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Original article

The influence of abiotic stress and phenotypic plasticity on the distribution of invasive *Alternanthera philoxeroides* along a riparian zone

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ABSTRACT

Relatively few studies have compared invasibility and species invasiveness among microhabitats within communities, synchronously. We surveyed the abundance and performance of non-native *Alternanthera philoxeroides* (Mart.) Griseb. (alligator weed), its co-occurring native congener, *Alternanthera sessilis* (L.) DC. (sessile joyweed), and other species in a wetland community along a riparian zone in southeast China to test the hypotheses that: i) degree of invasion differs between different types of microhabitats within the community; and ii) microhabitat types that differ in invasibility also differ in soil resource availability or in sediment characteristics likely to affect resource availability; iii) phenotypic plasticity of *A. philoxeroides* may play a key role in its adaptation to diverse habitats as can be concluded from its extremely low genetic diversity in China. The study riparian zone comprises different types of microhabitats including wet abandoned field, swamp, marsh dunes and gravel dunes. Consistent with these hypotheses, cover of *A. philoxeroides* was high in abandoned fields ($73 \pm 2.9\%$) and swamps ($94 \pm 1.3\%$), which had high soil nutrients and water availability. On the contrary, cover of native *A. sessilis* was relatively high in marsh dunes and gravel dunes, which had coarse gravel surfaces, low soil nutrients and low water availability. *A. philoxeroides* showed greater morphological plasticity in response to habitat variation. In abiotically harsh habitats, stems had limited growth, and were prostrate with weak adventitious roots at nodes, forming thin, scattered patches. In the two richer habitats, the highly branched plants spread over the water or soil surface, supporting dense stronger leaf-bearing stems which grew vertically. The growth pattern of *A. sessilis* among microhabitats did not exhibit significant variations. These results suggest that morphological plasticity and microhabitat types with high soil resources may facilitate invasions of *A. philoxeroides*.

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1. Introduction

Distributions of species along environmental gradients are thought to be the result of combinations of biotic and abiotic factors. Specifically, Tilman (1982, 1988) proposed a predict-

able sequence of species replacement along environmental gradients based on species' resource use strategies. A basic assumption is that, distributions might generally be limited by abiotic factors (e.g. limiting soil resources) at the more stressful end of a physical gradient, and by the ability to compete for light at the less stressful end. Therefore, this might be accompanied by a shift in community composition from plant species with the lowest requirement for soil nutrients to low-light tolerant species (Tilman, 1982; 1988;

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Wilson and Tilman, 1991). The related idea that plant community structure is governed by intraspecific tradeoffs between abiotic stress tolerance and competitive ability is a feature of many ecological theories (Connell, 1961; Grime, 1979; Brooker and Callaghan, 1998). In addition, the fact that some species are broadly distributed across environmental gradients suggests there may be a great role of within-species variation in the ability to tolerate abiotic stress or competitive conditions, e.g. ecotypic adaptation and phenotypic plasticity (Jurjavcic et al., 2002).

Biological invasions by non-native species have become a major environmental problem and a focus of ecological research (Vitousek et al., 1996; Brook et al., 1997; Dukes and Mooney 1999). What determines the susceptibility of a community or habitat to the establishment and spread of non-native species? Which traits enable a species to invade a new habitat? These two questions have long been main topics in invasion ecology (Elton, 1958; Alpert et al., 2000), and also in community ecology.

Comparisons of the degree to which alien invasive plants have spread into different communities suggest that some types of communities or habitats are more invasible than others (Lonsdale 1999; Alpert et al., 2000). A wide range of factors may underlie these differences, such as disturbance, resource availability, evolutionary history, propagule pressure, predation, mutualism, competition (see the review by Alpert et al., 2000). Many conceptual models state that increases in resource availability (including space, created by physical disturbance) can increase community susceptibility to invasion (e. g. Davis et al., 2000; Shea and Chesson 2002). Field and garden experiments provide evidence that availabilities of resources such as mineral nutrients and water are important determinants of the invasibility of communities by alien invasive plants. Adding nutrients to soils consistently promotes invasions (Wedin and Tilman, 1996; Li and Norland, 2001; Kolb et al., 2002). Adding water often promotes invasion (White et al., 1997; Kolb et al., 2002). One mechanism by which high resource availability might increase invasibility is by increasing the ability of non-native plant species to compete with natives (Davis and Pelsor, 2001; Shea and Chesson 2002).

In addition, there is clear evidence from a range of taxa that exotic invasive populations often quickly adapt to local conditions and express some genetically based “invasive” phenotypes following colonization (e. g. Siemann and Rogers, 2001; Lee, 2002; Blair and Wolfe, 2004). On the other hand, because invaders often have low initial genetic diversity owing to genetic bottlenecks or “genetic cleansing” (Tsutsui et al., 2000; Kaufman and Smouse, 2001; Giraud et al., 2002; Xu et al., 2003), a high degree of plasticity might be an alternative way of dealing with new environments. In fact, dating back to Baker’s classic work (Baker, 1974), many authors suggest that greater phenotypic plasticity is likely to confer greater invasiveness (Williams et al., 1995; Rejmanek and Richardson, 1996; Annapurna and Singh, 2003; also see the review by Daehler, 2003).

Moreover, invasibility and invasiveness interact: the probability of successful invasion depends on the fit between a particular exotic invasive species and a particular habitat (Dietz et al., 1998; Sans et al., 2004). In other words, biological

invasions are essentially context-specific processes (see the review by Alpert et al., 2000; Daehler, 2003).

Studying patterns of invasion within communities should be a good way to investigate the role of resource availability, local adaptation and/or phenotypic plasticity in successful invasion, as many of the other factors that may affect invasion, such as accessibility, history and predation, are likely to vary less within communities than between them. Relatively few studies have compared invasibility and species invasiveness between microhabitats within communities.

In the present study, we compared the abundance and performance of non-native *Alternanthera philoxeroides* (Mart.) Griseb. (alligator weed) and its co-occurring native congener, *Alternanthera sessilis* (L.) DC. (sessile joyweed), in a wetland community along a riparian zone in southeast China to test the hypotheses that: i) the degree of invasion differs between different types of microhabitats within the community; and ii) microhabitat types that differ in invasion also differ in soil resource availability or in sediment or soil characteristics likely to affect resource availability. Intensive studies have shown that *A. philoxeroides* maintained extremely low genetic diversity throughout China. For example, Xu et al. (2003) first reported that fragments amplified by 31 RAPD (Random amplified polymorphic DNA) primers showed no genetic variation within or among eight *A. philoxeroides* populations from southeast China. Fragments amplified by both 28 RAPD primers and 23 ISSR (inter simple sequence repeat) primers had no polymorphic bands within and among the seven populations sampled from the south of China (Wang et al., 2005). Using 81 ISSR markers, the mean Nei’s gene diversity of 193 individuals from 11 land-grown *A. philoxeroides* populations from South China was 0.0203 ± 0.008 , and the total diversity was 0.0286 (Ye et al., 2003). These results suggested that plants of alligator weed in China might have come from clones of the same genotype. Thus, we expected that: iii) phenotypic plasticity must have played a key role in adaptation to diverse habitats for *A. philoxeroides* in China.

2. Materials and methods

2.1. Plant materials

A. philoxeroides, a native to South America, was first brought to China as a forage crop from Japan during the 1930s, and later widely cultivated and spread in southern China as fodder during 1950s (Li and Xie, 2002). Now, *A. philoxeroides* is one of the 12 most harmful alien invasive species in China (Li and Xie, 2002). Alligator weed grows abundantly in habitats ranging from open waterways to shaded sites under dense vegetation. Typically, it forms floating mats in still or running water (Fig. 1A). The mats are composed of both leaf-bearing erect and prostrate stems that float on the surface of the water, or run along the soil surface and root at the nodes (Fig. 1B, C). The stems generally are rooted in shallow sediments or soils bordering the edge of waterways. Also, alligator weed can be found in semiaquatic (e.g. in gardens, plantations, and cultivated crops) or even drier conditions (e.g. on ditch bank, along roadsides, and the margins of floodplain

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