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RESEARCH PROJECT

Does herbivory by slugs influence the invasiveness of perennial Brassicaceae?

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Summary

1 It is often assumed that invasive plants escape control by their natural herbivores and pathogens in the introduced area. The EICA-hypothesis (Evolution of Increased Competitive Ability) suggests that release from natural enemies and pathogens results in higher plant vigour or that poorly defended but rapidly growing genotypes are selectively favoured in the absence of herbivores. Alternatively or in addition, invasive plants may be either less palatable or better able to compensate for biomass losses by herbivory than related, non-invasive species in the same area.

2 The objective of this study is to investigate whether release from slug herbivory and/or an increased ability to compensate for damage by slug herbivory is a possible reason for invasiveness. The family of the Brassicaceae has a high number of invasive species and for many of these plants slugs appear to be the main herbivores.

3 To investigate the EICA hypothesis, we compare life-history and fitness parameters of plants from native and introduced populations of four invasive Brassicaceae forbs. Plants or leaf material will be subjected to slug herbivory in controlled field and glasshouse experiments using *Arion lusitanicus,* a slug that is very abundant and a real pest in Europe but has only recently been found at one location in the United States.

4 To investigate the alternative hypothesis that invasive species are less susceptible to attack, we compare life-history and fitness parameters and the susceptibility to herbivory of invasive and non-invasive species. In this experiment six Brassicaceae species are offered to two common European slug species, *Deroceras reticulatum* and *Arion lusitanicus.*

5 The results of the project will help to assess whether herbivory is a significant factor influencing the success of Brassicaceae forbs as invaders and to establish by which mechanisms herbivory interacts with species invasiveness. Additionally, the study will contribute to our understanding of variations in the effects of herbivory upon similar plant species and among different life stages within species.

Keywords: *Arion lusitanicus,* compensatory growth, *Deroceras reticulatum,* EICA hypothesis, invasive plants, palatability.

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Introduction

The search for general characteristics of successful plant invaders (i.e. traits conferring high invasiveness) has proved to be difficult; each invasion appears to be a unique case (e.g. Radford & Cousens 2000). However, some ecological attributes seem to be more often associated with invading species than others. These include large plant size, high seed output, high phenotypic plasticity, rapid growth and, for historical reasons, pre-adaptation to anthropogenic site conditions (e.g. Noble 1989; Weber & Schmid 1993; Crawley *et al.* 1996; Williamson 1996).

It has often been observed that plants grow more vigorously and attain a larger size in the introduced area than plants of the same species growing in the native range (Noble 1989; Blossey & Nötzold 1995; Crawley *et al.* 1996; Rees & Paynter 1997). It has been suggested that release from natural enemies and pathogens results in higher plant vigour (e.g. Fowler *et al.* 1996) or that poorly defended but rapidly growing genotypes are selectively favoured in the absence of herbivores (EICA hypothesis, Blossey & Nötzold 1995).

For invasive plants growing in rather low herbaceous vegetation, differences in herbivore pressure between the introduced and the native range could be partly due to grazing by slugs. In Europe slugs are among the most important herbivores in this type of vegetation (e.g. Rathke 1985; Hulme 1996; Rodríguez & Brown 1998) and can influence both the biomass and the species composition of plant communities (e.g. Silva 1992; Hanley *et al.* 1995; Hulme 1996; Bruelheide & Scheidel 1999). It has been suggested that this is because plant species differ in their palatability to herbivores and in their capacity for regeneration and compensatory growth following herbivory (e.g. Louda *et al.* 1990; Silva & Teresa 1992). It has been shown, for example, that successful invasive species often have a particularly high capacity for compensatory growth and flexible resource allocation (e.g. Schierenbeck *et al.* 1994).

We hypothesise that presence or absence of slug herbivory is an important factor influencing the invasiveness of forbs of the Brassicaceae. In previous comparative studies slugs were often observed to prefer species of the Brassicaceae over other taxa despite the characteristic presence of mustard oils in Brassicaceae (e.g. Cates & Orians 1975; Dirzo 1980; Rathke 1985; Briner & Frank 1998). In addition, the Brassicaceae is a family with a high proportion of invasive species (e.g. Sebald *et al.* 1993), including perennial forbs. Several species that are native to the south-eastern or central parts of Europe have increased their range into northern and western Europe, and many species are invading North America (cf. Sebald et al. 1993; Jalas & Suominen 1994; Jalas *et al.* 1996; USDA 2000).

Whereas several voracious slug species have long been abundant in Europe, high levels of slug herbivory appear to be a more recent phenomenon in some regions of the US and are mainly related to just one species, *Deroceras reticulatum* (McCracken & Selander 1980). This slug was introduced approximately 150 years ago and is now expanding its range. In contrast, slug species native to North America have not been considered to be serious pests because of their rather low abundance (South 1992). Therefore, the lower intensity of slug herbivory in the US may contribute to an increased invasiveness of European Brassicaceae forbs in this area.

Research questions, hypotheses, and experimental approaches

The main objective of this study is to understand the role of slug herbivory for differences in the invasiveness within and among species of the rather homogeneous family Brassicaceae. The work comprises common garden, glasshouse and climate chamber experiments in Zurich, Switzerland. Depending on the experimental approach, four or six perennial forb species from Europe (northern Bavaria, Germany and eastern Austria) and from the USA (Great Lakes region) are used for comparative investigations.

The project focuses on two main questions and the related hypotheses.

1. Are there intraspecific differences in life-history traits, in fitness parameters and in the amount of feeding damage by slugs between plants from native European and introduced American populations?

To investigate this question which underlies the EICA hypothesis (Evolution of Increased Competitive Ability), we compare plants of four invasive species from native and introduced populations. The EICA hypothesis is derived from optimal defence theory (e.g. Coley et al. 1985; Herms & Mattson 1992). It is argued that in the absence of specialist herbivores, selection in the introduced range favours poorly defended but rapidly growing genotypes. Based on these assumptions, our hypothesis is that plants in the introduced range show more vigorous growth and are more palatable to herbivores and pathogens than plants in the native range.

Native plants grown from material collected in the Vienna area in Austria (south-eastern Central Europe) and in northern Bavaria (western Central Europe) will be compared with introduced plants grown from material that was mainly collected in the southern Great Lakes region of the US-American Midwest (Table 1). Three types of experiments are used to investigate how susceptible plants from native and introduced populations are to slug herbivory: (1) In a common garden experiment, established plants are exposed to slug herbivory under field-like conditions. (2) In microcosm experiments, the susceptibility of young plants to slug herbivory is compared (the seedling stage of Brassicaceae may be especially vulnerable to slug attack; cf. Frank 1998). (3) In food-choice bioassays, leaf discs are offered to slugs to test their palatability.

2. Are brassicaceous forbs introduced to western Central Europe less attacked by slugs and/or do they show higher compensatory growth following slug herbivory than related species that are native to this area?

The hypothesis is that native Brassicaceae species are more susceptible to slug herbivory than the invasive species, and that the latter show a higher compensatory growth. In this interspecific approach, we compare life-history and fitness parameters and the susceptibility to herbivory between invasive and non-invasive species. An experimental test of this kind for more than only two species is still lacking.

Six species of Brassicaceae, three of them introduced from south-eastern Europe and invasive in Central Europe and three of them native in Central Europe were selected for this part of the study. The experimental procedures are similar to those used in the intraspecific studies.

Methods

SPECIES

A total of six species are used, *Barbarea vulgaris* R.Br., *Bunias orientalis* L., *Cardaria draba* (L.) Desv., *Diplotaxis tenuifolia* (L.) DC., *Isatis tinctoria* L. and *Rorippa austriaca* (Crantz) Besser (Brassicaceae). Besides sharing traits characteristic of this homogeneous family

Table 1. *Regeneration strategy and status of the study species in the three different areas surveyed (SE-Eur, Southeastern Central Europe; W-Eur, Western Central Europe; N-Am, North America; N, species native and non invasive; I, species introduced and invasive; (?), status not clear)*

Species	Regeneration	Status		
		SE-Eur	W-Eur	N-Am
Barbarea vulgaris	sexual	N	N	I
Bunias orientalis	sexual (vegetative)	N	I	I (?)
Cardaria draba	clonal (sexual)	N	I	I
Diplotaxis tenuifolia[1]	sexual	N	N (?)	I (?)
Isatis tinctoria[1]	sexual	N (?)	N	I
Rorippa austriaca	clonal	N	I	I

[1] Only material from Western Central Europe included in this study

(Hedge 1976), the species are relatively similar in life-form and habitat preference. They are polycarpic herbaceous perennials with a semi-rosette growth form and mostly deep-reaching storage root systems; all grow in sun-exposed, moderately disturbed vegetation on calcareous soils with high nutrient availability (Oberdorfer 1990). Important differences between the species include the presence or absence of clonal growth, the importance of sexual reproduction (Table 1), the longevity of individuals and the type of the seed bank (Hegi 1986; Dietz & Ullmann 1998; Dietz *et al.* 2002; Dietz *unpublished*).

All species are native in south-eastern Europe and some also occur in western Central Europe (Table 1). *B. vulgaris, D. tenuifolia* and *I. tinctoria* are native or archaeophytic in Central Europe while *B. orientalis, C. draba* and *R. austriaca* have been introduced to at least the western parts of Central Europe (Jalas & Suominen 1994; Jalas *et al.* 1996). The species were introduced to North America (probably before 1900, cf. Voss 1985) where they are invasive to different degrees (Table 1).

Except for *D. tenuifolia,* two or three populations per species were sampled between 1998 and 2000 in each of the three different geographical areas surveyed. Seeds of *D. tenuifolia* were obtained from a commercial supplier. Sixty to 90 individuals per species were grown either from seeds (*B. vulgaris, B. orientalis, D. tenuifolia, I. tinctoria*) or regenerated from plant fragments if seeds were not available in sufficient numbers (*C. draba, R. austriaca*).

The two most common slug species in Central Europe, *Deroceras reticulatum* Müller and *Arion lusitanicus* Mabille (Reischütz 1986; Frank 1998), were chosen for this study, being important natural herbivores of at least some of the species. While *D. reticulatum* is also widely introduced to North America (McCracken & Selander 1980), *A. lusitanicus* was found there for the first time in 1999 (R. Hammond, pers. comm.). The slugs were collected in the surroundings of the experimental area at Hönggerberg in Zurich, Switzerland.

COMMON GARDEN EXPERIMENTS

The common garden experiments have been established in 2000 in a homogeneous, horizontal, sun-exposed area on bare, loamy and calcareous soil of our experimental garden at ETH Hönggerberg in Zurich. There are two separate experimental arrangements reflecting

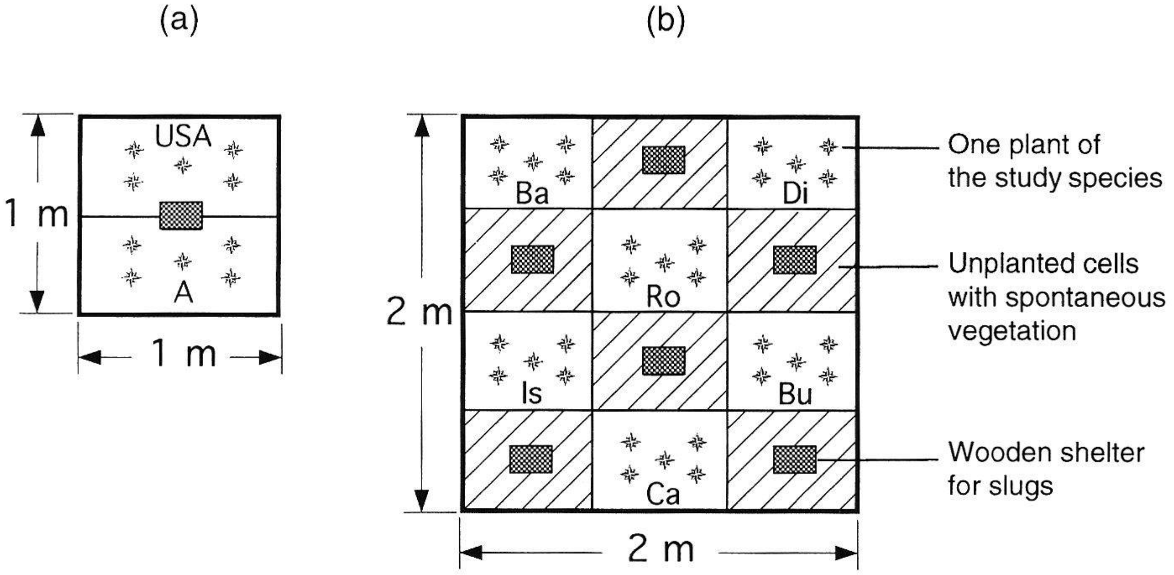

Fig. 1. *Design of the experimental plots (slug frames) used to investigate (a) intraspecific differences between populations from different areas (invasive vs. native range) and (b) interspecific differences in slug damage and compensatory growth between invasive and native species of one area. USA = populations from North America; A = populations from Austria; Ba =* Barbarea vulgaris; *Bu =* Bunias orientalis; *Ca =* Cardaria draba; *Di =* Diplotaxis tenuifolia; *Is =* Isatis tinctoria; *Ro =* Rorippa austriaca.

the two main research objectives in this study. In both experiments, we measure a number of characters that are related to life-history variation, phenology and fitness of the plants. These include: number of leaves and leaf damage by slug herbivory (measured twice a year in spring and autumn), number of shoots per plant, basal diameter of the shoots, time of flowering, number of developed fruits, mean number of seeds per fruit, mean seed mass (measured once a year in summer) and aboveground dry mass (measured at the end of the experiments, in autumn 2002).

Intraspecific differences between native and introduced populations

In this experiment, we examine species that are invasive in parts of Europe or the United States (*Barbarea vulgaris, Bunias orientalis, Cardaria draba, Rorippa austriaca*) and test for differences between plants from the introduced range and plants from the native range. Five plants per species from each of the two source areas (from the native and invasive range, respectively) were planted in one half of each plot frame (a slug-proof frame of 1 x 1 m^2 size, Fig. 1a) in autumn 2000. The slug species used in this experiment, *A. lusitanicus*, was chosen because it is abundant in Europe but almost absent from the North American continent (see above).

Origin of the plants and presence or absence of the slugs are the treatment factors. Half of the plots have been treated with five slugs per plot of *A. lusitanicus* since autumn 2000, while slugs are excluded from the remainder of the plots. A wooden shelter in the middle of each plot (Fig. 1a) protects the slugs from drought and helps to maintain the number of individuals (cf. Keller *et al.* 1999). Three replicates per treatment are arranged in a randomised block design.

Interspecific differences between invasive and non-invasive species

In this experiment we compare species collected in Central Europe that have been successful invaders (*Bunias orientalis, Cardaria* *draba, Rorippa austriaca*) with similar species that are not invasive in Central Europe (*Barbarea vulgaris, Diplotaxis tenuifolia, Isatis tinctoria*).

Commercially available metal frames are used to enclose slugs in the experimental plots (2 x 2 m^2). The area enclosed by each frame is subdivided into a grid of 12 equally sized cells (Fig. 1b). Five individuals each of the six plant species were planted into one cell within each frame in autumn 2000 (Fig. 1b). To present the slugs with less artificial foraging conditions, every second cell was left unplanted and vegetation was allowed to develop spontaneously.

The six experimental treatments (each replicated three times) are: (1) Slugs excluded from the plots, (2) *A. lusitanicus* added in autumn 2000, (3) *A. lusitanicus* added in spring 2001, (4) *D. reticulatum* added in autumn 2000, (5) *D. reticulatum* added in spring 2001, and (6) slugs excluded from autumn 2000 to spring 2001, followed by the removal of frames and spontaneous immigration of slugs. The slug numbers used in this experiment (20 individuals of *A. lusitanicus,* 40 individuals of the smaller *D. reticulatum*) simulate high natural slug densities (cf. Frank 1998). Six shelters placed into each plot (Fig. 1b) are used for slug monitoring.

SEEDLING BIOASSAYS

The susceptibility of the seedlings to grazing by slugs will be tested in spring 2002 in plastic flats (45 x 28 x 5 cm^3) filled with potting soil. Both intraspecific and interspecific differences will be tested, i.e. each flat will be planted either with seedlings from native and invasive populations of the same species or with seedlings from the six different species. The seedlings will be grown from seeds collected from surplus individuals of the plants that were cultured separately so as to avoid gene flow between individuals obtained from distinct areas. Three grazing treatments will be applied: no slugs, a controlled number of slugs present per flat, and exposure to ambient grazing pressure by slugs. All flats will be placed in the surrounding of the experimental plots of the common garden experiments at the Hönggerberg.

In further experiments, seedlings will be offered to the slugs in plastic boxes (20 x 10 x 5 cm^3) in a climate chamber (17 °C, 12 h light : 12 h dark). The bottom of each box will be covered with 2 cm of commercial potting soil. Twenty-four hours after transplanting the seedlings into the boxes, one slug will be introduced in each box and allowed to feed for 48 h. Half of the slugs will be starved and the other half will be fed *ad libitum* with *T. officinale* for 24 h before the onset of the experiments. The number of damaged and dead seedlings will be scored regularly.

LEAF DISC BIOASSAYS

In palatability experiments leaf discs obtained from fresh, mature leaves of surplus plants will be offered to *D. reticulatum* and *A. lusitanicus* in Petri dishes prepared with wet filter paper (to maintain increased air moisture). In one experiment (testing intraspecific differences) six leaf discs (same size as above) from plants of the native and the invasive populations of the same species will be placed in one dish (one species per dish). In the other experiment (testing interspecific differences) two (*D. reticulatum*) or three (*A. lusitanicus*) discs per study species and three discs of *Taraxacum officinale* will be offered to the slugs in each Petri dish. *T. officinale* is used as a standard in the palatability bioassays because it is known as one of the most palatable plants for slugs (e.g. Frank & Friedli 1999).

One slug will be introduced to the centre of each dish and will be allowed to feed for 12 h in the dark (17 °C) in a climate chamber. The slugs will be pre-treated as in the seedling bioassay. The bioassays will be conducted in spring and in autumn using juvenile and adult slugs, respectively. At the end of the experiments the amount of leaf damage will be determined using image analysis (cf. Dietz & Steinlein 1996).

Relevance of the research project

The results of our research project will provide the basis for assessing the importance of slug herbivory as a factor affecting the invasiveness of Brassicaceae forbs. As such they will complement parallel studies in progress in our institute on the role of life-history traits and anthropogenic disturbance as factors determining the invasiveness of perennial Brassicaceae and comparable species.

Several features of this study allow a particularly thorough examination of the effects of slug herbivory on invasiveness. First, we test different hypotheses relating variations in palatability, growth characteristics after grazing damage and changes in life-history traits due to reduced grazing pressure to plant species invasiveness. Second, we analyse the effects of slug grazing for different life stages of the plants and compare the results with leaf palatability assays to pinpoint the most sensitive phases in the life cycle of the plants and the discriminating plant traits that explain differences in grazing damage.

A third important feature of this study is the use of a set of taxonomically related species that can be compared in their responses to slug herbivory depending on species identity, the degree of invasiveness and native or introduced status. In this way, more robust results can be expected than in studies involving just a single species. While the species differ considerably in abundance and invasiveness, relatively few traits distinguish the forbs of the homogeneous family Brassicaceae. Thus, key factors influencing invasiveness should be easier to detect.

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