interspecific competition in invaded habitats (Güsewell and Bollens, 2003; Güsewell, 2004; Suding et al., 2004; Baribault and Kobe, 2011; Yuan et al., 2013). Nutrient level and N/P ratio have heterogeneous

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distributions in nature and often change as a result of deposition, pollution discharge and fertilizer loss from farmland, particularly in areas characterized by disturbance (Peršić et al., 2009; Lapointe and Bedford, 2011; Li et al., 2016). It is accordingly important to elucidate the pattern of growth and competitive dominance of invasive species under various nutrient levels and N/P ratios.

Alternanthera philoxeroides, commonly referred to as alligator weed, is a plant native to South America that has heavily invaded most regions of the world, especially in China (Julien et al., 1995; Xu et al., 2003; Zhang et al., 2016). Many studies have shown that clonal integration and phenotypic plasticity facilitate the success of invasive *A. philoxeroides* (Geng et al., 2007; Wang et al., 2009; Dong et al., 2015; Zhang et al., 2016). Although comparative studies between *A. philoxeroides* and native species have reportedly identified invasive mechanism of *A. philoxeroides*, in most cases, these species were cultivated in monocultures to access the invasive traits of *A. philoxeroides* (Geng et al., 2006; Chen et al., 2013; Wang et al., 2014; You et al., 2014). Gooden and French (2015) reported that it is the identity of resident species rather than resource availability that determines the impact of exotic plant invasion on native plant communities. Thus, in order to identify the factors contributing to the success of *A. philoxeroides* as an invasive species, it is necessary to examine the growth and competitive dominance of this alien plant when grown with other species, especially under conditions of differing nitrogen and phosphorus supply.

To this end, in the present study, we planted *A. philoxeroides* with either one of two noninvasive species (*Oenanthe javanica* or *Iris pseudacorus*) or *A. philoxeroides* (all three of which are riparian species) to explore the effects of nutrient level and N/P ratio on both the growth and competitive dominance of *A. philoxeroides*. Specifically, we sought to address the following questions:

(1) Would the culture pattern of *A. philoxeroides* (monoculture and mixed culture) modify the effects of nitrogen and phosphorus supply (nutrient level and N/P ratio) on the growth of *A. philoxeroides*?
(2) How do nutrient levels, N/P ratios, and co-occurring species affect the competitive dominance of *A. philoxeroides*?

2. Materials and methods

2.1. The species

The experiment was carried out using the following three plant species: the invasive *A. philoxeroides*, the native *O. javanica*, and the non-invasive alien *I. pseudacorus*. *Oenanthe javanica*, native to China, is a rhizomatous perennial plant and is often used for sewage purification (Zhou and Wang, 2010). During our pilot field investigation, we found that *O. javanica* grew in the same community as *A. philoxeroides*. *Iris pseudacorus*, an alien but noninvasive species in China, inhabits niches similar to those populated by *A. philoxeroides*, and is often used in water purification and the design of wetland landscape (Yousefi and Mohseni-Bandpei, 2010).

2.2. Study site and material preparation

The experiments were conducted in the greenhouse of Fanggan Research Station of Shandong University (36°26′N, 117°27′E). During the experiments, the average daytime temperature in the greenhouse ranged from 20 °C to 36 °C and the illumination intensity was maintained at 80% of natural light.

A. philoxeroides seedlings were collected from Nansi Lake wetland, Shandong Province, in April 2011. The seedlings of *O. javanica* and *I. pseudacorus* were purchased in May 2011. All three species were cultured in a nursery located in the greenhouse. In mid-June, individual shoots of the species were planted in pots (32 cm height × 29 cm diameter) filled with 8 kg washed river sand. The seedlings of *A. philoxeroides* and *O. javanica* were approximately 10 cm tall with four leaves, whereas those of *I. pseudacorus* were approximately 20 cm tall with four leaves.

2.3. Experimental design

For the mixed culture condition, one seedling of *A. philoxeroides* was planted in a pot together with a seedling of either *O. javanica* (AO) or *I. pseudacorus* (AI), whereas for the monoculture condition, two seedlings of *A. philoxeroides* (AA) were planted in the same pot. The nutrient treatments consisted of three N/P ratios (1, 10, and 100; labeled R1, R10, and R100, respectively) and three levels of nutrient supply (low [L], medium [M] and high [H]). Accordingly, there were a total of nine different nutrient treatments. The different N/P ratios respectively represented N-limited conditions (R1), balanced N and P supply (R10), and P-limited conditions (R100). In terms of total nutrient supply (N and P), the concentration of H was five times higher than that of M, which in turn was five times higher than that of L (Table 1). Each treatment contained eight replicate pots.

Table 1
Nitrogen and phosphorus added in different treatments. The numerical values represent mg/kg and each pot contained 8 kg of dry sand.

Total nutrient	R1		R10		R100	
	N	P	N	P	N	P
L	20	20	20	2	20	0.2
M	100	100	100	10	100	1
H	500	500	500	50	500	5

Table 2
The three-way analysis of variance (ANOVA) results of growth and relative dominance index of *Alternanthera philoxeroides* with nutrient level (N), N/P ratio (R) and culture pattern (C) as the main factors.

Indices	Source	df	*F*	*p*
Total biomass	N	2	1308.200	<0.001
	R	2	140.237	<0.001
	C	2	349.078	<0.001
	N × R	4	15.270	<0.001
	N × C	4	5.620	<0.001
	R × C	4	1.007	0.405
	N × R × C	8	1.229	0.282
Root to shoot ratio	N	2	117.054	<0.001
	R	2	6.378	0.002
	C	2	3.077	0.048
	N × R	4	6.159	<0.001
	N × C	4	2.468	0.045
	R × C	4	3.326	0.011
	N × R × C	8	4.011	<0.001
Total stolen length	N	2	1084.935	<0.001
	R	2	237.927	<0.001
	C	2	284.898	<0.001
	N × R	4	38.377	<0.001
	N × C	4	3.740	0.006
	R × C	4	0.482	0.749
	N × R × C	8	1.253	0.269
Relative dominance index	N	2	18.403	<0.001
	R	2	15.004	<0.001
	C	1	245.592	<0.001
	N × R	4	3.243	0.014
	N × C	2	2.792	0.065
	R × C	2	2.293	0.105
	N × R × C	4	0.959	0.433