

## NOTE / NOTE

## Parallel patterns of clinal variation in *Solidago altissima* in its native range in central USA and its invasive range in Japan

Julie R. Etterson, Daniel E. Delf, Timothy P. Craig, Yoshino Ando, and Takayuki Ohgushi

**Abstract:** The ability of exotic species to proliferate and expand their range may hinge critically upon their potential for adaptive evolution. The finding of parallel patterns of genetically based clinal variation in native and non-native ranges across similar environmental gradients supports the hypothesis that adaptive evolution has played a role in establishment and spread. In this common garden study, we compared patterns of phenotypic variation among 12 populations of *Solidago altissima* L. that were sampled across similar latitudes in the native range in central USA (25°N–43°N) and across its invasive range in Japan (26°N–43°N). Significant clinal variation in phenotype corresponding to latitude was found among US and Japanese populations for height, leaf number, leaf length, leaf width, stem diameter, and stomatal guard-cell size. Only the slope of leaf width differed significantly between the native and invasive range, and the slope was significantly steeper in Japan. These results indicate that patterns of selection across latitude are similar in these two countries. We suggest that populations of *S. altissima* have rapidly differentiated in response to the cline in selection in Japan, possibly by the sorting of lineages from multiple introductions, and this has contributed to their success as an exotic invader.

**Key words:** genetic differentiation, latitudinal variation, invasive species, cline.

**Résumé :** La capacité d'espèces exotiques à proliférer et à étendre leur aire de distribution peut dépendre fortement de leur capacité d'adaptation évolutive. L'observation de patrons parallèles basés sur la variation clinale dans les aires de plantes indigènes et adventices, le long de gradients environnementaux similaires, supporte l'hypothèse que l'évolution adaptative a joué un rôle dans leur établissement et leur expansion. Dans cette expérience en jardin commun, les auteurs comparent les patrons de variation phénotypique au sein de 12 populations du *Solidago altissima* L. ayant été échantillonnées sur des latitudes similaires, dans l'aire indigène du centre des USA (25°N–43°N) et l'aire d'invasion au Japon (26°N–43°N). Ils ont trouvé une variation clinale significative de phénotypes selon la latitude au sein des populations américaines et japonaises, quant à la hauteur, le nombre de feuilles, la longueur des feuilles, le diamètre de la tige, et la dimension des cellules de garde des stomates. Seule la pente de la largeur des feuilles diffère significativement entre les plantes des aires indigènes et adventices, et la pente est significativement plus prononcée au Japon. Ces résultats indiquent que les patrons de sélection selon la latitude sont semblables dans ces deux pays. Les auteurs suggèrent que les populations du *S. altissima* se différencient rapidement en réaction à la pente dans la sélection au Japon, possiblement en triant des lignées provenant de multiples introductions, ce qui a contribué à leur succès comme adventices envahissantes.

**Mots-clés :** différenciation génétique, variation altitudinale, espèce envahissante, pente.

### Introduction

Study of the genetic differentiation of populations along environmental gradients has a long history in plant evolutionary ecology (Turrison 1922; Claussen et al. 1940) and continues to be important as we try to understand how inva-

sive species evolve as they expand their ranges (Sakai et al. 2001; Lee 2002). Species with a broad geographic distribution frequently exhibit clinal patterns of variation in morphology, phenology, and physiology that correspond to gradients in environmental factors such as temperature, precipitation, and growing-season length. These clines in phe-

Received 16 April 2007. Published on the NRC Research Press Web site at botany.nrc.ca on 6 February 2008.

**J.R. Etterson,<sup>1</sup> D.E. Delf, and T.P. Craig.** Department of Biology, University of Minnesota Duluth, 207 Swenson Science Building, 1035 Kirby Drive, Duluth, MN 55812-3004, USA.

**Y. Ando and T. Ohgushi.** Center for Ecological Research, Kyoto University, Hirano 2, Otsu, 520-2113, Japan.

<sup>1</sup>Corresponding author (e-mail: jetterso@d.umn.edu).

notype are thought to represent adaptive responses to variation in natural selection (Endler 1977). Direct support for this hypothesis has come from studies that link clines in phenotype to estimates of the direction of natural selection along environmental gradients (Etterson 2004). Further support is provided by studies where phenotypic clines have evolved among populations of invasive species that have expanded into a range of environments (Reinartz 1984; Lacey 1988; Weber and Schmid 1998). Even stronger support comes from the cases where exotic species have expanded into environmental gradients similar to the native range and evolved latitudinal clines that parallel those of the ancestral range, as has been shown for short-lived insect species (Huey et al. 2000; Gilchrist et al. 2001).

It is assumed that adaptive evolution plays a key role in the establishment and spread of exotic species (Sakai et al. 2001; Lee 2002). Colonization of new habitats by invasive species is often accompanied by exposure to novel abiotic and biotic environmental conditions. Invading populations may encounter different climates, photoperiods, and resource bases. Exotic species may also escape biotic aspects of their native environment including predators, herbivores, and disease (Porter et al. 1997). Changes in abiotic and biotic aspects of the environment are likely to alter patterns of selection and influence the genetic structure of invading species (Ellstrand and Schierenbeck 2000). If traits that are targets of selection in the new range are heritable, adaptive evolution may ensue (Quinn et al. 2000). Exposure to novel environments has been shown to elicit rapid evolutionary responses in many species (Reznick and Ghalambore 2001).

*Solidago altissima* L. is a geographically widespread native North American species with a distribution extending throughout most of the USA and southern Canada (Gleason and Cronquist 1991). This species is an aggressive invasive species in Europe and in Japan and elsewhere in Asia (Weber 1998; Wu et al. 2004). In Europe, *S. altissima* was introduced as a horticultural plant in the middle of the 18th century, and it has since become one of the most abundant exotic species, having expanded across an extensive range. Populations across the invasive range in Europe have evolved latitudinal clines in morphology and phenology (Weber and Schmid 1998). *Solidago altissima* was introduced to Japan either as an ornamental flower or as a honey-bee plant in the early 1900s (Shimizu 2003). In recent decades, it has spread aggressively throughout a broad latitudinal range from the northernmost island of Hokkaido to the southern Okinawa Islands (Fujii 2003). *Solidago altissima* currently occupies a similar gradient in photoperiod and temperature in its native range in central USA and in its invasive range in Japan. However, little is known about the genetic differentiation of invasive populations here or elsewhere in Asia.

The objective of this study was to determine the extent to which parallel patterns of clinal variation have evolved in the invasive and native range of *S. altissima*. We grew populations sampled from latitudinal gradients in central USA and Japan, in a common garden experiment conducted in a greenhouse environment, to determine whether convergent evolution has occurred in the invasive range as populations spread into a latitudinal gradient similar to the native range.

**Table 1.** Location of 12 natural populations of *Solidago altissima* in the USA and Japan and the average annual temperature for each site.

Site	Latitude and longitude	Average annual temperature (°C)
<b>USA</b>		
Giddings, Texas	30° 11'N, 96°56'W	19.4
Hillsboro, Texas (two populations)	32° 01'N, 97°08'W	18.9
Winston, Missouri	39° 52'N, 94°08'W	12.3
Story City, Iowa	42° 11'N, 93°36'W	9.9
Northfield, Minnesota	44° 47'N, 93°10'W	6.4
Anoka, Minnesota	45° 12'N, 93°23'W	6.1
East Bethel, Minnesota	45° 19'N, 93°12'W	5.6
<b>Japan</b>		
Hakata, Fukuoka	33° 33'N, 130°22'E	16.6
Kobe, Hyogo	34° 43'N, 135°13'E	15.8
Seta, Shiga	34° 57'N, 135°58'E	14.8
Kyoto, Kyoto	35° 03'N, 135°45'E	15.6
Sapporo, Hokkaido	43° 05'N, 141°20'E	8.5

## Materials and methods

*Solidago altissima* is a self-incompatible polyploid species that includes diploid, tetraploid, and hexaploid cytotypes (Beaudry and Chabot 1959; Semple 1992). The geographical distribution of cytotypes is not well known, although this species is thought to be exclusively diploid in Europe (Weber 2000). This perennial species occurs in moist to dry open habitats and in sparse woods within its native range. In Japan, *S. altissima* inhabits disturbed sites such as previously cultivated fields, roadside ditches, and river banks (Ito et al. 1998). Once *S. altissima* individuals are established, they are thought to reproduce primarily through clonal propagation via persistent rhizomes (Werner et al. 1980). However, it also produces copious small seeds (max. ~200 000 per plant, Hurlbert 1970) that are wind-dispersed and likely play an important role in the colonization of new habitats and range expansion. The availability of disturbed environments is an important factor for seedling establishment, as was demonstrated in an experiment where artificial patches of bare ground were cleared within an existing population and germination rates monitored (Meyer and Schmid 1999).

In the current experiment, *S. altissima* seeds were bulk collected from eight natural populations in the United States between 30°N–45°N, and from five populations in Japan between 33°N–43°N (Table 1). Seeds were stored at 20 °C until germinated. In June 2003, seeds from each population were spread on separate 25 cm × 50 cm flats filled with a standard germination soil. Seeds were allowed to germinate in the University of Minnesota Duluth greenhouse (46°46'N, 92°07'W) without supplemental light (~15.5 h of ambient light per day). After 3 weeks, 30 seedlings from each population were randomly chosen and transplanted into 6-inch pots (1 inch = 2.54 cm) filled with ProMix BX (Premier Brands Inc., Rochelle, N.Y.). The pots were arranged in a fully randomized design across a single greenhouse bench and watered when necessary. When the plants were approximately 8 weeks old, the following measurements were

taken: plant height, leaf number, leaf length, leaf width, and stem diameter. These traits were chosen because they exhibit clinal patterns associated with latitude in other species (e.g., Li et al. 1998). Some of these traits were also found to differ in a study of native US and invasive European populations of a related species, *Solidago gigantea* Ait. (Güsewell et al. 2006). Two impressions of the lower surface of the uppermost fully expanded leaf on each plant were taken by applying clear acrylic (Naturistics, Del Laboratories, Inc., Farmingdale, N.Y.) to an intact leaf, peeling the replicate mold when dry, and permanently mounting it on a microscope slide. The average length of five stomatal guard cells on one of these impressions is reported. Stomatal guard cell size is associated with ploidy level in some species (Masterson 1994).

One week after these measurements were taken, the plants were moved to the University of Minnesota Duluth outdoor field research site where they were grown in pots under ambient conditions for the remainder of the growing season. Date of first flower emergence was recorded for the few plants that initiated floral development before the first frost.

To determine whether there was an overall difference between the plants in the USA and Japan and whether parallel patterns of clinal variation with latitude were evident, data were analyzed by ANCOVA and MANCOVA, with country considered a fixed factor and latitude a continuous covariate. A significant effect of country indicates that populations differ on average between their native range in central USA and in Japan. A significant effect of latitude indicates that the pattern of population-means corresponds to their latitudinal position and, therefore, clinal patterns of variation are present overall. A significant interaction between country and latitude indicates that the slope of population-means differs between USA and Japan.

Data were transformed where necessary to meet the assumptions of homoscedasticity and normality of the residuals. Leaf number was log transformed and leaf width was squared. Data from the two Hillsboro, Texas, populations were merged and treated as a single population in these analyses.

## Results

The mean of all traits tended to be greater for Japanese plants than US plants for all measurements (Fig. 1). Considering all traits jointly by MANCOVA, these differences were highly significant (Table 2). However, in univariate analyses, US and Japanese plants differed significantly only with respect to leaf width. On average, leaves of Japanese plants were 21% wider than those of US plants (Fig. 1D).

Significant patterns of clinal variation across latitude were found for all traits (Fig. 1; Table 2). Plants from higher latitudes tended to be taller and with more leaves, and had longer and wider leaves, thicker stems, and shorter stomatal guard cells. Furthermore, the slope of these phenotypic clines did not differ in Japan and the US for height, leaf number, leaf length, stem diameter, or stomatal guard cell size, as evidenced by a lack of significant country  $\times$  latitude interactions (Figs. 1A, 1B, 1C, and 1E). However, the slope of the cline in leaf width was significantly different in the US and Japan. Northern Japanese populations had substan-

tially wider leaves than the more southern Japanese populations, resulting in a steep cline for this trait. In contrast, the slope of leaf widths across latitude among US populations was negligible (Fig. 1D). Stomatal guard-cell size of one US population (Story City, Iowa) was significantly smaller than all other populations according to a post-hoc contrast ( $F_{1,362} = 140.82$ ,  $P < 0.0001$ ).

No Japanese plants initiated flowering before the first frost. Twenty-five US plants flowered before the first frost, but there was no clear relationship between the percent of plants that flowered and latitude (northern to southern population: 21%, 28%, 14%, 40%, 3%, 0%, 0%). In addition, the date of first flower emergence was not significantly associated with latitude among the US plants that did bloom ( $F_{1,23} = 3.4$ ,  $P = 0.08$ ).

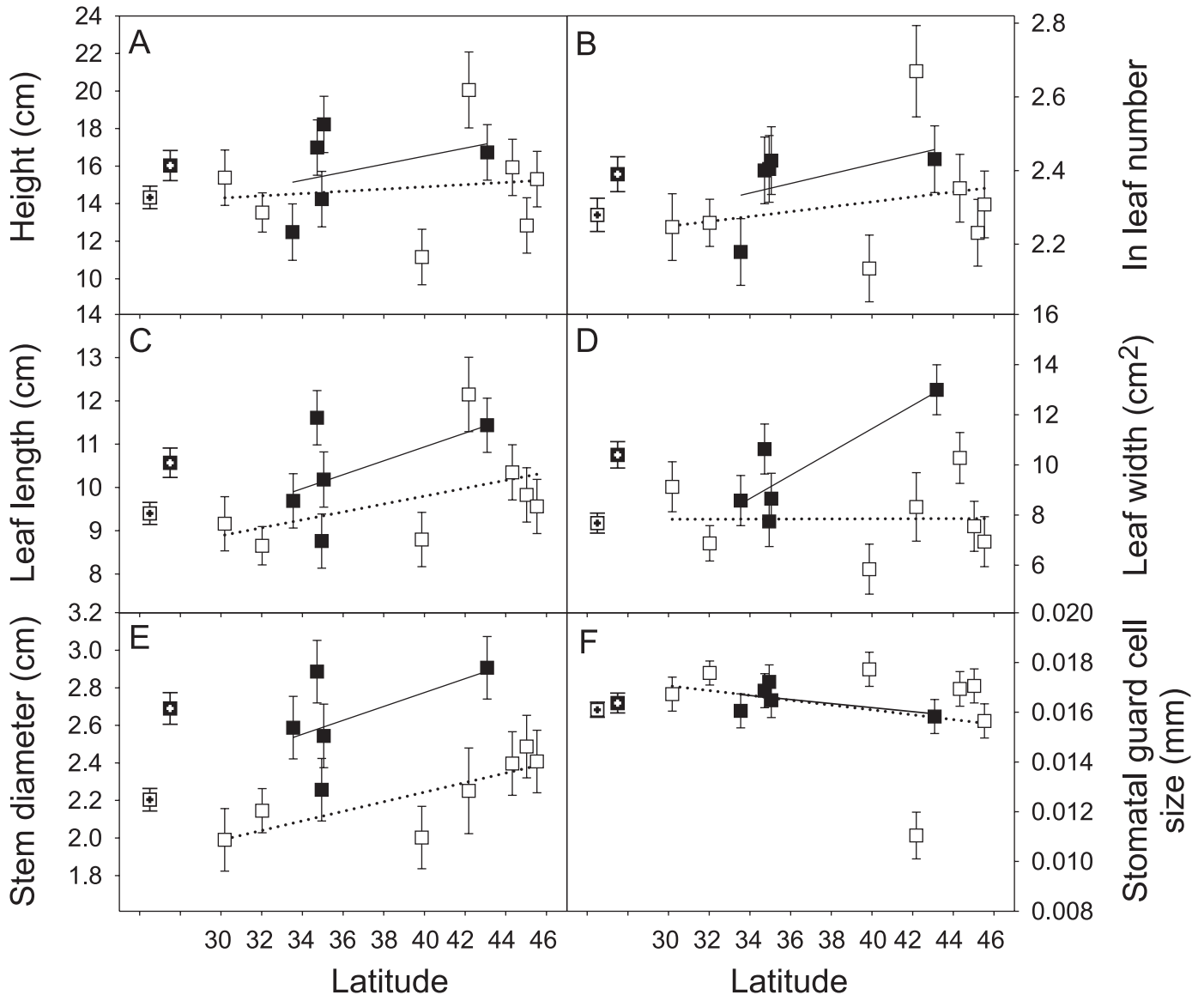
Mortality rates were generally low. No plants sampled from Japanese populations died during the course of the study. However, 92 of 200 (47%) of the Story City population died before measurement, as well as one plant from each of Hillsboro and Northfield, Minnesota.

## Discussion

*Solidago altissima* occupies a broad latitudinal gradient across its invasive range in Japan (26°N–43°N) and in its native range in the US (25°N–43°N). Our common garden study of populations sampled across the native and invasive ranges indicates that genetically based clinal patterns of variation that correspond to latitude have evolved for all measured traits. With the exception of one trait, leaf width, no significant differences were found between the overall means of Japanese and US populations, or the slopes of the means across latitude. This is in contrast to a similar common garden study of native US and invasive European populations of a related species, *S. gigantea*, that showed significant differences in growth pattern but no difference in leaf traits between continents (Güsewell et al. 2006). Our data suggest that similar clinal patterns of selection across latitude are molding plant phenotype in the US and Japan, producing parallel patterns of phenotypic divergence among populations.

The evolution of clinal variation among populations of *S. altissima* in Japan has occurred since it was introduced within the last century. Previous studies of invasive herbaceous species in North America have documented the evolution of clines in morphology and phenology over a similar time frame (*Daucus carota* L., Lacey 1988; *Verbascum thapsus* L., Reinartz 1984). In Europe where *S. altissima* is also invasive, phenotypic clines corresponding to latitude have evolved within the last 250 years after a putative single introduction (Weber and Schmid 1998). Photoperiod is likely an important agent of selection, because it varies clinally with latitude and is a reliable indicator of favorable conditions for growth (Fitter and Hay 1987). Many critical physiological processes including seed germination, stem elongation, and flower initiation rely upon photoperiodic cues (Garner and Allard 1920). Temperature also differs clinally with latitude across the US and Japan although the gradient is steeper in the mid-continent of the North America by comparison with the islands of Japan, presumably owing to the moderating effects of the nearby oceans.

**Fig. 1.** Least square means ( $\pm 2$  SE) of seven US populations (open symbols) and five Japanese populations (filled symbols) of *Solidago altissima* sampled from a latitudinal gradient and grown in a common garden experiment in a greenhouse environment. (A) Height; (B) leaf number; (C) leaf length; (D) leaf width; (E) stem diameter; and (F) stomatal guard-cell size. Trait means for each country are shown on the left of each panel (symbols with hatch marks). Lines show the slope of population means according to latitude in degrees north as estimated by ANCOVA for US populations (broken line) and Japanese populations (solid line).



*Solidago altissima* has become widespread in Japan in the last few decades, suggesting that there has been a recent and rapid expansion of this species (Ecological Society of Japan 2002; Shimizu 2003). Because the invasion history is not well known, however (i.e., site of introduction, pattern and rate of spread, number of introductions), it is not possible to precisely estimate the rate of evolutionary change among populations. If the Japanese populations were founded by a few individuals that have since propagated across this country, it is necessary to invoke substantial evolutionary change to explain the current geographic patterns of variation. For example, leaf width varies by 6.5 phenotypic standard deviations between the extreme Japanese populations. In contrast to the European invasion of *S. altissima*, where records

document a single intentional introduction of this species, there is no evidence to suggest a single founding event in Japan. Furthermore, the timing of the initial introduction corresponds to a period of heightened post World War II exchange between the US and Japan after 1945. Thus, it is more likely that *S. altissima* populations were established by individuals from multiple US locations. To some extent, the current pattern of clinal variation in Japan could then be accounted for by natural selection favoring clonal lineages that originated from similar US environments. However, given that propagation by seed is important for colonization in this species, it is also likely that genetic mixing of different US populations has occurred, which may produce unique genotypes and increase the range of phenotypes for selection

**Table 2.** ANCOVA and MANCOVA test statistics for analysis of morphological traits measured on 12 populations of *Solidago altissima* sampled across latitudinal gradients in the US and Japan and grown in a common garden experiment in a greenhouse environment.

	ANCOVA				MANCOVA					
	Height	Leaf number	Leaf length	Leaf width	Stem diameter	Stomatal cell size	All traits			
	df	F, P	df	F, P	df	F, P	df	Wilks' $\lambda$ , P		
Country	1, 369	0.98	1, 370	0.73	1, 370	0.004	3, 370	0.06	5, 365	<b>5.27</b> , <0.0001
Latitude	1, 369	<b>4.93</b> , <b>0.02</b>	1, 370	<b>25.60</b> , <0.0001	1, 370	<b>40.08</b> , <0.0001	1, 370	8.33, 0.004	5, 365	<b>12.10</b> , <0.0001
Country $\times$ latitude	1, 369	1.83	1, 370	2.14	1, 370	<b>33.77</b> , <0.0001	1, 370	0.008	5, 365	<b>6.31</b> , <0.0001

**Note:** Values in bold are statistically significant.

to differentiate among populations. By either mechanism, natural selection has quite rapidly produced a cline in phenotype that corresponds to latitude.

Clinal variation among populations in both the US and Japan may be associated with the distribution of diploid, tetraploid, and hexaploid cytotypes of this species. Numerous studies have shown marked differences in the geographic distributions of polyploid cytotypes (Soltis 1984; van Dijk et al. 1992; Keeler 1990; Burton and Husband 1999). Studies report that cytotypes are strikingly different in the field (Hardy et al. 2000), distinguishable only when reared in a common garden (van Dijk and van Delden 1990; Maceira et al. 1993; Keeler and Davis 1999). Our current understanding of the geographic distribution of *S. altissima* cytotypes in North America is very limited (Semple 1992) and is completely unknown for Japan. The stomatal guard-cell size data of this experiment does not suggest that there is extensive cytotype polymorphism in these populations. Only one US population has significantly smaller stomatal cells than other populations. However, further study of the relationship between this trait and ploidy level is necessary to determine whether this is a reliable indicator of cytotype.

Despite presumed similarities in the selection gradient across latitude in Japan and the US, some differences undoubtedly exist. For example, numerous insect herbivores native to North America, including an entire guild of stem gallers, are absent in the invasive range (Yukawa and Uechi 1999). The herbivore species that were introduced from North America with *S. altissima* differ in the timing, population densities, and impact on plant growth (Ohgushi 2007; Y.A. Ando, T.O. Ohgushi, and T.P. Craig, unpublished data, 2001-2003). Furthermore, the relative abundance of leaf chewers, leaf suckers, and leaf miners that attack *S. altissima* in Japan differs (Y.A. Ando and T.O. Ohgushi, unpublished data, 2001). Herbivores are potent agents of selection on *S. altissima*, reducing seed production at low herbivore abundance, completely eliminating sexual reproduction, and severely inhibiting vegetation growth at high abundances (Root 1996). Intense herbivory has also been shown to alter competitive interactions between *S. altissima* and other plant species and alter patterns of plant dominance in communities (Carson and Root 1999). In other plant species, insect herbivory has been associated with differences in plant morphology including leaf size (Whitham 1978; Ribeiro et al. 1994), stem diameter (Raman and Abrahamson 1995; Craig and Ohgushi 2002), shoot length (reviewed in Price 2003), trichome density, defensive compounds, and nutrient and water content (reviewed in Gutschick 1999; Pérez-Harguindeguy et al. 2003). Thus, the herbivore communities in the US and Japan could exert different patterns of selection on plant populations, and this could contribute to overall differences in morphology evident in this common garden study.

*Solidago altissima* is an extremely successful invasive species in Japan and Europe. The capacity for rapid adaptive evolution in response to different environments may have played a key role in its success. Future studies will help elucidate the pattern of spread of *S. altissima* across Japan and identify the agents of selection that have contributed to population divergence across both the native and invasive range.

## Acknowledgements

The authors thank M. Etterson for valuable comments made on a previous version of this manuscript. We would also like to thank J. Strange for seed collections in the US, and N. Schroeder for his assistance in data collection. This work was supported by a University of Minnesota Undergraduate Research Opportunities Grant to D. Delf, Grant-in-Aid of Research, Artistry and Scholarship to J. Etterson (A-15207003), the Japan Ministry of Education, Culture, and Sports, Science and Technology to T. Ohgushi, and the 21st Century COE Program (A14) to T. Ohgushi.

## References

- Beaudry, J.R., and Chabot, D.L. 1959. Studies on *Solidago* L. IV. The chromosome numbers of certain taxa of the genus *Solidago*. *Can. J. Bot.* **37**: 209–228. doi:10.1139/b59-017.
- Burton, T.L., and Husband, B.C. 1999. Population cytotype structure in the polyploid *Galax urceolata* (Diapensiaceae). *Heredity*, **82**: 381–390. doi:10.1038/sj.hdy.6884910. PMID:10383656.
- Carson, W.P., and Root, R.B. 1999. Top-down effects of insect herbivores during early succession: influence on biomass and plant dominance. *Oecologia*, **121**: 260–272. doi:10.1007/s004420050928.
- Claussen, J., Keck, D.D., and Hiesey, W.M. 1940. Experimental studies on the nature of species. I. The effect of varied environment on western North American plants. Publication 520. Carnegie Institution of Washington, Washington D.C.
- Craig, T.P., and Ohgushi, T. 2002. Preference and performance are correlated in the spittle bug *Aphorophora pectoralis* on four species of willows. *Ecol. Entomol.* **27**: 529–540. doi:10.1046/j.1365-2311.2002.00448.x.
- Ecological Society of Japan. 2002. Handbook of alien species in Japan. Chijinshokan, Tokyo [in Japanese].
- Ellstrand, N.C., and Schierenbeck, K.A. 2000. Hybridization as a stimulus for the evolution of invasiveness in plants? *Proc. Natl. Acad. Sci. U.S.A.* **97**: 7043–7050. doi:10.1073/pnas.97.13.7043. PMID:10860969.
- Endler, J.A. 1977. Geographic variation, speciation, and clines. Princeton University Press, Princeton, N.J.
- Etterson, J.R. 2004. Evolutionary potential of *Chamaecrista fasciculata* in relation to climate change. I. Clinal patterns of selection along an environmental gradient in the Great Plains. *Evolution*, **58**: 1446–1458. PMID:15341148.
- Fitter, A.H., and Hay, R.K.M. 1987. Environmental physiology of plants. Academic Press, San Diego, Calif.
- Fujii, Y. 2003. Asian-Pacific alien species database [online]. Available from apasd-niaes.dc.affrc.go.jp/ [accessed in 2007].
- Garner, W.W., and Allard, H.A. 1920. Effect of length of day on plant growth. *J. Agric. Res.* **18**: 553–606.
- Gilchrist, G.W., Huey, R.B., and Serra, L. 2001. Rapid evolution of wing size clines in *Drosophila subobscura*. *Genetica*, **112–113**: 273–286. doi:10.1023/A:1013358931816. PMID:11838770.
- Gleason, H.A., and Cronquist, A. 1991. Manual of the vascular plants of northeastern United States and adjacent Canada, 2nd ed. New York Botanical Garden, New York, N.Y.
- Güsewell, S., Jakobs, G., and Weber, E. 2006. Native and introduced populations of *Solidago gigantea* differ in shoot production but not in leaf traits or litter decomposition. *Funct. Ecol.* **20**: 575–584. doi:10.1111/j.1365-2435.2006.01141.x.
- Gutschick, V.P. 1999. Biotic and abiotic consequences of differences in leaf structure. *New Phytol.* **143**: 3–18. doi:10.1046/j.1469-8137.1999.00423.x.
- Hardy, O.J., Vanderhoeven, S., De Loose, M., and Meerts, P. 2000. Ecological, morphological and allozymic differentiation between diploid and tetraploid knapweeds (*Centaurea jaceae*) from a contact zone in the Belgian Ardennes. *New Phytol.* **146**: 281–290. doi:10.1046/j.1469-8137.2000.00631.x.
- Huey, R.B., Gilchrist, G.W., Carlson, M.L., Berrigan, D., and Serra, L. 2000. Rapid evolution of a geographic cline in size in an introduced fly. *Science (Wash.)*, **287**: 308–309. doi:10.1126/science.287.5451.308. PMID:10634786.
- Hurlbert, S.H. 1970. Flower number, flowering time, and reproductive isolation among ten species of *Solidago* (Compositae). *Bull. Torrey Bot. Club*, **97**: 189–195. doi:10.2307/2483456.
- Ito, I., Kobayashi, K., and Yoneyama, T. 1998. Fate of dehydromatricaria ester added to soil and its implications for the allelopathic effect of *Solidago altissima* L. *Ann. Bot. (Lond.)*, **82**: 625–630. doi:10.1006/anbo.1998.0722.
- Keeler, K.H. 1990. Distribution of polyploid variation in big bluestem (*Andropogon gerardii*, Poaceae) across the tallgrass prairie region. *Genome*, **33**: 95–100.
- Keeler, K.H., and Davis, G.A. 1999. Comparison of common cytotypes of *Andropogon gerardii* (Andropogoneae, Poaceae). *Am. J. Bot.* **86**: 974–979. doi:10.2307/2656614. PMID:10406720.
- Lacey, E.P. 1988. Latitudinal variation in reproductive timing of a short-lived monocarp, *Daucus carota* (Apiaceae). *Ecology*, **69**: 220–232. doi:10.2307/1943178.
- Lee, C.E. 2002. Evolutionary genetics of invasive species. *Trends Ecol. Evol.* **17**: 386–391. doi:10.1016/S0169-5347(02)02554-5.
- Li, B., Suzuki, J.-I., and Hara, T. 1998. Latitudinal variation in plant size and relative growth rate in *Arabidopsis thaliana*. *Oecologia*, **115**: 293–301. doi:10.1007/s004420050519.
- Maceira, N.P., Jacquard, P., and Lumaret, R. 1993. Competition between diploid and derivative autotetraploid *Dactylis glomerata* L. from Galicia. Implications for the establishment of novel polyploid populations. *New Phytol.* **124**: 321–325. doi:10.1111/j.1469-8137.1993.tb03822.x.
- Masterson, J. 1994. Stomatal size in fossil plants: evidence for polyploidy in majority of angiosperms. *Science (Wash.)*, **264**: 421–423. doi:10.1126/science.264.5157.421. PMID:17836906.
- Meyer, A.H., and Schmid, B. 1999. Seed dynamics and seedling establishment in the invading perennial *Solidago altissima* under different experimental treatments. *J. Ecol.* **87**: 28–41. doi:10.1046/j.1365-2745.1999.00316.x.
- Ohgushi, T. 2007. Nontrophic, indirect interaction webs of herbivorous insects. In *Ecological communities: plant mediation in indirect interaction webs*. Edited by T. Ohgushi, T. P. Craig, and P.W. Price. Cambridge University Press, Cambridge, UK. pp. 221–245.
- Pérez-Harguindeguy, N., Díaz, S., Vendramini, F., Cornelissen, J.H.C., Gurvich, D.E., and Cabido, M. 2003. Leaf traits and herbivore selection in the field and in cafeteria experiments. *Austral Ecol.* **28**: 642–650. doi:10.1046/j.1442-9993.2003.01321.x.
- Porter, S.D., Williams, D.F., and Patterson, R.S. 1997. Intercontinental differences in the abundance of *Solenopsis* fire ants (Hymenoptera: Formicidae): Escape from natural enemies? *Environ. Entomol.* **26**: 373–384.
- Price, P.W. 2003. Macroevolutionary theory on macroevolutionary patterns. Cambridge University Press, Cambridge.
- Quinn, T.P., Unwin, M.J., and Kinnison, M.T. 2000. Evolution of temporal isolation in the wild: genetic divergence in timing of migration and breeding by introduced Chinook salmon populations. *Evolution*, **54**: 1372–1385. PMID:11005303.
- Raman, A., and Abrahamson, W.G. 1995. Morphometric relationships and energy allocation in the apical rosette galls of *Solidago altissima* (Asteraceae) induced by *Rhopalomyia-Solidaginis* (Diptera, Cecidomyiidae). *Environ. Entomol.* **24**: 635–639.

- Reinartz, J.A. 1984. Life history variation of common mullein (*Verbascum thapsus*). I. Latitudinal differences in population dynamics and timing of reproduction. *J. Ecol.* **72**: 897–912. doi:10.2307/2259539.
- Reznick, D.M., and Ghalambore, C.K. 2001. The population ecology of contemporary adaptations: what empirical studies reveal about the conditions that promote adaptive evolution. *Genetica*, **112**: 183–198. doi:10.1023/A:1013352109042. PMID:11838765.
- Ribeiro, S.P., Pimenta, H.R., and Fernandes, G.W. 1994. Herbivory by chewing and sucking insects on *Tabebuia ochraceae*. *Biotropica*, **26**: 302–307. doi:10.2307/2388851.
- Root, R.B. 1996. Herbivore pressure on goldenrods (*Solidago altissima*): its variation and cumulative effects. *Ecology*, **77**: 1074–1087. doi:10.2307/2265577.
- Sakai, A.K., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A., Baughman, S., Cabin, R.J., Cohen, J.E., Ellstrand, N.C., McCauley, D.E., O'Neil, P., Parker, I.M., Thompson, J.N., and Weller, S.G. 2001. The population biology of invasive species. *Annu. Rev. Ecol. Syst.* **32**: 305–332. doi:10.1146/annurev.ecolsys.32.081501.114037.
- Semple, J.C. 1992. A geographic summary of chromosome number reports for North American asters and goldenrods (Asteraceae: Astereae). *Ann. Mo. Bot. Gard.* **79**: 95–109. doi:10.2307/2399812.
- Shimizu, T. 2003. Naturalized plants of Japan. Heibobsha, Tokyo [in Japanese].
- Soltis, D.E. 1984. Autopolyploidy in *Tolmiea menziesii* (Saxifragaceae). *Am. J. Bot.* **71**: 1171–1174. doi:10.2307/2443640.
- Turreson, G. 1922. The genotypic response of the plant species to the habitat. *Hereditas*, **3**: 211–350.
- van Dijk, P., and van Delden, W. 1990. Evidence for autotetraploidy in *Plantago media* and comparisons between natural and artificial cytotypes concerning cell size and fertility. *Heredity*, **65**: 349–357.
- van Dijk, P., Hartog, M., and van Delden, W. 1992. Single cytotype areas in autopolyploid *Plantago media* L. *Biol. J. Linn. Soc.* **46**: 315–331.
- Weber, E. 1998. The dynamics of plant invasions: a case study of three exotic goldenrod species (*Solidago* L.) in Europe. *J. Biogeogr.* **25**: 147–154. doi:10.1046/j.1365-2699.1998.251119.x.
- Weber, E. 2000. Biological flora of Central Europe: *Solidago altissima* L. *Flora*, **195**: 123–134.
- Weber, E., and Schmid, B. 1998. Latitudinal population differentiation in two species of *Solidago* (Asteraceae) introduced to Europe. *Am. J. Bot.* **85**: 1110–1121. doi:10.2307/2446344.
- Werner, R.P., Bradbury, I.K., and Gross, R.S. 1980. The biology of Canadian weeds. 45. *Solidago canadensis* L. *Can. J. Plant Sci.* **60**: 1393–1409.
- Whitham, T.G. 1978. Habitat selection by *Pemphigus* aphids in response to resource limitation and competition. *Ecology*, **59**: 1164–1176. doi:10.2307/1938230.
- Wu, S., Hsieh, C., and Rejmánek, M. 2004. Catalogue of the naturalized flora of Taiwan. *Taiwania*, **49**: 16–31.
- Yukawa, J., and Uechi, N. 1999. Can galls expand the host range to alien plants within a short period of time? *Esakia*, **39**: 1–7.