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Original article

Phenotypic variation and water selection potential in the stem structure of invasive alligator weed

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ABSTRACT

The morphological and anatomical characteristics of stems have been found to be related to drought resistance in plants. Testing the phenotypic selection of water availability on stem anatomical traits would be useful for exploring the evolutionary potential of the stem in response to water availability. To test the phenotypic variation of the stem anatomical traits of an invasive plant in response to water availability, we collected a total of 320 individuals of *Alternanthera philoxeroides* from 16 populations from terrestrial and aquatic habitats in 8 plots in China and then analyzed the variation, differentiation, plasticity and selection potential of water availability on the stem anatomical traits. We found that except for the thickness of the cortex, all of the examined phenotypic parameters of the *A. philoxeroides* stem were significantly and positively correlated with soil water availability. The phenotypic differentiation coefficient for all of the anatomical structural parameters indicated that most of the variation existed between habitats within the same plot, whereas there was little variation among plots or among individuals within the same habitat except for variation in the thickness of the cortex. A significant phenotypic plasticity response to water availability was found for all of the anatomical traits of *A. philoxeroides* stem except for the thickness of the cortex. The associations between fitness and some of the anatomical traits, such as the stem diameter, the cortex area-to-stem area ratio, the pith cavity area-to-stem area ratio and the density of vascular bundles, differed with heterogeneous water availability. In both the aquatic and terrestrial habitats, no significant directional selection gradient was found for the stem diameter, the cortex area-to-stem area ratio or the density of vascular bundles. These results indicated that the anatomical structure of the *A. philoxeroides* stem may play an important role in the adaptation to changes in water availability.

1. Introduction

Phenotypic plasticity, i.e., the capacity of an organism to express variable phenotypes in different environments, is a widespread phenomenon among many animals, plants and other organisms (Agrawal, 2001; Engel et al., 2011; Nicotra et al., 2010). Phenotypic plasticity plays an important role in the adaption of species to heterogeneous environments and is a prerequisite for evolution by natural selection (Agrawal, 2001; Stanton et al., 2000). Functionally adaptive plasticity, i.e., the capacity for specific appropriate environmental responses, can play major roles in both the ecological distribution of organisms and their patterns of evolutionary diversification from individual to population to species (Sultan and Spencer, 2002; Sultan, 2003). Adaptive plasticity may also contribute specifically to species invasiveness by allowing rapid colonization of diverse new habitats without the need to undergo local selection (Williams et al., 1995), which might allow a species to exhibit broader ecological amplitude and greater environmental tolerance than is required in their native regions (Williamson, 1996) and facilitate successful invasions in the introduced range (Buswell et al., 2011). Understanding how invasive plants adaptively evolve in response to environmental stress during the invasive process may help us predict the invasiveness of plants in the context of global climate change.

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Phenotypic selection, known as the differences in fitness (or its components) associated with phenotypic variation among individuals, is used to estimate the strength of natural selection (Munguia-Rosas et al., 2011; Kingsolver et al., 2012). Some studies have shown that phenotypic selection in natural populations is strong (Kingsolver et al., 2001; Kingsolver and Pfennig, 2007), whereas other studies show that it is weak (Kingsolver et al., 2012). The strength of phenotypic selection can be influenced by selection-driven force and environmental factors (Munguia-Rosas et al., 2011; Bartkowska and Johnston, 2012). Bartkowska and Johnston (2012) found that pollinators cause a stronger selection than herbivores on floral traits in *Lobelia cardinalis* (Lobeliaceae). Based on meta-analysis data, Munguia-Rosas et al. (2011) found that phenotypic selection on flowering phenology is influenced by latitude.

To date, selection has been detected in hundreds of populations in nature, with thousands of estimates of the strength and form of selection on numerous phenotypic traits (Kingsolver et al., 2001; Siepielski et al., 2009). Kingsolver et al. (2012) proposed that phenotypic selection on physiological and behavioral traits from natural populations is a promising area for expanding our understanding of selection in the wild (Kingsolver et al., 2012). Most studies in this area have focused on ecophysiological traits (Dudley, 1996), particularly leaf traits (Donovan et al., 2007, 2009) and flower traits (Beans and Roach, 2015). For example, Donovan et al. (2007) documented phenotypic selection on leaf water-use efficiency and related ecophysiological traits in natural populations of desert sunflowers. Donovan et al. (2009) examined spatial and temporal variation in phenotypic selection on leaf ecophysiological traits for 10 *Helianthus* populations. However, little attention has been paid to the anatomical structure of plants, particularly that of the stem. The stem is an important organ that exhibits high plasticity in adapting to variable environments (Ackerly et al., 2000). For example, Dudley and Schmitt (1996) found that the stem elongation response to density contributes to the fitness differences and presents adaptive properties. In particular, the morphological and anatomical characteristics of stems have been found to be related to drought resistance in plants (De Micco and Aronne, 2012). Therefore, testing the phenotypic selection on stem anatomical traits would be useful for exploring the evolutionary potential of the stem in response to water stress.

Alternanthera philoxeroides (Martius) Grisebach (Amaranthaceae) originated in the Parana River region of South America and is now widely distributed around the world (Li and Ye, 2006). *A. philoxeroides* was introduced into Shanghai, China, in the 1930s and occurs in most regions of southern China (Ye et al., 2003). *A. philoxeroides* causes severe damage to sectors such as agriculture, forestry, fisheries and irrigation and causes serious economic losses and ecological disasters (Ye et al., 2003). This species has been listed as one of the 12 most harmful alien invasive species in China (Li and Xie, 2002). *A. philoxeroides* is an aquatic plant in its native range but is widely distributed in different habitats in its introduced range, including terrestrial, aquatic and semi-aquatic habitats (Li and Ye, 2006).

A. philoxeroides is a stoloniferous and rhizomatous perennial plant that uses asexual reproduction as an important strategy for the colonization of new habitats (Li and Ye, 2006). Pan et al. (2006a) indicated that its high degree of plasticity may be an alternative strategy that *A. philoxeroides* uses to adapt to new environments. The anatomical structure of the *A. philoxeroides* stem has both terrestrial and aquatic characteristics (Tao et al., 2009). The phenotypic variation observed in the *A. philoxeroides* stem has been shown to be shaped by the water conditions in its habitat (Tao et al., 2009). In this study, *A. philoxeroides* was employed as the experimental material, and phenotypic selection was used to analyze the selection potential of water availability on the anatomical phenotypic traits of *A. philoxeroides*. We sought to determine 1) the variation, differentiation and plasticity of the stem anatomical structure among and within populations of *A. philoxeroides* under different water availability levels and 2) the strength of the selection potential of environmental conditions (water availability) on the phenotypic variation of invasive *A. philoxeroides*. These results will help elucidate the mechanisms underlying the rapid evolution of *A. philoxeroides* in adapting to habitats with differing water availability levels and will provide an important reference for the management of this species.

2. Materials and methods

2.1. Study area and sampling

This study was conducted in Linhai City, Zhejiang Province, China, which is located at 28°40′–29°04′ N, and 120°49′–121°41′ E. This area has a typical subtropical monsoon climate with abundant illumination and rainfall. The annual average temperature is 17.1 °C, rainfall is 1522.4 mm, relative humidity is 82%, and the amount of radiation is 1009.5 kcal/cm^2. Although *A. philoxeroides* is distributed widely in China, we chose only one location for this study to exclude the phenotypic plasticity caused by climate, soil and other abiotic or biotic factors.

In July 2012, 8 sampling plots were selected for this study. All eight plots were located in farmland or abandoned land with similar soil types and physical and chemical properties (Table 1), and the vegetation was dominated by *A. philoxeroides*. Among every plot, two populations of *A. philoxeroides* were collected from two different habitats: aquatic habitat (*A. philoxeroides* plants growing in ditches) terrestrial habitat (*A. philoxeroides* plants growing on dry land near ditches). The water regimes of all 16 populations were determined at a depth of 3 cm using an HH2 Handheld Moisture Meter (Version 2.0, Delta-T Devices Ltd., Cambridgeshire, UK). *A. philoxeroides* weeds showing good growth with low levels of infestation by pests and diseases and seldom consumption by herbivores were collected for further analysis. In every population, twenty individuals of *A. philoxeroides* separated by a distance at least 5 m were randomly collected and transported to the laboratory immediately in cooler bags at 4 °C. The plants were stored at 4 °C and used to measure the stem traits within 12 h. The experiment was continued in one week, i.e. from July 12 to July 18, 2013. A total of 320 individuals from 16 populations, 8 plots were analyzed in this study. No specific permits were required for collection in the localities sampled in this study, and none of the populations were privately owned or protected in any way. Additionally, we verified that the field studies did not involve endangered or protected species.

2.2. Measurements

The third fully developed stem of *A. philoxeroides* from the top of every individual was used for further analysis. The diameter of the stem (DS) was measured with a Vernier Caliper with a precision of 0.002 cm. Then, the third stem from the top was cut, and three freehand cross-section slices of the stem were prepared using a single blade. Anatomical structural features of the *A. philoxeroides* stem, including the thickness of the cortex (TCx), the diameter of the pith cavity (DPC), the number of vascular bundles (NVB), the diameter of vascular bundles (DVB) and the density of vascular bundles (DsVB), were measured under a microscope (Leica DM/LS, Leica MicroSystems Ltd., Wetzlar, Germany) using an objective microruler with a precision of 10 μm. The cortex area-to-stem area ratio (Cx/S) was calculated as the cortical area/total area of stem cross-sections. The