

Latitudinal and longitudinal clines of phenotypic plasticity in the invasive herb *Solidago canadensis* in China

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Abstract Phenotypic plasticity is thought to be important for plants in variable environments. The climatic variability hypothesis poses that populations at higher latitudes, due to the stronger variation in temperature, there should be more plastic in response to temperature than populations at lower latitudes. Similarly, populations at locations with stronger precipitation fluctuations should be more plastic in response to water availability than populations at locations with less variable precipitation. We sampled seven and nine populations of *Solidago canadensis*, a North American native that is invasive in China, along a latitudinal (temperature variability) and a longitudinal (precipitation variability) gradient, respectively, in China, and grew them under two temperature treatments and two water-availability treatments, respectively. Among the four traits with significant variation in plasticity among populations in response to temperature, plasticity of leaf length-to-width ratio was

significantly positively correlated with latitude and temperature seasonality of the populations. In addition, root/shoot ratio and water-use efficiency showed significant variation in plasticity among populations in response to water availability, and plasticities of these two traits were significantly negatively correlated with longitude and positively correlated with precipitation seasonality. The observed geographic clines in plasticity suggest that phenotypic plasticity of *S. canadensis* may have evolved rapidly in regions with different climatic conditions, and this may have contributed to the spread of this invasive species.

Keywords Climatic variability hypothesis · Latitudinal pattern · Longitudinal pattern · Morphological plasticity

Introduction

Phenotypic plasticity, i.e. the capacity of an organism to express different phenotypes in different environments (Bradshaw 1965), is a widespread phenomenon (Agrawal 2001; Engel et al. 2011), and is likely to play an important role in the adjustment of organisms to changing environments (Agrawal 2001). Compared to narrowly distributed species, widespread ones are expected to be characterized by a higher level of phenotypic plasticity because of larger variation in environmental conditions that they experience (Bradshaw 1965; Pintor et al. 2015). High phenotypic plasticity is also likely to contribute to the spread of invasive alien plants (Baker 1965; Richards et al. 2006; Molina-Montenegro et al. 2013; Keser et al. 2014; but see Davidson et al. 2011). Rapid adaptive evolution along environmental gradients is also commonly observed in invasive plants (Maron et al. 2004; Colautti et al. 2009; Moran and Alexander 2014; Oduor et al. 2016). However, while

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phenotypic plasticity can evolve in response to environmental variability (Scheiner and Lyman 1991; van Kleunen and Fischer 2005), few studies have addressed whether this might have happened during the spread of invasive plants to different latitudes and longitudes (Molina-Montenegro and Naya 2012).

Phenotypic plasticity of widespread species may show clear geographical patterns (Swallow et al. 2005; Overgaard et al. 2011). According to the climatic variability hypothesis (Janzen 1967; Stevens 1989), individuals of a species should show higher phenotypic plasticity in physiological and morphological traits or a broader range of physiological tolerance when climatic variability increases, as happens for temperature with increasing latitude. Empirical evidence for thermal traits mostly supports the prediction of the climatic variability hypothesis, since a positive relationship between thermal tolerance ranges and latitude has been reported for many different taxa (see Brattstrom 1968; Addo-Bediako and Chown 2000; Cruz et al. 2005; Calosi et al. 2008; Deutsch et al. 2008; Naya et al. 2012). However, studies testing relationships between latitude and phenotypic plasticity of traits underlying the thermal tolerance are much scarcer (Addo-Bediako and Chown 2000; Naya et al. 2008, 2012; Molina-Montenegro and Naya 2012). Furthermore, the few existing studies focused mostly on animals (Addo-Bediako and Chown 2000; Maldonado et al. 2011; Naya et al. 2008, 2012). For instance, a positive correlation was reported between plasticity of small intestine length and latitude in rodents (Naya et al. 2008) and between physiological plasticity to temperature and latitude in insects (Addo-Bediako and Chown 2000). On the other hand, Maldonado et al. (2011) did not find a positive relationship between the magnitude of digestive-tract plasticity and latitude in rufous-collared sparrows. To the best of our knowledge, only one study to date has tested such a relationship in plants. Molina-Montenegro and Naya (2012) clearly showed that plasticity in ecophysiological traits to temperature in *Taraxacum officinale* was positively correlated with latitude. So, while most of the few studies on this topic found positive relationships between plasticity and latitude, more studies, particularly on plants, are required to test how common this relationship is.

Because temperature seasonality increases with latitude, empirical studies testing geographic patterns of phenotypic plasticity focused on the relationship between latitude and phenotypic plasticity in response to temperature (Stevens 1989; Addo-Bediako and Chown 2000; Sunday et al. 2011; Molina-Montenegro and Naya 2012). However, little is known about how precipitation and its seasonality therein, another major climatic axis, affect phenotypic plasticity of plants. In many parts of the world, the amount and variation of precipitation change with longitude. For instance, Shi

(2004) found that in parts of China precipitation increases with decreasing longitude, i.e. there is more precipitation in the east (at larger longitude, near the ocean) and less in the west (at smaller longitude, far away from the ocean). Therefore, if the climatic variability hypothesis holds, then one would expect a relationship between longitude and phenotypic plasticity in response to water availability in China.

To examine how phenotypic plasticities in response to temperature and water availability change with latitude and longitude, respectively, we collected plants of the widespread invasive rhizomatous species *Solidago canadensis* along a latitudinal and a longitudinal gradient in China. A previous study has suggested that high phenotypic plasticity is an important trait contributing to the invasiveness of *S. canadensis* (Dong et al. 2006). We grew ramets (asexually produced individuals) of *S. canadensis* under two levels of temperature and two levels of water availability. On these plants we measured physiological traits on the efficiency of photosynthesis [light-use efficiency (LUE), water-use efficiency (WUE)], morphological traits on root allocation (root/shoot ratio) and leaf shape (leaf length-to-width ratio) and performance traits (plant height, biomass). We used these data to address the following questions: (1) Is phenotypic plasticity in response to temperature change positively related to latitude and temperature seasonality of the population of origin? (2) Is phenotypic plasticity in response to water-availability change negatively related to longitude and positively related to precipitation seasonality of the population of origin?

Materials and methods

Study species

Solidago canadensis L. (Asteraceae) is a rhizomatous clonal perennial forb native to North America, and is one of the most widespread invasive alien plants in China and in many other countries (Schittko and Wurts 2014). In China, the species was first recorded in the east, in Shanghai, in 1935, and spread from there to the west, north and south of China, where it is now widely distributed (Dong et al. 2006; Lu et al. 2007). Extensive clonal growth of *S. canadensis* leads to dense stands of shoots, which reduces native species diversity (Dong et al. 2006), but without apparent impact on the native soil seed bank (Kundel et al. 2014). Its seeds are small, numerous and wind dispersed, which facilitates long-distance dispersal (Dong et al. 2006). The species occurs between 23°N and 39°N in China, but it could be based on species distribution modelling that occur up to 50°N latitude (Lu et al. 2007).

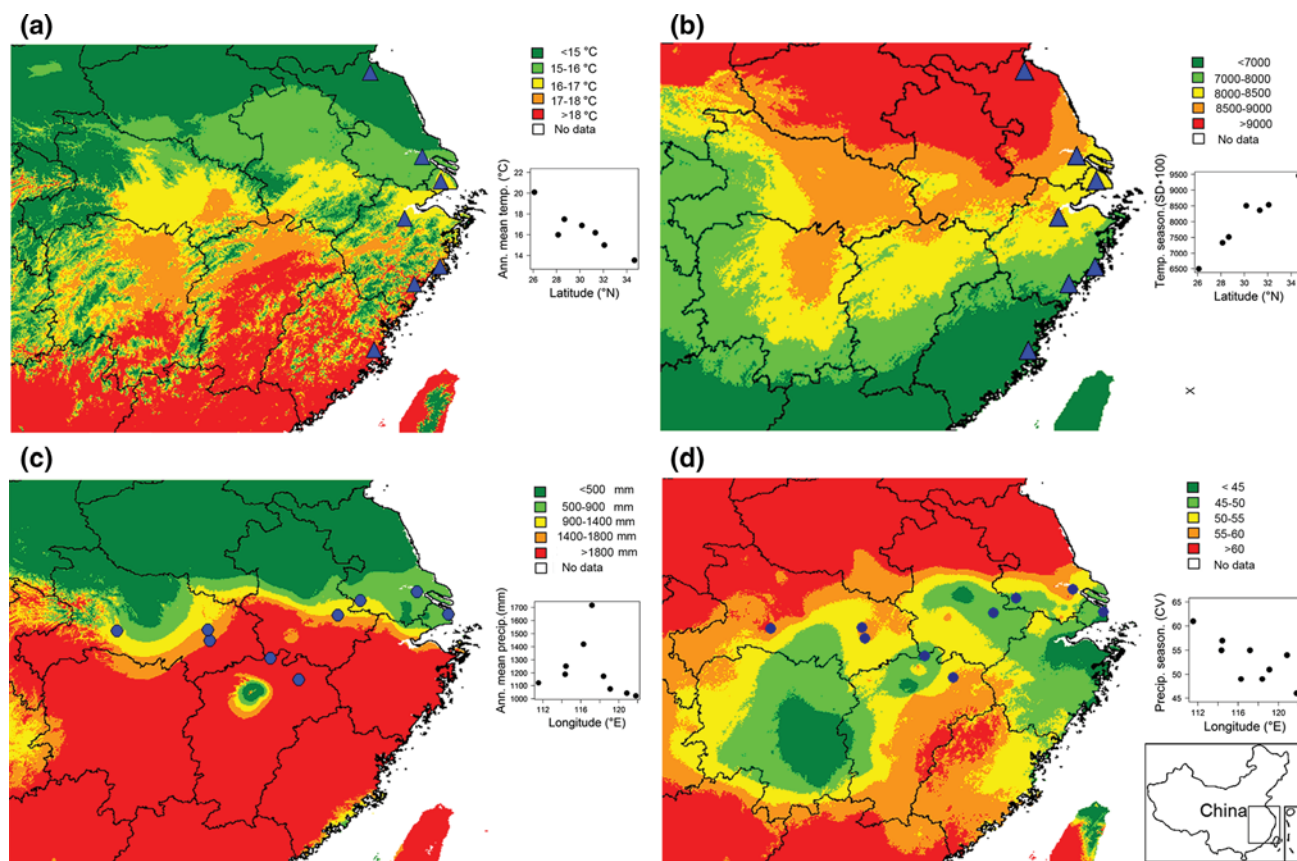


Fig. 1 Sampling locations of *Solidago canadensis* populations along a latitudinal (north–south) transect across China in relation to **a** mean annual temperature and **b** temperature seasonality gradients and along a longitudinal (east–west) transect of **c** mean annual precipitation and

d precipitation seasonality gradients. The annual mean temperature and temperature seasonality vs. latitude, and annual mean precipitation and precipitation seasonality against longitude for all sampling locations are shown as inserts. Color version is available online

Sampling and propagation of plant material

In October 2012, rhizomes of *S. canadensis* were collected from seven populations along a latitudinal transect (Fig. 1a, b, ESM Appendix 1) and nine populations along a longitudinal transect across China (Fig. 1c, d, ESM Appendix 1). Because one population was on both transects, there were 15 populations in total (ESM Appendix 1). The latitude of the populations ranges from 26.0968°N to 34.654°N, and the longitude ranges from 111.532°E to 121.804°E. The two transects span most of the recorded range of *S. canadensis* in China (Lu et al. 2007), and coincide with climatic gradients, especially with regard to variability in temperature and precipitation. This is because in the sampling areas the length of the vegetation period and mean temperature decrease, while temperature seasonality therein increases, with increasing latitude, and mean precipitation and its seasonality therein decrease with increasing longitude (Fig. 1). The sampled populations grew near roads, mostly in ruderal vegetation, which is the typical habitat for this species in China. The geographic coordinates of each

population were recorded using an Explorist 600 potable GPS receiver (Magellan Corporation, Santa Clara, California, USA).

Within each population, 12 randomly selected shoots (ramets) with attached rhizomes were dug out. Shoots were removed, and the shoot bases with attached rhizomes were kept moist until replanted. Individual clones of *S. canadensis* can easily be recognized in the field, because they form dense clusters of stems. Nevertheless, to reduce the chance of sampling the same genet more than once, the distances between collected rhizomes were at least 10 m. A molecular genetic analysis based on five microsatellite loci (see Zuo 2014) confirmed that all collected rhizomes belonged to different genotypes (genets). As *S. canadensis* is known to have different ploidy levels in its native North American range (Croat 1972), and ploidy level might affect plasticity (Levin 2002), we examined the ploidy level of the sampled plants. Therefore, we conducted flow cytometry analysis on fresh young leaf material using an Attune[®] NxT Acoustic Focusing Cytometer (Grand Island, New York, USA). We found that all sampled plants of *S. canadensis* were

hexaploid. This indicates that the *S. canadensis* invasion in China happened independently from the one in Europe, where all *S. canadensis* plants are diploid (van Kleunen and Schmid 2003).

Rhizomes were individually planted in pots (diameter: 30 cm, depth: 30 cm), filled with a soil mixture consisting of six parts of yellow clay soil collected from a field in Linhai City, Zhejiang Province, China, three parts of sand and one part of peat soil. The soil mixture had a final pH of 6.80 ± 0.10 (mean \pm SE, $n = 3$), an organic matter content of 27.66 ± 0.69 g kg⁻¹, a total nitrogen content of 361.00 ± 19.05 mg kg⁻¹, an available phosphorus content of 8.00 ± 0.66 mg kg⁻¹ and an available potassium content of 12.00 ± 0.58 mg kg⁻¹. To reduce environmental carry-over effects, all plant materials used in this study were vegetatively propagated in a greenhouse for at least 4 months.

Temperature experiment

On May 6, 2013, newly produced ramets with a height of about 15 cm were cut off from the stock genotypes of *S. canadensis* and individually planted in pots (diameter: 16 cm, depth: 14 cm) filled with the same soil mixture as used for the stock population. Pots were randomly allocated to positions on the bench of a walk-in growth chamber (3.6 m long \times 2.7 m wide \times 2.2 m high; Ningbo Jinnan Biological Instrument Co. Ltd., Zhejiang Province, China) in Taizhou University. Inside the chamber the photon flux density was $170 \mu\text{mol m}^{-2} \text{s}^{-1}$, the photoperiod was set to 14/10 h in light/dark, the humidity was 85 % and the temperature was 22/17 °C in day/night.

On May 20, 2013, we started the temperature experiment using two growth chambers with different temperature regimes. Two ramets from each of 6–9 genets of the seven *S. canadensis* populations (totaling 102 ramets) along the latitudinal transect across China were allocated to two treatments; a control and a high-temperature treatment (one replicate per genotype per treatment). The temperature of the control treatment was set at 22/17 °C in day/night, and the temperature of the high-temperature treatment was set at 32/27 °C in day/night. The experimental temperatures were chosen to cover a large amplitude that is still within the range of temperatures that all source populations can experience in nature (all populations have maximum temperatures of the warmest month over 30 °C and mean annual temperatures below 22 °C).

As we had only one replicate growth chamber per treatment, each temperature treatment had only one true replicate. However, as we were not interested in the temperature effect per se, but in differences in plastic responses among the populations, the pseudo-replication should not invalidate the comparison of plastic responses among populations. The positions of the pots were randomly changed

every week within each growth chamber to reduce position effects.

On July 21, 2013, several physiological and morphological traits that are potentially important with regard to responses to temperature and water availability were measured on the *S. canadensis* plants. As physiological traits, we determined LUE and WUE, which are traits that plants frequently adjust in response to environmental change to maximize photosynthesis (Rowlan et al. 2015; Zhou et al. 2015). As morphological traits, we determined root/shoot ratio, which plants frequently adjust to maximize the uptake of the most limiting resource (Bloom et al. 1985), and leaf length-to-width ratio, which is a measure of leaf shape important for thermoregulation (Nicotra et al. 2011). In addition, we measured plant height and total biomass as performance traits.

In situ measurements of photosynthesis were made on the third fully expanded leaf, counted from the shoot tip, using a portable photosynthesis-measurement system (LI-6400 XT, Li-COR Inc., Lincoln, NE, USA) between 9:00 and 11:00 am under a photosynthetically active radiation of $1400 \mu\text{mol m}^{-2} \text{s}^{-1}$ (i.e. under light saturation) with a leaf temperature of 25 °C, a CO₂ concentration of 400 ppm and a relative humidity of 70 %. Net photosynthetic rate (P_n), transpiration rate (E) and intercellular CO₂ concentration (C_i) were measured. Light-use efficiency (LUE) was calculated as P_n/PAR (Long et al. 1993), and instantaneous water-use efficiency (WUE) was calculated as P_n/E (Hamid et al. 1990). For every plant, six consecutive measurements were made, and their averages were used in the analyses. After the physiological measurements, we measured the height, length and width of the third leaf of each plant using a flexible ruler with a precision of 0.1 mm. Then, each plant was divided into roots and shoots, dried in an oven at 70 °C to a constant weight, and weighed. Total biomass and root/shoot ratio (R/S) were calculated.

Water-availability experiment

On March 6, 2013, newly produced ramets of about 15 cm high were cut off from the stock genotypes of *S. canadensis*, and planted individually in pots (diameter: 16 cm, depth: 14 cm) filled with the same soil mixture as used for the stock population. Pots were randomly allocated to positions in the greenhouse of Taizhou University in Linhai City, Zhejiang Province, China (121°17'E, 28°87'N).

On March 20, 2013, a water-availability experiment was started in the greenhouse. Maximum water-holding capacity of the soil mixture used in the experiment was measured gravimetrically (Gotsch et al. 2010) as follows. Soil samples were saturated with water and weighed. Then the samples were dried at 50 °C for 3 days, and weighed again. Two ramets from each of the 4–9 genets of the nine

S. canadensis populations (totaling 122 ramets) along the longitudinal transect across China were allocated to two treatments, a well-watered control and a drought treatment (one replicate per genotype per population per treatment). So, we used the same genetic material in each treatment. In the control treatment, the soil-available moisture was maintained at 75–80 % of the maximum water-holding capacity of the substrate. In the drought treatment, it was maintained at 20–25 %. Although we do not have data on the soil-available moisture in the populations of origin, the chosen amplitude is likely to be within the range of values that plants experience in natural populations. Water content of the soil was daily measured gravimetrically, and water was added as necessary to maintain the treatment differences. The positions of the pots were randomly changed every week to reduce position effects. From May 21 to 27, 2013, the same physiological, morphological and performance-related traits were measured as in the temperature experiment described above.

Climate data

For each population, we extracted data on climatic variables from the WorldClim data base (<http://www.worldclim.org/current>) using the DIVA-GIS software (version 7.2.1.1, <http://www.diva-gis.org>). The bioclimatic variables were calculated from monthly temperature and rainfall data in the period 1950–2000, interpolated at 30-s resolution (c. 1 km² resolution, see <http://www.worldclim.org/> and Hijmans et al. 2005). Although these interpolated climate data might deviate from the true values, they are the best data available. Bioclimatic variables used in our study are annual mean temperature (°C) and temperature seasonality (standard deviation × 100) for the populations in the temperature experiment, and annual mean precipitation (mm) and precipitation seasonality (coefficient of variation) for the populations in the water-availability experiment.

Statistical analyses

To test whether traits related to physiology (LUE, WUE), morphology (leaf length-to-width ratio, root/shoot ratio) and performance (plant height, biomass) were significantly affected by the treatments and varied among populations, we used two-way ANOVAs. In these models, treatment (either water availability or temperature) was included as a fixed factor. Because populations were randomly chosen along the geographic/climatic gradients, population and its interaction with the treatment were included as random factors.

To test whether plasticity in the physiological, morphological and performance traits is correlated with latitude and longitude and variation in climatic variables of the

populations, we calculated for each population an average phenotypic plasticity index (PPI) of each trait based on the PPI values of the individual genotypes. The PPI was calculated as: $(\max(x_0, x_i) - \min(x_0, x_i)) / \max(x_0, x_i)$, where x_0 and x_i stand for the mean values of the control and the drought or high-temperature treatments, respectively. $\max(x_0, x_i)$ is the larger value of x_0 and x_i , and $\min(x_0, x_i)$ the smaller value of x_0 and x_i (Cheplick 1995; Valladares et al. 2006). PPI per population was calculated as the mean of the PPI values of the genotypes in each population. Although PPI quantifies the magnitude of plasticity very well, it does not consider the direction of the plastic response. Therefore, we also calculated a directional plasticity index as $(x_0 - x_i) / x_0$ (Valladares et al. 2006). However, as the results were very similar (compare Tables 1, 2 with ESM Appendices 2 and 3), we only represent the results of PPI in the main text, as the climatic variability hypothesis makes no clear predictions regarding the direction of plasticity. The relationships of phenotypic plasticity (PPI) with latitude, longitude and climate data were evaluated using Pearson's correlation tests (see also Molina-Montenegro and Naya 2012). As tests for such correlations assume that populations differ in plasticity, we only did these tests for traits with significant environment × population interactions in the two-way ANOVAs. All statistical analyses were conducted using SPSS 16.0 software.

Results

Correlations of temperature induced plasticity with latitude, mean temperature and its variability

Averaged across all populations in the temperature experiment, plants of *S. canadensis* significantly decreased their WUE and root/shoot ratio, and increased their LUE in response to increased temperature. For plant height, leaf length-to-width ratio and biomass, the average values of the plants were not significantly different between the control and high-temperature treatment (Table 1). Nevertheless, for all of the latter traits, as well as for LUE, there was significant variation in plasticity among populations (significant temperature × population interactions in Table 1).

Among the four traits with significant variation among populations in plasticity to temperature, phenotypic plasticity of leaf length-to-width ratio was higher in the northern than in the southern populations, and consequently significantly positively related with latitude (Fig. 2a; Table 1). This coincided with a significant positive correlation of plasticity in leaf length-to-width ratio with temperature seasonality (Fig. 2c; Table 1), and a significant negative correlation with annual mean temperature (Fig. 2b; Table 1).

Table 1 Physiological, morphological and performance traits of *Solidago canadensis* in the control and high-temperature treatment and phenotypic plasticity index (PPI) of each of these traits

Trait	Temperature effect				Phenotypic plasticity index			
	Control (mean \pm SE)	High temp. (mean \pm SE)	Temp. $F_{1,6}$	Temp. \times pop. $F_{6,88}$	Mean \pm SE	r (latitude)	r (annual mean temperature)	r (temperature seasonality)
Plant height (cm)	43.83 \pm 4.29	56.93 \pm 3.95	3.74	28.56***	0.28 \pm 0.07	-0.30	-0.04	-0.30
Leaf length-to-width ratio	5.15 \pm 0.18	4.89 \pm 0.25	0.89	3.11**	0.17 \pm 0.02	0.82*	-0.73*	0.77*
Biomass (g)	4.68 \pm 0.40	4.70 \pm 0.57	<0.01	7.61***	0.35 \pm 0.03	0.50	-0.78*	0.46
Root/shoot ratio	0.50 \pm 0.03	0.22 \pm 0.01	138.16***	1.02	0.53 \pm 0.02	-	-	-
Light-use efficiency ($\mu\text{mol mmol}^{-1}$)	3.13 \pm 0.09	4.80 \pm 0.36	17.205**	2.66*	0.36 \pm 0.04	-0.65	0.42	-0.55
Water-use efficiency ($\mu\text{mol mmol}^{-1}$)	4.37 \pm 0.14	1.59 \pm 0.11	320.15***	0.26	0.55 \pm 0.03	-	-	-

F values and their significances for temperature effect and temperature \times population interaction from a two-way ANOVA are given. Pearson correlation coefficients (r) between mean PPI values and latitude, annual mean temperature and temperature seasonality of populations ($n = 7$) are also given for variables where the temperature \times population interaction is significant

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Table 2 Physiological, morphological and performance traits of *Solidago canadensis* in the control and drought treatment and phenotypic plasticity index (PPI) of each of these traits

Trait	Drought effect				Phenotypic plasticity index			
	Control (mean \pm SE)	Drought (mean \pm SE)	Drought $F_{1,8}$	Drought \times pop. $F_{8,104}$	Mean \pm SE	r (longitude)	r (annual mean precipitation)	r (precipitation seasonality)
Plant height (cm)	58.55 \pm 2.05	18.70 \pm 1.60	260.38***	1.63	0.67 \pm 0.03	-	-	-
Leaf length-to-width ratio	5.93 \pm 0.28	5.66 \pm 0.23	0.92	1.63	0.17 \pm 0.02	-	-	-
Biomass (g)	3.95 \pm 0.22	1.49 \pm 0.18	204.35***	0.37	0.61 \pm 0.04	-	-	-
Root/shoot ratio	0.38 \pm 0.02	0.87 \pm 0.08	36.60***	2.39*	0.49 \pm 0.04	-0.74*	-0.10	0.72*
Light-use efficiency ($\mu\text{mol mmol}^{-1}$)	7.39 \pm 0.23	3.25 \pm 0.15	176.88***	1.73	0.55 \pm 0.03	-	-	-
Water-use efficiency ($\mu\text{mol mmol}^{-1}$)	1.53 \pm 0.04	12.94 \pm 2.52	29.17**	5.55***	0.81 \pm 0.02	-0.71*	-0.32	0.83*

F values and their significances for drought effect and drought \times population interaction from a two-way ANOVA are given. Pearson correlation coefficients (r) between mean PPI values and longitude, annual mean precipitation and precipitation seasonality of populations ($n = 9$) are also given for variables when the drought \times population interaction is significant

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Correlations of water-availability induced plasticity with longitude, mean precipitation and its variability

Averaged across all populations in the water-availability experiment, plants of *S. canadensis* significantly decreased their height, biomass and LUE, and increased their root/shoot ratio and WUE in response to drought (Table 2). Leaf length-to-width ratio was not significantly affected by the

drought treatment (Table 2). For root/shoot ratio and WUE the degree of plasticity varied significantly among populations (significant drought \times population interactions in Table 2).

For both traits with significant variation among populations in plasticity to water availability, i.e. root/shoot ratio and WUE, their plasticities were higher in the western populations than in the eastern populations, and consequently

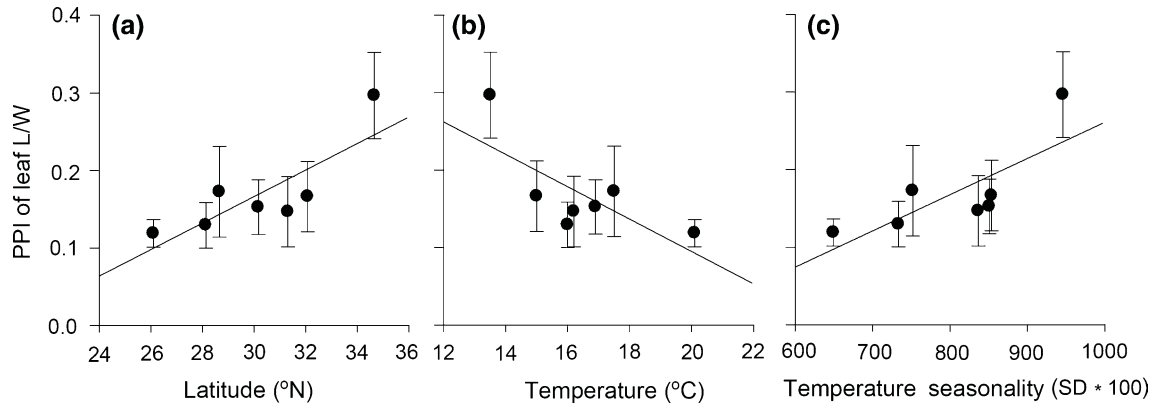


Fig. 2 Relationships of mean (\pm SE) phenotypic plasticity index (PPI) of leaf length-to-width ratio (L/W) of *Solidago canadensis* populations in response to changing temperature with **a** latitude, **b** annual mean temperature and **c** temperature seasonality of the populations of origin

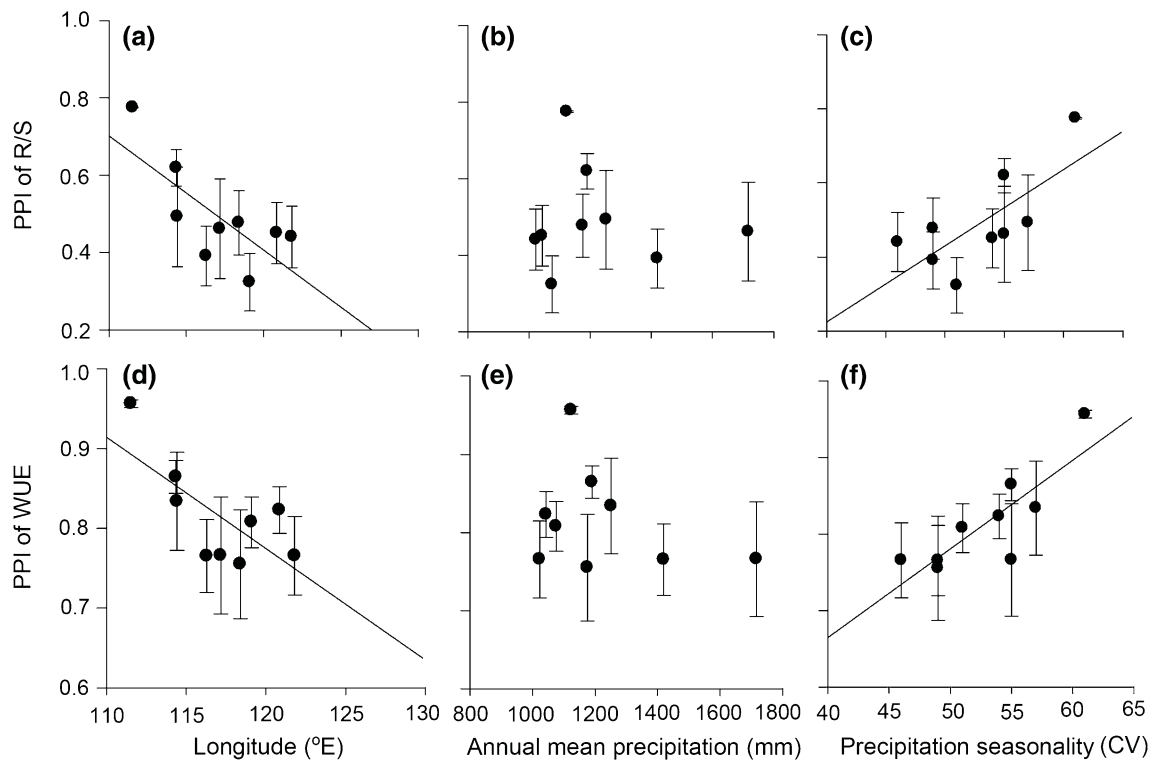


Fig. 3 Relationships of mean (\pm SE) phenotypic plasticity index (PPI) of **a–c** root/shoot ratio (R/S) and **d–f** water utilization efficiency (WUE) of *Solidago canadensis* populations in response to drought

with **a, d** longitude, **b, e** mean annual precipitation and **c, f** precipitation seasonality of the population of origin

significantly negatively related with longitude (Fig. 3a, d; Table 2). This coincided with significant positive correlations of plasticities of both traits with precipitation seasonality, but not with mean annual precipitation (Fig. 3b, c, e, f; Table 2).

Discussion

Plants of *S. canadensis* responded to temperature and water availability with plastic changes in physiological, morphological and performance traits. Populations also

varied in the degree and/or direction of many of their plastic responses. For several of the measured traits, variation in the degree of plasticity was related to the latitude and longitude of origin, in such a way that plasticity increased with seasonality in temperature and seasonality in precipitation, respectively. Our results thus provide support for the climatic variability hypothesis (Janzen 1967; Stevens 1989).

Latitudinal pattern of phenotypic plasticity to temperature in *S. canadensis*

For four of the six traits measured in our study, there was significant variation in plasticity in response to temperature among the seven populations. This suggests that evolutionary change has resulted in genetic differentiation in plasticity in response to temperature among populations. However, there are also several alternative possibilities than evolutionary change. First, it could be that different strains of *S. canadensis* have been introduced to different parts of China. Second, it could be that environmental maternal carry-over effects (e.g. Galloway 2005) or epigenetic differences are responsible for the observed among-population differentiation (Bossdorf et al. 2008). Future common garden experiments using seed material instead of rhizome pieces and studies using molecular genetic and epigenetic markers might reveal which of these scenarios is most likely.

For leaf length-to-width ratio, the magnitude of plasticity increased with the latitude of origin, decreased with annual mean temperature and increased with temperature seasonality. Other studies on invasive plants have frequently revealed latitudinal clines with regard to mean trait values (van Kleunen and Fischer 2008; Colautti et al. 2009), and that at least some of these latitudinal clines may reflect local adaptation (Colautti and Barrett 2013). Although our data do not allow to separate the effects of annual mean temperature and temperature seasonality in the populations of origin, the correlation between plasticity and temperature seasonality is in line with the predictions of the climatic variability hypothesis (Janzen 1967; Stevens 1989). This finding thus suggests that *S. canadensis* may have rapidly adapted after its introduction to Shanghai in 1935 and during its subsequent spread to the north and south of China by changing the plasticity of at least one of its traits to temperature. Similarly, Molina-Montenegro and Naya (2012) demonstrated that phenotypic plasticity of photosynthesis, foliar angle, number of flowers, WUE, biomass and seed-output of the invasive plant *T. officinale* in response to temperature increased with increasing latitude. Although the climate variability hypothesis was developed for widespread native species, and has been tested for native animals, we are not aware of any study that has tested it for a native plant species.

Latitude is correlated with several climatic and ecological factors that could affect the evolution of mean trait values and of phenotypic plasticity (e.g. Neuffer and Hurka 1986; Weber and Schmid 1998; Molina-Montenegro and Naya 2012). Indeed many studies have revealed evidence for genetic latitudinal clines in the native as well as non-native ranges of species (Colautti et al. 2009). We are not aware of any studies that tested for genetic latitudinal clines in the native range of *S. canadensis*. However, Weber and Schmid (1998) tested in a common-garden experiment for such clines in the non-native range of *S. altissima*, which is now considered to be *S. canadensis*, in Europe. They found that plants of this species from higher latitudes flowered earlier and at a smaller size than the ones from lower latitudes, which suggests that rapid evolution within the non-native ranges of invasive species is possible. However, to the best of our knowledge, no previous study had yet tested for latitudinal clines in phenotypic plasticity of *S. canadensis*.

Longitudinal pattern of phenotypic plasticity to water availability in *S. canadensis*

Of the studies that tested for geographical clines in plasticity, the majority focused on either latitudinal or altitudinal clines because of their clear associations with the mean and variation in temperature (Moran and Alexander 2014). However, climatic variables and variation therein can also change along longitudinal clines (Shi 2004). Indeed, plants from western populations of *S. canadensis* in China showed significantly stronger plasticity in root/shoot ratio and water use efficiency in response to water availability than plants from more eastern populations. Our study is thus, to the best of our knowledge, the first one to report significant longitudinal clines in phenotypic plasticity.

In parts of China, precipitation and variation therein are significantly affected by the distance from the ocean in the east (Shi 2004). Along our longitudinal transect, annual mean precipitation was highest at intermediate longitudes, while precipitation seasonality clearly decreased with longitude (Fig. 1c, d). Although plasticity in root/shoot ratio and WUE were correlated with longitude, the magnitude of plasticity was not associated with annual mean precipitation. However, plasticity in both traits was significantly correlated with precipitation seasonality. These findings indicate that the longitudinal clines in plasticity of *S. canadensis* in China are driven by seasonality in precipitation rather than by the mean precipitation. These findings thus strongly support the climatic variability hypothesis.

Implications for invasiveness and conclusions

High phenotypic plasticity has frequently been invoked to be a mechanism that promotes a species' invasiveness

(Baker 1965; Richards et al. 2006). Meta-analyses have not revealed consistent patterns in this regard (Davidson et al. 2011), but this could be because most studies have compared invasive species to native instead of to non-invasive alien species (van Kleunen et al. 2010). Here, we showed that within the non-native range of an invasive species, there can also be among-population variation in phenotypic plasticity of physiological and morphological traits. This shows that plasticity is not a static characteristic of a species, but is variable and may also change.

Since its introduction in 1935 to Shanghai, along the eastern coast of China, *S. canadensis* has spread to large parts of China. Its currently expanding range margins are in the west and north of China, exactly where plasticity in the measured traits is highest. Other studies on geographical patterns in plasticity have hypothesized that plasticity should be highest in peripheral populations because environmental variation is likely to be high there (Volis et al. 1998). Others, however, argued that due to founder effects and limited genetic variation, plasticity should be lower at the margins than in the center of a species' range (Mägi et al. 2011). While the latter is not supported by our findings, the former is. We could not explicitly test whether the observed plastic responses are adaptive (i.e. increase reproductive fitness) in this study. However, if we assume they are, the higher plasticity at this species' western and northern range margins is likely to have helped this species to rapidly invade China, and is likely to further speed up its expansion.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Author contribution statement JML, WBG, FHY and MK conceived and designed the experiments. LSD performed the experiments. JML, FHY, MK analyzed the data. JML, FHY, MK wrote the manuscript.

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