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Invasive *Chromolaena odorata* has similar size but higher phenolic concentration than native conspecifics

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ABSTRACT

Background: *Chromolaena odorata*, a perennial shrub, is native to tropical America and invasive in Asia. In Asia it interferes with agriculture, forestry, and stockbreeding, and threatens biodiversity.

Hypothesis: Invasive populations of *C. odorata* have adapted rapidly to new local environments, and this adaptation is at least partly responsible for their success. They show a cline with climatic conditions absent in the natives. And they have evolved increased competitive ability and decreased defensive ability (the EICA hypothesis) by growing to be larger than they had been in their native range.

Locations: Tlayacapan, Morelos, Mexico and Menglun, Mengla, Yunnan, China.

Methods: Conduct two common garden experiments. Plant seedlings of 13 native and 13 invasive *C. odorata* populations in the garden in Mexico, and plant seedlings of eight native and eight invasive populations in another garden in China. In the garden in Mexico, compare native and invasive *C. odorata* populations. After 8 months, compare several of their functional traits, and after 2 months, compare their leaf phenolic contents and their stem phenolic contents.

Results: Genetic differentiation in response to variation in mean annual temperature and precipitation occurred in invasive populations but was not significant in native populations. Inconsistent with the EICA hypothesis, invasive *C. odorata* were of similar size or even smaller than natives. Total phenolics in leaves and stems of invasives were higher than in natives.

Keywords: *Chromolaena odorata*, common garden experiment, EICA hypothesis, evolution, genetic differentiation.

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INTRODUCTION

Invasive alien plants alter species composition, structure and function of invaded ecosystems, often cause significant environmental damage, and are responsible for marked economic losses worldwide (D'Antonio and Kark, 2002). Identifying the factors that contribute to the success of invasives is very important for predicting and controlling potentially invasive plants. The rapid evolution hypothesis proposes that the invasive success of alien plants depends on their rapid adaptation to new environments (Hänfling and Kollman, 2002; Lee, 2002; Maron *et al.*, 2004; Rogers and Siemann, 2004; Bossdorf *et al.*, 2005; Hierro *et al.*, 2005; Lachmuth *et al.*, 2011). Changes to morphology, behaviour, and hereditary traits can be observed in some invasive plants after only a few generations in the introduced range (Whitney and Gabler, 2008). In the introduced range, the selection pressure of new environments is one important driver of evolution in invasive plants, and the pressure can be from biotic or abiotic factors.

Enemy release is an important biotic factor driving the evolution of invasive plants, and the EICA (evolution of increased competitive ability) hypothesis is an important theory to explain the mechanisms of invasion. It states that in the introduced range, exotic plants are liberated from their natural specialist enemies. In time, the exotics may lose costly defensive traits, and reallocate resources and energy from their defensive system to growth (Blossey and Nötzold, 1995; Wolfe *et al.*, 2004; Zou *et al.*, 2006, 2008). Daehler and Strong (1997) found that herbivore resistance was reduced in *Spartina alterniflora* after a century of herbivore-free growth in the introduced range. Siemann and Rogers (2001, 2003a, 2003b) also found an increase in competitive ability of invasive populations of *Sapium sebiferum*, and decreased leaf defensive ability compared with native populations. However, Bossdorf *et al.* (2004) reported a decrease in the size of invasive *Alliaria petiolata*, and Schaffner *et al.* (2011) found no significant difference in enemy defence between invasive and native populations of *Centaurea stoebe*.

Acclimation to environmental gradients is one important abiotic factor driving the evolution of invasive plants. Local adaptation is an important strategy with which plants acclimate to heterogeneous habitats (Williams *et al.*, 2008; Feng *et al.*, 2009). When a plant enters a new environment, it can adapt to that environment through genetic differentiation. Many studies have indicated that genetic differentiation often occurs in invasive plants, and this differentiation can sometimes be observed after a few generations only (Dlugosch and Parker, 2008a; Whitney and Gabler, 2008). The common garden study is one powerful method to determine genetic variation and local adaptation of invasive plants. In the common environment, phenotypic plasticity can be excluded to identify performance differences among populations. Sexton *et al.* (2002) found that in a common environment, *Tamarix ramosissima* from the northern range had a higher root mass fraction than conspecifics from the southern range. They suggested that greater allocation of biomass to the roots improved defence against frost (Sexton *et al.*, 2002). In another common garden experiment, 25 invasive populations of *Lythrum salicaria* showed a strong latitudinal cline in initiation of flowering and size at flowering, with plants from higher latitudes flowering earlier and at a smaller size than those at lower latitudes (Montague *et al.*, 2008). Local adaptation was also observed in the response of invasive *Senecio inaequidens* to different altitudes. When different populations of *S. inaequidens* were grown in a common environment, height and biomass were lower for populations from high altitudes than populations from low altitudes (Monty and Mahy, 2009).

Multiple introductions of an alien plant can increase genotype variation in invasive populations (Ellstrand and Schierenbeck, 2000; Bossdorf *et al.*, 2005; Lavergne and Molofsky, 2007; Dlugosch and Parker,

2008b). If these genotypes are coincidentally pre-adapted to various environments in the introduced range, genetic differentiation may simply result from the redistribution of various genotypes in the invaded ranges (Maron *et al*., 2004; Bossdorf *et al*., 2008; Dlugosch and Parker, 2008b), and not adaptive evolution after introduction. If invasive and native populations show similar performance and cline patterns in a common garden experiment, this indicates that genetic differentiation of invasive populations is caused by the redistribution of various genotypes (Etterson *et al*., 2008). In contrast, genetic differentiation was inferred to be a result of adaptive evolution within the invaded range where the performance of native and invasive populations differed, and only phenotypic traits of invasive populations displayed cline patterns (Dlugosch and Parker, 2008a; van Kleunen and Fischer, 2008).

Chromolaena odorata is a perennial shrub, native to Central and South America. It has invaded much of the tropics and subtropics, impacting agriculture, forestry, and stock-breeding, threatening biodiversity and causing environmental deterioration (Muniappan and Viraktamath, 1993; McFadyen and Skarratt, 1996; Raimundo *et al*., 2007). *Chromolaena odorata* was probably introduced into Asia as an ornamental plant in the early 1840s, through the Botanical Gardens in Kolkotta (Calcutta, India) (McFadyen, 1989; Gautier, 1993). By the 1870s, the plant had become naturalized in Dacca and the Ganges flood plain (present-day India and Bangladesh). From Calcutta, it spread east into Assam and Burma, and then progressively eastwards into China and south into Indonesia, particularly during the Second World War (McFadyen, 1989, 2002), although it was already present in both of these countries in the 1930s. *Chromolaena odorata* was first recorded in the Philippines in the late 1960s (Pancho and Plucknett, 1971), in Guam in 1963 (Marutani and Muniappan, 1991), and in the Marianas in 1973 (Fosberg and Falanruw, 1973). It had spread to most of the Micronesian islands by 2000 (Muniappan *et al*., 2004). In its invasive range, *C. odorata* can grow in diverse habitats, from rainforest to tropical savannas, but whether adaptive evolution has facilitated its wide distribution is not clear. Identifying the reason for genetic differentiation of invasive populations is very important for predicting the potential area to which they might spread, while most previous studies included only a few populations (Dlugosch and Parker, 2008a; Etterson *et al*., 2008; van Kleunen and Fischer, 2008; Monty and Mahy, 2009).

In the present study, we conducted a common garden experiment in Mexico (native range) to explore the biogeographical differences in performance (biomass and height) of *C. odorata*, and to determine whether invasive *C. odorata* display adaptive evolution to major environmental factors (mean annual temperature or precipitation). Phenolics are important chemicals in plant defence: they decrease leaf palatability and digestibility, and some are also toxic to herbivores (Müller-Schärer *et al*., 2004). Thus, we conducted a second common garden experiment in China (invasive range) to compare leaf and stem phenolic content (defensive ability) between native and invasive *C. odorata*.

MATERIALS AND METHODS

Study site and seed collection

In this study, we performed two common garden experiments, one in Tlayacapan, Morelos, Mexico (18°57′N, 98°58′W; 1634 m above sea level) and another in Menglun, Mengla, Yunnan, China (21°56′N, 101°150′E; 570 m above sea level). In Tlayacapan, the mean annual temperature is 19.3°C; the mean temperature in June (the hottest month) is 22.9°C and that in January (the coolest month) is 16.9°C; mean annual precipitation is 988.8 mm

with a dry period lasting from November to April (García, 1988). In Menglun, the mean annual temperature is 21.7°C; the mean temperature in July (the hottest month) is 25.3°C and that in January (the coolest month) is 15.6°C; the average annual precipitation is 1557 mm with a dry period lasting from November to April.

Seeds of *Chromolaena odorata* were collected in 2009 from 15 populations in its native range (Central America) and 15 populations in Asia (evolutionary-ecology.com/data/2861Appendix.pdf). In each population, seeds were collected from 10 individuals that were at least 20 m apart from one another, and saved separately in paper bags (10 seed families per population).

Common garden in Mexico

We used seeds of *C. odorata* from 13 native populations and 13 invasive populations in this experiment (evolutionary-ecology.com/data/2861Appendix.pdf). The seeds of 26 populations were sown into a seed bed in a greenhouse in Tlayacapan in April 2010. For each population, seeds from each family were raised separately. In late June, similar-sized (10 cm tall) seedlings from each population were transplanted into the common garden. Ten seedlings from 26 populations were planted 60 cm apart in rows of 26 (one seedling per population). Weeds were pulled out carefully when necessary, and the seedlings were watered every other day in the dry season at a rate of 2000 mL per seedling.

In February 2011, 50–100 leaves from each population were selected to determine leaf area with a Li-3000C Leaf Area Meter (Li-Cor, Lincoln, Nebraska, USA). Leaves were oven-dried at 60°C for 48 h, then weighed. The ratio of leaf area to dry mass was measured to calculate specific leaf area (SLA), and average leaf size (single leaf area) was calculated for each population. After measuring height, the aboveground parts of each individual were harvested, oven-dried at 60°C for 48 h, then weighed. At the same range, for each variable, the coefficient of variation was calculated as the ratio of standard deviation to mean value (mean of each population as replicates).

Common garden in China

We used seeds of *C. odorata* from eight native populations and eight invasive populations in this experiment (evolutionary-ecology.com/data/2861Appendix.pdf). In June 2009, seeds of each population were sown separately in seedling trays in a shade house with 50% irradiance. The germination medium was a mixture of river sand and forest topsoil (1:1). In August 2009, when the seedlings were about 5 cm tall, similar-sized vigorous seedlings were transplanted into 15-litre pots located under shade netting that allowed 50% irradiance. Pots contained a mixture of 70% topsoil of a secondary forest (dominated by *Phoebe lanceolata* and *Castanopsis indica*; excluding plant litter and stones) and 30% river sand. Each pot contained one seedling. We planted 10 seedlings per population. After 2 weeks of growth at 50% irradiance, all seedlings were grown in full sunshine by removing the shade net. In October 2009, the stem and fully expanded leaves were collected from five plants per population, and were dried at 60°C to constant mass and powdered to measure phenolics. Total phenolics in leaf and stem were measured using the Folin Ciocalteu method (McDonald *et al.*, 2001).

Statistical analysis

We used one-way nested ANOVA (population nested within range) to compare the differences in height, aboveground biomass, aboveground biomass to height ratio, leaf size, SLA, and phenolic content between native and invasive *C. odorata*. For *C. odorata* from each range, differences in each variable among populations (population effect) were tested by one-way ANOVA. In each range, stepwise regression analysis was used to analyse the relationship between each variable and mean annual temperature and precipitation. All analyses were conducted using SPSS v.17.0 (SPSS Inc., Chicago, Illinois, USA).

RESULTS

There were no significant differences in aboveground biomass and height between invasive and native *C. odorata* populations (Fig. 1a, b), while leaf size and SLA were higher but aboveground biomass to height ratio and leaf length to width ratio were lower for invasive populations than native populations (Fig. 1c; Fig. 2a–c).

Chromolaena odorata plants from the invasive range had higher leaf and stem phenolic content than plants from the native range (Fig. 3a, b). In each range, for all variables, there were significant differences among populations ($P < 0.05$ for all variables; Table 1). For all variables, the coefficients of variation were higher among native populations than among invasive populations. Using stepwise regression analysis, for invasive populations, the aboveground biomass to height ratio was significantly correlated with mean annual temperature (Fig. 4a), and leaf size and SLA were significantly correlated with mean annual precipitation (Fig. 4b, c). However, for native populations, there were no relationships between the variables and mean annual temperature (or precipitation).

DISCUSSION

Under identical conditions, single leaf area and specific leaf area (SLA) (Fig. 2a, b) were higher but leaf length to width ratio (Fig. 2c) and aboveground biomass to height ratio (Fig. 1c) were lower for invasive *Chromolaena odorata* populations than for native populations. The results suggest genetic differences between native and invasive *C. odorata*. The differences in leaf size and morphology might be due to lower precipitation in the native range (evolutionary-ecology.com/data/2861Appendix.pdf) than invasive range.

Table 1. Coefficient of variation (CV) for each variable in the same range, and population effect on each variable in each range

	CV (population effect)	
Variable	Native range	Invasive range
Aboveground biomass	0.50 ($P < 0.001$)	0.26 ($P = 0.003$)
Height	0.20 ($P < 0.001$)	0.13 ($P < 0.001$)
Aboveground biomass/height	0.41 ($P < 0.001$)	0.17 ($P = 0.012$)
Leaf size	0.44 ($P < 0.001$)	0.16 ($P < 0.001$)
Leaf length/leaf width	0.18 ($P < 0.001$)	0.07 ($P < 0.001$)
Specific leaf area	0.09 ($P < 0.001$)	0.06 ($P = 0.019$)

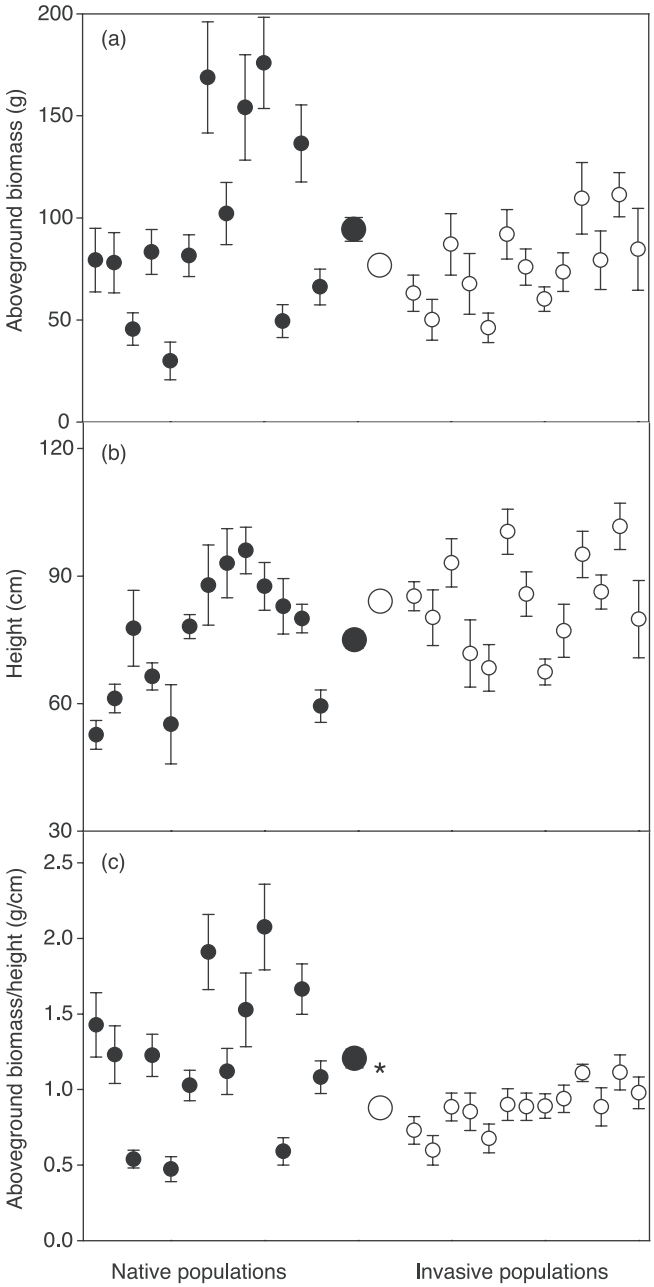

Fig. 1. Differences in aboveground biomass, height, and aboveground biomass to height ratio among *Chromolaena odorata* plants from native (solid circles) versus invasive (open circles) ranges. Small circles depict means and standard errors for each population; the two larger circles in the centre of the figure are means and standard errors for all populations from each range. Significant difference between ranges according to one-way nested ANOVA: $*P < 0.05$.

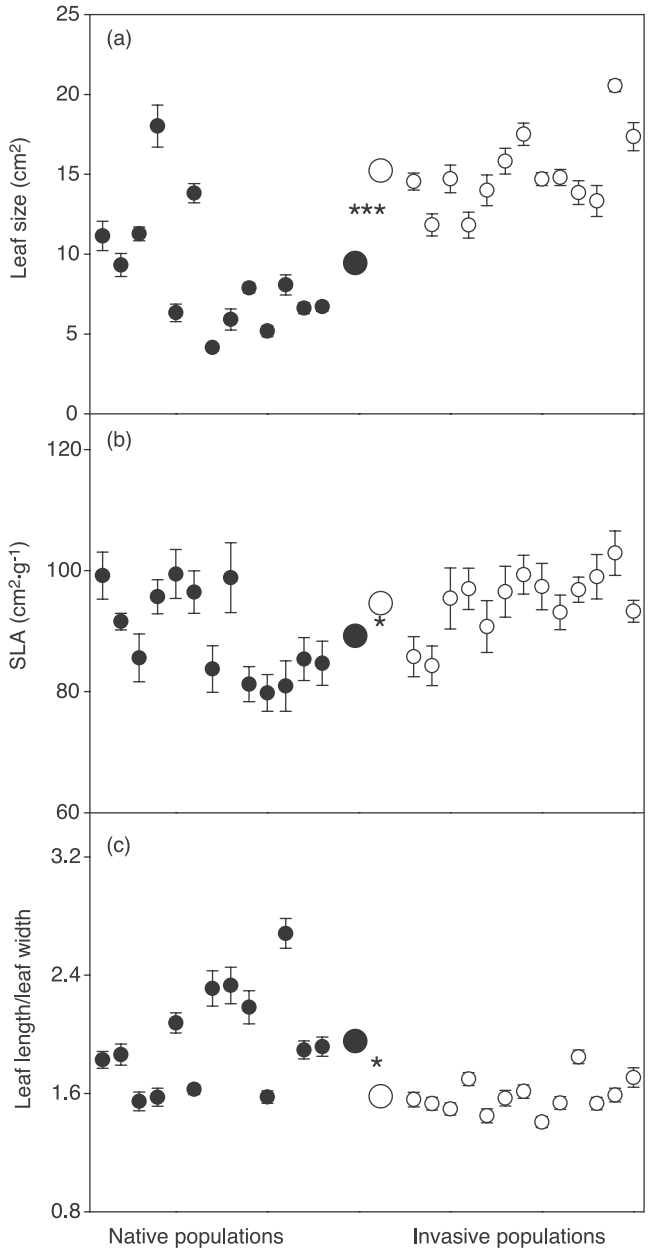

Fig. 2. Differences in leaf size, specific leaf area (SLA), and leaf length to width ratio among *Chromolaena odorata* plants from native (solid circles) versus invasive (open circles) ranges. Small circles depict means and standard errors for each population; the two larger circles in the centre of the figure are means and standard errors for all populations from each range. Significant difference between ranges according to one-way nested ANOVA: $*P < 0.05$, $***P < 0.001$.

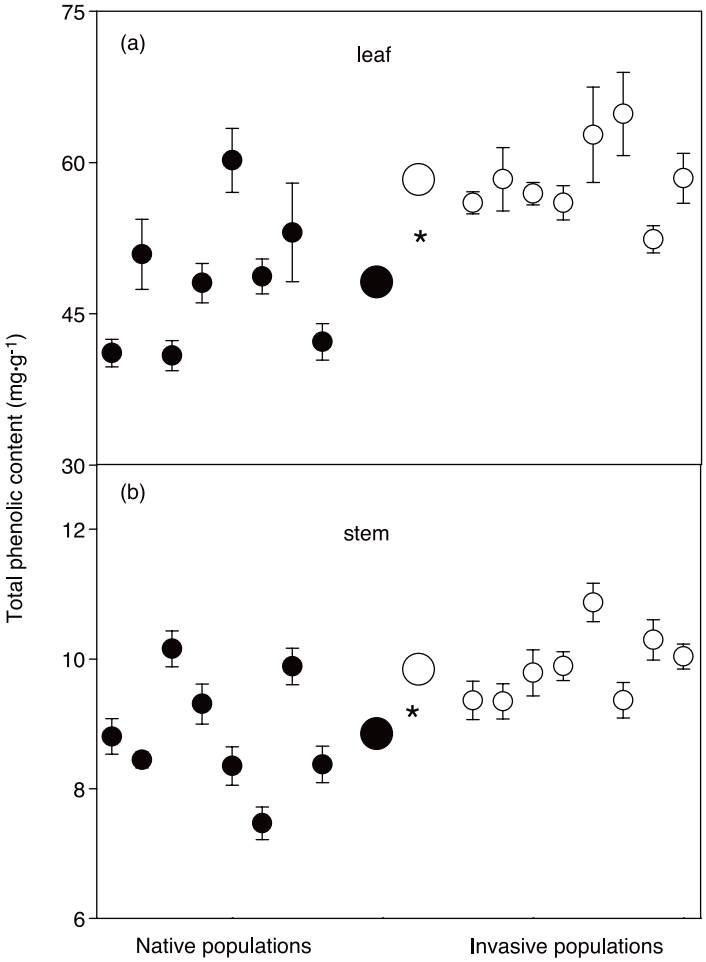

Fig. 3. Differences in leaf and stem phenolic content among *Chromolaena odorata* plants from native (solid circles) versus invasive (open circles) ranges. Small circles depict means and standard errors for each population; the two larger circles in the centre of the figure are means and standard errors for all populations from each range. Significant difference between ranges according to one-way nested ANOVA: $*P < 0.05$.

Larger leaves usually require greater evaporation due to the enhanced length of the boundary layer for energy and gaseous exchange (Royer *et al.*, 2005; Xu *et al.*, 2009). Similarly, the narrowing of the leaves is thought to be an adaptation to xeric environments, because narrow leaves reduce transpiration by reducing the size of the boundary layer. Specific leaf area, which is the ratio of leaf area to dry mass, is also positively correlated with transpiration rate (Reich *et al.*, 1997; Wright *et al.*, 2007). In water-limited environments, the cell walls of lamina are thicker and often strongly lignified, leading to a lower SLA. This structure can enhance the epidermal resistance of water vapour through cuticles to reduce water loss (Niinemets, 2001; Xu *et al.*, 2009). The lower aboveground biomass to height ratio (Fig. 1c) of invasive *C. odorata* was due to its lower biomass but greater height than native counterparts.

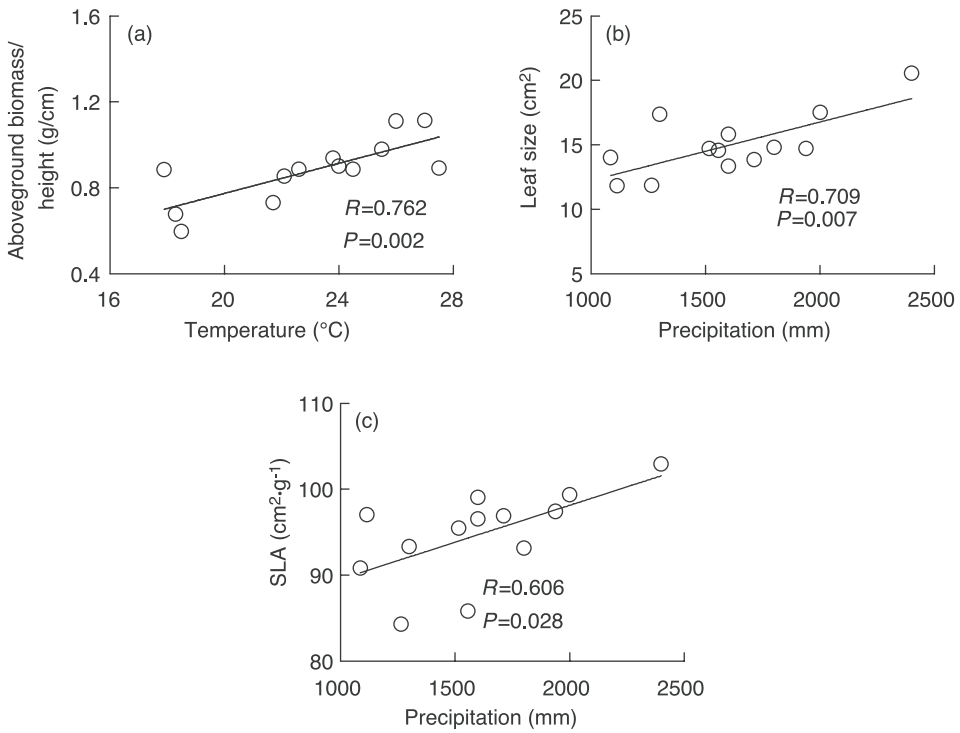

Fig. 4. Aboveground biomass to height ratio, leaf size, and specific leaf area (SLA) as a function of (a) mean annual temperature and (b, c) precipitation in invasive *Chromolaena odorata*. Mean values of each population were used for stepwise regression analysis. No significant relationships were found in native populations, thus data are not shown.

The aboveground biomass to height ratio reflects the architecture of the plant. In invasive *C. odorata*, a lower aboveground biomass to height ratio means fewer branches and smaller canopy than native populations, and a sparser canopy can decrease intraspecific competition at high density, thus helping invasion to succeed.

Inconsistent with the EICA prediction, invasive *C. odorata* were not larger (aboveground biomass and height) than native populations (Fig. 1a, b). Similarly, Vilà *et al.* (2003) found introduced *Hypericum perforatum* individuals not to be larger than native conspecifics. Furthermore, invasive *Alliaria petiolata* were similar in size or even smaller than native populations (Bossdorf *et al.*, 2004). In contrast with the EICA, Callaway and Ridenour (2004) proposed another mechanism for the evolution of increased competitive ability: If the invasive plants possess allelochemicals that provide greater competitive advantages in their new habitats than in their original ranges, then selection may act directly on those traits. Qin *et al.* (2013) showed that neighbouring plants in the invasive range in China are indeed more vulnerable to allelochemicals (presumably present in the leachate made from *C. odorata*) than natives from the native range in Mexico. In this case, natural selection might facilitate increased production of allelochemicals by invasive *C. odorata*. Indeed, we also found that the phenolic contents of leaf and stem were significantly higher for invasive *C. odorata* populations than native populations (Fig. 3). Vilà *et al.* (2003) proposed another explanation for size reduction of the invader. In the invasive range, if neighbouring plants of the invader

were smaller than neighbours in the native range, natural selection might favour the reduction of individual size but increase its competitive advantage at the population level (Vilà *et al.*, 2003; Bossdorf *et al.*, 2004). In a previous study of *C. odorata*, neighbouring plants from the native range (Mexico) were indeed found to be larger than neighbouring plants from the invasive range (China) (Qin *et al.*, 2013). According to our field investigation, the community structure and composition of neighbouring species is very different between the native (Mexico) and the invasive range (China), and the average size of neighbouring plants in Mexico is also larger than that of neighbouring plants in China (Y. Zheng *et al.*, unpublished data). In the invasive range, weaker and more vulnerable neighbouring plants might induce invasive *C. odorata* to reallocate biomass and energy from growth to allelochemical production. This evolution would decrease individual size but increase the allelopathic effect of the invader, which, in turn, could increase competitive ability (stronger allelopathic effect), reduce intraspecific competition, and facilitate successful invasion.

In each range, population effects on all variables were significant (Table 1), indicating there are genetic differences not only between native and invasive *C. odorata*, but also among populations in each range. For all variables, the coefficients of variation were higher in the native range than the invasive range (Table 1). Table 1 indicates that the genetic difference among native populations was higher than among invasive populations, which was consistent with previous studies. Although we do not know the genetic make-up of the *C. odorata* populations when they were first introduced to Asia, other studies also show that *C. odorata* populations in Asia are genetically rather homogeneous (Scott *et al.*, 1998; von Senger *et al.*, 2002; Ye *et al.*, 2004). Perhaps *C. odorata* in Asia originate from a restricted population? Based on nuclear (ITS) DNA sequences, W.-T. Li *et al.* (unpublished data) found that *C. odorata* in Asia might originate from Trinidad and Tobago or Florida, USA. But they also found its genetic diversity in those locations to be significantly higher than in Asian populations.

For invasive populations, the aboveground biomass to height ratio was significantly correlated with mean annual temperature (Fig. 4a), and leaf size and SLA were significantly correlated with mean annual precipitation (Fig. 4b, c). But there was no such pattern among native populations. These results indicate that adaptive differentiation in response to variation in environmental factors (mean annual temperature and precipitation) has occurred in the invasive range, but not in the native range. Yet *C. odorata* has occupied its native range much longer than its invasive range, and should have adapted to local climatic conditions there better than in its invasive range. That our results indicate the opposite might be due to selective pressure from other factors (such as enemies, community structure, and composition of neighbouring plants, soil conditions, etc.) being more powerful selective forces in the native range than the invasive range (Vilà *et al.*, 2003; Bossdorf *et al.*, 2004; Phillips *et al.*, 2010). In the invasive range, perhaps *C. odorata* experience lower enemy attack (enemy release) and weaker competition. Thus, the role of climatic factors would be more important in the invasive range, leading to genetic differentiation of *C. odorata* in response to climatic gradients.

Rapid evolution in response to local environments might be one important strategy for successful invasion. This is consistent with *C. odorata* evolving in response to mean annual temperature and precipitation, reducing its growth, and increasing its allelochemical production. But this strategy did not lead to larger size in invasive *C. odorata* populations.

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REFERENCES

Blossey, B. and Nötzold, R. 1995. Evolution of increased competitive ability in invasive non-indigenous plants: a hypothesis. *J. Ecol.*, **83**: 887–889.

Bossdorf, O., Prati, D., Auge, H. and Schmid, B. 2004. Reduced competitive ability in an invasive plant. *Ecol. Lett.*, **7**: 346–353.

Bossdorf, O., Auge, H., Lafuma, L., Rogers, W.E., Siemann, E. and Prati, D. 2005. Phenotypic and genetic differentiation between native and introduced plant populations. *Oecologia*, **144**: 1–11.

Bossdorf, O., Lipowsky, A. and Prati, D. 2008. Selection of preadapted populations allowed *Senecio inaequidens* to invade Central Europe. *Divers. Distrib.*, **14**: 676–685.

Callaway, R.M. and Ridenour, W.M. 2004. Novel weapons: invasive success and the evolution of increased competitive ability. *Front. Ecol. Environ.*, **2**: 436–443.

Daehler, C.C. and Strong, D.R. 1997. Reduced herbivore resistance in introduced smooth cordgrass (*Spartina alterniflora*) after a century of herbivore-free growth. *Oecologia*, **110**: 99–108.

D'Antonio, C.M. and Kark, S. 2002. Impacts and extent of biotic invasions in terrestrial ecosystems. *Trends. Ecol. Evol.*, **17**: 202–204.

Dlugosch, K.M. and Parker, I.M. 2008a. Invading populations of an ornamental shrub show rapid life history evolution despite genetic bottlenecks. *Ecol. Lett.*, **11**: 701–709.

Dlugosch, K.M. and Parker, I.M. 2008b. Founding events in species invasions: genetic variation, adaptive evolution, and the role of multiple introductions. *Mol. Ecol.*, **17**: 431–449.

Ellstrand, N.C. and Schierenbeck, K.A. 2000. Hybridization as a stimulus for the evolution of invasiveness in plants? *Proc. Natl. Acad. Sci. USA*, **97**: 7043–7050.

Etterson, J.R., Delf, D.E., Craig, T.P., Ando, Y. and Ohgushi, T. 2008. Parallel patterns of clinal variation in *Solidago altissima* in its native range in central USA and its invasive range in Japan. *Botany*, **86**: 91–97.

Feng, Y.-L., Lei, Y.-B., Wang, R.-F., Callaway, R.M., Valiente-Banuet, A., Inderjit *et al*. 2009. Evolutionary tradeoffs for nitrogen allocation to photosynthesis versus cell walls in an invasive plant. *Proc. Natl. Acad. Sci. USA*, **106**: 1853–1856.

Fosberg, F.R. and Falanruw, M.V.C. 1973. Noteworthy Micronesian plants, Part 1. *Micronesia*, **11**: 77–80.

García, E. 1988. *Modificaciones al sistema de clasificación cimática de Köppen para adaptarlo a las condiciones de la República Mexicana*. Instituto de Geografia, Universidad Nacional Autónoma de México, México.

Gautier, L. 1993. Establishment of *Chromolaena odorata* in a savanna protected from fire: an example from Lamto, Central Côte d'Ivoire. In *Proceedings of the Third International Workshop on Biological Control and Management of Chromolaena odorata* (U.K. Prasad, R. Muniappan, P. Ferrar, J.P. Aeschliman and H. de Foresta, eds.), pp. 54–67. Mangilao, Guam: Agricultural Experiment Station, University of Guam.

Hänfling, B. and Kollman, J. 2002. An evolutionary perspective on invasions. *Trends. Ecol. Evol.*, **17**: 545–546.

Hierro, J.L., Maron, J.L. and Callaway, R.M. 2005. A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range. *J. Ecol.*, **93**: 5–15.

Lachmuth, S., Durka, W. and Schurr, F.M. 2011. Differentiation of reproductive and competitive ability in the invaded range of *Senecio inaequidens*: the role of genetic Allee effects, adaptive and nonadaptive evolution. *New Phytol.*, **192**: 529–541.

Lavergne, S. and Molofsky, J. 2007. Increased genetic variation and evolutionary potential drive the success of an invasive grass. *Proc. Natl. Acad. Sci. USA*, **104**: 3883–3888.

Lee, C.E. 2002. Evolutionary genetics of invasive species. *Trends. Ecol. Evol.*, **17**: 386–391.

Maron, J.L., Vilà, M., Bommarco, R., Elmendorf, S. and Beardsley, P. 2004. Rapid evolution of an invasive plant. *Ecol. Monogr.*, **74**: 261–280.

Marutani, M. and Muniappan, R. 1991. Interactions between *Chromolaena odorata* (Asteraceae) and *Pareuchaetes pseudoinsulata* (Lepidoptera: Arctiidae). *Ann. Appl. Biol.*, **119**: 227–237.

McDonald, S., Prenzler, P.D., Antolovich, M. and Robards, K. 2001. Phenolic content and antioxidant activity of olive extracts. *Food Chem.*, **73**: 73–84.

McFadyen, R.E.C. 1989. Siam weed: a new threat to Australia's north. *Plant Protect. Quart.*, **4**: 3–7.

McFadyen, R.E.C. 2002. *Chromolaena* in Asia and the Pacific: spread continues but control prospects improve. In *Proceedings of the Fifth International Workshop on Biological Control and Management of Chromolaena odorata* (C. Zachariades, R. Muniappan and L.W. Strathie, eds.), pp. 13–18. Pretoria, South Africa: ARC–PPRI.

McFadyen, R.E. and Skarratt, B. 1996. Potential distribution of *Chromolaena odorata* (Siam weed) in Australia, Africa and Oceania. *Agr. Ecosyst. Environ.*, **59**: 1–2.

Montague, J.L., Barrett, S.C.H. and Eckert, C.G. 2008. Re-establishment of clinal variation in flowering time among introduced populations of purple loosestrife (*Lythrum salicaria*, Lythraceae). *J. Evol. Biol.*, **21**: 234–245.

Monty, A. and Mahy, G. 2009. Clinal differentiation during invasion: *Senecio inaequidens* (Asteraceae) along altitudinal gradients in Europe. *Oecologia*, **159**: 305–315.

Müller-Schärer, H., Schaffner, U. and Steinger, T. 2004. Evolution in invasive plants: implications for biological control. *Trends Ecol. Evol.*, **19**: 417–422.

Muniappan, R. and Viraktamath, C.A. 1993. Invasive alien weeds in the Western Ghats. *Curr. Sci.*, 64: 555–558.

Muniappan, R., Englberger, K., Bamba, J. and Reddy, G.V.P. 2004. Biological control of *Chromolaena* in Micronesia. In *Proceedings of the Sixth International Workshop on Biological Control and Management of Chromolaena odorata* (M.D. Day and R.E. McFadyen, eds.), pp. 11–12. ACIAR Technical Report 55. Canberra, ACT: ACIAR.

Niinemets, Ü. 2001. Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. *Ecology*, **82**: 453–469.

Pancho, J. and Plucknett, D. 1971. *Chromolaena odorata* (L.) R. M. King and H. Robinson – a new record of a noxious weed in the Philippines. *Philippines J. Anim. Sci.*, **8**: 143–149.

Phillips, B.L., Brown, J.P. and Shine, R. 2010. Life-history evolution in range-shifting populations. *Ecology*, **91**: 1617–1627.

Qin, R.M., Zheng, Y.L., Valiente-Banuet, A., Callaway, R.M., Barclay, G.F., Carlos, S.P. *et al*. 2013. The evolution of increased competitive ability, innate competitive advantages, and novel biochemical weapons act in concert for a tropical invader. *New Phytol.*, **197**: 979–988.

Raimundo, R.L.G., Fonseca, R.L., Schachetti-Pereira, R., Peterson, A.T. and Lewinsohn, T.M. 2007. Native and exotic distributions of Siam weed (*Chromolaena odorata*) modeled using the genetic algorithm for ruleset production. *Weed Sci.*, **55**: 41–48.

Reich, P.B., Walters, M.B. and Ellsworth, D.S. 1997. From tropics to tundra: a global convergence in plant functioning. *Proc. Natl. Acad. Sci. USA*, **94**: 13730–13734.

Rogers, W.E. and Siemann, E. 2004. Invasive ecotypes tolerate herbivory more effectively than native ecotypes of the Chinese tallow tree *Sapium sebiferum*. *J. Appl. Ecol.*, **41**: 561–570.

Royer, D.L., Wilf, P., Janesko, D.A., Kowalski, E.A. and Dilcher, D.L. 2005. Correlations of climate and plant ecology to leaf size and shape: potential proxies for the fossil record. *Am. J. Bot.*, **92**: 1141–1151.

Schaffner, U., Ridenour, W., Wolf, V.C., Bassett, T., Müller, C., Müller-Schärer, H. *et al*. 2011. Plant invasions, generalist herbivores, and novel defense weapons. *Ecology*, **92**: 829–835.

Scott, L.J., Lange, C.L., Graham, G.C. and Yeates, D.K. 1998. Genetic diversity and origin of Siam weed (*Chromolaena odorata*) in Australia. *Weed Technol.*, **12**: 27–31.

Sexton, J.P., McKay, J.K. and Sala, A. 2002. Plasticity and genetic diversity may allow saltcedar to invade cold climates in North America. *Ecol. Appl.*, **12**: 1652–1660.

Siemann, E. and Rogers, W.E. 2001. Genetic differences in growth of an invasive tree species. *Ecol. Lett.*, **4**: 514–518.

Siemann, E. and Rogers, W.E. 2003a. Reduced resistance of invasive varieties of an alien tree *Sapium sebiferum* to a generalist herbibore. *Oecologia*, **135**: 451–457.

Siemann, E. and Rogers, W.E. 2003b. Increased competitive ability of an invasive tree may be limited by an invasive beetle. *Ecol. Appl.*, **13**: 1503–1507.

van Kleunen, M. and Fischer, M. 2008. Adaptive rather than non-adaptive evolution of *Mimulus guttatus* in its invasive range. *Basic Appl. Ecol.*, **9**: 213–223.

Vilà, M., Gómez, A. and Maron, J.L. 2003. Are alien plants more competitive than their native conspecifics? A test using *Hypericum perforatum* L. *Oecologia*, **137**: 211–215.

von Senger, I., Barker, N.P. and Zachariades, C. 2002. Preliminary phylogeography of *Chromolaena odorata*: finding the origin of South African weed. In *Proceedings of the Fifth International Workshop on Biological Control and Management of Chromolaena odorata* (C. Zachariades, R. Muniappan and L.W. Strathie, eds.), pp. 90–99. Pretoria, South Africa: ARC-PPRI.

Whitney, K.D. and Gabler, C.A. 2008. Rapid evolution in introduced species, 'invasive traits' and recipient communities: challenges for predicting invasive potential. *Divers. Distrib.*, **14**: 569–580.

Williams, J.L., Auge, H. and Maron, J.L. 2008. Different gardens, different results: native and introduced populations exhibit contrasting phenotypes across common gardens. *Oecologia*, **157**: 239–248.

Wolfe, L.M., Elzinga, J.A. and Biere, A. 2004. Increased susceptibility to enemies following introduction in the invasive plant *Silene latifolia. Ecol. Lett.*, **7**: 813–820.

Wright, I.J., Ackerly, D.D., Bongers, F., Harms, K.E., Ibarra-Manriquez, G., Martinez-Ramos, M. *et al*. 2007. Relationships among ecologically-important dimensions of plant trait variation in seven neotropical forests. *Ann. Bot.*, **99**: 1003–1015.

Xu, F., Guo, W.H., Xu, W.H., Wei, Y. and Wang, R.Q. 2009. Leaf morphology correlates with water and light availability: what consequences for simple and compound leaves? *Prog. Nat. Sci.*, **19**: 1789–1798.

Ye, W.H., Mu, H.P., Cao, H.L. and Ge, X.J. 2004. Genetic structure of the invasive *Chromolaena odorata* in China. *Weed Res.*, **44**: 129–135.

Zou, J.W., Rogers, W.E., DeWalt, S.J. and Siemann, E. 2006. The effect of Chinese tallow tree (*Sapium sebiferum*) ecotype on soil–plant system carbon and nitrogen processes. *Oecologia*, **150**: 272–281.

Zou, J.W., Rogers, W.E. and Siemann, E. 2008. Increased competitive ability and herbivory tolerance in the invasive plant *Sapium sebiferum. Biol. Invasions*, **10**: 291–302.