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Ecological Genetics of Plant Invasions: a Case Study on *Alliaria petiolata*

Dissertation

zur

Erlangung der naturwissenschaftlichen Doktorwürde

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Chapter 1

General introduction

General introduction

In the last centuries, there has been a drastic breaching of the biogeographic barriers that previously isolated continental biotas for millions of years. As a result of increasing global trade and transport, the numbers of plant and animal species translocated by humans, either deliberately or by accident, has increased dramatically (Drake et al. 1989, Vitousek et al. 1996, Williamson 1996, Mack et al. 2000). Some of these introduced species have become pests in their new range and caused major environmental and economic problems. Biological invasions are regarded as one of the greatest threats to global biodiversity (Wilcove et al. 1998, Sala et al. 2000). Introduced crop pests, in particular, are causing large economic costs (Perrings et al. 2000), estimated as \$137 billion per year for the US alone (Pimentel et al. 2000). A considerable amount of biological research has therefore already been done on the causes and consequences of biological invasions, and their control. One motivation for this research has been to control and prevent invaders. A second one, however, has been the realization that invasive species provide some of our best opportunities to study contemporary ecological and evolutionary processes (Mack 1985, Vermeij 1991, Lodge 1993, Auge et al. 2001, Mooney & Cleland 2001, Sakai et al. 2001, Lee 2002).

Ecological mechanisms

Out of 1000 introduced plant species, only 10 become established in natural vegetation, and one turns into a pest that spreads and causes serious damage (Williamson & Fitter 1996). Why do these species become invaders and so many others don't? And why are some habitats more susceptible to invasion than others? If biologists could answer these questions, they should be able to predict and hence to prevent future invasions (Mack et al. 2000, Kolar & Lodge 2001).

Previous research in this context has often used a comparative approach to identify the common characteristics of successful invaders and vulnerable habitats (e.g. Gray 1986, Crawley 1987, Roy 1990, Crawley et al. 1996, Rejmanek & Richardson 1996, Daehler 1998, Pysek 1998). Although the success of these studies has been somewhat limited (Gilpin 1990, Lonsdale 1999), a number of generalizations can be made. Many invasive plants possess characters associated with weedy colonizers (Baker 1965, 1974), such as a wide ecological niche, a short life cycle with high growth rates, and a large number of seeds that disperse well. Given such "pre-adaptation" and an overall climate matching, the chances of a species to become invasive are further increased by its number of introductions (Williamson 1996), and the extent to which it benefits from enemy release in the new range (Maron & Vilà 2001, Keane & Crawley 2002, Mitchell & Power 2003).

Although few habitats are resistant to invasion (Usher 1988, Lodge 1993), those with high resource availability and a disturbance regime that has been altered by humans appear to be parti-

cularly vulnerable (Sher & Hyatt 1999, Alpert et al. 2000, Davis et al. 2000). In addition, habitats might be vulnerable if niches have remained vacant during evolutionary history (Elton 1958, Mack 2003) or newly created by humans (Levine & D'Antonio 1999, Davis et al. 2000). The evidence for a general relationship between diversity and invasibility, however, remains ambiguous (e.g. Tilman 1997, Lavorel et al. 1999, Levine & D'Antonio 1999, Dukes 2001, Wardle 2001).

Impacts of invaders

The primary concern about plant invaders has of course been their economic impact in terms of crop and forage losses. For instance, the introduced weeds *Cirsium arvense* and *Barbarea vulgaris* greatly reduce crop yields in North America (Pimentel et al. 2000), and toxic weeds like *Euphorbia esula* and *Senecio jacobaea* cause serious trouble in Australian pastures (Lonsdale et al. 1994). However, invasive plants also threaten the structure and functioning of natural ecosystems (Mack et al. 2000, Pimentel et al. 2000, Levine et al. 2003).

At the most basic level, invaders compete with native species and may therefore cause their extinction. Islands (e.g. Fritts & Roda 1998) and other isolated biota such as the Cape Flora (Richardson et al. 1996) appear to be particularly vulnerable in this respect. Invasive plants also change the structure and composition of natural communities (e.g. Holmes & Cowling 1997) and disrupt trophic interactions (e.g. Richardson et al. 2000). Several studies, for instance, found that invasive plants altered plant-pollinator interactions in their new range (e.g. Chittka & Schurkens 2001, Brown & Mitchell 2001). Extreme, and therefore well-known, cases of community change after invasion are the almost complete take-over of the Florida everglades by the Australian *Melaleuca quinquenervia* (Gordon 1998), of Californian grasslands by introduced *Centaurea* species (Lejeune & Seastedt 2001), and of many US wetlands by purple loosestrife (*Lythrum salicaria*) (Blossey et al. 2001). Finally, invaders can affect important ecosystem processes (Vitousek et al. 1996, Mack & D'Antonio 1998, Ehrenfeld 2003). In many places of the world, introduced grasses have altered fire regimes (D'Antonio & Vitousek 1992). On Hawaii, the frequency of fires has been greatly increased by introduced fountain grass (*Pennisetum setaceum*) (Hughes et al. 1991), while another invader, the nitrogen-fixing shrub *Myrica faya*, changes nutrient cycles and therefore the development of entire ecosystems (Vitousek et al. 1987, Vitousek & Walker 1989).

Evolutionary processes

In addition to the ecological causes and consequences described above, there might also be evolutionary processes that play a role in the success of invaders and their impact on native ecosystems. In fact, biologists are just beginning to realize that invasive species provide some of

the best model systems to study rapid evolution in action (Thompson 1998, Mooney & Cleland 2001, Reznick & Ghalambor 2001, Sakai et al. 2001, Hänfling & Kollmann 2002, Lee 2002).

The invader itself might evolve for several reasons: First, there might be evolution by genetic drift and inbreeding in founder populations (Brown & Marshall 1981, Barrett & Richardson 1986). Second, inter- or intraspecific hybridization may create novel genotypes, in some cases polyploids. There is some evidence that polyploid hybrids become invasive particularly often (Brown & Marshall 1981, Ellstrand & Schierenbeck 2000), e.g. *Spartina anglica* in southern England (Thompson 1991b). Third, invasions into novel environments may often involve drastic changes in selection regimes (Mooney & Cleland 2001) that cause adaptive evolution, either by sorting out of the most suitable genotypes or by rapid local adaptation, in the invaders (e.g. Baker 1974, Rice & Mack 1991b, Weber & Schmid 1998, Neuffer & Hurka 1999). Many of the species that become invasive do so only after a lag time (Williamson 1996, Mack et al. 2000), probably after such evolutionary adjustments have taken place (Mooney & Cleland 2001). One hypothesis that has been particularly influential in this context is the Evolution of Increased Competitive Ability (EICA) hypothesis by Blossey & Nötzold (1995). It proposes that after enemy release in the novel range, selection has favoured less defended but more vigorous invader genotypes. Although the experimental evidence for EICA remains ambiguous (see Chapter 2 of this thesis), the EICA hypothesis has stimulated much of the recent research on evolution in plant invaders.

Just as invaders rapidly evolve in response to novel environments, so may the invaded in response to the invaders. Invasive species, particularly if they become dominant, will impose novel, direct or indirect, selection pressures and therefore cause niche displacement in native species (Vitousek et al. 1996, Mooney & Cleland 2001, Sakai et al. 2001, Lee 2002). In the extreme, hybridization and introgression between native and invasive species may result in extinction of the native species (Rhymer & Simberloff 1996, Huxel 1999). In addition, because invasive plants often have complex effects across trophic levels (e.g. Richardson et al. 2000), they may cause rapid evolution of species interactions (Thompson 1999). However, apart from some well-documented cases of host race formation after plant introductions (Singer et al. 1993, Carroll et al. 1998, Filchak et al. 2000), little is known about the evolutionary consequences of plant invasions for native competitors, mutualists, and antagonists.

Structure of this thesis

This thesis is concerned with rapid evolution in invaders. It consists of a literature review and four experiments that test for genetic differentiation in invasive plant populations. My model species has been *Alliaria petiolata*, a European herb that is one of the most serious invaders of

deciduous forests in the US (Nuzzo 2000; see chapter 3 for a description of the species). Because of its detrimental effects on native ecosystems, the species is target of an ongoing biocontrol program (Hinz & Gerber 1998, 2001, Blossey et al. 2001). A time lag of almost 100 years between introduction and spread of *A. petiolata* suggests that evolutionary changes such as EICA might play a role in the species' invasion success. I have addressed this issue in a series of comparative experiments. In each, plants were raised from seed under identical conditions and then used to test for genetic variation in ecologically relevant traits among and between native and invasive populations.

Chapter 2 is a review of the current empirical evidence for genetic differentiation between native and invasive plant populations. The review is divided into three sections: First, field comparisons of native and invasive populations. Most of these tested for increased vigour in the invasive range, the phenomenon the EICA hypothesis is based upon. Second, studies that compared molecular genetic variation in native versus invasive populations with DNA markers. Third, experiments that compared quantitative traits in a common environment.

Chapters 3 and 4 are a test of the EICA hypothesis with *Alliaria petiolata*. I use palatability tests with a specialist and a generalist herbivore, as well as simulated herbivory (chapter 3) to test the first prediction of the EICA hypothesis, reduced anti-herbivore defence in invasive populations. The second prediction, increased competitive ability in invasive populations, is addressed in a competition diallel experiment (chapter 4) in which offspring from native and invasive populations are grown alone or in all possible pairwise combinations. Because, taken together, these experiments address plant growth, competitive ability, resistance to specialist and generalist herbivores, and plant tolerance, this is to date the most comprehensive test of the EICA hypothesis.

Chapter 5 investigates allelopathy as a potential mechanism of *Alliaria* invasion, as well as the degree to which its effect depends on the continental origin of *Alliaria* and the target species. A novel approach is used to contribute to the controversy about the allelopathic potential of *Alliaria* (McCarthy & Hanson 1998, Vaughn & Berhow 1999). Soil contaminated by *Alliaria* is used for germination experiments with a congeneric pair of neighbour species, and activated carbon is used to eliminate allelopathy and hence to test for its effect.

Chapter 6 explores evolution of phenotypic plasticity in the invasion of *Alliaria petiolata*. I hypothesize that because general-purpose genotypes should have an advantage in a novel environment, there should be evolution of increased plasticity in invasive populations. I use a greenhouse shading experiment to test this prediction and to compare phenotypic plasticity and integration in native versus invasive populations.

Chapter 2

Phenotypic and genetic differentiation in invasive plant populations

(with Daniel Prati, Lucile Lafuma, William E. Rogers, Evan Siemann, Harald Auge)

Abstract. Plant invasions often involve rapid evolutionary change. Founder effects, inbreeding, and rapid adaptation to novel environments cause genetic differentiation between native and invasive populations and may contribute to the success of invaders. An influential idea in this context has been the evolution of increased competitive ability (EICA) hypothesis. It proposes that after enemy release plants rapidly evolve to be less defended but more competitive, thereby increasing plant vigour in the invasive range. To detect evolutionary changes in invaders, comparative studies of native versus invasive populations are needed. Here, we review the current empirical evidence from (1) comparisons of phenotypic variation in natural populations, (2) comparisons of molecular genetic variation with DNA markers, and (3) comparisons of quantitative genetic variation in a common environment. The field data suggest that increased vigour and reduced herbivory is common in invasive plant populations. In molecular studies, the genetic diversity of invasive populations was equally often lower and equal to that of native populations. Multiple introductions of invasive plants appear to be the rule rather than the exception. However, field comparisons and molecular studies are still few. In contrast, there have been many tests of the EICA hypothesis in a common environment. The majority found increased growth or decreased resistance in invasive populations. Thus, there is reasonable support for the EICA hypothesis, and enough empirical evidence to suggest that rapid evolution is important in plant invasions. We discuss conceptual and methodological issues associated with cross-continental comparisons and make recommendations for future research. When testing for EICA, greater emphasis should be put on competitive ability and plant tolerance. Moreover, previous research has been largely restricted to testing for EICA. It is now important to address evolutionary change in other characteristics that could play a role in plant invasions, especially those related to belowground interactions with other species.

Introduction

Some invasive plant species grow more vigorously and produce larger and denser populations in their introduced range than in their native range. Some of these species cause major economic and environmental problems. They outcompete native species, change the structure and functioning of native communities and ecosystems, and cause substantial problems in agriculture and forestry (Drake et al. 1989, Vitousek et al. 1996, Mack et al. 2000). In fact, biological invasions are regarded as one of the greatest threats to global biodiversity (Sala et al. 2000). In addition to these applied concerns, invasive species represent a major challenge for ecological research because they reveal our limited understanding of the population dynamics of plants, ecological interactions between species, and the stability of ecosystems (Lodge 1993, Sakai et al. 2001). Many questions on the success of invasive plants are still open. How often does it actually occur that plants grow larger in their invasive range? And if so, is this a consequence of a benign environment, probably mediated through the release from natural enemies (Keane & Crawley 2002, Mitchell & Power 2003)? Or is it because these plants evolved towards greater invasiveness in the new range (Blossey & Nötzold 1995)? Here, we review the current empirical evidence that is available to answer these questions, and we identify some of the remaining gaps in our knowledge.

Although the greater vigour of invasive plants outside their native range has long been observed (e.g. Pritchard 1960), scientists have only recently begun to systematically compare native and invasive populations. To explain the increased vigour, several hypotheses have been put forward: According to the enemy release hypothesis, many of the natural herbivores and pathogens are absent in the invasive range of plants, and the increased growth is a plastic response to this benign environment (Maron & Vilà 2001, Keane & Crawley 2002, Mitchell & Power 2003). Alternatively, because plant defence against herbivores might be costly, there could have been subsequent evolution of less defended but more competitive plant genotypes in the invasive range (Blossey & Nötzold 1995). According to this “evolution of increased competitive ability” (EICA) hypothesis, increased vigour would result from rapid evolutionary change rather than from a plastic response.

Defence and competitive ability are important characteristics of invasive plants, but they are almost certainly not the only ones. Many other scenarios of evolutionary change in invasive plants are possible (e.g. Baker 1974, Brown & Marshall 1981, Mooney & Cleland 2001, Sakai et al. 2001). Rapid genetic differentiation will occur in any trait that is beneficial under the novel selection regime, given there is genetic variation for it. In the initial phase of colonization, for instance, traits commonly associated with weeds, such as a short life cycle, high growth rates and reproductive effort may be selected (Baker 1965, 1974).

The potential for evolutionary change in the invasive range depends on the amount of genetic variation introduced. If several introductions from different source regions occurred, rapid local adaptation is much more likely than if there was only a single introduction. In the latter case, introduced species are expected to undergo a phase of inbreeding before they are able to spread (Barrett & Richardson 1986). Therefore, a comprehensive analysis of the population biology of invasive plants also requires a knowledge of the amount and distribution of genetic variation in native and invasive populations.

Here, we review of the current empirical evidence for phenotypic and genetic differentiation between native and invasive plant populations. The review is divided into three sections: (1) Field comparisons of plant sizes, populations sizes, or herbivore loads in native versus invasive populations, (2) studies that addressed genetic variation among and between native and invasive populations with DNA markers or allozymes, and (3) common garden or greenhouse experiments that compare quantitative traits in offspring from native and invasive populations.

Material and Methods

In order to review all currently available data about comparisons of native versus introduced plant populations, we carried out a literature search, using databases and the references in published papers. In addition, we included a number of unpublished studies by colleagues and by ourselves. A study was included if comparisons were made between continents or disjunct areas within continents, and if the data from native and invasive populations were collected by the same author(s) according to the same protocol. Cases of range expansion were not considered. We compiled three data sets: (1) comparisons of phenotypic variation in field populations, (2) comparisons of neutral genetic variation with either DNA markers or allozymes, and (3) comparisons of quantitative genetic variation in common garden or greenhouse experiments.

For each study, we recorded the numbers of populations compared, whether a difference had been found between native and invasive populations, and the direction of that difference. Field studies were included if they compared the plant sizes or fecundities, herbivores loads, or population sizes in the native and invasive range. The molecular studies included all cross-continental comparisons with either DNA markers or allozymes that gave estimates of genetic variation within and among populations in the native and invasive range, and in some cases the number of introductions to the new range.

The third data set contained all studies that used offspring from native and invasive populations to compare quantitative traits in a common environment. For each species and independent experiment, we created one entry in the data table that was classified into the broad categories

plant growth (G), competitive ability (C), and resistance (R) and tolerance (T) to herbivory. We also recorded the method used and the most important variables tested. In addition, several experiments compared phenotypic plasticity of native and invasive populations. These studies differed as they compared the response to environmental change of native and invasive populations, rather than their behaviour in a single common environment. We created a separate data table for plasticity studies which also contained information about the environmental factors manipulated.

Results

The few available field data suggest that plant performance is indeed better in the invasive range than in the native range (Table 1). Three out of four studies of population sizes found larger average sizes in the invasive range. In addition, two studies found greater individual plant sizes, and four studies found greater individual plant fecundity in the invasive range. The opposite, lower plant fitness or smaller population sizes was never reported. To date, three published studies have estimated herbivory in native versus invasive plant populations. All of them found lower herbivore loads in the invasive range. One study (Memmott et al. 2000) distinguished between specialist and generalist herbivores and found that only the specialists were fewer in the invasive range.

The data from molecular studies must be treated with caution because there were great differences in how genetic diversity within populations and genetic differentiation between populations were calculated. Therefore, to interpret our data, several measures, such as F -statistics, AMOVA (analysis of molecular variance), and simple descriptive statistics, were considered together. We found a total of ten species in twelve analyses for which molecular variation was studied in the native and invasive range (Table 2). In four cases, within-population genetic variation was reduced in invasive populations, whereas in one case (Squirrell et al. 2001) it was higher. Genetic differentiation among populations was mostly smaller in the invasive range (six out of eight studies). Nonetheless, most studies suggest that multiple introductions have occurred. In *Rubus alceifolius*, single introductions occurred to several Indian Ocean islands, on which the species spread by apomixis (Amsellem et al. 2001). For *Senecio inaequidens*, the data suggest that it was introduced to Europe twice (Lafuma et al. 2004).

Table 1. Field studies that compared population sizes, size or fecundity of individual plants, or herbivore loads in native versus invasive populations. “+” indicate an increase in the invasive range, “-“ a decrease in the invasive range, and “0” that there was no difference between native and invasive populations. *n* denotes the numbers of native / invasive populations used in a study.

Species	<i>n</i>	Pop. Size	Plant Size	Plant fecundity	Herbivory	Reference
<i>Carduus nutans</i>	n.a.			+		Woodburn & Sheppard 1996
<i>Cytisus scoparius</i>	10 / 10				-	Memmott et al. 2000
<i>Lythrum salicaria</i>	5 / 6			+		Edwards et al. 1998
<i>Lythrum salicaria</i>	102 / 102	+				Eckert et al. 1996
<i>Senecio inaequidens</i>	18 / 5-10	+	+	+	-	Prati & Bossdorf 2004a
<i>Silene latifolia</i>	50 / 36	0			-	Wolfe 2002
<i>Solidago gigantea</i>	46 / 45	+	+	+		Jakobs et al. 2004

n.a.: not available

Table 2. Comparisons of molecular variation in native versus invasive plant populations, using DNA markers or allozymes. *n* denotes the numbers of native / invasive populations used. "Div" refers to genetic diversity within populations, "Diff" to genetic differentiation among populations, and "Intro" to the number of introductions suggested by the data. "+" indicates an increase in the invasive range, "-" a decrease in the invasive range, and "0" that there was no difference between native and invasive populations.

Species	Life history	Marker	<i>n</i>	Div ¹	Diff ²	Intro	Reference
<i>Alliaria petiolata</i>	Biennial, selfing	ISSR	3 / 8	0			Meekins et al. 2001
<i>Alliaria petiolata</i>	Biennial, selfing	Microsatellites	27 / 25	-	0	multiple	W. Durka, unpubl.
<i>Apera spica-venti</i>	Annual, outcrossing	Isozymes	6 / 9	0	-	multiple	Warwick et al. 1987
<i>Bromus mollis</i>	Annual, selfing	Isozymes	10 / 10	0			Brown & Marshall 1981
<i>Bromus tectorum</i>	Annual, selfing	Isozymes	51 / 60	-	-	multiple	Novak et al. 1991, Novak and Mack 1993
<i>Capsella bursa-pastoris</i>	Biennial, selfing	Isozymes	593 / 88	0		multiple	Neuffer & Hurka 1999
<i>Epipactis helleborine</i>	Perennial, mixed	Isozymes	35 / 12	+	-		Squirrell et al. 2001
		cpDNA	17 / 12	+	-		
<i>Hypericum perforatum</i>	Perennial, outcrossing	AFLP	18 / 32	0		multiple	Maron et al. 2004
<i>Rhododendron ponticum</i>	Perennial, outcrossing	AFLP	30 / 21	0			Roß 2003
<i>Rubus alceifolius</i>	Perennial, apomict	AFLP	16 / 16	-	-	single	Amsellem et al. 2000
<i>Senecio inaequidens</i> (Netherlands introduction)	Perennial, outcrossing	Isozymes	2 / 2	0	0	single	L. Lafuma, unpubl.
		cpDNA					
<i>Senecio inaequidens</i> (Southern France introduction)	Perennial, outcrossing	Isozymes	2 / 2	-	-	single	L. Lafuma, unpubl.
		cpDNA					

¹Depending on the study, number and percentage of polymorphic loci, genetic diversity from AMOVA, or Shannon diversity indices

²F_{st} and G_{st} values

Table 3. Experiments that compared growth (G), competitive ability (C), resistance (R), or tolerance (T) in native versus invasive plant populations. Each line represents an independent experiment. “+” indicate an increase in the invasive range, “-“ a decrease in the invasive range, and “0” that there was no difference between native and invasive populations. *n* denotes the numbers of native / invasive populations used.

Species	G	C	R	T	<i>n</i>	Methods ¹	Variables ²	Reference
<i>Alliaria petiolata</i>	-	-			8 / 8	GR, intraspecific diallel	PF	Bossdorf et al. 2004a
			0/-		8 / 6	HB (generalist/specialist)	consumption	Bossdorf et al. 2004b
				0	7 / 5	GR, SH	PF	Bossdorf et al. 2004b
<i>Barbarea vulgaris</i>	+		0		3 / 3	CG, HB (generalist)	PF, consumption	H. Buschmann, unpubl.
<i>Bunias vulgaris</i>	0		0		3 / 3	CG, HB (generalist)	PF, consumption	H. Buschmann, unpubl.
<i>Cardaria draba</i>	-		0		3 / 3	CG, HB (generalist)	PF, consumption	H. Buschmann, unpubl.
<i>Carduus nutans</i>	0				7 / 7	CG	PB	Willis et al. 2000
<i>Carduus pycnocephalus</i>			-		1 / 1	host-specificity of rust fungus	growth reduction	Olivieri 1984
<i>Centaurea solstitialis</i>	0		0		2 / 5	CG	natural herbivory	Clement 1994
<i>Clidemia birta</i>	0				4 / 4	GR	growth rates	DeWalt et al. 2004
<i>Digitalis purpurea</i>	0				6 / 4	CG	PB	Willis et al. 2000
<i>Echium vulgare</i>	0				6 / 6	CG	PB	Willis et al. 2000
<i>Eschscholzia californica</i>	+	0			10 / 10	CG, interspecific comp.	PF	Leger & Rice 2003
<i>Euphorbia esula</i>			0		1 / 6	HB (specialist)	consumption, HD	Lym & Carlson 2002
<i>Hypericum perforatum</i>	0	0			10 / 20	GR, interspecific comp.	PB	Vilà et al. 2003
	0				18 / 32	CG (transplant)	PF	Maron et al. 2004
<i>Lythrum salicaria</i>	+		0/0		6 / 6	HB (generalist/specialist)	PB, HD, phenolics	Willis et al. 1999
	+		-		1 / 1	CG, HB (specialist)	PB, HD	Blossey & Nötzold 1995
	+		-		13 / 23	CG	PB, natural herbivory	Blossey & Kamil 1996
	+				6 / 4	CG (transplant)	PB, growth rates	Willis & Blossey 1999

	+			3 / 3	GR	PF, growth rates	Bastlova & Kvet 2002
<i>Mabonia aequifolium</i>	+			8 / 5	GR	PB	H. Auge, unpubl.
<i>Rorippa austriaca</i>	-	0		3 / 3	CG, HB (generalist)	PF, consumption	H. Buschmann, unpubl.
<i>Sapium sebiferum</i>	+	-		1 / 3	CG	PB, tannins	Siemann & Rogers 2001, 2003a
	+	-		2 / 1	CG, HB (generalist)	PB, consumption	Siemann and Rogers 2003b
		0		1 / 1	HB (generalist)	PB, consumption	Lankau et al. 2004
	-	-	+	1 / 1	CG, SH, interspecific comp.	PB, growth rates	Rogers & Siemann 2004
<i>Senecio inaequidens</i>	+/-		+	12 / 11	GR, aphid infestations	PF	A. Winkler, unpubl.
<i>Senecio jacobaea</i>	0			6 / 6	CG	PB	Willis et al. 2000
		+/-		13 / 16	HB (generalist/specialist)	HP, HD, alkaloids	J. Joshi, unpubl.
	+		-	13 / 16	SH	PB	J. Joshi, unpubl.
<i>Solidago canadensis</i>		-	0	3 / 9	CG, SH	PF	van Kleunen & Schmid 2003
	0	0		3 / 9	HB (generalist)	PF, consumption	Rahm 2003
<i>Solidago gigantea</i>	+			26 / 12	CG	PB	G. Jakobs, unpubl.
	+	+		5 / 5	CG, interspecific comp.	PF	G. Jakobs, unpubl.
<i>Spartina alterniflora</i>			-	1 / 2	GR, HB (generalist)	PB, HP, plant mortality	Daehler & Strong 1997

¹CG = common garden, GR = greenhouse, HB = herbivore bioassay, SH = simulated herbivory

²HD = herbivore development, HP = herbivore preference, PB = plant biomass, PF = plant fecundity

Table 4. Experiments that compared phenotypic plasticity in native versus invasive plant populations. + = greater plasticity in invasive populations; 0 = no difference between native and invasive populations. *n* denotes the numbers of native / invasive populations used.

Species	Result	<i>n</i>	Plasticity to what?	Variables	Reference
<i>Alliaria petiolata</i>	0	8 / 8	shading	biomass, morphology, photosynthesis	O. Bossdorf, unpubl.
<i>Clidemia birta</i>	0	4 / 4	shading	growth rate, morphology, photosynthesis	DeWalt et al. 2004
<i>Hypericum perforatum</i>	0	9 / 10	nutrients/moisture	biomass, growth rate, morphology	S. Elmendorf, unpubl.
<i>Mabonia aequifolium</i>	0/0	8 / 5	shading/pH	biomass	H. Auge, unpubl.
<i>Melaleuca quinquenervia</i>	+ / 0	3 / 4	pH/water stress	biomass, growth rate	Kaufman and Smouse 2001
<i>Sapium sebiferum</i>	-	1 / 1	nutrients	biomass, growth rate	Rogers and Siemann 2004
<i>Senecio inaequidens</i>	+	12 / 11	nutrients	root biomass, growth form, reproduction	A. Winkler, unpubl.
<i>Solidago gigantea</i>	+ / +	26 / 12	shading/nutrients	biomass, height, reproduction	G. Jakobs, unpubl.
	+	5 / 5	nutrients	biomass, reproduction	G. Jakobs, unpubl.

We found a total of 41 comparisons – 31 independent studies using 23 different species – of quantitative traits in native versus invasive populations (Tables 3 and 4). Most of these were common garden experiments (19 comparisons), herbivore bioassays (11 comparisons) and greenhouse experiments (8 comparisons). Overall, the majority of comparisons found significant genetic differences between native and invasive populations. Most previous studies were tests of the EICA hypothesis that compared growth (27 comparisons) or resistance (16 comparisons) of native and invasive populations. In contrast, only five studies addressed competitive ability, and four studies tolerance to herbivory. Taken together, the data suggest reasonable support for the EICA hypothesis with increased growth in 14 out of 27 studies, and decreased resistance in 8 out of 16 studies, whereas contradictory results were rare (Table 3). We found nine comparative studies of phenotypic plasticity in native versus invasive plant populations. Most of these manipulated light or nutrient availability. Increased plasticity in invasive populations was found in four studies, whereas the opposite was found in only one.

Discussion

What is the empirical evidence?

The available field studies suggest that plants and populations are indeed often larger in the invasive range. In addition, there is some evidence for enemy release. This contradicts a recent comparison of plant sizes in American and European common floras (Thébaud & Simberloff 2001) which did not find a general tendency for plants to be taller in their invasive range. A likely reason for this difference is however that our data are not only few, but also based on case studies where people often chose problematic pest species, such as *Lythrum salicaria* in North America or *Solidago gigantea* in Europe. Flora comparisons are based on all species listed, including established ones that are inconspicuous. The basic population for statistical inference differs in the two approaches, hence the opposing results.

The results from molecular studies are ambiguous and do not yet allow a general conclusion. Reduced genetic variation in invasive populations has been found in some species (e.g. Novak & Mack 1993, Amsellem et al. 2000), but this does not appear to be the rule. Particularly in North America, multiple introductions seem to be common. There are many more studies that analysed molecular variation only among invasive populations (e.g. Saltonstall 2003, Walker et al. 2003). Often they found overall genetic variation to be low and explained this by a genetic bottleneck during introduction. However, without comparing invasive to native populations, we will not be able to adequately assess the role of genetic bottlenecks. Clearly, more studies are needed that compare molecular genetic variation among and between native and invasive plant populations.

Overall, there is reasonable support for the evolution of increased competitive ability (EICA) hypothesis in invasive plants (Blossey & Nötzold 1995): increased growth and decreased resistance was found in 52 % and 50 % of the studies, respectively. A major caveat of previous studies, however, is that growth was often measured in isolated plants, i.e. in the absence of competition. Growth is one determinant of plant competitive ability, but at high densities it may not be an adequate measure of it (Grime 1979, Goldberg 1996). Many plants invade natural communities, so growth in isolation might have little relevance for their success. In fact, those studies that compared native and invasive populations under competitive conditions found no difference or even results that contradict the EICA hypothesis (Table 3). Another problem with previous studies is that plant defence was often tested in bioassays with generalist herbivores. However, invasive plants are mostly released from specialist herbivores in their invasive range (Memmott et al. 2000, Keane & Crawley 2002), and that is also what EICA is based upon (Blossey & Nötzold 1995). Because resistance against specialists and generalists are likely based on different mechanisms, studies that address both simultaneously often find different results (e.g. Bossdorf et al. 2004b). Finally, while plant resistance has received much attention previously, another important component of plant defence, plant tolerance, has not (Müller-Schärer & Steinger 2004). We strongly recommend testing for EICA under competitive conditions, and we suggest that in future studies greater emphasis should be put on resistance to specialist herbivores and plant tolerance.

Several of the studies that compared phenotypic plasticity in native versus invasive plant populations found a higher degree of plasticity in invasive populations (Table 4). One explanation for this might be that plasticity allows introduced species to naturalize across a range of environments. This might be particularly beneficial in founder populations with reduced additive genetic variation (Baker 1974, Rice & Mack 1991a, Sexton et al. 2002). As a result, there might be evolution of increased plasticity in invasive plant populations. More research is needed to clarify the role of evolution of plasticity in plant invasions.

What are we comparing?

When comparing plant populations from the native and the introduced range, an important question is whether we are comparing the appropriate taxonomic units. Species often vary in their chromosome numbers and in some cases only one type is invasive. For instance, the South African *Senecio inaequidens* occurs in diploid and tetraploid populations in its native range, but all invasive European populations are tetraploid (Lafuma et al. 2004). To investigate evolutionary change in invasive populations of this species, comparisons should therefore be restricted to tetraploids. However, if both diploids and tetraploids have been introduced initially, but only the

tetraploids became invasive, a comparison between the two types may yield insight into an early sorting-out of plant traits that are associated with diploidy.

A related problem occurs when invaders hybridize, either among formerly distant genotypes, or with different species. Hybridization has been recognized as an important factor influencing genetic variation and adaptation in invasive plants (Brown & Marshall 1981, Ellstrand & Schierenbeck 2000). However, it is unclear to what extent comparisons between native and invasive populations make sense in such a context. In addition, many ornamental species have been deliberately crossed and selected to produce a variety of cultivars, some of which have escaped to become invasive (e.g. *Mahonia aequifolium*). In these cases it is probably more informative to compare the traits of invasive and non-invasive cultivars.

In our review we did not consider cases of range expansion, i.e. cases where species spread into new ranges adjacent to the ones already occupied. Although such species are often listed as invasive in many floras, we excluded them for three reasons: First, it was difficult to find cases that met our methodological criteria. The declaration of invasives is often very arbitrary in these cases and based on political rather than biogeographic boundaries. Second, range expansion is a natural process which every species once underwent. Cross-continental introductions, in contrast, are mostly man-made, and they add the important dimension of tearing down biogeographic barriers (Mooney & Cleland 2001). Third, both the enemy release hypothesis (Maron & Vilà 2001, Keane & Crawley 2002) and the EICA hypothesis (Blossey & Nötzold 1995) do not apply to range expansions, because plants do not have faster migration rates than their enemies. Comparisons of central with marginal populations can certainly provide insights into the nature of plant colonization and adaptation, just as comparisons of mainland and island populations (e.g. Husband & Barrett 1991, Cody & Overton 1996), but they were outside of the scope of this review.

Other methodological issues

When seeds from wild population are used to cultivate and compare plants in a common environment, population differentiation, and thus evolutionary divergence in invasive species, will likely be overestimated due to environmental maternal effects (Roach & Wulff 1987). None of the studies in Table 3 and 4 controlled for such carry-over effects by pre-cultivating plants for one or several generations before the comparisons were made. In addition, if there are systematic environmental differences between the native and the invasive range which can be carried over to the next generation via seeds, this might cause serious misinterpretation of cross-continental studies. It would be certainly rewarding to conduct a study that attempts to estimate this bias.

In general, cross-continental comparisons require a large sample of native and invasive populations. Sample size should be as high as possible, because it increases statistical power for testing continent effects, and it reduces the likelihood of systematic environmental differences. Alternatively, if the invasion history of a species is well known, one might study a chronological sequence of invasive populations (Barrett & Shore 1989, Daehler & Strong 1997) or compare the known founder population to other, younger populations in the invasive range. A good example for the latter approach is the research on *Sapium sebiferum* (Siemann & Rogers 2001, 2003a,b), which is one of the strongest cases in support of the EICA hypothesis. However, in most cases multiple introductions (Table 2) or a lack of historical information will preclude such approaches, so that often a large sample size is the best solution.

Future perspectives

The need for invasive plants to adapt to novel environments is often invoked with little detail on which environmental factors are expected to be novel. Most plants occur in similar climatic and edaphic conditions in their invasive range (Williamson 1996), so selection will more likely be exerted by novel competitors, herbivores or pathogens. The documentation of such changes, however, has been very limited so far (Table 1). For instance, herbivore loads in native and invasive ranges were studied in only three species. More comparative field studies are needed of the diversity and abundance of natural enemies on invasive plants.

A similar lack of data concerns the distribution of neutral genetic variation assessed by molecular markers or allozymes. Because such data can help to distinguish between multiple versus single to few introductions, it is important for the interpretation of genetic divergence between native and invasive populations. If multiple introductions from different source regions occurred, genetic differentiation among invasive populations may result from unequal survival of pre-adapted genotypes (“sorting-out”; Müller-Schärer & Steinger 2004). However, in the case of few introductions, the same result would suggest that differentiation was created *de novo* through recombination, mutation and selection. Thus, it would make a stronger case for rapid evolutionary change in a novel environment.

The evolution of increased competitive ability hypothesis (Blossey & Nötzold 1995) has stimulated much of the recent research on native versus invasive plant populations. However, as already mentioned above, this research has mostly compared growth of isolated plants or resistance to generalist herbivores in laboratory bioassays. Future studies should test for EICA under competitive conditions and address resistance to specialist herbivores and plant tolerance. Admittedly, a problem with competition experiments is the choice of appropriate competitors. Plants

encounter different sets of competitors in their native and invasive range, and they may be adapted to some extent to their native ones (Callaway & Aschehoug 2000). One solution to this might be intraspecific competition experiments (e.g. Bossdorf et al. 2004a). The best, albeit very laborious, solution are reciprocal transplant experiments across continents (e.g. Willis & Blossey 1999, Maron et al. 2004).

Defence and competitive ability are certainly not the only important traits of invasive plants. Rapid evolution might occur in any trait that is beneficial under the novel selection regime, given there is genetic variation for it. To date, only one empirical study did not address EICA or phenotypic plasticity in native versus invasive populations: Buckley et al. (2003) found that the seeds of *Cytisus scoparius* were heavier in its invasive range, whereas no difference was found in *Ulex europaeus*. Although the study did not distinguish between genetic differences and maternal carry-over effects, it has been a valuable step towards a more general approach of testing for evolutionary change in traits commonly associated with weediness (Baker 1965).

Müller-Schärer & Steinger (2004) proposed an evolutionary change of plant life cycles towards polycarpy in the invasive range. If herbivores preferentially attack larger plant individuals and this has a significant effect on plant fitness, then selection should favour early reproduction and monocarpy. The release from these enemies, in turn, may result in a selective advantage of polycarpic genotypes in the invasive range. A trend towards polycarpy has been observed in several invasive plants (e.g. *Cynoglossum officinale*, *Senecio jacobaea*, *Centaurea stoebe*). Future research should examine the genetic basis of this phenomenon.

Finally, there is increasing evidence that belowground interactions play a key role in plant invasions. Invasive plants may dominate invaded communities through allelopathic inhibition of competitors (Callaway & Aschehoug 2000, Bais et al. 2003) or through manipulation of the mycorrhiza community and other micro-organisms in the soil. In fact, invasive species appear to "cultivate" a soil community suitable for their own proliferation (Klironomos 2002). However, so far only one study directly compared native and invasive plant populations in this context. Prati & Bossdorf (2004b) investigated allelopathic inhibition of the germination of co-occurring species through native and invasive populations of *Alliaria petiolata*. They found that the allelopathic effect depended on the origins of both *A. petiolata* and the target. More research on evolutionary divergence in belowground interactions is highly needed.

Chapter 3

Palatability and tolerance to simulated herbivory in native and introduced populations of *Alliaria petiolata* (Brassicaceae)

(with Daniel Prati, Stefan Schröder, Harald Auge)

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Abstract. The European herb garlic mustard (*Alliaria petiolata*) is a serious invader of North American deciduous forests. One explanation for its success could be that in the absence of specialized herbivores, selection has favored less defended but more vigorous genotypes. This idea was addressed by comparing offspring from several native and introduced *Alliaria* populations with respect to their palatability to insect herbivores and their tolerance to simulated herbivory. Feeding rates of a specialist weevil from the native range were significantly greater on US plants, suggesting a loss of resistance in the introduced range. In contrast, there was significant population variation but no continent effect in the feeding rates of a generalist caterpillar. After simulated herbivory, *A. petiolata* showed a substantial regrowth capacity that involved changes in plant growth, architecture, and allocation. Removal of 75% leaf area or of all bolting stems reduced plant fitness to 81% and 58%, respectively, of the fitness of controls. There was no indication of a difference in tolerance between native and introduced *Alliaria* populations, or of a trade-off between tolerance and resistance.

Introduction

One explanation for the success of invasive plants is that they are released from their native specialist herbivores (Maron & Vilà 2001, Keane & Crawley 2002). Resources normally lost to these enemies are allocated to growth and reproduction, thereby increasing plant vigour and abundance in the new range. Invoking optimal defence theory and the possibility of rapid evolutionary change, Blossey & Nötzold (1995) recently expanded this idea to propose the “evolution of increased competitive ability” (EICA) hypothesis: if there is a trade-off between growth and defence, then selection should favour less defended but more competitive genotypes in the new range. Although several tests of the EICA hypothesis have been carried out recently (Daehler & Strong 1997, Willis et al. 1999, 2000, Siemann & Rogers 2001), two points have received little attention: the distinction between specialist and generalist herbivores, and between resistance and tolerance components of plant defence. A reasonable next step would be to include these into the conceptual framework of the EICA hypothesis and to adjust its predictions accordingly.

Plant defence includes a range of strategies that are commonly divided into those associated with resistance, i.e., any trait that reduces the preference or performance of herbivores and those associated with tolerance, the degree to which plant fitness is affected by herbivory relative to fitness in the undamaged state (Strauss & Agrawal 1999). Because specialist insects often adapt to or even utilize plant toxins (Berenbaum & Zangerl 1992a), these are assumed to be primarily a defence against generalists (Van der Meijden 1996), whereas the effect of specialists may be reduced by quantitative deterrents or by tolerance.

Even if invasive plants are released from their specialist enemies, generalists may have similar attack rates in the new range (Jobin et al. 1996, Memmott et al. 2000). Thus, there is little reason to expect an invader to be less defended overall. In contrast, one might expect the following: (1) If the primary defence against specialists is tolerance and tolerance is costly, then there might be selection against it in the new range. Moreover, if there is a trade-off between resistance and tolerance (Van der Meijden et al. 1988), then resources might even be re-allocated to chemical defence, so that one would expect lower tolerance and equal or even higher resistance to generalists in invasive genotypes. (2) If the primary defence against specialists is a class of chemicals other than those acting against generalists, then selection might reduce the former, but, again, resources might be re-allocated to growth or generalist defence. As a result, invasive genotypes should be less resistant against specialists, but equal or more resistant to generalists.

We addressed these ideas in a series of experiments with native and introduced populations of *Alliaria petiolata*, a European crucifer that has become a serious pest in North American deciduous forests. We used palatability tests to estimate plant resistance to a native specialist and to a

common bioassay generalist herbivore. In addition, we carried out clipping experiments in which we estimated plant tolerance to different types of simulated herbivory.

Material & methods

Study species

Garlic mustard [*Alliaria petiolata* (M. Bieb.) Cavara and Grande] is a hexaploid member of the mustard family (Brassicaceae) native to the Eurasian temperate zone. Plants typically germinate in early spring, form a rosette in the first year, overwinter as a rosette, develop flowering stems in the following spring, produce seeds in June/July, and die. Selfing seems to be very frequent (Anderson et al. 1996, Cruden et al. 1996). In Europe, garlic mustard occurs in mesic semi-shade habitats such as forest edges and moist woodlands. Introduced to North America in the 19th century, the species has continuously expanded its range and is now present in 34 US states and four Canadian provinces (V. Nuzzo, Nature Conservancy, unpublished report). Garlic mustard invades the understory of North American deciduous forests where it may displace native plant species (McCarthy 1997), disrupt plant–insect associations (Porter 1994, Huang et al. 1995) and eventually collapse native food webs (B. Blossey, Cornell University, personal communication). As a consequence, garlic mustard has become the target of a recently established biocontrol research program (Blossey et al. 2001).

Previous ecological studies on garlic mustard either described life-history variation in its new range (Anderson et al. 1996, Byers & Quinn 1998, Meekins & McCarthy 2002) or focused on its reproductive biology (Baskin & Baskin 1992, Cruden & McClain 1996, Susko & Lovett-Doust 1999, 2000), its potential for competitive and allelopathic interference (Meekins & McCarthy 1999, Vaughn & Berhow 1999, Roberts & Anderson 2001), or its response to environmental variation (Meekins & McCarthy 2000, 2001). There is a lack of research in two areas: (1) comparisons of native and introduced populations testing for genetic differentiation in invasion-related traits, and (2) the ecology of plant-herbivore interactions and plant defence.

Alliaria contains glucosinolates, particularly sinigrin and its breakdown products (Larsen et al. 1983, Vaughn & Berhow 1999), which are part of its defence chemistry but also act as feeding stimulants for specialist weevils (Nielsen et al. 1989) and *Pieris* larvae (Renwick & Lopez 1999). Other compounds that may play a defensive role include flavonoids that appear to be feeding deterrents for *Pieris* larvae (Haribal & Renwick 1998, 2001, Renwick et al. 2001). Little is known about the herbivore communities on natural *Alliaria* populations. A recent literature survey found 69 insect species associated with *Alliaria* in Europe (Hinz & Gerber 1998). No surveys have been made yet in invasive US populations.

Table 1. Native (Europe) and introduced (US) populations of *Alliaria petiolata* that were used in this study. MON, HF, and HW were used only in the palatability tests. OHA was used only in the stem removal experiment.

ID	Location	Latitude	Longitude
<i>Europe</i>			
BRU	Bruck, Austria	47°18' N	12°49' E
BUD	Budweis, Czech Republic	48°58' N	14°29' E
HAL	Halle, Germany	51°28' N	11°58' E
IAS	Iasi, Romania	47°09' N	27°38' E
KOP	Copenhagen, Denmark	55°43' N	12°34' E
MON	Montpellier, France	43°36' N	03°53' E
PAR	Ascot, UK	51°25' N	00°41' W
SOY	Soyhières, Switzerland	47°24' N	07°22' E
<i>USA</i>			
CAS	Ipswich, MA	42°41' N	70°51' W
FF	McLean, IL	40°29' N	89°00' W
HF	Petersham, MA	42°54' N	72°17' W
HW	Mahomet, IL	40°23' N	88°09' W
OHA	Athens, OH	39°20' N	82°83' W
OHB	Athens, OH	39°19' N	82°07' W
VRO	Danville, IL	40°09' N	87°37' W

In this study we used seeds from eight European and seven US populations (Table 1). As in other highly selfing species, most of the genetic variation in *Alliaria* appears to be between rather than within populations (Meekins et al. 2001). The populations were not selected for specific habitat criteria but chosen among those available to cover a reasonable geographic range. We regard them to be random samples within continents. In fall 2000, mature siliques were collected from several mother plants in each population. The seeds were cleaned and stored under cold, dry conditions.

Palatability tests

In January 2002, seeds from several maternal families in each of eight European and six US populations (Table 1) were placed in petri dishes filled with a sterilized 1:1 mixture of sand and seeding compost (COMPOSANA[®] Anzuchterde; COMPO GmbH, Münster, Germany) and dark stratified at 4°C for 100 days. The petri dishes were then placed in a climate chamber with a

12/12 h light/dark cycle at 8/12°C, where germinated seedlings were transferred to planting trays filled with a 1:1 mixture of sand and potting soil (LAT Terra[®] Typ P, HAWITA-Gruppe GmbH, Vechta, Germany). They were kept in the chamber for several weeks, until no further germination was observed. At the end of May, six replicates from four families per population, altogether 336 plants, were planted into 0.5 L pots filled with the same substrate described, plus 1 g slow-release fertilizer (Osmocote[®] Exact 8-9 M Standard, Scotts International BV, Geldermalsen, The Netherlands). The pots were placed in an unheated greenhouse and watered as needed. To prevent the spread of an aphid infestation in July, all plants were treated three times with an organic insecticide (Neudosan, W. Neudorff GmbH KG, Emmerthal, Germany), a potassium soap solution that suffocates the aphids but does not leave any residues in the plant. Very few plants had been colonized by aphids. None were observed afterwards. Two no-choice palatability tests were done 2–3 months later with new leaves that developed after the insecticide treatment. In each test we used three replicates from each *Alliaria* family, so that each plant and insect was used once.

Half of the replicates from each *Alliaria* family were used in a test with *Ceutorhynchus scrobicollis* (Coleoptera: Curculionidae), a monophagous weevil that is currently tested as a biocontrol agent for garlic mustard (Blossey et al. 2001). The weevil has been found in several native Central European *Alliaria* populations, with great abundance in some of them (Hinz & Gerber 2000). The larvae of *C. scrobicollis* mine the root crowns of garlic mustard, while adult beetles feed on the leaves in the fall. In October 2002, adult weevils were collected in natural populations in northeastern Germany, brought to a climate chamber where they were kept at 15°C and a 12/12 h light dark cycle and fed with *Alliaria* leaves from a nearby population not included in this study. The palatability tests were done in this chamber, using male beetles only. Prior to the experiment, each beetle was placed in a petri dish with moist filter paper and starved for 24 h. Two identical 4-mm discs were taken from the youngest fully expanded rosette leaf of each plant. In pilot feeding trials with a range of disc sizes, 4 mm was optimal for maximizing the effect size relative to measurement error, given the small size of the weevils. In each case, we determined the fresh weights of the two leaf discs and immediately dried the control disc to a constant weight at 80°C. The test disc was randomly assigned to one of the petri dishes where a weevil fed on it for 24 h. After that, the remainder of the test disc was also dried. We calculated the dry weight by fresh weight ratio of the control disc and used this ratio to estimate dry weight of the test disc before feeding. This value minus dry weight after feeding estimated the leaf mass consumed by each beetle. We used this estimate as a direct measure of plant palatability.

The second test was done with third-instar larvae of *Spodoptera littoralis* (Lepidoptera: Noctuidae), a widely employed generalist herbivore known to feed on plants in over 40 families world-

wide. Laboratory strains of *S. littoralis* had been provided by Gero Eck (University of Düsseldorf, Düsseldorf, Germany) and bred at our institute since May 2002. The larvae were raised on artificial diet at 26°C and a 12/12 h light/dark cycle. The experiment was identical to the one with *C. scrobicollis*, except that, because the caterpillars are larger, 13-mm leaf discs were used. Also, there was no initial starvation period, because, unlike in weevils, starvation is not needed to stimulate feeding of caterpillars, but may even kill them.

Clipping experiments

To estimate plant tolerance, herbivory was simulated by manual clipping in two experiments. The first experiment was a defoliation study that imposed damage typical of generalist herbivores such as snails in natural *Alliaria* populations. Seeds were germinated in 2001 and plants cultivated in a climate chamber as described above. In June 2001, we planted four seedlings from each of eight European and eight US populations in 1.5-L containers filled with a 1:1 mixture of sand and potting soil. The plants were placed in an unheated greenhouse and watered as needed. In the fall, all plants received 2 g slow-release fertilizer (Osmocote[®] Plus 3-4M, Scotts International BV, Geldermalsen, Netherlands) and were treated against aphids with a systemic insecticide (Bi-58, BASF AG, Ludwigshafen, Germany). To ensure plant vernalization under realistic conditions, the first-year rosettes were brought to an experimental garden in November, where they were packed into bark mulch and overwintered. A harsh frost period killed some rosettes, so that in March 2002, when the plants were returned to the greenhouse, 52 of 64 had survived. These consisted of 25 European and 28 US plants. On 10 April, we recorded the diameter of each rosette. We randomly selected half of the European and the US plants and removed 75% of the area of each leaf with scissors. The others were left as controls. On 24 April, we clipped on newly produced leaves. The plants were randomized on a greenhouse bench, watered as needed, and harvested at fruit maturity. On each plant, we counted the numbers of stems and siliques. Siliques and remaining vegetative aboveground parts were separately dried to a constant weight at 80°C and weighed. Total aboveground biomass was calculated as the sum of the two fractions, and reproductive allocation was the ratio between reproductive and vegetative biomass. We used the number of siliques and their biomass as estimates of plant fitness.

In the second experiment, we simulated herbivory by removing all apical meristems, which has a fundamentally different effect than leaf removal (Tiffin & Rausher 1999). In *Alliaria*, similar damage is caused by the root crown-mining larvae of *C. scrobicollis*, which often kill entire developing stems (Blossey et al. 2001). The plants were raised and overwintered as described, with 20 seedlings from each of eight European and eight US populations grown in 1-L pots.

Unfortunately, winter mortality was much higher in these plants, with only 146 survivors of 320. Some additional plants died before the start of the experiment. We used only populations that could still be replicated in each treatment, so that eventually our experiment consisted of 113 plants from seven European and five US populations (Table 1), with 4-19 replicates per population. From each population, half of the plants were randomly chosen to be clipped; the others were used as controls. There was great phenological variation among populations, so we clipped at a common phenological stage rather than at the same time. Plants were clipped when they had developed five immature fruits at least 1 cm long. The first flowers and fruits of *Alliaria* appear when bolting starts, so the clipping took place at an early stage of flowering. We recorded the initial diameters of each plant and cut off all flowering stems above their second cauline leaf. The first plants were clipped on 12 April, the last on 21 May. Control plants were measured at the same stage. The plants were harvested at fruit maturity. For each, we recorded the numbers of stems and siliques, dried the biomass fractions to a constant weight at 80°C, and calculated total aboveground biomass and reproductive allocation as described.

Statistical analyses

The palatability data were standardized to zero mean and unity variance and analyzed as nested ANOVA models using the GLM procedure in SAS (SAS Institute 2001). Each model included continent, population nested within continent, family nested within population, and herbivore weight as a covariate. We used a sequential (type I sum of squares) model in which the covariate was fitted first. As a surrogate for the genetic correlation between resistance to specialist and generalist herbivores, we calculated Pearson's product-moment correlations between the feeding rates of the two herbivores. These correlations were done across continents, both at the level of family and population means.

The leaf removal data were analyzed as a two-factorial ANOVA with clipping, continent and their interaction as fixed factors. Due to the low sample size, we did not include a population level in this analysis. Prior to the analyses, stem numbers, silique numbers, and silique biomass were square root transformed. The stem removal data were analyzed as a nested ANOVA with clipping, continent, and their interaction as fixed factors. Populations and their interaction with clipping were random factors nested within continent and continent \times clipping, respectively. Silique numbers were square root transformed prior to analyses. In both analyses, we used type III sum of squares to account for the unbalanced design, and we included plant diameter as a covariate to control for the effect of plant size at the beginning of the experiment. Differences

among continents or populations in their tolerance to herbivory are indicated by significant continent \times clipping and population \times clipping interactions, respectively (Stowe et al. 2000).

In addition, the stem removal data were used to examine costs of tolerance and the relationship between resistance and tolerance. Costs of tolerance were analyzed as a regression of fitness in the damaged vs. undamaged state (Strauss & Agrawal 1999). We used a major axis (model II) regression (Legendre 2001) on log-transformed population means, so that costs of tolerance were indicated by a deviation of the slope from unity. The 11 populations that had been used both in the palatability tests and the stem removal experiment (Table 1) were used to test for a relationship between resistance and tolerance. We calculated population-level tolerance as the ratio between damaged and undamaged trait means. A ratio of unity indicates perfect compensation, whereas < 1 indicates under- and > 1 overcompensation. Using these indices, we calculated the correlations between standardized specialist and generalist feeding rates and tolerance in terms of silique numbers, silique biomass, and total biomass.

Results

The feeding rates of *C. scrobicollis* were more variable than those of *S. littoralis* (Fig. 1). As a result, the full ANOVA model explained 67% of the variance in *S. littoralis* feeding, but only 30% in the weevil data (Table 2). Native and introduced *Alliaria* populations differed in their palatability to *C. scrobicollis*, which had higher feeding rates on leaf discs from US populations (Fig. 1A). There was a significant population effect in the feeding of *S. littoralis*. This effect was not only caused by the Romanian outlier population (IAS, Fig. 1B); it remained significant when IAS was excluded. There was no correlation across continents between the mean feeding rates of specialists and generalists at population ($r_s = -0.099$, $P = 0.736$) or family ($r_s = -0.080$, $P = 0.561$) levels.

Simulated herbivory reduced plant fitness in both experiments, although *Alliaria* had a great capability to compensate for damage. After 75% leaf area removal, damaged plants ended up with 81% of the silique biomass of controls (Table 3). Removal of bolting stems had a greater impact and reduced silique biomass to 58% (Table 4). Stem removal significantly increased stem numbers from 2.9 in undamaged to 5.7 in damaged plants, but there was no such effect after leaf removal (Table 3). Stem removal decreased reproductive allocation from 0.99 to 0.80 (Table 4), whereas after leaf removal there was an increase from 0.80 to 0.95 in damaged plants (Table 3). In the stem removal experiment, plants from European populations had a significantly higher fitness in terms of silique biomass than plants from US populations, and there were significant population effects for total biomass and reproductive allocation (Table 4). However, we found

no differences among plants in their tolerance to herbivory, as indicated by continent \times clipping or population \times clipping interactions (Tables 3 and 4).

Table 2. Summary of analyses of variance for two no-choice palatability tests with a specialist weevil, *Ceutorhynchus scrobicollis*, and a generalist caterpillar, *Spodoptera littoralis*, on *Alliaria petiolata* plants from several native European and invasive US populations. Plants were raised from seed in a common environment, and palatability tests were done with fresh leaves in a climate chamber. Effects with $P < 0.05$ are in boldface type.

Source	d.f.	<i>C. scrobicollis</i>		<i>S. littoralis</i>	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Herbivore weight	1	5.28	0.023	21.48	< 0.001
Continent	1	5.82	0.033	0.61	0.450
Population [C]	12	0.60	0.833	10.92	< 0.001
Family [P, C]	42	0.80	0.787	1.14	0.293
Error	111				

The slope of the major axis regression across continents of damaged vs. undamaged population means did not differ from unity for any measure of fitness. For silique biomass, the slope was 1.19 (95% confidence interval: 0.69-2.17), indicating a positive linear relationship between fitness in the two treatments. Feeding rates of *C. scrobicollis* and *S. littoralis* did not correlate with tolerance in terms of silique numbers, silique biomass, or total biomass ($n = 11$, $P > 0.50$ for all correlations). Thus, there was no evidence for a trade-off between resistance and tolerance to stem removal. If the outlier population IAS was excluded, there was even a marginally significant positive correlation between resistance (1 – palatability) to *S. littoralis* and tolerance in terms of silique numbers ($n = 11$, $r_s = 0.549$, $P = 0.099$).

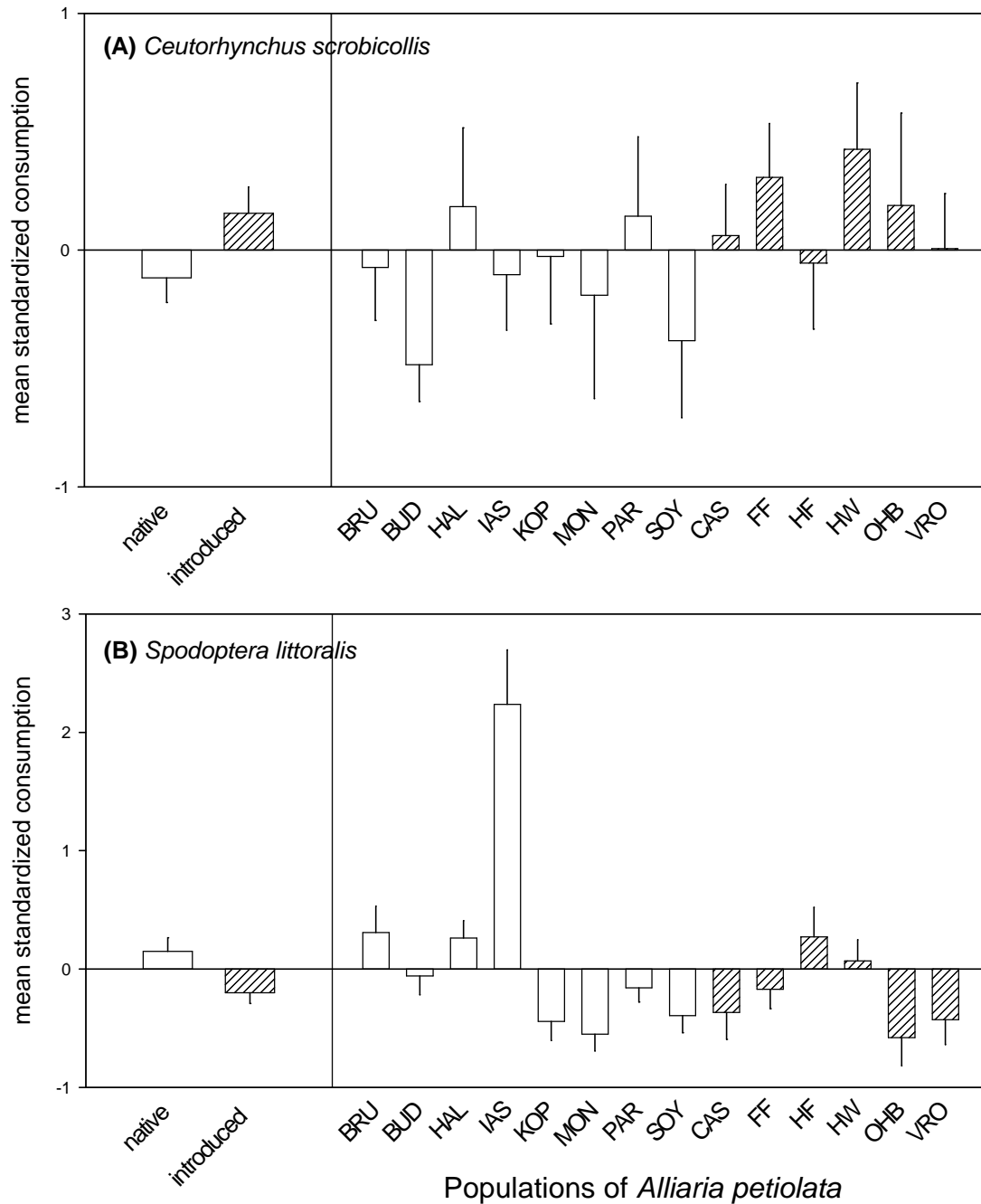


Fig. 1. Palatability of native European (white bars) and invasive US (hatched bars) populations of *Alliaria petiolata* to a specialist weevil, *Ceutorhynchus scrobicollis* (A), and a generalist caterpillar, *Spodoptera littoralis* (B). Plants were raised from seed in a common environment, and their leaves were used for no-choice palatability tests in a climate chamber. The values are continental (left) and population (right) means (\pm SE) of standardized consumption estimates. See Table 1 for population details, and Table 2 for the associated analyses of variance.

Table 3. Tolerance to 75% leaf area removal in native European and invasive US genotypes of *Alliaria petiolata*. Plants of different origin were raised from seed in a common environment and subjected to simulated herbivory at the beginning of the second growing season. For each trait, the treatment by continent means (\pm SD) are given, followed by its analysis of variance. Effects with $P < 0.05$ are in boldface type.

	# Stems		# Siliques		Silique biomass [g]		Total biomass [g]		Reprod. allocation	
EU Control (n = 12)	9.17 \pm 1.90		336.8 \pm 45.9		20.05 \pm 3.00		48.89 \pm 8.00		0.74 \pm 0.20	
US Control (n = 13)	9.23 \pm 2.09		329.9 \pm 79.5		20.11 \pm 3.30		44.32 \pm 7.71		0.84 \pm 0.11	
EU Clipped (n = 13)	9.54 \pm 1.76		266.5 \pm 54.6		17.21 \pm 4.11		35.11 \pm 5.21		0.98 \pm 0.27	
US Clipped (n = 14)	9.21 \pm 1.53		263.9 \pm 56.3		15.33 \pm 4.50		32.03 \pm 8.19		0.92 \pm 0.19	
Analyses of variance										
Source (d.f.)	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Plant diameter (1)	4.53	0.039	0.03	0.856	4.52	0.039	3.32	0.075	0.00	0.946
Clipping (1)	0.20	0.655	16.62	< 0.001	12.33	0.001	39.81	< 0.001	7.95	0.007
Continent (1)	0.16	0.687	0.13	0.725	0.03	0.861	1.53	0.223	0.14	0.709
Clip \times Cont (1)	0.36	0.553	0.06	0.814	1.10	0.300	0.08	0.776	1.95	0.170
Error (47)										

Table 4. Tolerance to removal of all apical meristems in native European and invasive US populations of *Alliaria petiolata*. Plants of different origin were raised from seed in a common environment and subjected to simulated herbivory at the beginning of the flowering period. For each trait, the treatment by continent means (\pm SD) are given, followed by its analysis of variance. Effects with $P < 0.05$ are in boldface type.

	# Stems		# Siliques		Silique biomass [g]		Total biomass [g]		Reprod. allocation	
EU Control (n = 31)	3.26 \pm 1.37		196.1 \pm 40.8		13.48 \pm 2.77		26.67 \pm 6.10		1.07 \pm 0.22	
US Control (n = 28)	2.57 \pm 1.69		188.5 \pm 98.1		10.71 \pm 4.85		22.74 \pm 9.90		0.89 \pm 0.28	
EU Clipped (n = 32)	6.00 \pm 2.33		130.9 \pm 40.9		7.75 \pm 2.60		17.13 \pm 5.22		0.84 \pm 0.20	
US Clipped (n = 22)	5.27 \pm 2.64		126.3 \pm 43.3		6.12 \pm 3.18		13.96 \pm 6.20		0.75 \pm 0.24	
Analyses of variance										
Source (d.f.)	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Plant diameter (1)	90.91	< 0.001	16.37	< 0.001	30.08	< 0.001	58.61	< 0.001	0.46	0.500
Clipping (1)	63.39	< 0.001	30.42	< 0.001	73.73	< 0.001	74.71	< 0.001	15.11	< 0.001
Continent (1)	1.44	0.258	0.03	0.863	6.28	0.031	2.33	0.158	2.88	0.120
Population [C] (10)	1.66	0.104	1.38	0.204	1.40	0.196	2.59	0.009	2.04	0.039
Clip \times Continent (1)	0.20	0.663	1.12	0.314	1.41	0.262	0.54	0.479	0.05	0.823
Clip \times Population [C] (10)	0.64	0.773	0.54	0.855	0.74	0.688	0.83	0.597	0.71	0.715
Error (87)										

Discussion

This is the first study that compared both resistance and tolerance in native and introduced populations of an invasive plant. We hypothesized that invasive populations of *Alliaria petiolata* would be equally resistant to generalist herbivores but either less resistant to specialists or less tolerant to damage. Results from palatability tests were in accordance with these predictions: while the specialist weevil *Ceutorhynchus scrobicollis* had significantly higher feeding rates on introduced populations, there was no difference in the feeding rates of the generalist herbivore *Spodoptera littoralis* (Fig. 1, Table 2), presumably because generalists are abundant in the new range, too. After simulated herbivory, *A. petiolata* showed a tremendous regrowth capacity (Tables 3 and 4), but in contrast to our predictions, tolerance was not lower in plants from the new range. Next, we discuss possible mechanisms behind these findings and their implications for biocontrol and garlic mustard research.

Palatability tests

The population effect in *Spodoptera* feeding rates indicates genetic variation for resistance, probably because of variation in glucosinolate levels. Glucosinolates are regarded as a first line of defence against generalist herbivores on Brassicaceae (Renwick 2002). Many previous studies found natural variation in glucosinolate levels (e.g. Stowe 1998a, Haribal & Renwick 2001, Kliebenstein et al. 2002) and demonstrated its ecological relevance (e.g. Mauricio et al. 1997, Siemsen & Mitchell-Olds 1998, Agrawal et al. 2002). Also, glucosinolates act as feeding deterrents and toxins against *Spodoptera* (Li et al. 2000, Wallace & Eigenbrode 2002). Other compounds that could play a role in the resistance against *Spodoptera* are proteinase inhibitors. Trypsin inhibitor, in particular, is a toxin and feeding deterrent to *S. littoralis* (De Leo & Gallerani 2002). Cipollini (2002) found significant environmental variation for trypsin inhibitor levels in a natural *Alliaria* population.

Little is known about the chemical defence of *Alliaria* against specialist herbivores, so we can only speculate about the increased feeding rates of *C. scrobicollis* on US populations. Glucosinolates, again, could be involved if *C. scrobicollis* is affected by types other than *S. littoralis*. In most Brassicaceae, there is a complex system of glucosinolates (Fahey et al. 2001). At least some also have negative effects on specialists (Siemsen & Mitchell-Olds 1996, Stowe 1998a, Li et al. 2000). Kliebenstein et al. (2001) examined 34 glucosinolates in 39 *Arabidopsis* ecotypes and found a limited set of characteristic glucosinolate profiles. Such a modular system may allow differential responses to various herbivores. Alternatively, another class of chemicals might be involved. Flavonoids, for instance, inhibit feeding by larvae of the oligophagous *Pieris napi oleracea* on

Alliaria (Renwick et al. 2001). They could play a role in the resistance against other specialist herbivores, too.

Plant tolerance

Alliaria petiolata had a great capability to tolerate damage. After a 75% loss of leaf area or removal of all bolting stems, damaged plants regained 81% and 58%, respectively, of the fitness of controls (Tables 3 and 4). Regrowth of *Alliaria* involved increased growth, activation of dormant meristems, as well as changes in plant architecture and allocation pattern. After stem removal, damaged plants quickly produced new stems from lateral buds, which caused a more branchy growth form than in undamaged plants (Table 4). Changes in allocation pattern depended on the type of damage: leaf removal increased but stem removal decreased reproductive allocation (Tables 3 and 4). This diversity of mechanisms possibly indicates past selection by herbivores unaffected by resistance (Stowe et al. 2000). Specialist herbivores may have been important in the evolution of *A. petiolata*.

Apart from two comparisons of a native and an invasive species (Schierenbeck et al. 1994; Rogers & Siemann 2002), plant tolerance has received little attention in the context of plant invasions. To our knowledge, no one has ever tested the possibility that tolerance may have evolved during an invasion. Here we have made a first attempt to address this question. However, we found no differences between native and introduced populations (Tables 3 and 4). One reason for this could be that the reduced number of samples caused by winter mortality made the detection of presumably small continent effects difficult. Alternatively, tolerance might not have evolved in the new range because it has other functions than defence against specialists (Strauss & Agrawal 1999), or it may not have evolved yet, given a timescale of 150 years (~ 75 generations).

A plant that has maximal resistance will not be damaged. A highly tolerant one will not need to be resistant. If resistance and tolerance serve the same function and both have a cost, then we should expect a trade-off between the two (van der Meijden et al. 1988, Herms & Mattson 1992). The empirical evidence for this trade-off, however, is ambiguous (e.g. Simms & Triplett 1994, Fineblum & Rausher 1995, Mauricio et al. 1997, Stowe 1998b, Strauss & Agrawal 1999, Tiffin & Rausher 1999). There was no indication of a trade-off in our data, and it is unlikely that this was due to low statistical power, because there was even a marginally significant positive correlation between tolerance and resistance to *S. littoralis*. Resistance and tolerance might not be mutually exclusive, but to some extent, be complementary (Mauricio et al. 1997, “less-than-additive”) mechanisms of the defence of *Alliaria*. Also, we found a positive relationship between fitness in

the damaged vs. undamaged state in the stem removal experiment, so the assumption of costs of tolerance might not be true.

Implications for biocontrol

One of the basic assumptions of biocontrol theory is that invasive plants have been released from their specialist enemies (van Driesche & Bellows 1996). If defence against specialists has become redundant, selection might act against costly defence mechanisms (Blossey & Nötzold 1995). This would make invasive genotypes even more vulnerable to biocontrol. Our data on *A. petiolata* support this hypothesis: leaves from invasive populations were more palatable to the specialist weevil and potential biocontrol agent *C. scrobicollis*. Still, the plant populations varied greatly in their resistance to both herbivores (Fig. 1). Many biocontrol studies are done on a single target population, although genetic variation for defence traits is common in natural plant populations (e.g. Fritz & Price 1988, Berenbaum & Zangerl 1992b). Biocontrol programs should profit from taking this genetic variation of their targets into account.

Garlic mustard, plant defence, and the EICA hypothesis

The EICA hypothesis makes two major predictions. First, plants from the invasive range should be defended less. Second, they should have a higher fitness in the absence of herbivores. Here, we have found experimental support for the first prediction, but we do not know yet whether this translates into greater fitness of invasive *Alliaria* genotypes. The significant continent effect in the stem removal experiment (Table 4) suggests the opposite, but clearly further work that explores this EICA prediction is needed. Also, we have no quantitative data yet on the actual extent of an enemy release in US populations of *Alliaria*. Wolfe (2002) recently showed that both specialists and generalists were reduced in the invasive range of *Silene latifolia*. Hence, the assumption that only specialists are absent may not always be true. Finally, we do not know enough about the defence chemistry of *Alliaria*, in particular about its defence against specialists such as *C. scrobicollis*. Closing these gaps in our knowledge would enable us to test more precise hypotheses about the evolution of defence in garlic mustard invasions.

Chapter 4

Reduced competitive ability in an invasive plant

(with Daniel Prati, Harald Auge, Bernhard Schmid)

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Abstract. One explanation for successful plant invaders is that they evolved to be more competitive. An intuitive prediction of this Evolution of Increased Competitive Ability (EICA) hypothesis never previously tested is that invasive populations should outcompete their native “ancestors” in a common environment. We tested this idea in a diallel competition experiment with *Alliaria petiolata* where offspring from native and invasive populations were grown alone or in all pairwise combinations. While without competition there were no differences between native and invasive populations, native populations outperformed invasive ones when competing against each other. Our results contradict the EICA hypothesis and we conclude that it does not hold for *Alliaria petiolata*. Instead, we formulate a new ERCA (Evolutionary Reduced Competitive Ability) hypothesis: if there is less competition in the invasive range and competitive ability involves traits that have a fitness cost, then selection might act against it, thereby reducing intraspecific interactions, too.

Introduction

Evolutionary change can be rapid and therefore relevant to ecological studies (Thompson 1998). In this context, invasive, nonindigenous species offer excellent model systems (Thompson 1998, Mooney & Cleland 2001, Sakai et al. 2001, Lee 2002). In fact, there are several reasons why evolutionary processes might be expected to play a role in invasions: First, invasive species are brought into environments that are characterized by novel selection pressures (Mooney & Cleland 2001). Second, only few of those species introduced actually become invasive (Williamson 1996), suggesting selection upon key characters. Third, many of the species that become invaders do so after a lag time (Mack et al. 2000, Sakai et al. 2001), possibly after evolutionary adjustments to the novel environments (Weber & Schmid 1993, Mooney & Cleland 2001). Understanding such evolutionary mechanisms might be crucial for the successful management of biological invasions.

One evolutionary hypothesis to explain plant invasions is based on the observation that introduced species are often released from many of their specialized herbivores and pathogens (Maron & Vilà 2001, Keane & Crawley 2002, Wolfe 2002, Mitchell & Power 2003). At the same time, some invasive plants appear to perform better in their introduced than in their native range (e.g. Crawley 1987). Invoking a trade-off between plant growth and defence (Herms & Mattson 1992), Blossey & Nötzold (1995) proposed that this might be due to rapid evolution. In the absence of specialized enemies selection might favour less defended but more competitive invader genotypes. This Evolution of Increased Competitive Ability (EICA) hypothesis makes two major predictions: when compared to native populations in a common environment, plants from the introduced range should be (1) less resistant to (specialized) enemies but (2) more competitive where enemies are excluded.

Recent tests of the EICA hypothesis were often restricted to one of the predictions and compared fitness (usually biomass) or resistance of offspring from native and invasive populations in a common environment (Blossey & Nötzold 1995, Daehler & Strong 1997, Willis & Blossey 1999, Willis et al. 1999, 2000, Siemann & Rogers 2001, Leger & Rice 2003, van Kleunen & Schmid 2003, Vilà et al. 2003). Another simple, albeit intuitive prediction has never been tested: if invasive genotypes have evolved to be more competitive, they should be able to outcompete their “ancestors” from the native range. We tested this idea in a greenhouse study with garlic mustard (*Alliaria petiolata*), a European herb that is a serious invader in North American deciduous forests. We used a diallel design in which offspring from several native and invasive populations were either grown alone or in all pairwise combinations in a herbivore-free environment.

Our approach differed in two ways from previous EICA studies: First, it allowed separating fitness in the absence of competition from different aspects of competitive ability. Second, our focus on intra- rather than interspecific competition avoided the problem of competitor choice. If local adaptation, species-specific interactions and possibly coevolution play a role in plant invasions (Callaway & Aschehoug 2001, Klironomos 2002, Prati & Bossdorf 2004b), then using one or few interspecific competitors from either of the two ranges will give a biased picture.

We asked the following questions: (1) when grown alone, do plants from invasive *Alliaria* populations have a higher fitness than plants from native populations? (2) do plants from invasive *Alliaria* populations outperform plants from native populations in competition? (3) is there a correlation between the mean performance of *Alliaria* populations in the absence of competition and their performance in competition?

Material & methods

Study species

Garlic mustard (*Alliaria petiolata* [M. Bieb.] Cavara and Grande) is a member of the mustard family (Brassicaceae) native to the Eurasian temperate zone where it grows in mesic semi-shade habitats such as forest edges and moist woodlands. Plants typically germinate in early spring, form a rosette in the first year, overwinter as rosette, develop flowering stems in the following spring, produce seeds in June/July, and die. The species was first introduced to North America in the middle of the 19th century. Microsatellite data suggest that several independent introductions have occurred since then (O. Bossdorf, unpublished microsatellite data). Over the last few decades, the species rapidly expanded its range and is now present in at least 34 US states and four Canadian provinces (Nuzzo 2000). Garlic mustard invades the understory of North American deciduous forests where it may displace native plant species (McCarthy 1997) and disrupt plant-insect associations (Porter 1994, Huang et al. 1995). In a recent study, we found that invasive US populations of garlic mustard are less resistant to a specialist herbivore than native European populations (Bossdorf et al. 2004b).

In this study we used seeds from eight European and eight US populations (Table 1). The species is self-compatible and primarily autogamous (Anderson et al. 1996), so that most genetic variation is found between rather than within populations (Meekins et al. 2001, O. Bossdorf, unpublished data). In both continents, the populations came from a mixture of forest, forest edge and roadside habitats. We regard them to be random samples within continents. Based on a long-term data set of climatic records (New et al. 2000), European and US populations did not differ in mean elevation, annual temperature, or precipitation (two-sample *t*-tests, $n = 14$, all $P > 0.1$).

In autumn 2000, mature siliques were collected from several mother plants in each population. The seeds were cleaned and stored under cold, dry conditions.

Table 1. Native and invasive populations of *Alliaria petiolata* that were used in this study. For each, the numbers of surviving plants used in analyses of “singles” (one plant per pot) or “pairs” (two plants per pot) are given.

ID	Location	Longitude	Latitude	Singles	Pairs
<i>Native</i>					
BRU	Bruck, Austria	12°49' E	47°18' N	13	15
BUD	Budweis, Czech Republic	14°29' E	48°58' N	11	19
HAL	Halle, Germany	11°58' E	51°28' N	15	18
IAS	Iasi, Romania	27°38' E	47°09' N	12	20
KOP	Copenhagen, Denmark	12°34' E	55°43' N	7	19
MON	Montpellier, France	03°53' E	43°36' N	4	11
PAR	Ascot, UK	00°41' W	51°25' N	15	22
SOY	Soyhières, Switzerland	07°22' E	47°24' N	1	7
<i>Invasive</i>					
CAS	Ipswich, MA	70°51' W	42°41' N	8	25
FF	McLean, IL	89°00' W	40°29' N	12	18
HF	Petersham, MA	72°17' W	42°54' N	4	2
HW	Mahomet, IL	88°09' W	40°23' N	5	16
OHA	Athens, OH	82°83' W	39°20' N	14	16
OHB	Athens, OH	82°07' W	39°19' N	15	20
VRO	Danville, IL	87°37' W	40°09' N	9	12
WI	Milwaukee, WI	87°53' W	43°05' N	14	14

Experimental design

In January 2001, seeds from 20 maternal families per populations were placed in petri dishes filled with a sterilized 1:1 mixture of sand and seeding compost (Composana[®] Anzuchterde, Compo GmbH, Münster, Germany) and dark stratified at 4°C for 100 days. Hereafter the petri dishes were placed in a climate chamber with a 12/12 h light/dark cycle at 15/10°C, where germinated seedlings were transferred to planting trays filled with a 1:1 mixture of sand and potting soil (Latterra[®] Typ P, Hawita-Gruppe GmbH, Vechta, Germany; a peat-based substrate with approx. 150 mg N, 150 mg P₂O₅ and 250 mg K₂O per litre). At the end of May, the seedlings were taken to an unheated greenhouse and planted into 0.5 litre pots filled with the same substrate as above. In addition, each pot received 5 g of slow-release fertilizer (Osmocote[®] Plus 3-4M

with 15% N, 11% P₂O₅, 13% K₂O, 2% MgO + trace elements, Scotts International BV, Geldermalsen, The Netherlands). The final size and seed output of plants in our experiment was similar to that of plants in a typical natural population, so we assumed our common environment to be a reasonable match of the nutrient-rich natural habitats (Nuzzo 2000) of garlic mustard.

Each population was grown in monoculture at two densities (one plant per pot and two plants per pot), and in pairwise mixture with each of the other populations (two plants per pot). There were three replicates for each treatment yielding a total of 456 pots and 864 plants. Within each population, plants were chosen at random from the available seed families. Due to unequal germination success and chance we eventually used 9-16 families per population. We measured the lengths of all leaves on each plant and calculated a sum of squared leaf lengths which was used as an estimate of initial plant size. A pilot study showed that this was a reasonable predictor for seedling biomass ($r^2 = 0.884$, $n = 100$).

The pots were randomly arranged on two benches in an unheated greenhouse, watered as needed, and re-randomised twice in the course of the experiment. In November 2001, all pots were taken to an experimental garden where they were packed into bark mulch and overwintered. By the end of March 2003, when the plants were returned to the greenhouse, 413 of all plants had survived (see Table 1). Similar rates of rosette mortality are possible in natural *Alliaria* populations (Nuzzo 1993). Winter mortality, analysed by logistic regression (McCullagh & Nelder 1989), was random across competition treatments and continents (all $P > 0.2$) but did range from 11% to 69% between populations within continents ($P < 0.001$). In April, all pots were treated with a systemic insecticide (Bi-58; BASF AG, Ludwigshafen, Germany). The plants were harvested at fruit maturity. For each one we measured plant height and counted the numbers of siliques. Siliques and the remaining aboveground parts were dried separately at 80°C and weighed. Total aboveground biomass was calculated as the sum of the two fractions.

To estimate the precision of different fitness estimates we randomly chose ten siliques on each plant, weighed them and removed the seeds which were counted and weighed. There were close correlations between silique biomass and seed number ($r^2 = 0.729$, $P < 0.001$) as well as silique biomass and seed biomass ($r^2 = 0.864$, $P < 0.001$), suggesting that silique biomass is a reasonable predictor for fitness in terms of seed output in *Alliaria*.

Statistical analyses

The winter mortality among plants caused our final data set to be unbalanced with missing values, including the loss of some population monocultures. This ruled out a calculation of traditional competition indices (Weigelt & Jolliffe 2003) as well as a full diallel analysis (McGilchrist

1965). Instead, we tested the effects of the target and neighbour plant origins by analysis of variance (Schmid & Bazzaz 1987). The target effect is the mean fitness of a population i , averaged over all neighbour populations. Likewise, the neighbour effect is the mean fitness of all plants that have population i as neighbour. Although target and neighbour effect are conceptually similar to competitive response and effect (Goldberg 1990), they differ in that they are not independent from each other. Each plant in a pair is used to estimate both target and neighbour effect.

Plant fitness (height, aboveground biomass, silique number and silique biomass) was analysed with a nested ANOVA. We carried out one analysis of the full data set that included all harvested plants, then we split up the data into single plants and plant pairs and analysed each set separately. With the full data set, the ANOVA model included initial plant size as a covariate, and plant density, target continent and neighbour continent nested within density as fixed effects. Target and neighbour population were random effects nested within continent. We used after-winter density (1 or 2 plants per pot) rather than initial density, since the latter had no significant effect on any of the dependent variables (all $P > 0.2$), i.e. plants that had been growing alone since the start of the experiment did not differ from those that ended up alone due to winter mortality. With single plants, the model included initial plant size, continent and population of origin. With plant pairs it included initial plant size and the nested target and neighbour effects. In all three analyses we used type-III sum of squares since the data were unbalanced (SAS Institute 2001).

Although the variables analysed were not independent, we did not carry out a multivariate analysis of variance (MANOVA), since this would have been difficult with unbalanced, nested data, and because MANOVA is sensitive to departures from multivariate normal distribution of data (Kendall 1980, Cole et al. 1994). To account for multiple statistical tests of the same hypothesis, we calculated the expected probabilities of finding significant results and compared these to observed frequencies instead of using overly conservative Bonferroni procedures (Moran 2003). To examine the relationship between plant fitness in the absence and presence of competition, we extracted the population least square means from the analysis of singles, as well as the population least square means of target and neighbour effects from the analysis of plant pairs. Similar to regression analyses for maternal and paternal arrays in genetic diallels (Mather & Jinks 1982), we calculated Pearson's product-moment correlations between the fitness of singles, target effects and neighbour effects with regard to plant height, aboveground biomass, silique number and silique biomass. In this analysis a perfect negative correlation is expected between population target and neighbour effects if competitive interactions were fully reciprocal whereas a weaker, absent, or even positive correlation indicates departure from full reciprocity (Assémat & Oka 1980). One

population (HF) was excluded because it was an extreme outlier based on only two surviving plants in pairs.

Results

Single plants produced 67% more aboveground biomass, 66% more silique biomass, and 99% more siliques than plants in pairs, suggesting that there was strong competition for soil resources in our experiment (Table 2, Fig. 1). Plant fitness also strongly depended on the population origin (Tables 2 and 3) and its interaction with density (Table 2). Thus, fitness had a genetic component.

In the analyses of the full data set, native plants were significantly taller than plants from the invasive range (Table 2, term “Continent”). The differences between continents were revealed more clearly in the analysis restricted to plant pairs. Plants of native origin growing in pairs were significantly taller (+22%) and produced significantly more siliques (+48%) (Table 3, term “Continent”). In addition, the neighbour effects of native plants were stronger than those of American plants, i.e. the former reduced the fitness of target plants with respect to silique number and silique biomass more than did the latter (Table 3, term “Neighbour Continent”). When single plants were analysed separately, there was hardly any genetic variation detectable. Apart from a population effect on silique number ($F_{14,142} = 3.45$, $P < 0.001$), all continent and population effects were non-significant. Overall, single plants were remarkably similar in terms of their size and fecundity.

As expected, there was a strong negative correlation between target and neighbour effect for total aboveground biomass and silique biomass (Table 4). However, there was no correlation between the mean fitness of populations as singles and their mean target and neighbour effects in plant pairs for any of the traits investigated (Table 4, Fig. 2).

In a table with four statistical tests of the same hypothesis, the probability of finding a particular effect to be significant by chance is $1 - 0.954 = 0.185$ (Moran 2003), i.e. less than one out of four tests. Since in our analysis of plant pairs (Table 3) both continent and neighbour continent effect were significant twice, we are confident that the observed differences between native and invasive populations are not a product of chance.

Table 2. Summary of analyses of variance of the full data set with all harvested plants. Square brackets indicate nesting of terms; degrees of freedom in parentheses are for silique biomass. Levels of significance: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Source	d.f.	Height		Total biomass		Silique number		Silique biomass	
		<i>MS</i>	<i>F</i>	<i>MS</i>	<i>F</i>	<i>MS</i>	<i>F</i>	<i>MS</i>	<i>F</i>
Initial plant size	1	19.1	0.04	1.69	0.11	0.74	0.16	1.41	0.50
Density	1	3043.2	6.95**	1784.27	111.04***	470.80	103.06***	277.72	98.56***
Continent	1	7792.6	4.66*	79.11	1.99	53.92	3.55	5.60	0.82
Population[C]	14	1670.9	3.82***	39.82	2.48**	15.19	3.32***	6.81	2.42**
D × C	1	1012.9	1.85	39.98	1.94	14.13	1.64	15.46	3.09
D × P[C]	14	548.0	1.25	20.59	1.28	8.63	1.89*	5.01	1.78*
Neighbour Continent[D]	1	86.4	0.14	79.33	3.10	12.52	3.20	16.98	4.19
Neighbour Population[NC, D]	14	606.6	1.39	25.57	1.59	3.91	0.86	4.05	1.44
C × NC[D]	1	787.6	1.51	3.23	0.25	4.99	1.02	0.00	0.00
P[C] × NP[NC, D]	120 (118)	521.4	1.19	12.67	0.79	4.90	1.07	2.15	0.76
Residual	244 (240)	437.8		16.07		4.57		2.82	

Table 3. Summary of the analyses of variance of plant pairs. Square brackets indicate nesting of terms; degrees of freedom in parentheses are for silique biomass. Levels of significance: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Source	d.f.	Height		Total biomass		Silique number		Silique biomass	
		<i>MS</i>	<i>F</i>	<i>MS</i>	<i>F</i>	<i>MS</i>	<i>F</i>	<i>MS</i>	<i>F</i>
Initial plant size	1	225.0	0.40	27.56	1.50	0.69	0.16	1.671	0.59
Continent	1	8224.2	5.11*	153.54	3.99	68.85	5.36*	24.977	3.13
Population[C]	14	1608.3	2.84**	38.47	2.09*	12.84	2.89**	7.974	2.80**
Neighbour Continent	1	127.1	0.21	91.47	3.55	20.30	5.94*	19.064	4.67*
Neighbour Population[NC]	14	616.9	1.09	25.76	1.40	3.42	0.77	4.082	1.43
C × NC	1	688.0	1.35	1.42	0.12	1.17	0.29	0.104	0.05
P[C] × NP[NC]	120 (118)	508.8	0.90	11.67	0.64	4.05	0.91	2.015	0.71
Residual	101 (97)	567.2		18.38		4.45		2.846	

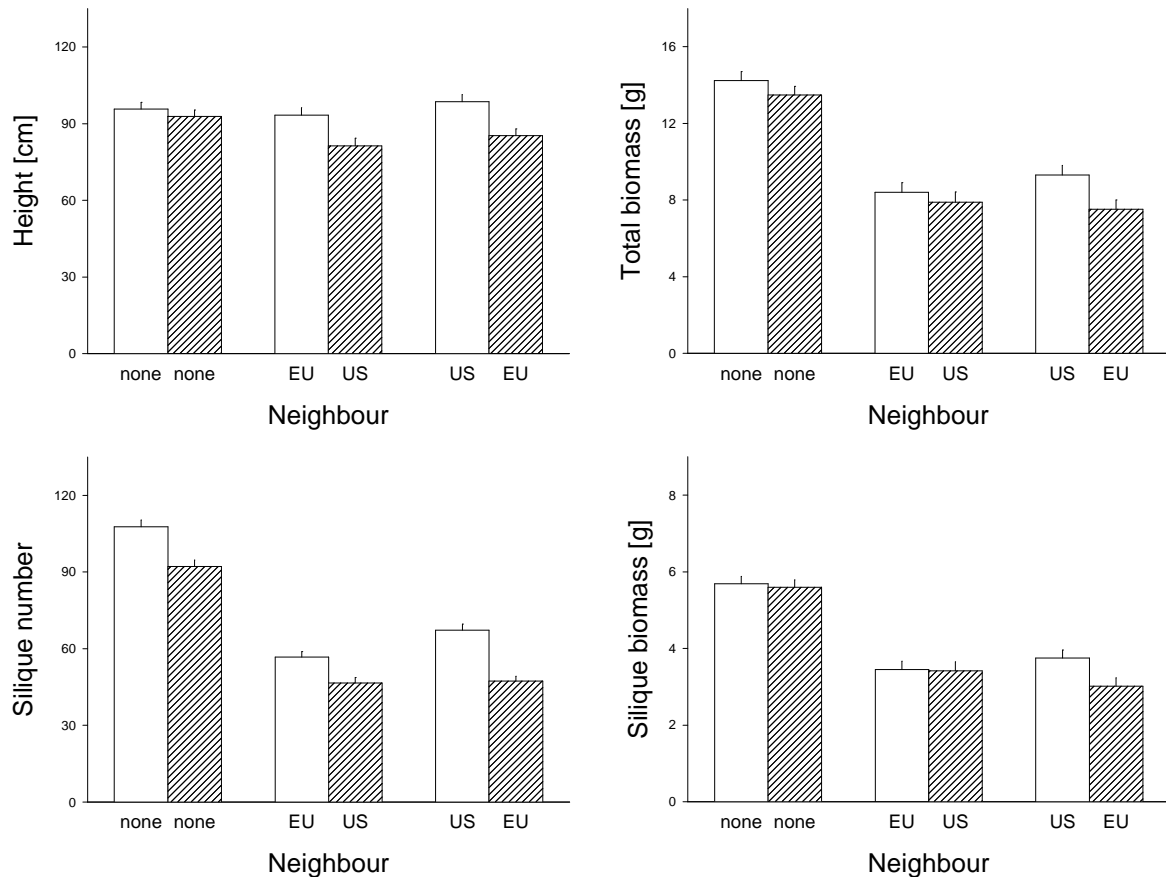


Fig. 1. Mean size and fitness (+ s.e.) of native European (open bars) and invasive North American (hatched bars) plants of *Alliaria petiolata* in an intraspecific competition experiment. Plants were either grown without neighbours (none) or in pairs with neighbours from the same or the other continent (EU, US).

Table 4. Correlations among 15 populations of *Alliaria petiolata* between the mean fitness when growing alone and the mean target and neighbour effects when growing in pairs. The values are correlation coefficients; *P*-values in parentheses.

	Height	Total biomass	Silique biomass	Silique number
Fitness alone	0.189	0.372	0.182	0.405
– target effect	(0.499)	(0.172)	(0.516)	(0.134)
Fitness alone	0.148	0.026	0.131	0.303
– neighbour effect	(0.598)	(0.927)	(0.642)	(0.272)
Target effect	–0.149	–0.798	–0.786	–0.251
– neighbour effect	(0.595)	(0.000)	(0.001)	(0.366)

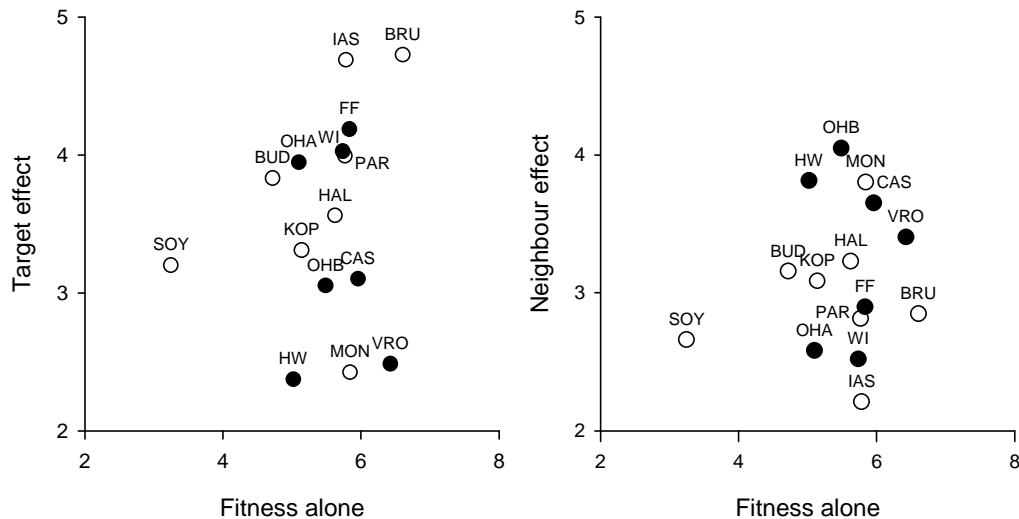


Fig. 2. The relationship between mean fitness of European (white circles) and North American (black circles) populations of *Alliaria petiolata* when growing alone and their mean target and neighbour effects when growing in pairs. All values are ANOVA least-square means of silique biomass [g]. See Table 1 for population details.

Discussion

A major prediction of the EICA hypothesis is that because of resource re-allocation from defence to growth, plants from the invasive range will be more competitive than those from the native range. In this study we found that under optimal, competition-free conditions there were no differences between native and invasive populations of *Alliaria petiolata*. When plants were competing against conspecifics, however, native populations outperformed those from the invasive range. This completely contradicts the EICA hypothesis and we therefore conclude that it does not hold for *Alliaria petiolata*.

A potential caveat of this study could be that we assume no adaptive evolution to environmental conditions, except for the absence of herbivores, in the introduced range. Although we have shown that the source environments of native and invasive populations were comparable with regard to several important climatic variables, we cannot exclude the possibility that local adaptation to other environmental factors is responsible for the observed differences. Another limitation of our study is that winter mortality substantially reduced the sample size, so the results should be viewed with some caution.

Many recent tests of the EICA hypothesis compared native and invasive populations in competition-free environments. Results were ambiguous: invasive populations had a greater fitness in *Lythrum salicaria* (Willis & Blossey 1999) and *Sapium sebiferum* (Siemann & Rogers 2001), but there were no differences in four invasive biennials (Willis et al. 2000). Still, fitness in the absence of

competition might not necessarily translate into competitive ability, for instance if the ability of a plant to rapidly exploit resources has a different mechanistic basis than its ability to tolerate low resource levels (e.g. Grime 1979; Goldberg 1996). There was no relationship between the average fitness of *Alliaria* populations when growing alone and their competitive ability in pairs (Fig. 2). Had our experiment been restricted to plant singles, we would have concluded that there are no differences among native and invasive *Alliaria* populations.

To date, few studies used a competitive environment when testing for EICA. Leger & Rice (2003) found that invasive populations of *Eschscholzia californica* were superior only when grown without competition by horticultural poppies. Vilà et al. (2003) used a native grass as competitor and found no differences between native and invasive populations of *Hypericum perforatum*. Here, we have argued that interspecific competitors might give a biased picture, and that one way to tackle this problem is to focus on intraspecific competition instead. Interestingly, those two studies that did so found counterevidence for EICA. Invasive populations of *Solidago canadensis* had a lower fitness than native ones when growing in dense monospecific stands (van Kleunen & Schmid 2003). In our study, native populations of *Alliaria petiolata* outperformed invasive populations in a competition diallel.

Reduced competitive ability could be the consequence of a genetic bottleneck with subsequent inbreeding depression or random changes through genetic drift (Barrett & Husband 1990). Both processes could have caused changes in traits that confer competitive ability. However, we think that this explanation is rather unlikely since *Alliaria* has a high selfing rate (Anderson et al. 1996) with low within-population genetic variation in both its introduced and native range (Meekins et al. 2001, O. Bossdorf, unpublished data). Also, significant differentiation among invasive populations suggests sufficient genetic variation for evolutionary responses.

Another explanation for reduced competitive ability in invasive populations would be directional selection. If there are fewer or weaker competitors in the North American habitats invaded by *Alliaria petiolata*, and at the same time resource competition involves traits that have a fitness cost – such as a particular growth form, allocation scheme, or physiological apparatus – then there might be selection against it in the invasive range. Furthermore, if plants in invasive populations have usually more intra- than interspecific neighbours, an Evolutionary Reduced Competitive Ability (ERCA) may increase stand-level fitness (King 1990) by reducing intraspecific interactions, too. It is conceivable that ERCA allows invasive populations of *Alliaria* to use the savings not spent for resource competition in other processes that may contribute to their invasion success, such as plasticity, tolerance to herbivory (Bossdorf et al. 2004b), or allelopathy (Prati & Bossdorf 2004b). Clearly further research is needed to test this new ERCA hypothesis.

Chapter 5

Allelopathic inhibition of germination by *Alliaria petiolata* (Brassicaceae)

(with Daniel Prati)

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Abstract. Garlic mustard (*Alliaria petiolata*, Brassicaceae) is an invasive, nonindigenous species currently invading the understory of North American woodlands where it is a serious threat to the native flora. Part of this success might be due to allelopathic interference by garlic mustard. Two congeneric species, the European *Geum urbanum* and the North American *Geum laciniatum*, were tested for allelopathic inhibition of germination by garlic mustard. Seeds were germinated either on substrate contaminated by garlic mustard or on substrate with contamination neutralized by activated carbon. Allelopathic effects of native European and invasive North American garlic mustard populations were also compared. Activated carbon increased germination by 14%, indicating that garlic mustard contaminated the substrate through root exudates. Activated carbon in turn counteracted this effect. The two test species differed in their sensitivity to allelopathic interference. North American *G. laciniatum* had a much stronger increase in germination when activated carbon was added to the substrate, independent of the origin of garlic mustard. In contrast, the European *G. urbanum* germinated better in substrate precultivated with North American garlic mustard, whereas activated carbon increased its germination only in substrate precultivated with European garlic mustard.

Introduction

Allelopathic interference between plant species has often been invoked to explain why some invasive, nonindigenous plants have become extremely dominant, out-compete native species or even produce monospecific stands (Wardle et al. 1993, Dolling et al. 1994, Ridenour & Callaway 2001). However, empirical evidence that allelopathic interference plays an important role in plant invasions is still ambiguous. Controlled bioassays to test putative allelochemicals often failed to show allelopathic effects (Choesin & Boerner 1991, Dietz et al. 1996, Keay et al. 2000, Conway et al. 2002) and are generally criticized for their artificial nature (Harper 1977, Williamson 1990). On the other hand, a number of experiments revealed large differences in the outcome of competition when allelopathic interference was reduced by adding activated carbon to the substrate (Nilsson 1994, Ridenour & Callaway 2001, Callaway & Aschehoug 2000, Siemens et al. 2002). Wardle et al. (1998) have argued that allelochemicals may alter plant competition also indirectly through changes in ecosystem properties. For instance, the presence of decomposing leaves of invasive plant *Carduus nutans* decreased nitrogen fixation in legume species through a reduction in nodulation.

Allelopathic interference must be species-specific to explain why nonindigenous species dominate an invaded community while they normally do not reach high dominance in their native community. It is possible that co-occurring species adapt to allelochemicals released by competitors; hence, it might be difficult to find pronounced effects in established communities (Harper 1977). Invasive species, however, do not share a coevolutionary history with the community they invade, and one might therefore expect greater allelopathic effects in such systems. However, only a few studies compared the allelopathic effects of an invasive species on competitors from the native and the invaded range. Callaway & Aschehoug (2000) found that the outcome of competition between the invasive *Centaurea diffusa* and grass species from the new and the old range depended on whether or not activated carbon reduced allelopathic interference among them. To our knowledge, no one has ever tested the possibility that the degree of allelopathy of an invader may change as a result of encountering new competitors.

Garlic mustard [*Alliaria petiolata* (Bieb.) Cavara & Grande (Brassicaceae)] is a biennial (and sometimes perennial) species native to Europe that was introduced to North America in the mid of the 19th century. In the last few decades it started to expand rapidly its range and has invaded the understory of mesic forests in northern United States and in southern Canada (Nuzzo 1999). Garlic mustard reduces the abundance of native species and decreases diversity in its new range in North America because of its high competitive ability (McCarthy 1997, Meekins & McCarthy 1999, B. Blossey, Cornell University, personal communication). In addition, a number of putative

allelopathic chemicals have been isolated (glucosinolates and their degradation products) that could be responsible for the success of garlic mustard (Vaughn & Berhow 1999, but see also McCarthy & Hanson 1998).

Here, we tested for allelopathic inhibition of germination through the presence of garlic mustard in two congeneric competitor species. *Geum urbanum* is a native European species that often co-occurs with garlic mustard, whereas *Geum laciniatum* is a member of the invaded North American communities (McCarthy 1997). In addition to comparing an old with a new competitor, we used plants from native European and invasive North American garlic mustard populations and asked whether their allelopathic potential differed depending on the origin of the plants. In contrast to the laboratory bioassays often used to test for allelopathic effects, our approach was to grow garlic mustard in flower pots and let the species contaminate the substrate with root exudates. Seed germination was then tested in the contaminated substrate and compared with a control where activated carbon was added to neutralize contamination.

Material & methods

Study species

Seeds of garlic mustard were collected from natural populations in North America and Europe. For a better geographic representation, we sampled seeds from three different locations on each continent (Halle [Germany, 51°28' N, 11°58' E], Copenhagen [Denmark, 55°43' N, 12°34' E], and Soyhières [Switzerland, 47°24' N, 07°22' E] in Europe; Athens [OH, 39°19' N, 82°07' W], Ipswich [MA, 42°41' N, 70°51' W], and Milwaukee [WI, 43°05' N, 87°53' W] in North America), but no attempt was done to test for population differences. *Geum urbanum* L. and *G. laciniatum* Murr. (Rosaceae) are both perennial woodland herbs that co-occur with garlic mustard either in its native and invasive range, respectively. Seeds of *G. urbanum* and *G. laciniatum* were bought from commercial seed suppliers (Rieger-Hofmann GmbH, Blaufelden-Roldshausen, Germany, and Ernst Conservation Seeds, Meadville, Pennsylvania, USA).

Garlic mustard cultivation

Seeds of garlic mustard were dark-stratified for 3 months at 5°C. Transplanted seedlings were cultivated in small pots of 125 cm³ for 4 weeks. Then 28 seedlings of European and 28 of North American origin were planted into pots containing 0.5 L of a 1:1 mixture of sand and compost substrate. To half of the pots, finely ground activated carbon was added at a concentration of 20 ml per litre substrate. Activated carbon is often used to reduce interference by allelopathic chemicals in the soil because it has a high affinity to organic compounds and a weak affinity to inorga-

nic nutrients (Ridenour & Callaway 2001, Callaway & Aschehoug 2000). Activated carbon did not have any direct effect on the growth (+6% aboveground biomass, $F_{1,52} = 0.767$, $P > 0.3$) and reproduction (+16% number of pods, $F_{1,52} = 0.774$, $P > 0.3$) of garlic mustard. From spring 2001 to early summer 2002, the plants were grown in a greenhouse with a 25/15°C day/night cycle and additional light provided by 500 W lamps. During winter, the plants were vernalized in an unheated greenhouse or in a climate chamber at 5°C when the greenhouse was too cold. Plants were harvested after seed set, and the substrate was carefully separated from the roots.

The germination experiment

Ten petri dishes were filled with the substrate from each flower pot totalling 560 dishes. In half of these, we placed 10 seeds of *Geum urbanum*, and in the other half of the petri dishes, 10 seeds of *G. laciniatum*. To test for a direct effect of activated carbon on the germination of either species, 10 control petri dishes were filled with the same 1:1 mixture of sand and compost substrate but without precultivation with garlic mustard. Activated carbon was added at the same concentration to half of these dishes. The petri dishes were kept in a refrigerator for 1 week and transferred to a climate chamber at 15°C with 14 h light. The number of germinated seeds was recorded weekly for 8 weeks.

Statistical analysis

The total number of seedlings that germinated after 8 weeks was analyzed using a split-plot analysis of deviance with activated carbon and origin of garlic mustard (Europe vs. North America) as plot level treatment and with species (*G. urbanum* vs. *G. laciniatum*) and its interactions as within-plot treatment. As seed germination follows a binomial distribution, a likelihood-ratio test was used with logit-link function to calculate variance ratios that are approximately *F*-distributed (McCullagh & Nelder 1989, pp. 98ff). The analyses were computed using the program GENSTAT 6 (Payne et al. 1987).

Results

Germination of between the two test species differed significantly, with *G. laciniatum* germinating more than twice that of *G. urbanum* during the first six weeks, and no further germination was observed thereafter (Table 1, Fig. 1). Overall, there was a marginally significant increase by about 14% in germination when activated carbon was added to the substrate, indicating that garlic mustard contaminated the substrate through root exudates and adding activated carbon in turn counteracted this effect. The control experiment using substrate without a history of garlic

mustard showed no direct effect of activated carbon on seed germination (Quasi- $F = 0.227$; $df = 1, 16$; $P > 0.6$). Here, activated carbon even reduced germination slightly from 50% to 47%. Thus, the observed increase of germination in the main experiment cannot be a direct effect of activated carbon.

Table 1. Summary of analysis of deviance of the germination success of the two species *Geum urbanum* and *G. laciniatum*. Seeds germinated on substrate previously containing garlic mustard of European or North American origin either with or without activated carbon.

Sources of variation	d.f.	Mean deviance	Quasi- F
Activated carbon	1	19.205	2.928(*)
Origin of garlic mustard	1	2.355	0.359
Activated carbon \times origin	1	2.587	0.394
Flower pot residual	52	6.560	4.591***
Species	1	580.6	406.2***
Species \times activated carbon	1	9.954	6.966**
Species \times origin	1	12.694	8.883**
Species \times activated carbon \times origin	1	9.592	6.712*
Residual	500	1.429	

Levels of significance: (*) $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

The two species differed in their reaction to activated carbon, i.e. in their response to allelochemicals. Germination of North American *G. laciniatum* consistently increased when activated carbon was added to the substrate (Table 1, Fig. 2). This effect was independent from the origin of garlic mustard. For the European *G. urbanum*, the pattern was more complex. *Geum urbanum* germinated better in substrate in which North American populations of garlic mustard were previously cultivated. Moreover, activated carbon slightly decreased germination in substrate precultivated by North American garlic mustard. In contrast, activated carbon increased germination when substrate was precultivated with European garlic mustard. This complex pattern for *G. urbanum* was indicated by a significant two-way interaction between the two test species and the origin of garlic mustard and a significant three-way interaction between species, origin, and activated carbon (Table 1). The difference in the reaction to activated carbon between *G. urbanum* and *G. laciniatum* showed that the sensitivity to the presence of allelochemicals in the substrate was species-specific.

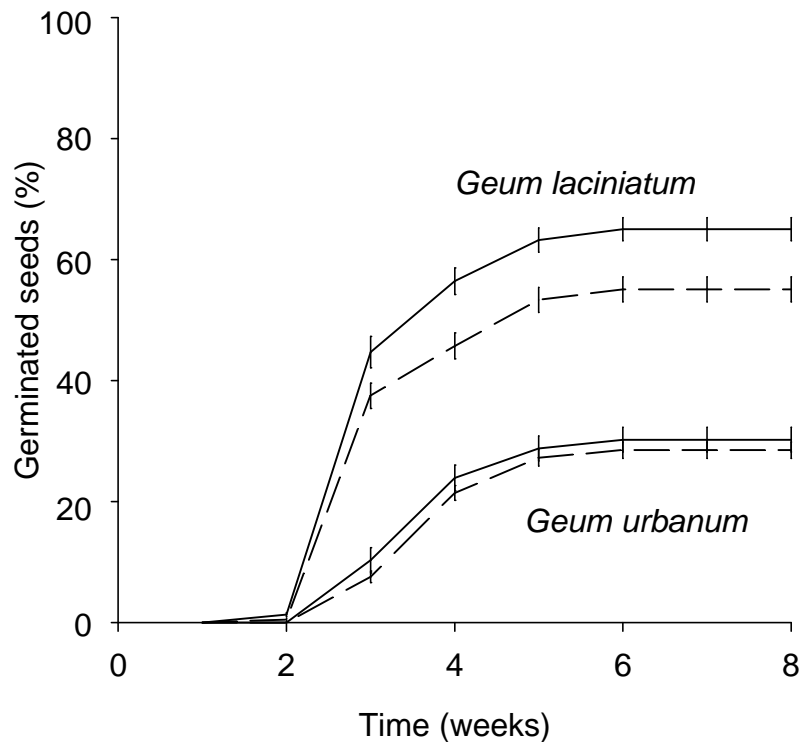


Fig. 1. Germination success (%) over time of two test species *Geum urbanum* and *G. laciniatum* in substrate previously contaminated by root exudates of *Alliaria petiolata* (broken lines) or contamination neutralized with activated carbon (solid lines). Given are weekly means \pm 1 SE.

Discussion

This study showed that garlic mustard negatively affected the germination of co-occurring species, but the result depended intricately on the identity of test species and the origin of garlic mustard. The overall effect of allelopathy was rather small: germination increased only by 14% when activated carbon neutralized the adverse effects of either root exudates or decomposing dead roots. However, individual-based models on the role of allelopathy in invasion showed that even moderate sensitivity to allelochemicals might shift the outcome of between-species competition (Goslee et al. 2001). Our approach to grow garlic mustard in flower pots and let the species contaminate the substrate by root exudates represented a more realistic test of allelopathy than bioassays, at a cost of not being able to quantify dose-response relationships or to identify the chemicals responsible for allelopathy. Although it does not meet all criteria to prove allelopathy outlined by Williamson (1990), the use of activated carbon could improve our ability to understand allelopathy. Vaughn & Berhow (1999) isolated several phytotoxic chemicals from garlic mustard (mainly allyl isothiocyanate and benzyl isothiocyanate), but we do not know whether these chemicals are involved in our study. Field experiments are now needed to test the effect of

allelopathy under more natural conditions and to estimate its magnitude relative to resource competition or other interactions.

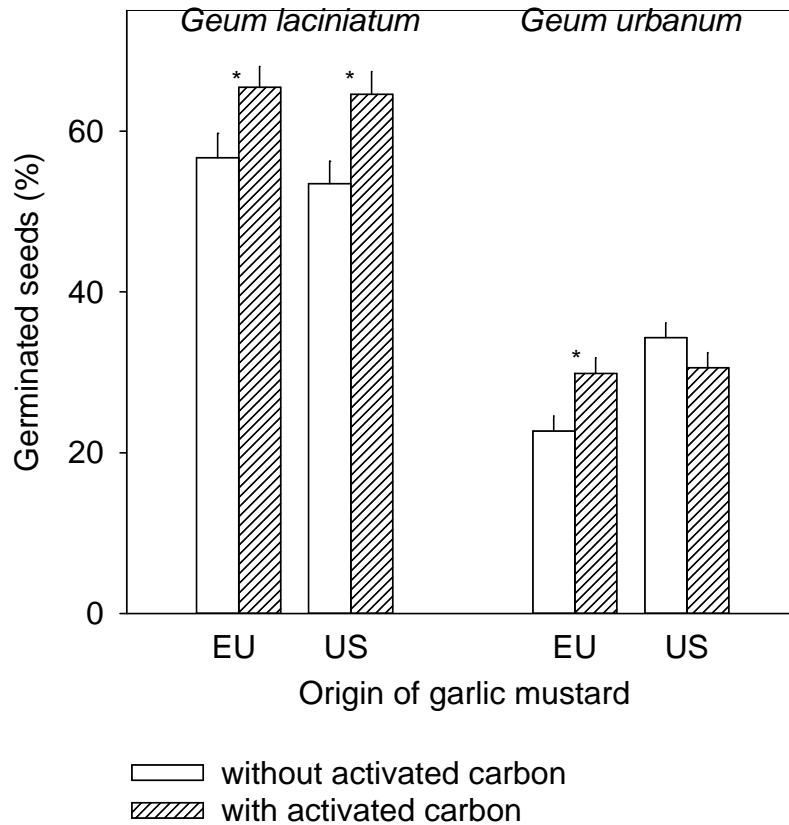


Fig. 2. Germination success (%) of two test species *Geum urbanum* and *G. laciniatum* on substrate previously contaminated by root exudates of garlic mustard (*Alliaria petiolata*) from either European (EU) or North American (US) origin and either with (hatched bars) or without (open bars) activated carbon added to the substrate. Bars are means + 1 SE. Asterisks above the bars indicate statistically significant differences between with and without activated carbon.

We found that the two species of *Geum* differed in their sensitivity to allelochemicals. When activated carbon was added there was a much greater increase of germination in the American *G. laciniatum* than in the European *G. urbanum*. There still was allelopathic inhibition of *G. urbanum* when growing in substrate precultivated with European garlic mustard, but North American garlic mustard has obviously lost its “nastiness” to a former competitor. This was the most remarkable finding of our experiment: germination of *G. urbanum* depended on the origin of garlic mustard populations. It is tempting to invoke local adaptation to explain this pattern. However, in how far evolutionary changes actually occurred in garlic mustard during the coloni-

zation of North America was out of the scope of this paper. Our results do suggest that North American garlic mustard behaved differently than European garlic mustard, but whether this resulted from a single introduction of one particular population that then spread in North America or whether the two types of garlic mustard differ consistently must remain open. One would need to know more on the number of initial populations and the colonization history in North America, but still little information is available on these aspects (Cavers et al. 1979). Alternatively, one would have to compare a much larger number of European and North American populations of garlic mustard to test the consistency of the difference. Nevertheless, our results suggest that plant material should be carefully selected when testing allelopathy in invasive species.

In conclusion, our data suggest that allelopathy may contribute to the success of garlic mustard as an invader of North American forests, but field trials are needed to examine the relative importance of allelopathy vs. other factors. The use of activated carbon to test for allelopathy is a fruitful approach as compared with laboratory bioassays. Finally, the degree of allelopathic interference is species-specific and can even vary within species. This is particularly important for invasive species that compete with different sets of species in the native and invasive range. Target species should be used that co-occur with the allelopathic species in nature to produce meaningful data.

Chapter 6

Evolution of plasticity and reduced phenotypic integration in invasive populations of *Alliaria petiolata*

(with Daniel Prati, Harald Auge, Bernhard Schmid)

Abstract. In order to become successful invaders, introduced plants must be able to establish themselves in a range of novel environments. Because plastic “general-purpose” genotypes may have a fitness advantage in such situations, we may expect evolution of increased phenotypic plasticity in invasive populations. Phenotypic integration, the pattern of covariation among traits, will however constrain the adaptive potential of invaders. A novel environment should therefore select against phenotypic integration. We tested this idea in a greenhouse shading experiment with offspring from native and invasive populations of garlic mustard (*Alliaria petiolata*). The species showed a strong, typical shading response. There was significant genetic variation among populations with respect to trait means and their plasticities, hence a potential for plasticity to evolve. When plant traits were analysed separately, there was little evidence for a general difference in plasticity between native and invasive populations. However, there were differences in how phenotypic integration was affected by shading. Phenotypic correlation matrices were less correlated across environments in invasive populations, indicating greater multivariate plasticity in invasive populations of *A. petiolata*. It is possible that this reflects selection for greater overall phenotypic flexibility in the introduced range. Because evolutionary changes in invaders might be more complex than previously thought, the rapidly expanding field of ecological genetics of invaders should benefit from a complex phenotype perspective.

Introduction

Invasive species offer excellent model systems for studying rapid evolutionary change (Thompson 1998, Reznick & Ghalambor 2001, Mooney & Cleland 2001, Sakai et al. 2001, Lee 2002). Adaptive evolution to novel biotic or abiotic conditions in the invasive range (Blossey & Nötzold 1995, Bossdorf et al. 2004), genetic drift and inbreeding depression in founder populations, and intraspecific hybridisation between formerly distant genotypes (Ellstrand & Schierenbeck 2000) may cause rapid genetic differentiation between native and introduced populations and explain the frequent lag times between introduction and spread of invasive species (Mack et al. 2000, Sakai et al. 2001, Müller-Schärer & Steinger 2004).

An ecological characteristic that is considered to be particularly important in plant invasions is phenotypic plasticity, i.e. the ability of an organism to express different phenotypes, depending on the environment (Bradshaw 1965). Evolution of increased plasticity in invaders could occur for two reasons: First, plasticity allows introduced species to become naturalized across a range of environments (Baker 1974, Agrawal 2001, Sexton et al. 2002). Plastic “general-purpose” (Baker 1965) genotypes should have a fitness advantage in founder populations where local adaptation has not occurred yet (Sexton et al. 2002), or cannot occur because of a lack of additive genetic variation (Marshall & Jain 1968, Baker 1974, Rice & Mack 1991a, Williams et al. 1995). Hence there should be an evolutionary “sorting out” (Weber & Schmid 1998, Müller-Schärer & Steinger 2004) of the more plastic genotypes. Second, phenotypic plasticity of a trait is a trait in itself that can evolve independently (Sultan 1987, Thompson 1991, Schmid 1992, Scheiner 1993, Schlichting & Pigliucci 1998). As such, evolution of plasticity might be part of local adaptation. Given sufficient genetic variation and a novel environment that is more variable or unpredictable than the native environment, evolution should maximize fitness by increasing plasticity (adaptive plasticity hypothesis, e.g. Schmid 1992, Via et al. 1995).

Typically, phenotypic traits are not independent from each other. There is a complex pattern of covariation among functionally related traits (“phenotypic integration”, Schlichting 1989, Pigliucci 2003) which may reflect genetic, functional, or developmental relationships (Schlichting & Pigliucci 1998). Phenotypic plasticity can be investigated not only at the level of individual traits, but also with regard to the correlation structure among traits, i.e. how the phenotype as a whole responds to environmental change. Under rapid environmental change, phenotypic integration will constrain an organism’s potential for adaptation (Schlichting 1989, Arnold 1992, Mitchell-Olds 1996, Wagner & Altenberg 1996, Merilä & Björklund 2004). Thus, a novel environment should not only select for increased plasticity but also against phenotypic integration.

Most previous studies that addressed plasticity in the context of plant invasions compared the plasticity of native and invasive species (e.g. Williams & Black 1994, Pattison et al. 1998, Durand & Goldstein 2001, McDowell 2002), of several invasive species (e.g. Marshall & Jain 1968, Weber & D'Antonio 1998) or several populations of an invasive species (e.g. Wu & Jain 1978, Rice and Mack 1991, Williams et al. 1995, Sexton et al. 2002, Parker et al. 2003) in the introduced range. Overall, these studies found that many invasive species are highly plastic, there is often genetic variation for plasticity, and invaders often display a greater plasticity than native congeners or co-occurring species. To date, few studies addressed the idea that plasticity might evolve in invasive plants by comparing native and introduced populations in a common environment (but see Kaufman & Smouse 2001, DeWalt et al. 2004). None of them addressed phenotypic integration.

Here, we tested for evolution of phenotypic plasticity and integration in a greenhouse experiment with garlic mustard (*Alliaria petiolata*), a European herb that is a serious invader in North American deciduous forests. We focused on plasticity to shading, because light is an important factor in the forest understory habitats of garlic mustard (Byers & Quinn 1998, Meekins & McCarthy 2000), and because the shading response is a well understood case of plasticity in plants (Schmitt et al. 1999). Specifically, we asked the following questions: (1) Is there genetic variation for plasticity to shading among garlic mustard populations? (2) Do plants from introduced populations have a greater plasticity than plants from native populations? (3) Do native and introduced populations differ in their degree of phenotypic integration and how it is affected by shading?

Material & methods

Study species

Garlic mustard (*Alliaria petiolata* [M. Bieb.] Cavara and Grande) is a member of the mustard family (Brassicaceae) native to the Eurasian temperate zone. It grows in mesic semi-shade habitats such as forest edges and moist woodlands. Plants typically germinate in early spring, form a rosette in the first year, overwinter as rosette, develop flowering stems in the following spring, produce seeds in June/July, and die. The species has been introduced to North America in the middle of the 19th century. Microsatellite data suggest that several independent introductions have occurred since then (O. Bossdorf, unpublished data). In the last few decades, the species rapidly expanded its range and is now present in at least 34 US states and four Canadian provinces (Nuzzo 2000). *A. petiolata* invades the understory of North American deciduous forests where it may displace native plant species (McCarthy 1997) or disrupt plant-insect associations (Porter 1994; Huang et al. 1995).

In this study we used seeds from eight European and eight US populations (Table 1). The species is self-compatible and primarily autogamous (Anderson et al. 1996), therefore most genetic variation is found between rather than within populations (Meekins et al. 2001; O. Bossdorf, unpublished data). In both continents, the populations came from a mixture of forest, forest edge, and roadside habitats. We regard them to be random samples within continents. Based on a long-term data set of climatic records (New et al. 2000), European and US populations did not differ in mean elevation, annual temperature, or precipitation (two-sample *t*-tests, $n = 14$, all $P > 0.1$). In autumn 2000, mature siliques were collected from several mother plants in each population. The seeds were cleaned and stored under cold, dry conditions.

Table 1. Native and invasive populations of *Alliaria petiolata* that were used in this study.

ID	Location	Longitude	Latitude
<i>Native</i>			
BRU	Bruck, Austria	12°49' E	47°18' N
BUD	Budweis, Czech Republic	14°29' E	48°58' N
HAL	Halle, Germany	11°58' E	51°28' N
IAS	Iasi, Romania	27°38' E	47°09' N
KOP	Copenhagen, Denmark	12°34' E	55°43' N
MON	Montpellier, France	03°53' E	43°36' N
PAR	Ascot, UK	00°41' W	51°25' N
SOY	Soyhières, Switzerland	07°22' E	47°24' N
<i>Invasive</i>			
CAS	Ipswich, MA	70°51' W	42°41' N
FF	McLean, IL	89°00' W	40°29' N
HF	Petersham, MA	72°17' W	42°54' N
HW	Mahomet, IL	88°09' W	40°23' N
OHA	Athens, OH	82°83' W	39°20' N
OHB	Athens, OH	82°07' W	39°19' N
VRO	Danville, IL	87°37' W	40°09' N
WI	Milwaukee, WI	87°53' W	43°05' N

Experimental design

In January 2001, seeds from 20 maternal families per population were placed in petri dishes filled with a sterilized 1:1 mixture of sand and seeding compost (Composana[®] Anzuchterde, Compo GmbH, Münster, Germany) and dark stratified at 4°C for 100 days. Hereafter the petri

dishes were placed in a climate chamber with a 12/12 h light/dark cycle at 15/10°C, where germinated seedlings were transferred to planting trays filled with a 1:1 mixture of sand and potting soil (Latterra® Typ P, Hawita-Gruppe GmbH, Vechta, Germany). They were kept in the chamber for several weeks, until no further germination was observed. At the end of May, six replicates from four seed families per population, altogether 384 plants, were planted into 1-L pots filled with the same substrate as above. On each plant, we measured cotyledon length which was used as an estimate of initial plant size.

Shading treatments were created with photosensitive plastic foils (Lee Colortran Int., Andover, UK) which, similar to natural shading, modify photosynthetically active radiation (PAR) and the red:far red ratio (R:FR) of light. Half of the replicates from each seed family were grown at 85% PAR and a R:FR of 0.8 (Lee Filter No. 246), the other half at 15% PAR and a R:FR of 0.1 (Lee Filter No. 089). In the remainder of this paper, we will refer to these treatments as “light” and “shade”. The experiment had a randomised block design with six blocks in an unheated greenhouse. Each block consisted of two boxes representing the two shading treatments. The plants were randomly assigned to blocks, with the constraint that each population should be present in each block at the same frequency. There were 32 plants per box and 64 plants per block. Each seed family occurred in three blocks only. The pots were watered as needed and re-randomised within boxes after three and six weeks. After five weeks, all pots were treated with a systemic insecticide (Bi-58; BASF AG, Ludwigshafen, Germany). After ten weeks, the plants were harvested.

On each plant we estimated leaf thickness as an average of three measurements on fresh leaves with a dial thickness gauge. Leaf chlorophyll content was estimated based on five measurements with a SPAD-502 greenness meter (Minolta Co., Osaka, Japan), a hand-held device that calculates relative chlorophyll content based on absorbance rates at 650 and 940 nm (Richardson et al. 2002). We counted the number of rosette leaves, measured leaf and petiole length on the three largest rosette leaves, and calculated the average leaf length:petiole length ratio, a typical variable for quantifying the shading response of plants (e.g. Solangaarachichi & Harper 1987). The plants were divided into roots, shoots, and leaves. Total leaf area was determined with a LI-3100 leaf area meter (LI-COR Inc., Lincoln, Nebraska, USA). All biomass samples were dried to a constant weight at 80°C and weighed. Total biomass was calculated as the sum of the three biomass fractions, root:shoot ratio as root biomass divided by the sum of the remaining fractions, and specific leaf area (SLA) as leaf area divided by leaf biomass. The dry leaves were crunched, fine-milled and homogenized in a ball mill, and analysed for leaf nitrogen concentration (mg g^{-1}) in a Vario EL elemental analyser (Elementar Analysensysteme GmbH, Hanau, Germany).

Statistical analyses

Individual plant traits were analysed with nested analysis of variance using the GLM procedure in SAS (SAS Institute 2001). Because the data were balanced, we used type I sum of squares. Treatment and block effects were analysed at the plot level, i.e. the block \times treatment interaction was used as error term when calculating F-ratios. Continent, population nested within continent, seed family nested within population, and their interactions with treatment were analysed at the pot level. Initial plant size was included as a covariate. To avoid trivial correlations and to keep the number of non-independent tests as low as possible, we a priori restricted our analyses to the following eight variables: total biomass, root:shoot ratio, leaf number, specific leaf area, leaf thickness, leaf length:petiole length ratio, leaf greenness, and leaf nitrogen concentration. Prior to the analyses, total biomass, root:shoot ratio and leaf number were sqrt-transformed. Specific leaf area, leaf thickness, leaf length:petiole length, and leaf nitrogen were log-transformed.

To address phenotypic integration in native versus introduced populations, we calculated separate phenotypic correlation matrices for European and US plants growing in light and shade, respectively. Plants were pooled across populations, so that each of the four matrices was based on 96 plants. The patterns of character correlations were visualised with star diagrams in which traits were connected by solid lines if they were positively correlated, and by broken lines if they were negatively correlated (Fig. 2). As an index of phenotypic integration of each matrix we calculated the average absolute correlation strength in each.

Next, we analysed matrix similarity across treatments for European and US plants, respectively, and between European and US matrices within treatments. As there is no consensus on the most appropriate method for matrix comparison (Murren 2002, Stepan et al. 2002), we used several approaches. First, we tested for overall matrix correlation with Mantel tests in NTSYS (Rohlf 2000). Second, we calculated the amount of change between two matrices with an element by element approach suggested by Roff et al. (1999):

$$T\% = \frac{\sum_{i=1}^c |\hat{q}_{i1} - \hat{q}_{i2}| / c}{(\hat{q}_1 + \hat{q}_2) / 2} \times 100$$

where c is the number of off-diagonal elements in a matrix, \hat{q}_j is the average absolute correlation strength in matrix j , and \hat{q}_{ij} is the i th element of the j th matrix. Basically, $T\%$ quantifies the average relative change per matrix element. Finally, we used common principal component analysis (CPCA; Flury 1988), currently the most popular method for comparing genetic and phenotypic correlation matrices (Mezey & Houle 2003). CPCA tests a series of hypotheses about matrix

similarity, including full equality, proportionality, or partially shared eigenstructures (Phillips & Arnold 1999, Steppan et al. 2002). We used the jump-up approach in the software by Patrick Phillips (<http://darkwing.uoregon.edu/~pphil/>). However, unlike the other two methods, CPCA indicated no relationship between the correlation matrices of native and invasive populations, and no difference in their multivariate response to shading. CPCA does have its limitations (Houle et al. 2002, Mezey & Houle 2003), and we think it was unable to capture some of the pattern in our data. We will therefore not consider it in the results and discussion of this paper.

Results

Experimental shading strongly affected plant phenotypes in the expected ways (Schmitt et al. 1999; see Tables 2 and 3, Fig. 1). On average, shading reduced total plant biomass to 45%. Shade plants had a greater SLA and a lower root:shoot ratio, i.e. they allocated more resources to above-ground structures. Also, shade plants developed leaves that were thinner and had higher chlorophyll content and nitrogen concentration. In addition, they had a lower leaf length:petiole length ratio, i.e. relatively longer petioles.

Table 2. Trait means of native European and invasive US plants of *Alliaria petiolata* grown at 85% PAR (“Light”) or 15% PAR (“Shade”) for 10 weeks. Greenness values are a relative measure of chlorophyll content. Sample size $n = 96$ for each column. The data are back-transformed least-square continent means from the analyses of variance.

	Light		Shade	
	Native	Invasive	Native	Invasive
Total biomass [g]	3.536	2.964	1.493	1.413
Root:shoot ratio	0.840	0.810	0.270	0.293
Leaf number	5.119	5.046	5.048	4.885
Specific leaf area [cm ² g ⁻¹]	247.4	253.5	453.2	465.0
Leaf thickness [mm]	33.06	32.10	23.74	22.26
Leaf length:petiole length	0.646	0.688	0.450	0.477
Greenness	16.58	16.82	24.40	23.10
Leaf N [mg g ⁻¹]	17.94	17.63	32.59	28.94

Initial plant size significantly affected the final biomass and leaf number of plants, as well as their SLA and root:shoot ratio (Table 3). There were highly significant population main effects and population \times shading interactions in most characters investigated, indicating genetic variation for trait means and their plasticities (Table 3, Fig. 1). In addition, family main effects were signifi-

cant for root:shoot ratio, leaf number and leaf nitrogen concentration (Table 3). With two exceptions, there were no significant differences between native and invasive populations in terms of traits means (Table 3, term “Continent”) and their plasticities (Table 3, term “Treatment \times Cont”): in response to shading, plants from invasive populations showed a weaker increase in leaf chlorophyll content but a stronger decrease in leaf thickness than did plants from native populations (Tables 2 and 3). However, only the first of these two results in the expected direction of decreased plasticity in invasive populations.

There was considerable variation in phenotypic correlation patterns of light and shade plants, as well as of plants from native and invasive origins (Fig. 2). Overall, shade plants tended to have a stronger average correlation strength among phenotypic traits (Table 4), i.e. they were more tightly phenotypically integrated. When compared within treatments, matrices of native and invasive plants were correlated and had a similar average correlation strength (Tables 4 and 5). However, shading caused greater relative change per matrix element in invasive plants (Table 5). Hence, matrix correlation across treatments was lower in invasive plants than in native plants.

Table 4. Phenotypic integration in offspring from native European and invasive US populations of *Alliaria petiolata*, when grown under experimental light or shade conditions. The four correlation matrices consisted of 28 correlations among 8 traits. Each matrix was based on $n = 96$ plants.

	Mean correlation strength	% Correlations > 0.3
Native Light	0.194	25%
Invasive Light	0.185	21%
Native Shade	0.245	25%
Invasive Shade	0.254	39%

Table 5. Comparisons of phenotypic correlation matrices in native European and invasive US populations of *Alliaria petiolata*, when grown under experimental light or shade conditions. Each matrix consisted of 28 correlations, and was based on $n = 96$ plants. All matrix correlations are significant at $P < 0.001$. $T\%$ is the average relative change per matrix element.

	Matrix correlation	$T\%$
EU Light vs EU Shade	0.713	65.2 %
US Light vs US Shade	0.652	90.9 %
EU Light vs US Light	0.697	75.8 %
EU Shade vs US Shade	0.710	74.5 %

Table 3. Results of analysis of variance of individual plant traits.

Source	d.f.	Skeleton analysis		Total biomass		Root:shoot ratio		Leaf number	
		<i>MS</i>	<i>F</i>	<i>MS</i>	<i>F</i>	<i>MS</i>	<i>F</i>	<i>MS</i>	<i>F</i>
Initial plant size	1	MS_I	MS_I/MS_{R2}	2.283	58.33***	0.095	15.53***	0.520	13.37***
Block	5	MS_B	MS_B/MS_{R1}	0.543	5.59*	0.080	12.89**	0.053	0.65
Shading treatment	1	MS_T	MS_T/MS_{R1}	34.108	351.39***	13.674	2194.45***	0.066	0.82
Residual 1 (B × T)	5	MS_{R1}		0.097		0.006		0.081	
Continent	1	MS_C	MS_C/MS_P	0.997	1.98	0.003	0.03	0.099	0.32
Population [C]	14	MS_P	MS_P/MS_F	0.503	11.77***	0.115	9.96***	0.307	4.72***
Family [P,C]	48	MS_F	MS_F/MS_{R2}	0.043	1.09	0.012	1.89***	0.065	1.67**
Shading × Cont.	1	$MS_{T \times C}$	$MS_{T \times C}/MS_{T \times P}$	0.382	3.74	0.036	2.36	0.010	0.06
Shading × Pop. [C]	14	$MS_{T \times P}$	$MS_{T \times P}/MS_{T \times F}$	0.102	3.50***	0.015	1.86	0.173	4.96***
Shading × Fam. [P,C]	48	$MS_{T \times F}$	$MS_{T \times F}/MS_{R2}$	0.029	0.75	0.008	1.32	0.035	0.90
Residual 2	245	MS_{R2}		0.039		0.006		0.039	

Table 3. continued.

Specific leaf area		Leaf thickness		Leaf length:petiole length		Leaf greenness		Leaf nitrogen concentration	
<i>MS</i>	<i>F</i>	<i>MS</i>	<i>F</i>	<i>MS</i>	<i>F</i>	<i>MS</i>	<i>F</i>	<i>MS</i>	<i>F</i>
0.066	10.63**	0.001	0.17	0.032	2.21	3.99	1.04	0.052	3.23
0.067	3.83	0.321	5.16*	0.084	3.22	94.14	4.41	0.452	4.11
35.258	2012.61***	11.670	187.66***	12.737	485.28***	4781.28	224.18***	28.659	260.23***
0.017		0.062		0.026		21.33		0.110	
0.064	0.78	0.226	3.61	0.435	2.05	18.53	0.55	0.434	1.71
0.082	9.90***	0.063	8.89***	0.212	10.48***	33.78	6.33***	0.253	9.04***
0.008	1.35	0.007	0.88	0.020	1.41	5.34	1.39	0.028	1.74**
0.000	0.00	0.030	6.44*	0.001	0.02	56.98	5.08*	0.247	3.68
0.021	2.75**	0.005	1.06	0.041	4.18***	11.21	2.99**	0.067	4.11***
0.008	1.26	0.004	0.54	0.010	0.68	3.75	0.98	0.016	1.02
0.006		0.008		0.014		3.84		0.016	

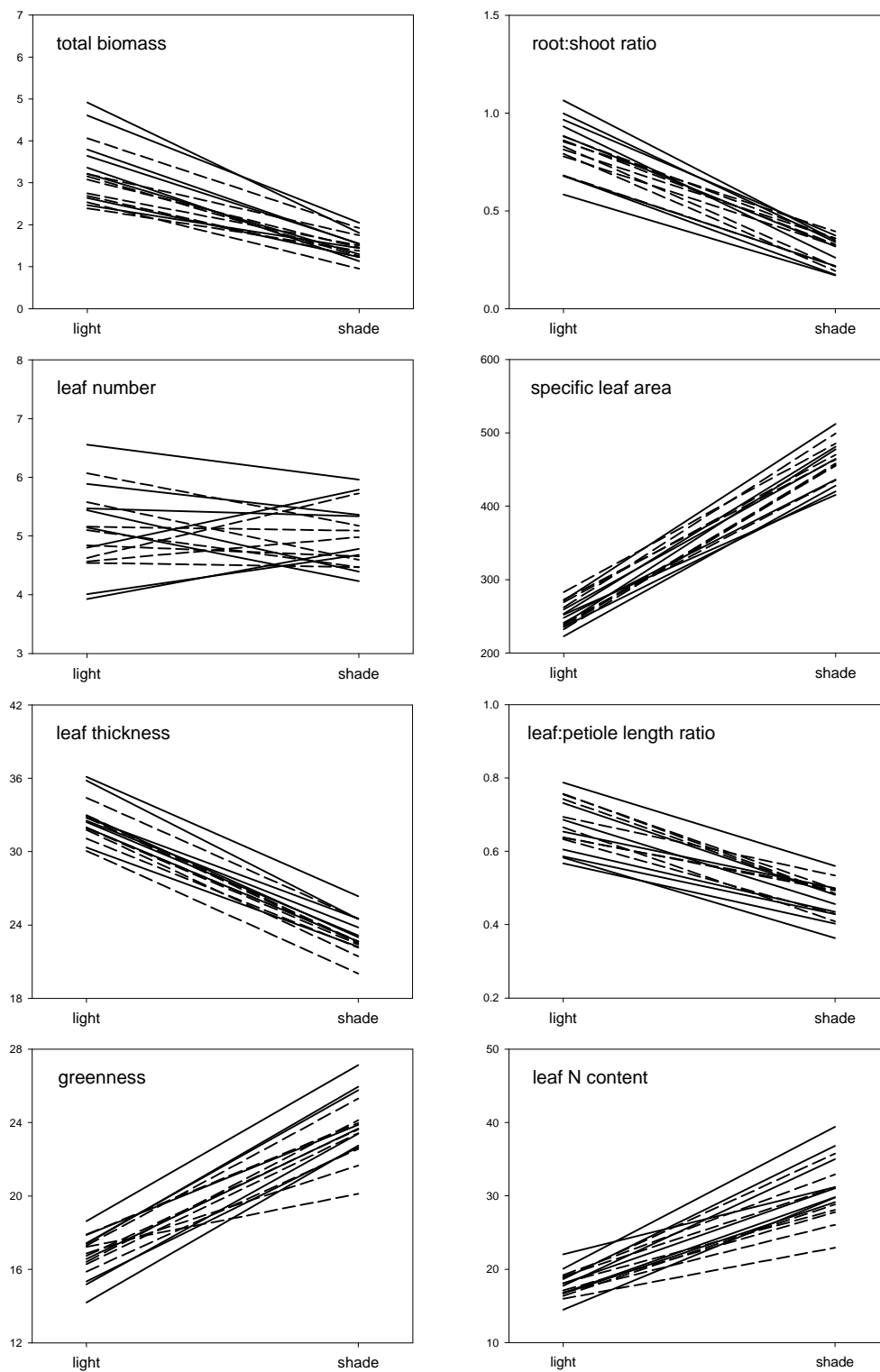


Fig. 1. Reaction norms to shading of eight native European (solid lines) and eight invasive US (broken lines) populations of garlic mustard (*Alliaria petiolata*). Plants were raised under identical conditions and subjected to experimental shading in a greenhouse experiment. The data are back-transformed least-square population means from the analyses of variance.

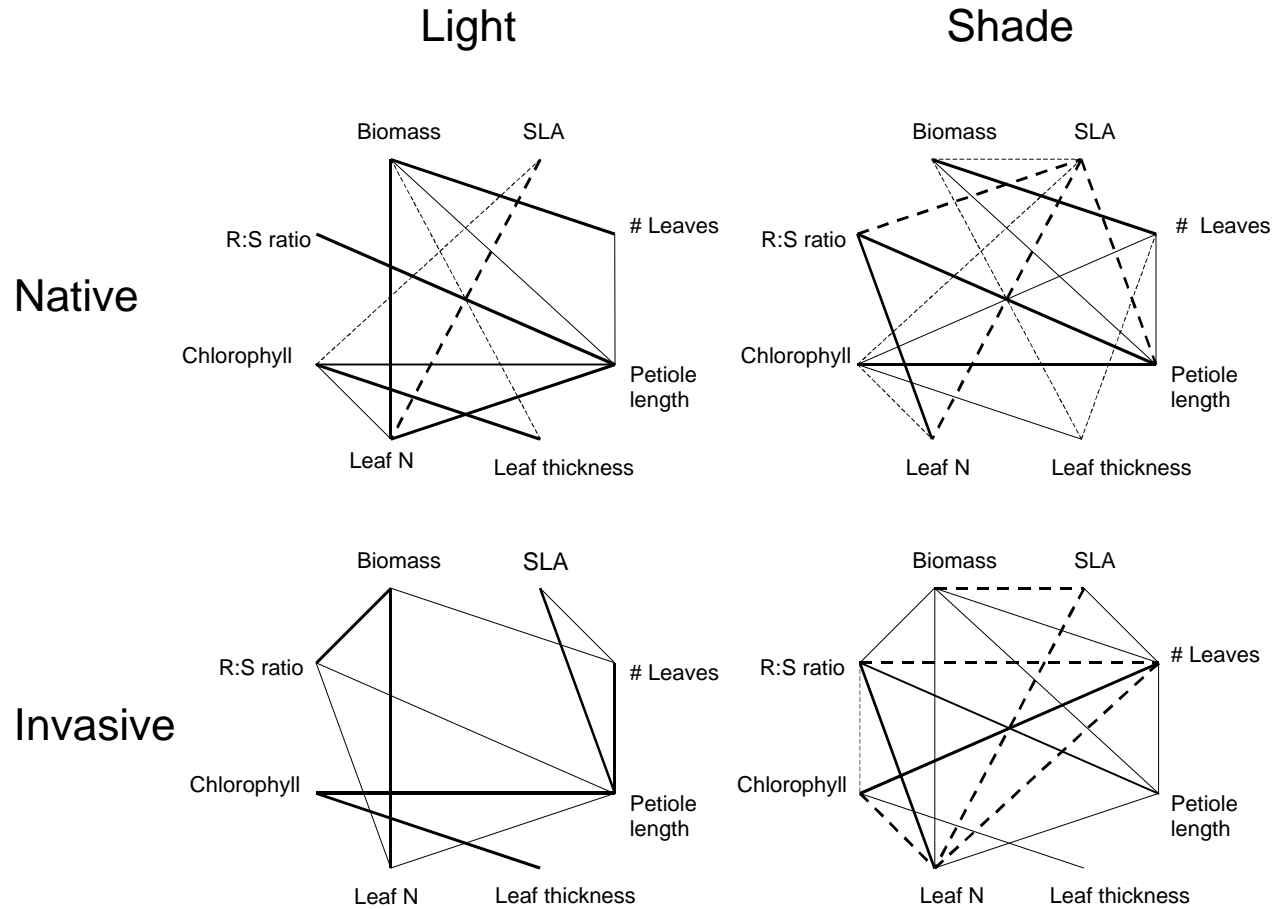


Fig. 2. Patterns of phenotypic integration in native and invasive populations of garlic mustard (*Alliaria petiolata*). Offspring from several native European and invasive US populations were raised under identical conditions and subjected to experimental shading in a greenhouse experiment. Solid lines are significant positive correlations ($P = 0.05$), broken lines significant negative correlations ($P = 0.05$). Thick lines are correlations significant at $P = 0.001$.

Discussion

In order to become successful invaders, introduced plants must be able to establish themselves in a range of novel environments. Because plastic “general-purpose” (Baker 1965) genotypes may have a fitness advantage in such situations (Agrawal 2001, Sexton et al. 2002), we may expect evolution of increased phenotypic plasticity in invasive populations. In this study we grew offspring from several native and invasive populations of *Alliaria petiolata* in a greenhouse shading experiment. When phenotypic traits were analysed separately, we found little difference in the plasticity of native and invasive populations. However, there were differences in how phenotypic integration was affected by shading. Greater change across environments in their phenotypic correlation structure indicated increased multivariate plasticity in invasive populations.

The invasion success of *A. petiolata* has been attributed by many authors to its plasticity in response to various environmental factors, including light, soil pH, soil moisture, and nutrient availability (Anderson & Kelley 1995, Byers & Quinn 1998, Dhillon & Anderson 1999, Meekins & McCarthy 2000). Our experimental data support this idea. *A. petiolata* displayed a strong plastic response to shading, with morphological changes typical for shaded plants (e.g. Pigliucci & Kolodnynska 2002, Sleeman et al. 2002, DeWalt et al. 2004). In spite of a 80% reduction of photosynthetically active radiation, the development, among others, of thinner leaves with a higher chlorophyll content allowed shaded plants to maintain a productivity of almost 50% of that of plants grown in light. Moreover, the significant population \times shading interactions in most traits (Table 3, Fig. 1) indicate genetic variation for plasticity and hence the potential for plasticity to evolve in *A. petiolata*.

To date, few studies compared phenotypic plasticity of native and invasive populations in a common environment. Kaufman & Smouse (2001) compared the growth of native and invasive populations of the tree *Melaleuca quinquenervia* at different water and pH levels. They found a greater environmental component in the response to pH of invasive populations and interpreted this as increased plasticity. DeWalt et al. (2004) investigated morphological and physiological plasticity to shading in the invasive shrub *Clidemia hirta* and found little difference in the plasticity of native and invasive populations. Both studies, however, were done with seedlings of long-lived species that one would expect to have rather slow evolutionary responses to the novel environments because of their long generation times. Here, we used *A. petiolata* as a model system, a biennial herb that has been naturalized in its introduced range for at least 50-75 generations. Still, when phenotypic traits were analysed separately, there was little evidence for evolution of plasticity in invasive populations.

One reason for this lack of a difference in plasticity could be that costs of plasticity (e.g. De Witt et al. 1998, Van Kleunen et al. 2000) prevented evolution of increased plasticity in a species that appears to be generally well adapted to heterogeneous environments. After all, genetic constraints on the evolution of plasticity are one of the reasons why “Darwinian monsters” – species capable to perfectly adapt to any environment through plasticity (Pigliucci 2001) – as well as “ideal weeds” (Baker 1965) do not exist.

It is now widely recognized that patterns of covariation among phenotypic traits are not fixed within a species, but may depend on genotype and environmental context (e.g. Murren 2002, Pigliucci 2003, and references therein). Moreover, if character correlations have a genetic basis, evolution might act on suites of correlated characters rather than on single traits (Schlichting 1989, Wagner & Altenberg 1996, Pigliucci & Preston 2004). Here, we have found that both shading and continent of origin affected phenotypic integration in garlic mustard. Specifically, we found that phenotypic integration was tighter under shaded conditions, which could represent some kind of canalization under stress, i.e. trade-offs are stronger under conditions of low resource availability. Phenotypic correlation matrices were less correlated across environments in invasive populations, indicating greater multivariate plasticity in the invaders. It is conceivable that this indeed reflects selection for greater overall phenotypic flexibility in invasive populations.

In conclusion, our study addressing phenotypic integration and multivariate plasticity in native versus invasive plant populations suggests that evolutionary changes in invaders can be complex. The rapidly expanding field of ecological genetics of invaders should benefit from considering both univariate and multivariate phenotypic responses to novel environments.

Chapter 7

Summary / Zusammenfassung

Summary

As a result of global trade and transport, the number of plant species introduced to novel areas by humans, either deliberately or by accident, has increased dramatically. Some of these species have become pests in their new range and cause major environmental and economic problems. Today, invasive species are regarded as one of the greatest threats to biodiversity. However, only one out of 1000 introduced species turns into a pest. Understanding why these few become invaders and so many others don't would be an important step towards being able to predict and control invaders. It is therefore a great challenge for basic research.

One approach to this question have been comparative studies of the ecological characteristics of invaders. They found that many invasive plants possess traits usually associated with agricultural weeds, but there are many exceptions to this rule. Thus, to be or not to be an invader is not a simple question of having the right traits. One reason for this might be that traits evolve. Evolutionary change can be rapid, and biologists are just beginning to realize that invasive species provide some of the best opportunities to study rapid evolution in action. As invasions often involve drastic changes in selection regimes, invaders should rapidly adapt to the novel environments. Many of the species that become invasive do so only after a lag time, probably after such evolutionary adjustments have taken place.

A hypothesis that has been very influential in this context is the Evolution of Increased Competitive Ability (EICA) hypothesis. It is based on the observation that many plants appear to grow more vigorously in their invasive range. Usually this has been attributed to a release from natural enemies. The EICA hypothesis, in contrast, proposes that after enemy release plants evolved to be less defended but more competitive. The increased vigour would therefore result from rapid evolution rather than from a plastic response. The EICA hypothesis predicts that, when compared in a common environment, plants from invasive populations should be less defended against natural enemies but more competitive than plants from native populations.

Chapter 2 of this thesis has reviewed the current evidence for EICA and found reasonable support for it. Field comparisons of native and invasive populations mostly found greater fitness in invasive ones. and the majority of common environment studies found either increased growth or decreased resistance in invasive populations. Another conclusion, however, has been that previous research has been one-sided. Although EICA is concerned with competitive ability, most previous studies dealt with growth in a competition-free environment. Also, while many studies used herbivore bioassays to estimate resistance in native versus invasive populations, another component of plant defence, tolerance, has hardly been addressed. Finally, because EICA has been so popular, previous research has been largely restricted to testing its predictions, whereas

evolutionary change in other characteristics that could play a role in the success of plant invaders, such as allelopathy or phenotypic plasticity, have received much less attention. I have attempted to address these shortcomings in the experimental part of my thesis.

As a model system I used *Alliaria petiolata* (garlic mustard), a European herb that has become a serious pest in North American deciduous forests. A time lag of almost 100 years between introduction and spread suggests that evolutionary changes such as EICA might play a role in the invasion success of *A. petiolata*. I used seeds from several native European and invasive US populations to raise plants under identical conditions and to test for genetic differentiation among and between native and invasive populations.

Chapter 3 tested the first prediction of the EICA hypothesis. I used palatability tests as well as simulated herbivory experiments to compare resistance and tolerance in native versus invasive populations of *A. petiolata*. Indeed, feeding rates of the specialist weevil and potential future bio-control agent *Ceutorhynchus scrobicollis* were significantly greater on US plants, suggesting a loss of resistance in the new range. In contrast, there was significant population variation but no continent effect in the feeding rates of the generalist caterpillar *Spodoptera littoralis*. After simulated herbivory, *A. petiolata* showed substantial regrowth and changes in plant architecture and allocation. However, there was no difference in the tolerance of native and invasive populations.

In chapter 4 I tested the second EICA prediction with a diallel competition experiment. Offspring from native and invasive populations were grown alone or in all pairwise combinations. The advantage of this novel approach was that it allowed separating growth from competitive ability, and it avoided the problem of competitor choice. If local adaptation and coevolution play a role in invasions, any interspecific competitor would likely have given a biased picture. There was no difference between native and invasive populations when growing alone. However, when competing against each other, native populations outperformed invasive ones. To explain the results I formulate a new Evolutionary Reduced Competitive Ability (ERCA) hypothesis: if there is less competition in the invasive range and competitive ability involves traits that have a fitness cost, then selection might act against it, thereby reducing intraspecific interactions, too. Taken together, chapters 3 and 4 provide no consistent evidence for the EICA hypothesis and I therefore conclude that it does not hold in *Alliaria petiolata*.

Defence and competitive ability are important characteristics of invasive plants, but they are certainly not the only ones. Rapid genetic differentiation will occur in any trait that is beneficial under the novel selection regime, given there is genetic variation for it. In chapters 5 and 6 of this thesis, I went beyond EICA to investigate the role of two other traits that could play an important role in invasive populations of *A. petiolata*.

In chapter 5 I tested for allelopathic inhibition of germination by *A. petiolata*. Seeds of *Geum urbanum* and *Geum laciniatum*, which co-occur with *A. petiolata* in its native and invasive range, respectively, were germinated on soil that *A. petiolata* had previously been growing in. To half of the experiment, I added activated carbon which adsorbs organic substances in the soil. Activated carbon significantly increased germination, indicating that *A. petiolata* had contaminated the soil through root exudates. Also, the allelopathic effect depended on the origins of *A. petiolata* and the target. The European *Geum* species was negatively affected only by European *A. petiolata*. This experiment is the first evidence for allelopathic inhibition of germination by *A. petiolata*, and it demonstrates that allelopathic interference can be complex and species-specific.

In chapter 6 I compared phenotypic plasticity and integration in native and invasive populations of *A. petiolata*. Plastic “general-purpose” genotypes should have a fitness advantage in novel environments, whereas phenotypic integration, the pattern of trait covariation, will constrain the evolutionary potential of invaders. Thus, I expected increased plasticity but reduced phenotypic integration in invasive populations. In a shading experiment, I found significant genetic variation for plasticity among populations, hence a potential for plasticity to evolve. When traits were analysed separately, there was no evidence for a difference in plasticity between native and invasive populations. There were differences, however, in how phenotypic integration was affected by shading. Phenotypic correlation matrices were less correlated across environments, indicating greater multivariate plasticity in invasive populations of *A. petiolata*. It is possible that this reflects selection for greater overall phenotypic flexibility in invasive populations.

To summarize my experimental work, I found reduced resistance to a specialist herbivore, reduced competitive ability, and reduced phenotypic integration in invasive populations of *Alliaria petiolata*. In addition, I was able to show that the species can inhibit germination of neighbours through root exudates. Overall, the study of native versus invasive populations in a common environment has proven to be a useful tool for detecting evolutionary change. However, to explain the invasion success of *A. petiolata*, other mechanisms than EICA must be sought. I suggest that phenotypic plasticity and allelopathy likely play a role.

Our understanding of the invasion of *A. petiolata* will be greatly improved if future research addresses (1) plant fitness, herbivore loads, and the dynamics of natural populations in the native and invasive range, (2) the defence against specialist herbivores such as *C. scrobicollis*, as well as genetic variation in this defence, (3) mechanisms of belowground interference between *A. petiolata*, its competitors and associated soil biota, and (4) invasion pathways and molecular genetic variation in both ranges, using molecular markers. After all, it is the amount of genetic variation that determines the potential for rapid adaptive evolution in *Alliaria petiolata*.

Zusammenfassung

Die Zahl der Pflanzenarten, die durch den Menschen in neue Gebiete verschleppt werden, ist durch die Globalisierung von Handel und Transport dramatisch angestiegen. Einige dieser Arten haben sich in ihrem neuen Areal stark ausgebreitet und verursachen dort wirtschaftliche Schäden und Umweltprobleme. Invasive Arten gelten heute als eine der größten Gefahren für die Biodiversität. Tatsächlich wird jedoch nur jede 1000. eingeschleppte Art zu einem Problem. Warum ausgerechnet diese, gibt der Wissenschaft nach wie vor Rätsel auf. Würde sie dies verstehen, dann wäre sie in der Lage, Invasionen vorherzusagen, und somit, diese zu verhindern.

Ein Ansatz, mit dem man versucht hat, diese Frage zu beantworten, ist der Vergleich ökologischer Merkmale invasiver Arten. Man fand, dass invasive Pflanzen oft Merkmale von Ackerunkräutern besitzen. Es gibt jedoch so viele Ausnahmen von dieser Regel, dass die Aussichten, anhand weniger Merkmale vorherzusagen zu können, ob eine Pflanze invasiv wird, nach wie vor gering sind. Eine mögliche Ursache hierfür ist, dass Merkmale sich durch Evolution verändern können. Evolutionäre Prozesse können mitunter schnell ablaufen. Invasive Arten sind ein gutes Beispiel dafür, da sie in ihrem neuen Areal oft drastisch veränderten Selektionsbedingungen ausgesetzt sind. Es ist zu vermuten, dass sie darauf mit entsprechender Anpassung reagieren. Bei vielen invasiven Arten beginnt die Ausbreitung im neuen Areal erst nach einer Verzögerungsphase. Es ist denkbar, dass diese durch evolutionäre Anpassungsprozesse verursacht wird.

Eine neue wissenschaftliche Hypothese, die in diesem Zusammenhang eine wichtige Rolle spielt, ist die EICA-Hypothese (Evolution of Increased Competitive Ability = Evolution größerer Konkurrenzstärke), die zu beantworten versucht, warum invasive Pflanzen im neuen Areal oft besser wachsen als im einheimischen. Bisher wurde dies oft durch eine geringere Anzahl natürlicher Fraßfeinde (Herbivore) erklärt. Die EICA-Hypothese hingegen vermutet, dass nach dem Verlust der Fraßfeinde eine Selektion weniger resistenter, dafür aber konkurrenzstärkerer Pflanzen-Genotypen stattgefunden hat. Der Erfolg invasiver Pflanzen wird hier durch schnell ablaufende evolutionäre Prozesse erklärt. Die EICA-Hypothese sagt voraus, dass im direkten Vergleich invasive Genotypen bzw. Populationen (1) schwächer gegen Fraßfeinde verteidigt, dafür aber (2) konkurrenzstärker sein werden als einheimische.

In Kapitel 2 dieser Dissertation habe ich die gegenwärtige Beweislage für EICA zusammengestellt und überwiegend Unterstützung für die Hypothese gefunden. Vergleiche natürlicher Populationen zeigen meist, dass Pflanzen im invasiven Areal eine höhere Fitness aufweisen als im einheimischen. Ebenso fand die Mehrzahl der Studien, die EICA-Vorhersagen unter kontrollierten Bedingungen testeten, bei invasiven Genotypen ein stärkeres Wachstum oder eine verringerte Resistenz gegen Herbivore. Eine allgemeine Schlussfolgerung aus der Übersicht empirischer

Arbeiten ist, dass die Forschung auf diesem Gebiet bisher auf zu wenige Aspekte beschränkt war. Obwohl die EICA-Hypothese Vorhersagen zur Konkurrenzkraft macht, wurde bisher meist nur konkurrenzfreies Wachstum einheimischer und invasiver Pflanzen-Genotypen verglichen. Herbivorenabwehr von Pflanzen wurde fast ausschließlich in Form von Fraßtests untersucht, die die Resistenz gegen Herbivore schätzen. Ein anderer wichtiger Aspekt von Abwehr wurde kaum berücksichtigt: Toleranz, d.h. die Fähigkeit von Pflanzen, Fraßschäden durch gesteigertes Wachstum zu kompensieren. Da die bisherige Forschung stark auf die EICA-Hypothese fokussiert war, wurden evolutionäre Prozesse in anderen Merkmalen, die ebenso wichtig sein könnten für den Erfolg invasiver Pflanzen, kaum untersucht. Ich habe versucht, einige dieser Punkte im experimentellen Teil meiner Arbeit zu berücksichtigen.

Als Beispielart wählte ich die Knoblauchsrauke (*Alliaria petiolata*), eine europäische Pflanze, die in Nordamerika invasiv ist und sich dort vor allem im Unterwuchs von Laubwäldern ausbreitet. Die starke Ausbreitung von *A. petiolata* in Nordamerika begann erst circa 100 Jahre nach ihrer Einschleppung durch den Menschen, was evolutionäre Anpassungsprozesse als Ursache für den Erfolg der Art nahe legt. Samenmaterial von mehreren europäischen und nordamerikanischen Populationen wurde verwendet, um Pflanzen unter identischen Bedingungen aufzuziehen und genetische Differenzierung zwischen einheimischen und invasiven Populationen zu untersuchen.

Kapitel 3 ist ein Test der ersten EICA-Vorhersage mit *A. petiolata*. Mit Hilfe von Fraßtests und simulierter Herbivorie verglich ich Resistenz und Toleranz von einheimischen und invasiven Populationen. Der auf *Alliaria* spezialisierte Rüsselkäfer *Ceutorhynchus scrobicollis* zeigte signifikant stärkeren Fraß auf amerikanischen Pflanzen, was tatsächlich auf eine verringerte Resistenz der invasiven Populationen schließen lässt. Bei einem unspezialisierten Herbivoren hingegen, den Raupen von *Spodoptera littoralis*, waren keine Unterschiede zwischen einheimischen und invasiven Populationen festzustellen. Starke, künstlich erzeugte Herbivorie führte zu deutlichem Kompensationswachstum und morphologischen Veränderungen bei *A. petiolata*, jedoch ohne Unterschieden zwischen einheimischen und invasiven Populationen.

Kapitel 4 ist ein Test der zweiten EICA-Vorhersage mittels eines Konkurrenz-Diallel-Experiments, in dem Nachkommen einheimischer und invasiver *Alliaria*-Populationen einzeln wuchsen oder in allen möglichen Kombinationen gegeneinander konkurrierten. Der Vorteil dieses Ansatzes war, dass zwischen Wachstum und Konkurrenzstärke unterschieden werden konnte, und der Einsatz einer anderen Konkurrenzart vermieden wurde. Da Pflanzen im einheimischen und invasiven Areal mit unterschiedlichen Arten konkurrieren, sie zudem an ihre einheimischen Konkurrenten durch Koevolution angepasst sein können, wäre mit keiner Art ein objektiver Vergleich der Konkurrenzstärke möglich gewesen. Es gab keinen Unterschied zwischen einheimischen und

invasiven Pflanzen, wenn diese einzeln wuchsen. Unter Konkurrenzbedingungen hingegen waren einheimische Genotypen signifikant erfolgreicher. Dies steht im Widerspruch zur EICA-Vorhersage. Insgesamt bieten Kapitel 3 und 4 keinen überzeugenden Beleg dafür, dass die EICA-Hypothese als Erklärung für den Invasionserfolg von *Alliaria petiolata* dienen kann.

Konkurrenzstärke und Verteidigungsmechanismen gegen Fraßfeinde sind wichtige Merkmale invasiver Pflanzen, aber sicher nicht die einzigen. Genetische Differenzierung im neuen Areal kann in jedem Merkmal erfolgen, das unter den veränderten Selektionsbedingungen von Vorteil ist. In Kapitel 5 und 6 dieser Arbeit habe ich zwei andere Merkmale untersucht, die beim Invasionserfolg von *A. petiolata* eine wichtige Rolle spielen könnten.

In Kapitel 5 wird untersucht, inwiefern *A. petiolata* allelopathisch, d.h. mittels durch Wurzeln abgesonderte organische Verbindungen, die Keimung anderer Pflanzen hemmt. Hierzu wurden Samen von *Geum urbanum* und *Geum laciniatum*, zweier Arten, die im einheimischen bzw. invasiven Areal zusammen mit *A. petiolata* vorkommen, auf Boden gekeimt, in dem vorher *A. petiolata* gewachsen war. Zur Hälfte des Versuchs wurde Aktivkohle beigemischt, die organische Substanzen adsorbiert. Die Aktivkohle hatte einen deutlich positiven Effekt auf die Keimung der beiden *Geum*-Arten, was darauf schließen lässt, dass *A. petiolata* den Boden mit einer keimungshemmenden Substanz kontaminiert hatte. Die Stärke dieses allelopathischen Effekts hing aber sowohl von der Herkunft der Zielart als auch der *Alliaria*-Population ab. Die Keimung der europäischen *Geum*-Art wurde nur durch einheimische, also europäische, *Alliaria*-Pflanzen gehemmt. Dieses Experiment ist der erste Beweis dafür, dass *A. petiolata* allelopathisch die Keimung anderer Arten beeinflusst. Es zeigt zudem, dass allelopathische Effekte komplex und artabhängig sind.

Kapitel 6 vergleicht einheimische und invasive Populationen von *A. petiolata* hinsichtlich ihrer phänotypischen Plastizität und Integration. Phänotypische Plastizität, die Fähigkeit eines Genotypen, umweltabhängig verschiedene Phänotypen auszubilden, sollte bei der Besiedlung neuer Areale vorteilhaft sein. Phänotypische Integration, die Korrelationsstruktur zwischen Merkmalen, hingegen wirkt einschränkend auf evolutionäre Prozesse. In invasiven Populationen sollte deshalb Selektion für Plastizität, aber gegen phänotypische Integration stattfinden. Um diese Hypothese zu testen, führte ich ein Beschattungsexperiment durch. Ich fand genetische Variation in Plastizität zwischen Populationen, aber keinen Unterschied zwischen einheimischen und invasiven Populationen in der Plastizität einzelner Merkmale. Die Korrelationsstruktur invasiver Populationen wurde jedoch durch Beschattung stärker verändert, was man als größere multivariate Plastizität interpretieren kann. Möglicherweise findet im neuen Areal tatsächlich eine Selektion in Richtung phänotypischer Flexibilität statt.

Im experimentellen Teil meiner Arbeit habe ich herausgefunden, dass invasive Populationen von *Alliaria petiolata* weniger resistent gegen einen spezialisierten Herbivoren und weniger konkurrenzstark sind, und dass sie größere multivariate Plastizität aufweisen als einheimische Populationen. Ich konnte außerdem zeigen, dass *A. petiolata* durch allelopathische Substanzen die Keimung anderer Arten hemmen kann. Die Invasion von *Alliaria petiolata* kann nicht durch die EICA-Hypothese erklärt werden. Stattdessen spielen vermutlich Allelopathie und phänotypische Plastizität eine wichtige Rolle. Der experimentelle Vergleich einheimischer und invasiver Genotypen unter kontrollierten Bedingungen hat sich als gute Methode bewährt, um evolutionäre Prozesse bei Invasionen zu untersuchen.

Um den Invasionserfolg von *Alliaria petiolata* besser zu verstehen, sollte in Zukunft folgendes besser untersucht werden: (1) Pflanzengröße, Herbivorie und Populationsdynamik in natürlichen Populationen des einheimischen und invasiven Areals, (2) chemische und molekulare Grundlagen der Verteidigung gegen spezialisierte Herbivore, (3) Wechselwirkungen zwischen *A. petiolata* und seinen Konkurrenten, die über Allelopathie oder Bodenorganismen vermittelt werden, sowie (4) mit Hilfe von molekularen Markern der Ursprung der invasiven Populationen, die Anzahl der Einführungen, und die genetische Diversität in einheimischen und invasiven Areal. Das evolutionäre Potential einer invasiven Art hängt nicht zuletzt davon ab, wie viel genetische Variation ihr zur Verfügung steht.

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Dissertation	<p><i>Ecological genetics of plant invasions: a case study on <i>Alliaria petiolata</i></i> (2004)</p> <p>Supervision: Dr. H. Auge, Dr. D. Prati (Department of Community Ecology, UFZ Centre for Environmental Research Halle), Prof. B. Schmid (Institute of Environmental Sciences, University of Zurich)</p>
Publications	<p>Bossdorf O, Schurr F, Schumacher J (2000) Spatial patterns of plant association in grazed and ungrazed shrublands in the semi-arid Karoo, South Africa. <i>J Veg Sci</i> 11: 253-258.</p> <p>Bossdorf O, Prati D, Auge H, Schmid B (2004) Decreased competitive ability in an invasive plant. <i>Ecol Lett</i> 7: 346-353.</p>

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Erklärung

Hiermit erkläre ich, dass ich bei der selbständigen Abfassung meiner Dissertation keine anderen Quellen und Hilfsmittel als die darin angegebenen benutzt habe.

Halle, den 31. März 2004

Oliver Boßdorf