INDIVIDUAL-AND GROUP-BASED INTERSPECIFIC COMPETITION BETWEEN ALIEN INVASIVE PLANT *ERIGERONANNUUS* AND TWO CO-EXISTING HERBS

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ABSTRACT

Individual- and group-based interspecific competition played the important role on growth and distribution of invasive plant species and further influenced growth and diversity of plant communities. However, none has examined the both effects of interspecific competition on a worst alien invasive plant *Erigeron annuus*. In the greenhouse experiments, seedlings of invasive plant *E. annuus* and two co-existing herbs (a native herb *Artemisia indica* and a common crop *Ipomoea batatas* in the farmland) were subjected to the individual-based (without and with interspecific competition) and group-based competition [i.e. without and with interspecific competition under two distribution types (aggregation and segregation) of *E. Annuus*]. Individual-based interspecific competition significantly affected aboveground mass, belowground mass and biomass of native *A. indica* and *I. batatas*, but did not affect growth of invasive *E. annuus*. Interspecific relative competition intensity (RCI) of aboveground mass and biomass mass were significantly lower in *E. annuus* than those in other two co-existing species. Group-based interspecific competition significantly decreased all growth measures of *E. annuus*. Under the segregation distribution, aboveground mass and biomass of *E. annuus* were significantly greater in the no competition than in the competition treatments, but was statistically the same between two competition treatments under the aggregation distribution. Moreover, RCI of biomass in *E. annuus* was significantly lower under the aggregation than under the segregation distribution. Therefore, *E. annuus* has high individual-based competitive ability, and aggregation distribution of *E. annuus* can increased the group-based interspecific competitive ability with two co-existing herbs.

Keywords: *Erigeron annuus*, plant invasion, interspecific competition, aggregation distribution, relative competition intensity

INTRODUCTION

In natural habitats, invasive plant species are the serious ecological and conservation threat to native biodiversity and ecosystem functions on a global scale (Huenneke *et al*. 1990; Simberloff 2005; Funk and Vitousek, 2007). Invasion success depends on competitive interactions between invasive plants and native plants of the communities to be invaded (Funk and Vitousek, 2007, Qin *et al*. 2013). Comparing with native species, most invasive plants showed inherent competitive advantage and performance in novel environments by allelopathic compounds effects, higher resource uptake, faster growth rates, or by release from specialist natural enemies (Ridenour *et al*. 2008; Qin *et al*. 2013; Callaway and Ridenour, 2004; Liu *et al*. 2016).

Competition among plants has been considered as the most important driver of plant community diversity and dynamics and plays the important role on growth, distribution and abundance of alien plant species (Emeterio *et al*. 2007; Tilman 1997). Theoretically, neighboring plants can act as obstacles for sharing limited resources (light, nutrient, and water) resulting in the different scales of competition (from individual to group / community level) and interfere the normal growth of co-occurring plants (Wang *et al.* 2016a, c). Recent studies have shown that invasive species seems to have an innately superior competitive ability over native species. In the process, some individual traits, such as higher leaf area, lower tissue construction costs and more efficient resource use strategies, might confer a competitive advantage over native species (Daehler *et al*. 2004; Funk and Vitousek, 2007; Zhang *et al*. 2016). However, communities were structured in more complex ways than simply the collection of all species. Thus, when the individual traits referred to competition were translated into community structure, it required consideration of two levels of comparison (Gough *et al*. 2001).

The distribution types (aggregation or segregation) of alien plants is likely to affect the growth of plant communities in the group-based competition. Under field conditions, intraspecific distribution of most species are aggregated at one or several spatial scales (Herben *et al*. 2000). The distribution of invasive plants can create the effects of spatial heterogeneity on native species, which might alter interspecific competition by modifying availabilities of resource heterogeneity in light and water supply (Dong *et al*. 2013; Wang, 2016b). For instance, recent study has shown that ramet aggregation negatively affects the competitive ability of target species for increasing the overlapping zones of influence (Lenssen *et al*. 2005, Dong *et al*. 2013). In contrast, experimental research also found the spatial aggregation of species reduces the strength of interspecific competition sufficiently to facilitate invasion (Rejmanek 2002). Moreover, Tilman and Karevia (2005) have emphasized that intraspecific aggregation can changes the frequency of inter- or intra-specific encounters and thus contributes to species coexistence. To our knowledge, however, few studies have explicitly tested both individual-based and the effect of distribution type on group-based interspecific competition in invasive plant species.

In this study, we conducted the greenhouse experiments to discuss whether individual- and group-based interspecific competition will affect the growth of invasive plant *Erigeron annuus* and two co-existing herbs (a native herb *Artemisia indica* and a common crop *Ipomoea batatas* in the farmland). Invasive plant *E. annuus* and two co-existing herbs were subjected to without and with individual-based competition (i.e. one plant of each species was planted alone, and one plant of invasive plant was planted with one plant of each co-existing herb), and subjected to without and with group-based competition [i.e. six plant of invasive plant were planted alone under the two distribution types (aggregation and segregation), and six plants of invasive plant were planted with 12 plants of each co-existing herb]. Therefore, we addressed the following questions: (1) Whether individual-based interspecific competition has the different effects on growth between *E. annuus* and two co-existing herbs? (2) Whether distribution type of *E. annuus* can alter growth and interspecific competition intensity at the group-based level?

MATERIALS AND METHODS

Study species: *Erigeron annuus* (Asteraceae) is an annual herb and originates from North America. It is commonly distributed in arable lands, pasture and wastelands over large areas in southern China (Liu 2008). The species was introduced in China in the 1886 and reproduced to establish population via viable seeds. Dispersal of seeds by human activities, trade and transportation has resulted in a rapid expansion of the geographical range of *E. annuus* in China, where the species has become an important ecological and agricultural problem in a broad range of habitats.

In the natural habitats, there are two main dominant co-existing herbs (a native herb *A. indica* and a common crop *I. batatas* in the farmland) with *E. annuus* in farming areas by the previous plot survey. *Artemisia indica* (Asteraceae), a perennial native herb, is widespread from tropical to warm temperate farmland habitats in China. The dispersal of *A. indica* relies mainly on sexual reproduction (i.e. seeds). *Ipomoea batatas* (Convolvuloideae) is an annual clonal herb and one of main crops distributed in farmland. This species can produce tubers that can be potential to produce an inducing ramet.

We selected seeds of *E. annuus* and *A. indica, and* tubers of *I. batatas* from at least five locations at the fields of Huazhong Agriculture University (over 100 ha) (30°28′49″N; 114°21′21″E), Wuhan, Hubei Province, Central China. On 17 February 2014, we sowed the seeds and tubers in pots filled with a 1:1 mixture of sand and fine vermiculite. Pre-cultivation took place in the experiment garden of Huazhong Agriculture University. On 20 April 2014, seedlings of three species were transplanted in the greenhouse. The sufficient water was added to each container until seedlings had recovered and established. After two weeks of cultivation, 480 individuals of *E. annuus*, 346 individuals of *A. indica* and *I. batatas* with identity size were selected from pre-cultivation seedlings in the experiment. Of them, 12 seedlings of each species were randomly selected for testing initial height and dry mass. No differences between species were detected in initial size (dry weight and initial height) of the plants ($P > 0.05$, n = 12). Then the other seedlings were used for experiment described below.

Experimental design

The study consisted of two experiments. In the first experiment, we tested the effects of individual-based interspecific competition on growth of invasive plant *E. annuus* and two co-existing herbs. There were the five treatments, i.e., three competition-free (none) treatments (*E. annuus*, *A. indica* and *I. batatas*) and two competition treatments (*E. annuus* competed with *A. indica* ($E.\ annuus_{Art}$) and with *I. batatas* ($E.\ annuus_{Ipo}$)). In the competition-free treatments, one plant of target species was planted alone in the center of each plastic container (16 cm diameter × 12 cm high). In the competition treatments, one plant of *E. annuus* was grown with one plant of *A. indica* or *I. batatas*. Each treatment had twelve replicate containers and thus there were 60 plastic containers.

In the second experiment, we tested the effects of group-based interspecific competition on growth of invasive plant *E. annuus* and two co-existing herbs under the two distribution types of invasive plant. There were three competition treatments (none – six individuals of *E. annuus* was planted alone, $E.\ annuus_{Art}$ – six individuals of *E. annuus* was planted with twelve individuals of *A. indica*, $E.\ annuus_{Ipo}$ – six individuals of *E. annuus* was planted with twelve individuals of *I. batatas*) and two distribution treatments (aggregation – six seedlings of *E. annuus* were grown in aggregation and were close to the center of the container, segregation – six seedlings of *E. annuus* were grown in segregation and were closer to the inner borders of the container). There were twelve replicates of containers (60 cm diameter × 45 cm high) for each of the six treatments and thus 72 containers in total.

The experiments was started on 25 April 2014 and ended on 28 June 2014, lasting 9 weeks. All containers were filled with a mixture of sand and yellow-brown soil (2:1 v/v). During the experiment, the mean temperature and mean relative humidity in the greenhouse were 22.5°C and 72.2%, respectively (measured by Amprobe TR300, Amprobe, Everett, WA, USA). The containers were randomly placed in the greenhouse experimental base. Sufficient tap water were also added to each container for maintaining the demand of plant growth. Furthermore, the containers were randomly repositioned every week to avoid potential effect of environment patchiness.

Measurements and data analysis: At the end of the experiment, all plants of each species were separated into belowground mass and aboveground mass, dried at 80℃ for 48h and weighed . Total biomass was the sum of aboveground and belowground mass. Before analysis, values of all variables in the competition treatments were divided by six or twelve so that the values were scaled to the level of per initial plant.

To measure the intensity of interspecific competition, we calculated the interspecific relative competition intensity as RCI= $(B_0 – B_+) / B_0$, where B_0 is mean growth measure of target species without competition and B_+ is mean growth measure of target species with competition. Positive values mean competition, negative values mean facilitation and zero means neutral.

We used one-way ANOVA to test the effects of different competition treatments (none (i.e. competition-free), *E. annuus$_{Art}$* and *E. annuus$_{Ipo}$*) on biomass, aboveground mass and belowground mass of *E. annuus* at the individual level. We used two-way ANOVAs to examine the effects of native species (*A. indica* and *I. batatas*) and interspecific competition (with vs. without competition) on their growth measures at the individual level. When significant effects were found, *Tukey* multiple comparison tests were conducted to examine for differences between the four treatments. We further employed two-way ANOVAs to test the effects of interspecific competition (with vs. without competition), distribution (aggregation and segregation) and their interactive on biomass，aboveground mass and belowground mass of *E. annuus* at the group level. In the these analysis, we conducted the effects of interspecific competition with different interspecific competitors, *A. indica* and *I. batatas*, respectively. We also employed one-way ANOVA to examine the effects of interspecific competition on RCI in all species at the individual level. We used one-way ANOVA to test the effects of different interspecific competitors and distribution on RCI of *E. annuus*. All analyses were conducted using SPSS Statistics 17.0 (IBM Corp., Armonk, NY, USA) . The effects were considered significant if $P<0.05$.

RESULTS

Effects of interspecific competition at the individual level: Interspecific competition (with *A. indica* and *I. batatas*) affected none of aboveground mass, belowground mass and biomass of invasive plant *E. annuus* at the individual level (Fig. 1). However, individual-based interspecific competition dramatically decreased all growth measures of native plants *A. indica* and *I. batatas* (Fig. 2). Interspecific relative competition intensity (RCI) of above-ground mass and biomass were significantly lower in *E. annuus* than in other two native plant species (Fig. 3). The results suggested that there were significant differences in growth response between invasive *E. annuus* and two co-existing native species *A. indica* or *I. batatas* under individual-based interspecific competition.

Effects of distribution and interspecific competition at the group level

Group-based interspecific competition significantly decreased aboveground mass, belowground mass and biomass of invasive *E. annuus* at the group level (Fig. 4). There was no significant effect of distribution type of *E. annuus* on the three growth measures. However, the interaction between group-based interspecific competition and distribution type significantly affected aboveground mass and biomass of *E. annuus* (Fig. 4). Under the segregation distribution, aboveground mass and biomass of *E. annuus* were significantly greater in the no competition than in the competition treatments, but was statistically the same between two competition treatments under the aggregation distribution (Fig. 4). Such interactions were observed in both interspecific competitors. Interspecific relative competition intensity (RCI) of biomass of *E. annuus* was also significantly higher under the segregation distribution than under the aggregation distribution treatment in both interspecific competitors (Fig. 5). These results suggested that distribution of *E. annuus* can alter interspecific competitive intensity, and aggregation distribution of *E. annuus* increased the interspecific competitive ability at the group level.

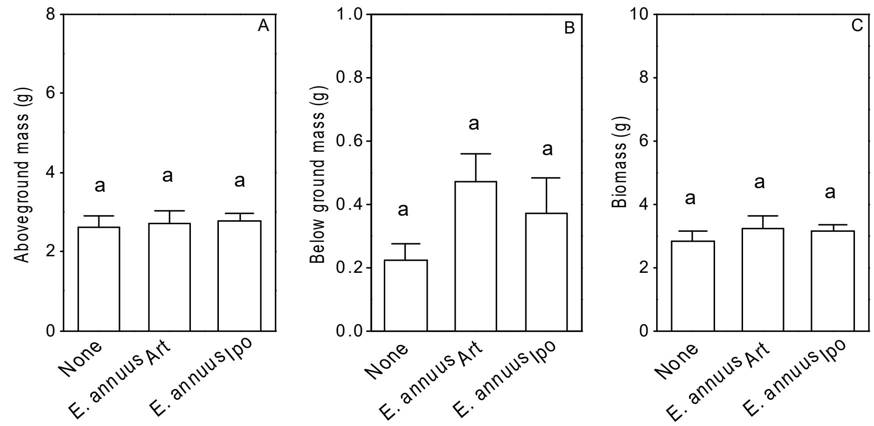

Fig.1. Above ground mass (A), below ground mass (B) and biomass (C) of invasive plant *Erigeronannuus* in the competition-free (None), competition with *Artemisiaindica* (*E.annuus$_{Art}$*) and with *Ipomoeabatatas* (*E.annuus$_{Ipo}$*) treatments at the individual level. Error bars how +SE. Bars sharing the same letters are not different at P=0.05 (*Tukey* test).

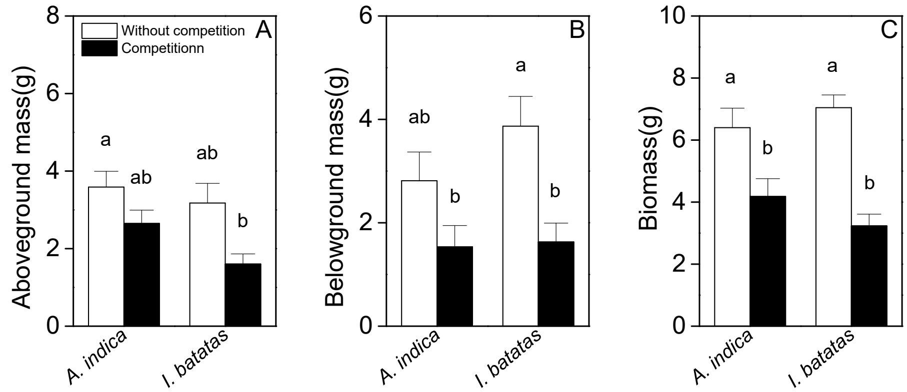

Fig. 2 Aboveground mass (A), belowground mass (B) and biomass (C) of native plants *A. indica* and *I. batatas* in the two interspecific competition (with and without competition) treatments at the individual level. Error bar show +SE. Bars sharing the same letters are not different at P=0.05 (*Tukey* tests).

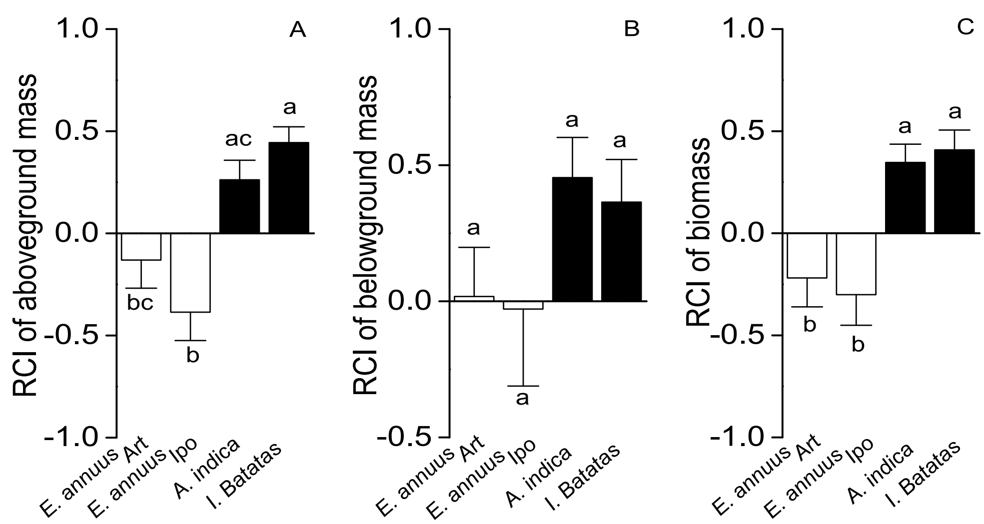

Fig. 3 Interspecific relative competition intensity (RCI) of aboveground mass (A), belowground mass (B), biomass (C) of different species at the individual level. Bars sharing the same letter are not significantly different at P=0.05 (*Tukey* tests). Mean + SE are given. *E. annuus$_{Art}$* = *E. annuus* competed with *A. indica*; *E annuus$_{Ipo}$* = *E. annuus*

competed with *I. batata*

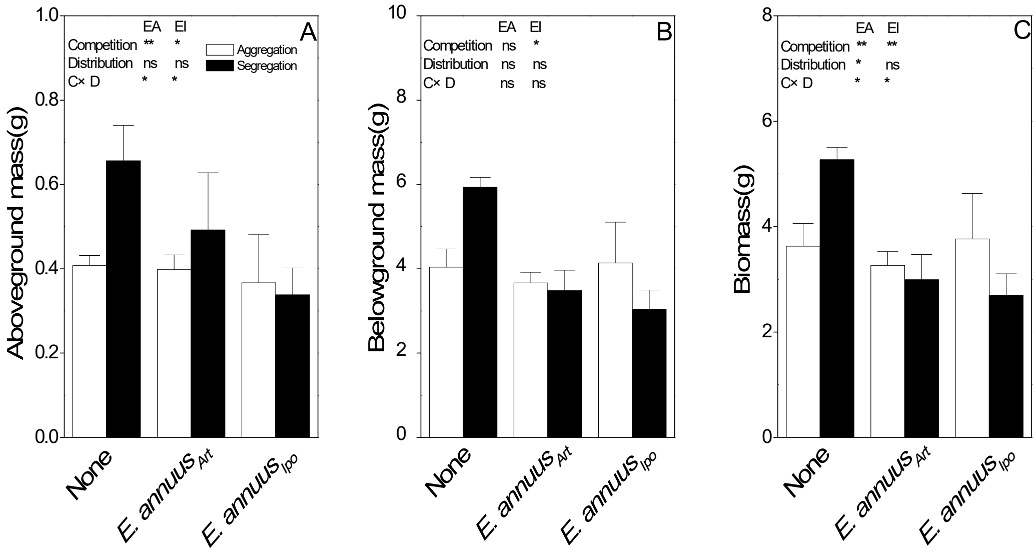

Fig. 4 Effects of competition treatments (None, competition with *Artemisia indica* (*E. annuus*$_{\mathrm{Art}}$) and with *Ipomoea batatas* (*E. annuus*$_{\mathrm{Ipo}}$)) and distribution type (aggregation and segregation) on aboveground merass (A), belowground mass (B) and biomass (C) of *E. annuus* at the group level. Error bar show +SE. Bars sharing the same letters are not different at P=0.05 (*Tukey* tests). Significant result of two-way ANOVAs on the effects of competition (C), distribution (D) and their interaction are indicated. ns, $P \geq 0.05$; *, $P<0.05$; **, $P<0.01$. EA = competition between *E. annuus* and *A. indica*, EI = competition between *E. annuus* and *I. batatas*

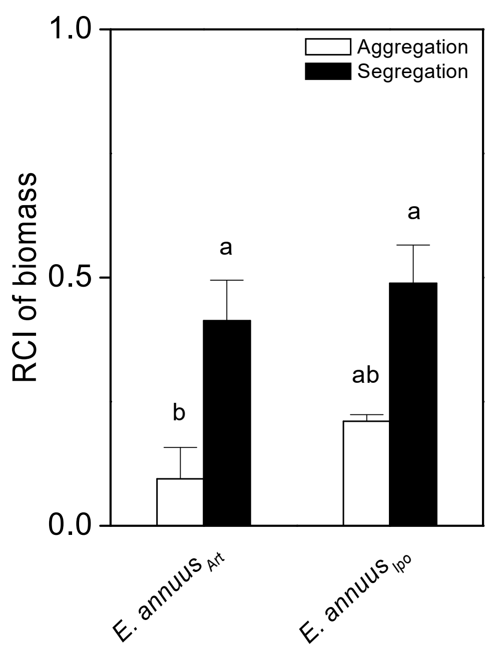

Fig. 5 Interspecific relative competition intensity (RCI) of biomass of *Erigeron annuus* in different competition (competition with *A. indica* (*E. annuus*$_{Art}$) and with *I. batatas* (*E. annuus*$_{Ipo}$)) and distribution (aggregation and segregation) treatments at the group level. Error bar show +SE. Bars sharing the same letters are not different at P=0.05 (*Tukey* tests).

Discussion and conclusion

Although some studies have tested effects of individual-based or group-based interspecific competition on growth of plants (Gough *et al*. 2001), none has examined the effects of both individual-based and group-based interspecific competition on *E. annuus*. Our results indicated individual-based interspecific competition significantly negatively affected on growth of native *A.*

indica and *I. batatas*, but did not affect growth of invasive *E. annuus*. Furthermore, at the group-based interspecific competition, distribution of *E. annuus* can alter interspecific competitive intensity, and aggregation distribution of *E. annuus* increased the interspecific competitive ability.

Be consistent with another studies on *E. annuus*, it demonstrated greater competitive ability than co-existing native species in individual-based competition (Trtikova 2009). Difference in functional traits (i.e. growth traits)between invasive and native species may help to explain the stronger interspecific competitive ability (van Kleunen *et al*. 2010). A high growth rate and the ability to rapidly exploit higher source conditions was widely recognized as a potential determinant of invasion success (Richards *et al.* 2006). As we known, *E. annuus* belongs to composite family had strong reproductive capacity and high propagation rate. The high growth rates allow plants to grow laterally, thereby occupying more space for growth, and also resulted in high annual biomass production (van Kleunen *et al*. 2010). On the other hand, root systems also played a significant role in the growth of *E. annuus*. The belowground mass of *E. annuus* were relative higher under competition treatment. The trait differences reflected the differential ability of species to pre-empt the same resources and increased resource capture in novel environments, resulting in a competitive hierarchy (Herben and Goldberg, 2014). Moreover, that novel chemicals from invaders might have stronger effects on native plants contribute to high performance of invaders with competition. For instance, Uesgi (2013) found a high concentration of *cis*-dehydromatricaria ester (DEM) released by the root of *Solidago altissima* could effectively suppress the growth of competitors that come into contact.

In the group-based competition, spatial distribution might modify the relative strength of intra- and inter-specific competition (Hart and Marshall, 2009). Thus, it had the potential to affect coexistence between invasive and native species. Compared with aggregation, initial ramet segregation significantly decreased aboveground mass and biomass of *E. annuus* in the presence of competition, suggesting that ramet aggregation positively affects the growth of *E. annuus*. The likely reason is that, species aggregation may increase the number of intraspecific contacts relative to interspecific contacts (Neuhauser and Pacala, 1999) and thereby gained a substantial advantage. When interspecific competition was relative weak or absent, aggregation of initial plants may release a higher concentration chemical signal attracting mutualists and altering their metabolism or impacting their soil community mutualists (Morris *et al.* 1998; Fernandez *et al.* 2016). Furthermore, species with tight aggregation become competitively superior for correlated life history traits such as physiological integration or shoot production rate (Winkler *et al*. 1999).

Although the presence of competitors decreased all growth measures of *E. annuus* under segregation treatments, interspecific competition have relatively little effect on the growth of *E. annuus*. The results provided the evidence that difference in distribution of conspecifics can markedly alter competitive interactions. One obvious consequence of species with segregation was to have lower resistance ability (Gough *et al*. 2001). In addition, segregation may was adverse to find available space for roots, it provided a possible explanation for the pattern that the belowground biomass of *E. annuus* was reduced in segregation treatment.

Simultaneously, interspecific competition had negative effects on the growth of two co-existing natives. Our results supported the theory that introduced plants would suppress natives for attaining dominance in their new range (Vila` and Weiner, 2004; He *et al*. 2009; Inderjit *et al*. 2011).

Therefore, *E. annuus* has high individual-based competitive ability, and the aggregation distribution of *E. annuus* can increased the group-based interspecific competitive ability. In our study, *E. annuus* negatively affected growth of common crop *I. batatas* and native herb *A. indica* in the farmland in both levels of competitions. However, allelopathic effects in spatial heterogeneous distribution of *E. annuus* was not analyzed to assess the influence of distribution type of invasive plant. Therefore, further studies should be explore the mechanism of heterogeneous distribution of invasive plant and the interaction of heterogeneous distribution and the invasion process of invasive plants.

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