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Identity recognition and the invasion of exotic plant

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ABSTRACT

Identity recognition (competition or altruism depending on genetic relationship) in plants was reported more infrequently than in animals. Few studies found identity recognition can help reducing competition between kin plants, and increasing population fitness. The exotic invasive plants usually form dense monoculture distribution, but native plants rarely distribute similarly. It might due to the invader had higher identity recognition ability, which could reduce intraspecific competition and enhance overall population fitness. In this study, we compared identity recognition ability between invasive *Eupatorium adenophorum* and two native congeners (*Eupatorium fortunei* and *Eupatorium lindleyanum*) in different nutrient condition and planting density. The results indicated that all three species did not show identity recognition ability in low and intermediate density condition. However, in high density condition, invasive *E. adenophorum* shew higher identity recognition ability than two native congeners. Recognition could alleviate intraspecific competition of invasive *E. adenophorum* through reducing carbon accumulation and RMF, but increasing the height to enhance light use efficiency. This strategy might contribute to high population fitness of *E. adenophorum* when it grew in high densities. This is the first study to explore the relationship between identity recognition and exotic plant invasion.

1. Introduction

Identity recognition (Kin selection) theory, which was proposed by Hamilton (1964), has been proved broadly in animals. This theory is usually used to explain altruism in social animals, and the altruism degree depends on genetic relationship (closer relationship usually indicates greater altruism) (Hamilton, 1963). For example, the probability of the success of an intruder to honeycomb is related with the genetic relationship between the intruder and the defender of the honeycomb, and the possibility is higher for closer intruder (Gadagkar, 1997). Identity recognition allows plant or animal to favor close relatives preferentially over distant relatives, reducing the cost of positive interaction (Waldman, 1988).

Whether identity recognition existing in plants is a hot topic in ecology. In recent years, evidence for identity recognition was found in some plants, and these plants usually grow better when grown together with more closely related plants (Donohue, 2003; Dudley and File, 2007; Murphy and Dudley, 2009; Li et al., 2018). For example, compared with growing singly, the annual plant *Cakile edentula* increased biomass allocation to roots when grown together with strangers (seedlings from different maternal plants of the same species), but not when growing with siblings (seedlings from the same maternal plant) (Dudley and File, 2007). Murphy and Dudley (2009) found that compared with grown singly, *Impatiens pallida* increased leaf to root allocation when grown with strangers, but increased stem elongation and branchiness in response to siblings. Similar patterns were also found in *Arabidopsis thaliana* (Biedrzycki et al., 2010). These results indicate that plant may compete more strongly with strangers than with kins.

Identity recognition can not only adjust biomass allocation strategies to reduce kin competition but also increase defense ability against enemies (Delory et al., 2016; Trewavas, 2016). Karban et al. (2009; 2013) found that *Artemisia tridentata* plants experienced lower leaf herbivory when receiving the cues of volatile chemicals from experimentally clipped close relative than distant relatives. The results indicated that *A. tridentata* respond differently to cues from plants with different phylogenetic distance. For *Ambrosia artemisiifolia* plants grown with close relative to distant relatives, the abundance of beneficial microbes in their mycorrhizal network increased, while the infection of pathogen

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decreased (File et al., 2012). Some studies even found that identity recognition in plants can affect nutrient cycling and nutrient utilization efficiency (Semchenko et al., 2017; Li et al., 2018). However, the mechanisms underlying plant identity recognition are still unclear. Root touch or root exudation may play an important role in identity recognition (Biedrzycki et al., 2010; Chen et al., 2012).

In introduced range, invasive plants are usually distributed in large area with higher densities than in native range, and also than co-occurring native plants (Zheng et al., 2015; Iqbal et al., 2020; Zhao et al., 2020). The difference in identity recognition ability between the invasive and native plant may contribute to their different densities. We postulate that identity recognition ability is higher for invasive plants relative to native plants, i.e., the invader can increase overall population fitness more greatly through adjusting growth strategy to reduce intra-specific competition. To our knowledge, however, no studies have yet compared the difference in identity recognition ability between invasive and native plants.

Eupatorium adenophorum (also known as *Ageratina adenophora* (Sprengel) R. M. King and H. Robinson), native to Central America, is a critical invasive weed in southwest China and still expanding its invaded range into northern and eastern China (Wang and Wang, 2006). Seed production of *E. adenophorum* is very high, and its seed dispersal is mainly by wind. This weed often occurs in dense monocultures in invasive range, suppressing co-occurring native plants significantly (Inderjit Et Al., 2011). It has higher resource-use efficiencies than some native plants (Lei et al., 2012), and can dominate infertile habitats (Feng, 2008). In harsh environments, identity recognition may facilitate *E. adenophorum* to increase population fitness by decreasing intraspecific competition through reducing root mass fraction. Some studies have found that soil nutrient condition and planting density can affect identity recognition ability of plants (Chen and Li, 2015). In this study, we compared identity recognition ability of *E. adenophorum* and its native congeners (*Eupatorium fortunei* and *Eupatorium lindleyanum*) in different nutrient conditions and planting densities. We hypothesize that identity recognition ability is higher for *E. adenophorum* (1) than for the two native congeners, (2) in high relative to low planting density, (3) in low relative to high nutrient condition, (4) and that higher identity recognition ability of the invader causes a reduction in root mass fraction.. There are several levels for identity recognition in plants, seedlings from the same maternal plant; seedlings from same species, and seedlings from different species, etc. (Murphy et al., 2017a). In this study, identity recognition was performed among seedlings from the same species.

2. Materials and methods

2.1. Study site

This study was conducted in a greenhouse of Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences (XTBG-CAS) (21°56′ N, 101°15′E) located in Menglun, Mengla, Yunnan Province, southwest China. In this area, the mean annual temperature is 21.7 °C. In July, the hottest month, the mean temperature is 25.3 °C, and in January, the coolest month, the mean temperature is 15.6 °C. The average annual precipitation of this area is 1557 mm, with a dry period lasting from November to April (Zheng et al., 2020).

2.2. Study materials

Seeds of *E. adenophorum* and the two native congeners (*E. fortunei* and *E. lindleyanum*) were collected in Yunnan Province, China in 2018. For each species, seeds were collected from more than 10 individuals, mixed uniformly, and stored in paper bags, respectively. In May 2019, the seeds were germinated in the greenhouse. In June, when the seedlings were approximately 10 cm tall, they were transplanted into planting boxes, which were 60 cm (length) × 40 cm (width) × 25 cm (depth). Two, four and eight seedlings of each species were grown in each box (density treatments), and the seedlings in each box were separated with plastic board to prevent root interaction of different individuals (no recognition treatment) or not separated as identity recognition treatment (Appendix 1). Half boxes were fertilized with compound fertilizer (nitrogen: phosphorus: potassium 21:8:11) as fertilization treatment (1 g per seedling in August and September, respectively); and half boxes were treated as non-fertilization. In total, we had 180 boxes, i.e., 3 species × 3 density treatments × 2 recognition treatments × 2 nutrition treatments × 5 replicates=180 boxes of plants.

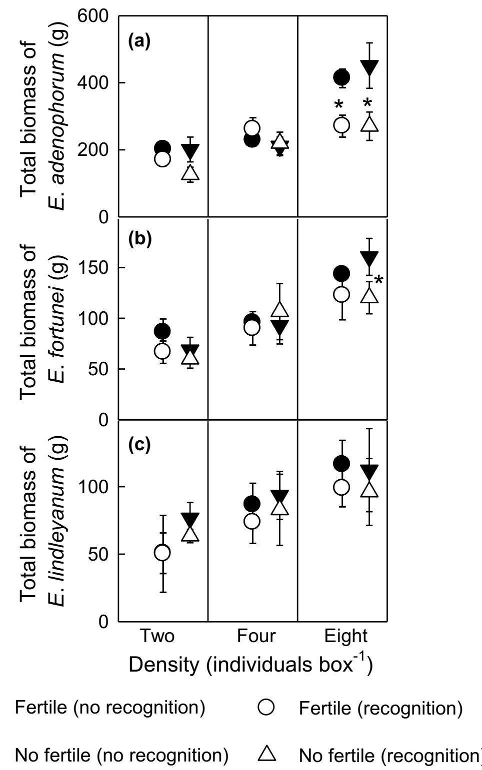

Fig. 1. Total biomass (whole biomass in the box) of *Eupatorium adenophorum* and two native congeners in different density conditions.

2.3. Measurements

In October, height of each individual was determined using a ruler, and all plants were harvested. Before harvest, net photosynthetic rate (P_n) was measured on newly matured leaves of each individual plant using Li-6400 Portable Photosynthesis System (Li-Cor, Lincoln, NE, USA). Light intensity on leaf surface was set at 1000 μmol m^{-2} s^{-1}, CO_2 concentration in reference chamber at 380 μmol mol^{-1}, leaf temperature at 25 °C, and humidity in leaf chamber at 80%. For each individual plant, the root, leaf and support organ (including stem, branch, and petiole) were separated, oven-dried at 60 °C for 72 h, and then weighed. Leaf area was determined using Li-3000A leaf area meter (Li-Cor, Lincoln, NE, USA). According to Feng et al. (2007), root mass fraction (RMF) was calculated as root mass / total individual biomass (the sum of roots, leaves and support organs). Then, total biomass and total leaf area of each box were calculated as the sum of all plant individuals in the box.

2.4. Statistical analysis

Four-way ANOVA was used to detect the effects of species, fertilization treatment, density, recognition treatment and their interactions on each variable. In order to further detect the effects of recognition treatment, the difference in each variable between recognition and no recognition treatments was determined using independent sample *t*-test

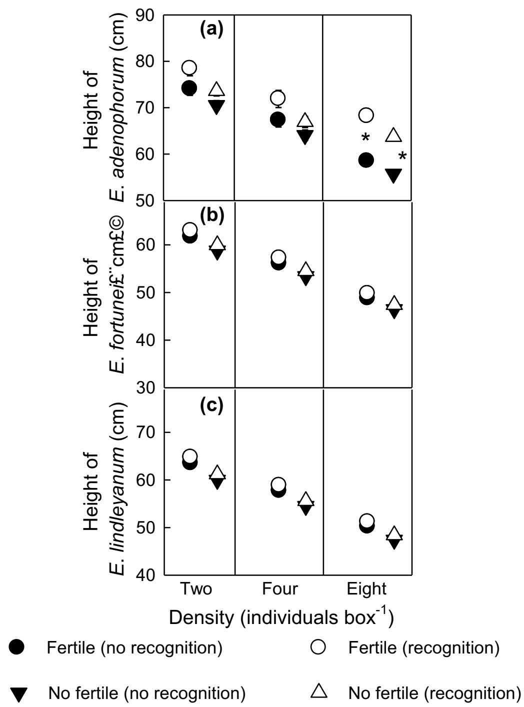

Fig. 2. Height (mean value of each box) of *Eupatorium adenophorum* and two native congeners in different density conditions.

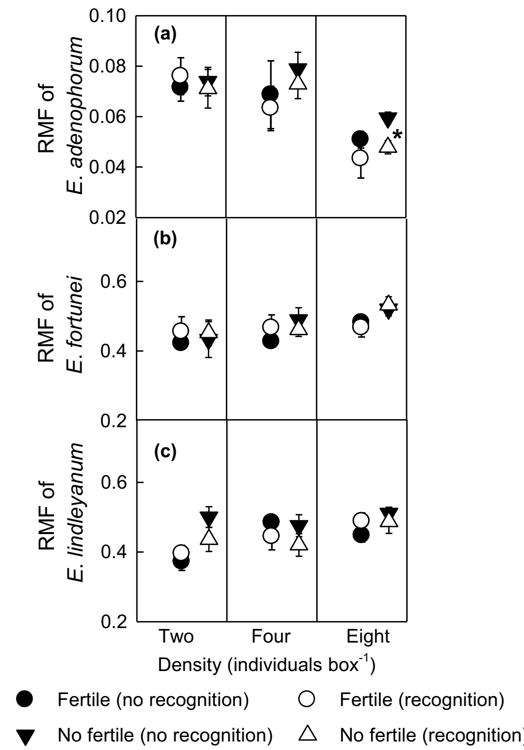

Fig. 3. Root mass fraction (RMF; mean value of each box) of *Eupatorium adenophorum* and two native congeners in different density conditions.

for each plant at each density and nutrient treatment. Linear regression was used to analyze the relationships between total biomass and total leaf area, and between P_n and height.

3. Results

Species and density have significant effects on all five variables, fertilization treatment had significant effects on total leaf area, P_n and height but not for total biomass and RMF, and recognition treatment had significant effects on all variables. The interactions of fertilization and density, fertilization and recognition, and species, fertilization, density and recognition had no significant effects on any variable. However, the interaction of species and fertilization had significant effect on total biomass, the interaction of species and density had significant effects on RMF, total leaf area, P_n and total biomass, the interaction of species and recognition had significant effects on RMF, total biomass and height, and the interaction of density and recognition had significant effects on RMF and total biomass.

Under the highest density treatment (eight individuals per box), recognition relative to no recognition treatment decreased total biomass significantly for *Eupatorium adenophorum* in both fertilization treatments (Fig. 1a), and for *E. fortunei* in no fertilization addition treatment (Fig. 1b), but not for *E. lindleyanum* in either fertilization treatment (Fig. 1c). Recognition relative to no recognition treatment also decreased RMF (only in no fertilization addition treatment with 8 individuals per box, Fig. 3a) and total leaf area (in both fertilization treatments with 8 individuals per box, Fig. 4a), and increased plant height (in both fertilization treatments with 8 individuals per box, Fig. 2a) significantly for *E. adenophorum* in both fertilization treatments, but not for the two native species in either fertilization treatment (Figs. 2–4). Net photosynthetic rates were not influenced significantly by recognition treatment for the invasive and native species (Fig. 5).

Under the lowest and intermediate density treatments (two and four individuals per box), the effects of recognition treatment were not significant for any of the variables of any of the invasive and native species in either fertilization treatment (Figs. 1–5).

For each of the species, total biomass and total leaf area increase significantly with the increase of planting density, while plant height and P_n decrease (Table 1; Figs. 1,2,4,5). With the increase of plantation density, RMF decrease significantly for *E. adenophorum* (Fig. 3a), but not

Table 1
Effects of species, fertile treatment, density, recognition treatment and their interactions on each variable by four way annovas.
(* $P<0.05$; ** $P<0.01$; *** $P<0.001$).

Source	*F* Value Root mass fraction	Total leaf area	P_n	Total biomass	Height
Species	169.6***	236.4***	771.5***	169.6***	374.09***
Fertile treatment	0.012	6.313*	39.5***	0.01	63.94***
density	46.89***	22.96**	453.1***	46.9***	317.19***
Recognition treatment	13.44***	3.62*	45.7***	13.44***	52.58***
Species×Fertile	0.475	0.922	1.19	0.623***	0.80
Species×density	8.89***	4.81**	12.57***	8.89***	0.35
Species×recognition	4.47*	2.18	1.03	4.47*	10.93***
Fertile×density	0.266	0.042	0.802	0.266	0.20
Fertile×recognition	0.507	0.021	0.219	0.507	0.56
Density×recognition	6.87**	1.952	0.646	6.87***	2.06
Species×fertile×density×recognition	0.066	0.765	0.013	0.066	0.003

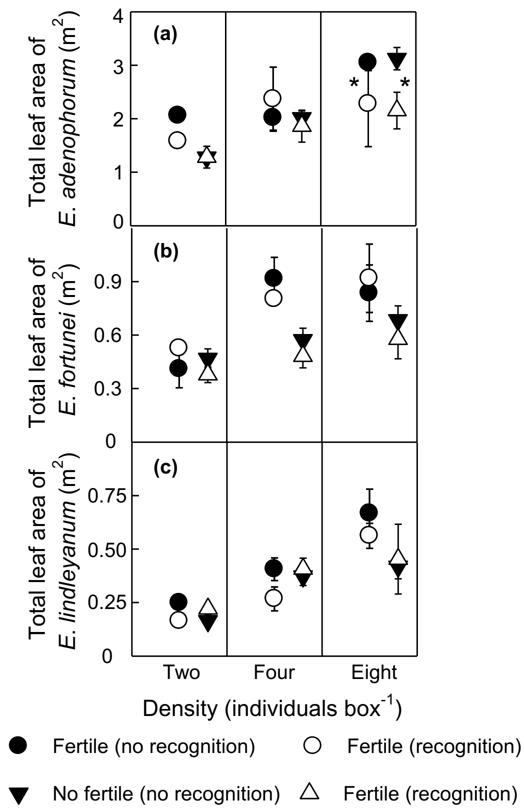

Fig. 4. Total leaf area (whole leaf area in the box) of *Eupatorium adenophorum* and two native congeners in different density conditions.

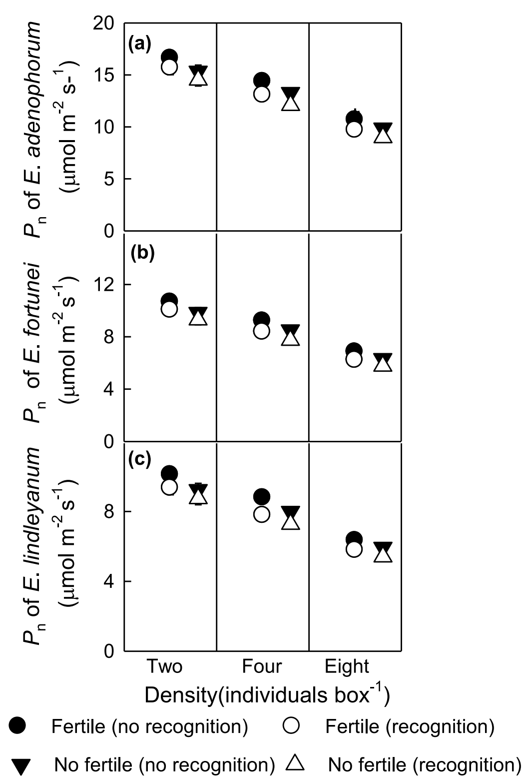

Fig. 5. Net photosynthetic rates (P_n) of *Eupatorium adenophorum* and two native congeners in different density conditions.

for two native plants (Fig. 3b). Biomass is positively correlated with leaf area (Fig. 6a), and height is positively related with P_n (Fig. 6b).

4. Discussion

Consistent with our prediction, invasive *E. adenophorum* show recognition ability in total biomass, height, RMF and total leaf area under highest density (8 individuals per box), but not under the lowest and intermediate density (2 and 4 individuals per box). Except *E. fortunei* show recognition ability in total biomass under highest density (only in no fertile treatment, Fig. 2b), two native congeners did not show recognition ability (Figs. 1–5). Previous study also proved identity recognition responses are species-specific (Murphy et al., 2017b). Lepik et al. (2012) found identity recognition was density-dependent for some temperate grassland plants. In high density, *E. adenophorum* has lower biomass in recognition treatment than in no recognition treatment. It might be due to intraspecific competition was higher in high density condition, and recognition facilitated *E. adenophorum* decreasing biomass allocation to root (Fig. 1a) and leaf area (Fig. 2a), which led to lower biomass of *E. adenophorum*, potentially lowering intraspecific competition. Light is usually poor in high density condition, recognition facilitate *E. adenophorum* decreasing total leaf area but increasing the height (Fig. 5a), which can increase the light use efficiency. Murphy and Dudley (2009) also found identity recognition decreased RMF but increased stem elongation and branchiness for *Impatiens pallida*.These strategies may benefit *E. adenophorum* gaining a reproductive advantage and increase long-term population fitness (Chen et al., 2012; Martín-Forés et al., 2018; Ehlers and Bilde, 2019). In another study, we also found lower biomass but higher reproduction mass fraction for invasive *Chromolaena odorata* than native conspecifics (Liao et al., 2020).

A few studies found that identity recognition might be nutrient-dependent (Palmer et al., 2016; Li et al., 2018). Consistent with our prediction, we also found RMF of *E. adenophorum* and total biomass of *E. fortunei* were significantly different between recognition and no recognition treatments at no fertile condition (Figs. 1–5). Belowground competition usually leads to the increase of RMF (Berendse and Moller, 2009), but in highest density and no fertile treatment, the RMF of *E. adenophorum* in box without separation (recognition) was significantly lower than RMF in box with separation (no recognition, Fig. 3a). It indicated that for *E. adenophorum*, recognition play more important role than belowground competition in this condition (Bhatt et al., 2011). According to the design, identity recognition of invasive *E. adenophorum* may by root communication, because the root communication of each individual is blocked in no recognition treatment. Several studies also found rice recognition was regulated by physical contact of root tips or root exudates (Fang et al., 2013; Wang et al., 2020). In future, we will detect the detailed mechanism of identity recognition of *E. adenophorum*, which may help controlling the spread of *E. adenophorum.*

5. Conclusions

In conclusion, in high density condition, recognition can alleviate intraspecific competition of invasive *E. adenophorum* by reducing biomass accumulation and RMF, but increasing the height to enhance light utilization efficiency. This strategy may contribute to high population fitness of *E. adenophorum* when it grew in high density condition.

CRediT authorship contribution statement

Yu-long Zheng: Conceptualization, Data curation, Writing - review & editing. **Jean H. Burns:** Writing - review & editing. **Rui-fang Wang:** Writing - review & editing. **An-du Yang:** Data curation. **Yu-long Feng:** Writing - review & editing.

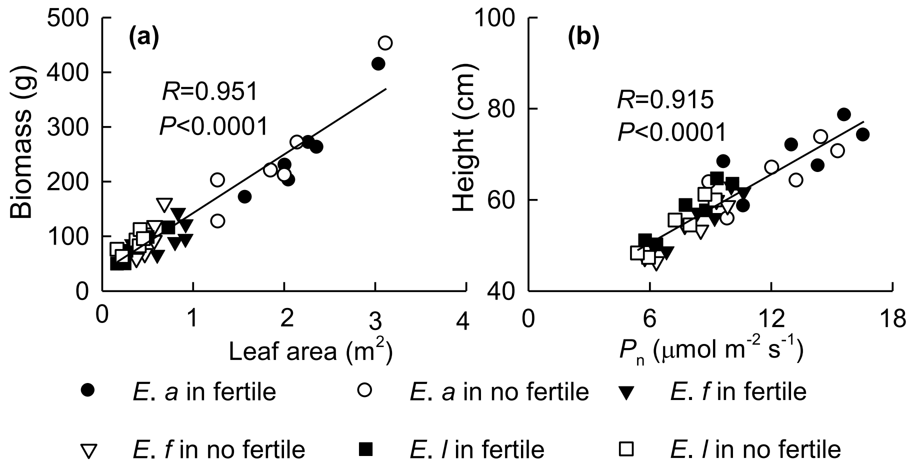

Fig. 6. The relationships of biomass-total leaf area, and net photosynthetic rate (P_n)-height.

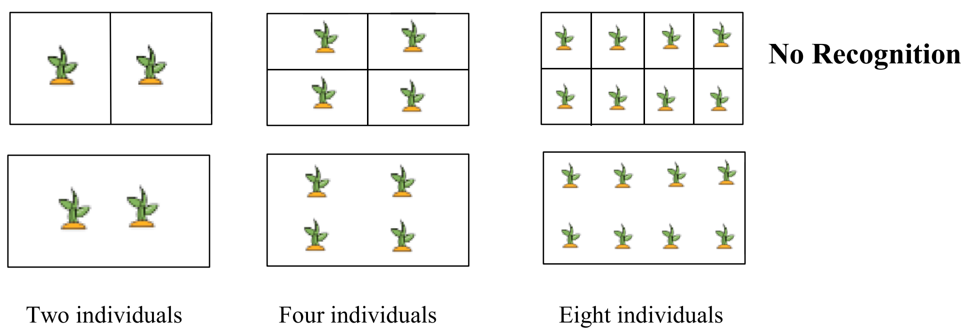

Fig. A1. The planting pattern of each species in this study.

Declaration of Competing Interest

This manuscript has not been published or presented elsewhere in entirety or in part and is not under consideration by another journal. We have read and understood your journal's policies, and we believe that neither the manuscript nor the study violates any of these. There are no conflicts of interest to declare.

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Appendix

See Fig. A1.

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