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Functional trait similarity of native and invasive herb species in subtropical China—Environment-specific differences are the key

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ABSTRACT

The attempt to identify traits associated with plant invasions has revealed ambiguous results to date. Accounting for environmental and temporal variation in multispecies trait comparisons of native and invasive species might help explain such inconsistency.

The relative importance of light and nutrient availability was tested in a greenhouse experiment on trait expression and variation of 15 native and 15 invasive herb species from Southeast China. In addition, N uptake of a subset of these species and its temporal pattern were assessed by means of a ^{15}N tracer experiment.

A predominant lack of significant differences between the two status groups indicated strong overall trait similarities, thus supporting the 'join-the-local' hypothesis. However, at high light levels, the invasive species displayed significantly higher trait relative growth rates, whereas the native species had a higher tissue quality as displayed in a higher dry matter content of shoots and leaves. The invasion success of the invasive species could neither be explained by a general higher N uptake nor by a distinction in temporal N uptake strategy between native and invasive species.

Despite comparable fundamental niches of the species, increased growth rates under beneficial light conditions may provide a head start advantage for invasive species compared to native ones. The present study confirms the assumption of an opportunistic strategy for invasive species and emphasizes the need to assess trait variation between native and invasive species in different environmental contexts.

1. Introduction

Biological invasions have become a major threat to diversity and ecosystem functioning and have attracted increasing scientific interest in recent years (Mack et al., 2000; Pimentel et al., 2000). One central aim in research on plant invasion ecology is to identify traits, i.e. morphological and physiological characteristics (Violle et al., 2007; van Kleunen et al., 2010), which are associated with the success of exotic invasive plant species and, thus, help explain the mechanisms behind this success. So far, much effort has been made to find such general traits (Pattison et al., 1998; Grotkopp et al., 2002; Cadotte et al., 2006; Richardson and Pyšek, 2006; Hawkes, 2007). Thereby, the results are often ambiguous and to date, it has not been possible to find a set of 'invasive' traits that apply consistently to all vascular plants. While many studies focus only on the role of traits in isolation, particular traits also work in concert and may facilitate successful invasions in combinations (Küster et al., 2008). Such trait combinations might also be caused by physiological constraints, as evidenced, for example, by a trade-off between relative growth rate and tissue density (Enquist et al., 1999). Successful invasive species are thought to be better at acquiring resources or to use resources more efficiently than native species (Vitousek, 1986; Pattison et al., 1998; Niinemets et al., 2003; Feng et al., 2007; Funk and Vitousek, 2007). In contrast, Tecco et al. (2010) raised the 'join-the-locals' concept, which implies strong environmental filters to be the main control agent for community composition by favouring species with similar traits that fit best to the environmental situation encountered. However, successful invasions depend on a number of factors such as the resource availability or the regions' climate and it is crucial to evaluate the characteristics of invaders and their trait interactions in the context of the characteristics of the recipient environment (Shea

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and Chesson, 2002; Hayes and Barry, 2008). The success of invasive plants in resource-rich or disturbed habitats may be facilitated by attributes of high resource acquisition and fast growth. However, attributes of resource conservation are needed in resource-poor or pristine habitats, where invasions occur as well (Tecco et al., 2010). Daehler (2003) found that the competitive ability of invasive species was not generally superior but rather changed under different conditions. Accordingly, Richards et al. (2006) set the terminology of opportunistic invasive strategy for some invasive species that often succeed only under favourable conditions.

However, accounting for environmental variability does not only refer to spatial variation but also includes the possibility of variation in time (Davis et al., 2000). Since growth and biomass allocation are related to resource use, they might also change temporally (Crawley, 1989; Poorter and Pothmann, 1992; Wright and McConnaughay, 2002). To date, only few studies (e.g. James et al., 2008) have taken temporal variation of growth- and biomass-related traits or resource uptake for explaining invasion success into account. Successful colonization in an established community is particularly favoured if an invasive species can use resources at times when they are unavailable for the native residents (Shea and Chesson, 2002). Thus, a high resource uptake and rapid growth of the invasive species at the beginning of the growing season would enhance their establishment success by profiting from a head start in phenological or developmental features.

The present study makes use of an experimental multispecies approach and focuses on short-living ruderal species of comparable habitats to characterize morphological and physiological characteristics. In the context of the first biodiversity and ecosystem functioning experiment in subtropical forests in China (BEF-China), we studied each 15 invasive and 15 native herb species of resource-rich ruderal habitats, currently occurring in the study area. It can be assumed that in the course of this experiment, increasing canopy closure and thus light exclosure in time will induce changes in herb layer composition and invasibility. In addition, seed addition experiments previously conducted in a Chinese common garden situation (Both et al., 2012) have shown that productivity of invasive herb species was strongly enhanced by nutrient addition while native species showed no such response. Accordingly, we refer to these 30 species to study the relative importance of different environmental conditions in terms of light and nutrient availability on the trait expression as well as the trait expression during the development. Trait differences between the native and the invasive species and both their spatial and temporal variation were assessed in a greenhouse study with different light and nutrient conditions. In addition, a ^{15}N tracer experiment was conducted to investigate N uptake and allocation in the course of time. The experiments were designed to test the following hypotheses: (i) Differences in growth- and biomass-related traits between the invasive species and the native species are context-dependent. The invasive species should display superiority over the native species under favourable conditions, namely beneficial light and nutrient conditions. (ii) Differences in growth- and biomass-related traits as well as differences in the nitrogen uptake between the invasive and the native species change temporally. These differences are supposed to be more evident in earlier stages of the development.

2. Materials and methods

2.1. Study species

About 40 species were selected according to their status, habitat and distribution as well as their frequency of occurrence in China and included herb species and two grass species from Southeast China (in the following all referred to as herbs). Seeds of all species were collected in 2008 in Zhejiang province, from comparable habitats in rural areas of Hangzhou, Wenzhou, Quzhou and near the Gutianshan National Nature Reserve and were sampled across several individuals per sampling location. Since not all species germinated, the study was carried out with each 15 species that are native, non-invasive in China and 15 are exotic ones that are considered invasive (sensu Richardson and Pyšek, 2006) in both study provinces of the BEF-China Experiment, Zhejiang and Jiangxi. The classification of the species is based on information from local experts and is supported by information of the Flora of China. (http://hua.huh.harvard.edu/china/) the Flora of Zhejiang and review studies on major invasive plant species in all of China (Liu et al., 2005, 2006; Weber et al., 2008). In the following, the exotic invasive species are referred to as invasive species and the native non-invasive species as native species. Both status groups comprise annuals, bi-annuals and perennials (Table A.1). The study species mostly occur in grassland, disturbed areas or forest margins, and in young successional forest stands.

2.2. Greenhouse experiment 1: light and nutrient variation

Individuals of all 30 species were propagated from seeds in a greenhouse chamber and cultivated in pots with a substrate mixed by 1/3 sand and 2/3 potting soil (Type 0, Einheitserdewerk Hameln, Germany). After germination the seedlings were transplanted into 0.77 L pots. At the beginning of the experiment, half of the pots were enriched in nutrients ('*rich nutrient conditions*') by adding granules of a slow-release fertilizer (4 g per L substrate of Basacote® Plus 6M, NPK 16:8:12, Compo, Münster, Germany). The other half served as control ('*poor nutrient conditions*'). Plants were transferred to larger pots (0.98 L) containing the same soil mixtures after seven weeks.

Three levels of light availability were applied by using shading nets which reduced full light (300 $\mu E\,m^{-2}\,s^{-1}$) provided by greenhouse lamps (pressure mercury lamps, Philips HQI, 400W) down to medium light (150 $\mu E\,m^{-2}\,s^{-1}$) and low light (15 $\mu E\,m^{-2}\,s^{-1}$), respectively. Each light level treatment (light block) was replicated three times. Growing conditions were set to 25 °C/20 °C (day/night) with air humidity of 80% and 12 h daytime. Both levels of nutrient treatments were represented in each light block. Each treatment × species combination was replicated three times with each two individuals by species in each of the nine light blocks. For reasons of low germination for *Artemisia anomala* and *Celosia argentea*, these two species were replicated only once per treatment, thus, yielding a total number of 516 individuals randomly positioned within blocks.

The plants were watered every two days during the experiment that ran from February to May 2009 at the Institute of Biology/Geobotany and Botanical Garden, University of Halle, Germany.

2.3. Greenhouse experiment 2: ^{15}N tracer addition

In a second experiment, several ^{15}N tracer applications were repeatedly conducted during the plants' life-span for assessing nitrogen uptake pattern in time. We focused on annual species only with the advantage of investigating N uptake and allocation over nearly the entire plants' life period in a short-term experiment. The species set comprised eight annual invasive and eight annual native species, the latter group including one annual/biennial species (Table A.1).

The experiment ran from May to July 2009 in the greenhouse and was conducted with 30 individuals per species. A ^{15}N tracer was applied six times during the experiment on five individuals per species at each time.

The cultivation of species was done as described in experiment 1. Two weeks old seedlings were transplanted into 0.98 L pots with a medium fertilizer addition (2 g per L substrate of Basacote® Plus 6M,