RESEARCH PROJECT

Life-history and genetic variation of native vs. introduced populations of the perennial *Solidago gigantea* Ait. (Asteraceae)

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Summary

1 Introduced and invasive plant species are often more vigorous and taller than conspecifics in the native range. It has been suggested that the apparent increase in plant vigour is a plastic response either to a more favourable environment in the non-native range or to release from natural enemies and pathogens.

2 The EICA-hypothesis (Evolution of Increased Competitive Ability) suggests that in the introduced range, continued low herbivore and pathogen pressure has lead to the evolution of plants that grow larger and have a higher competitive ability, but that are less defended against herbivores than plants in the native range.

3 In this project, *Solidago gigantea* is used as a model system to test EICA. This rhizomatous perennial of North American origin is invasive in Central Europe, where it often forms monospecific stands of high shoot density.

4 Common garden experiments are set up in Zurich and in Wisconsin, U.S.A., with plants from American and European populations of *S. gigantea.*

5 In Zurich, life-history and genetic variation of the populations is being assessed, and the competitive ability against native plant species is investigated. In Wisconsin, it is tested whether or not European plants show lower allocation to defence than native plants if exposed to naturally occurring insect herbivores and pathogens.

6 Preliminary results from Zurich indicate a high amount of variation among populations in many growth-associated plant traits and in phenology, with little difference between American and European populations. European populations grown in Wisconsin seem to be more susceptible to at least some insects and diseases than their American native relatives.

7 The results of these studies will show whether EICA applies to *S. gigantea* and whether it is a possible explanation for the invasion success of this species in Europe.

Keywords: common garden experiment, competition, EICA-hypothesis, herbivore effects, invasive plants

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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). Since the period of European colonization plant species have increasingly been transported outside their original biogeographical range, thus overcoming natural dispersal barriers. Some of these exotic species have the potential to rapidly spread in the new environment and to alter native plant communities by outcompeting native taxa and reducing the local biodiversity. Plant invasions have therefore become an important issue in nature management and restoration programs. They are often enhanced by disturbances and habitat fragmentation.

Although invasive alien plant species are represented by many different life forms and families, some characteristics are more commonly observed than others: the ability to form dense, monospecific stands, clonal growth, and a high growth rate (Blossey & Kami 1996; Crawley 1987). In addition, plants of introduced populations often appear to grow more vigorously and to reach a greater size than their conspecifics in the native range (Noble 1989; Blossey & Nötzold 1995; Crawley *et al.* 1996; Rees & Paynter 1997). For example, Pritchard (1960) grew *Hypericum perforatum* L. from seeds collected in Australia and Europe together and observed that Australian plants were on average taller than European plants. Similarly, Blossey & Kamil (1996) compared the growth of *Lythrum salicaria* L. from the native European range and from the introduced American range. Plants from the introduced range grew taller and achieved a higher biomass than those from the native range.

The high performance of invasive plants in the introduced range might be explained by more favourable environmental conditions compared to the native range or by the absence of natural enemies (herbivores, pathogens) that used to limit plant growth in the native range. In both instances, the reaction of the plant would be due to phenotypic plasticity. An alternative explanation is proposed by the EICA-hypothesis (Evolution of Increased Competitive Ability) by Blossey & Nötzold (1995). According to this hypothesis, plants introduced to another continent are free of herbivores and pathogens and thus experience changed selection pressures. These would lead to the evolution of genotypes that grow faster and have a higher competitive ability, but are less defended against herbivores. If EICA applies, genetic differences between native and introduced plants with respect to these characters may be expected. Indeed, the genetic composition after introduction can rapidly alter as a result of founder effects (Novak & Mack 1993), leading to new genotypes in the introduced range.

The aim of this study is to compare life-history and genetic variation of native and introduced populations of the invasive species *Solidago gigantea* in order to test whether or not EICA applies to this species. *Solidago gigantea* is native to North America and introduced in Europe, where it invades riparian habitats, forest edges, meadows, and ruderal communities. The main questions of the study are:

(1) Are European plants less defended against herbivores and pathogens than American plants when exposed to native herbivores?
(2) Do European plants differ from American plants with respect to growth-related characters, if grown in a common garden?
(3) Do plants of European origin invest more resources into clonal growth than their native conspecifics?

(4) What is the amount of genetic variation within and between introduced and native populations of *S. gigantea*?
(5) Do European plants show a higher competitive ability than American plants?

Study species

Solidago gigantea is a rhizomatous perennial herb of 1–2 m height that was introduced from North America 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. The current range in Europe includes Central and Eastern Europe, the southern part of Scandinavia, and the northern part of South Europe (Weber 2001). The species is considered invasive in Central Europe. Due to clonal growth, it forms dense monocultures and subsequently outcompetes native species. The long-creeping rhizomes easily fragment and root at the nodes under favourable conditions. Above-ground shoots emerge in spring and die back in autumn or early winter. Plants flower in late summer with numerous yellow flower heads. Seeds (achenes) are small and wind-dispersed; a single shoot may produce up to 19'000 seeds. In established populations it can be assumed that plants multiply mainly vegetatively as is the case in the closely related *S. altissima* (Meyer & Schmid 1999). In the native range, *S. gigantea* occurs as diploid (2n = 18) or tetraploid (2n = 36) cytotypes, whereas only tetraploid plants have been found in Europe (Weber 1997).

Methods

SEED COLLECTIONS

Seeds were collected from 12 American and 26 European populations in late summer 1999. Populations from the native range were sampled in eastern and midwestern USA, and populations from the introduced range in Central Europe. Seeds were collected either as separate seed families or as bulk samples (small populations). In the first case distances between mother plants were kept large enough to ensure that seed families originated from different genets. Seeds were stored at room temperature until germination.

Fig. 1. *The experimental garden at Hönggerberg, Zurich, at the end of the season*

ASSESSING LIFE-HISTORY VARIATION

Plants of all populations were grown in a common garden at the Hönggerberg experimental facility of the ETH Zurich for one growing season (Fig. 1). Seeds were germinated in March 2000, and plants were transferred to the garden in May 2000. The experiment consisted of 48 plots, each with 38 plants (one plant per population) separated by 20-cm spaces. Half of the plots (randomly assigned) were fertilized during the growing season with a commercial liquid NPK-fertilizer (Wuxal, Maag Agro, Dielsdorf; 0.6%; 10 l per plot). Unfertilized plots received an equal amount of water.

During the growth period a number of characters was measured: shoot height, status (rosette, shoot, flowering) and length of the longest leaf in May, July and late autumn. All plants were harvested after fading of the inflorescence of the main shoot in autumn 2000. At this stage, stem diameter as well as height and width of inflorescences were recorded. Phenology was scored by noting the day of first flower opening. The leaves were scored for variation in leaf serration and degree of leaf pubescence. After harvesting, shoots were dried at 70 °C and weighed to determine the biomass.

CLONAL GROWTH

A subset of five American and five European populations were planted in sand (about 20 cm deep) in spring 2000 in order to follow rhizome growth patterns. 18 plants per population were established with 60-cm spaces to minimize competition during the course of the experiment. An initial harvest of six plants per population took place in fall 2000. Further subsets of six plants each will be harvested in spring and fall 2001, respectively.

At each harvest the number of rhizomes as well as the length and dry weight of each rhizome will be measured. Shoots will be separated into vegetative and reproductive parts. Thus, biomass allocation to rhizomes and to sexual organs can be compared among populations.

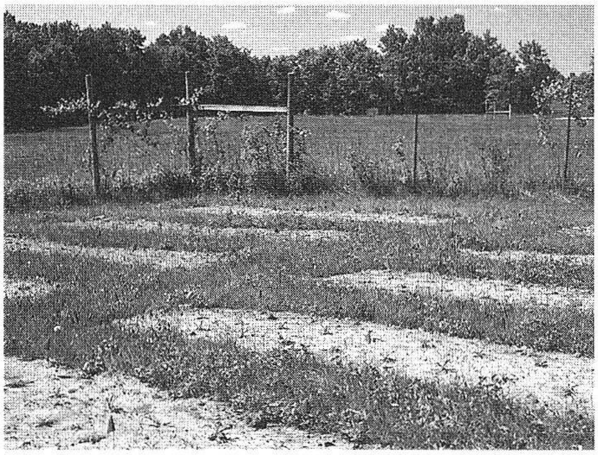

***Fig. 2.** The experimental garden at the UWM field station, USA, at planting*

RESISTANCE TO HERBIVORES

At the University of Wisconsin-Milwaukee Field Station in Saukville, WI, USA, a common garden experiment has been set up with plants from 10 American and 20 European populations (Fig. 2). Plants are arranged in plots, and half of the plots are treated with insecticides to exclude herbivores. Plants in the untreated plots are exposed to naturally occurring herbivores and pathogens. Herbivore damage and plant performance are assessed, and leaves of American and European plants are tested in food choice experiments with selected herbivores.

COMPETITIVE ABILITY

Plants from a subset of five American and five European populations will be grown in 2001 with and without competitors, respectively. Plants with competitors will be surrounded either by four plants of *Lythrum salicaria* as a strong above-ground competitor or by four plants of *Anthoxanthum odoratum* as a strong below-ground competitor (S. Güsewell, personal comm.). Distances between targets and competitors will be 8 cm. Half of the plots will be fertilised with a commercial liquid NPK-fertilizer (Wuxal, Maag Agro, Dielsdorf). Each combination of population, competition treatment and fertilizer treatment will be replicated four times.

Significance of the project and preliminary results

The EICA hypothesis as a possible explanation for the colonization success of introduced species has recently been challenged (Willis 2000; Thébaud & Simberloff 2001). To test whether an introduced plant species shows characteristics that are consistent with the EICA hypothesis, it is not sufficient to compare one population from the native range with one from the introduced range in a common garden setting and to test for differences in plant size or other fitness-related traits. Indeed, significant genetic variation among populations may be expected within each range, e.g. due to differences in latitude and soil conditions at the site of origin. This variation would be confounded with differences between the introduced and the native range unless it is taken into account by investigating multiple populations from each range. In addition, testing the EICA hypothesis should include the direct comparison of introduced and native plants with respect to herbivore resistance and competitive ability.

The ongoing study addresses all aspects of EICA and thus represents a rigorous test of this hypothesis. The results will demonstrate whether or not introduced *Solidago gigantea* has become more susceptible to the herbivores occurring in its native range, and whether the presumed genetic differences between American and European plants translate into a higher competitive ability of the latter.

Preliminary results indicate that all morphological characters measured so far in the garden experiments are quite variable, both within and between populations. In Wisconsin, American plants were more likely to flower than European ones (61% vs. 55% flowering). Flowering rate was higher in Zurich, since about 90% of the plants came to flower. Final shoot height of plants at Zurich ranged from 32 to 227 cm. Shoot height in May was on average larger for European than for American plants, but this difference had disappeared by the end of the experiment.

Previous studies have shown a considerable variation in life-history and floral traits of *S. gigantea* within Europe (Voser-Huber 1983; Weber 1997; Weber & Schmid 1998), and thus the patterns found so far were as expected. As argued above, the results of all parts of this project will be necessary to really demonstrate the presence of EICA in *S. gigantea.*

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