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Short Communication

Extension of the EICA hypothesis for invasive *Chromolaena odorata*

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ABSTRACT

Invasive plants usually occur in limited areas in their native range but may spread into diverse environments in non-native ranges. Therefore, besides increasing competitive ability, evolution may also increase the tolerance of invading plants to environmental stress. In our previous study, we found that evolution facilitates invasive *Chromolaena odorata* by increasing the allelopathic effect. In this study, we compared drought tolerance of *C. odorata* between six native and six non-native populations. The results indicated that invasive *C. odorata* displayed higher drought tolerance than native conspecifics. This study proved that invasive *C. odorata* had not only evolved increased competitive ability but also drought tolerance, which may have contributed to its wide distribution in non-native ranges.

1. Introduction

The Evolution of Increased Competitive Ability (EICA) hypothesis proposes that when introduced into non-native habitats, invasive plants may reallocate resources from defense to growth in response to the absence of natural predation (Blossey and Notzold, 1995). Muller--Scharer et al. (2004) further refined the EICA hypothesis proposing that, in the non-native habitats, invasive plants may adjust the allocation of resources from high-cost quantitative defenses (i.e., resisting specialist herbivores) to growth and low-cost qualitative defenses (i.e., resisting generalist herbivores). The lack of natural predation may play a role in the greater competitive ability of invasive plants (Lakeman-Fraser and Ewers, 2013), but invasion success also strongly depends on local environmental conditions (Siemann et al., 2017).

Some studies found that invaders could rapidly adapt to local environmental conditions (Buswell et al., 2011; Zenni et al., 2014), enhancing their spread into diverse environments in novel ranges. Consequently, as an extension of EICA, it is reasonable to infer that the invader not only responds evolutionarily to biotic factors, such as the lack of predation and competitor shift, but also to abiotic factors, such as water and nutrient conditions, among others. For example, Dlugosch et al. (2015) found that different species compositions present in native and non-native habitats contributed to the evolution of drought stress tolerance in invasive *Centaurea solstitialis* L. In addition, Qin et al. (2013) and Li et al. (2020) showed that the relative performance between native and invasive populations of *Chromolaena odorata* depended on nutrient conditions.

Chromolaena odorata (L.) R. M. King and H. Robinson is native to Central and South America but is now recognized as an invasive species in most tropical and subtropical regions of the world (Zheng et al., 2015), from rainforests to savannas (Derouw, 1991; Wei et al., 2017). In the present study, we hypothesized that when a species is introduced into a new habitat, natural selection may favor an increase in drought tolerance of the invader. To test this hypothesis, we compared drought tolerance between invasive and native *C. odorata* plants in a common garden under drought and control conditions.

2. Material and methods

2.1. Materials

Seeds of *C. odorata* were collected in 2009 from the native range (Central and South America) as well as from the non-native range (Asia) (Table 1). Seeds of 10 individuals spaced at least 20 m apart were collected from each population. These seeds were germinated, and seedlings were planted in a common garden at the Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences as a genotype bank.

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Table 1
Background information on locations of sampled populations of *Chromolaena odorata* for comparison of drought resistance in native and non-native populations.

Population	Latitude/longitude	Elevation (m)
Natives		
Pinardel Río, Cuba	N22°45′/W82°50′	565
Martin, Florida, USA	N27°06′/W80°15′	1–5
Coahuayana, Michoacan, Mexico	N19°01′/W103°36′	950
Sur de Cd. Victoria, Mexico	N23°40′/W99°11′	600
Ponce, Puerto Rico	N18°11′/W66°51′	300
Manati, Puerto Rico	N18°47′/W66°47′	390
Non-natives		
Nakorn Nayok, Thailand	N14°25′/E101°23′	739
Vientiane, Laos	N17°58′/E102°37′	170
Menglun, Yunnan, China	N21°56′/E101°15′	544
Simao, Yunnan, China	N22°46′/E100°56′	1380
Jingdong, Yunnan, China	N24°17′/E100°50′	1263
Melaka, Malaysia	N 2°22′/E102°21	50

2.2. *Comparison of drought tolerance between native and invasive C. odorata*

In April 2013, we randomly selected *C. odorata* seeds from 6 native and 6 non-native populations from the genotype bank to germinate in a greenhouse. In June 2013, when the seedlings were approximately 6 cm tall, 120 similar sized seedlings (10 individuals per population) were transplanted into 15 L pottery pots (one seedling per pot). The pots were filled with equal proportions of river sand and a top layer (0–15 cm) of forest soil. All pots were placed in the greenhouse, and the seedlings were watered at two different levels, 1500 mL per seedling every 2 weeks (drought conditions) and 1500 mL per seedling every 3 days (control) from July to September 2013.

In September 2013, the photosynthetic response to drought stress was measured. At approximately 10:00 A.M., when studied plants were known to achieve the highest daily photosynthetic rates, net light saturated photosynthetic rate (P_n) was measured using a Li-6400 Portable Photosynthesis System (Li-Cor, Lincoln, NE, USA) under 1000 μmol m^{-2} s^{-1} photosynthetic photon flux density. Relative humidity and CO_2 concentration in the reference chamber as well as leaf temperatures were maintained at 80%, 400 μmol mol^{-1}, and 22 °C, respectively. Leaf chlorophyll fluorescence was measured using a Dual PAM-100 fluorometer (Heinz Walz, Effeltrich, Germany). The following chlorophyll fluorescence parameters were calculated:

$F_v/F_m = (F_m - F_o)/F_m$ (1);

$Y(II) = (F_m' - Fs)/F_m'$ (2);

$Y(NO) = F_s/F_m$ (3);

and

$$Y(NPQ) = F_s/F_m' - F_s/F_m \tag{4}$$

(Hendrickson et al., 2004; Huang et al., 2013), where F_o is the minimum fluorescence in the dark-adapted state, F_m and F_m' are the dark-adapted and light-adapted (800 μmol m^{-2} s^{-1}) maximum fluorescence upon illumination of a pulse (300 ms) of saturating light (10,000 μmol m^{-2} s^{-1}), respectively, F_v/F_m is the maximum quantum yield of photosystem II (PSII) after dark adaptation, F_s is the light-adapted steady state fluorescence, and Y(II) is the effective quantum yield of PSII. Additionally, Y(NO) is the fraction of energy that is passively dissipated in the form of heat and fluorescence, and Y(NPQ) is the fraction of energy dissipated in the form of heat via the regulated non-photochemical quenching mechanism.

Drought-induced change in each parameter was calculated as

(the value in drought − the value in control)/(the value in control) (5)

2.3. *Statistical analysis*

Differences between the changes in each of the parameters of native and invasive *C. odorata* were compared via *t*-test (mean value of each population as replicates). The differences of Y(II) and Y(NO) between *C. odorata* and resident plants were compared via one-way analysis of variance. The analyses were performed using SPSS ver. 16.0 for Windows (SPSS, Inc., Chicago, Illinois, USA).

3. Results and discussion

Following a water deficient period of 2 months, the increases in F_o (Fig. 1a) and Y(NO) (Fig. 3a) were significantly greater for native *C. odorata* populations than those for non-native populations, and the decreases in F_m, F_v/F_m, P_n, and Y(NPQ) were also significantly greater for native populations than those for non-native populations (Figs. 1b, 2a and 2b, 3b). However, there were no significant differences among F_o, F_m, F_v/F_m, P_n, Y(NO), and Y(NPQ) in the control treatment (Figs. 1–3).

Following a drought treatment lasting 2 months, the increase in F_o (Fig. 1a), the decrease in F_m (Fig. 1b), and F_v/F_m (Fig. 2a) were greater in native *C. odorata* populations than in non-native populations, indicating that photo damage for native populations was higher than that for non-native populations.

A high Y(NO) (the fraction of energy that is passively dissipated in the form of heat and fluorescence) value reflects the inability of a plant to protect itself against damage due to excessive light energy (Busch et al., 2009; Huang et al., 2013). Additionally, a high Y(NPQ) (the fraction of energy dissipated in the form of heat via the regulated non-photochemical quenching mechanism) value indicates the inability of the plant to protect itself by dissipating excess light energy (Klughammer and Schreiber, 2008). Following a drought treatment lasting 2 months, the increase in Y(NO) and the decrease in Y(NPQ) were higher for native *C. odorata* than for invasive conspecifics (Fig. 3), suggesting that invasive *C. odorata* populations were more drought tolerant than native populations. This finding agrees with results of Hodgins et al. (2020) who also reported that invasive *Cirsium arvense* displayed higher performance and nutrient stress tolerance than native populations.

In conclusion, our results indicated that following 2 months of drought treatment, the increase in Y(NO) was significantly lower in invasive *C. odorata* than in native *C. odorata*. Thus, in an introduced range, natural selection may favor genotypes of *C. odorata* with stronger drought tolerance, leading to invasive *C. odorata* developing a higher degree of drought tolerance than native conspecifics.

As an evolutionary strategy, increased drought tolerance may favor the spread of invasive plants in an introduced region. Thus, this study provides an example for the extension of EICA theory, which contends that evolution improves competitive ability of the invader not only by increasing growth or allelopathy but also by increasing tolerance to harsh environmental conditions.

Author contributions

YLZ designed experiment; YLZ and WTL collected and analyzed data; WTL, YLZ and RFW wrote or revised the paper.

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These have been reviewed.

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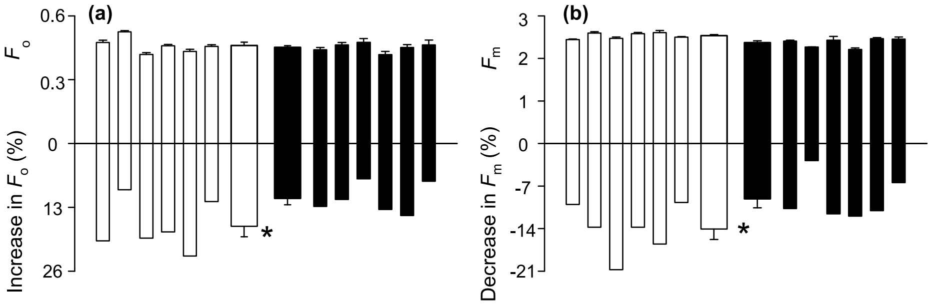

Fig. 1. Minimum fluorescence in the dark-adapted state (F_o) (a) and dark-adapted maximum fluorescence upon illumination of a pulse of saturating light (F_m) (b) of invasive (indicated by black bars) and native *Chromolaena odorata* (indicated by white bars), above the midline, and their changes following drought treatment, below the midline. Narrow bars indicate the mean ± standard error (SE) for each population. The two thicker bars in the center depict the mean ± SE for *C. odorata* from each range (* indicates significant differences between native and invasive *C. odorata*, $P < 0.05$).

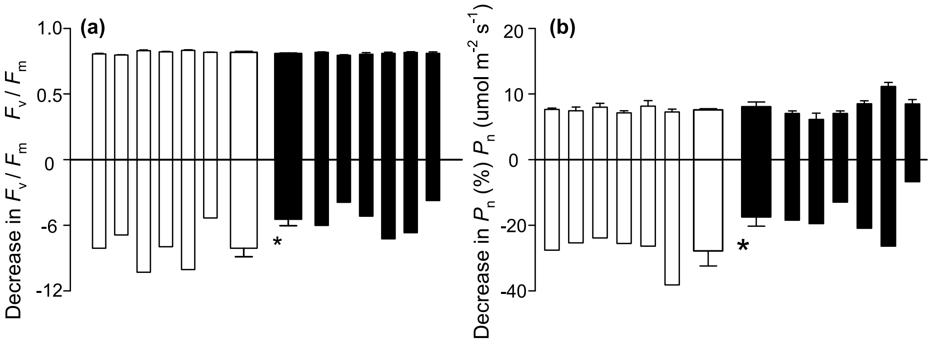

Fig. 2. The maximum quantum yield of PSII after dark adaptation (F_v/F_m) (a) and net light saturated photosynthetic rate (P_n) (b) of invasive (indicated by black bars) and native *Chromolaena odorata* (indicated by white bars) (above the midline) and their changes following drought treatment (below the midline). Narrow bars indicate the mean ± standard error (SE) for each population. The two thicker bars in the center depict the mean ± SE for *C. odorata* from each range (* indicates significant differences between native and invasive *C. odorata*; $P < 0.05$).

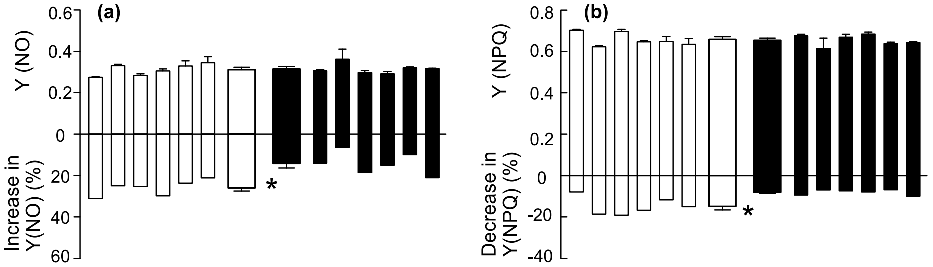

Fig. 3. The fraction of energy that is passively dissipated in the form of heat and fluorescence (Y (NO)) (a) and the fraction of energy dissipated in the form of heat via the regulated non-photochemical quenching mechanism (Y(NPQ)) (b) of invasive (indicated by black bars) and native *Chromolaena odorata* (indicated by white bars) (above the midline), and their changes following drought treatment (below the midline). Narrow bars indicate the mean ± standard error (SE) for each population. The two thicker bars in the center depict the mean ± SE for *C. odorata* from each range (* indicates significant differences between native and invasive *C. odorata*, $P < 0.05$).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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