Effects of latitudinal variation on field and common garden comparisons between native and introduced groundsel (Senecio vulgaris) populations

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Abstract

Background: Field and common garden comparisons are commonly performed to test the rapid evolution of increased vigor in introduced plant populations. Latitudinal clines in phenotypic traits can obscure such evolutionary inferences, particularly when native or introduced populations are distributed across large geographic ranges. We tested whether the latitudinal clines influence the comparisons between introduced and native populations of Senecio vulgaris. We compared plant height, number of branches and number of capitula in the field in Europe and China, and in a common garden in Switzerland.

Results: The Chinese introduced populations performed better than the European native populations in the field in terms of plant height and number of capitula, which was consistent with the prediction of the evolution of increased competitive ability (EICA) hypothesis. The Chinese populations exhibited more capitula than the European populations when the latitudinal cline was considered in the common garden comparison. When we compared the traits of the northeast Chinese, southwest Chinese and European populations in both the field and common garden, the northeast Chinese populations, at latitudes similar to those of the European populations, exhibited greater plant size and more capitula than the European populations in both the field and common garden. However, the southwest Chinese populations, at latitudes that are much lower than those of the European populations, did not perform better in terms of reproduction than the native populations.

Conclusion: Latitudinal clines in phenotypic traits should be considered in field and common garden comparisons when introduced populations are geographically structured.

Background

A common phenomenon in plant invasions is that plants tend to perform better (larger plant size and higher fecundity) in their introduced range than in their native range [1, 2]. This phenomenon gave rise to several hypotheses explaining invasion success [3]. The evolution of increased competitive ability (EICA) hypothesis suggests that the advantages in plant size and fecundity in the introduced range results from the absence of specific herbivores and the subsequent evolution of increased competitive ability [4, 5]. According to this hypothesis, the better performance of invasive plants is genetically determined rather than a plastic response to the environment [4, 6]. Therefore, it is crucial to assess the variation in plant phenotypic traits in the native and introduced ranges to test this hypothesis [7].

Field comparisons can establish whether there are any patterns of phenotypic differences between native and introduced populations. However, surprisingly little attention has been paid to such field comparisons, and the available literature provides inconsistent results. Thebaud and Simberloff found there was no general tendency for species to be taller in their introduced ranges by comparing the size of introduced plant species [8]. The overall results from analyses of published studies that compared native and introduced populations in the field suggest that invasive plant species perform better in their introduced range relative to their native range, although there was some variation across species [2, 9].

Further comparative studies are needed to assess the phenotypic differences and ecological processes of invasive plant species in their introduced and native ranges in the field, and these studies should be connected with the genetically-based phenotypic differences identified in common garden experiments [9].

Common garden comparison, a classical approach used to quantify genetically-based phenotypic differentiation among populations, is widely used to test the EICA hypothesis. As the EICA hypothesis predicts, under identical growing conditions, individuals from the introduced range will increase in size and/or fecundity and be attacked more by specialized herbivores than those from the native range [4]. However, the available studies show mixed results [9–11]. Even the individuals from the introduced range show an increase in size and fecundity compared with those from the native range in common gardens, which does not provide unequivocal support for EICA [9, 12–17]. One potential explanation for the departure from expectations of EICA is that only plants that were introduced from poor native habitats may invest more resources to defense and hence exhibit better growth and reproductive performance after the evolution of decreased defense in introduced ranges [18–20]. In addition, considering the among-population variation in traits within native and/or introduced ranges [21–23], Colautti et al. hypothesized that clinal variation in plant traits might explain certain differences between native and introduced populations that have previously been used to support or reject the EICA hypothesis [12]. If a particular phenotypic trait, such as size or reproduction, covaries with latitude, then among-population variation can potentially complicate statistical comparisons between native and introduced populations [12]. Rosche et al. found that climate conditions, changed with latitude, explained more variations in neutral genetic differentiation and common garden performance than native vs. nonnative range affiliation [24].

In fact, along the latitudes, abiotic and/or biotic factors will change and impose selection on plant fitness. For example, when plants are introduced from high latitudinal areas to low latitudinal areas, the environments with high temperature and precipitation may be more stressful for introduced plants. As a result, the plants may evolve to invest more resources into defense [25, 26] and less into growth and reproduction in stress environments and depart from the expectations of EICA. An increasing number of case studies have demonstrated latitudinal variation in phenotypic traits in native and/or introduced populations [27–30], and nonparallel latitudinal changes in phenotypic traits between native and introduced ranges [31, 32]. Studies including field and common garden comparisons of native and introduced populations involved latitudinal clines are needed to increase our understanding of invasion biology.

This paper presents the results of field and common garden comparisons in which we compared the plant size and fecundity of common groundsel (*Senecio vulgaris* L.) collected from native European and introduced Chinese populations. Our main questions are as follows: (1) in the field comparison, will plants from introduced Chinese populations be larger in size and higher in fecundity than those from European native populations with or without considering the covariance of phenotypical traits with latitude; (2) in the common garden comparison, will the phenotypic patterns be the same as those in the field comparison?

Results

Field investigation

The field investigation indicated that the *Senecio vulgaris* individuals performed better in terms of both growth and reproduction in introduced populations than in native populations. The plants from Chinese populations were significantly taller (China: 25.6 ± 1.5 cm, mean ± se, Europe: 18.6 ± 1.5 cm, $P = 0.034$, Fig. 1a) and set more capitula (China: 42.1 ± 3.0, Europe: 29.2 ± 5.3, $P = 0.010$, Fig. 1c) than those from native populations (Table 2). Latitude had no effect on plant height ($P = 0.976$) or number of capitula ($P = 0.446$). The 'range and latitude' models did not differ from the 'range-only' models in terms of plant height ($P = 0.976$) or number of capitula ($P = 0.450$). The effect size of range did not vary much when latitude was dropped from the models (plant height: 6.909 ± 2.909 vs. 6.961 ± 2.350; number of capitula: 0.485 ± 0.188 vs. 0.401 ± 0.154). The 'region' models showed that both northeast Chinese populations (25.4 ± 1.7 cm, $P = 0.021$) and southwest Chinese populations (26.1 ± 3.2 cm, $P = 0.024$) were taller than European populations (Fig. 2a; Table S1). Plants from northeast Chinese populations (45.0 ± 4.0, $P = 0.004$) produced more capitula than European populations but southwest Chinese populations did not (37.0 ± 3.6, $P = 0.126$, Fig. 2c). No significant difference in the number of branches was detected between native and introduced populations regardless of whether latitude was included in the model ($P = 0.184$) or not ($P = 0.978$, Table 2), but plants from Chinese populations at higher latitudes tended to produce more branches based on the 'range and latitude' model ($P = 0.025$, Fig. 1b).

Common garden comparisons

Individuals from introduced populations also performed better in terms of both growth and reproduction than those from native populations when they were grown in the common garden in Switzerland. At harvest, plants from introduced populations were taller than those from native populations (China: 19.8 ± 0.6 cm, Europe: 16.9 ± 0.9 cm, Table 2, Fig. 3a) regardless of whether latitude was included in the models ($P = 0.730$, Table 2). However, a different scenario was detected in the comparison of the number of capitula when latitude was dropped from the models. The 'range and latitude' model suggested that both range and latitude significantly affected the number of capitula (Table 2). More capitula were found in plants from Chinese introduced populations than from native populations ($P = 0.013$, Table 2) and from populations at higher latitudes ($P = 0.003$, Table 2, Fig. 3b). When latitude was dropped, the 'range-only' model indicated significant difference in the patterns ($P = 0.010$, Table 2). No significant difference in the number of capitula was detected between introduced and native populations. Dry mass (China: 1.19 ± 0.13 g, Europe: 1.14 ± 0.12 g, Fig. 3c) did not vary significantly between introduced and native populations regardless of whether latitude was included in the models (Table 2). Both the 'range and latitude' models and 'range-only' models suggested no significant differences in plant height or number of capitula between introduced and native populations in all the three observations before harvest (Table S2).

Plant height and number of capitula at harvest exhibited similar patterns as those in the field investigation according to the 'region' models. Plants from northwest (19.8 ± 0.5 cm, $P = 0.038$) and Southeast Chinese populations (19.9 ± 1.2 cm, $P = 0.044$) were taller than those in European populations (16.9 ± 0.9 cm) (Fig. 4a; Table S1). However, only the plants from northeast Chinese populations where the latitude was similar to that of the native populations (23.1 ± 1.3, $P = 0.048$) produced more capitula than those from European populations (18.3 ± 1.2) (Fig. 4b; Table S1). Dry mass did not vary significantly between the two Chinese regions and the European region (Fig. 2c; Table S1).

Discussion

Invasive species are generally expected to perform better in their introduced ranges [2], and our field investigations of *Senecio vulgaris* supported this expectation in terms of both growth and reproduction (Fig. 1). In comparison to the European native populations, the *S. vulgaris* plants were significantly taller in the Chinese introduced populations regardless of whether they were from the southwest or northeast regions (Fig. 2a). The reproductive investment, as indicated by the number of capitula, was also significantly higher for plants from introduced populations than those from native populations. However, different patterns were detected between the two Chinese regions. Only plants from northeast Chinese populations which located at similar latitudes to those from European populations performed better in terms of the number of capitula than native populations (Fig. 2b).

The common garden comparisons of growth and reproduction between native and introduced populations confirmed again that *S. vulgaris* from the introduced ranges performed better (Fig. 3) and suggested that the difference in growth and reproduction between plants from the native and introduced ranges was not a result of phenotypic plasticity in response to the environment. The same patterns were found in the common garden comparisons and the field investigation. The *S. vulgaris* plants from Chinese introduced ranges were taller than those from the native range, and those from the northeast range set more capitula, but this was not that case for those from the southwest range (Fig. 4).

The different patterns in terms of reproductive investment in the comparison of European native populations to northeast and southwest Chinese populations may suggest the effects of latitudinal clines or habitat productivity [12, 18–20]. The 'range and latitude' model indicated that both range and latitude had significant effects on the number of capitula. However, when latitude was dropped from the model, the 'range-only' model suggested no significant difference in the number of capitula between the native and introduced ranges (Table 2). These results revealed the effects of latitudinal variation on tests of the expectations of EICA [12].

The latitudinal clines in the traits of introduced plants reported by several studies suggest physiological adaptation to the abiotic environment during invasion [21, 24, 33, 34]. Among our investigated introduced populations, the northeast Chinese populations were located at higher latitudes (41~46°N), while the southwest Chinese populations were located at lower latitudes (24~30°N). The *S. vulgaris* from southwest Chinese populations set fewer capitula than those from the northeast Chinese populations (Fig. 2). For the comparisons between northeast Chinese introduced populations and European native populations, the plants grew in ranges with similar latitudes (Table 1). If the ranges at similar latitudes showed similar habitat productivity, the plants in introduced ranges would invest more resources into growth and reproduction after enemy release and show more vigor [4, 18–20]. Our results from the common garden comparisons were consistent with this expectation. The southwest Chinese populations represented a different scenario. The plants from southwest Chinese populations grew at much lower latitudes (Table 1). If the environmental conditions at the lower latitudes at which the southwest Chinese populations occur are more stressful for *S. vulgaris,* which naturally occurs at higher latitudes, they are at greater risk for impacts from generalist pathogens, for example, and the introduced plants may have little potential to evolve significantly lower defenses [20]. Therefore, the resources invested in defense cannot be shifted to improve growth and reproduction. A previous study revealed such a trade-off between exposure to the rust fungus and vegetative vigor in this *S. vulgaris* species [35]. As a result, the southwest Chinese populations did not perform better than native populations in our common garden comparisons (Fig. 2). More information is needed to evaluate the investment in defense between Chinese introduced and European populations and between northeast and southwest Chinese introduced populations of *S. vulgaris.* In addition, more evidence is needed to exclude the likelihood that biotic factors such as herbivore and pathogen would cause rapid adaptations. The other possibility is that trait divergences are caused by history or chance demographic events (e.g. multiple introductions from different origins) [36]. Our previous study found that populations in northeast China were derived from different sources; in southwest China although half individuals were assigned to a population sampled from UK, the rest were from other sources. In addition, populations in these two Chinese ranges were not clustered into two genetic groups [37]. Therefore, the latitudinal trait variation observed in this study was less likely due to different origins but environmental difference between the northeast and southwest China.

Conclusions

The present study demonstrated the increased vigor of introduced populations in field and common garden experiments, consistent with one prediction of the EICA hypothesis. More importantly, this study highlighted the importance of considering latitudinal clines and the habitat productivity in comparisons of native and introduced populations.

Methods

Study species

Senecio vulgaris (Asteraceae) is a self-compatible annual herb that likely originated in southern Europe [38], and has been introduced to Asia, America, South Africa, New Zealand and Australia [39]. It was first reported in northeast China in the nineteenth century. Currently, *S. vulgaris* is distributed in northeast and southwest China and mainly inhabits ruderal and agricultural environments [40]. Genetic analyses based on microsatellite markers suggest multiple introductions of *S. vulgaris* to China and significant genetic differentiation among populations in China [37].

Field investigation

Field investigations were conducted in five populations sampled in Europe and 11 populations in China (Table 1). The European sampling sites are distributed in England and Switzerland. The Chinese sampling sites are distributed in Heilongjiang, Inner Mongolia and Jilin in northeast China and Yunnan, Sichuan and Guizhou in southwest China. At each sampling site, we randomly sampled more than 30 individuals and measured the three following phenotypic traits: plant height, number of branches and number of capitula.

Common garden experimental design

Mature seeds were collected from 30 groundsel plants within each of six native populations in Europe, three introduced populations in northeast China and three populations in southwest China in 2005 (Table 1). For each population, all mature seeds were mixed together and stored at 4°C in envelopes. Fifty high-quality seeds from each population were used for the common garden experiments.

Beginning on 26 April 2006, we conducted a common garden experiment at the University of Neuchatel, Switzerland, to evaluate the differences in growth and reproduction of offspring sampled from native and introduced ranges. All seeds were placed in 0.5% formaldehyde for 15 min, rinsed with water and then immersed in 1 mg/L gibberellin for 24 h. After the seeds were cleaned with water, all 50 high-quality groundsel seeds from each population were sown in 50 pots (one seed per pot). Thus, the experiment consisted of 600 pots separated from one another by 0.5 m.

To evaluate plant growth and reproduction in different stages, we measured the height and number of capitula of each plant 45, 51, and 57 days after the start of the experiment. Once a capitulum matured, the whole individual was harvested. At harvest, we measured the plant height, number of capitula. Then, the plant was oven dried at 80°C for 48 h to a constant weight, and we measured the dry mass.

Statistical analysis

To test the effects of range (native or introduced) and latitude on the phenotypic traits, we fitted linear mixed models by using plant height and dry mass as response variables and fitted generalized linear mixed models by using number of branches and number of capitula as response variables. In both model fittings, range and latitude were set as fixed effects without interaction, and population was set as a random effect. These models were defined as 'range and latitude' models.

To specifically test whether latitude affected estimates of the difference between native and introduced populations, we compared two models: 1) the previously described 'range and latitude' model including range and latitude without interaction and 2) the 'range-only' model excluding latitude. The -2 residual log-likelihood of the two models were compared and tested with X^2 test (chi-square test) in linear mixed model fitting. The deviance of the two models were compared and tested with X^2 test in generalized linear mixed model fitting. We used the parameter of range estimated in each model as the effect size for range and compared this value between the two models.

The sampling sites in China aggregate into two regions (northeast and southwest China). Therefore, we replaced the two fixed effects (range and latitude) with one fixed effect (region: Europe, northeast China or southwest China) in the 'range and latitude' models to compare the difference between native and introduced populations. These models were defined as 'region' models. All analyses were performed in R [41]. The linear mixed models were fitted using the function *'lme'* and the generalized linear mixed models were fitted using the function *'glmer'* in the package lme4.

Declarations

Abbreviations

EICA: evolution of increased competitive ability.

Ethics approval and consent to participate

Senecio vulgaris is an invasive plant, and no permissions were required to collect its plant specimens.

Consent for publication

Not applicable.

Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Competing interests

The authors declare that they have no competing interests.

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Authors' contributions

DYZ and WJL conceived and designed the experiments. WJL, XML and BRZ performed the experiments, analyzed the data and wrote the manuscript. All authors read and approved the final manuscript.

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Tables

Table 1 Populations of *Senecio vulgaris* involved in the common garden experiment (C) and field investigation (F).

Range	Population	Location (Latitude, longitude, altitude)	Investigation performed
Native			
	SWBI	47.13 N, 7.23 E, 437 m	C
	SWNE	47.01 N, 6.96 W, 527 m	C, F
	FRTR	48.23 N, 4.04 E, 125 m	C
	FRVA	45.04 N, 6.34 E, 1673 m	C
	GEBV	49.12 N, 11.28 E, 416 m	C
	GEFR	50.13 N, 8.69 E, 125 m	C
	UKAS1	51.41 N, 0.65 W, 46 m	F
	UKAS2	51.42 N, 0.64 W, 46 m	F
	UKOX1	51.74 N, 1.24 W, 47 m	F
	UKOX2	51.56 N, 1.28 W, 48 m	F
Introduced			
Northeast China			
	NCBX	41.34 N, 123.88 E, 124 m	C
	NCTH	41.74 N, 125.93 E, 371 m	C, F
	NCHL	45.76 N, 132.93 E, 95 m	C, F
	NCTM	44.47 N, 129.98 E, 98 m	F
	NCMD	44.60 N, 129.67 E, 214 m	F
	NCJD	45.23 N, 131.15 E, 196 m	F
	NCJX	45.31 N, 132.98 E, 130 m	F
	NCYK	49.29 N, 120.73 E, 640 m	F
Southwest China			
	SCKM	24.99 N, 102.62 E, 1910 m	C, F
	SCGY	26.70 N, 106.65 E, 1329 m	C, F
	SCLD	29.82 N, 102.22 E, 1609 m	C
	SCLP	26.59 N, 104.82 E, 1816 m	F
	SCMG	28.33 N, 103.13 E, 1951 m	F

Table 2 Parameter estimates of the mixed effects models for trait comparison in field and common garden.

Traits	Range and latitude model				Range-only model		Model comparison	
	Range		Latitude		Range			
	Estimates (mean±se)	*P*	Estimates (mean±se)	*P*	Estimates (mean±se)	*P*	Statistics	*P*
Field investigation								
Plant height (cm)	**6.909±2.909**	**0.034**	-0.004±0.141	0.976	**6.961±2.350**	**0.010**	0.001	0.976
No. branches	0.219±0.165	0.184	**0.018±0.008**	**0.025**	0.004±0.154	0.978	**4.365**	**0.037**
No. capitula	**0.485±0.188**	**0.010**	0.007±0.009	0.446	**0.401±0.154**	**0.010**	0.571	0.450
Common garden comparison								
Plant height (cm)	**3.288±1.412**	**0.045**	0.029±0.083	0.738	**2.949±1.018**	**0.016**	0.119	0.730
No. capitula	**0.374±0.151**	**0.013**	**0.026±0.009**	**0.003**	0.043±0.140	0.758	**6.568**	**0.010**
Dry mass (g)	0.127±0.234	0.600	0.005±0.014	0.713	0.063±0.164	0.707	0.143	0.705

For plant height and dry mass, linear mixed effects models were fitted. For number of branch and number of capitula the generalized linear mixed effects models were fitted. Estimates were the estimated values of the parameters of fixed effects in models. Bold numbers indicate significant level at p value < 0.05.

Figures

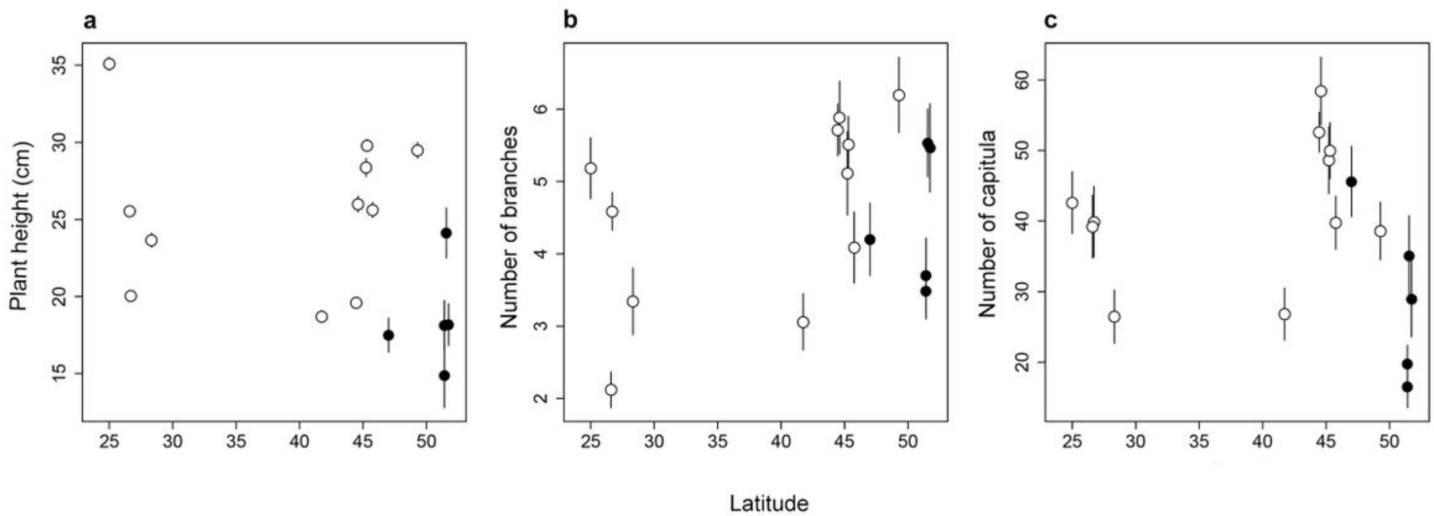

Figure 1

Plant height (a), number of branches (b) and number of capitula (c) in field populations in Europe (black dot) and China (empty dot). The dot represents mean and the error bar represents SE.

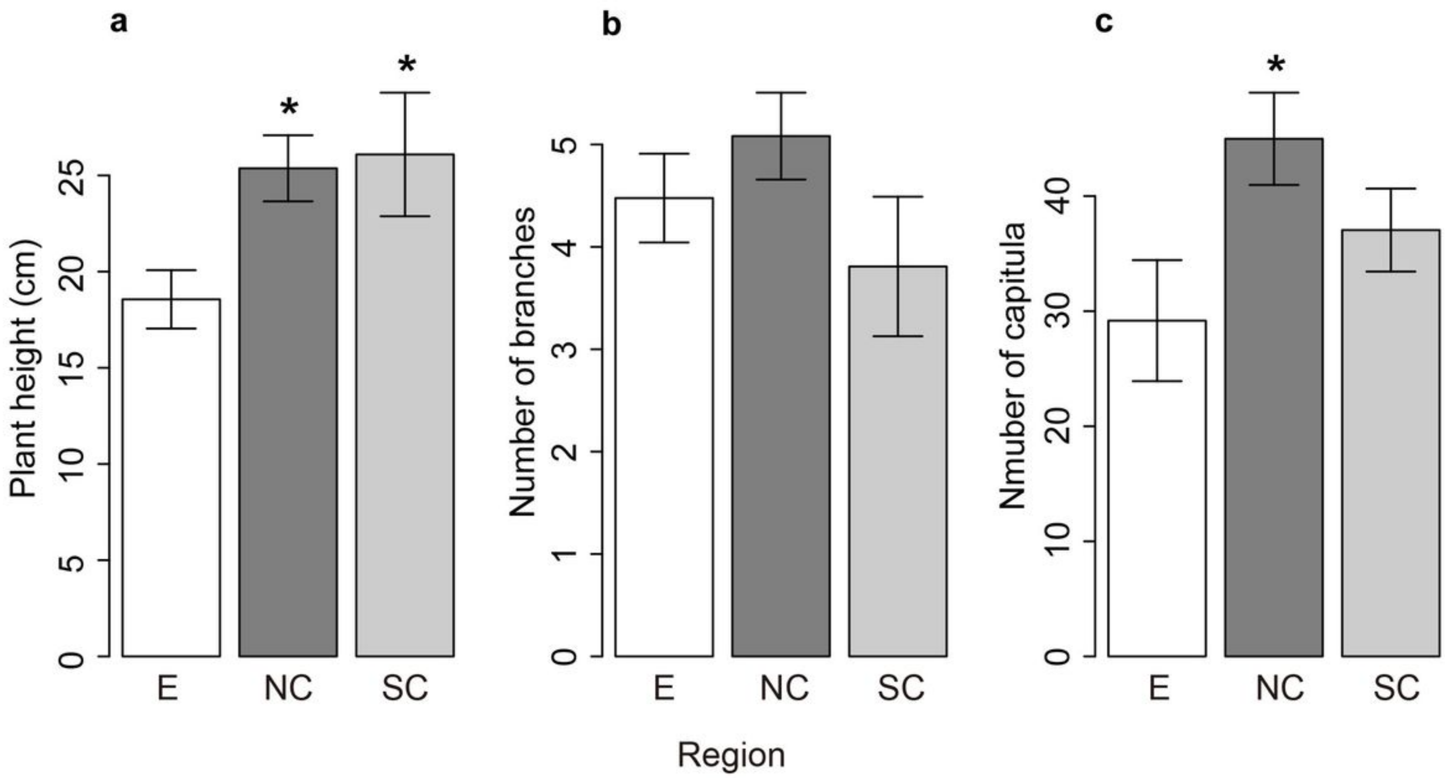

Figure 2

Comparisons of plant height (a), number of branches (b) and number of capitula (c) in field. Populations were from European (E: white), northeast Chinese (NC: dark grey) and southwest Chinese (SC: light grey) regions. The error bar represents SE. The star indicates significant difference (P < 0.05) compared to European populations.

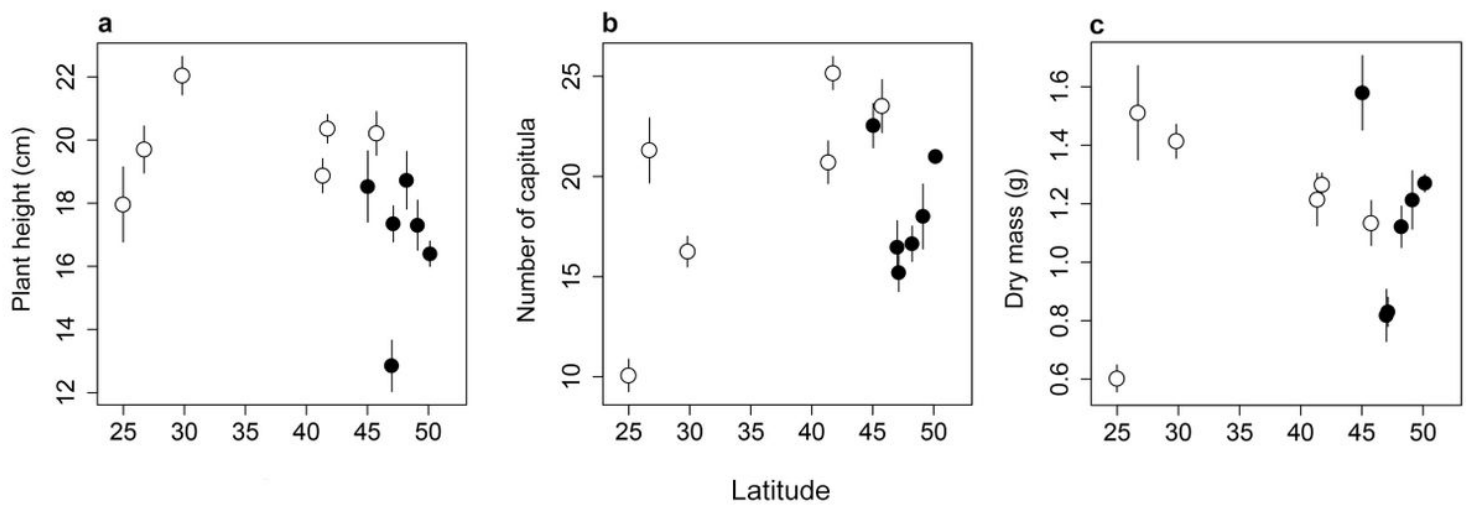

Figure 3

Plant height (a), number of capitula (b) and dry mass (c) in common garden populations in Europe (black dot) and China (empty dot). The dot represents mean and the error bar represents SE.

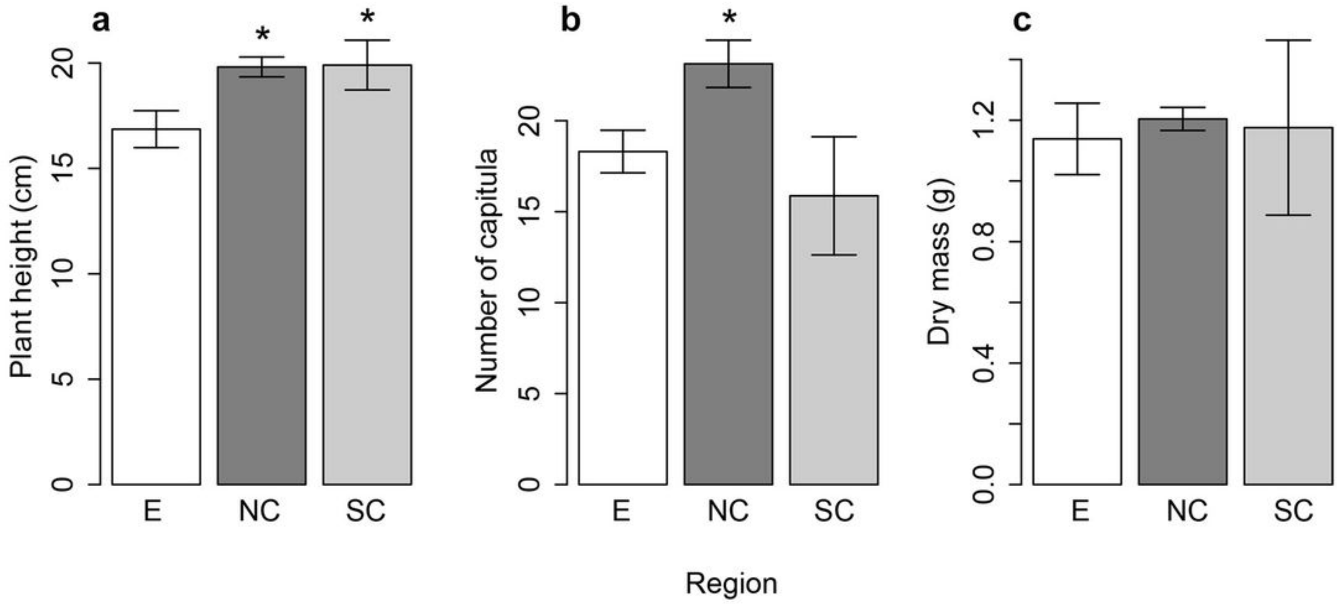

Figure 4

Comparisons of plant height (a), number of capitula (b) and dry mass (c) in common garden. Plants were from European (E: white), northeast Chinese (NC: dark grey) and southwest Chinese (SC: light grey) regions. The error bar represents SE. The star indicates significant difference ($P < 0.05$) compared to European populations.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- Supplementarydata.docx