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Short Communication

The effect of resource pulses on the competitiveness of a tropical invader depends on identity of resident species and resource type

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ABSTRACT

Different species have differential physiological requirements and ecological strategies, and the resident species and resource type may affect invasiveness of alien plants. Resource pulse is an important factor influencing the invasion status of alien plants. Here, we tested the effects of irradiance and nutrient pulse on the competitiveness of the invasive plant *Chromolaena odorata* when cultured with two resident plants, *Abelmoschus manihot* and *Xanthium sibiricum*. Our results suggest that the response of competitiveness to a resource pulse (nutrient and irradiance) depended on species identity – *Chromolaena odorata* was more competitive with *Abelmoschus manihot* than with *Xanthium sibiricum* under resource pulse. Moreover, *Chromolaena odorata* has higher advantage than resident species in competitive conditions but not in monoculture conditions. This study provided information for controlling the future spread of invasive *C. odorata*.

1. Introduction

Invasive plants threaten the integrity and biodiversity of invaded ecosystems, and have become a seriously environmental problem (D'Antonio and Kark, 2002; Zheng et al., 2009). Identifying the factors that contribute to the successful invasion is important for controlling and eradicating invasive plants. Resource variability has a strong influence on both the structure and function of ecosystems (Pederson et al., 2014; Seddon et al., 2016; Leruste et al., 2019). Some studies found invasive plants respond differently from native species to changes in resource availability (Radford, 2013), and resource pulse is an important factor controlling the successful invasion of alien plants (Davis et al., 2000; Thompson et al., 2001; Thomsen et al., 2006; Feng et al., 2007; Besaw et al., 2011; Mallon et al., 2015). Both magnitude and spatial distribution of resource pulses can influence invasion success of *Schismus arabicus* (James et al., 2006). Parepa et al. (2013) also demonstrated that increased nutrient variability significantly promotes the invasion of *Fallopia japonica*. The invasion of knotweed was also facilitated by nitrogen pulse (Parepa et al., 2019). The superior ability of invasive plants to take advantage of variable resources may be a key mechanism of their dominance. However, Li and Stevens (2012) demonstrated that resource pulses will differentially affect different invaders, likely due to the different physiological requirements and ecological strategies of the different species studied. Besaw et al. (2011) found annual and perennial alien plants responded variously to the same resource pulse. The invasion of *Hieracium pilosella* was also halted following abrupt increases in water and nutrient supply (Walker et al., 2005).

Chromolaena odorata (L.) R. M. King and H. Robinson (Compositae) is a perennial shrub, native to North, Central, and South America, and now is a noxious invasive species throughout most of tropical and subtropical Asia, Oceania, and Africa. It was first introduced into India as an ornamental plant in the middle of the 19 th Century, and has become one of the most invasive species in southern China (Qin et al., 2013). *C. odorata* is sparsely distributed in its native ranges but can form dense, mono-dominant stands in nonnative ranges – severely

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affecting agriculture, forestry, stockbreeding, biodiversity, and environments of invaded areas (Zheng et al., 2015).

Irradiance and nutrient are core resources regulating the survival, growth, and distribution of plants (Feng et al., 2007, 2009). In this study, we created irradiance and nutrient pulse environments, and compared the competitive performance of invasive *C. odorata* and two resident plants, *Abelmoschus manihot* and *Xanthium sibiricum*. The main purposes of this study were to detect (1) whether irradiance and nutrient pulse could facilitate the invasion of *C. odorata*, and (2) which traits are mainly related with the advantage of *C. odorata* under resource pulse conditions?

2. Materials and methods

2.1. Study site and materials

This study was carried out at Xishuangbanna Tropical Botanical Garden (21°56′ N, 101°15′ E) of Chinese Academy of Sciences located in Menglun, Mengla County, Yunnan Province, southwest China. The mean annual temperature in this area is 21.7 °C. The mean temperature of the hottest month (July) is 25.3 °C, and of the coolest month (January) is 15.6 °C. The average annual precipitation is 1557 mm, with a dry period lasting from November to April (Zheng et al., 2018).

In 2015, the seeds of *C. odorata*, *A. manihot,* and *X. sibiricum* were collected at Xishuangbanna. Both *A. manihot* and *X. sibiricum* are common and occurs sympatrically with *C. odorata*. For each species, seeds were collected from more than 10 individuals, spaced at least 10 m apart, and mixed uniformly in paper bags. To reduce maternal effects, seeds from the F1 generation (according to the following process) were used. These seeds were germinated in a seedbed in April 2016. Two months later, when the seedlings were approximately 8 cm tall, 90 similarly sized seedlings (30 per species) were planted in a common garden at Xishuangbanna Tropical Botanical Garden. Seeds of each species were collected from these plants and then used in this study.

2.2. Irradiance and nutrient pulse

In this study, we set up two irradiance levels: 20% and 100% of full exposure to sun. The 20% irradiance was created by covering shade houses with two layers of black nylon mesh, and open site as 100% irradiance. The relative irradiance in each shade house was estimated by comparing the integrated photosynthetic photon flux density (PPFD) with that in the open site during a clear day. Quantum sensors and a Li-1400 Datalogger (Li-Cor, Lincoln, NE) were used to measure PPFD. There were five pairs of shade houses and open sites as replicates for 20% and 100% irradiance.

In May 2017, seeds of *C. odorata*, *A. manihot*, and *X. sibiricum* were sown separately into a seedbed in a greenhouse. At the end of July 2017, similar-sized seedlings were transplanted into 10 L pottery pots. The pots were filled with equal proportions of river sand and top layer (0–15 cm) of forest soil (litters, roots and stones were removed). Forty individuals of *C. odorata* were grown alone for a total number of 120 pots. We also transplanted 40 individuals of *C. odorata* into pots with each individual of the two resident species (pairwise competition), with plants 10 cm apart, for a total number of 80 pots. In this study, we also set two nutrient levels: 0.6 g compound fertilizer (nitrogen: phosphorus: potassium 21:8:11) was added into each pot at the end of August as positive nutrient pulse (PNP), and no fertilizer addition as low-nutrient control (LC). Four pots of each species grown alone (or competition with another plant) were divided into each shade house or open site. Two pots were treated as PNP, and the other two pots as LC. At the end of September, half of the pots were switched between 20% and 100% irradiances. This meant that for each species grown alone (or with competition) at each shade house (or open site), one pot with PNP (or LC) was moved to open site, and half pots in open site were also moved to a shade house. Therefore, in this study, there were four irradiance treatments: 20% (stable), 20 → 100% (positive irradiance pulse, PIP), 100% (stable), 100%→20% (negative irradiance pulse, NIP). Fig. S1 shows the details of the experiment design.

2.3. Measurements and calculation

At the end of November, all plants were harvested, and each individual was separated into three parts: roots, leaves, and support organs (including stems, branches, and petioles). Each part was oven dried at 80 °C for 48 h, and the total biomass of each individual was the sum of the three parts. Leaf mass fraction (LMF) and root mass fraction (RMF) were calculated as leaf mass/total biomass and root mass/total biomass, respectively.

Before the harvest, $P_{\max}$ was measured on fully expanded leaves of each species, grown alone, with a Li-6400 Portable Photosynthesis System (Li-Cor, Lincoln, NE). Prior to the measurement, each sample leaf was illuminated with saturated light (1500 μmol mol^{-1}) provided by the LED light of the equipment for 10 min in order to achieve fully photosynthetic induction. Relative humidity and CO_2 concentration of the air in the leaf chamber was controlled at 75% and 380 μmol mol^{-1}, respectively, and the leaf temperature kept at 25 °C.

The competitiveness of *C. odorata* was evaluated by the change of biomass ratio between *C. odorata* and resident species, which was calculated by the following equations:

$\text{Ratio}_{\text{alone}}$ = (Biomass of *C. odorata*): (Biomass of resident) grown alone

$\text{Ratio}_{\text{competition}}$ = (Biomass of *C. odorata*): (Biomass of resident) grown in competition

Competitiveness = the change of biomass ratio = $(\text{Ratio}_{\text{competition}} - \text{Ratio}_{\text{alone}}) / \text{Ratio}_{\text{alone}}$

The same equations were used to calculate the change of LMF, RMF, and $P_{\max}$ ratio between *C. odorata* and resident species.

2.4. Statistical analyses

Three-way ANOVA was used to test the effects of species, irradiance, and nutrient on competitiveness. For each species, one-way ANOVA was used to test the competitiveness differences among treatments. Linear or nonlinear regression was used to analyze the relationship of competitiveness with LMF, RMF, and $P_{\max}$ ratio change. All analyses were carried out using SPSS 18.0.

For each variable, when grown alone, the differences among three species at the same irradiance and nutrient were analysed with one-way ANOVA; when grown in competition, the differences between *C. odorata* and *A. manihot* (or between *C. odorata* and *X. sibiricum*) were evaluated by *t*-test. Levene statistic was used to test homogeneity of variances.

3. Results

Species (S), irradiance (I), and nutrient (N) have significant effects on competitiveness, and their interactions were also significant for competitiveness (Table 1).

When competing with *A. manihot*, at the same irradiance, positive nutrient pulse (PNP) increased the advantage of *C. odorata* except for at 20% irradiance (Fig. 1a), and at the same nutrient, positive irradiance pulse (PIP) and negative irradiance pulse (NIP) also increased the competitiveness of *C. odorata* except for in LC at 20%→100% irradiance (Fig. 1a). When competing with *X. sibiricum*, at the same irradiance, PNP significantly reduced the competitiveness of *C. odorata* in 100%→20% irradiance but significantly increased the competitiveness in 20% irradiance (Fig. 1b), while there were no significant effects on the

Table 1
Effects of species, irradiance, nutrient and their interactions on competitiveness according to a three-way ANOVA.

Source	df	*F*-values	P-values
Species (S)	1	126.11	***
Irradiance (I)	3	11.75	***
Nutrient (N)	1	82.79	***
S × I	3	13.53	***
S × N	1	66.51	***
I × N	3	3.27	*
S × I × N	3	20.45	***

*$P < 0.05$, ***$P < 0.001$.

competitiveness from 20%→100% and 100% irradiances (Fig. 1b); at the same nutrient, irradiance pulse has no significant effects on the competitiveness except for NIP at low nutrient control (LC; Fig. 1b).

When grown in alone, the biomass of *C. odorata* was not higher than two resident species (Fig. 2) but significantly higher than them when grown in competition (Fig. 3). Root biomass fraction of invasive *C. odorata* was significantly higher than resident species when grown in competition (Fig. 5) but not in alone condition (Fig. 4). Competitiveness was significantly and negatively related with RMF ratio change but not significantly related with $P_{\max}$ ratio change (Fig. 6).

4. Discussion

Chromolaean odorata perform better than two resident species when *C. odorata* competed with them (Fig. 3), which indicated that invasive *C. odorata* has a greater advantage than resident species in competitive conditions. The change of biomass allocation might mainly contribute to this pattern, because the relative performance of $P_{\max}$ between *C. odorata* and resident species was not influenced by growing conditions (Fig. S2, 3). In competitive condition, compared with two resident species, *C. odorata* has lower root biomass fraction (Figs. 4 and 5). It indicated that more biomass was allocated to the aboveground parts (leaves and support organs), which could decrease root respiratory load but increase assimilation capability (D'Antonio et al., 2001; Lei et al., 2011) and shade the competitor (Feng et al., 2007). Previous studies also found that the lower root mass fraction and higher aboveground biomass fraction contributed to the successful invasion of the alien plants (te Beest et al., 2009; Zheng et al., 2009; Lei et al., 2011).

Nutrient pulse increased competitiveness greater when *C. odorata* competed with *A. manihot* than when it competed with *X. sibiricum* (Fig. 1). Irradiance pulse also significantly increased the competitiveness when *C. odorata* competed with *A. manihot* but has no effect on competitiveness when *C. odorata* competed with *X. sibiricum* except under LC in 20% irradiance (Fig. 1). It indicated that resource pulse (nutrient and irradiance) disproportionately influences the relative performance between *C. odorata* vs *A. manihot* and *C. odorata* vs *X. sibiricum*. The interactive effect of species and grown condition (alone or in competition) was significant on RMF but not significant on $P_{\max}$ (Table S1), and competitiveness was significantly and negatively related with RMF ratio change (Fig. 6) but not significantly related with $P_{\max}$ ratio change (Fig. S4). This proved that variation of biomass allocation caused by resource pulse mainly contributed to the inconsistent competitiveness pattern when *C. odorata* competed with *A. manihot* and *X. sibiricum*. Some studies also found the effect of resource pulses on invasion success depends on the resource type and identity of the neighbor plant (Walker et al., 2005; Radford, 2013; James et al., 2006). Furthermore, disturbance is one important factor that facilitates the invasion of alien plants (MacDougall et al., 2009; Maron et al., 2014), and its effect may be related with the resource pulses because disturbances usually cause the pulse of some resources (Radford, 2013).

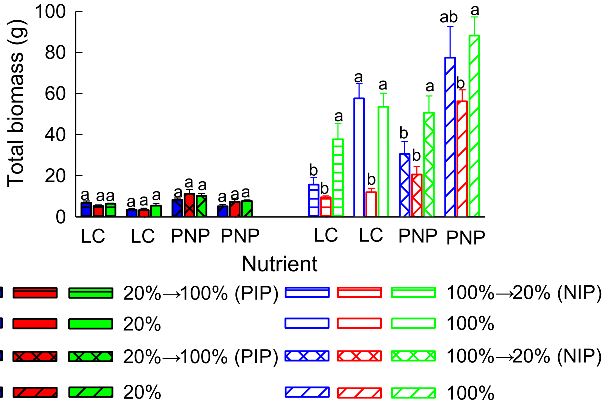

Fig. 2. The total biomass of *Chromolaena odorata* (blue), *Abelmoschus manihot* (red), and *Xanthium sibiricum* (green) when grown alone. LC: low-nutrient control; PNP: positive nutrient pulse; PIP: positive irradiance pulse, NIP: negative irradiance pulse. Different letters indicated there were significant differences among *C. odorata*, *A. Manihot* and *X. sibiricum*. . (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

In conclusion, *C. odorata* has higher performance than resident species in competitive condition but not in monoculture condition. The response of competitiveness to resource pulse (nutrient and irradiance) depends on species identity, and competitiveness was higher when *C. odorata* competed with *A. manihot* than when it competed with *X.*

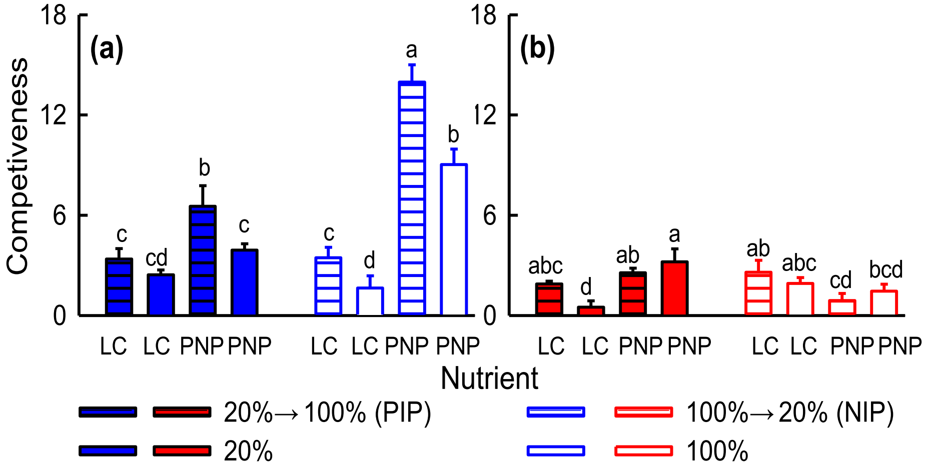

Fig. 1. The competitiveness of *Chromolaena odorata* when grown with *Abelmoschus manihot* (**a**) and *Xanthium sibiricum* (**b**). LC: low-nutrient control; PNP: positive nutrient pulse; PIP: positive irradiance pulse; NIP: negative irradiance pulse.

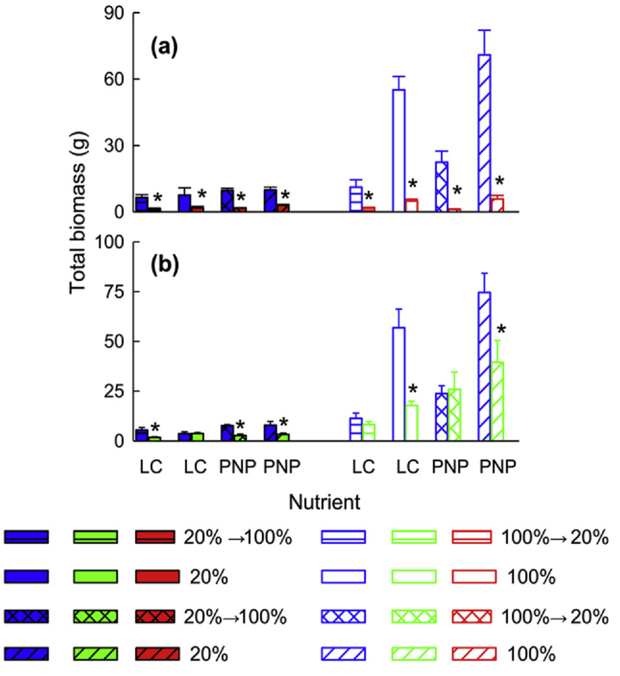

Fig. 3. The total biomass (**a**) of *Chromolaena odorata* (blue) and *Abelmoschus manihot* (red) when grown together; and the total biomass (**b**) of *Chromolaena odorata* (blue) and *Xanthium sibiricum* (green) when grown together. LC: low-nutrient control; PNP: positive nutrient pulse; PIP: positive irradiance pulse, NIP: negative irradiance pulse. The meaning of each legend is the same with Fig. S2. Asterisk indicated there was significant difference between *C. odorata* and *A. manihot* (or *X. sibiricum*). . (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

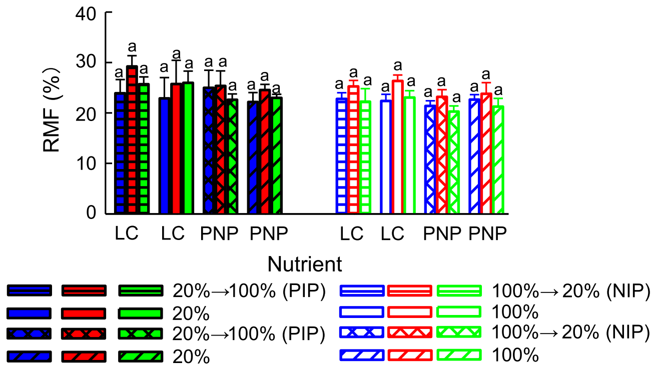

Fig. 4. The RMF of *Chromolaena odorata* (blue), *Abelmoschus manihot* (red) and *Xanthium sibiricum* (green) when grown alone. LC: low-nutrient control; PNP: positive nutrient pulse; PIP: positive irradiance pulse, NIP: negative irradiance pulse. Different letters indicated there were significant differences among *C. odorata*, *A. Manihot* and *X. sibiricum*. . (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

sibiricum.

Author contributions

YLZ designed experiment, YZL, ADY and LL collected data, YLZ and ZYL analysed data, YLZ, ZYL, WTL, RFW, YGZ and YLF wrote or revised the manuscript.

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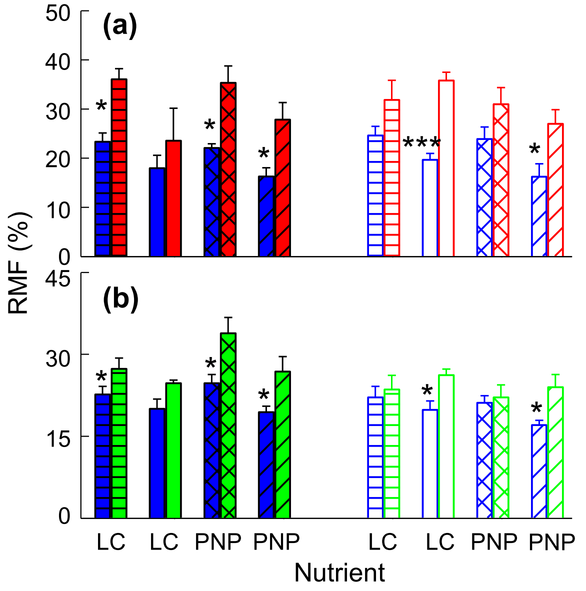

Fig. 5. The RMF (**a**) of *Chromolaena odorata* (blue) and *Abelmoschus manihot* (red) when grown together; and the $P_{\max}$ (**b**) of *Chromolaena odorata* (blue) and *Xanthium sibiricum* (green) when grown together. LC: low-nutrient control; PNP: positive nutrient pulse; PIP: positive irradiance pulse, NIP: negative irradiance pulse. The meaning of each legend is the same with Fig. S6. Asterisk indicated there was significant difference between *C. odorata* and *A. manihot* (or *X. sibiricum*). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

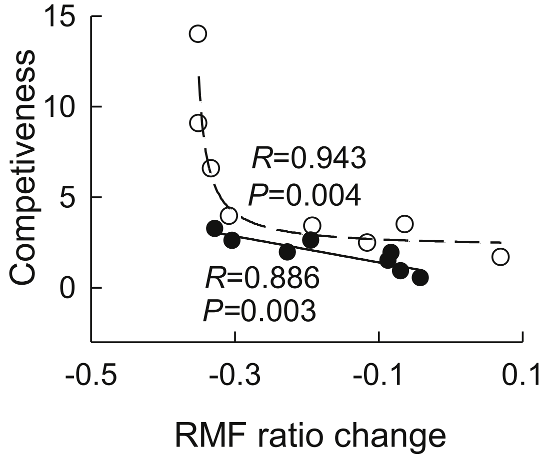

Fig. 6. The relationship between competitiveness and RMF ratio change. Open circles indicated the relationship when *C. odorata* competed with *A. Manihot*, and black circles indicated the relationship when *C. odorata* competed with *X. sibiricum*.

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Declaration of competing interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.actao.2019.103507.

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