

Introduced plants of the invasive *Solidago gigantea* (Asteraceae) are larger and grow denser than conspecifics in the native range

Gabi Jakobs*, Ewald Weber and Peter J. Edwards

Geobotanical Institute, Swiss Federal Institute of Technology, Zürichbergstr. 38, CH-8044 Zurich, Switzerland

ABSTRACT

Introduced plant species that became successful invaders appear often more vigorous and taller than their conspecifics in the native range. Reasons postulated to explain this better performance in the introduced range include more favourable environmental conditions and release from natural enemies and pathogens. According to the Evolution of Increased Competitive Ability hypothesis (EICA hypothesis) there is a trade-off between investment into defence against herbivores and pathogens, and investment into a stronger competitive ability. In this study, we conducted field surveys to investigate whether populations of the invasive perennial *Solidago gigantea* Ait (Asteraceae) differ with respect to growth and size in the native and introduced range, respectively. We assessed size and morphological variation of 46 populations in the native North American range and 45 populations in the introduced European range. Despite considerable variation between populations within continents, there were pronounced differences between continents. The average population size, density and total plant biomass were larger in European than in American populations. Climatic differences and latitude explained only a small proportion of the total variation between the two continents. The results show that introduced plants can be very distinct in their growth form and size from conspecifics in the native range. The apparently better performance of this invasive species in Europe may be the result of changed selection pressures, as implied by the EICA hypothesis.

Keywords

Biological invasions, clonal growth, competitive ability, EICA, exotic species, life history, *Solidago*.

*Correspondence: Gabi Jakobs, Geobotanical Institute, Swiss Federal Institute of Technology, Zürichbergstr. 38, CH-8044 Zurich, Switzerland. Tel.: +41 16324382. Fax.: +41 16321215. E-mail: jakobs@geobot.unmwn.ethz.ch

INTRODUCTION

Plant invasions are a significant component of global change with far-reaching consequences for the invaded communities (D'Antonio & Vitousek, 1992; Vitousek *et al.*, 1997; Rejmánek *et al.*, 2002). Since the period of European colonization, plant species have increasingly been transported by humans outside their original biogeographical ranges, thus overcoming natural dispersal barriers. Some of these non-indigenous species have the potential to establish and spread rapidly in the new environment and to alter native plant communities by outcompeting native taxa, thus reducing local biodiversity. Although invasive plant species vary greatly in their morphology and life history, there seem to be some traits commonly associated with successful invaders. These traits include a high phenotypic plasticity and high growth rate; many invasive species also have the ability to

spread clonally (Vogt-Anderson, 1995), which enables them to form dense, monospecific stands (Crawley, 1986; Blossey *et al.*, 1996).

A common observation is that introduced plants grow larger and are more vigorous than plants of the same species in the native range (Blossey & Nötzold, 1995; Bastlová-Hanzélyová, 2001). Despite numerous studies on invasive species, though, the reasons for this apparent increased vigour are not yet fully understood (Noble, 1989; Crawley *et al.*, 1996; Rees & Paynter, 1997). Introduced species could either profit from more favourable environmental conditions in the introduced range, or from the absence of specific herbivores and pathogens, as proposed in the Enemy-Release Hypothesis by Keane & Crawley (2002). The EICA hypothesis (Evolution of Increased Competitive Ability; Blossey & Nötzold, 1995) goes one step further, proposing that if the introduced plants have escaped their specialized herbivores

there may be selection for increased competitive ability rather than for defence.

Before these hypotheses can be tested it is necessary to assess the amount of variation in plant performance in both the introduced and native range, in order to see whether there are explicit differences that can be attributed to the above hypotheses. An empirical comparison of plant performance in both ranges may also contribute to an evaluation of biological characters that make a particular taxon invasive, and whether these characters are different in the introduced than in the native range.

The present study compares the morphological variation and size of native and introduced populations of *Solidago gigantea* in the field. This clonal perennial herb is highly invasive in central Europe, where it can become dominant in various habitats such as forest edges, riverbanks, and wetlands (Walter, 1987; Schuldes & Kübler, 1990). It is also highly variable in its growth habit within Europe (Weber, 1997). To investigate whether there are differences in the growth of plants in native and introduced populations, we recorded various aspects of their growth at both the population and the individual plant level. Our main hypotheses were: (1) European populations are larger and denser than the native populations in North America; (2) Above- and below-ground ramet sizes are larger in European populations; and (3) There is a shift in biomass allocation to reproductive parts among European plants. To help distinguish between the effects of environmental conditions and release from herbivores and pathogens, we also investigated the influence of the geographical location, and of weather and climatic conditions on the population differences in the two ranges.

METHODS

The study species

Solidago gigantea (Asteraceae) is a rhizomatous perennial herb of 0.5–2.5 m height. Its shoots are erect and unbranched except within the inflorescence. *S. gigantea* flowers in late summer and autumn, displaying numerous yellow flower heads. The wind-dispersed seeds are primarily important for long-distance dispersal; within established stands plants appear to multiply almost exclusively vegetatively, as was shown for the closely related *S. altissima* (Hartnett & Bazzaz, 1985). Under favourable conditions the long-creeping rhizomes of *S. gigantea* easily fragment and

become rooted. Due to this clonal growth the species can form dense stands which exclude almost all other species. *Solidago gigantea* is native to North America and was introduced to Europe as an ornamental plant some 250 years ago. First cultivated in gardens, it began to spread after an initial lag-phase of about 100 years (Weber, 1998). It is now invasive in central Europe and penetrates into margins of wetlands, meadows, afforestations and river banks. The current range in Europe includes central and eastern Europe, the southern part of Scandinavia and the northern part of South Europe (Weber, 2001).

Field survey

For a representative comparison of North American and European regions, a total of 91 populations were visited during summer 2001. The populations were distributed in three main regions in both continents (Fig. 1): 45 North American populations were located in Pennsylvania, Iowa and Wisconsin, and 46 European populations were located in Germany, Northern Switzerland/France (Alsace) and south of the Swiss Alps (Tessin and Italy). Even though the climate was generally more continental in the areas visited in North America, all regions were characterized by a temperate climate with a sufficient water supply throughout the year.

A population was defined geographically by a minimum separation of 1 km between plants of neighbouring populations. Distances within each of the six areas were comparable, whereas distances between the three areas were rather larger in America. Within each region, the populations selected for this survey represented the whole spectrum of habitats in which the species commonly occurs, including ruderal, seminatural and natural sites. Records made for each population included geographical location, altitude, soil moisture, the most frequent species in the accompanying flora, an estimate of the extent of herbivory, and notes on the surrounding environment (e.g. open vs. forests edge or forest populations, ruderal vs. (semi) natural sites, the slope and important landmarks, such as rivers or lakes). Whereas the primary goal of the study was to quantify the size variation of *Solidago gigantea*, we estimated soil moisture conditions and the degree of herbivory as an additional characterization of the habitat and conditions of the plants. Soil moisture was measured by taking five randomly spaced soil cores within each population and determining fresh and dry weight of the samples. The extent

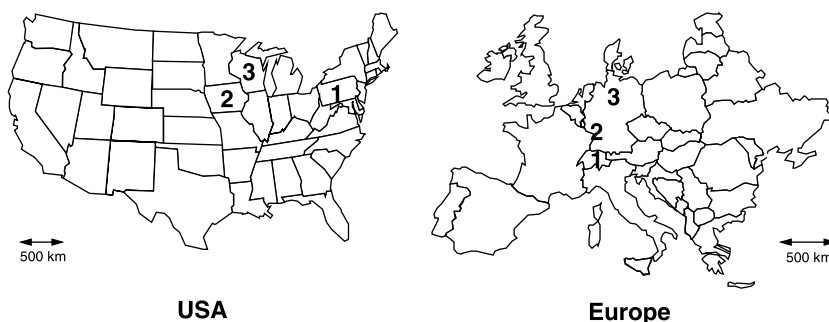


Figure 1 Maps of sampling areas in North America: 1 — Pennsylvania, 2 — Iowa State, 3 — Wisconsin and Europe: 1 — Italy and Tessin, 2 — Northern Switzerland, Southern Germany and Alsace (France), 3 — Northern Germany.

of herbivory was classified as heavily infested if at least half of the above-ground ramets were infested, and no further classification was done. The shoot density of the entire population was estimated from the mean of three randomly placed 1-m² plots; in very dense populations (more than 100 shoots per m²), the plot size was reduced to 0.25 m².

We measured plant height, stem diameter, inflorescence size, and number, length and diameter of rhizomes. All above-ground parameters were recorded as the mean of the three tallest ramets of a population; for the below-ground parts, 10 rhizomes were isolated and the largest three were measured. The deviation to the mean of 20 ramets measured along two transects through the population was less than 5% in a subsample of 10 populations measured both ways; subsequently this small number seemed representative for the entire population.

Above-ground biomass was estimated by calculating a regression between the size of the three largest shoots and the total biomass per m² for 20 populations of varying size and density. These measurements were conducted in October when the majority of ramets had produced seeds. Ramet size was equal to that in July and August, when the 91 populations included in this field study were measured. The biomass estimate was calculated as a function of ramet height (h), stem diameter (d) and inflorescence height (i):

$$f(\text{biomass}) = -130 + ((1.489 \times h) \times 59.228) \times 0.09 + (3.047 \times d - 86.754) \times 0.21 + ((4.197 \times i + 16.760) \times 0.79)$$

The regression coefficient r^2 for this relationship was 0.79 ($P < 0.001$).

Weather and climatic data

The weather in the previous year and long-term climatic data in the region were taken into account as possible parameters influencing plant growth and population dynamics. For each sampling site, climatic data for the nearest station were obtained. The annual precipitation (separately recorded for autumn and winter 2000 and spring and summer 2001) was obtained from the Global Precipitation Climatology Centre (<http://www.dwd.de/de/WundK/Klimadaten/index.html>). Mean January and July temperatures (representing the temperature of the coldest and warmest months), mean annual temperature and annual sunshine hours were available from the National Climatic Data Center and the World Climate Research Program (www.ncdc.noaa.gov/oa/ncdc.html). The length of the vegetation period and long-term precipitation and temperature data were recorded as the means for a thirty year period.

Statistical analyses

We used analysis of variance (ANOVA) methods for testing for differences in plant traits between continents and populations. If necessary, data were transformed to normalize their distribution prior to analysis. The effect of climatic parameters on the growth of *S. gigantea* was tested with linear regression analyses.

RESULTS

Site conditions

In the native range, *Solidago gigantea* occurred only in rather moist habitats such as wetlands, riverbanks, the lower parts of fields and in swales which were wetter than the surrounding area. The patches of *S. gigantea* were often clearly distinct from the surrounding vegetation. Drier areas nearby were frequently occupied by other *Solidago* species, mainly *S. altissima*, *S. canadensis*, *S. juncea* and *S. rugosa*. Typical species of the associated flora were various Euphorbiaceae, *Daucus carota* and *Coronilla varia*. In Europe, the ecological range of *S. gigantea* appeared to be larger, and the species was found both in wet and dry habitats. This impression is supported by information from European floras (Landolt, 1977; Ellenberg, 1982), which characterize *S. gigantea* as a species tolerant of a wide range of soil moisture conditions. Patches of *S. gigantea* were often less clearly defined than in North America, and borders could not be related to differences in soil moisture. Fewer populations were directly adjacent to rivers and lakes and more were in disturbed areas and beside roads. In Europe, *S. gigantea* was most commonly associated with *Artemisia vulgaris*, *Urtica dioica*, *Cirsium arvense* and *Rubus* spp. Especially in disturbed sites it often occurred together with other invasive species such as *Reynoutria japonica* and *Impatiens glandulifera*.

The total number of accompanying vascular plant species varied between the areas in each continent; the average was slightly higher in European populations, but due to a large variation from zero to 24 species the differences were not significant. The species richness was highest in the Alsace region of Europe with a mean of 15.2 species and in Wisconsin, USA, with 11.9 species. There were several monospecific populations in Europe (7%), but none in USA, not taking into account small patches within the entire population.

Growth characteristics of *Solidago gigantea*

The populations of *S. gigantea* analysed in this field survey varied considerably in their size and density. Population (patch) size varied from 2 to 50,000 m² in Europe and from 1.5–15,000 m² in North America. On average, European populations were four times larger than American populations. Many populations south of the Swiss Alps, however, were smaller than the average of European populations and thus more similar to American sites. The mean shoot density was significantly higher in European populations, namely 78.5 ± 4.6 ramets per m² compared to 35.6 ± 4.0 ramets per m² in American populations.

There was considerable variation in ramet size, both above and below ground; the ramets of European plants were on average larger than those of American plants. There were highly significant differences between the two continents in ramet height, stem diameter, inflorescence size, and the number, length and diameter of rhizomes (Table 1). The strongest difference between the two continents was apparent in the number of rhizomes which was almost three times as high in Europe than in North

	EU	US	F	Prob > F	Prob(lat) > F
Population traits					
Shoot density (m ⁻²)	78.9 ± 4.0	35.5 ± 4.1	58.1	< 0.0001	< 0.0001
Species number	10.2 ± 0.8	9.2 ± 0.8	0.7	n.s.	n.s.
Above-ground traits					
Biomass (g)	202 ± 4	126 ± 4	58.1	< 0.0001	< 0.0001
Shoot height (cm)	168 ± 5	131 ± 5	13.1	< 0.0001	< 0.0001
Inflorescence height (cm)	40 ± 3	24 ± 3	26.0	< 0.0001	< 0.0001
Stem diameter (0.1 mm)	77 ± 3	60 ± 2	22.4	< 0.0001	< 0.0001
Below-ground traits					
No. of rhizomes	16.8 ± 1.2	6.7 ± 1.0	42.6	< 0.0001	< 0.0001
Rhizome length (cm)	31 ± 2	24 ± 1	9.9	0.0071	0.007
Rhizome diameter (mm)	55 ± 3	47 ± 3	2.9	0.0224	0.026

Column Prob > F gives the *P*-values of an ANOVA, Prob (lat) > F gives *P*-values of an ANCOVA taking latitude as a covariate. Density = mean population density; species = number of species within the population. Plant traits are based on the mean of three ramets per population (see text).

America; above-ground biomass and the size of the inflorescences were also considerably higher in Europe. However, the coefficient of variation between populations in growth parameters was also larger in Europe, especially for the number of rhizomes (4.5 vs. 3.2) and the population density (1.8 vs. 0.4).

Ramet size and density varied within continents according to the geographical locations of the populations. On average, the further south the population was situated, the smaller were the ramets, this trend being particularly pronounced for rhizomes (Fig. 2). Despite the more northerly location of most European populations, the differences between the two continents were still significant if the latitude was considered (Table 1). The altitude of sites varied between 74 and 1000 m above sea level, but there were no significant relationships with plant growth.

The variation of ramet size within each continent can also be related to habitat characteristics. In America shoots of forest edge populations were particularly tall, whereas this was not the case in European populations. Some American populations grew beneath forest, and these plants had small, weak shoots with very thin, often elongated rhizomes. None of the European populations was within forest vegetation, although the species is described as shade tolerant. In Europe the tallest ramets with the largest inflorescences were found in large monospecific stands in open habitats.

Climatic influences

Weather and climatic differences between the regions appeared to have a considerable influence on the growth of *S. gigantea* (Table 2). The strongest performance was in areas with an oceanic climate with low thermal amplitudes throughout the year and high rates of precipitation. Thus high winter and low summer temperatures were associated with vigorous growth of *S. gigantea* (Fig. 3a,b), but annual mean temperature did not affect the ramet growth. A precipitation rate above the long-term annual mean enhanced the growth of ramets and the

Table 1 Size differences between European and American populations of *Solidago gigantea*, as measured in the field (Mean ± SE)

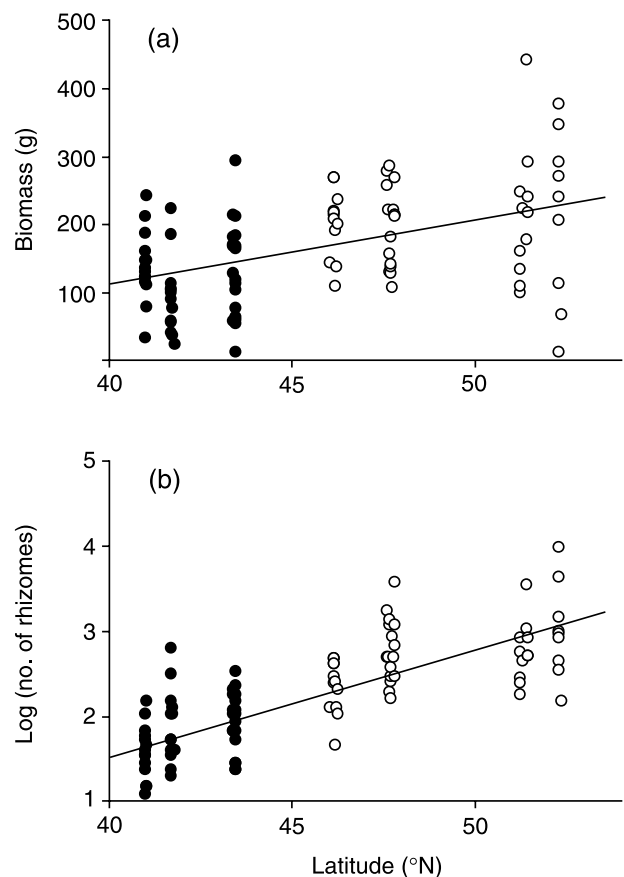


Figure 2 Clinal variation of American and European populations of *Solidago gigantea* of (a) above-ground biomass ($r^2 = 0.31$) and (b) the logarithm of the number of rhizomes ($r^2 = 0.58$). Lines represent regression lines. Filled circles represent North American populations; open circles European populations.

population density. Depending on the season, precipitation affected different parts of the plant: whereas above-ground parts were mainly influenced by the precipitation in the first half of the vegetation period, rhizome length and population density

Table 2 Correlation of climatic parameters and plant traits in populations of *Solidago gigantea*

	Above-ground biomass	Shoot height	Inflorescence height	No. of rhizomes	Shoot density
Precipitation					
Spring prec.	0.074*	n.s.	0.055*	0.046*	n.s.
Summer prec.	n.s.	0.098*	0.045*	0.07*	n.s.
Autumn prec.	0.098**	n.s.	0.089**	0.154***	0.082**
Winter prec.	n.s.	n.s.	n.s.	n.s.	n.s.
Temperature					
Mean annual temp.	n.s.	n.s.	n.s.	n.s.	n.s.
Mean temp. January	0.261***	0.090*	0.243***	0.323***	0.261***
Mean temp. July	0.217***	0.148***	0.281***	0.450***	0.262***
Sunshine	0.277***	0.206***	0.263***	0.462***	0.282***

Levels of significance are indicated as *for $\alpha = 0.05$, **for $\alpha = 0.01$ and ***for $\alpha = 0.001$.

Spring prec. = accumulated amount of precipitation from March–June 2001 in mm;

Summer prec. = accumulated amount of precipitation from July–September 2000;

Autumn prec. = accumulated amount of precipitation from October–November 2000;

Winter prec. = accumulated amount of precipitation from December 2000 and February 2001. The mean annual temperature was measured between August 2000 and July 2001. Sunshine = no. of sunshine hours from autumn 2000 to summer 2001.

were stronger correlated with autumn precipitation (Fig. 3c). In general, the rhizome system reacted much more strongly to differences in precipitation. The total number of sunshine hours was negatively correlated with the growth of *S. gigantea*.

Herbivory

Seventy percent of the American populations were severely damaged by herbivores, mainly by *Eurosta solidaginis*, *Rhopalomyia solidaginis*, *Philaenus spumarius* and *Uroleucon caligatum*, and most of the remaining populations showed some signs of herbivory. Rhizome herbivory was also observed occasionally. Only 20% of the populations in the forest and 50% at the forest edge were affected by herbivores, compared to almost 80% of the populations from open sites. Herbivory was not correlated with the mean ramet size, but the coefficient of variation was smaller in infested sites than in noninfested sites. None of the European populations was infested by herbivores though in two populations we found very few shoots with some branches within the inflorescences which had apparently been damaged; this limited damage could have been the result of herbivory earlier in the season.

DISCUSSION

Life-history traits

The comparison between North American and European populations of *Solidago gigantea* showed pronounced differences in both plant and population traits. Similar differences have been described for other invasive plant species, e.g. *Sapium sebiferum*

(Siemann & Rogers, 2001) and *Lythrum salicaria* (Willis & Blossey, 1999; Bastlová-Hanzélyová, 2001). Whereas all the plant traits investigated differed between the two ranges, the extent of these differences varied according to the trait. For example, the greatest differences between the two continents were in the number of rhizomes and the size of the inflorescences; this could be because traits related to reproductive capacity are under particularly strong selection in invasive populations. It is also interesting that there is a larger variability in many traits amongst invasive populations. We have no information about the reason for this difference, but it could indicate a higher plasticity in introduced populations. This would be consistent with the invasive genotypes growing in a wider range of habitats. Support for both these tentative conclusions comes from common garden experiments (Jakobs *et al.*, 2001), showing that in European populations the reproductive effort was higher and plants were more plastic in their response to varying environmental conditions (e.g. nutrient conditions). The garden experiments strongly suggest a genetic basis for the observed differences. Sexual and vegetative reproduction therefore seem to be essential postinvasive changes and may strongly influence the rapid establishment and spread of the species.

The two modes of reproduction are important at different stages during the establishment of a population of *S. gigantea*. Sexual reproduction ensures long-distance dispersal and the occupation of new habitats. This may guarantee the continuing spread of the species, as described in the literature (Balogh, 2001). Once established in an area, vegetative reproduction enables *S. gigantea* to compete strongly with other species. This is partly because a high rhizome density allows clones to increase the number of shoots produced in the following year, hence

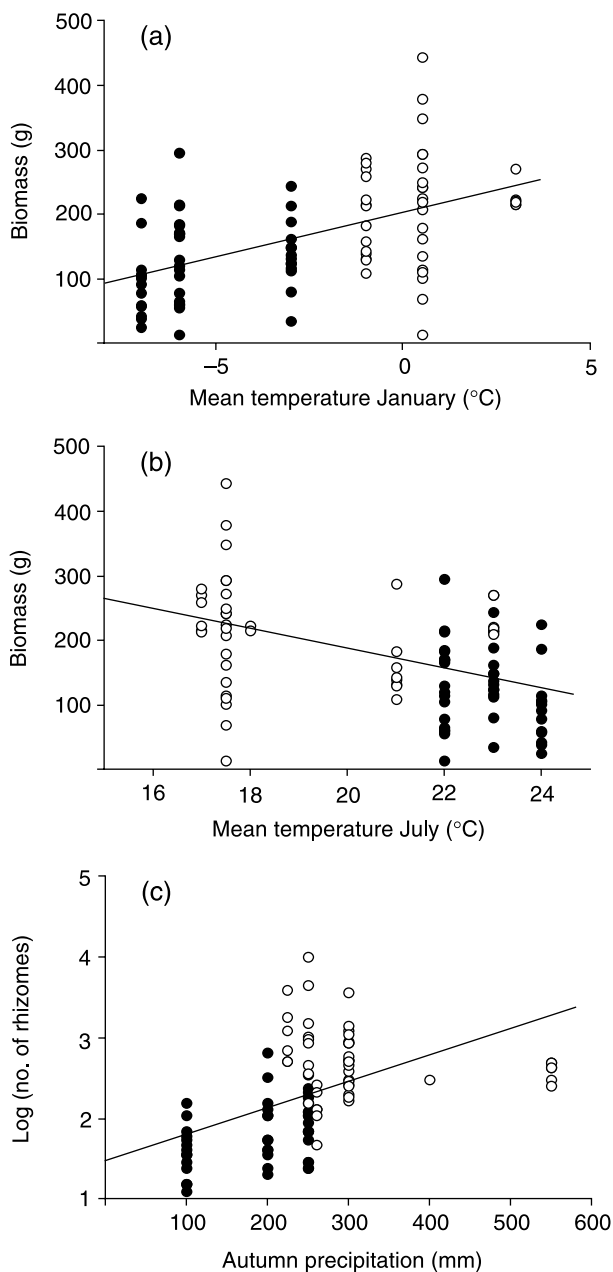


Figure 3 Influence of the climate of the previous year on above-ground biomass and number of rhizomes in American and European populations of *Solidago gigantea*. Lines represent regression lines, see Table 2 for correlation coefficients. Filled circles represent North American populations; open circles European populations. (a) influence of the mean temperature of the coldest month on biomass (b) influence of the mean temperature of the warmest month on biomass, and (c) influence of autumn precipitation on number of rhizomes. For definition of autumn precipitation, see Table 2.

strengthening the pressure of competition on other species. Secondly a larger rhizome system may permit an efficient use of resources in the habitat. Pysek *et al.* (1995) found that clonal plants often reach their maximum distribution earlier and are more likely to gain dominance in a certain habitat than

nonclonal species. This could be one reason for the occurrence of monospecific stands in the introduced range. Finally the larger number of rhizomes per shoot in invasive populations may also indicate a higher level of connections between ramets, and thus greater clonal integration. The extent of clonal growth and its plasticity may be important in determining whether a species can permanently establish itself in a new habitat.

Influence of environmental conditions

The high percentage of European populations occurring in disturbed habitats such as riverbanks, wastelands, railway and road embankments reflects the advantages of open and ruderal sites for successfully occupying new habitats. An establishment with seeds requires a gap in space and time (Grime, 2001). Once established, the ability for vegetative reproduction may allow a species to invade neighbouring closed vegetation.

Our data suggest that *S. gigantea* tends to grow best under the most temperate conditions. This is probably because moderate winter temperatures allow an early start to the vegetation period while low summer temperatures guarantee lower evaporation and subsequently better water supply throughout the season. Both factors are probably important in a large herbaceous perennial species which flowers late in the season. A sufficient water supply in summer seems particularly important for *S. gigantea*, since the plants respond to drought by reducing the leaf area, which in turn negatively influences the development and growth of the inflorescence (Botta-Dukát & Dancza, 2001). This might also explain the negative influence of sunshine, since the higher radiation might increase the evaporation, and subsequently decrease the amount of water available for the plant. Some of the parameters measured, such as shoot height, responded very plastically to the recent precipitation. Other parameters, for example the size of the inflorescence, seem to behave more conservatively, and show a higher correlation with the long-term annual mean. Rhizomes show their highest growth in autumn, which explains the strong influence of autumn precipitation on the size of the rhizome system and the population density. In dry soil the rhizome growth may be mechanically restricted. This influence was stronger in North American sites, probably because rhizomes were on average thinner.

Despite similar rates of precipitation, many European sites were more exposed and drier than North American sites, as revealed in the analysis of soil moisture contents. The restriction to wetter habitats in the native range reflects the species' known habitat preferences. In Europe, however, it is able to tolerate less favourable conditions. The frequent occurrence in drier habitats in Europe, as described by Botta-Dukát & Dancza (2001), can be interpreted as a broadening of the ecological niche; possibly this is enabled by the release from herbivores in the introduced habitat.

Climatic conditions only explain a proportion of the variation observed in *S. gigantea* populations. Equally important may be adaptations to local environmental conditions. Among other factors, a longer day length during the summer months may allow a higher biomass production and a higher allocation to the rhizome system in northern areas, evoking a clinal variation in

this species. Similar altitudinal or elevational clinal variation has been described for many other plant species, such as *Picea abies* (Modrzyński & Eriksson, 2002) and *Lythrum salicaria* (Olsson & Agren, 2002).

Herbivory

The absence of herbivores in the introduced range is consistent with earlier findings on goldenrods (Zwölfer, 1976). In a more recent study on invasive populations of *S. gigantea* and the closely related *S. altissima*, only a few potential herbivores were found on the plants and feeding activity was not verified (Jobin *et al.*, 1996; Bopp, 1997). It seems probable that the invertebrate herbivores of the native goldenrod, *S. virgaurea*, are unable to feed on any of the introduced species.

Release from herbivores and pathogens in the introduced range is an assumption of the EICA hypothesis. In the native range, the high abundance of herbivores suggests the relevance of defence or resistance. Although plant patches infested by herbivores were not necessarily smaller than less infested ones, herbivory can be assumed to have an impact on the population growth. Beetle folivory, for instance, has been shown to raise the probability of other plant species invading monocultures of goldenrods (Brown, 1994). This may be one reason for the lower population densities and the lower number of monospecific stands in North America. Furthermore, taller plants in denser populations are more often infested with herbivores and larger stem diameters improve the performance of gall forming invertebrates (Raman & Abrahamson, 1995; Craig *et al.*, 1999), which results in higher costs for the plant and reduced biomass. If larger plants are more frequently infested, potentially larger shoots may not reach their full height, either due to a direct constraint on the inflorescence growth, e.g. by the galls of *Eurosta solidaginis* or *Rhopalomyia solidaginis*, or indirectly through metabolic changes associated with wound responses (e.g. production of phenolics, tissue necrosis, early leaf senescence). On the other hand, smaller genotypes might benefit relative to larger ones from being less often infested. This benefit could partly take the form of greater clonal integration, because rhizome connections usually last longer in less infested sites (Abrahamson *et al.*, 1991).

Whereas in the native range herbivore susceptibility is likely to be an important selection factor, the situation is completely different in the introduced range in Europe. Non-infested sites in the introduced range may experience the same advantages as described above, but independently of ramet size and population density. According to Blossey & Kamil (1996), species are likely to experience rapidly changing selection pressures in the invaded habitats, favouring larger growing genotypes rather than well-defended ones. This altered selection pressure could lead to major changes in the genotype frequency and composition in European populations over only a few sexual generations. Common garden experiments in Wisconsin revealed that European plants are less defended against pathogens and herbivores (Meyer, submitted), which suggests that there is indeed a trade-off between defence mechanisms and competitive ability, as postulated in the EICA hypothesis.

In the case of *S. gigantea* there appears to have been an initial lag phase of about one hundred years before it began to invade seminatural and natural habitats strongly. A phenomenon lag has also been observed in other alien species. If the EICA hypothesis applies for *S. gigantea*, this delay could represent the time needed to select for genotypes with a higher competitive ability. We also suppose that the size differences between European populations along a north–south axis are the result of postinvasive ecophysiological adaptations rather than multiple introductions. We reject the alternative explanation — that there were numerous introductions with selection favouring the best-adapted genotypes in each region — since it seems unlikely that there have been multiple introductions on a large scale (Weber & Schmid, 1998). If this interpretation is correct, high genetic variability in combination with high plasticity have been important factors for the invasion success of *S. gigantea*.

CONCLUSIONS

If a particular plant species becomes invasive in the introduced range, the question arises to what extent this plant differs from its conspecifics in the native range. A direct comparison of plants growing in both ranges provides useful evidence of whether such differences exist. The results of this field survey show an increased growth performance of *Solidago gigantea* in the introduced range. The observed differences are rather pronounced and probably have a genetic basis, as they can only partly be explained by phenotypic plasticity or climatic differences. However, without common garden experiments we cannot be certain that the trends described here reveal genetic differences among continents; such studies are underway and will be reported elsewhere. Despite this limitation, we suggest that the increase in size, especially that of the reproductive traits, and the high plasticity of the European populations are probably the result of postinvasive genetic changes and help to explain the invasion success of *S. gigantea* in its introduced range.

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