

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

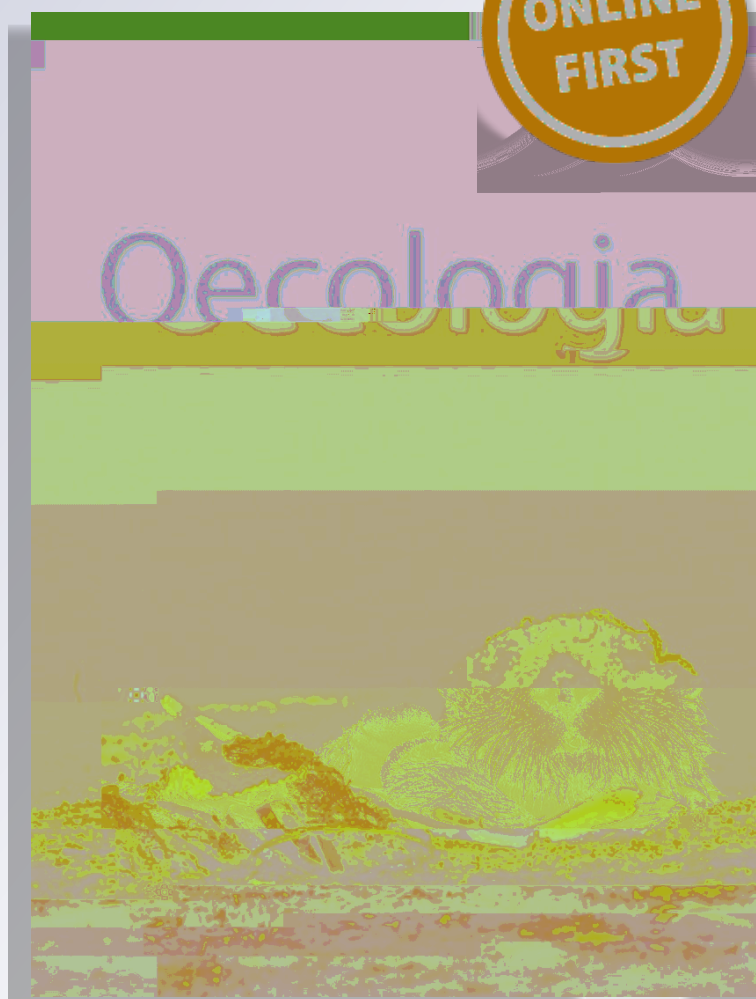
**Junmin Li, Leshan Du, Wenbin Guan,  
Fei-Hai Yu & Mark van Kleunen**

**Oecologia**

ISSN 0029-8549

Oecologia

DOI 10.1007/s00442-016-3699-x



**Your article is protected by copyright and all rights are held exclusively by Springer-Verlag Berlin Heidelberg. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your article, please use the accepted manuscript version for posting on your own website. You may further deposit the accepted manuscript version in any repository, provided it is only made publicly available 12 months after official publication or later and provided acknowledgement is given to the original source of publication and a link is inserted to the published article on Springer's website. The link must be accompanied by the following text: "The final publication is available at [link.springer.com](http://link.springer.com)".**

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

**Junmin Li<sup>1</sup> · Leshan Du<sup>1,2,4</sup> · Wenbin Guan<sup>2</sup> · Fei-Hai Yu<sup>2</sup> · Mark van Kleunen<sup>3</sup>**

Received: 5 December 2015 / Accepted: 27 July 2016  
© Springer-Verlag Berlin Heidelberg 2016

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 correlated traits (latitudinally positively correlated traits) were also significantly correlated with

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).

### 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 portable 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 *w neary/TJ m.016 Tw 38*

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  $6.80 \pm 0.10$  (mean  $\pm$  SE,  $n = 3$ ), an organic matter content of  $27.66 \pm 0.69$  g kg<sup>-1</sup>, a total nitrogen content of  $361.00 \pm 19.05$  mg kg<sup>-1</sup>, an available phosphorus content of  $8.00 \pm 0.66$  mg kg<sup>-1</sup> and an available potassium content of  $12.00 \pm 0.58$  mg kg<sup>-1</sup>. 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 CO<sub>2</sub> concentration of 400 ppm and a relative humidity of 70 %. Net photosynthetic rate ( $P_n$ ), transpiration rate ( $E$ ) and intercellular CO<sub>2</sub> concentration ( $C_i$ ) were measured. Light-use efficiency (LUE) was calculated as  $P_n/\text{PAR}$  (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'

*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 km<sup>2</sup>



**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

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

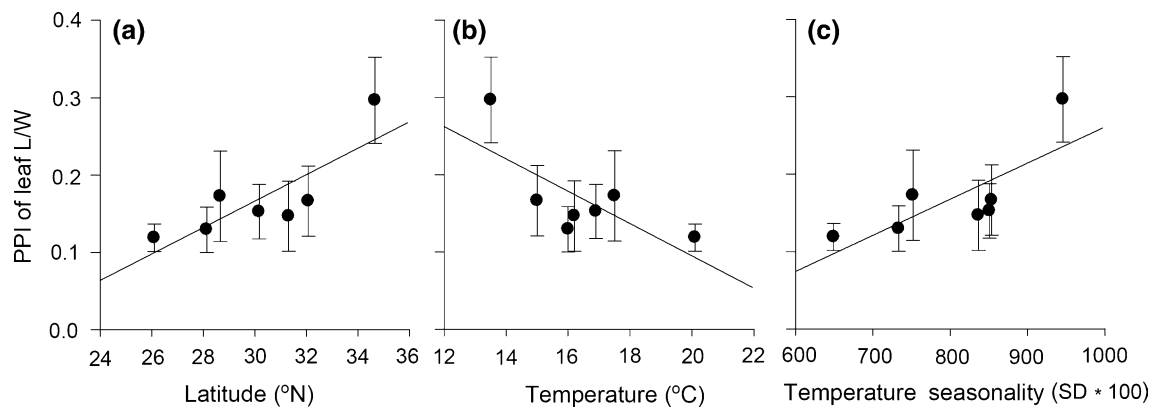
### Correlations of water-availability induced plasticity with longitude, mean precipitation and its variability

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

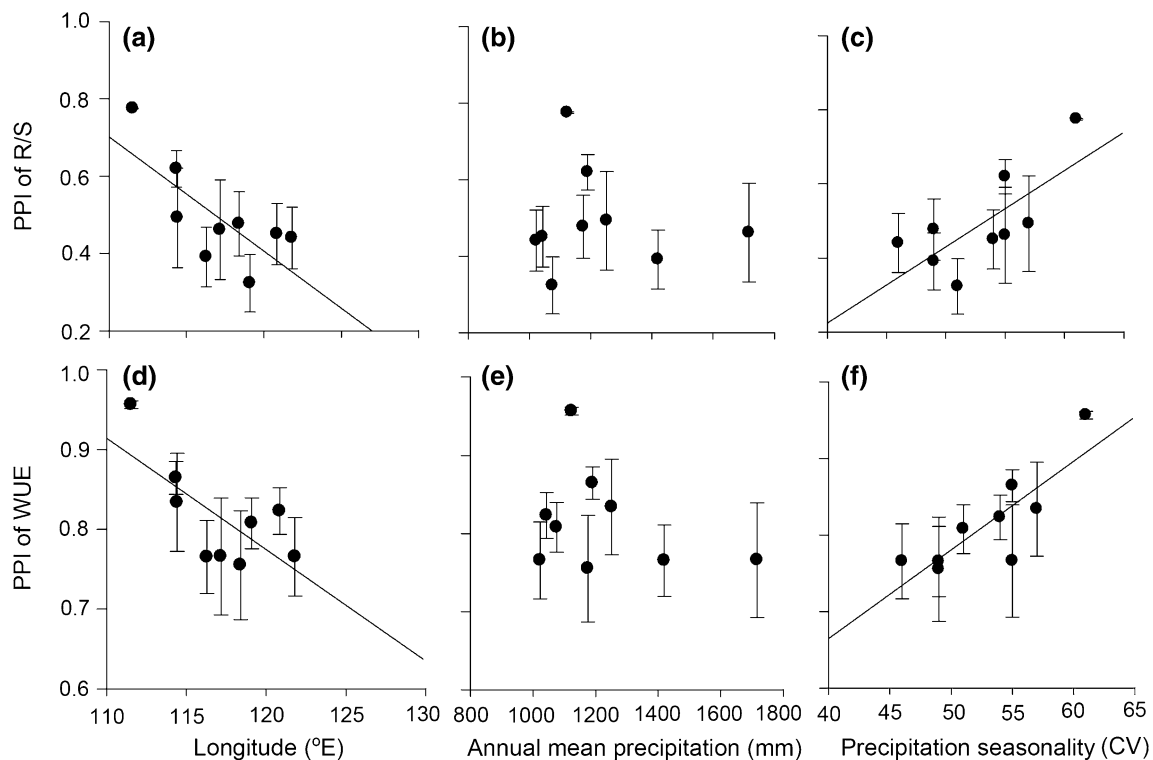
drought treatment (Table 2). For root/shoot ratio and WUE the degree of plasticity varied significantly among populations (significant drought  $\times$  population interactions in Table 2).

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

(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 norther range margins is likely to have helped this species to rapidly invade China, and is likely to further speed up its expansion.

**Acknowledgments** We thank Jianqing Ding and Zhengsheng He for their kind help in collecting plants. This work was financially supported by the National Natural Science Foundation of China (No. 31270461), the National Key Research and Development Program (2016YFC1201100) and the Qianjiang Talents Project of Zhejiang Province (type D), China (No. QJD1302021). MvK acknowledges financial support from the DFG SPP1819 Rapid Evolutionary Adaptation (KL 1866/10-1).

# 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.

# References

Addo-Bediako A, Chown SL, Gaston KJ (2000) Thermal tolerance, climatic variability and latitude. *Proc R Soc Lond B* 267:739–745. doi:[10.1098/rspb.2000.1065](https://doi.org/10.1098/rspb.2000.1065)

Agrawal AA (2001) Phenotypic plasticity in the interactions and evolution of species. *Science* 294:321–326. doi:[10.1126/science.1060701](https://doi.org/10.1126/science.1060701)

Baker HG (1965) Characteristics and modes of origin of weeds. In: Baker HG, Stebbins GL (eds) *The genetics of colonizing species*. Academic, New York, pp 147–172

Bloom AJ, Chapin FS III, Mooney HA (1985) Resource limitation in plants: an economic analogy. *Ann Rev Ecol System* 16:363–392. doi:[10.1146/annurev.es.16.110185.002051](https://doi.org/10.1146/annurev.es.16.110185.002051)

Bossdorf O, Richards CL, Pigliucci M (2008) Epigenetic for ecologists. *Ecol Lett* 11:106–115. doi:[10.1111/j.1461-0248.2007.01130.x](https://doi.org/10.1111/j.1461-0248.2007.01130.x)

Bradshaw AD (1965) Evolutionary significance of phenotypic plasticity in plants. *Adv Genet* 13:115–155. doi:[10.2307/1311135](https://doi.org/10.2307/1311135)

Brattstrom BH (1968) Thermal acclimation in anuran amphibians as a function of latitude and altitude. *Comp Biochem Physiol* 24:93–111. doi:[10.1016/0010-406X\(68\)90961-4](https://doi.org/10.1016/0010-406X(68)90961-4)

Calosi P, Bilton DT, Spicer JJ (2008) Thermal tolerance, acclimatory capacity and vulnerability to global climate change. *Biol Lett* 4:99–102. doi:[10.1098/rsbl.2007.0408](https://doi.org/10.1098/rsbl.2007.0408)

Cheplick GP (1995) Genotypic variation and plasticity of clonal growth in relation to nutrient availability in *Amphibromus scabrivalvis*. *J Ecol* 83:459–468. doi:[10.2307/2261599](https://doi.org/10.2307/2261599)

Colautti RI, Barrett SCH (2013) Rapid adaptation to climate facilitates range expansion of an invasive plant. *Science* 342:364–366. doi:[10.1126/science.1242121](https://doi.org/10.1126/science.1242121)

Colautti RI, Maron JL, Barrett SCH (2009) Common garden comparisons of native and introduced plant populations: latitudinal clines can obscure evolutionary inferences. *Evol Appl* 2:187–199. doi:[10.1111/j.1752-4571.2008.00053.x](https://doi.org/10.1111/j.1752-4571.2008.00053.x)

Croat T (1972) *Solidago canadensis* complex of the Great Plains. *Brittonia* 24:317–326. doi:[10.2307/2805669](https://doi.org/10.2307/2805669)

Cruz FB, Fitzgerald LA, Espinoza RE, Schuster JA II (2005) The importance of phylogenetic scale in tests of Bergmann's and Rapoport's rules: lessons from a clade of South American lizards. *J Evol Biol* 18:1559–1574. doi:[10.1111/j.1420-9101.2005.00936.x](https://doi.org/10.1111/j.1420-9101.2005.00936.x)

Davidson AM, Jennions M, Nicotra AB (2011) Do invasive species show higher phenotypic plasticity than native species and if so, is it adaptive? A meta-analysis. *Ecol Lett* 14:419–431. doi:[10.1111/j.1461-0248.2011.01596.x](https://doi.org/10.1111/j.1461-0248.2011.01596.x)

Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *Proc Natl Acad Sci* 105:6668–6672

Dong M, Lu JZ, Zhang WJ, Chen JK, Li B (2006) Canada goldernrod (*Solidago canadensis*): an invasive alien weed rapidly spreading in China. *Acta Phytotax Sinica* 44:72–85

Engel K, Tollrian R, Jeschke JM (2011) Integrating biological invasions, climate change and phenotypic plasticity. *Comm Integ Biol* 4:247–250. doi:[10.4161/cib.4.3.14885](https://doi.org/10.4161/cib.4.3.14885)

Galloway L (2005) Maternal effects provide phenotypic adaptation to local environmental conditions. *New Phyt* 166:93–100. doi:[10.1111/j.1469-8137.2004.01314.x](https://doi.org/10.1111/j.1469-8137.2004.01314.x)

Gotsch SG, Powers JS, Lerdau MT (2010) Leaf traits and water relations of 12 evergreen species in Costa Rican wet and dry forests: patterns of intra-specific variation across forests and seasons. *Plant Ecol* 211:133–146. doi:[10.1007/s11258-010-9779-9](https://doi.org/10.1007/s11258-010-9779-9)

Hamid MA, Agata W, Kawamitsu Y (1990) Photosynthesis, transpiration and water use efficiency in four cultivars of mungbean. *Photosynthetica* 24:96–101. doi:[10.1023/A:1015660213811](https://doi.org/10.1023/A:1015660213811)

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *Int J Climatol* 25:1965–1978. doi:[10.1002/joc.1276](https://doi.org/10.1002/joc.1276)

Janzen DH (1967) Why mountain passes are higher in the tropics. *Am Nat* 101:233–249

Keser LH, Dawson W, Song YB, Yu FH, Fischer M, Dong M, van Kleunen M (2014) Invasive clonal plant species have a greater

- root-foraging plasticity than non-invasive ones. *Oecologia* 174:1055–1064. doi:[10.1007/s00442-013-2829-y](https://doi.org/10.1007/s00442-013-2829-y)
- Kundel D, van Kleunen M, Dawson W (2014) Invasion by *Solidago* species has limited impacts on soil seedbank communities. *Basic Appl Ecol* 15:573–580. doi:[10.1016/j.baec.2014.08.009](https://doi.org/10.1016/j.baec.2014.08.009)
- Levin D (2002) *The Role of Chromosomal Change in Plant Evolution*. Oxford University Press, New York
- Long SP, Baker NR, Rains CA (1993) Analyzing the responses of photosynthetic CO<sub>2</sub> assimilation to long-term elevation of atmospheric CO<sub>2</sub> concentration. *Vegetation* 104:33–45. doi:[10.1007/BF00048143](https://doi.org/10.1007/BF00048143)
- Lu JZ, Weng ES, Wu XW, Weber E, Zhao B, Li B (2007) Potential distribution of *Solidago canadensis* in China. *Acta Phytotax Sin* 45:670–674. doi:[10.1360/aps06200](https://doi.org/10.1360/aps06200)
- Mägi M, Semchenko M, Kalamees R, Zobel K (2011) Limited phenotypic plasticity in range-edge populations: a comparison of co-occurring populations of two *Agrimonia* species with different geographical distributions. *Plant Biol* 13:177–184. doi:[10.1111/j.1438-8677.2010.00342.x](https://doi.org/10.1111/j.1438-8677.2010.00342.x)
- Maldonado K, Bozinovic F, Rojas JM, Sabat P (2011) Within-species digestive tract flexibility in Rufous-collared sparrows and the climatic variability hypothesis. *Physiol Biochem Zool* 84:377–384. doi:[10.1086/660970](https://doi.org/10.1086/660970)
- Maron JL, Vilà M, Bommarco R, Elmendorf S, Beardsley P (2004) Rapid evolution of an invasive plant. *Ecol Monogr* 74:261–280. doi:[10.1890/03-4027](https://doi.org/10.1890/03-4027)
- Molina-Montenegro MA, Naya DE (2012) Latitudinal patterns in phenotypic plasticity and fitness related traits: assessing the climatic variability hypothesis (CVH) with an invasive plant species. *PLoS One* 7:e47620. doi:[10.1371/journal.pone.0047620](https://doi.org/10.1371/journal.pone.0047620)
- Molina-Montenegro MA, Palma-Rojas C, Alcayaga-Olivares Y, Osés R, Corcuera LJ, Cavieres LA (2013) Ecophysiological plasticity and local differentiation help explain the invasion success of *Taraxacum officinale* (dandelion) in South America. *Ecography* 36:718–730. doi:[10.1111/j.1600-0587.2012.07758.x](https://doi.org/10.1111/j.1600-0587.2012.07758.x)
- Moran EV, Alexander JM (2014) Evolutionary responses to global change: lessons from invasive species. *Ecol Lett* 17:637–649. doi:[10.1111/ele.12262](https://doi.org/10.1111/ele.12262)
- Naya DE, Bozinovic F, Karasov WH (2008) Latitudinal trends in digestive flexibility: testing the climatic variability hypothesis with data on the intestinal length of rodents. *Am Nat* 172:122–134. doi:[10.1086/590957](https://doi.org/10.1086/590957)
- Naya DE, Spangenberg L, Naya H, Bozinovic F (2012) Latitudinal patterns in rodent metabolic flexibility. *Am Nat* 179:172–179. doi:[10.1086/665646](https://doi.org/10.1086/665646)
- Neuffer B, Hurka H (1986) Variation of development time until flowering in natural populations of *Capsella bursa-pastoris* (Cruciferae). *Plant System Evol* 152:277–296. doi:[10.1007/BF00989433](https://doi.org/10.1007/BF00989433)
- Nicotra AB, Leigh A, Boyce CK, Jones CS, Niklas KJ, Royer DL, Tsukaya H (2011) The evolution and functional significance of leaf shape in the angiosperms. *Funct Plant Biol* 38:535–552. doi:[10.1071/FP11057](https://doi.org/10.1071/FP11057)
- Oduor AMO, Leimu R, van Kleunen M (2016) Invasive plant species are locally adapted just as frequently and at least as strongly as native plant species. *J Ecol* 104:957–968. doi:[10.1111/1365-2745.12578](https://doi.org/10.1111/1365-2745.12578)
- Overgaard J, Kristensen TN, Mitchell KA, Hoffmann AA (2011) Thermal tolerance in widespread and tropical drosophila species: does phenotypic plasticity increase with latitude? *Am Nat* 178:S80–S96. doi:[10.1086/661780](https://doi.org/10.1086/661780)
- Pintor AFV, Schwarzkopf L, Krockenberger AK (2015) Rapoport's rule: do climatic variability gradients shape range extent? *Ecol Monogr* 85:643–659. doi:[10.1890/14-1510.1](https://doi.org/10.1890/14-1510.1)
- Richards CL, Bossdorf O, Muth NZ, Gurevitch J, Pigliucci M (2006) Jack of all trades, master of some? On the role of phenotypic in plant invasions. *Ecol Lett* 9:981–993. doi:[10.1111/j.1461-0248.2006.00950.x](https://doi.org/10.1111/j.1461-0248.2006.00950.x)
- Rowlan L, Lobo-do-vale RL, Christoffersen BO, Melem EA, Kruijt B, Vasconcelos SS, Domingues T, Binks OJ, Oliveira AAR, Metcalfe D, Da Costa ACL, Mencuccini M, Meir P (2015) After more than a decade of soil moisture deficit, tropical rainforest trees maintain photosynthetic capacity, despite increased leaf respiration. *Global Change Biol* 21:4662–4672. doi:[10.1111/gcb.13035](https://doi.org/10.1111/gcb.13035)
- Scheiner SM, Lyman RF (1991) The genetics of phenotypic plasticity. II. Response to selection. *J Evol Biol* 4:23–50. doi:[10.1046/j.1420-9101.1991.4010023.x](https://doi.org/10.1046/j.1420-9101.1991.4010023.x)
- Schittko C, Wurts S (2014) Above- and belowground effects of plant-soil feedback from exotic *Solidago canadensis* on native *Tanacetum vulgare*. *Biol Invas* 16:1465–1479. doi:[10.1007/s10530-013-0584-y](https://doi.org/10.1007/s10530-013-0584-y)
- Shi XY (2004) Regional climate meridional and zonal feature in China. Msc dissertation, Chinese Academy of Meteorological Science, Beijing, China
- Stevens GC (1989) The latitudinal gradient in geographical range: how so many species coexist in the tropics. *Am Nat* 133:240–256. doi:[10.1086/284913](https://doi.org/10.1086/284913)
- Sunday JM, Bates AE, Dulvy NK (2011) Global analysis of thermal tolerance and latitude in ectotherms. *Proc R Soc Lond B* 278:1823–1830. doi:[10.1098/rspb.2010.1295](https://doi.org/10.1098/rspb.2010.1295)