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NO EVIDENCE FOR AN EVOLUTIONARY INCREASED COMPETITIVE ABILITY IN AN INVASIVE PLANT

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Abstract. We tested whether *Solidago canadensis*, which was introduced from North America into Europe from the 17th century onward, has evolved an increased competitive ability (EICA) at the cost of tolerance against herbivory in its new range. We grew plants from nine introduced European and 10 native American populations in a common garden in Europe. In half of the plants, we simulated herbivory by removing 50% of the leaf area and by spraying them with jasmonic acid. Although plants from Europe had 30.5% larger leaves, they had 27.4% smaller inflorescences and tended to grow less tall (−7.0%) and produce fewer vegetative offspring (−5.0%) than plants from North America. The simulated herbivory treatment did not result in any significant differences in height, inflorescence biomass, or number of vegetative offspring between treatment and control plants. Moreover, there were no significant differences in the response of European and American plants to simulated herbivory, indicating that they did not differ in their tolerance against herbivory. We conclude that the EICA-hypothesis does not hold in the case of the *S. canadensis* complex, and the worldwide invasion success of this species must be based on other mechanisms.

Key words: alien species; biological invasions; EICA hypothesis; evolution; goldenrod; nonindigenous species; response to herbivory; Solidago canadensis.

INTRODUCTION

Some nonindigenous invasive plant species appear to perform better in their introduced range than in their native range (Crawley 1987). This may be a consequence of a plastic response in growth when the environment is more benign in the introduced range than in the native range due to the absence of natural competitors, herbivores, and pathogens (Crawley 1987, Keane and Crawley 2002). Moreover, selection pressures in the introduced range may differ from the ones in the native range and may have resulted in genetic differentiation in growth and reproduction (Blossey and Nötzold 1995).

Due to the absence of natural herbivores and pathogens, selection for resistance against them can be absent in the introduced range of an invasive plant species. Because the production of defense chemicals or structures may be at a cost of growth and reproduction (Bazzaz et al. 1987, Agrawal et al. 1999), it has been suggested that selection in the introduced range may have resulted in larger plants that invest more in reproduction and less in defense (Blossey and Nötzold 1995). This is known as the EICA (evolutionary increased competitive ability) hypothesis (Blossey and Nötzold 1995). In addition or as an alternative to defense mechanisms, plants may also tolerate damage by herbivores or pathogens by plastic changes in physiological traits increasing their growth (Rosenthal and Kotanen 1994). As the maintenance of the genetic and physiological machinery necessary for such plastic responses can be costly (DeWitt et al. 1998, van Kleunen et al. 2000), the increased competitive ability in the introduced range of invasive plants may also have evolved at a cost of tolerance against herbivores or pathogens. So far, the EICA hypothesis has been tested only for a few invasive plant species (Sakai et al. 2001).

We tested the EICA hypothesis for populations of *Solidago canadensis* L., which was introduced from North America into Europe in the 17th century (Wagenitz 1964, Weber and Schmid 1993). Now, this rhizomatous perennial is an aggressive weed in disturbed sites such as abandoned fields and along roads and railroads in large parts of Europe (Zwölfer 1976). Although the maximum height of *S. canadensis* in its native range is 150 cm (Steere 1966), it may easily reach >200 cm in its introduced range in Europe (Weber 2000), suggesting that an increased competitive ability may have evolved in Europe.

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We grew plants from nine European and 10 American populations of *S. canadensis* in a common garden in Zurich, i.e., in the introduced range. To test whether plants from the introduced and native ranges differed in their response to herbivory, we simulated herbivory in half of the plants by removing 50% of the leaf area and spraying them with jasmonic acid, which is a natural elicitor of chemical defenses against herbivores (Baldwin 1996).

We asked the following specific questions: (1) Do plants of *S. canadensis* from the introduced range (i.e., Europe) have a larger size, and more sexual and vegetative reproduction than the ones from the native range (i.e., North America)? (2) Are plants of *S. canadensis* from the introduced range less tolerant to herbivory than the ones from the native range?

Methods

Study species

Taxa of the *Solidago canadensis* L. species complex are rhizomatous perennials that occur over a large range in North America from Texas in the south to Nova Scotia in the north (Scoggan 1979). The rank of these taxa is difficult to define, two important groups having been referred to as *S. canadensis* L. s.str. (predominantly 2x = 2n = 18) and as *S. canadensis* var. *scabra* Torr. & Gray = *S. altissima* L. (Croat 1972, Melville and Morton 1982; predominantly 6x = 2n = 54). Plants with the morphology of var. *scabra* (Schmid et al. 1988), but with diploid cytotypes, found more commonly in *S. canadensis* s.str., have been introduced into Europe in the 17th century (Wagenitz 1964). This taxon presently ranges from northern Italy in the south to southern Scandinavia in the north (Weber 2000) and is considered to be one of the most aggressive invading species in Europe (Zwölfer 1976, Weber and Schmid 1993). Moreover, the species has also been introduced to Asia and Australia (Weber 2000). In view of the complicated unresolved taxonomy and the multiple ploidy levels within the taxa (see *Methods: Experimental design*), we collectively refer to the species complex with the binary name *S. canadensis* s.l., omitting the ''s.l.'' for simplicity.

Solidago canadensis grows mainly in disturbed sites such as in abandoned fields and along roads and railroads. Aboveground shoots of plants of *S. canadensis* are produced annually from a perennial branched rhizome system. In central Europe, shoots can rise to 2 m in height, produce up to 20 cm long lanceolate leaves, and end up in a branched inflorescence (Weber 2000). The species is self-incompatible (Schmid and Dolt 1994) and flowers in the period from July until October. Inflorescences consist of numerous flower heads along up to 60 short, recurved branches that are produced from the axils of leaves along the upper part of the main stem (Weber 2000). Flower heads consist of 5–15 female ray florets and 3–9 hermaphroditic disc florets, and are visited by several insect species (Weber 2000). One single inflorescence may produce >10 000 mainly wind-dispersed seeds (Meyer and Schmid 1991).

Plant material and precultivation

To comprehensively sample genetic variation both within and between European and North American populations of *S. canadensis*, seeds were collected from different plants in nine populations in Europe and 10 populations in North America (see Appendix A) at the end of the growing season in 1999. All collectors (see *Acknowledgments*) in both continents were experienced in recognizing the different taxa of *Solidago* in the field and collected seed material that according to morphological determination belonged to *S. canadensis* var. *scabra*.

On 2 May 2000, seeds of all plants (seed families) were sown into pots filled with potting compost and placed in a plant room at 25°C with 16 h of daily artificial light. To get clonal replicates of each plant and to reduce maternal environmental carryover effects, we first precultivated the plants for 1 yr in a common garden at the University of Zurich (47°32′60″ N, 8°34′60″ E). The following year, on 10 April 2001, we took two cuttings (3–10 cm long shoots connected to 1–3 cm of rhizome) of each of three plants (i.e., clones) of each of eight seed families of each population (totaling 912 cuttings) and planted them into multitop trays filled with potting compost.

Experimental design

For the experiment, which took place in the same garden as the precultivation, we prepared 48 1.2 × 0.9 m plots with 1 m distance between them. On 29 May 2001, we randomly assigned one of the two rooted cuttings of each clone to one of 20 planting positions in each of 24 randomly chosen plots with the restriction that there was only one plant per population in each plot. We filled the one remaining empty planting position in each plot as well as empty positions due to missing plants with remaining plants of unspecified genotype. Distances between plants within each plot were 30 cm. We did the same for the other 24 plots. The first set of 24 plots was assigned to the simulated herbivory treatment and the second set to the control treatment. At the start of the experiment, on 11 June 2001, we removed the distal half of each leaf of all plants in the simulated herbivory treatment with scissors and sprayed these plants with 1 mmol/L jasmonic acid (Sigma Chemical, St. Louis, Missouri, USA) solution until they were dripping wet. The used concentration was within the range of concentrations used by Thaler et al. (1996) to induce chemical defenses in *Lycopersicon esculentum* without being toxic to the plant. Results of another experiment with *S. canadensis* showed that the combination of leaf area removal and jasmonic acid induced growth responses more closely

to the ones induced by natural herbivory than did clipping alone (M. van Kleunen, G. Ramponi, and B. Schmid, *unpublished manuscript*). Plants in the control treatment were sprayed with only the solvent until they were dripping wet. The treatments were repeated after 4 wk.

Flow cytometry, using a Becton Dickinson (San Jose, California, USA) FACStrac flow cytometer, revealed that all European populations contained only diploid plants, and that of the American populations seven contained only hexaploid plants, two contained only diploid plants, and one contained both diploid and hexaploid plants (see Appendix B).

Measurements

To determine relative height growth rate (RhGR), we measured the height of each plant at the start of the experiment and 20, 41, and 138 d after the start of the experiment. RhGRs were calculated as the difference between two consecutive ln-transformed height measurements divided by the number of days between the two measurements (Meyer 1998). We measured the stomatal conductance of each plant on the sixth leaf counted from the shoot tip with a porometer (AP4, Delta-T Devices, Cambridge, UK) on two consecutive cloudless days (50 and 51 d after the start of the experiment). Subsequently, we harvested each measured leaf, determined its area with a CI-202 Area Meter (CID, Camas, Washington, USA), and weighed it after drying to constant mass at 70°C. We calculated the specific leaf area of this leaf by dividing its area by its mass. As an estimate of sexual reproductive effort, we harvested the inflorescences (i.e., all plant parts above the lowest flower-bearing side branch) at the end of the growing season before plants started to shed their seeds, and weighed them after drying to constant mass at 70°C. As an estimate of vegetative reproductive effort, we counted the number of vegetative offspring (number of shoots) of each plant in April 2002.

Analyses

Because the European plants most likely originate from diploid American ancestors, we only present results of diploid plants (data including the hexaploid plants are presented in Appendix C). The final data set consisted of 466 instead of 912 plants. All variables were analyzed with hierarchical analyses of variance using the statistical software SPSS (SPSS 1999). Simulated herbivory and continent of origin were considered as fixed factors and plots (within simulated herbivory treatment), population (within continent), and seed family (within population and continent) as random factors. Because it turned out that plants grew taller on one side of the experimental field probably as a consequence of a gradient in nutrient availability in the garden, we corrected for this by entering the position of each plant along the short (row *X*) and long (row *Y*) side of the field as covariates into the model before fitting the fixed and random factors. Means and standard errors of the traits were calculated after correcting the data for the gradient in the garden. This was done by adding the residuals, from an analysis with only the position covariates included, to the overall mean. In the analysis of stomatal conductance, we additionally corrected for the day of measurement and for the leaf temperature by including them as covariates in the model. Changes over time in RhGRs of plants were analyzed with repeated-measures analysis of variance. To have two independent estimates of RhGR over time (Poorter 1989), we only included the growth rates during the period of day 0–20 and the ones during the period of day 41–138 in this analysis. The between-subject effects refer to plants, and the within-subject effects refer to the two census periods. The leaf area, specific leaf area, stomatal conductance, and number of vegetative offspring were $\log_{10}$-transformed, and the inflorescence biomass was square-root transformed prior to analyses to achieve normality and homoscedasticity.

RESULTS

Growth of shoots

The RhGR was slightly lower for the European plants than for the American plants, and resulted in a 7.0% lower stem height at the end of the season (Fig. 1). However, these effects were not significant (Tables 1 and 2). Plants in the simulated herbivory treatment had a lower RhGR (−6.2%) in the period of day 0–20, and a higher one (+9.1%) in the period of day 41–138 than plants that were in the control treatment (Fig. 1, significant period-by-herbivory interaction in Table 1). As a consequence, there were no significant differences in final stem height between plants in the simulated herbivory treatment and the ones in the control treatment (Fig. 1, Table 2). Moreover, there were no significant differences in the response of RhGR and height to simulated herbivory between American and European plants (Fig. 1, no significant herbivory-by-continent interaction in Tables 1 and 2).

Leaf characteristics

European plants had 30.5% larger leaves, a 3.6% lower specific leaf area, and a 8.9% lower stomatal conductance than American populations (Fig. 1). This effect was only significant for leaf area (Table 2). Leaves of plants in the simulated herbivory treatment had an 11.2% larger area, a 3.5% higher specific leaf area, and a 2.7% higher stomatal conductance (Fig. 1). This effect was significant for the leaf area and the specific leaf area (Table 2). However, there were no significant differences in the effect of herbivory on leaf area, specific leaf area, and stomatal conductance between European and American plants (Fig. 1, Table 2).

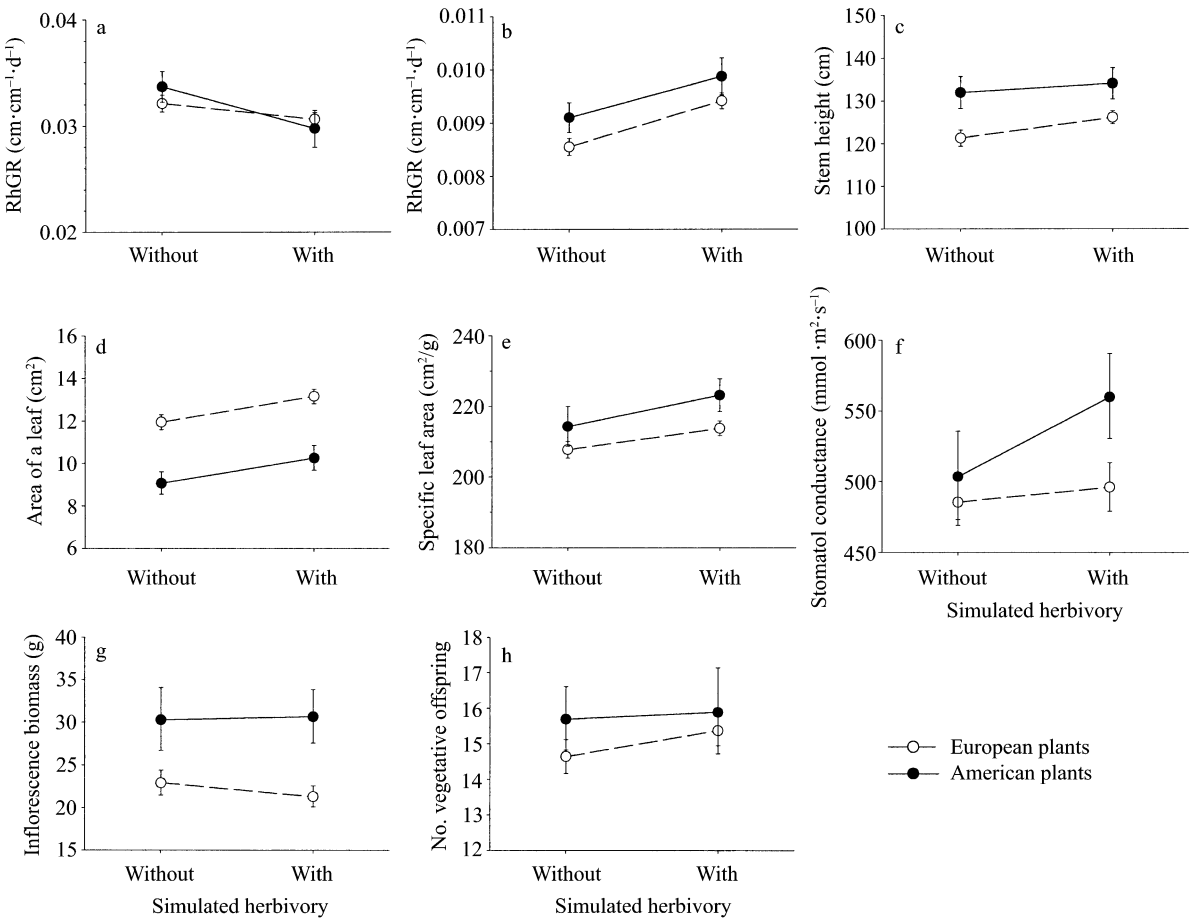

FIG. 1. The effect of simulated herbivory on the relative height growth rate (RhGR, mean ± 1 SE) during (a) day 1–20 and (b) day 41–138, (c) final stem height, (d) area of a leaf, (e) specific leaf area, (f) stomatal conductance, (g) inflorescence biomass, and (h) number of vegetative offspring of plants of *Solidago canadensis*. Experimental plants included plants from nine European populations (open circles and dashed lines) and plants from three American populations (solid symbols and solid lines).

Sexual and vegetative reproduction

European plants had a significantly lower inflorescence biomass (−27.4%), and tended to produce fewer vegetative offspring (−5.0%) than American plants (Fig. 1, Table 2). There were no significant differences between plants in the simulated herbivory treatment and the ones in the control treatment for inflorescence biomass, and the number of vegetative offspring (Fig. 1, Table 2). Neither were there significant differences in the effect of simulated herbivory between American and European plants (Fig. 1, Table 2).

DISCUSSION

In our common garden experiment, populations of *S. canadensis* from the introduced range in Europe had larger leaves, smaller inflorescences, and tended to have fewer vegetative offspring and to grow less tall than plants from the native range in North America. This indicates that there are genetic differences in performance between European and American populations of *S. canadensis*.

With the exception of differences in leaf size, the observed differences in performance are in opposite direction to the EICA-hypothesis, which predicts a higher performance for plants from the introduced range than for the ones from the native range (Blossey and Nötzold 1995). Moreover, the statistical power to detect differences between European and American plants was restricted by the fact that these differences were compared with the variation among populations within continents, which itself was often large and significant. If the differences had been tested at the level of individual families, thereby ignoring the problem of pseudoreplication (Hurlbert 1984), they would have been significant more often but mostly in the opposite direction of the EICA-predictions.

It could be argued that because *S. canadensis* is a perennial rhizomatous species, a higher performance of European plants may become apparent after a few

TABLE 1. Summary of analysis of variance of effects of position in the garden (row *X* and *Y*), simulated herbivory, continent of origin, plot, population of origin, and seed family on the relative height growth rate (RhGR) in the experiment with *Solidago canadensis*.

Effect	df	MS	*F*
Between plants			
Row *X*	1	4.623×10^{-3}	100.21***
Row *Y*	1	8.770×10^{-4}	19.01***
Herbivory	1	7.149×10^{-5}	0.690
Plot (within herbivory)	46	1.036×10^{-4}	2.25***
Continent	1	2.521×10^{-5}	0.15
Population (within continent)	11	1.719×10^{-4}	3.76***
Family (within population, continent)	76	4.572×10^{-5}	0.99
Herbivory × continent	1	2.969×10^{-5}	0.37
Herbivory × population (within continent)	11	7.960×10^{-5}	2.29†
Herbivory × family (within population, continent)	74	3.484×10^{-5}	0.76
Plant	227	4.613×10^{-5}	
Within plants			
Period	1	0.112	3049.48***
Period × row *X*	1	8.121×10^{-2}	220.57***
Period × row *Y*	1	1.141×10^{-3}	31.00***
Period × herbivory	1	4.551×10^{-4}	4.53†
Period × plot (within herbivory)	46	1.004×10^{-4}	2.73***
Period × continent	1	2.963×10^{-6}	0.02
Period × population (within continent)	11	1.858×10^{-4}	4.42***
Period × family (within population, continent)	76	4.200×10^{-5}	1.14
Period × herbivory × continent	1	2.879×10^{-5}	0.41
Period × herbivory × population (within continent)	11	7.073×10^{-5}	2.04†
Period × herbivory × family (within population, continent)	74	3.473×10^{-5}	0.94
Error	227	3.682×10^{-5}	

Note: We used repeated-measures analysis of variance to study both variation between plants (between subject) and variation within plants (within subject).
*** $P < 0.001$; † $P < 0.1$.

years as they might initially allocate more biomass to storage in rhizomes than American plants do. This, however, is unlikely because a followup experiment, which included part of the plants of this study, did not reveal larger rhizomes or a higher reproduction after two years of growth for European than for American plants (S. Rahm, *personal communication*). Therefore, we conclude that the EICA-hypothesis does not hold for *S. canadensis*, and that the apparently larger size of plants of *S. canadensis* in Europe than in North America represents a plastic response.

Although relative height growth rate was reduced shortly after application of the simulated herbivory treatment, at the end of the experiment there were no significant differences in height, inflorescence biomass, or the number of vegetative offspring between plants in the simulated herbivory and control treatment. This indicates that plants of *S. canadensis* are rather tolerant against herbivory. This tolerance is likely acquired through an increase in photosynthetic leaf area by means of plastic increases in the size of leaves and the specific leaf area in response to simulated herbivory.

In line with the results that European plants did not have a higher performance than American plants of *S. canadensis*, we did not find evidence that European plants are less tolerant against simulated herbivory than American plants. A possible explanation might be that there has not been sufficient additive genetic variation for selection to act on. However, latitudinal differentiation in phenological timing (Weber and Schmid 1998) suggests that there has been sufficient additive genetic variation for evolutionary responses. Another explanation might be that the few generalist species that feed on *S. canadensis* in Europe impose enough selection to maintain tolerance against herbivory in the invasive range.

So far, the only evidence for the EICA-hypothesis comes from studies on *Lythrum salicaria* in which plants from its introduced range in North America have a more vigorous vegetative growth and lower phenolic contents than, and are preferred by specialized herbivores over the ones from its native range in Europe (Blossey and Nötzold 1995, Blossey and Kamil 1996, Willis et al. 1999). Our results and the ones of a study on *Carduus nutans*, *Digitalis purpurea*, *Senecio jacobaea*, and *Echium vulgare* (Willis et al. 2000), however, show that the EICA-hypothesis does not generally hold. For *Hypericum perforatum* (Pritchard 1960) and the tree species *Sapium sebiferum* (Siemann and Rogers 2001), there is evidence that plants from the introduced range have a genetically based higher performance than the ones from the native range. However, these studies did not test whether this was at a cost to resistance against herbivores. A genetically based higher performance of plants from the introduced range could also be explained by a biased preference of the introducers for tall plants. Moreover, in the cases where plants from the introduced range are less resistant to herbivores or

TABLE 2. Summary of analyses of variance of effects of position in the garden (row *X* and *Y*), simulated herbivory, and continent of origin, plot, population of origin, and seed family on (a) stem height by the end of the growing season, area of a leaf, and specific leaf area and (b) stomatal conductance, inflorescence biomass, and number of vegetative offspring in the experiment with *Solidago canadensis*.

(a) Effects on stem height and leaf area

Source	df	Stem height		Log(area of a leaf)‡		Log(specific leaf area)§	
		MS	*F*	MS	*F*	MS	*F*
Row *X*	1	76 329.860	184.93***	0.101	3.88*	1.447×10^{-3}	0.39
Row *Y*	1	7260.440	17.59***	3.894×10^{-2}	1.50	3.254×10^{-2}	8.72**
Herbivory	1	2178.264	1.31	0.233	8.96**	2.093×10^{-2}	7.17**
Plot (within herbivory)	46	1657.358	4.02***	2.601×10^{-2}	1.00	2.922×10^{-3}	0.78
Continent	1	6862.665	3.17	0.861	9.42*	2.150×10^{-2}	2.32
Population (within continent)	11	2168.205	4.00***	9.148×10^{-2}	2.83**	9.262×10^{-3}	1.63
Family (within population, continent)	76	542.5357	1.31†	3.232×10^{-2}	1.24	5.678×10^{-3}	1.52**
Herbivory × continent	1	10.325	0.10	8.221×10^{-3}	0.35	2.052×10^{-4}	0.03
Herbivory × population (within continent)	11	108.313	0.39	2.319×10^{-2}	1.30	7.213×10^{-3}	2.44*
Herbivory × family (within population, continent)	75	275.075	0.67	1.786×10^{-2}	0.97	2.953×10^{-3}	0.79
Error	240	412.758		2.600×10^{-2}		3.731×10^{-3}	

(b) Effects on stomatal conductance, inflorescence biomass, and vegetative offspring

Source	df	Log(stomatal conductance)		Square root of inflorescence biomass‖		Log(no. vegetative offspring)¶	
		MS	*F*	MS	*F*	MS	*F*
Row *X*	1	0.833	28.91***	1034.521	330.17***	1.936	67.94***
Row *Y*	1	5.173×10^{-2}	1.80	55.027	17.562***	0.411	14.43***
Day of measurement	1	0.302	10.48***	…	…	…	…
Leaf temperature	1	3.672	127.48***	…	…	…	…
Herbivory	1	1.859×10^{-2}	0.65	2.229	0.19	3.965×10^{-2}	0.73
Plot (within herbivory)	46	2.843×10^{-2}	0.99	11.546	3.69***	5.404×10^{-2}	1.90***
Continent	1	0.142	1.48	40.742	7.64**	2.990×10^{-2}	0.78
Population (within continent)	11	9.560×10^{-2}	3.15***	5.336	1.31	3.818×10^{-2}	0.81
Family (within population, continent)	76	3.033×10^{-2}	1.05	4.086	1.30	4.695×10^{-2}	1.65**
Herbivory × continent	1	3.031×10^{-2}	1.96	1.545	0.78	3.922×10^{-3}	0.10
Herbivory × population (within continent)	11	1.549×10^{-2}	0.66	1.980	1.17	4.093×10^{-2}	1.74†
Herbivory × family (within population continent)	74	2.346×10^{-2}	0.85	1.696	0.54	2.353×10^{-2}	0.83
Error	225	2.880×10^{-2}		3.133		2.850×10^{-2}	

Note: For stomatal conductance we also included the day of measurement and the leaf temperature as covariables.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; † $P < 0.1$.
‡ The df of herbivory × family and error df for log(area of a leaf) were 74 and 225, respectively.
§ The df of herbivory × family and error df for log(specific leaf area) were 74 and 224, respectively.
‖ The df of herbivory × family and error df for sqrt(inflorescence biomass) were 75 and 235, respectively.
¶ The df of herbivory × family and error df for log(no. of vegetative offspring) were 75 and 241, respectively.

pathogens, it is not necessarily a consequence of adaptive evolution. Plants of *Carduus pycnocephalus* from the invasive range in Australia were more sensitive to a rust fungus from the native range in Europe, but did not have a higher performance in the absence of the rust than did European plants (Olivieri 1984). Moreover, plants from an introduced population of *Spartina alterniflora* in the state of Washington, where herbivores are absent, had a lower resistance to herbivores and also a lower growth in the absence of herbivores than the ones of an introduced population in California, where herbivores are present (Daehler and Strong 1997). This suggests that a decrease in the resistance to herbivores or pathogens in habitats where herbivores or pathogens are absent is not necessarily a result of selection for increased size at a cost of resistance, but could also be a simple consequence of increased importance of genetic drift when selection pressures for resistance are absent in the introduced range of an invasive plant species (Olivieri 1984, Daehler and Strong 1997).

The fact that European plants of *S. canadensis* had a lower instead of a higher performance than American plants, might be a consequence of a genetic bottleneck during its introduction (Sakai et al. 2001). Reduced genetic variation shortly after introduction might have resulted in inbreeding and fixation of deleterious mutations, and as a consequence in reduced fitness. There is, however, genetic differentiation between European populations in some traits (Weber and Schmid 1998),

suggesting that there is sufficient additive genetic variation for evolutionary responses. Such additive genetic variation might have resulted from conversion of non-additive genetic variation after population bottlenecks (Goodnight 1988).

In conclusion because European plants of *S. canadensis* do not have a higher performance than American plants, their success as an invasive plant cannot be explained by the EICA-hypothesis, and therefore needs other explanations. *S. canadensis* is also a successful species in its native range (Schmid and Bazzaz 1987), where it becomes one of the dominant species during succession in old fields (Bazzaz 1975). This suggests that the life-history characteristics of *S. canadensis* including its tall stature, and the production of large numbers of wind-dispersed seeds and perennial rhizomes, have predestinated *S. canadensis* to be a successful invader.

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APPENDIX A

A table showing the origin of populations of *Solidago canadensis* is available in ESA's Electronic Data Archive: *Ecological Archives* E084-074-A1.

APPENDIX B

A table showing the effects of simulated herbivory on hexaploid American plants is available in ESA's Electronic Data Archive: *Ecological Archives* E084-074-A2.

APPENDIX C

ANOVA tables of data including diploid and hexaploid plants are available in ESA's Electronic Data Archive: *Ecological Archives* E084-074-A3.

Ecological Archives E084-074-A1

Mark van Kleunen and Bernhard Schmid. 2003. No evidence for an evolutionary increased competitive ability in an invasive plant. *Ecology* 84:2816–2823.

Appendix A. A table showing the origin of populations of *Solidago canadensis*.

Table A1. Names, latitude, and longitude of the nearest place to, and number of diploid and hexaploid seed families of the European and North American populations of the *Solidago canadensis* complex used in our experiment. Between parentheses, we give the name of the country (in Europe) or state (in North America).

			Number of seed families	
Site	Latitude	Longitude	Diploid	Hexaploid
Europe				
Katowice (Poland)	50°15'45 N	19°01'26 E	8	0
Göttingen (Germany)	51°31'43 N	09°55'18 E	8	0
Friedrichsthal (Germany)	52°47'09 N	13°17'01 E	8	0
Prague (Czech Republic)	50°05'34 N	14°25'20 E	8	0
Sihlbrugg (Switzerland)	47°14'35 N	08°33'50 E	8	0
Hegenheim (France)	47°33'45 N	07°31'15 E	8	0
Chiasso (Switzerland)	45°50'16 N	09°01'25 E	8	0
Landeck (Austria)	47°08'25 N	10°34'42 E	8	0
Fribourg (Switzerland)	46°48'23 N	07°08'00 E	8	0
North America				
Haverhill (Massachusetts)	42°46'20 N	71°04'43 W	0	8
Ann Harbor A (Michigan)	42°27'03 N	83°45'34 W	7	1
Ann Harbor B (Michigan)	42°27'03 N	83°45'34 W	8	0
Ann Harbor C (Michigan)	42°27'03 N	83°45'34 W	0	8
Claremont (New Hampshire)	43°22'25 N	72°20'48 W	0	8
Huntington (Vermont)	44°19'01 N	72°59'42 W	0	4
Lone Tree (Iowa)	41°30'12 N	91°26'11 W	0	8
Petersburg (North Dakota)	48°00'49 N	97°59'24 W	2	0
Saukville (Wisconsin)	43°26'46 N	87°58'18 W	0	6
Ithaca (New York)	42°26'38 N	76°30'00 W	0	8

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Ecological Archives E084-074-A2

Mark van Kleunen and Bernhard Schmid. 2003. No evidence for an evolutionary increased competitive ability in an invasive plant. *Ecology* 84:2816–2823.

Appendix B. A table showing th effects of simulated herbivory on hexaploid American plants.

Table B1. The effect of simulated herbivory on relative height growth rate (RhGR) during day 1–20 and day 41–138, final stem height, area of a leaf, specific leaf area, stomatal conductance, inflorescence biomass, and number of vegetative offspring of hexaploid American plants of *Solidago canadensis*. Means are given ± 1 SE for non-transformed data, and ± upper SE/lower SE for log- and square root-transformed data after back transformation.

Trait	Simulated herbivory	
	Without	With
$RhGR_{day\ 1–20}$ ($cm \cdot cm^{-1} \cdot day^{-1}$)	0.0286 ± 0.0010	0.0242 ± 0.0007
$RhGR_{day\ 41–138}$ ($cm \cdot cm^{-1} \cdot day^{-1}$)	0.0086 ± 0.0002	0.0096 ± 0.0002
Stem height (cm)	123.2 ± 1.9	124.2 ± 1.8
Area of a leaf ($cm^{2)}$	9.23 ± 0.36/0.35	11.02 ± 0.36/0.35
Specific leaf area ($cm^2 \cdot g^{-1}$)	191.7 ± 2.6/2.6	195.6 ± 2.2/2.2
Stomatal conductance ($mmol \cdot m^{-2} \cdot s^{-1}$)	528.4 ± 19.2/18.6	550.9 ± 15.5/15.2
Inflorescence biomass (g)	26.5 ± 1.8/1.8	22.5 ± 1.7/1.5
Number of vegetative offspring	17.4 ± 0.9/0.8	17.8 ± 0.8/0.7

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Ecological Archives E084-074-A3

Mark van Kleunen and Bernhard Schmid. 2003. No evidence for an evolutionary increased competitive ability in an invasive plant. *Ecology* 84:2816–2823.

Appendix C. ANOVA tables of data including diploid and hexaploid plants.

Hexaploid plants were only present in populations from North America. We corrected for this by fitting "ploidy" before "continent" in the analyses of variance. Therefore, the continent effect in the tables below refers to differences between diploid American and European plants.

Table C1. Summary of analysis of variance of effects of position in the garden (row X and Y), simulated herbivory, ploidy level, continent of origin, plot, population of origin, and seed family on the relative height growth rate (RhGR) in the experiment with *Solidago canadensis*. We used repeated-measures analysis of variance to study both variation between plants (between subject) and variation within plants (within subject).

Effect	df	MS	*F*
Between plants			
Row X	1	7.610×10^{-3}	153.93***
Row Y	1	1.095×10^{-3}	22.15***
Herbivory	1	3.324×10^{-4}	3.21†
Plot (within herbivory)	46	1.036×10^{-4}	2.10***
Ploidy	1	2.168×10^{-3}	18.82***
Continent	1	2.178×10^{-5}	0.19
Population (within continent)	17	1.152×10^{-4}	2.24**
Family (within population, continent)	119	5.143×10^{-5}	1.04
Herbivory × ploidy	1	1.303×10^{-4}	2.06
Herbivory × continent	1	3.113×10^{-5}	0.49
Herbivory × population (within continent)	17	6.339×10^{-5}	1.38
Herbivory × family (within population, continent)	115	4.576×10^{-5}	0.93
Plant	388	4.944×10^{-5}	
Within plants			
Period	1	0.148	3621.20***
Period × row X	1	1.230×10^{-2}	300.23***
Period × row Y	1	1.437×10^{-3}	35.06***
Period × herbivory	1	1.232×10^{-3}	11.96**
Period × plot (within herbivory)	46	1.030×10^{-4}	2.52***

Period × ploidy	1	2.173×10^{-3}	16.97***
Period × continent	1	4.990×10^{-6}	0.04
Period × population (within continent)	17	1.280×10^{-4}	2.60**
Period × family (within population, continent)	119	4.919×10^{-5}	1.201
Period × herbivory × ploidy	1	1.316×10^{-4}	2.37
Period × herbivory × continent	1	3.025×10^{-5}	0.55
Period × herbivory × population (within continent)	17	5.548×10^{-5}	1.35
Period × herbivory × family (within population, continent)	115	4.106×10^{-5}	1.00
Error	388	4.097×10^{-5}	

† $P < 0.1$; ** $P < 0.01$; *** $P < 0.001$.

Table C2.Summary of analyses of variance of effects of position in the garden (row X and Y), simulated herbivory, ploidy level, and continent of origin, plot, population of origin, and seed family on (a) final stem height, area of a leaf, specific leaf area, (b) stomatal conductance, (c) inflorescence biomass, and number of vegetative offspring in the experiment with *Solidago canadensis*. For stomatal conductance we also included the day of measurement and the leaf temperature as covariables.

(a)		Stem height		Log(area of a leaf)[#1]		Log(specific leaf area)[#2]	
Effect	df	MS	*F*	MS	*F*	MS	*F*
Row X	1	120147.332	341.38***	0.355	14.11***	2.013×10^{-2}	5.49*
Row Y	1	10268.061	29.175***	2.571×10^{-3}	0.10	3.660×10^{-2}	9.98**
Herbivory	1	1783.762	0.81	0.604	18.16***	2.904×10^{-2}	7.91**
Plot (within herbivory)	46	2198.458	6.25***	3.327×10^{-2}	1.32	3.676×10^{-3}	1.00
Ploidy	1	673.170	0.30	0.751	9.76**	0.250	30.00***
Continent	1	6789.514	3.01	0.897	11.64**	1.646×10^{-2}	1.98
Population (within continent)	17	2257.241	3.90***	7.702×10^{-2}	1.79*	8.327×10^{-3}	1.67†
Family (within population, continent)	119	579.147	1.65***	4.312×10^{-2}	1.71***	4.976×10^{-3}	1.36*
Herbivory × ploidy	1	389.492	4.36†	3.956×10^{-2}	1.99	6.211×10^{-4}	0.09
Herbivory × continent	1	0.057	0.00	6.898×10^{-3}	0.35	3.002×10^{-4}	0.04
Herbivory × population (within continent)	17	89.446	0.34	1.992×10^{-2}	1.07	6.875×10^{-3}	2.32**
Herbivory × family (within pop., continent)	116	261.349	0.74	1.870×10^{-2}	0.74	2.960×10^{-3}	0.81
Error	406	351.951		2.516×10^{-2}		3.668×10^{-3}	

(b)	Stomatal conductance		
Effect	df	MS	*F*
Row X	1	1.099	42.81***
Row Y	1	1.032×10^{-3}	0.04
Day of measurement	1	0.602	23.47***
Leaf temperature	1	4.926	191.99***
Herbivory	1	3.688×10^{-2}	0.93
Plot (within herbivory)	46	3.960×10^{-2}	1.54*
Ploidy	1	0.176	2.17
Continent	1	0.132	1.63
Population (within continent)	17	8.114×10^{-2}	2.49**
Family (within population, continent)	119	3.253×10^{-2}	1.27*
Herbivory × ploidy	1	6.576×10^{-3}	0.58
Herbivory × continent	1	2.320×10^{-2}	2.05
Herbivory × population (within continent)	17	1.131×10^{-2}	0.54
Herbivory × family (within population continent)	116	2.115×10^{-2}	0.82
Error	386	2.566×10^{-2}	

(c)		Sqrt(inflorescence biomass)[#3]		Log(number of vegetative offspring)	
Effect	df	MS	*F*	MS	*F*
Row X	1	1432.476	472.34***	2.658	74.88***
Row Y	1	84.601	27.90***	0.577	16.25***
Herbivory	1	8.094	0.53	4.767×10^{-2}	0.84
Plot (within herbivory)	46	15.340	5.06***	5.649×10^{-2}	1.59*
Ploidy	1	0.887	0.10	0.729	5.26*
Continent	1	42.048	4.64*	2.701×10^{-2}	0.20
Population (within continent)	17	9.056	2.19**	0.139	2.75***
Family (within population, continent)	119	4.138	1.36	5.047×10^{-2}	1.42**
Herbivory × ploidy	1	2.305	1.67	1.596×10^{-2}	0.52
Herbivory × continent	1	2.063	1.49	1.812×10^{-3}	0.06
Herbivory × population (within continent)	17	1.382	0.78	3.079×10^{-2}	1.20
Herbivory × family (within pop., continent)	117	1.764	0.58	2.574×10^{-2}	0.73
Error	407	3.033		3.549×10^{-2}	

[#1]Error df for log(area of a leaf) was 386.

[#2]Error df for log(specific leaf area) was 385.

[#3]Error df of sqrt(inflorescence biomass) was 399.

† $P < 0.1$; * $P < 0.05$;** $P < 0.01$; *** $P < 0.001$.

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