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Biomass reallocation and increased plasticity might contribute to successful invasion of *Chromolaena odorata*

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ABSTRACT

Invasive plants are often genetically different from their native conspecifics. In the introduced range, the evolution of functional traits or plasticity might occur as an adaptive response to novel environmental pressures. *Chromolaena odorata* originates from the Americas, but now is a noxiously invasive species in some other tropical and subtropical areas. In this study, plant growth, morphology, photosynthesis and plasticity were compared between *C. odorata* plants from five introduced and five native populations under three light intensities (low, medium and full light). Compared to native *C. odorata*, introduced conspecifics had higher height under medium and full light, but lower root to shoot biomass ratio across all light conditions, and lower leaf N under medium light. This indicates genetic differences between native and introduced *C. odorata*. Furthermore, plasticity was higher for introduced *C. odorata* plants than for native conspecifics under various light environments. Our results indicate that biomass reallocation (from belowground into aboveground) and stronger plasticity could contribute to successful invasion of introduced *C. odorata* in frequently disturbed environments.

1. Introduction

One of the popular hypotheses in invasion biology is that invasive species often perform better in the introduced range than in their native range (Blossey and Nötzold, 1995). Rapid adaptive evolution might contribute to increased performance of invasive plants in the introduced range (Bossdorf et al., 2005). However, most studies focused on differences in functional trait means between introduced and native populations (evolution of traits, Matesanz et al., 2010), whereas phenotypic plasticity (i.e. the responses of these traits to different environmental conditions) were seldom compared (Bossdorf et al., 2005; Matesanz et al., 2010).

Phenotypic plasticity is crucial for invasive plants to colonize new environments as it increases ecological breadth and potentially available resources, thus facilitating performance and invasion especially in changing environments (Sultan and Bazzaz, 1993; Ghalambor et al., 2007; Matesanz et al., 2010). A plant's ability to compete for light is crucial for its fitness. Traits related to light capture and utilization efficiency (Martin and Pfennig, 2009; Valladares and Niinemets, 2008) and plastic responses of these traits are directly related with the performance of plants under different light conditions (Corliss and Sultan, 2016; Liu et al., 2016; Matesanz et al., 2010; Sultan et al., 2013). Highly disturbed habitats are usually easily invaded, which might be due to disturbance usually causing light variation in an ecosystem, in which invasive plants have a higher performance and stronger plastic responses than native species (Martin et al., 2009; van Kleunen et al., 2015). Moreover, natural selection might increase the performance and plasticity of invasive plants even further. However, studies comparing functional traits and plasticity between introduced and native populations of invasive species are inconsistent (Corliss and Sultan, 2016; Flory et al., 2011; Sultan et al., 2013; Zhang et al., 2015). For example, Flory et al. (2011) found that introduced *Microstegium vimineum* populations accumulated consistently greater biomass under both shade and sun conditions than native populations, but they found no differences in

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plasticity of growth across light treatments. Sultan et al. (2013) found that invasive *Polygonum cespitosum* genotypes had higher reproductive output when grown in open, sunny conditions, but its plasticity was higher when grown in moist and sunny conditions.

Chromolaena odorata (L.) R. M. King & H. Robinson (Asteraceae) is a perennial subshrub, which is native to the Americas. It is now widely distributed in (sub-)tropics of the Old World (Kriticos et al., 2005), and has become one of the worst terrestrial invasive plants in these regions. It is distributed sparsely in the native range (Zachariades et al., 2009), while it can form dense mono-dominant stands in the introduced range, especially in greatly disturbed habitats (Honu and Dang, 2000; Zheng et al., 2015). Stronger adaptation to various light environments is thought to be important for its successful invasion (Cabi, 2018). Since rapid adaptive evolution might contribute to this adaptive ability, we hypothesized that *C. odorata* plants from introduced populations have higher performance and plasticity than their conspecifics from native populations under various light environments.

In order to test our hypothesis, *C. odorata* from five introduced and five native populations were grown under three light intensities (i.e. low, medium and full light). Growth and functional traits related to light capture and utilization ability were compared between introduced and native *C. odorata*. Specifically, we asked the following questions: (1) Do plants from introduced *C. odorata* populations show a stronger plastic response to the light treatment than plants from native populations? (2) Do plants from introduced *C. odorata* populations perform better than plants from native populations?

2. Materials and methods

2.1. Study site and seed materials

This study was carried out in Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences (21°56′N, 101°15′E, 560 m above sea level), Yunnan Province, southwest China. The mean annual temperature is 21.7 °C, with a mean of 25.3 °C in the hottest month (July) and 15.6 °C in the coolest month (January). The annual precipitation is about 1500 mm, of which 87% falls in the rainy season from May to October (Feng et al., 2002). Seeds of *C. odorata* from five native and five introduced populations were used in this study (Table 1). Within each population, seeds were collected from 10 to 15 individuals (i.e. seed families) that were at least 10 m apart. All seeds were kept separately in paper envelopes at room temperature until sowing.

Table 1
Locations of the 10 sampled *Chromolaena odorata* populations from the native and the introduced range and the number of seed families included in the experiment.

Location	Latitude	Longitude	Elevation (m)	Seed families
Native				
Mamoral, Trinidad & Tobago	N 10°27′	W 61°17′	63	7
Felicity, Trinidad & Tobago	N 10°31′	W 61°25′	10	9
Chiapas, Mexico	N 16°44′	W 93°09′	640	10
Quintana Roo, Mexico	N 18°38′	W 88°47′	29	10
Veracrus, Mexico	N 19°23′	W 96°58′	1160	13
Introduced				
Melaka, Malaysia	N 2°22′	E 102°21′	50	11
Central Province, Sri lanka	N 7°11′	E 80°25′	451	12
Iligan city, Philippines	N 8°10′	E 124°10′	107	13
DongNai Province, Vietnam	N 11°22′	E 107°24′	125	10
Vientiane, Laos	N 17°58′	E 102°37′	170	7

2.2. Experimental design

Seeds from each seed family were sown on 6 March 2010 separately in seedling trays which were filled with sand and forest topsoil (volume ratio 1:1). Seedling trays were placed in a shade house with one layer of black nylon mesh (*c*. 50% of natural irradiance based on manufacturer's information of nylon mesh) for germination. On 1 June 2010, when seedlings were about 10 cm in height, they were transplanted into 15 L pots (each pot containing one seedling). Pots were filled with a mixture of 70% topsoil of a secondary forest (dominated by *Phoebe lanceolata* and *Castanopsis indica*; plant litter, roots and stones were excluded) and 30% river sand. All plants were grown under 50% irradiance for 2 weeks to overcome the transplant shock. In order to ensure that each treatment had similar genotypes, three individuals from each seed family were divided into three groups and then were separately moved into three shade houses. Due to failure of germination in some families, 7–13 seed families for each population were included in the experiment.

To minimize differences in other environmental factors, three similar shade houses were built (each room size: length × width × height: 10.0 m × 5.0 m × 2.5 m). The lower 30 cm of the shade houses were left open to facilitate ventilation and also to allow herbivores moving in and out freely. Shade treatments were created by covering the shade houses with different layers of black nylon mesh: two layers of mesh to achieve low light, one layer of mesh for medium light, and no shade mesh for the full light treatment. Relative light intensity in each shade treatment was estimated by comparing the integrated photosynthetic photon flux density (PPFD) over six consecutive clear days during the experimental period (Fig. S1). Four quantum sensors (one in full light and one in medium and two in low light treatment; Hobo Weather Stations data logger) were mounted and leveled at 1.5 m above-ground height to quantify PPFD. Similar with many previous studies, we had no replication of the shade house for each treatment, and the seedlings in each shade house were used as replicates for statistical analyses (Baltzer and Thomas, 2007; Semchenko et al., 2012; Zheng et al., 2012).

All pots were fertilized monthly from July to November by granules of compound fertilizer (N:P:K, 15:15:15; Nitrophosha R, BASF, Belgium) at the rate of 4 g per pot. All pots were watered from the top until saturation every one to two days when necessary. All plants remained healthy and no obvious herbivore damage was observed during the experiment. In order to avoid position effects during the experimental period, all pots were rerandomized every two weeks within each shade house.

Two weeks after the transplantation, plant height was measured as initial plant size. In October 2010, six individuals per population per light treatment were used to determine photosynthetic ability by using a Li-6400 Portable Photosynthesis System (Li-Cor, Lincoln, NE). The seed families were randomly selected before our measurement, and individuals from the same seed family in different light treatments were used. For all measurements, a recently matured leaf (the fifth or sixth leaf from the top of the main stem) was used. Plants were watered a day before the measurement to minimize the effects of variation in water availability on plant performance. A preliminary measurement was carried out to detect the saturating light intensity for plants grown under different light intensities. The same saturating light intensity was used for all plants grown under different shade treatments, because no photoinhibition was observed during measurements. Thus, all photosynthetic measurements were carried out under PPFD of 1500 μmol m^{-2} s^{-1} and at a CO_2 concentration of 400 μmol mol^{-1}. Relative humidity of the leaf chamber was kept at about 70%, and leaf temperature was kept at about 30 °C. All leaf samples were illuminated with saturating PPFD by a LED light source in the leaf chamber for 5–10 min before measurement. The maximum photosynthetic rate (A_{max}, μmol$m^{-2}s^{-1}$) was recorded when photosynthetic rate and stomatal conductance were relatively constant.

After the photosynthetic measurements, leaf samples were taken for measurements of specific leaf area (SLA, $m^2 g^{-1}$) and leaf nitrogen (N, $g m^{-2}$) content. For each SLA measurement, 3–5 recently matured leaves of each individual were chosen (all plants were sampled and leaves used for the photosynthetic rate measurements were included). Leaf area was determined by using a Li-3000C portable area meter (LI-COR, Lincoln, NE) and then leaves were oven dried at 60 °C for 72 h. SLA was determined as the ratio of leaf area to dry mass of the leaves. Leaf samples were then ground and used for leaf N content measurements. Leaf N content was determined by using a Vario MAX CN Element Analyzer (Elementar Analysensysteme, Hanau, Germany).

In mid-December 2010, all plants were harvested. Before the harvest, the height of each plant was recorded. Plants were separated into leaves, stems and roots, oven dried at 80 °C for 72 h until constant weight and then weighed. Total biomass was determined as the sum of leaf, stem and root biomass. Root to shoot ratio (RTSR, $g g^{-1}$) was calculated as the ratio of root to aboveground biomass, and total leaf area (TLA, cm^2) was calculated as leaf mass × SLA of each individual.

2.3. Data analysis

We ran linear mixed-effects models in order to detect the overall effects of light treatment and plant origin (introduced vs. native range) and their interaction on plant growth, morphological and eco-physiological traits. Light, origin and their interaction were treated as fixed factors. Population nested within origin was treated as random factor. Initial plant size was used as covariate when analysing plant growth and morphological traits. Kenward-Roger degrees of freedom approximation were applied to account for unbalanced replicates of each population in plant growth, morphological traits and SLA. A significant origin effect would indicate genetically based differentiation of a trait between plants from the introduced and native range, a significant light effect would indicate an overall plastic response of a trait to the light treatments, and a significant origin by light interaction would indicate a genetic difference in plasticity of a trait between plants from the two ranges in response to different light intensities. For each species, the emmeans package (Russell, 2018) was used to conduct post-hoc Tukey's tests for multiple comparisons of trait differences between native and introduced populations under each light environment when origin by light interaction was significant. Data were either square-root or natural-logarithm transformed to improve normality when necessary. Analyses were carried out using the lmerTest package (Kuznetsova et al., 2017) in R (R Core Team, 2019).

3. Results

Light treatments had significant effects on all measured traits, except on total leaf area (TLA) (Table 2). Generally, plants grown under stronger light conditions had higher biomass, root to shoot ratio (RTSR), maximum photosynthetic rate (A_{max}), and leaf N content, but lower specific leaf area (SLA) (Table 2; Figs. 1 and 2). Height was highest under medium light (Fig. 1a).

Significant origin effects were detected in height, RTSR, TLA, and leaf N, and a marginally significant origin effect was detected in SLA (Table 2). Compared to plants from native populations, *C. odorata* plants from introduced populations had higher height (introduced vs. native, mean ± se: 173.2 ± 19.0, 153.8 ± 18.5; $P = 0.041$), TLA (introduced vs. native, mean ± se: 5210.9 ± 476.6, 4519.9 ± 211.6; $P = 0.028$), and SLA (introduced vs. native, mean ± se: 328.3 ± 84.5, 312.3 ± 80.6; $P = 0.089$), but lower RTSR (introduced vs. native, mean ± se: 0.156 ± 0.038, 0.227 ± 0.057; $P < 0.001$) and leaf N (introduced vs. native, mean ± se: 1.51 ± 0.22, 1.60 ± 0.25; $P = 0.048$). No significant origin effects were detected in total biomass or A_{max} between plants from both ranges (Table 2).

Significant origin by light interactions were detected in height, total biomass and TLA (Table 2). Under low light, no differences in height, total biomass and TLA between plants from the two ranges were observed. Under full and medium light, introduced *C. odorata* were significantly taller than native conspecifics. Under full light, *C. odorata* from introduced populations were significantly higher in total biomass and TLA than those from native populations (Fig. 1a–c). No significant effect of origin by light interaction was detected in RTSR, SLA, A_{max} and leaf N between *C. odorata* from both ranges (Table 2).

4. Discussion

4.1. Trait differentiation between introduced and native populations

Our results are consistent with some previous studies showing that higher biomass reallocation to aboveground biomass might be associated with successful invasion of invasive plants (Huang et al., 2012; te Beest et al., 2009; Zou et al., 2007). For example, in a greenhouse experiment, Zou et al. (2007) found that introduced *Sapium sebiferum* populations differed from native populations in most morphological and physiological traits. They found lower RTSR, higher TLA and higher CO_2 assimilation in introduced populations, and these traits contributed to the invasion success of *S. sebiferum*. In this study, we also found that introduced *C. odorata* had lower RTSR than conspecifics from native populations. Lower RTSR might contribute to higher performance of *C. odorata* when belowground nutrients are not limited, as competition for resources would shift from competition for soil nutrients (especially nitrogen) to competition for light (Feng et al., 2007; Liao et al., 2013).

Shifts in biomass allocation patterns might reflect adaptation to new selection pressures during the invasion process (Liao et al., 2013; te Beest et al., 2009; Zou et al., 2007). For example, invasive plants might

Table 2

Differences in plant traits between five introduced and five native *Chromolaena odorata* populations under different light environments. Marginal and conditional R^2 are given for each linear mixed-effects model.

Variables	Light (L)		Origin (O)		L*O			
	df, ddf	*F* value	*df, ddf*	*F* value	*df, ddf*	*F* value	R^2_m	R^2_c
Plant growth and morphological traits								
Plant height (cm)	2, 291.2	142.23***	1, 8.0	5.92*	2, 291.0	4.24*	0.500	0.614
Total biomass (g, log10)	2, 291.0	255.91***	1, 8.1	1.26	2, 290.1	6.52**	0.632	0.647
RTSR ($g g^{-1}$, log10)	2, 290.8	149.40***	1, 8.1	26.67***	2, 290.1	0.13	0.550	0.578
TLA (cm^2, log10)	2, 289.9	2.81	1, 8.1	7.17*	2, 289.11	11.62***	0.169	0.211
Leaf ecophysiological traits								
SLA ($cm^2 g^{-1}$, log10)	2, 290.8	1564.28***	1, 8.1	3.73	2, 290.1	0.52	0.908	0.914
A_{max} ($\mu mol m^{-2} s^{-1}$)	2, 166.0	108.03***	1, 8.0	0.70	2, 166	0.08	0.503	0.590
N ($g m^{-2}$, log10)	2, 165.0	280.91***	1, 8.0	5.46*	2, 165.0	0.13	0.735	0.776

Light, origin, and their interaction were treated as fixed factor, population nested within origin was treated as random factor. Initial plant height was used as covariate when analysing plant growth and morphological traits. * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

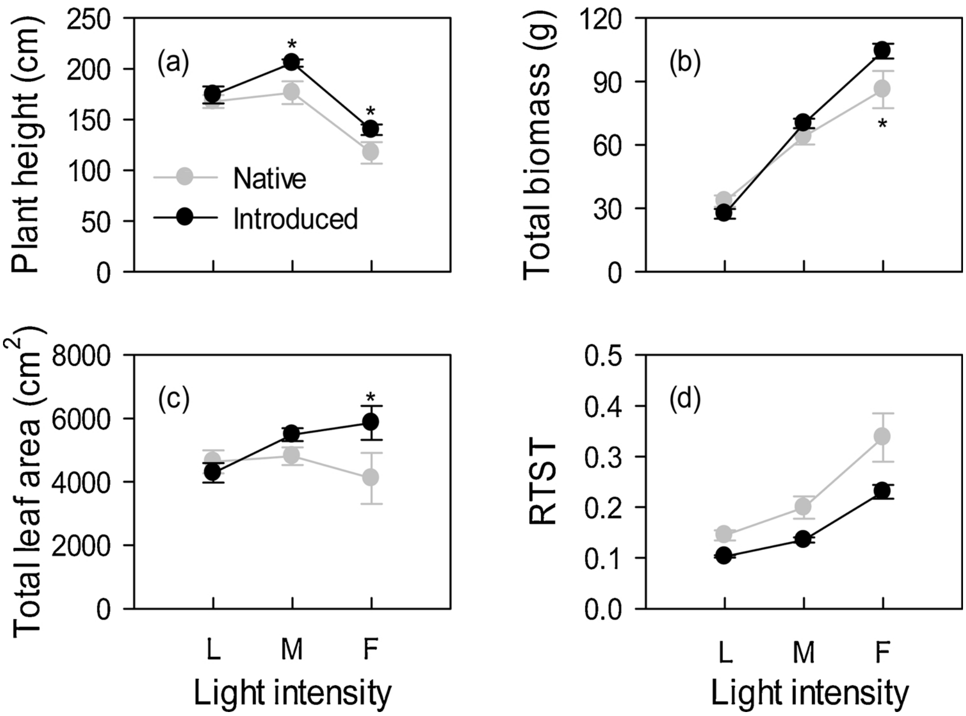

Fig. 1. Plant height (a), total biomass (b), total leaf area (c), and root to shoot ratio, RTSR (d) of plants from five introduced and five native *Chromolana odorata* populations under different light environments. Trait differences between two ranges under each light condition were tested by post-hoc Tukey's tests, and significant differences are indicated with asterisks (*). L, M, and F represent low, medium and full light, respectively.

evolve lower RTSR in response to the absence of natural enemies in the introduced range (te Beest et al., 2009; Zou et al., 2007), or in response to more frequently disturbed habitats (Flory et al., 2011; Zhang et al., 2015). In Asia, *C. odorata* usually occupies frequently disturbed habitats and forms dense monocultures by outcompeting native plants through shading (Zheng et al., 2015; Zheng and Liao, 2017). In addition, lower RTSR might confer advantage to invasive *C. odorata* plants by reducing intraspecific competition (Bossdorf et al., 2004; Liao et al., 2013). Enemy composition is different between introduced and native ranges, and novel enemy fauna in the introduced ranges could also lead to shifts in biomass allocation patterns (Liao et al., 2014; Qin et al., 2013; te Beest et al., 2009). Further experiments should be carried out to test whether enemy composition has played a role in the shift in allocation patterns of *C. odorata*.

Differences in eco-physiological traits have been shown to be pivotal for the invasion success (Feng et al., 2009; Pattison et al., 1998). Compared with *C. odorata* from native populations, introduced *C. odorata* had higher SLA but lower leaf N (Table 2, Fig. 2c) and grew taller under medium and full light conditions (Fig. 1a). SLA of introduced *C. odorata* populations tended to be higher compared to native populations across all light levels. Maximum height is one of the most important determinants related to intrinsic growth rate (Rüger et al., 2012), because taller plant height would favor introduced *C. odorata* plants competing for light much more than their native conspecifics. In spite of lower leaf N content, introduced *C. odorata* attained a similar level of A_{max} compared to native conspecifics (Fig. 2b). This might be due to differences in leaf N allocation among photosynthetic and structural organs, such as cell walls (Feng et al., 2009; Lei et al., 2011). For example, in a common garden experiment by growing introduced and native populations of the invasive *Ageratina adenophora*, Feng et al. (2009) found no differences in leaf N between native and introduced *A. adenophora*, but higher N was allocated to photosynthetic organs in introduced *A. adenophora*, which lead to higher photosynthetic rate of introduced *A. adenophora* than native conspecifics, and contributed to its successful invasion.

4.2. Differences in plastic responses to light between introduced and native populations

Except for TLA, light treatment had significant effects on all parameters (Table 2). Plastic responses of morphological and physiological traits to light treatments were consistent with previous studies on adaptive plasticity (Valladares and Niinemets, 2008; van Kleunen and Fischer, 2005). In unpredictable habitats, higher phenotypic plasticity might be adaptive and thus be selected (van Kleunen and Fischer, 2005). For example, introduced Floridan *Melaleuca quinquenervia* populations were more plastic in growth rate and biomass in response to water and pH treatments than native Australian populations (Kaufman and Smouse, 2001). In the presence of disturbance, introduced Spanish *Senecio pterophorus* populations had higher fitness and plasticity than native South African populations (Caño et al., 2008). Increased plasticity of introduced genotypes could increase their ability to use resources in frequently disturbed habitats, and natural selection might favor genotypes with higher plasticity and fitness (Caño et al., 2008). We did not compare the disturbance between introduced *C. odorata* habitats and their native habitats. However, we found in the introduced region in Asia that *C. odorata* often occupied habitats with high disturbances such as frequent deforestation, fire, construction or plantation (see also Roder et al., 1995). Light levels usually altered dramatically after such disturbances. Therefore, *C. odorata* genotypes with higher performance and stronger plasticity to variable light regimes could have been selected in the introduced range, which could have caused the introduced *C. odorata* to evolve higher plasticity in height, total biomass and TLA than their native conspecifics, and to outperform native conspecifics under full light (Table 2; Fig. 1a–c).

5. Conclusions

We found that compared to native populations, introduced populations of *C. odorata* had lower RTSR across all light environments, grew taller under medium and full light conditions, and had lower leaf N under medium light. Introduced *C. odorata* populations were also more plastic than native populations in response to light treatments. Frequent disturbance events in the introduced range might have caused the

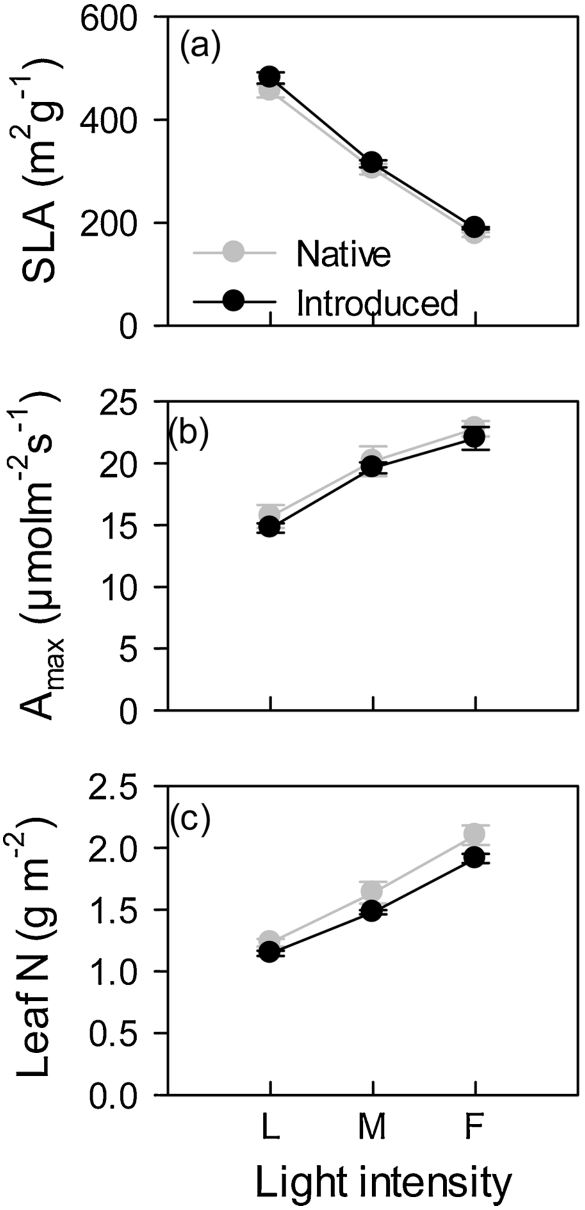

Fig. 2. Specific leaf area, SLA (a), maximum photosynthesis rate, A_{max} (b), and leaf N (c) of plants from five introduced and five native *Chromolana odorata* populations under different light environments. Trait differences between two ranges under each light condition were tested by post- hoc Tukey's tests, and significant differences are indicated with asterisks (*). L, M, and F represent low, medium and full light, respectively.

evolution of this biomass reallocation and higher plasticity of introduced *C. odorata*, which may have contributed to the successful invasion of *C. odorata*.

Author's contributions

Z.Y.L. and Y.L.F. conceived the ideas; Z.Y.L. and Y.L.Z. collected the data; Z.Y.L. and Y.L.F. analysed the data; Z.Y.L., J.F.S. and Y.L.F. wrote the manuscript. All authors contributed critically to the drafts.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.flora.2019.05.004.

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