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Plant invasion, insect herbivory and competition: insights into the ecological interactions between invasive goldenrod (*Solidago canadensis*) and native tansy (*Tanacetum vulgare*)

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"..the study of invasions has resulted in significant intellectual shifts in the way that old paradigms are perceived by ecologists and have led us into new and uncharted territory."

(Ragan M. Callaway and John L. Maron; 2006)

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Preface

This PhD-thesis “Plant invasion, insect herbivory and competition: insights into the ecological interactions between invasive goldenrod (*Solidago canadensis*) and native tansy (*Tanacetum vulgare*)” was designed to contribute to a better understanding in fundamental mechanisms of invasive plants to have higher performance in the invaded range and the response of native plants in the altered environment. In this thesis several approaches were used to investigate the interaction of different processes which are adaptation, competition and herbivory and their effects on performance of native and invasive plants and their herbivores, which indirectly will affect higher trophic levels. Each of these issues is represented in an autonomous research paper.

As a general introduction, chapter 1 describes the importance of a better understanding of biological invasions. It includes different mechanism that are proposed to explain better performance for invasive species in the invaded range.

The following chapters (chapter 2-6) attempt to answer the following questions: i) Are invasive plants performing differently in their invaded compared to their native range (chapter 2, 3)? ii) What are the best mechanisms that can explain different performance of invasive plants (chapter 3, 4, 5)? iii) What is the response of native plants to the invaded environment (chapter 3, 4)? iv) What is the effect of invasive species on the native herbivores and higher trophic level (chapter 5, 6)?

In chapter 7, the specific research topics are discussed from a general perspective. In the following, the references of the introduction and discussion are cited. The publications that derived from this project are attached in the appendix, and last but not least the acknowledgements.

Summary

There is no doubt that plant invasions are threatening biodiversity and altering fundamental ecosystem processes worldwide, but scientists are still looking for answers to basic questions about the mechanisms, which help invasion. Better performance of invasive species often is due to a release of invasive plants from their herbivores in the invaded range. Invasive plants then show increased competitive ability due to a shift of resources from defence into growth. Yet, the outcome of competition between an invasive and a particular native plant does also depend on other factors such as the interaction of the native plant with its herbivores or previous exposure of the plant to the competitor. As model system, goldenrod (*Solidago canadensis* L.) which is a successful invasive plant in Europe, and its co-occurring native plant tansy (*Tanacetum vulgare* L.) which is aggressively invading a variety of habitats throughout the United States, were used. These two species present an interesting case of mutual invasion. To understand if invasive plants have the ability to increase their invaded range, in chapter 2 the current distribution of native tansy and invasive goldenrod were compared to their distribution 10 years ago in a field survey. In chapter 3, individual performance of native and invasive plants in both their invasive and native range was compared in a field experiment. A greenhouse was used to compare performance of plants which were grown from seeds collected in their native and invaded range in chapter 3. The outcomes of competition between tansy and goldenrod were tested in the presence and absence of experimental herbivory in chapter 3 by spraying with insecticide in a field. In chapter 4 intra- vs. interspecific competition of tansy and goldenrod grown in pairs with different types of herbivory were contrasted. Therefore, the caterpillar *Spodoptera* was placed on either one plant, both plants, or no plants. As a control, single plants were grown with and without herbivory. Competition history of the tansy seeds used in the experiment in chapter 4 was also manipulated: they either were collected from tansy growing in the vicinity of goldenrod, or from plants that had grown without competition to goldenrod in the field. In addition, the effect of invasive plant competition on native herbivores and higher trophic level was studied in a greenhouse experiment in chapter 5 and 6. Results showed that after being introduced to a new area, invasive goldenrod increased its invaded range and both tansy and goldenrod appear to have higher performance in their exotic than in their native range. For both plant species, competition reduced plant performance. For goldenrod, interspecific competition was stronger than intraspecific competition. In contrast, plant performance was more strongly reduced by intraspecific competition for tansy. Because herbivory on both species was lower in the invaded ranges, enemy release could underlie these differences in performance between the native and invaded ranges. For tansy, insecticide application increased biomass in the native range in Europe and decreased it in USA. In addition goldenrod had higher performance when caterpillars were only present on tansy, supporting the enemy release hypothesis in both field and greenhouse experiments. For goldenrod, however, adding caterpillar or removing herbivory by insecticide treatment did not increase performance. We found strong evidence that plants in the invaded ranges differed from those in the native habitat: as in the greenhouse experiment, plants derived from populations in the invaded range were larger than plants from populations in the native range, which is consistent with the EICA hypothesis. The effect of competition history was surprisingly strong. When the competitor was goldenrod, tansy with competition history had more biomass. Our results showed that the main effect of competition was the reduced size of competing plants. Therefore native-invasive plant competition not only decreased the quality of native plants but also affected their herbivores, this can consequently have an effect on higher trophic levels and therefore the biodiversity of the habitat as well. Our results give no support to the hypothesis that tansy will be outcompeted by the successful invader goldenrod. In contrast, the low impact of competition by the invasive goldenrod on native tansy performance indicates the potential for at least temporary coexistence of tansy and goldenrod in USA and stable coexistence in Europe. It is concluded that coexistence of two competing species is possible when intraspecific competition over-rules interspecific competition. The other possibility is that evolution may help native plants to adapt to the new environments, which may contribute to the coexistence between two species.

Zusammenfassung

Es besteht kein Zweifel darin, dass invasive Pflanzen eine Bedrohung für Biodiversität darstellen und fundamentale Ökosystemfunktionen weltweit verändern können, dennoch sucht die Wissenschaft immer noch nach Antworten auf grundlegende Fragen zu den Mechanismen die Invasionen begünstigen. Eine bessere Leistungsfähigkeit invasiver Arten ist oft einer Befreiung invasiver Pflanzen von deren Herbivoren im neuen Lebensraum geschuldet. Invasive Pflanzen zeigen dann eine erhöhte Konkurrenzfähigkeit da sie Ressourcen von der Verteidigung zum Wachstum verlagern können. Dennoch kann das Ergebnis von Konkurrenz zwischen einer invasiven Pflanze und bestimmten heimischen Pflanzen von weiteren Faktoren abhängig sein, wie zum Beispiel von der Interaktion zwischen den heimischen Pflanzen und deren Herbivoren oder früherer Exposition der Pflanze mit ihrem Konkurrenten. Als Modellsystem wurden Goldrute (*Solidago canadensis* L.) -eine erfolgreiche invasive Pflanze in Europa- und der gemeinsam auftretende heimische Rainfarn (*Tanacetum vulgare* L.) –welcher sich in einer Vielfalt an Habitaten in den USA aggressiv ausbreitet- verwendet. Diese zwei Arten repräsentieren einen interessanten Fall von gegenseitiger Ausbreitung. Um zu verstehen, ob invasive Arten die Fähigkeit besitzen ihren neuen Lebensraum auszuweiten wurde in Kapitel 2 die heutige Verbreitung heimischen Rainfarns und invasiver Goldrute mit der Verbreitung vor 10 Jahren in einer Freilandstudie verglichen. In Kapitel 3 wurde in einer Freilanduntersuchung die individuelle Leistungsfähigkeit von heimischen und invasiven Pflanzen sowohl im heimischen als auch im neuen Lebensraum verglichen. Um die Leistungsfähigkeit von Pflanzen zu vergleichen wurden in einem Gewächshausexperiment Goldrute und Rainfarn aus Samen des heimischen und des neuen Lebensraum angezogen (Kapitel 3). Das Ergebnis dieser Konkurrenz zwischen Rainfarn und Goldrute wurde des Weiteren unter Anwesenheit und Abwesenheit von experimenteller Herbivorie getestet. Um Herbivorie im Feldversuch auszuschließen wurde ein Insektizid gesprüht (Kapitel 3). In Kapitel 4 wurden die intra- und interspezifische Konkurrenz von Rainfarn und Goldrute die als Paare angezogen wurden mit unterschiedlichen Arten von Herbivorie getestet. Dafür wurden *Spodoptera* Raupen auf eine der Pflanzen, beide Pflanzen oder keine der beiden Pflanzen der Rainfarn Goldruten Paare gesetzt. Zur Kontrolle wurden einzelne Pflanzen mit und ohne Herbivorie getestet. In Kapitel 4 wurde außerdem die „Konkurrenz-Erfahrung" der verwendeten Rainfarn-Samen manipuliert: sie wurden entweder von Pflanzen gesammelt, welche im Freiland in der unmittelbaren Nähe von Goldrute oder ohne Konkurrenz mit Goldrute gewachsen waren. Zusätzlich wurde in Kapitel 5 und 6 der Einfluss von Konkurrenz invasiver Pflanzen auf heimische Herbivore und höhere trophische Ebenen im Gewächshaus untersucht. Die Ergebnisse zeigen, dass invasive Goldrute in der Lage war ihren

Lebensraum auszuweiten nachdem sie neu eingeführt wurde, und dass sowohl Rainfarn als auch Goldrute eine höhere Leistungsfähigkeit im neuen Lebensraum haben. Für beide Pflanzenarten reduzierte Konkurrenz mit anderen Pflanzen die Leistungsfähigkeit. Für Goldrute war der interspezifische Konkurrenzdruck größer als der intraspezifische Konkurrenzdruck. Im Gegensatz dazu wurde die Leistungsfähigkeit von Rainfarn stärker durch intraspezifische Konkurrenz reduziert. Für beide Arten waren die Herbivorieraten im neuen Lebensraum geringer, was möglicherweise an einer Befreiung von Fraßfeinden liegt und somit auch den Unterschieden in der Leistungsfähigkeit erklären könnte. Für Rainfarn führte das Applizieren von Insektiziden zu einer Zunahme an Biomasse im heimischen Lebensraum und zu einer Abnahme der Biomasse in den USA. Zusätzlich hatte Goldrute eine erhöhte Leistungsfähigkeit wenn Raupen nur auf Rainfarn vorhanden waren, was die „Enemy- Release" Hypothese sowohl im Freiland als auch im Gewächshaus bestätigt. Andererseits führten weder das Hinzufügen von Raupen noch die Behandlung mit Insektiziden zu einer erhöhten Leistungsfähigkeit von Goldrute.Wir fanden überzeugende Hinweise darauf dass sich Pflanzen im neuen Lebensraum von denen im heimischen Lebensraum unterscheiden: im Gewächshausexperiment waren Pflanzen aus dem neuen Lebensraum größer als Pflanzen aus dem heimischen Lebensraum, was die „EICA" Hypothese bestätigt. Der Effekt von „Konkurrenz-Erfahrung" war überraschend stark. Mit Goldrute als Konkurrent hatte Rainfarn eine höhere Biomasse. Unsere Ergebnisse zeigen, dass der Haupteffekt von Konkurrenz die verringerte Größe der konkurrierenden Pflanzen war. Das bedeutet dass die Konkurrenz zwischen heimischen und invasiven Pflanzen nicht nur die Qualität heimischer Pflanzen verringert, sondern auch deren Herbivore beeinflusst, was wiederrum einen Effekt auf die höheren trophischen Ebenen und somit auf die gesamte Biodiversität des Habitats haben kann. Unsere Ergebnisse stützen die Erwartung, dass Rainfarn durch die erfolgreiche invasive Goldrute verdrängt wird nicht. Im Gegenteil deuten der geringe Einfluss von Konkurrenz durch die invasive Goldrute mit heimischem Rainfarn auf eine potentielle (zumindest zeitweise) Koexistenz von Rainfarn und Goldrute in den USA und eine stabile Koexistenz in Europa hin. Es kann gefolgert werden, dass die Koexistenz zweier konkurrierender Arten möglich ist, wenn intraspezifische Konkurrenz die interspezifische Konkurrenz übertrifft. Eine weitere Möglichkeit ist, dass evolutionäre Mechanismen der heimischen Pflanzen dabei helfen, sich an die veränderten Umweltbedingungen anzupassen was zu einer Koexistenz zweier Arten beiträgt.

Chapter 1

General introduction

1-1 Biological invasion: Concepts and definitions

In recent years, more attention has been drawn to the wide-ranging impacts of the worldwide increase of invasive species and their globally rising effect on ecosystems biodiversity, agriculture, and public health (Doorduin and Vrieling 2011). Invasive species are species that become dominant out of their native range and cause harm to the ecosystems they invade (Crawley 1986, Mack et al. 2000, Keane and Crawley 2002). Indeed, biological invasion is the disruption of natural communities and ecosystems by the increase in distribution and abundance of invasive species (Barbier 2001, Keane and Crawley 2002, Valery et al. 2008). It is the outcome of the successful transport, colonization, and subsequent spread of species in areas not previously occupied (Richardson et al. 2000, Keane and Crawley 2002). With the onset of modern global transportation and commerce which overcomes biogeographic barriers, the frequency and rapidity at which novel species are introduced to new areas has dramatically increased (Van der Putten et al. 2010).

1-2 The global effect of invasive species

Whether deliberate or accidental, this movement of species represents one of the most important conservation concerns (Mack et al. 2000, Pimentel et al. 2000). Successful invaders can impact the abundances of native species (Colautti and MacIsaac 2004, Fridley et al. 2007) or even exclude native species due to competition, trophic interaction or change in abiotic condition (Tilman and Lehman 2001). They increase the homogenization of the global community composition (Olden and Poff 2003, McKinney 2004) and can alter ecosystem function and cause a decrease in biodiversity (Mack et al. 2000, Pimentel et al. 2000, Colautti and MacIsaac 2004, DeWalt et al. 2004, DeAngelo et al. 2007). Invasive plants may also have cascading effects within the food web and impact higher trophic levels associated with plants impacted by invaders (Simao et al. 2010). Finally they also cause billions of dollars of economic damage, especially when invasive species affect agricultural ecosystems (Mack et al. 2000, Pimentel et al. 2000, Foster and Motzkin 2003, Colautti and MacIsaac 2004, Henderson et al. 2006). In the United States, the cumulative losses from harmful invaders were estimated to be almost $100 billion, and rising annually (Barbier 2001). Indeed, not only the severity of the problems caused by invasive plants is increasing but the number of new arising problems seems to be increasing as well. The number of species moved out of their native ranges by accidental or intentional introduction is increasing (Lockwood et al. 2007). The negative effects of some invasive species have grown too large to ignore. Every year there are many species which are introduced into new areas but few of them become successful invasive species (Williamson and Fitter 1996), yet it is still not clear how invasive plants which are minor components of their native communities, become dominant components of invaded communities (Callaway and Maron 2006). Consequently, to limit the environmental impacts of invasive species, we need to understand the mechanisms behind exotic invasions that help only some species become invasive (Keane and Crawley 2002).

1-3 What causes a species to become invasive? Mechanisms of how invasive species take over plant communities

Several mechanisms have been formulated on how invasive plants are able to become dominant in their new environment. They also look at factors that have been proposed to limit the invasion success of an invasive plant. Here I briefly discuss the main mechanisms on success and limitation of plant invasion.

1-3-1 Invasive species outcompete native plant species

Competition is a primary ecological process and refers to any direct or indirect negative interference of one plant with another (Fowler 1986, Casper and Jackson 1997). Individuals within a plant community typically suffer from competition through reduced fecundity, growth rate, performance, nutrient uptake, and consequently the nutritional quality of the plant's tissue and phloem (Schädler et al. 2007). Evolutionary theory states that competition plays an important role in natural selection and affects ongoing processes in the structuring and other dynamics of populations (Bengtsson 1991). The presence of competitors may influence the regional distribution of plants by affecting probabilities of extinction or colonization (Goldberg and Barton 1992). Therefore, it is necessary to understand the role of intra- and interspecific competition which determines the species distribution an abundance when investigating the effects of invasive plants on native communities (Mangla et al. 2011).

For a plant to become invasive, it has to outcompete plants from the native community (Sakai et al. 2001, Vila and Weiner 2004). Pair-wise experiments between invading and native plant species suggest that the effect of invasive species on native is usually stronger than vice versa (Vila and Weiner 2004). High competitive ability of non-native species has been mentioned as a key factor promoting successful invasive potential. Indeed, many researchers have demonstrated invasive plants to be competitively superior compared to native species (Vila and Weiner 2004, Abela-

Hofbauerova and Munzbergova 2011, Ferrero-Serrano et al. 2011, Evans et al. 2013, Kumschick et al. 2013, Parker et al. 2013, te Beest et al. 2013). Thereby native plant species can be displaced by invasive species (Paini et al. 2008). However, competition can have indirect influences as well. Negative effects of neighbours due to consumption of limited resources can be one example. In this case the dominance of an invader can be attributed to other factors than competition itself, such as interaction with herbivores (Vila and Weiner 2004).

1-3-2 Invasive species are often free of herbivory – the enemy release hypothesis (ERH)

Herbivory is an antagonistic relationship between plants and animals (-/+) and can modify the growth rate and other plant traits determining the performance and competitive ability of plants (Crawley 1983, Louda et al. 1990b, Maron and Vila 2001, Levine et al. 2004). Even low herbivores densities may have significant effects on plant performance and fecundity (Crawley 1983). Indeed lots of studies illustrate that herbivory can have a strong effect on fitness and population dynamics of their host plant. This is confirmed furthermore by lots of successful classical biological control in controlling the population dynamics of invasive plants (Colautti et al. 2004). Suffering less from herbivory damage in the invaded range, may help invasive plants to be competitively superior. Escaping from native herbivores is believed to be one of the primary causes contributing to the successful invasion of many invasive plants. The “enemy release hypothesis” (ERH) (Maron and Vila 2001, Keane and Crawley 2002, Colautti et al. 2004) is one of the most important hypotheses for explaining the success of invasive plants in their new area and was confirmed by a number of recently published studies (Fenner and Lee 2001, Keane and Crawley 2002, Mitchell and Power 2003, Torchin et al. 2003, Reinhart and Callaway 2004, Stastny et al. 2005, Callaway and Maron 2006, Liu et al. 2007). The enemy release hypothesis (ERH) states that invasive species are able to succeed in the new habitat because they are not attacked by specialist herbivores that kept their population in check in the native range. This is because often only the plant is transported into the area but not the herbivores specific to the them. This hypothesis is based on a three-point logical argument: (1) natural enemies have the ability to keep population in check and are important regulators; (2) the effect of enemies is greater on native than on invasive plants; and (3) invasive plants gains a reduction in enemy regulation, resulting in increased population growth (Keane and Crawley 2002). Being free from their natural enemies can greatly benefit invasive species which are competing with native plants because herbivory can alter or even reverse the outcome of competition. In general, herbivores do not need to consume a large amount of plant material in order to have a large effect on plant community composition, they need only reverse the outcome of competition (Louda et al. 1990a). Until now, only few experiments have explicitly compared the effects of competition and herbivory in both the native and invaded range (Callaway and Aschehoug 2000, Rogers and Siemann 2004). With a clearer understanding of the role of enemy release in exotic plant invasions, we can begin to build a comprehensive predictive model of exotic plant invasions (Keane and Crawley 2002).

1-3-3 Invasive species evolve to better competitors in their new habitat – The Evolution of Increased Competitive Ability (EICA)

The hypothesis of the evolution of increased competitive ability hypothesis (EICA, Blossey and Nötzold 1995) is an extension of the ERH hypothesis. The ERH-hypothesis proposes that the release from coevolved herbivores can initiate an evolutionary change resulting into the success of many invasive plants (Wolfe et al. 2004, Felker-Quinn et al. 2013). If invasive plants are considered to be more vigours in the new area, insect herbivores may contribute to this fact because invasive plants frequently have low losses to herbivores in their introduced range (Siemann and Rogers 2003). Consequently invasive plants may evolve to be competitively superior, by allocating resources previously needed for anti-herbivore defense into growth (Blossey and Nötzold 1995, Thebaud and Simberloff 2001, Leger and Rice 2003, Wolfe et al. 2004). Then their performance is likely to increase in the invaded range compared with their native range (Blossey and Nötzold 1995, Leger and Rice 2003, Wolfe et al. 2004).

Using the common garden approach, a number of studies confirmed the EICA hypothesis. They show that individuals of plants sampled from the invaded range had a higher performance than plants of the same species growing in their native range (Siemann and Rogers 2001, Wolfe 2002, Blair and Wolfe 2004). Beaton et al. (2011) provide evidence for EICA in the noxious grassland invader *Lespedeza cuneata*, by comparing the native (Japanese) genotypes. They show that the invasive genotype was a better competitor than the native genotype. Their results suggest that selection has played a essential role in shaping this invasive plant species into a more aggressive, but less constitutively defended competitor. However, this general rule was not confirmed for all species tested (Willis et al. 2000).

1-3-4 Invasive species competition via allelopathy– New weapon

The role of consumer interactions in plant invasions is crucial, but interactions between plants as determinants of invasive success have been overlooked (Callaway and Ridenour 2004). One mode of competition between plants is to release allelochemicals (toxic metabolites) into the environment (Inderjit et al. 2006). Long-term species associations allow co-evolution of tolerance to the biochemical effects of neighbors. This tolerance is absent in new associations in novel habitats. The novel weapons hypothesis states that some invasive species transform from native weaklings to invasive bullies by exuding biochemicals that are highly inhibitory (allelopathic) to other plants species (Callaway and Ridenour 2004). Such plants with allelopathic effects, can reduce fitness, seed germination, or growth of affected plants (Callaway and Aschehoug 2000, Inderjit and Callaway 2003, Callaway and Ridenour 2004, Cappuccino and Arnason 2006). For example, root exudates and root extracts of goldenrod, *Solidago canadensis*, have been documented to have an inhibitory effect on the growth of competing plants (Butcko and Jensen 2002, Abhilasha et al. 2008).

In addition to affecting plants, allelochemicals produced by a plant can also act as feeding deterrents for herbivores, and may reduce herbivore growth rates, resulting in e.g. smaller adult size and increased mortality (Harvey et al. 2005). However, potential cascading effects of allelochemicals on herbivores feeding on co-occurring plants, that do not have the ability to produce allelochemicals itself are unclear.

1-4 Native species and the outcome of competition with invasive plants

The effect of interspecific competition between an invasive and a native plant in the invaded community can be larger, smaller or similar in magnitude compared to the intraspecific competition by other individuals of the same native plant (Bengtsson 1991, Mangla et al. 2011). This can lead to exclusion, facilitation or coexistence between invasive and native plants (Aarssen 1983). The outcome of competition between an invasive and a particular native plant does depend on properties of the native plant and may depend on other factors such as native plant traits or previous exposure of the native plant to the competitor (Leger 2008). Consequently, invasive plants might exclude not all native plants under all conditions.

1-4-1 Natives evolved to the presence of an invasive plant

Because of the dramatic effects of invasive species in invaded communities, the environment for native plants can be changed. Consequently, native species might be exposed to new selective pressures due to the presence of invaders. They have to adapt to the new habitat or they may eventually go extinct (Leger 2008). To date there are few studies that address the most fundamental question of whether there are any ecological differences between native plants growing in invaded and uninvaded areas (Lau 2006, Leger 2008). Whether native species can evolve in response to the effects of exotic species invasion is very important for the future of native plant communities (Leger 2008). The best way of testing for an evolutionary change in the resident plant community is to compare the growth of native plants that were never in contact with invasive plants to those from communities invaded by invasive plants.

1-4-2 Native herbivores and the effect of invasive plants on them

The success of invasive plant species in their new range, in turn, also depends on the interactions with native plants and herbivore. By competing and excluding native plants, invasive can affect native communities and also by disrupting a wide range of trophic interactions that are associated with them (Bezemer et al. 2014). They may influence associated herbivores, which can have strong ecological consequences (Simao et al. 2010). Insects such as pollinators, decomposers, and predators of pest insects are important links in the food web and influence ecosystems (Simao et al. 2010). As a new resource invasive plants can affect the performance of native insect herbivores and their natural enemies such as parasitoids and predators, and this can lead to decrease population of these herbivores and natural enemies (Bezemer et al. 2014). Although, lots of studies has demonstrated the negative impact of invasive plants in their new range, few studies have explicitly included interactions with other trophic levels, such as interactions between invasive plants, herbivores and their natural enemies (Bezemer et al. 2014). By gaining a better understanding of the mechanisms through which invasive plants alter arthropod habitats one could predict whether herbivore groups will respond positively or negatively to plant invasions (Simao et al. 2010, Bezemer et al. 2014).

1-5 The study system

Designing an experimental study so that the invasive species of interest is occupying a similar habitat to native species can provide a better understanding of the mechanisms responsible for invasion. Using field observations and historical characteristics of an invasive plants can reveal many important facts about the performance of plant species under natural conditions. However experimental manipulations are more likely to reveal single mechanisms responsible for the dominance of an aggressive invasive species and its interaction with native plants (Rogers and Siemann 2004).

In this thesis, I describe a complementary suite of experimental field studies, as well as greenhouse studies examining how enhancing or reducing insect herbivory, competition and competition history influences the success of invasive plant species. My work involves long-term monitoring, field and common garden and greenhouse experiments. In this study, I used goldenrod (*Solidago canadensis* L.) which is a successful invasive plant in Europe, and its co-occurring native plant tansy (*Tanacetum vulgare* L.) which is aggressively invading a variety of habitats throughout the United States, as a model system. As these two species present an interesting case of mutual invasion and they co-occurrence, they are a good model to investigate the effects of competitors in both native and invaded range with and without herbivores. In my thesis I examine if this mutual invasion leads to a reversal of competitive hierarchies in the two different areas, Europe and the USA.

Goldenrod

Goldenrod (*Solidago canadensis* L.) was chosen because it is documented as being allelopathic, it is important in successional systems, has a high potential to expand its current geographical range and is becoming invasive worldwide (Weber 1998, 2000b, 2001). Goldenrod was introduced to Europe as an ornamental plant 100 years ago.

Considering the large native ranges of goldenrod in northern America (from Florida to Canada along the east coast), it is not surprising that its potential distribution covers large parts of Europe (Weber 2001). Although goldenrod is widely recognized as one of the most aggressive invasive species, there is little knowledge of its actual distribution in Europe. Goldenrod can overwhelm natural communities by outcompeting native plant communities and reducing the species diversity (Priede 2008). Goldenrod is often a component of the weedy vegetation on abandoned pastures and unmanaged roadsides as well as in human-disturbed habitats in urban areas and settlements (Weber 2001, Priede 2008, Walter and Binimelis 2009). Goldenrod is frequently attacked by insect herbivores in its native habitats (Maddox and Root 1990, Root and Cappuccino 1992, Fontes et al. 1994), unlike the situation in Europe where herbivory has usually little influence on invasive goldenrods (Guesewell et al. 2006, Jacobs 2008).

Tansy

Tansy (*Tanacetum vulgare* L.) is a perennial, herbaceous plant, native to Europe and is normally found along roadsides and railroads, fields and pastures, ditch banks, riparian areas, and other moist places (Mitch 1992a). Volatile oils produced in the leaves and flowers deter grazing by cows and horses. Historically, the oils have been used medicinally and the literature is fairly rich in common tansy’s pharmacological characteristics, but scant in its invasive ecology. Escaped cultivated plants brought to North America as early as the 1600’s are most likely the original sources of common tansy infestations. Today, tansy is common in riverbanks, wastelands, along roadsides, and in rural and urban-industrial areas (Rebele 2000). Populations often grow in thick clumps that crowd out grasses, forbs, and shrubs resulting in reduced livestock forage and wildlife habitat. In the native range tansy hosts more than 23 aphid species (Blackman and Eastop 2006, Holman 2009).

Tansy aphids

One of the specialized herbivores on tansy is the tansy aphid (*Macrosiphoniella tanacetaria*, Hemiptera: Aphididae, Kaltenbach). It has wingless oviparae and winged males. This species produce both sexual and asexual morphs (holocylic) spends its complete life-cycle on tansy plant (monoecious). The distribution of this species includes Europe, West Asia, Siberia and it has been introduced to America (Blackman and Eastop 2006). It is not ant–attended (Stadler 2004) and feeds in loose colonies mainly on new shoots and flowering heads of tansy.

1-6 Research objective

The general aim of this study is to increase knowledge about the effect of invasive plants on native vegetation. In my thesis I use a number of approaches to investigate the interaction of different processes which are adaptation, competition and herbivory and their effect on growth, survival and reproduction of native and invasive plants and their herbivores which indirectly will affect higher trophic level. More specifically, the objectives were:

- To compare the performance of invasive plants in their invasive and native range (Chapter 2, 3).
- To explore different mechanisms that can explain a higher performance in the invaded range such as

  i) release from herbivores (Chapter 3, 4), ii) evolution effect (Chapter 3, 4), iii) competition via allelopathy (Chapter 5)

- To investigate the outcome of competitive interactions between native and invasive plants and to see if these outcomes are different with adding or removing herbivory (Chapter 3, 4, 5).
- To study the response of native plants to the invaded environment (Chapter 3, 4, 5).
- To understand the effect of invasive species on the native herbivores and higher trophic level (Chapter 5, 6).

Chapter 2

Does invasive goldenrod replace tansy in Germany?

Abstract

Invasive species are thought to lead to declines in native species diversity. Yet, the long-term impacts of such invasions on community structure are poorly understood. Once invasive plants have successfully colonized a habitat, their control is difficult and expensive. In 2011/2013, we conducted a survey where we revisited sites which were mapped in 2001 for the occurrence of tansy in Jena, Germany. We wanted to monitor how many of them are still occupied by tansy or whether invasion and competitive replacement by goldenrod had occurred. In most of the sites tansy was still present (81%) and our results provide only little indication of exclusion of tansy by goldenrod (3% of sites). But about 26% of sites occupied by tansy in 2001 were replaced by human activity in 2011/2013. In the some sites where tansy was occurring, it was co-occurring with goldenrod and these two plants still coexisted (59% of sites with vegetation). In contrast to our hypothesis, tansy was not replaced by goldenrod invasion over a period of 10 years and these two plants coexisted in most of the sites where tansy occurred. Consequently, our result does not indicate a danger of tansy to be replaced by goldenrod in Germany. In contrast, our results showed a danger of management and building activates which are destroying habitats of tansy (and goldenrod).

Key words: goldenrod, tansy, survey, coexistence.

Introduction

In a world without borders, the accidental or intentional introduction of non-native organisms continues to threaten natural and agricultural ecosystems worldwide (Agrawal and Kotanen 2003). Few if any areas remain sheltered from these immigrations and some areas are subject to high rates of invasion (Mack et al. 2000, Keane and Crawley 2002) which cause serious economic and social costs (Davis et al. 2000, Abramova 2012). Once invasive plants have successfully colonized a habitat, their control is difficult and expensive (Blossey and Hunt 1999, Shuster et al. 2005).

The probability of successful invasion increases with longer time since the first introduction. Because with time increases the chance that safe sites for establishment appear, as a result of natural disturbances and human-made changes in site conditions (Pyšek and Jarošík 2005). The massive disturbances created by city growth not only destroy the habitat of native species but they create habitat for invasive species that are adapting to urban and suburban conditions (McKinney 2006). In roughly 300 cases, introduced plant species have been demonstrated to spread in and have negative effects on urban and sub-urban areas where they have become invasive (Dozier 2000). These potentially heavily infested urban areas may also serve as jumping off points for invasion into natural areas (McKinney and Lockwood 1999, Dozier 2000).

Invasive species not only cause costs in urban and natural areas but also have important biological impacts. Successful invasive species often replace native species causing local and global extinctions (Bennett and Owens 1997, McKinney and Lockwood 1999, Rahel 2002). Thereby invasions can reduce biodiversity because of the replacement of specialized native species by widespread invasive species (Lockwood et al. 2000) and promote biotic homogenization resulting in the loss of local and regional distinctiveness (McKinney 2004).

While many studies focused on the mechanisms of invasion and their impacts, relatively little attention has been directed to the long-term consequences of invasive species on native plants (Olden and Poff 2003, McKinney 2004, Phillips et al. 2007). Thus to evaluate the current status of invasive species distribution and their actual effect on the invaded community over a time period, invasive plant surveys and motoring is necessary. These help to document replacement of vegetation by invasive species and studying of expansion ranges leads to a better understanding of the reasons of success and failures of invaders and also the potential for their future spread (Weber 1998). Few empirical studies have been done to measure whether the actual effect of invasive spices, either extinction or replacement of native, does and does not occur in different sites along a time period (Phillips et al. 2007).

Goldenrod (*Solidago canadensis* L.) is a good model system of invasive plants to study as Weber (2001) already suggests goldenrod has a high potential to expand its current geographical range. Goldenrod was introduced to Europe as ornamental plant and now is one of the most aggressive weeds in its invaded range. Considering the large native ranges of goldenrod in northern America (from Florida to Canada along the east coast), it is not surprising that the potential distribution of the species covers large parts of Europe (Weber 2001) and in particular Germany. Although goldenrod is widely recognized as one of the most aggressive invasive species, there is little knowledge on its actual distribution in Germany. Goldenrod may overwhelm the natural communities outcompeting the native plant communities and locally reducing the species diversity (Priede 2008). Often it is a weedy component of vegetation on abandoned pastures and unmanaged roadsides as well as in human-disturbed habitats in urban areas and settlements (Weber 2001, Priede 2008, Walter and Binimelis 2009). There, it frequently co-occurs with tansy (*Tanacetum vulgare*) one important native plant in Europe use for medical purposes (Keskitalo et al. 2001, Dragland et al. 2005). Tansy also introduced to Europe and now it considered as a serious pest along fencerows, urban areas and roadside (Mitch 1992a). As both of these species are of management concern, their movement and range expansion are of particular interest. Because at least in Germany there are worries, that tansy might be replaced by goldenrod over time.

In 2011/2013, we conducted a survey of 255 sites in Jena revisiting sites that were mapped in 2001 for the occurrence of tansy. We aimed at monitoring how many sites remained occupied by tansy in Jena- Germany or whether invasion and competitive replacement by goldenrod occurred. We hypothesized that I) goldenrod is increasing its invaded range and II) tansy is suffering from the invasion of goldenrod in its habitats being excluding over time.

Materials and Methods

Model system:

Goldenrod

Goldenrod (*Solidago canadensis* L.) is native to North America and has been introduced to Europe as garden ornamentals in the 17th century (Hartnett and Bazzaz 1985, Weber 1998, 2000a). Goldenrod in its native range occurs in tall grass prairies and light forest edges. It develops relatively stable secondary communities in old fields (Hartnett and Bazzaz 1985). Likewise tansy, goldenrod also is sensitive to management and mowing and by mowing shoot density of goldenrod will decrease strongly (Kabuce 2006).

Tansy

Tansy (*Tanacetum vulgare* L.) is a tall perennial herbaceous flowering plant from Asteraceae family that is originally native to Central and Eastern Europe. Escaped cultivated plants brought to North America as early as the 1600's and become serious pest in some area (Mitch 1992a). Today, tansy is common in riverbanks, wastelands, along roadsides, and in rural and urban-industrial areas (Rebele 2000). Repeated mowing, will reduce flowering and seed production and may replace tansy over time with mowing (Jacobs 2008).

Survey

In 2011/2013, we conducted a survey in Jena revisiting 255 sites that were mapped 2001 for the presence of tansy. In both surveys also information about the presence of goldenrod and management practices were recorded. When revisiting the sites in 2011/2013 they were grouped into two main groups and five different categories. I) Non-suitable habitat: 1) "lost due to building activity": at these sites, vegetation had been replaced by new buildings, parking spaces or roads causing the loss of potential habitat. 2) "Lost due to intensive management": these vegetated sites were intensively managed by mowing more than once per month (by asking from local people) causing the loss of potential habitat for tansy or goldenrod. II) Suitable habitat: The rest of the sites were suitable habitat for tansy and goldenrod with extensive or no management. 3) "Tansy present, with or without goldenrod": at these sites, tansy was found independent of the presence or absence of goldenrod. 4) “Tansy replaced by goldenrod”: at these sites, there were monoculture of goldenrod and no tansy. 5) “Tansy replaced by other vegetation”: at these sites, there were no tansy and goldenrod but other vegetation.

Analysis

For all five categories and the two groups of tansy status in 2011/2013 defined above, we calculate the proportion of sites by dividing the number of sites within each category/group by the total number of sites revisited in 2011/2013 (255 sites). To quantify the potential of tansy to be replaced by goldenrod independent of human activities at the sites, we also calculated proportions based only on sites with suitable habitat for tansy (i.e. sites with vegetation and extensive or no management). For each category in this group we divided the number of sites assigned to the category by the total number of sites with suitable habitat.

In addition, we aimed at quantifying if goldenrod is increasingly occupying sites in the study region over the studied 10 year period. To do so, we compared the number of sites that were invaded by goldenrod by calculating the proportion of sites where tansy was present together with or without goldenrod for both the 2001 and 2011/2013 census.

Result

In total, 255 sites were checked in 2011-2013 where tansy occurred in 2001. Within these sites 52 sites were replaced by building activity (20% of total sites) and addition 15 sites were replaced by other vegetation due to intensified management during the last 10 years (6% of total sites). For 188 sites there still was vegetation with only extensive or no management so that these sites were potential habitat for the occurrence of tansy.

In 152 out of these 188 potentially suitable sites, tansy was present (81% of potential habitat sites) in 2011/2013 (Table 1, Fig 1). In contrast to our hypothesis, there was only little indication that tansy had been replaced by goldenrod because only in 3% of the revisited potential habitat sites tansy was replace by goldenrod. The chance that tansy was replaced by other plants between 2001 and 2011/2013 was much higher than to be replace by goldenrod as in 30 sites tansy was replaced with other vegetation (16 % of the potential habitat sites; Table 1, Fig 1).

In 59% of the sites where tansy was occurring in 2011/2013 it was co-occurring with goldenrod. This was an increase of 16 percent- points compared to 2001 where in 43% of sites that tansy was present goldenrod also was present (Fig 2). These results provide evidence that from 2001 to 2011/2013 goldenrod was increasing its invaded range. Despite that, there was very limited evidence that goldenrod was replacing tansy over last 10 years and indeed in most of the sites where these two plants were present they coexisted.

Discussion

In summary we found evidence that goldenrod was continued to expand their invaded range in Germany. Yet only in few sites (3%) tansy was replaced by goldenrod and in most of the site tansy was still present (80%) which was in contrast to our hypothesis. Tansy and goldenrod were coexisting in most of the site in which tansy was present. Rather than replacement by invasive goldenrod, tansy is more threatened by human activities because we found that in most of the sites where tansy was lost this was due to human construction or by intensive management (26% of the total sites monitored).

Does invaded site by goldenrod increased during last 10 years?

According to our results goldenrod continues to increase the number of its invaded sites during last 10 years in Jena. These observations suggest that goldenrod is still in the process of range expansion and has not yet achieved a state of equilibrium in Germany. Several comprehensive studies on introduced goldenrod species and their expansion in Europe were previously published by others (Weber and Schmid 1998, Weber 2000a, 2001, Priede 2008), which show an exponential expansion of invasive goldenrods in Europe. In our and the above-mentioned studies goldenrod occurred mostly on roadsides, fallows, railway verges, in grasslands and ruderal sites (weed-laden sites, waste dumps, and urban areas). The dispersal success of goldenrods had been greatly facilitated by land use changes, human alteration of ecosystems, and development of transportation networks beside its specific biological features. Short life cycle, high seed production, efficiency in seed dispersal of invasive goldenrod allow it to achieve the maximum possible success in invasions (Cornelius 1990, Priede 2008).

Does goldenrod invasion translate into tansy replacement?

In contrast to our hypothesis, our results show that although the proportion of sites where tansy was present and which were invaded by goldenrod increased from

2001 to 2011/2013, this did not translate into a high replacement of tansy by invasive goldenrod, because only in 3% of tansy sites, the species was replaced by goldenrod. Rather and in contrast to expectation, in most of the vegetation sites these two plants coexisted. These results were in agreement with Rebele (2000) who showed in over 5 years of field experiment tansy and goldenrod to coexist. Although competition decreased performance of tansy and goldenrod compared to control plants without competition, effects of interspecific competition by goldenrod were smaller for tansy than effect of interspecific competition by another tansy.

As mentioned above, only in few sites (3%) tansy was replaced by goldenrod. As competitive exclusion of tansy by goldenrod seems to be unlikely, other mechanisms have to explain the replacement of tansy by goldenrod in these sites. This replacement could be because of rare and extreme climatic or environmental effects or because goldenrod suffers less form herbivory in the invaded range (Jobin et al. 1996). Selective herbivory on tansy in its native range could translate into replacement by goldenrod in this few sites, although outbreak situations of the native herbivores might be necessary to cause sufficient high herbivory pressure (Rebele 2000). For example Rebele (2000) showed the slug outbreak caused the switch in dominant plant species that were already coexisted 4 years.

What is the real threat for tansy?

According to our results, 26% of our sites were replaced by human activities such as buildings, new parking spaces, roads or intensified management. There is no doubt that human civilization has a negative impact on biodiversity (Hunter 2007). Our results show that urbanization is one of the leading causes of species extinction

(McKinney 2006) and human activity had more negative effect on tansy presence than invasion by goldenrod.

Conclusion

In contrast to our hypothesis tansy was not replaced by goldenrod invasion over a period of 10 years and these two plants were coexisting in most of the sites where tansy occurred. Consequently, our result does not indicate a danger of tansy to be replaced by goldenrod in Germany. In contrast, our results showed a threat of management and building activates which are destroying habitats of tansy (and goldenrod). Our results showed that a better understanding of the ecological impacts of invasive species is crucial for arranging management efforts.

Acknowledgement

We wish to thank Silke Schroeckh and Robert Schaelike for their assistance in conducting the survey.

Table1- Results from a mapping of tansy (*Tanacetum vulgare*) and goldenrod (*Solidago canadensis*) in Jena–Germany. Sites were mapped in 2001 and revisited in 2011/2013. Given are the number and the proportions of sites separated into different types based on the status of tansy occurrence in 2011/2013.

Status in 2011/2013	**Number**	**Proportion of total sites (%)**	**Proportion of suitable habitat sites (%)**
Site revisited	255	100%	-
Sites with non-suitable habitat	67	26%	
Lost due to building activity	52	20%	-
Lost due to intensive management	15	6%	-
Sites with suitable habitat (vegetation with extensive or no management)	**188**	**74%**	**100%**
Tansy present, with or without goldenrod	152	60%	81%
Tansy replaced by goldenrod	6	2%	3%
Tansy replaced by other vegetation	30	12%	16%

Figure. 1: Proportion of sites in Jena– Germany that are potentially suitable habitat for tansy (*Tanacetum vulgare*) in 2011/2013 and where tansy had been mapped to occur in 2001, separated into the different fates of tansy.

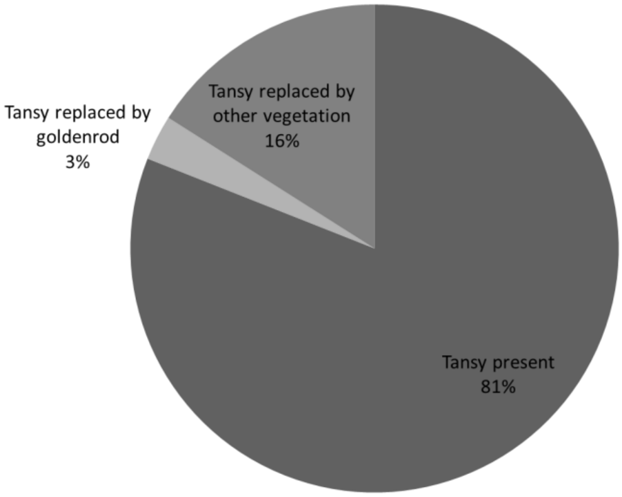
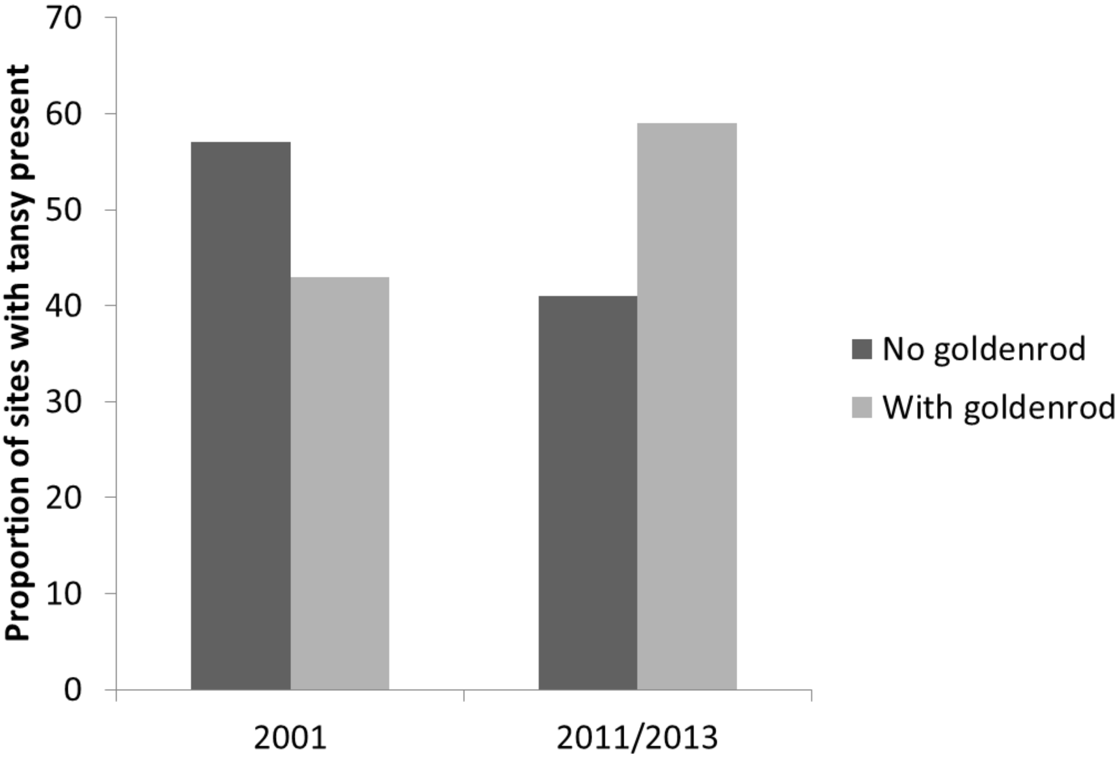


Figure 2- Proportion of sites where tansy (*Tanacetum vulgare*) was present together with or without goldenrod (*Solidago canadensis*) in 2001 and 2011/2013.



Chapter 3

The role of insect herbivores in the interaction between *Solidago canadensis* and *Tanacetum vulgare* in a cross continental experiment

Abstract

Invasive plant invasions are threatening biodiversity and altering fundamental ecosystem properties and processes worldwide, but the mechanisms underlying successful species invasion remain poorly understood. Some invasive species may suffer less from their co-evolved specialist herbivores in the invaded range (enemy release hypothesis) and show increased competitive ability due to a shift of resources from defence into growth (EICA - the evolution of increased competitive ability).

Solidago canadensis (Canada goldenrod; hereafter goldenrod) is native to North America and invasive in Europe while *Tanacetum vulgare* (common tansy; hereafter tansy) is native to Europe and invasive in North America. Both species often co-occur and appear to suffer less from herbivory in the invaded range. The broad objective of this study was to determine if this mutual invasion leads to reversed competitive hierarchies among the two plant species in Europe and North America.

We set up a reciprocal field experiment where goldenrod and tansy were grown with and without application of insecticide to remove any insect herbivores. In addition, we used a greenhouse experiments to compare plant performances in a common garden design. Both tansy and goldenrod showed greater biomass and height in their invaded ranges compared to their native ranges. Because herbivory of both species was lower in the invaded ranges, enemy release could underlie these differences in performance between the native and invaded ranges. For tansy, insecticide application increased biomass in the native range in Europe and decreased it in USA, supporting the enemy release hypothesis. For goldenrod, however, insecticide treatment did not increase performance despite high herbivory in the native range. There was strong evidence that plants in the invaded ranges differed from those in the native habitat: in the greenhouse experiment, plants derived from populations in the invaded range were larger than plants from populations in the native range, for both species, consistent with the EICA hypothesis.

While both plant species have invaded the native habitat of the other species where they show better growth than in their native range, competition between the species was low. In mixed plantings, individual tansy plants generally performed better than goldenrod, compared to tansy monocultures, while for goldenrod there was no measurable effect of competition. In the US only, application of insecticide decreased tansy performance in mixed planting, when tansy was in competition with goldenrod, i.e. the competitive advantage of tansy over goldenrod was reduced by application of insecticide. Overall, however, the weak impacts of competition by the invasive plants on native plant performance indicate the potential for at least temporary coexistence in USA and stable coexistence in Europe between tansy and goldenrod. Thus, while both plants are invasive and showed patterns of herbivory and growth consistent with current hypotheses on plant invasion, they are more likely to displace other native plants than one another.

Key words: herbivory, competition, enemy release hypothesis, the evolution of increased competitive ability hypothesis

Introduction

Invasive plants are deliberately or accidentally introduced to new areas and are often an ecological threat (Pimentel et al. 2000, Grotkopp et al. 2002). They are able to become dominant, have higher abundance, densities, growth rates and less herbivory in the invaded range compared to their native range (Mack et al. 2000, Keane and Crawley 2002, Colautti et al. 2004) but see also (Thebaud and Simberloff 2001). Such successful invaders can alter ecosystem function, impact the abundance of native species, homogenize global community composition and cause billions of dollars of cost due to economic damage (Blossey and Nötzold 1995, Mack et al. 2000, Keane and Crawley 2002, Colautti et al. 2004). Therefore, understanding the mechanisms causing invasive plant to be successful can help to avoid future and mitigate current effects of invasive plants.

Competition is one of the main factors shaping plant communities and for a plant to become invasive, it has to outcompete plants from the native community (Sakai et al. 2001, Vila and Weiner 2004) as has been shown for a number of invasive plants (Paini et al. 2008). The outcome of competitive interactions between native and invasive plants also depends on properties (traits) of the native plant and interacting herbivores. Consequently, not all native plants might be excluded by invasive plants under all conditions. The effect of interspecific competition between a non-native and native plant in the invaded community can actually be larger, smaller or similar in magnitude compared to intraspecific competition by other individuals of the same native plant (Mangla et al. 2011). This can lead to exclusion, facilitation or coexistence between invasive and native plants (Aarssen 1983).

Hypotheses explaining higher performance of invasive species in invaded range

There are several theories explaining how invasive plants are able to become dominant in their invaded range.

a) Enemy release hypothesis

Escape from native herbivores is believed to be one of the primary causes contributing to the successful invasion of many invasive plants, called the "enemy release hypothesis" (ERH; Keane and Crawley 2002). This hypothesis is based on a three-point logical argument: (1) natural enemies are important to keep population in check; (2) effect of enemies is higher on native than on invasive species; and (3) invasive plants have less in enemy than their native range, their population will increase (Keane and Crawley 2002). This hypothesis is supported by a number of recently published studies which show that native plants had more herbivores and greater levels of herbivory damage than invasive plants (e.g. Fenner and Lee 2001, Wolfe 2002, Mitchell and Power 2003, Torchin et al. 2003, Reinhart and Callaway 2004, Liu et al. 2007). Despite lots of studies on invasive plants to test the enemy release hypothesis, there are still two limitations of current studies: First, Maron and Vila (2001) suggested that to test the ERH, a precise empirical experiment is needed by parallel excluding herbivores from both native and invasive plants in the native and invasive invaded range, yet insecticide is generally not applied in reciprocal transplant experiments aiming at testing the ERH. Releasing from enemies can greatly benefit invasive species competing with native plants, because herbivory could alter or even reverse the outcome of competition. Yet, only few experiments have explicitly compared the effects of competitors in both native and invaded range with and without herbivores (Callaway and Aschehoug 2000). Consequently, the ability of the ERH to explain patterns of invasion remains less well studied than the impression created by the large number of studies on invasion and ERH.

b) EICA hypothesis

The evolution increase competitive ability hypothesis (EICA) (Blossey and Nötzold 1995) is an extension of the ERH hypothesis assuming that invasive plants are superior and have higher performance, because they have evolved in their invaded range to allocate resources previously needed for anti-herbivore defence into growth (Stamp 2003, Stastny et al. 2005). The best way of testing this hypothesis is to grow invasive plants from their native and invaded range in a common garden to evaluate their phenotypic plasticity and genetic differences (Wolfe et al. 2004). Using this common garden approach a number of studies confirmed the EICA hypothesis by showing that plant performances of individuals sampled from their invaded range was higher than that of plants from the native range (Siemann and Rogers 2001, Blair and Wolfe 2004). However, this general rule was not confirmed for all species tested (Willis et al. 2000).

In this study we used goldenrod (*Solidago canadensis* L.) and tansy (*Tanacetum vulgare* L.) as a model system. These two species present an interesting case of mutual invasion, where each species has invaded the native range of the other species. These species often co-occur in both Europe and North America and both species have become dominant in parts of their new invaded range (Weber and Schmid 1998, Jacobs 2008). This study tests if these mutual invasions lead to a reversal of competitive hierarchies between the two continents. To answer this question, we set up a reciprocal field experiment a by planting both the native and invasive species in isolation and mixtures to assess competition and the dominance in Europe or the USA. To test for interactions with herbivores, half of both the native and invasive plants were relieved from herbivory by spraying insecticides. A common garden experiment in a greenhouse was set up to supplement the field experiment by comparing of all seed origins used in the field experiments on plant performance. Plants arise from seeds of invaded range named "exotic" origin and plants arise from seeds of native range named "native origin".

We specifically asked

(1) Do tansy and goldenrod perform differently in their native and invaded range? (2) Can a hypothesized higher performance in the invaded range be explained by (2a) release from herbivores or (2b) differences between plant origins? (3) Are tansy and goldenrod such strong competitors in their invaded range that they will replace each other in their native range?

Materials and methods

Description of species

Goldenrod (*Solidago canadensis* L.) is native to America and was introduced to Europe in the 17th century. The flowers are self-sterile and the seeds are wind-dispersed. Goldenrod is forming large clonal colonies making it one of the most aggressive weeds in Central Europe in old fields, urban areas and industrial wastelands (Weber and Schmid 1998, Weber 2001). In America, goldenrod is attacked by a rich community of insect herbivores that has been shown to impact its growth, fecundity and competitive ability (e.g. Cain et al. 1991, Carson and Root

1999, 2000, Long et al. 2003). The phytophagous community on goldenrod is reduced in Europe compared to America (Jobin et al. 1996).

Like goldenrod invading Europe, tansy (*Tanacetum vulgare* L.) is invading America where it turned out to be a serious pest (Jacobs 2008). Tansy originally occurred on riverbanks and meadows. Tansy nowadays also is part of ruderal communities in Central and Eastern Europe (Keskitalo et al. 2001, Dragland et al. 2005). In America, tansy occupies its original habitats along riverbanks (Mitch 1992b) where also goldenrod occurs. In its native range, tansy is attacked by a large number of often specialized herbivorous insects (Schmitz 1998). More than 169 herbivores were reported on tansy and between these herbivores; 29 species of them are specialized on it (Schmitz 1998). Little is known about herbivory on tansy in the US.

Study sites

The experiment was replicated in three different sites spanning the native and invaded range of both plant species, two European sites in Germany (Jena) and Hungary (Pellérd), and one site in North America (Montana, Missoula). The site in Jena is located in the floodplain of the river Saale in Jena (Thuringia, Germany, 50_550N, 11_350E, 130 m a.s.l.). Mean annual air temperature is 9.3 °C, average annual precipitation amounts to 587 mm.

The site in Hungary is located in a hilly area called South-Baranya-Hills (46°01'N, 18°08'E, 138 m a.s.l.). Mean annual temperature is 10-11 °C, while mean annual precipitation ranges between 650 and 700 mm.

The Montana site is located in the Rocky Mountains (46°50'N, 113°59'E, 995 m a.s.l.). At the Montana sites mean annual temperature is 7-8 °C, while mean annual precipitation ranges between 346 and 405 mm.

Experimental design

I- Cross-continental experiment on plant-plant competition and effects of herbivory

In a fully factorial field experiment that was replicated at all three locations: Germany (GER), Hungary (HUN) and North America (USA), a plant competition treatment was crossed with an insecticide treatment. In the experiment plant density was held constant, by planting six pregrown, two month old seedlings into plots of 50 × 50 cm. We planted monocultures of tansy (6 plants), monocultures of goldenrod (6 plants), and mixtures of tansy and goldenrod (3 plants each). Half of all plots were sprayed with insecticide while the other half served as control. The insecticide used was mixture of a systemic insecticide Biscaya (active ingredient *Thiacloprid, (*Z)-3-(6-chloro-3-pyridylmethyl)-1, 3-thiazolidin-2-ylidenecyanamide) and a knock-down insecticide Decis (deltamethrin,(S)-cyano-3-pehoxybenzyl(1R)-cis-3-(2,2-dibromovinyl)-2,2-dimethy lcyclopropane carboxylate). We used the recommended rate of 0.1% water solution of both insecticides. Three sprayed and three unsprayed plots formed a block (in total 6 plots per block). All treatment combinations were replicated 15 times per location, resulting in 15 blocks. The size of one block was 1.2 × 2m and surrounded by walking paths of 50 cm width. The experimental setup (same size, same number of blocks) was the same in each country. The other side of a block where no insecticide was used was covered by a big plastic foil during application.

Different variables describing plant performance were measured after plants had stopped growing in the fall (September). For each plant the number of shoots was counted and the height of the tallest shoot was measured (in cm). Proportion of flowering was recorded as the number of shoots with flowers per number of shoots for each plant. For total plant biomass (g), aboveground parts of plants were harvested, dried to constant mass at 70 °C for 48 hours, and weighed. To quantify potential impacts of consumers on plants in different sites and to verify the effectiveness of the insecticide application, herbivory was measured as the total number of leaves showing damage (including chewed holes and leaf mines) on leaves of the tallest shoot. Then herbivory was measured as the total number of leaves showing damage on plants because in the three experimental locations different variables were measured for herbivory. In one experimental location, we did not count the number of leaves. Then herbivory was measured as total number of leaves showing damage on plants. Because of frequent colonisation by tansy aphids (*Macrosiphoniella tanacetaria*), aphids were counted in GER before and after treatment with insecticide, on the tallest shoot and on the entire plant for all tansy plants.

II- Greenhouse experiment

Each location in the field experiment used seeds from local seed sources to set-up the experiment. To test for the effect of seed source on plant performances, seeds from all three origins: America (usa), Hungary (hun), and Germany (ger) were planted under standardized conditions excluding herbivores in a greenhouse. Thereby, we can directly compare any differences in performance of plants from all three (native and invasive) origins. Seeds were planted in 50ml pots and after one month seedlings were transplanted individually into 500 ml pots with 20 replicates per plant species and origin. After three months, plant performance was measured when plants had stopped growing and started to flower. For each plant the height of the tallest shoot was measured (in cm). Also the number of leaves and flowers was recorded.

Statistical analysis

A linear model was used to test for differences in the average proportion of herbivory experienced by tansy and goldenrod and the number of aphids found on tansy in the field experiment as a function of the differences between the two plant species, the application of insecticide, and competition by the other species. Due to generally high rates of herbivory in HUN, the proportion of plants with damage rather than the proportion of leaves with damage was analyzed for the data from HUN. Because of these different measures of herbivory, data from the three locations: GER, HUN and USA were analyzed in separate models.

A Linear mixed-effects model (LME) was used to compare mean values for each measure of plant performance by fitting location, insecticide, competition, and their interaction as fixed effects and block as a random effect. The average values of the performance measures from the individuals per plot were used for the analyses and all tests were done for each plant species separately.

The data from the greenhouse experiment to test for origin effects was analyzed using a linear model to compare mean values for each performance variable separately with origin as a single explanatory variable. All models were estimated using the R software (Version 2.14.1; R Development Core Team 2011) employing the base function “lm” for linear models and the function “lme” in the nlme package (Pinheiro et al. 2012) for mixed effect models. Variables were transformed as necessary (indicated in Table1-4). In all analyses, not significant terms were removed during model simplification (in the order indicated in Table 1-4). All data are presented as mean ± standard error (SE).

Results

1) Performance of tansy and goldenrod in native and invaded range

The location where the experiment took place significantly affected all measures of goldenrod and tansy performance (Table 1). As predicted, both species showed higher biomass in their invaded ranges compared to their native ranges. Goldenrod had more biomass and was taller in GER and HUN (invaded range) compared to USA (native range; Figure 1A, Figure S1A). In contrast to biomass, however, the proportion of flowering shoots and the number of shoots for goldenrod was higher in HUN and USA and significantly lower in GER (Figure S1E & C), such that overall goldenrod performance was highest in HUN.

Tansy had most biomass in USA (invaded range), which was lower in HUN (native range) and lowest in GER (native range; Figure 1B). Tansy height and the number of shoots were also lowest in GER and highest in USA but in contrast to biomass height and number of shoots were also high in HUN (Figure S1B & D). The proportion of flowering shoots was highest in USA and lower in Hungary like for biomass, yet there was a high proportion of flowering shoots in GER (Figure S1F). Thus, overall tansy tended to show lowest performance in GER and highest in USA (Figure S1).

2.1. Competition between tansy and goldenrod in different experimental locations

Overall, there was little effect of competition on the two plant species and plants tended to profit from the interspecific competition treatments, i.e. growth of plants was better when intra-specific competition was replaced by inter-specific competition. For goldenrod, the effect of competition depended on the experimental location (Table 1). In GER, competition with tansy increased goldenrod biomass and number of shoots compared to goldenrod monocultures but decreased them in the USA, i.e. only in the native range was interspecific competition stronger than intraspecific competition (Table 1, Figure 2A, Figure S4 C). For tansy, interspecific competition in fact increased both biomass and number of shoots independent of experimental location, i.e. in tansy intra-specific competition was always stronger than inter-specific competition (Table 1, Figure 2B, and Figure S4 D).

2.2. Herbivory on tansy and goldenrod in different experimental locations

Overall, tansy incurred higher levels of herbivory than goldenrod. Consistent with the enemy release hypothesis, there was higher herbivory in the native range for both species (Table 3, Figure 2C and D). In GER, tansy suffered strongly from insect herbivores while goldenrod was hardly attacked. This pattern was reversed in USA where a high proportion of goldenrod plants showed herbivory damage. In

HUN herbivory was strong for both species (Figure 2C and D). In addition to attack by chewing herbivores, tansy was infected by a high number of aphids (*Macrosiphoniella tanacetaria*) in GER while aphids were never observed on goldenrod (Table 3, Figure S3), and aphid attack in the other two experimental locations was not noticeably strong. The insecticide treatment reduced levels of leaf herbivory for both tansy and goldenrod (Table 3, Figure 2C and D) to about half of the control plant levels. Only in HUN did the effect of insecticide treatment depend on species and had a stronger effect on goldenrod, while in GER and USA there was no interaction between the species and insecticide treatments (Table 3, Figure 2C and D). In GER aphid numbers were strongly reduced by the application of insecticide (Table 3, Figure S3).

2.3. Herbivore exclusion and its effect on plant growth and the competitive interaction between tansy and goldenrod

For goldenrod, insecticide treatment had no effect of insecticide on any measure of goldenrod performance, despite high herbivory in the native range. For tansy, insecticide application increased biomass (and also height, and proportion of flowering shoots) in GER and HUN and decreased performance in the USA (Figure 2B, Figure 4SB & F). Because there was little inter-specific competition between the two species, removing herbivores had few effects. For goldenrod there was no interaction between experimental location, insecticide and competition (Table 1). For tansy the interactions between experimental location and insecticide and between insecticide and competition were significant (Table 1). Tansy profited more from insecticide in the absence of competition. While the interaction between competition and insecticide appeared to be different in Europe vs. the USA, the three-way interaction location*insecticide*competition was not significant.

3. Performance of tansy and goldenrod from different seed origin

In the common garden greenhouse experiment, the origin (usa, hun & ger) of seed material used significantly affected all measures of tansy and goldenrod performance (Table 2). For both tansy and goldenrod, performance of the plants from the exotic origin was higher than for those with a native origin (Figure 3A and B, Figure S2A-C).

While goldenrod seeds from hun did not germinate, goldenrod plants from ger (exotic origin) had significantly more leaves compared to plants from usa (native origin; Figure 3A). There were no differences in height (Figure S2A) and no initiation of reproduction after three months.

Tansy plants grown from seeds from usa had more leaves and were growing higher compared to plants from Europe (hun, ger; Figure 3B, Figure S2B). After three months some of the plants from usa started flowering and some plants from hun produced flower buds, at the same time none of the plants from ger did so. The proportion of plant with reproductive shoots was the same for plants from usa and hun (Figure S2c). Overall, Tansy performance was highest for plants from usa (exotic origin), lowest for plants from ger and intermediate for plants from hun (both native origin).

Discussion

Although biological invasions consider as a serious threats to biodiversity, they also provide the opportunity to better understand interactions between the ecological and evolutionary processes structuring populations and communities (Pintor et al. 2011). In our experiment both tansy and goldenrod showed greater biomass and height in their invaded ranges compared to their native ranges, While herbivory of both species was lower in the invaded ranges. For tansy, insecticide application increased biomass in the native range in Europe and decreased it in USA. For goldenrod, however, insecticide treatment did not increase performance despite high herbivory in the native range. In a common greenhouse experiment, plants derived from populations in the invaded range were larger than plants from populations in the native range.

Higher performance of both species in invaded range

In the cross-continental experiment, plants in the invaded range showed higher performance compared to their native ranges. Although we did not find comparable study for tansy and goldenrod, other studies that compared native and introduced populations in the field show the same results for other species (Jakobs et al. 2004, Bossdorf et al. 2005, Prati and Bossdorf 2004). Different performance in invaded range compared to native range could be caused by at least two distinct mechanisms which are the release from herbivores and the evolutionary increased competitive ability of the plants in their invaded range. Both mechanisms were partially supported by our experiments.

Effects of herbivory on plant performance in native and invaded range (Enemy release hypothesis)

Herbivory on both spices was higher in their native ranges which could potentially explain higher performance in the invaded range, as has been hypothesized (ERH; Keane and Crawley 2002) and documented for a range of invasive species (reviewed in Hierro et al. 2005, Liu et al. 2007). A release from herbivores might contribute to a higher tansy performance in the invaded range, as tansy biomass increased when applying insecticide in the native range but not in the invaded range. This indicates a reduced importance of herbivores in the invaded range as suggested by the ERH. Several other studies have found evidence that herbivores are either more abundant or have greater effects on plants performance in their native than in their invaded ranges. Mitchell and Power (2003) examined 473 plant species introduced to the United States from Europe and found 84% fewer fungal pathogen and 24% fewer viral pathogen species on the plants in the United States. While we found convincing evidence for enemy release hypothesis for tansy in USA, insecticide treatment did not affect goldenrod performance despite high herbivory in its native range. This result agrees with DeWalt et al. (2004) who showed that the exclusion of herbivory had no effect on relative growth or survival of plants in native range in Costa Rica or in either invaded range in Hawaii.

The effect of releasing invasive plants from natural enemies in their invaded range is only partly attributed to a direct effect of reduced herbivory damage and partly to a change in the competitive balance between invasive and native plants due to increased invader performance because of reduced herbivory (Keane and Crawley 2002). This part of the ERH was supported only by the effects of insecticide application observed in the part of our experiment in the USA. In USA, application of insecticide decreased tansy performance when tansy was in competition with goldenrod. Thus, the competitive advantage of tansy over goldenrod was reduced by application of insecticide. This result is consistent with the ERH as lower herbivory on tansy compared to goldenrod contributes to the success of tansy in its invaded range and this effect can be reduced by applying insecticide. While insecticide application did reduce herbivory on goldenrod, it did not change goldenrod performance and consequently also not its competitive ability. This prediction was not supported by ERH due to the competitive ability of tansy was influenced by herbivores but not the way that we expected. In Europe tansy profited from insecticide only in the absence of competition with goldenrod. It means that there was no negative effect of herbivory when in competition with goldenrod that could be alleviated by insecticide. Thus, again there was no support for the ERH explaining the success of goldenrod in Europe.

Seed origin effects on the performance in native and invaded range (EICA-hypothesis)

In the common garden experiment in the greenhouse, plants derived from populations in the invaded range were larger than plants from populations in the native range, for both species. Thus, the possible mechanisms to explain higher performance of tansy and goldenrod in the invaded range could be EICA Hypothesis. The results show that plants in the invaded range have evolved higher growth rates or represent a subset of genotypes from the native range. Similar origin effects have been shown for tansy (Wolf et al. 2011) and other invasive plant species (Willis et al. 1999, Blair and Wolfe 2004, Bossdorf et al. 2005, Stastny et al. 2005). In contrast, the single published study investigating the effect of origin on goldenrod performance did not find evidence for EICA (van Kleunen and Schmid 2003).

Which mechanisms can best explain the higher performance of the two plants in their invaded range?

Our results for goldenrod did not agree with the ERH because adding or removing herbivory did not change goldenrod interaction with native tansy. That is the reason why the higher performance of goldenrod in the invaded range is unlikely to be explained by the Enemy Release Hypothesis. While we do not have direct evidence of performance of different goldenrod genotypes, the results from the greenhouse experiment indicate some genotypic differences between native and invaded range of goldenrod that could be explained by the appearance of more vigorous goldenrod genotypes that is consist with EICA hypothesis.

Our results suggest that a release from herbivores might contribute to a higher tansy performance in its invaded range (USA), as tansy biomass increased with applying insecticide in the native range but did not change in the invaded range. This means that tansy is free from herbivory in the invaded range; hence applying insecticide did not further increase tansy performance. Tansy plants derived from populations in the invaded range grew larger and flower earlier than plants from populations in the native range. The possibility is, over time, invasive tansy plants show increased vigour compared with plants from populations within the native range which is consist with EICA hypothesis.

Does the increased performance in the invaded range translate into higher competitive abilities?

In Europe, both species showed higher performance in mixtures of the two species compared to monocultures, i.e. lower interspecific than intraspecific competition. Consequently there was no evidence for a higher competitive ability of goldenrod in its invaded range as tansy in fact profited from the presence of goldenrod. Although other studies show that goldenrod is a well-established invader in most invaded community (Lu et al. 2007, Crutsinger et al. 2008, Zhang et al. 2008) and it is putative to outperform the native plants even under some special condition like pollution.

In USA, tansy showed a strongly increased performance when in competition with goldenrod compared to monocultures of tansy and goldenrod suffered in competition with tansy showing reduced biomass. Thus the higher performance of tansy in its invaded range translated into a higher competitive ability.

Evidence for competitive exclusion or coexistence?

Our experiment yielded no evidence for the competitive exclusion of native species by invaders, neither in Europe nor USA.

In USA, there was no competitive exclusion of native plants (goldenrod) despite tansy showing higher performance and competitive ability which decreased goldenrod performance. It could be that the two species in the experiment coexisted because the time observed in the experiment was not long enough for competitive exclusion of goldenrod. Additional, longer term experiments should investigate if a continued reduced performance of goldenrod when in competition with tansy eventually leads to a suppression of goldenrod and dominance by tansy.

In Europe, plants coexisted until the end of the experiment and despite high performance of goldenrod in its invaded range individual tansy plant performance even increased in mixtures with goldenrod compared to tansy monocultures. This reduced interspecific competition between tansy and goldenrod compared to intraspecific competition within tansy stands points at niche separation between the two species and implies the potential for stable coexistence of this two species in Europe.

Conclusions

Tansy and goldenrod present an interesting case of mutual invasion, each species having invaded the native range of the other species. Therefore, they are a good model system to test the predictions of the ERH and EICA hypothesis as effects of competition in native and invaded range can be tested without changing species identity. Both species showed higher performance in their invaded range. Regarding the mechanisms for higher performance, there was some indication for the release from natural enemies for tansy in USA but not for goldenrod and evidence supporting evolutionary increased competitive ability for both species. As plants in the experiment were coexisting until end of the experiment, our results did not confirm the general view that all invasive species are competitively superior and exclude native plant species. In contrast, the low impacts of competition by the invasive plants on native plant performance indicate the potential for at least temporary coexistence of tansy and goldenrod in USA and stable coexistence in Europe.

Acknowledgments

We wish to thank Dr. Anne Ebeling, Sylvia Creutzburg, Silke Schroeckh and Gardening team of the Jena experiment (Jena, Germany) and many student helpers for their assistance in the field experiment.

Table 1- Results from linear mixed-effects models for a range of response variables measuring tansy (*Tanacetum vulgare)* and goldenrod (*Solidago canadensis)* performance in a field experiment in three locations spanning the native and exotic range of both species: Germany (GER), Hungary (HUN) and America (USA). Plant species were grown individually or in competition with the other species in a substitutive design which was crossed with an insecticide treatment. Results for tansy and goldenrod were analyzed in separate models. In addition to the fixed effects location, insecticide, competition, and their interactions a blocking variable nested within location was included as a random effect in the models (not shown). Minimum adequate models are presented together with terms removed from the models given in brackets. Superscripts give the order in which terms have been removed from the model starting with highest order interactions based on least significance. Significant terms in the final models are given in bold. For definitions of variables, see materials and methods.

Variable	Species	Location	Insecticide	Competition	Location × Insecticide	Location ×Competition	Insecticide× Competition	Location× Insecticide× Competition
	Goldenrod							
Biomass*		**$F_{2,33}$=49.1; p<<0.001**	($F_{1,139}$=0.638; p=0.426)^{4}	$F_{1,140}$=2.85; p=0.094	($F_{2,136}$=0.09; p=0.905)^{2}	**$F_{2,140}$=4.55; p=0.012**	($F_{1,138}$=0.74; p=0.390)^{3}	($F_{2,134}$=0.27; p=0.757)^{1}
Height		**$F_{2,33}$=124.0; p<<0.001**	($F_{1,142}$=0.020; p=0.889)^{6}	($F_{1,141}$=0.00; p=0.964)^{5}	($F_{2,139}$=0.53; p=0.585)^{4}	($F_{2,137}$=0.48; p=0.618)^{3}	($F_{1,136}$=0.00; p=0.981)^{2}	($F_{2,134}$=0.10; p=0.897)^{1}
Proportion flowering shoots		**$F_{2,33}$=21.1; p<<0.001**	($F_{1,142}$=0.523; p=0.471)^{6}	($F_{1,141}$=0.46; p=0.497)^{5}	($F_{2,136}$=0.54; p=0.582)^{2}	($F_{2,139}$=1.22; p=0.297)^{4}	($F_{1,138}$=0.74; p=0.391)^{3}	($F_{2,134}$=0.22; p=0.799)^{1}
Shoots number °		**$F_{2,33}$=69.9; p<<0.001**	($F_{1,139}$=0.709; p=0.401)^{4}	$F_{1,140}$=1.28; p=0.259	($F_{2,136}$=0.09; p=0.914)^{2}	**$F_{2,140}$=4.50; p=0.013**	($F_{1,138}$=2.25 p=0.136)^{3}	($F_{2,134}$=0.06; p=0.939)^{1}
	Tansy							
Biomass*		**$F_{2,33}$=71.1; p<<0.001**	**$F_{1,139}$=4.907; p=0.028**	**$F_{1,139}$=5.44; p=0.021**	**$F_{2,139}$=4.81; p=0.010**	($F_{2,137}$=2.47; p=0.088)^{2}	**$F_{1,139}$=4.99; p=0.027**	($F_{2,135}$=0.33; p=0.719)^{1}
Height		**$F_{2,33}$=80.8; p<<0.001**	**$F_{1,139}$=4.372; p=0.038**	$F_{1,139}$=1.64; p=0.202	**$F_{2,139}$=4.95; p=0.008**	($F_{2,137}$=1.04; p=0.353)^{2}	**$F_{1,139}$=6.35; p=0.013**	($F_{2,135}$=2.61; p=0.077)^{1}
Proportion flowering shoots"		**$F_{2,33}$=40.5; p<<0.001**	$F_{1,141}$=3.236; p=0.074	($F_{1,140}$=0.08; p=0.773)^{4}	**$F_{2,141}$=3.07; p=0.049**	($F_{2,137}$=0.87; p=0.419)^{2}	($F_{1,139}$=1.52; p=0.218)^{3}	($F_{2,135}$=0.05; p=0.945)^{1}
Shoots number °		**$F_{2,33}$=16.6; p<<0.001**	($F_{1,142}$=0.147; p=0.702)^{6}	**$F_{1,143}$=8.62; p=0.004**	($F_{2,137}$=0.88; p=0.414)^{2}	($F_{2,139}$=2.32; p=0.102)^{3}	($F_{1,141}$=3.82; p=0.053)^{4}	($F_{2,135}$=0.01; p=0.987)^{1}

* linear model on cube root-transformed values , ° linear model on square root-transformed values , " linear model on squared-transformed values

Table 2: Results from Linear model and generalized linear models for performance of tansy and goldenrod raised form three different seed origins spanning the native and exotic range of both species: Germany (ger), Hungary (hun) and America (usa) in a greenhouse. Significant models are given in bold.

Treatment	Species	Leaves Nr.″	Height (cm)*	Flower Nr.°
Origin	Goldenrod	**Chi$^{2}_{1,38}$=26.44; p<<0.001**	F$_{1,38}$=2.168; p=0.149	
Origin	Tansy	**Chi$^{2}_{2,\,57}$=15.12; p=0.001**	**F$_{2,\,57}$=17.98; p<<0.001**	**Chi$^{2}_{2,\,57}$=7.88; p=0.028**

* linear model on log-transformed values , ″GLM with poison error distribution, °GLM with binomial error distribution

Table 3- Results from linear models on the proportion of herbivory experienced by tansy (*Tanacetum vulgare)* and goldenrod (*Solidago canadensis)* and number of aphids found on tansy in a field experiment located in three different locations: Germany, Hungary and America. Due to different measures of herbivory locations were analyzed in different models. Differences between plant species were analyzed by including the factor "species" which was crossed in the experiment with the application of insecticide and competition by the other species. Minimum adequate models are presented together with terms removed from the models given in brackets. Superscripts give the order in which terms have been removed from the model starting with highest order interactions based on least significance. Significant terms in the final models are given in bold. For definitions of variables, see materials and methods.

Treatment	**Location**			
	Germany	**Germany**	**Hungary**	**America**
	Proportion of herbivory*	**number of aphids on Tansy"**	**Proportion of herbivory°**	**Proportion of herbivory°**
Block	$\text{Chi}_{14,105}$=8.57; p=0.857	$F_{14,44}$=1.336; p=0.226	**$\text{Chi}_{14,105}$=534.9; p<<0.001**	$\text{Chi}_{5,113}$=15.82; p=0.075
Species	$\text{Chi}_{1,104}$=41.20; p<<0.001	no aphids on Goldenrod	**$\text{Chi}_{1,104}$=2132; p<<0.001**	**$\text{Chi}_{1,112}$=148.0; p<<0.001**
Competition	($\text{Chi}_{1,103}$=0.819; p=0.365)^{5}	($F_{1,43}$=0.223; p=0.639)^{2}	($\text{Chi}_{1,103}$=0.410; p=0.847)^{4}	($\text{Chi}_{1,111}$=0.001; p=0.980)^{5}
Insecticide	**$\text{Chi}_{1,102}$=45.48; p<<0.001**	**$F_{1,44}$=140.64; p<<0.001**	**$\text{Chi}_{1,102}$=1465; p<<0.001**	**$\text{Chi}_{1,110}$=49.62; p<<0.001**
Species×Competition	($\text{Chi}_{1,101}$=0.179; p=0.673)^{4}	-	($\text{Chi}_{1,101}$=12.46; p=0.286)^{3}	($\text{Chi}_{1,109}$=1.881; p=0.275)^{3}
Species×Insecticide	($\text{Chi}_{1,100}$=0.116; p=0.734)^{3}	-	**$\text{Chi}_{1,100}$=137.8; p<0.001**	($\text{Chi}_{1,108}$=3.605; p=0.131)^{4}
Competition×Insecticide	($\text{Chi}_{1,99}$=0.481; p=0.488)^{2}	($F_{1,42}$=0.412; p=0.524)^{1}	($\text{Chi}_{1,99}$=0.500; p=0.831)^{2}	($\text{Chi}_{1,107}$=0.571; p=0.548)^{2}
Species×Competition×Insecticide	($\text{Chi}_{1,98}$=2.113; p=0.146)^{1}	-	($\text{Chi}_{1,98}$=16.56; p=0.219)^{1}	($\text{Chi}_{1,106}$=1.543; p=0.323)^{1}

*glm with binomial error distribution, "linear model on square root-transformed values, °glm with quasibinomial error distribution

Figure 1: Results of goldenrod (*Solidago canadensis,* A) and tansy (*Tanacetum vulgare,* B) performance. These results quantified as whole plant biomass at the end of the growing season in three locations in the fields of Germany (GER), Hungary (HUN) and America (USA).

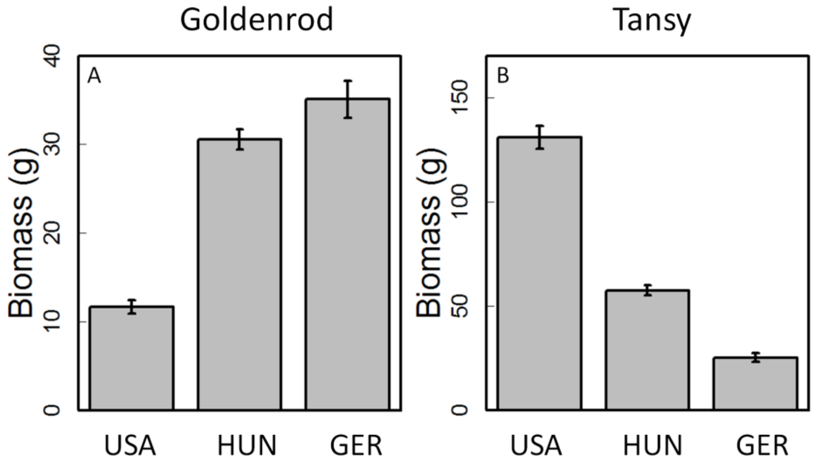


Figure 2: A & B: Performance of goldenrod (*Solidago canadensis*, A) and tansy (*Tanacetum vulgare*, B) quantified as whole plant biomass at the end of the growing season in three locations, Germany (GER), Hungary (HUN) and America (USA) with the experimental treatment of competition by the other species of (without: -C and with: +C) and application of insecticide (without: -I and with: +I).

C & D: Proportion of herbivory suffered by goldenrod (C) and tansy (D) with (+I) or without (-I) application of insecticide in the different countries. In GER and USA the proportion of plants showing herbivory damage is shown. *Due to generally high rates of herbivory in HUN all plants showed signs of herbivory and the proportion of individually counted leaves with herbivory damage is shown.

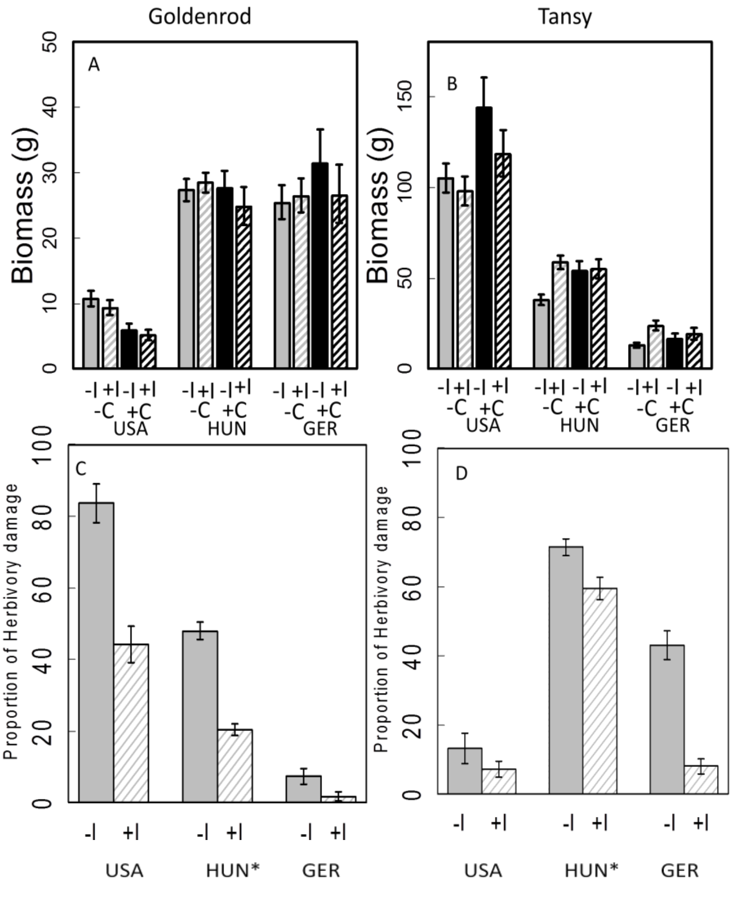
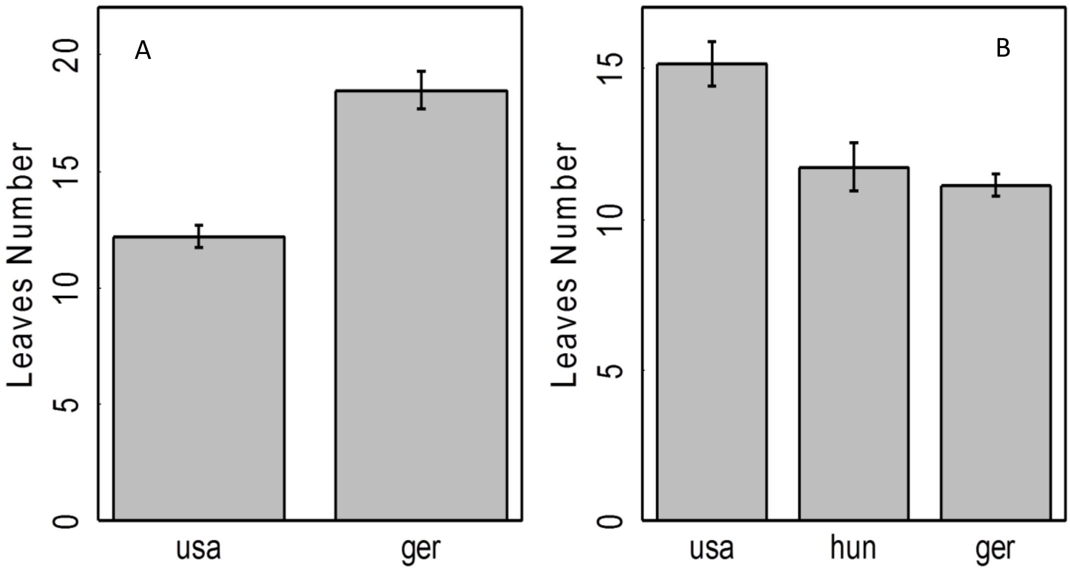


Figure 3: Number of leaves of goldenrod (A) and tansy (B) from different origin America (usa), Hungary (hun) and Germany (ger) in a common greenhouse. Because seeds of goldenrod from hun did not germinate there is no number of leaves given.



Supplementary information

Figure S1: Different measurements for the performance of goldenrod (*Solidago canadensis,* A, C and E) and tansy (*Tanacetum vulgare,* B, D and F) in three locations, Germany (GER), Hungary (HUN) and America (USA). The proportion of flowering in panel E and F is the proportion of shoots on which flowers have been observed.

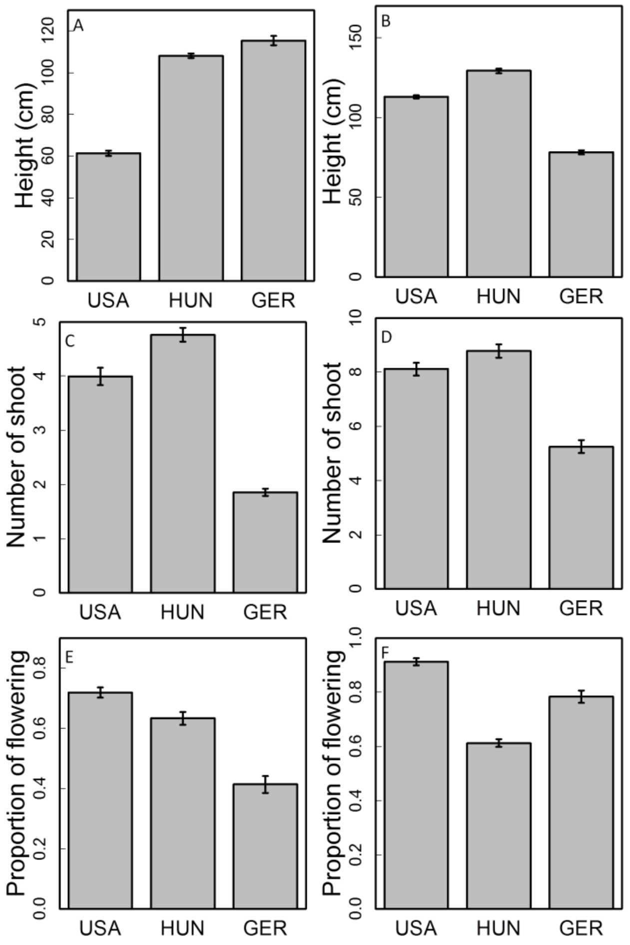


Figure S2: Performance of goldenrod (*Solidago canadensis*, A) and tansy (*Tanacetum vulgare,* B-C) from different origin America (usa), Hungary (hun) and Germany (ger) in the greenhouse in 2012-2013. The proportion of flowering in panel C is the proportion of shoots on which flowers have been observed.

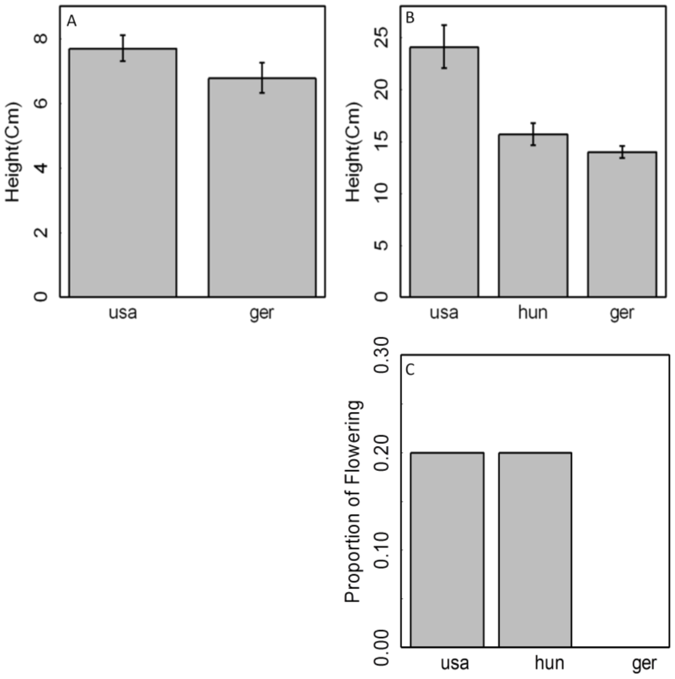


Figure S3: In Germany, tansy (*Tanacetum vulgare*) was in addition infected by a high number of aphids (*Macrosiphoniella tanacetaria*) which was reduced to zero in all plots where insecticide was applied. Aphids never occurred on goldenrod in Germany Applying insecticide killed all aphids on treated plants and even four weeks after insecticide applications (prior to the next application) aphid numbers were still significantly reduced on treated plants by about 50% (F1, 44=9.033; p=0.004).

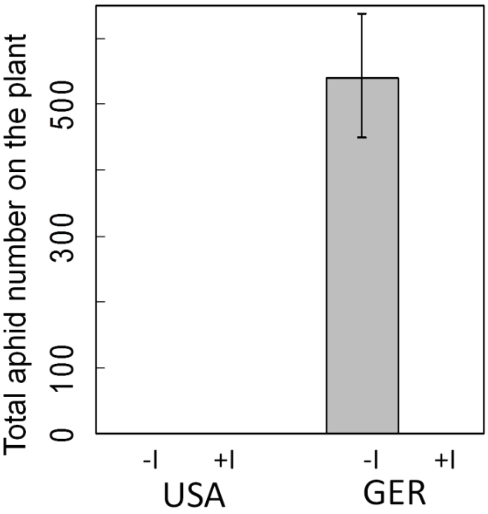
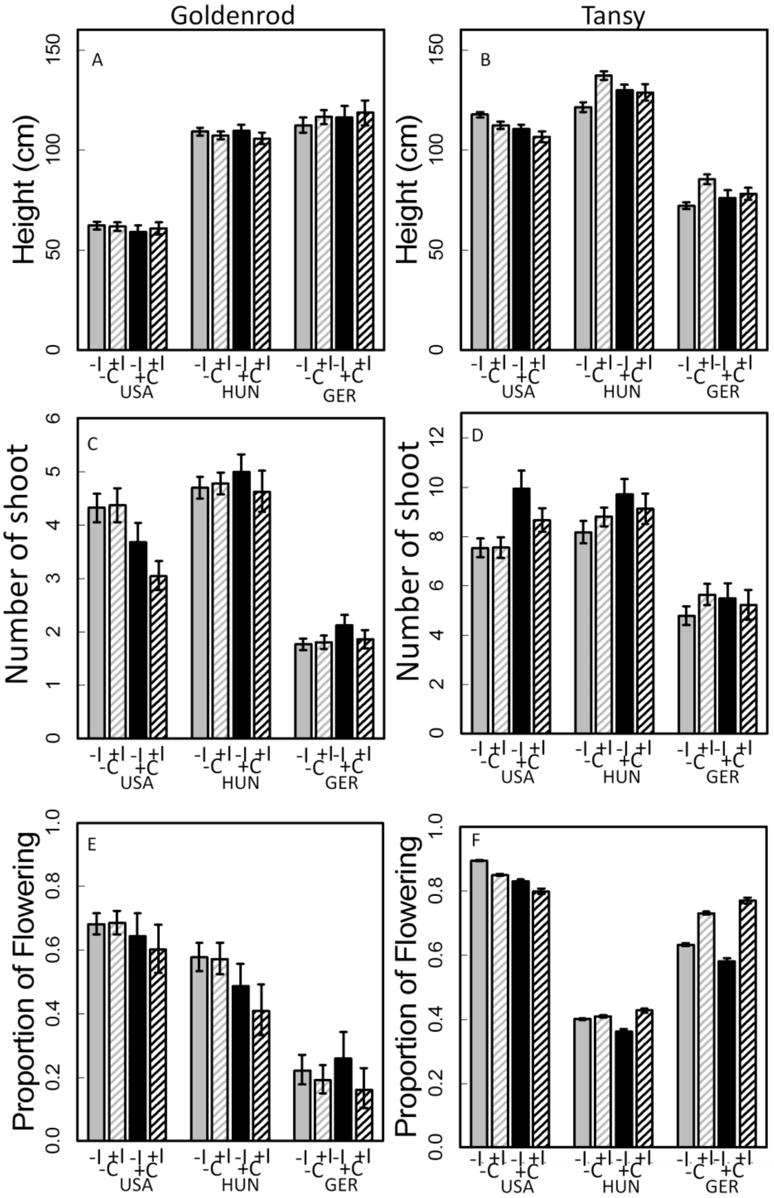


Figure S4: Different performance of goldenrod (*Solidago canadensis*, A, C & E) and tansy (*Tanacetum vulgare*, B, D & F) at the end of the growing season in three locations, Germany (GER), Hungary (HUN) and America (USA) with the experimental treatment of competition by the other species of (without: -C and with: +C) and application of insecticide (without: -I and with: +I). The proportion of flowering in panel E and F is the proportion of shoots on which flowers have been observed.



Chapter 4

Effects of herbivory and competition history on the competitive interactions between tansy and goldenrod

Abstract

Worldwide, invasive species threaten biodiversity because they outcompete native plant species causing local or global extinctions. Often, this is due to a release of invasive plants from their coevolved herbivores in the invaded range. The outcome of competition between an invasive and a particular native plant does, however, also depend on properties of the native plant and may depend on other factors such as the interaction of the native plant with its herbivores or previous exposure of the plant to the competitor. Goldenrod (*Solidago canadensis*) was introduced to Europe from North America where it continues to spread in habitats such as urban or industrial wastelands. There, it frequently co-occurs with native tansy (*Tanacetum vulgare*), that appears to be able to co-exist with goldenrod. While a large range of herbivores attacks tansy, goldenrod suffers very little from herbivory in the invaded range, in contrast to the situation in North America. We tested for the outcome of competition between tansy and goldenrod in the presence and absence of experimental herbivory by *Spodoptera* caterpillars in a greenhouse experiment. We contrasted intra- vs. interspecific competition of plants grown in pairs and with herbivory on either one plant, both plants, or no plants. As a control, single plants were grown with and without herbivory. We also manipulated the competition history of the tansy seeds used in the experiment: they either were collected from tansy growing in the vicinity of goldenrod, or from plants that had grown without competition to goldenrod in the field. For both plant species, adding a second plant to the pot strongly reduced plant biomass, height, number of shoots and the proportion of shoots that were flowering. For goldenrod, interspecific competition was stronger than intraspecific competition. In contrast, for tansy, the opposite was true: plant performance was more strongly reduced by intraspecific competition. While herbivory generally reduced plant biomass, the reduction on plants that a caterpillar had fed on was always less than 15% of total biomass. Herbivory did not change the outcome of competitive interactions between the two plant species even when only one plant was subjected to a caterpillar. The effect of competition history was surprisingly strong. For tansy plants grown from seeds collected from plants found in competition with goldenrod in the field, the difference in plant biomass between plant in intraspecific competition with tansy and those in interspecific competition with goldenrod was larger than for plants grown from seeds with no competition history. For plants grown without competition, there was no effect of competition history. This indicates that exposure to competition with goldenrod increases the competitive ability of tansy through maternal effects. Our results give no support to the hypothesis that tansy will be outcompeted by the successful invader goldenrod. This coexistence is not affected even when herbivory was strongly favouring one over the other plant species. Our results also point to the importance of responses of native plants to an invader. Studies on invasive-native plant interactions should thus not only focus on adaptive processes in the invasive plants but also investigate changes in the native plant populations, as illustrated by the strong effect of competition history on tansy performance.

Keywords: invasive plant, invader, native, competition history, coexistence, herbivory, caterpillar, competition, competitor identity, introduced species, adaptation

Introduction

Invasive plants and their effect on the ecosystem and biodiversity

Competition plays an important role in structuring plant communities (Freckleton and Watkinson 2001) and for a non-native plant to establish successfully and become invasive it has to outcompete plants from the local flora (Keane and Crawley 2002). Indeed, many successful invaders become dominant after having been introduced into a new area and cause harm to the original plant community by reducing native species diversity via competitive exclusion (Wolfe 2002, Colautti et al. 2004, Doorduin and Vrieling 2011). Yet, the outcome of competition between an invasive and a particular native plant does also depend on traits of the native plant and other factors such as previous exposure of the plant to the competitor (Leger 2008) and the interaction of the native plant with its herbivores (Maron and Vila 2001, Keane and Crawley 2002).

Herbivory effect

Herbivory can reduce the growth rates and other traits determining plant performance and competitive ability (Crawley 1983, Louda et al. 1990b, Maron and Vila 2001, Levine et al. 2004). This is true for both invasive and native plants from the invaded community. Symmetric herbivory occurs if individuals of both plants in competition are affected in the same magnitude and direction by herbivores. In contrast, during asymmetric herbivory one of the plant species in competition suffers less from herbivory and as a result should have a competitive advantage over the other species with higher herbivory. Asymmetric herbivory is assumed to be typical for pairs of invasive and native plants because of differences in the associated herbivore communities. While the effect of invasive plants on native community is increasing globally, studies that examine the effect of herbivores on both native and invasive plants are essential for understanding the influence species invasions on community dynamic and ecosystem function.

Hypothesis explain success of invasive species

The success of invasive species in the invaded range and their high competitive ability have been explained by a lack of natural enemies (e.g. herbivores) in their invaded range as detailed in the enemy release hypothesis (ERH; Jones and Lawton 1991, Keane and Crawley 2002, Colautti et al. 2004). As a consequence, the absence of herbivores may result in selection against costly herbivore-resistance traits in vigour or competitive ability traits (which typically show trade-offs with herbivore resistance traits) as predicted by the evolution of increased competitive ability (EICA; Blossey and Nötzold 1995).

Interactions of competition and herbivory

It is well known that herbivory and competition are two of the most important stressors that (native and invasive) plants encounter (Li et al. 2013). These stressors do not act independently and their effects can interact in a synergistic or antagonistic way. Synergistic effects that arise if neighbouring plants reduce a plant's tolerance to tissue loss to herbivores and when negative effects of herbivory reduce the plant's competitive ability are assumed to be the norm (Herms and Mattson 1992, Mcevoy et al. 1993, Meiners and Handel 2000, Hämback and Beckerman 2003). In contrast, some studies have revealed, the effects of competition and herbivory that were smaller in combination than their individual effects, indicating an antagonistic interaction between herbivory and competition (Callaway et al. 2006, Schädler et al.

2007, Li et al. 2013). The combined effects of interspecific competition and herbivory on invasive plant species performance, although potentially important, are much less explored (Meiners and Handel 2000; Hämback and Beckerman 2003; Lau and Strauss 2005). In general, herbivores need not consume a large amount of plant material to have a large effect on plant community composition, they need only reverse the outcome of competition (Louda et al. 1990a, Rogers and Siemann 2004).

Effect of competition history

Higher competitive ability due to herbivore release, however, may not be the only or even the primary selective pressure on invasive plant populations. Since an invasive species must successfully disperse and then survive to reproduce in a region where it has no previous history, EICA studies suggested that shifts in performance traits for plant species in invaded ranges may indicate adaptation to local condition (Felker-Quinn et al. 2013). Because of dramatic effects of invasive species on the invaded communities, the environment for native plants can be changed. Consequently, native species might be exposed to new selective pressures due to the presence of invaders. They have to adapt or they may eventually go extinct (Leger 2008). To date there are few studies that address the fundamental question of whether there are any ecological differences between native plants growing in invaded and uninvaded areas (Lau 2006, Leger 2008). Whether native species are able to evolve in response to the effects of invasive species invasion is very important for the future persistence of native plant communities (Leger 2008).

In this study

We used goldenrod (*Solidago canadensis* L.) and tansy (*Tanacetum vulgare* L.) as a model system, because they present an interesting case of reciprocal invasion patterns. There is a possibility that both native plants are suffering from this invasion and might be replaced over time. Goldenrod in its native habitats is frequently attacked by insect herbivores (Maddox and Root 1990, Root and Cappuccino 1992, Fontes et al. 1994), unlike the situation in Europe where herbivory has usually little influence on invasive goldenrod (Guesewell et al. 2006, Jacobs 2008). In contrast to goldenrod, native tansy is attacked by a large number of often specialized herbivorous insects in Europe with only few herbivory in USA. Consequently, the lack of herbivory in the invaded, and the strong herbivory in the native range for both plant species, potentially shifts the competitive balance towards the invasive plants. We tested for the outcome of competition between tansy and goldenrod in the presence and absence of experimental herbivory by *Spodoptera* caterpillars. In a greenhouse experiment, we contrasted intra- vs. interspecific competition of plants grown in pairs and with herbivory on either one plant, both plants or no plants. As a control, single plants were grown with and without herbivory. We also manipulated the competition history of the tansy seeds used in the experiment: they were collected either from tansy growing in the vicinity of goldenrod, or from plants that had grown without competition to goldenrod in the field. We specifically asked

1) Does the outcome of interspecific competition between tansy and goldenrod differ from intraspecific competition? 2) Do plants with a competition history perform

differently from plants without? 3) Can herbivory change the competitive interactions between tansy and goldenrod?

Material and Methods

Study system

Goldenrod (*Solidago canadensis* L.) is a perennial herb, native to US and was introduced to Europe in the 17th century. It is now one of the most aggressive weeds in Central Europe occurring in rural and urban-industrial areas in the habitats of the native tansy (*Tanacetum vulgare* L.). Tansy is a tall perennial herbaceous flowering plant from the Asteraceae family that is originally native to Central and Eastern Europe, has been introduced to America, and become a serious pest there. While in many places this two plant species are still coexisting, there are worries that in invaded range these two plant might replace by each other over time.

In this study, two greenhouse experiments were performed to evaluate effects of competition and competition history on goldenrod and tansy performance with and without including effects of herbivory.

Experiment I: Effects of competition and competition history on goldenrod and tansy performance

To evaluate the competitive ability of tansy and goldenrod, seeds of 20 mother plant of tansy growing in the vicinity of goldenrod (less than 1m away from a goldenrod) so that they had "competition history" (CH) and seeds of 20 tansy plants that had no goldenrod close by (no goldenrod in a zone of at least 2m around tansy) were collected from an old field in Freising, Germany. To grow the plants, seeds for all mother plant were sown in 50 ml pots in the greenhouse in separate groups (20 pots per plant and 10 seeds per pot). At the same time goldenrod were sown in 600 pots (10 seeds per pot) in the same way. Plants maintained under controlled greenhouse conditions (temperature ~ 25°C during the day and ~ 20°C at night and with a 16 h light: 8 h dark light regime). Plants germinated within the first 2 weeks after which the strongest plant individual was kept in each pot and the rest was removed. After one month, seeds from 17 tansy mother plant without and 15 with CH had germinated. At the start of the experiment, seedlings were transplanted to 1.25-L pots combining tansy (T) and goldenrod (G) and in the following design: a single plant without competition (T/G), plants in competition with the same species (TT/GG) or one plant in competition with the other species (TG=GT) in four replicates (32 × 5 × 4= 640). For two conspecific individuals in competition, random plant was labelled at the start of the experiment and only measurements of these plants were used in the analysis. After plants had stopped growing and had flowered, variables describing plant performance were measured. For each plant the number of shoots was counted and the height of the tallest shoot was measured (in cm). Proportion of flowering was recorded as the presence or absence of flowering shoot. For total plant biomass (g), aboveground parts of plants were harvested, dried to constant mass at 70°C for 48 hours, and weighed.

Experiment II: Effects of competition crossed with herbivory and competition history on goldenrod and tansy performance.

After the first vegetation period the experiment was continued with the resprouting plants from the previous experiment to investigate the effect of experimental herbivory on the competitive interactions between both species in addition to the CH. Plant were grown for two months in the same combination of CH and competitor identity as in experiment I. When the plants reached at height of 20 cm, an additional experimental herbivory treatment was applied. Herbivory was applied to the focal plant (measured plant) or competing plant and all possible combinations of these treatments. This resulted in three groups of plants: i) No-herbivory treatment in which herbivory was applied in combination plants in competition to none of the two (--) ii) Symmetric herbivory in which herbivory was applied to both plants in competition (++) and iii) Asymmetric herbivory in which in each pot only one of the plants in competition was exposed to herbivory (+-/-+). All herbivory treatments were applied to plant combination of the same (TT/GG) and different species (TG). When there were two plants with the same treatment combination in one pot (i.e. symmetric or no herbivory on TT or GG) only measurement of one plant randomly selected at the start of experiment were used in the analysis (32×10=320). In this experiment to have a comparison for the effect of competition per species, additional control pots of both tansy and goldenrod individuals (T/G) without competition (single plants) were performed. Half of these plants were also exposed to herbivory (32×4=128).

Experimental herbivory

To impose herbivory damage to plants in experiment II, a forth larval instar of *Spodoptera litoralis* (Noctuidae) was placed on the upper portion of individual plants for five days in the design detailed above. To avoid cross infection between plants by escaping caterpillars, each plant was covered with one air-permeable cellophane bag fixed to the root grown of the plants with elastic bands. In case of two plants in a single pot both being exposed to herbivory, each plant received an individual caterpillar and was bagged individually. To control for potential side effect of the bags, also plants in the treatment without herbivory were covered in the same way with cellophane bags. During the five days of the herbivory treatment, caterpillars removed about 30% of the total leaves of the plants.

Spodoptera litoralis, known as the Cotton leaf worm is a very generalist herbivore. Its larvae have been recorded to feed on a wide range of plants from over 40 plant families (Hill 1987). In a pre-trial, the caterpillars had been tested for the suitability of tansy and goldenrod as food plants. The caterpillars had readily accepted both plant species. Because of the high degree of generalism and wide feeding range, the caterpillar is a very suitable herbivore when an experimental herbivory treatment is applied to different plant species *Spodoptera litoralis* is major pest of many crops because of which the species is under special legal restrictions. Special quarantine measures have been taken during the experiment to ensure that no individuals could have escaped during rearing of the caterpillars from eggs or during the greenhouse experiment. Permits for the import of the species (050/2013) from the Institute of Biology, University of Neuchâtel, Switzerland and to work with the caterpillars (18/2013) were received from the Bayerische Landesanstalt für Landwirtschaft, Institut für Pflanzenschutz, Plfanzengesundheit – Quarantäne, Lange Point 10, 85354 Freising-Weihenstephan.

Statistical analysis

In the first experiment, linear models (LM1, LM2) were used to compare mean value for response variables measuring plant performance by fitting block, competition, CH and their interactions as fixed factor for a range of. In first model (LM1), competition, as a factor, had three different levels (T, TT & TG), whereas in second model (LM2) levels were decreased to two, so that plants in competition (TT & TG) considered as one level. Comparison of these two models tests for the effect of competitor identity. In our second experiment for a range of response variables measuring control plants of tansy and goldenrod, a linear model was used to compare mean value for each variable by fitting block, caterpillar treatment (no-herbivory, herbivory), CH and their interactions. Plants in competition were analysed in separate model, comparing mean value for each response variables measuring plant performance by fitting block, competitor identity, focal plant with herbivory, competing plant with herbivory, CH and their interactions. All tests were done for each plant species separately. For plant biomass we calculated log response ratios (plant biomass LogRR) to directly quantify the effects of competition on plant growth, by calculating the log of the biomass of conspecific individuals in competition divided by the biomass of plants in competition with the other species. Values of plant biomass LogRR <0 indicate that the biomass of plants competing with the other species was higher than the biomass of plants with conspecific competition and thus intraspecific competition decreases plant biomass. In contrast, LogRR values >0 indicate that conspecific competition increases plant biomass thus interspecific competition decreases plant biomass. All models were estimated using the R software (Version 2.14.1; R Development Core Team 2011). Variables were transformed as necessary (indicated in Table 1-2). In all analyses, not significant terms were removed during model simplification (in the order given in Table 1-2). All data are presented as mean ± standard error (SE).

Results

Experiment I

For both plant species, adding a second plant to the pot (i.e. competition) strongly reduced plant biomass, height, number of shoots and the proportion of shoots that were flowering (Table 1). Competition decreased goldenrod biomass and height but its effect was stronger when goldenrod was in competition with tansy compared to competition with goldenrod (Table 1, Fig. 1A, B). Thus, interspecific competition reduced goldenrod performance more while tansy performance was reduced more from intraspecific competition. Tansy performance (i.e. biomass, height, shoot number and proportion of flowering) decreased more in competition with tansy compared to goldenrod (Table 1, Fig. 1D-G). The important difference between competition with tansy and goldenrod was confirmed also by a significant difference between a model including competitor identity and a simpler model including only competition (F_{376}=48.193; p<<0.001). CH had a significant effect on tansy proportion of flowering (Table 1) but no other measures of tansy performance. Generally tansy plants had higher proportion of flowering with CH compared to plants without CH (with CH: 0.7 ± 0.034; without CH: 0.61 ± 0.034, Fig. S1). In contrast to tansy, CH had no effect on any measured of goldenrod (Table 1).

Experiment II

After the first vegetation period and harvest of the aboveground biomass, the experiment was continued with the resprouting plants. An additional experimental herbivory treatment was applied to remove 30% of plant foliar. Herbivory decreased the performance of control individuals of both tansy and goldenrod almost 15% (i.e. single plants without competition; Table 2, Fig. 2A, D and G). These control plants without competition were bigger than plants in competition by a factor of about two (Tansy: 2.34±0.06 vs 1.17±0.04; Goldenrod: 2.59±0.06 vs1.1±0.04, average over level of herbivory and competitor identity).

For goldenrod plants exposed to competition, competitor identity had a significant effect on biomass and height. The competition effect was stronger when goldenrod was in competition with tansy compared to competition with goldenrod (Table 3A, Fig. 3A, B), causing an overall positive LogRR in response to competitor identity and confirming results from the first experiment (Table 3A, Fig. S2A). There was no effects of herbivory applied to the focal plant on any measure of goldenrod performance. Herbivory applied to the competing plants affected goldenrod height (Table 3A) so that goldenrod was growing higher when the competing plant didn’t have herbivory compared to competing plants with herbivory (Fig. 3B). CH had no significant effect on any measure of goldenrod performance in contrast to competitor identity and herbivory (Table 3A).

For tansy exposed to competition, competitor identity affected all measured of tansy performance in the experiment. Tansy performance decreased more in competition with tansy compared to competition by goldenrod (Table 3B, Fig. 3 D-G). Herbivory applied to the focal plant decreased tansy biomass (Fig. 3D, Fig. S3).

Because we reduced 30% of plant foliar by herbivory and this resulted in smaller plant that had at 15% less biomass. In addition, herbivory applied to competing plant had a significant effect on tansy height but this effect depended also on competitor identity and CH (Table 3B). Tansy plants with CH were tallerwhen the competitor was goldenrod while for plants without CH, tansy was only higher if the competing goldenrod had herbivory (Table 3B, Fig. 3E). In contrast to goldenrod, CH affected tansy performance. The reduction of tansy biomass for plants in competition with goldenrod was smaller when plants had a CH (Table 3B, Fig. 3 D). Consequently average plant biomass LogRR in response to competitor identity was more negative when plants had CH (Table 3B, Fig. S2B).

Discussion

Summary of main results

In this study, we have demonstrated that both species suffered from competition while the magnitude depended on competitor identity. Goldenrod suffered more from competition with tansy compared to competition with goldenrod. In contrast, tansy performance was reduced stronger by competition with tansy compared to goldenrod. Generally, there were only weak effects of herbivory reducing the performance of plants that caterpillars fed on. Even the strongly asymmetric herbivory imposed in our experiment did not change the outcome of competitive interactions between the two plant species. A history of competition with goldenrod increased the competitive ability of tansy. The reduction of tansy biomass for plants in competition with goldenrod was smaller when plants had a CH, while there was no effect of CH on goldenrod.

Effect of competition

Competition plays an important role in structuring plant communities and experimental evidence supports this view (Fowler 1986, Weiner 1990, Casper and Jackson 1997). High competitive ability of invasive species has been mentioned as a key factor promoting successful invasive potential, and competitive exclusion by native plant species seems to be a major force resisting invasive plants (Keane and Crawley 2002). Studies on the control of invasive species suggest that competition can reduce invasive plant growth more than herbivory (Vila and Weiner 2004). The main effect of competition is to reduce the size of competing plants, and in our experiment, control plants without competition were bigger than plants in competition by a factor of about two. These results indicate that resource reduction and competition for soil nutrients which were in short supply might have occurred. The presence of competing plants in a given volume of soil can induce nutrient stress in a given plant as neighbours acquire limiting resources (Craine and Dybzinski 2013). While plants compete mainly for light and soil nutrients (Casper and Jackson 1997), in our experiment aboveground competition for light cannot be ruled out completely, it is unlikely because plants were sufficiently spaced to cause competition for light to be strongly reduced. Consequently, mostly below ground competition affected our plants.

Competitor identity

The effect of competition on plant biomass depended on competitor identity confirming our first hypothesis. Thus, interspecific and intraspecific competition between tansy and goldenrod had differently strong effects. In this study, competition with native tansy did decrease the growth of invasive goldenrod significantly more than competition with another goldenrod plant, i.e. for goldenrod competition with a conspecific is less intense than with a tansy plant. This pattern was reverse for tansy. Tansy plants suffered less from competition by a goldenrod plant compared to competition with a conspecific tansy plant. This is in agreement with a pervious study by Rebele (2000) that suggested that tansy is a stronger competitor for soil nutrients (P, Ca and Mg) compared to goldenrod. In addition, the competitive ability tansy species appears to involve long-term pre-emption of underground space by bulky roots, possession of winter- green leaves, rapid shoot growth in early spring, and a canopy that casts a dense shade at ground level (Crawley et al. 1999). Despite the strong effect of competition, as indicated by the drastic reduction in performance of the control plants, species in competition coexisted until the end of experiment. The possibility is weaker interspecific competitive effects than intraspecific effects, because trade-offs among the competitors, give each species unique advantages for exploiting environmental resource requirements (reviewed by Chesson 2000, Moll and Brown 2008).

Herbivory effects

Both competition by native species and herbivory could affect the invasiveness of introduced species and often limit the success of invasive species in a recipient community. While experimentally imposed herbivory damage (loss of about 30% of the leaf area) induced by feeding of a caterpillar decreased both plant species' performance its effect was generally weak. More importantly, and contrary to general theoretical expectations, we found no clear evidence of interaction between competition and herbivory (synergic or antagonistic) on key parameters of both plant species' growth and fitness. Even the strongly asymmetric herbivory imposed in our experiment did not change the outcome of competitive interactions between the two species. This result is in contrast with other studies that they found an interaction between competition and herbivory for plant growth and reproduction (e.g. Lee and Bazzaz 1980, Belsky 1986, Mcnaughton 1986, Louda et al. 1990a, Müller-Schädler 1991, Mullerscharer 1991, Meiners and Handel 2000, Lei 2009).

There are two potential explanations why this study did not find interactive effects between herbivory and competition I) Too week effects of herbivory on plant performance to change competitive abilities, i.e. the intensity of herbivory may not have been high enough to require a trade-off between defense or tolerance of herbivory versus growth. Consequently the competitive interaction between the plants would not have changed. II) Stronger interactions between competition and herbivory might have occur if we used an earlier life stage, when plants have fewer stored resources to invest for both growth and defence (Suwa et al. 2010). Well stablished plants have ability to allocate more biomass to tissues responsible for capturing a limiting resource (Haag et al. 2004). Consequently, it was possible for plants to allocate resources to growth after herbivory compensating for losses to herbivory via regrowth (Briske and Anderson 1992, Siemann and Rogers 2001) As the direct effects of herbivory on the plant that suffered were relatively small, the indirect effects on the competing plant were also small. Yet, in competition treatments, when only tansy was affected with herbivory, goldenrod performance was higher. These results are consistent with the predictions of the ERH for tansy in

USA where tansy is free from herbivory and goldenrod suffers from herbivory. This can explain the higher performance of tansy in its invaded range (Fenner and Lee 2001, Torchin et al. 2003, Colautti et al. 2004, DeWalt et al. 2004).

Competition history

Our results showed that there is a difference between the performances of native tansy with CH compared to tansy without CH. When the competitor was goldenrod, tansy with CH, had more biomass and grew higher. We see this pattern in both experiments but in the first experiment only for the proportion of flowering, while this pattern was strong for all measures of tansy performance in the second experiment. This indicates that plants had to become older to show stronger effects of CH. As EICA suggested, for invaders, shifts in performance traits in invaded ranges may indicate adaptation to local condition (Felker-Quinn et al. 2013). Our results indicate that in addition to invaders, also natives respond evolutionarily to the novel selection regimes by adapting to the presence of the exotic plant. The possibility is increases in competitive ability of native species over time and low impacts of competition on plant performance stabilizing coexistence (Chesson 2000). Prior studies which compared plants from native and invaded sits, also suggested native species can respond evolutionarily to novel environmental conditions, such as invasion by invasive species (Callaway et al. 2005, Lau 2006, Mealor and Hild 2006, Leger 2008, Goergen et al. 2011). For example Goergen et al. (2011) study the response of native plants to the selective pressure of invasion *Bromus tectorum* on a variety of communities and across large areas. Their results indicate that some, but not all, populations of native grasses may be evolving in response to *B. tectorum* invasion. Yet previous studies compare different invaded and uninvaded area (Leger 2008, Goergen et al. 2011), we extended this comparison to the individual native plants that had grown to the vicinity of invasive, or had grown without competition with invasive. Our results showed even within population in the invaded area, plant evolved differently in response to invasion depending on the distance of being exposed to the invasive species.

Ecological consequences

Goldenrod is a well-established invader in that the region where the invasion is happening (Lu et al. 2007) and it putatively outperforms the native plants (Zhang et al. 2008). In contrast to our expectation not only did goldenrod not supressed tansy, even more, tansy showed to be a better competitor compared to goldenrod. In addition herbivory also did not change the outcome of competitive interactions between the two plant species even when only one plant was subjected to a caterpillar. Thus our greenhouse experiment does not indicate a danger of tansy to be replaced by goldenrod in Europe even when tansy was under herbivory. If such a replacement is occurring in the field, it would have to be caused by other mechanisms like maybe extreme climatic events. In contrast, because of the competitive effect of tansy on goldenrod, especially when tansy was free of herbivory, invasive tansy could be considered a threat for native goldenrod in North America. Our initial evidence for the tansy response to presence of an invasive neighbour showed that it is possible that adaptation allows tansy to persist in altered environments which indicates potential evolutionary responses of native species to invasion. Tansy may evolved tolerance to invasive goldenrod and eventually contributes to coexistence among these two plants.

Conclusion

Biological invasions provide exceptional opportunities to investigate the evolutionary responses of native community members to novel species additions. Our experiment showed no competitive exclusion or strongly reduced tansy performance in presence of goldenrod not even when experimental herbivory was strongly favouring goldenrod. On the contrary, tansy competing with goldenrod performed better than tansy competing with another tansy. This effect was especially strong for tansy plants with a history of competition with goldenrod. Our results also point to the importance of responses of native plants to an invader as illustrated by the strong effect of CH on tansy performance. Thus, studies on invasive-native plant interactions should not only focus on adaptive processes in the invasive plants but also investigate changes in the native plant populations.

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Table 1- Results from linear models of the effect of competition and competition history (experiment I) for a range of response variables measuring goldenrod (*Solidago canadensis*) and tansy (*Tanacetum vulgare*) performance in a greenhouse experiment in Germany. Plant species were grown individually or in competition with the same or the other species (i.e. competitor identity). Tansy seeds used in the experiment differed in competition history with goldenrod (i.e. they either were collected from tansy growing in the vicinity of goldenrod, or from plants that had grown without competition to goldenrod in the field). Results for tansy and goldenrod were analyzed in separate models. Minimum adequate models are presented together with terms removed from the models given in brackets. Superscripts give the order in which terms have been removed from the model starting with highest order interactions based on least significance. Significant terms in the final models are given in bold.

Variable	Species	Block	Competition(C)	Competition history(CH)	C×CH
	Goldenrod				
Biomass*		**$F_{3,378}$=8.577; p<<0.001**	**$F_{2,378}$=104.61; p<<0.001**	($F_{1,377}$=0.073; p=0.787)^{2}	($F_{2,375}$=1.787; p=0.169)^{2}
Height		**$F_{3,378}$=5.849; p=0.001**	**$F_{2,378}$=81.87; p<<0.001**	($F_{1,377}$=0.036; p=0.85)^{2}	($F_{2,375}$=1.071; p=0.343)^{2}
Proportion flowering shoots °		-	-	-	-
Shoots number **		$Chi_{3,380}$=3.75; p=0.289	($Chi_{2,378}$=0.004; p=0.997)^{3}	($Chi_{1,377}$=3.475; p=0.062)^{2}	($Chi_{2,375}$=0.857; p=0.651)^{1}
	Tansy				
Biomass		**$F_{3,377}$=3.44; p=0.016**	**$F_{2,377}$=168.89; p<<0.001**	($F_{1,376}$=0.264; p=0.608)^{2}	($F_{2,374}$=0.134; p=0.874)^{1}
Height		**$F_{3,377}$=6.33; p=0.001**	**$F_{2,377}$=79.94; p<<0.001**	($F_{1,376}$=0.001; p=0.993)^{2}	($F_{2,374}$=0.100; p=0.904)^{1}
Proportion flowering shoots °		**$F_{3,376}$=3.91; p=0.008**	**$F_{2,376}$= 39.54; p<<0.001**	**$F_{1,376}$= 4.331; p=0.038**	($F_{2,374}$= 0.445; p=0.641)^{1}
Shoots number**		**$Chi_{3,377}$=10.19; p=0.016**	**$Chi_{2,377}$=23.18; p<<0.001**	($Chi_{1,376}$=3.74; p=0.062)^{2}	($Chi_{2,374}$=0.584; p=0.746)^{1}

* linear model on sqrt-transformed values , ** glm with poisson error distribution, ° glm with quasibinomial error distribution

Table 2- Results from linear models of the herbivory effect (experiment II) for control plants in the absence of competition on a range of response variables measuring goldenrod (*Solidago canadensis)* and tansy (*Tanacetum vulgare*) performance in a greenhouse experiment in Germany. Tansy seeds used in the experiment differed in competition history with goldenrod (i.e. they either were collected from tansy growing in the vicinity of goldenrod, or from plants that had grown without competition to goldenrod in the field). Effect of herbivory (Caterpillars of the general herbivore *Spodoptera litoralis*) was crossed with the effect of competition history. Results for tansy and goldenrod were analyzed in separate models. Minimum adequate models are presented together with terms removed from the models given in brackets. Superscripts give the order in which terms have been removed from the model starting with highest order interactions based on least significance. Significant terms in the final models are given in bold.

Variable	**Species**	**Block**	**Herbivory(H)**	**Competition history(CH)**	**H×CH**
	Goldenrod				
Biomass*		$F_{1,61}$=2.82; p=0.09	**$F_{1,61}$=4.683; p=0.034**	($F_{1,60}$=0.001; p=0.996)^{2}	($F_{1,59}$=2.78; p=0.1)^{1}
Height		$F_{1,62}$=0.273; p=0.628	($F_{1,61}$=0.296; p=0.588)^{3}	($F_{1,60}$=2.569; p=0.114)^{2}	($F_{1,59}$=3.606; p=0.062)^{1}
Proportion flowering shoots		-	-	-	-
Shoots number **		$F_{1,62}$=1.47; p=0.229	($F_{1,61}$=0.012; p=0.913)^{3}	($F_{1,60}$=0.190; p=0.664)^{2}	($F_{1,59}$=0.3; p=0.585)^{1}
Tansy					
Biomass		$F_{1,60}$=1.158; p=0.286	**$F_{1,60}$=13.38; p=0.001**	($F_{1,59}$=0.226; p=0.635)^{2}	($F_{1,58}$=0.001; p=0.989)^{1}
Height		$F_{1,61}$=0.005; p=0.935	(**$F_{1,60}$**=1.28; p=0.262)^{3}	($F_{1,59}$=0.158; p=0.692)^{2}	**(**$F_{1,58}$=3.173; p=0.08))^{1}
Proportion flowering shoots *		$F_{1,60}$=2.121; p=0.15	**$F_{1,60}$=10.81; p=0.001**	($F_{1,59}$=0.544; p=0.463)^{2}	($F_{1,58}$=0.804; p=0.373)^{1}
Shoots number**		$F_{1,61}$=0.2; p=0.656	(**$F_{1,60}$**=0.726; p=0.397)^{3}	($F_{1,59}$=0.033; p=0.856)^{2}	**(**$F_{1,58}$=0.232; p=0.631)^{1}

* linear model on log-transformed values, ** glm with poisson error distribution

Table 3A- Results from linear models of the herbivory effect (experiment II) for a range of response variables measuring goldenrod (*Solidago canadensis)* performance in a greenhouse experiment in Germany. Plant species were grown in competition with the same or the other species (i.e. competitor identity). Tansy seeds used in the experiment differed in competition history with goldenrod (i.e. they either were collected from tansy growing in the vicinity of goldenrod or from plants that had grown without competition to goldenrod in the field). Effect of herbivory (Caterpillars of the general herbivore *Spodoptera litoralis*) was crossed with the effect of competition history and competitor identity. Results for tansy and goldenrod were analyzed in separate models. Minimum adequate models are presented together with terms removed from the models given in brackets. Superscripts give the order in which terms have been removed from the model starting with highest order interactions based on least significance. Significant terms in the final models are given in bold.

Variable	**Species**	**Biomass***	**LogRR plant biomass**	**Height***	**Shoots number***
	Goldenrod				
Block		$F_{1,233}=0.870; p=0.351$	$F_{1,112}=1.36; p=0.245$	$F_{1,232}=0.062; p=0.803$	$F_{1,234}=0.008; p=0.926$
Competitor identity (CI)		**$F_{1,233}=18.91; p<<0.001$**	--	**$F_{1,232}=4.32; p=0.03$**	$(F_{1,233}=0.084; p=0.77)^{15}$
Focal plant with herbivory (FWH)		$(F_{1,230}=0.077; p=0.780)^{12}$	$(F_{1,111}=0.2.73; p=0.101)^{7}$	$(F_{1,230}=0.056; p=0.813)^{12}$	$(F_{1,232}=0.015; p=0.902)^{14}$
Competing plant with herbivory (CWH)		$(F_{1,231}=2.24; p=0.135)^{13}$	$(F_{1,110}=2.56; p=0.112)^{6}$	**$F_{1,232}=6.25; p=0.013$**	$(F_{1,230}=0.001; p=0.991)^{12}$
Competition history (CH)		$(F_{1,232}=2.66; p=0.103)^{14}$	$(F_{1,109}=0.114; p=0.736)^{5}$	$(F_{1,231}=0.173; p=0.677)^{13}$	$(F_{1,231}=0.001; p=0.965)^{13}$
CI : FWH		$(F_{1,229}=3.789; p=0.052)^{11}$	--	$(F_{1,226}=0.214; p=0.643)^{8}$	$(F_{1,228}=1.09; p=0.295)^{10}$
CI : CWH		$(F_{1,227}=2.310; p=0.129)^{9}$	--	$(F_{1,228}=0.634; p=0.426)^{10}$	$(F_{1,224}=0.001; p=0.980)^{6}$
FWH : CWH		$(F_{1,228}=2.697; p=0.103)^{10}$	$(F_{1,108}=302; p=0.583)^{4}$	$(F_{1,225}=0.024; p=0.876)^{7}$	$(F_{1,227}=0.275; p=0.599)^{9}$
CI : CH		$(F_{1,226}=0.196; p=0.655)^{8}$	--	$(F_{1,229}=2.377; p=0.124)^{11}$	$(F_{1,225}=0.004; p=0.946)^{7}$
FWH:CH		$(F_{1,225}=0.194; p=0.659)^{7}$	$(F_{1,106}=0.005; p=0.942)^{2}$	$(F_{1,227}=0.391; p=0.532)^{9}$	$(F_{1,229}=3.55; p=0.059)^{11}$
CWH:CH		$(F_{1,224}=0.106; p=0.744)^{6}$	$(F_{1,107}=0.08; p=0.773)^{3}$	$(F_{1,224}=0.002; p=0.961)^{6}$	$(F_{1,226}=0.039; p=0.843)^{8}$
CI : FWH :CWH		$(F_{1,223}=0.963; p=0.327)^{5}$	--	$(F_{1,222}=0.625; p=0.430)^{4}$	$(F_{1,222}=2.708; p=0.099)^{4}$
CI : FWH : CH		$(F_{1,222}=0.144; p=0.703)^{4}$	--	$(F_{1,223}=0.930; p=0.335)^{5}$	$(F_{1,220}=0.110; p=0.739)^{2}$
CI : CWH :CH		$(F_{1,220}=0.003; p=0.925)^{2}$	--	$(F_{1,220}=0.054; p=0.816)^{2}$	$(F_{1,221}=0.400; p=0.326)^{3}$
FWH: CWH : CH		$(F_{1,221}=0.032; p=0.856)^{3}$	$(F_{1,105}=0.007; p=0.9291)^{1}$	$(F_{1,221}=0.448; p=0.503)^{3}$	$(F_{1,223}=3.148; p=0.075)^{5}$
CI: FWH: CWH : CH		$(F_{1,219}=0.160; p=0.899)^{1}$	--	$(F_{1,219}=0.177; p=0.673)^{1}$	$(F_{1,219}=0.189; p=0.597)^{1}$

* linear model on sqrt-transformed values

Table 3B- Results from linear models of the herbivory effect (experiment II) for a range of response variables measuring tansy (*Tanacetum vulgare*) performance in a greenhouse experiment in Germany. Plant species were grown in competition with the same or the other species (i.e. competitor identity). Tansy seeds used in the experiment differed in competition history with goldenrod (i.e. they either were collected from tansy growing in the vicinity of goldenrod or from plants that had grown without competition to goldenrod in the field). Effect of herbivory (Caterpillars of the general herbivore *Spodoptera litoralis*) was crossed with the effect of competition history and competitor identity. Results for tansy and goldenrod were analyzed in separate models. Minimum adequate models are presented together with terms removed from the models given in brackets. Superscripts give the order in which terms have been removed from the model starting with highest order interactions based on least significance. Significant terms in the final models are given in bold.

Variable	**Species**	**Biomass**	**LogRR plant biomass**	**Height***	**Shoots number***	**Proportion flowering**
	Tansy					
Block		**$F_{1,230}$=6.55; p=0.011**	$F_{1,112}$=0.322; p=0.572	$F_{1,224}$=2.84; p=0.092	**$F_{1,236}$=6.024; p=0.014**	$F_{1,236}$=0.300; p=0.584
CI		**$F_{1,230}$=20.43; p<<0.001**	--	**$F_{1,224}$=9.105; p=0.002**	**$F_{1,236}$=6.87; p=0.009**	**$F_{1,236}$=17.52; p<<0.001**
FWH		**$F_{1,230}$=7.242; p=0.007**	($F_{1,111}$=1.077; p=0.301)^{6}	$F_{1,224}$=0.638; p=0.425	($F_{1,233}$=0.098; p=0.735)^{12}	($F_{1,235}$=1.005; p=0.317)^{14}
CWH		$F_{1,230}$=0.419; p=0.517	(F_{110}=0.125; p=0.724)^{5}	**$F_{1,224}$**=0.723; p=0.395	($F_{1,235}$=1.026; p=0.311)^{14}	($F_{1,233}$=0.478; p=0.489)^{12}
CH		$F_{1,230}$=1.64; p=0.201	**$F_{1,112}$=6.993.; p=0.009**	**$F_{1,224}$**=0.541; p=0.462	($F_{1,234}$=0.398; p=0.528)^{13}	($F_{1,234}$=0.627; p=0.429)^{13}
CI : FWH		$F_{1,230}$=1.285; p=0.258	--	**$F_{1,224}$**=1.304; p=0.254	($F_{1,227}$=0.118; p=0.731)^{6}	($F_{1,228}$=0.173; p=0.677)^{7}
CI : CWH		$F_{1,230}$=8.307; p=0.634	--	**$F_{1,228}$**=0.449; p=0.503	($F_{1,230}$=3.15; p=0.226)^{9}	($F_{1,230}$=0.364; p=0.546)^{9}
FWH : CWH		($F_{1,229}$=1.87; p=0.171)^{8}	($F_{1,107}$=1.27; p=0.260)^{2}	**$F_{1,224}$**=0.097; p=0.754	($F_{1,231}$=2.27; p=0.136)^{10}	($F_{1,227}$=0.001; p=0.973)^{6}
CI : CH		**$F_{1,230}$=8.307; p=0.004**	--	$F_{1,224}$=3.19; p=0.075	($F_{1,229}$=0.699; p=0.403)^{8}	($F_{1,231}$=0.951; p=0.330)^{10}
FWH:CH		($F_{1,227}$=0.001; p=0.988)^{6}	($F_{1,108}$=1.30; p=0.256)^{3}	**$F_{1,224}$**=0.435; p=0.51	($F_{1,228}$=0.580; p=0.446)^{7}	($F_{1,229}$=0.214; p=0.567)^{8}
CWH:CH		($F_{1,228}$=0.259; p=0.611)^{7}	($F_{1,109}$=1.30; p=0.256)^{4}	**$F_{1,224}$**=2.64; p=0.105	($F_{1,232}$=3.11; p=0.078)^{11}	($F_{1,232}$=2.129; p=0.145)^{11}
CI : FWH :CWH		($F_{1,225}$=1.08; p=0.299)^{4}	--	**$F_{1,224}$**=1.865; p=0.173	($F_{1,224}$=0.322; p=0.571)^{3}	($F_{1,224}$=0.305; p=0.580)^{3}
CI : FWH : CH		($F_{1,224}$=0.605; p=0.437)^{3}	--	$F_{1,224}$=0.874; p=0.350	($F_{1,223}$=0.185; p=0.666)^{2}	($F_{1,223}$=0.162; p=0.687)^{2}
CI : CWH :CH		($F_{1,226}$=1.27; p=0.259)^{5}	--	**$F_{1,224}$=4.321.; p=0.038**	($F_{1,226}$=0.493; p=0.483)^{5}	($F_{1,226}$=1.18; p=0.277)^{5}
FWH: CWH : CH		($F_{1,223}$=0.225; p=0.613)^{2}	($F_{1,106}$=0.952; p=0.331)^{1}	($F_{1,223}$=0.642; p=0.423)^{2}	($F_{1,225}$=0.471; p=0.493)^{4}	($F_{1,225}$=0.555; p=0.456)^{4}
CI: FWH: CWH : CH		($F_{1,222}$=0.57; p=0.450)^{1}	--	($F_{1,222}$=0.141; p=0.707)^{1}	($F_{1,222}$=0.142; p=0.706)^{1}	($F_{1,222}$=0.081; p=0.801)^{1}

* linear model on log-transformed values , ** glm with quasibinomial error distribution

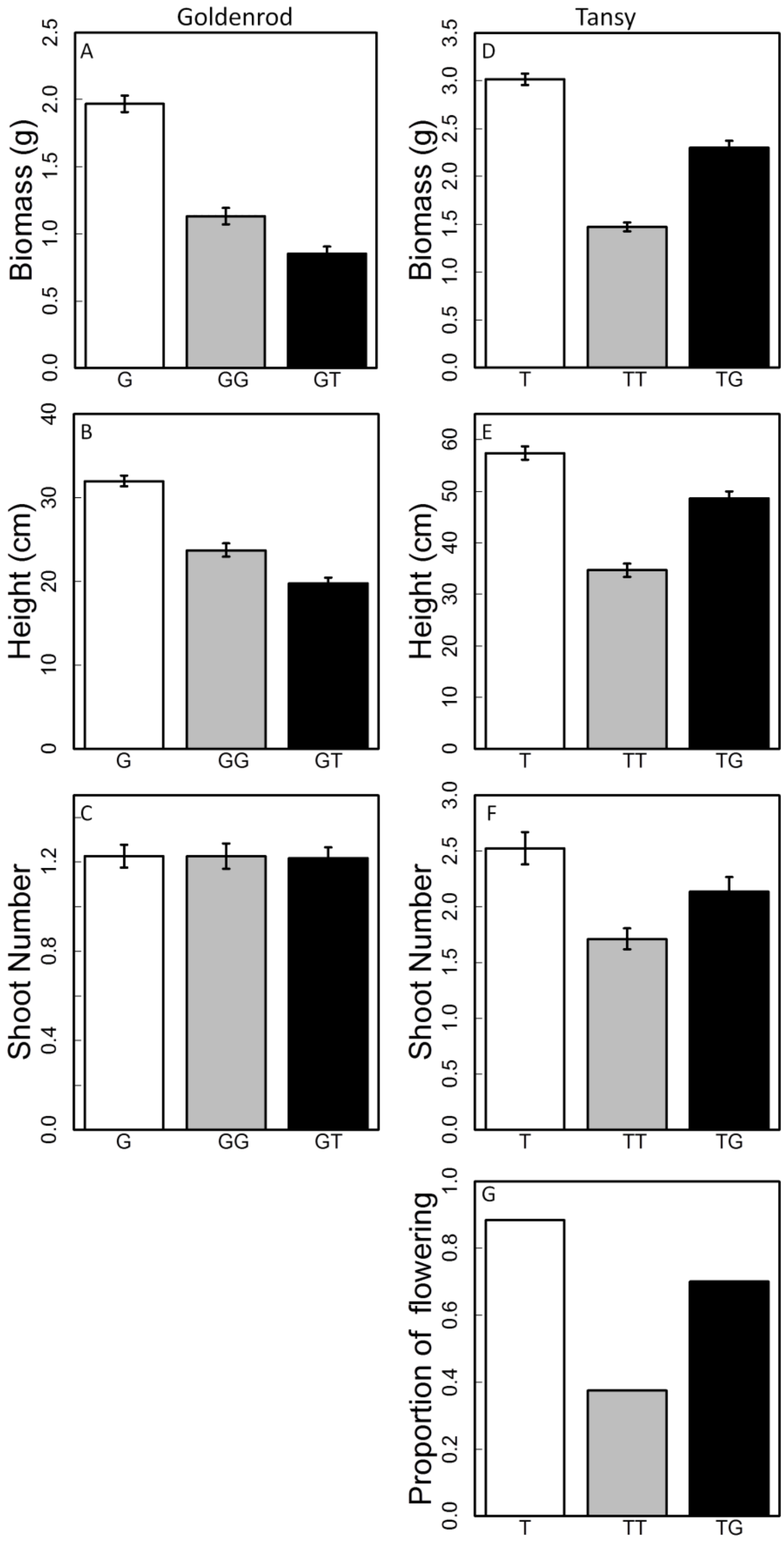


Figure1- Different measurements for the performance of goldenrod (*Solidago canadensis,* A-C) and tansy (*Tanacetum vulgare,* D-G) performance to test the effect of competition (experiment I) in a greenhouse experiment in Germany. Plant species were grown individually (G/T) or in competition with the same (GG/TT) or the other species (TG, GT).

Figure 2. Different measurements of control plants for a range of response variables measuring goldenrod (*Solidago canadensis*, A-C) and tansy (*Tanacetum vulgare*, D-G) performance to test the effect of herbivory (experiment II) in the absence of competition in a greenhouse experiment in Germany. Tansy seeds used in the experiment differed in competition history with goldenrod (+ competition history: seeds were collected from tansy growing in the vicinity of goldenrod, -competition history: from plants that had grown without competition to goldenrod in the field). Herbivory as caterpillars of the general herbivore *Spodoptera litoralis;* +: herbivory on plant, - : no-herbivory. T/G: Tansy/ goldenrod.

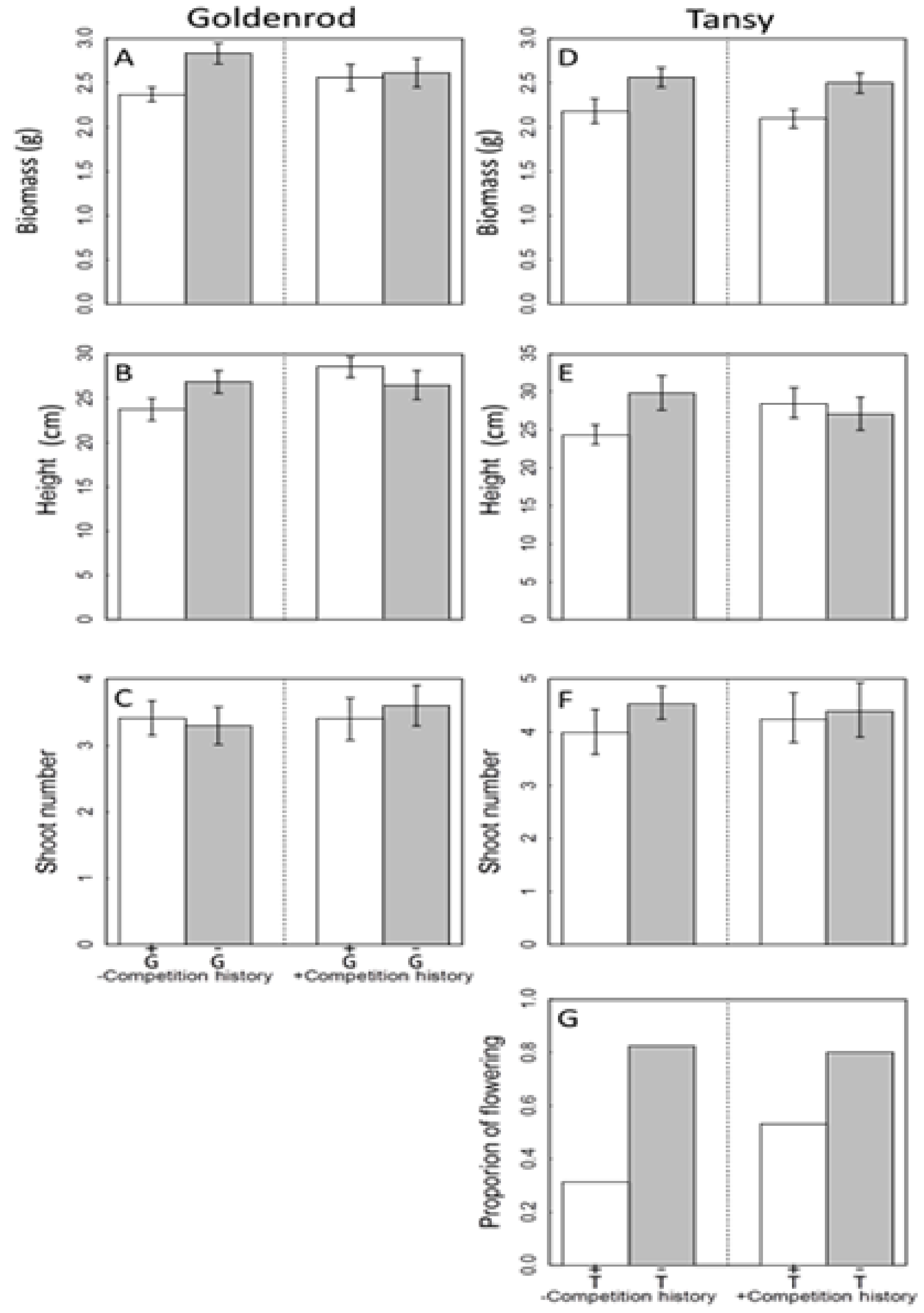


Figure 3. Different measurements for a range of response variables measuring goldenrod (*Solidago canadensis*, A-C) and tansy (*Tanacetum vulgare*, D-G) performance to test the herbivory effect in the presence of competition (experiment II) in a greenhouse experiment in Germany. Tansy seeds used in the experiment differed in competition history with goldenrod (+ competition history: seeds were collected from tansy growing in the vicinity of goldenrod, -competition history: from plants that had grown without competition to goldenrod in the field). Effect of competitor identity (TT/GG: Tansy/ goldenrod in competition with the same species, TG, GT: Tansy/ goldenrod in competition with the other species) was crossed with the competition history to the other species and effect of herbivory (Caterpillars of the general herbivore *Spodoptera litoralis;* ++: herbivory on both focal and competing plant, +-: with herbivory on focal plant, -+: with herbivory on competing plant, --: no-herbivory).

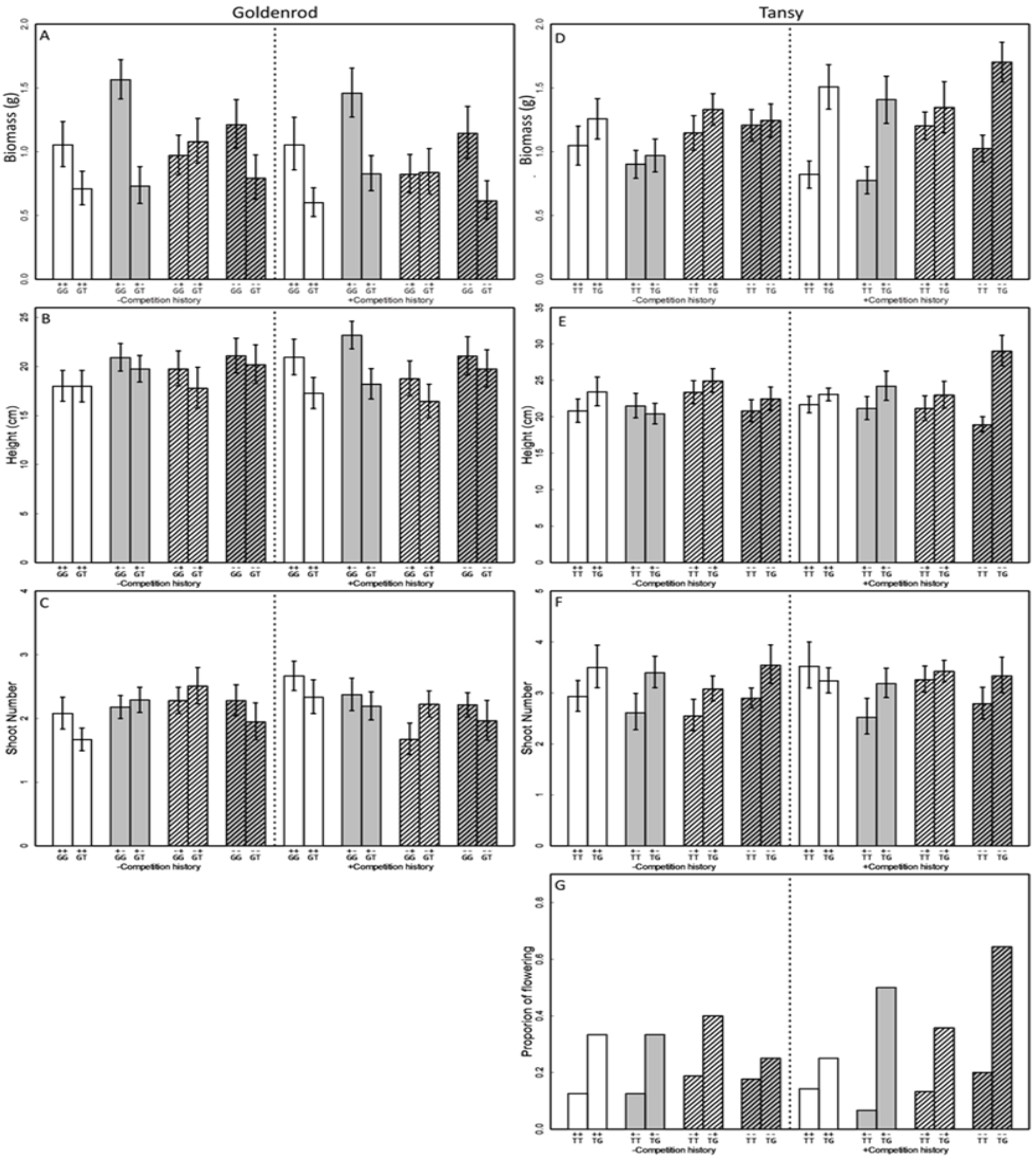


Figure S1. Measurement of proportion of tansy flowering (*Tanacetum vulgare*) to test the effect of competition (experiment I) in a greenhouse experiment in Germany. Plant species were grown individually (G/T) or in competition with the same (GG/TT) or the other species (TG, GT). Tansy seeds used in the experiment differed in competition history with goldenrod (+ competition history: seeds were collected from tansy growing in the vicinity of goldenrod, -competition history: from plants that had grown without competition to goldenrod in the field).

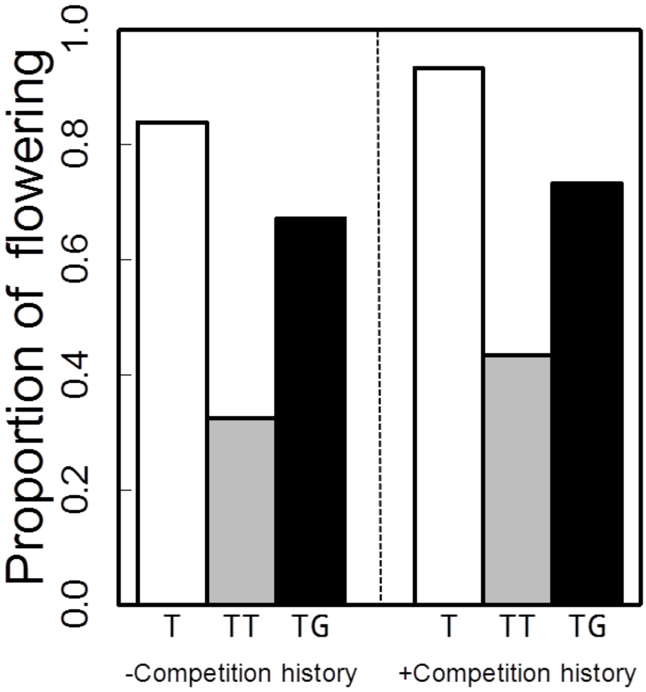


Figure S2. Log response ratio (LogRR) for goldenrod (*Solidago canadensis*, A) and tansy (*Tanacetum vulgare*, B) plant biomass which was measured as plant biomass in the presence of competitor divided by plant biomass without competition. Tansy seeds used in the experiment differed in competition history with goldenrod (+ competition history: seeds were collected from tansy growing in the vicinity of goldenrod, -competition history: from plants that had grown without competition to goldenrod in the field). Herbivory (Caterpillars of the general herbivore *Spodoptera litoralis*) was applied as ++: herbivory on both focal and competing plant, +-: with herbivory on focal plant, -+: with herbivory on competing plant, - -: no-herbivory.

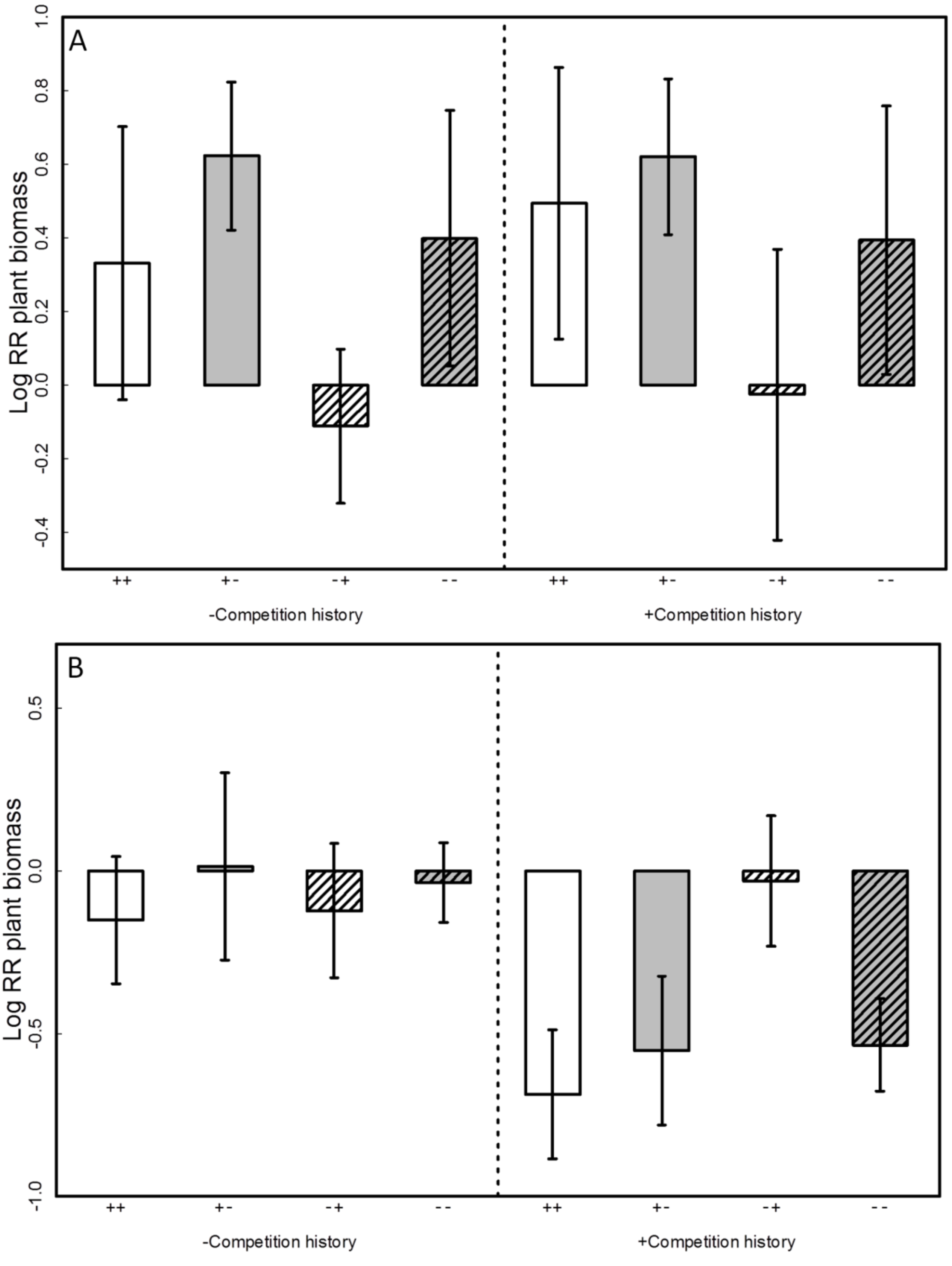
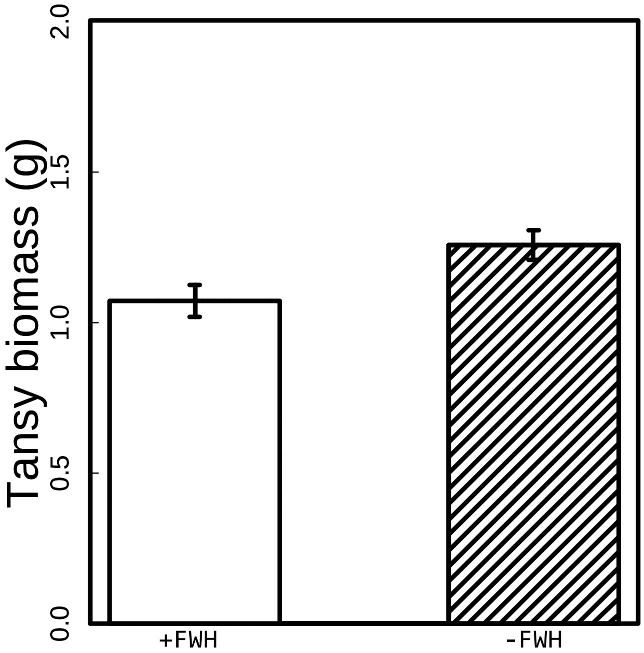


Figure S3. Applying herbivory to the tansy (*Tanacetum vulgare*) focal plant decreased tansy biomass. +FWH: tansy biomass when focal plant had herbivory, +FWH: tansy biomass when focal plant was without herbivory (- FWH).



Chapter 5

Complex effects of fertilization on plant and herbivore performance in the presence of a plant competitor and activated carbon

Published in PLoS ONE

Abstract

Plant-herbivore interactions are influenced by host plant quality which in turn is affected by plant growth conditions. Competition is the major biotic and nutrient availability a major abiotic component of a plant's growth environment. Yet, surprisingly few studies have investigated impacts of competition and nutrient availability on herbivore performance and reciprocal herbivore effects on plants. We studied growth of the specialist aphid, *Macrosiphoniella tanacetaria*, and its host plant tansy, *Tanacetum vulgare*, under experimental addition of inorganic and organic fertilizer crossed with competition by goldenrod, *Solidago canadensis.* Because of evidence that competition by goldenrod is mediated by allelopathic compounds, we also added a treatment with activated carbon. Results showed that fertilization increased, and competition with goldenrod decreased, plant biomass, but this was likely mediated by resource competition. There was no evidence from the activated carbon treatment that allelopathy played a role which instead had a fertilizing effect. Aphid performance increased with higher plant biomass and depended on plant growth conditions, with fertilization and AC increasing, and plant competition decreasing aphid numbers. Feedbacks of aphids on plant performance interacted with plant growth conditions in complex ways depending on the relative magnitude of the effects on plant biomass and aphid numbers. In the basic fertilization treatment, tansy plants profited from increased nutrient availability by accumulating more biomass than they lost due to an increased number of aphids under fertilization. When adding additional fertilizer, aphid numbers increased so high that tansy plants suffered and showed reduced biomass compared with controls without aphids. Thus, the ecological cost of an infestation with aphids depends on the

balance of effects of growth conditions on plant and herbivore performance. These results emphasize the importance to investigate both perspectives in plant herbivore interactions and characterize the effects of growth conditions on plant and herbivore performance and their respective feedbacks.

Chapter 6

Diet–mediated effects of specialized tansy aphids on survival and development of their predators: Is there any benefit of dietary mixing?

Published in Biological Control

Abstract

Some predators have a broad prey range, but not all prey are equally suitable for a predator. We tested the suitability of three specialized tansy (*Tanacetum vulgare*) aphids, *Macrosiphoniella tanacetaria*, *Metopeurum fuscoviride* and *Uroleucon tanaceti*, on biological parameters of their major predators, *Coccinella septempunctata* and *Chrysoperla carnea*, when aphid species were offered either alone, or as a mixed diet of all the three aphid species. For the lacewing, *C. carnea*, a diet consisting only of the generally ant-tended *M. fuscoviride* resulted in the shortest larval and total developmental time, in highest larval survival and pupation success. For the ladybird, *C. septempunctata*, a pure diet of the non-tended *M. tanacetaria* was most suitable, resulting in the shortest total developmental time, heaviest fresh and dry weight. Larvae of both predator species had low survival and none of them developed to pupal stage when offered only *U. tanaceti* that has a bright red colour, is not ant-tended and feeds on the underside of lower leaves. The mixed diet of all three aphid species was worse than the best single-aphid diet for both predators, for almost all fitness parameters. Thus, while diet mixing may allow predators to avoid the negative impact of unsuitable prey, diet mixing does not necessarily result in the highest fitness of predators.

Chapter 7

General discussion

Biological invasions are regarded as one of the greatest current threats to global biodiversity (Sala 2000) and are a large and growing environmental problem with tremendous societal costs (Rogers and Siemann 2004). Successful invaders often demonstrate high levels of plasticity that allow them to succeed in a wide range of habitat conditions (Claridge and Franklin 2002). Because of these negative effects, much research had already been carried out on the causes and consequences of biological invasions, and their control (for overviews see e.g. Williamson and Fitter 1996, Mack et al. 2000). However, these works has often been showed our inadequate understanding of population dynamics, ecological interactions among species and the stability of ecosystems (Bossdorf et al. 2005). Within the chapters of this thesis I demonstrated that it is important to consider different interactions such as competition, herbivory and adaptation among both the invasive and native plants if we want to understand the effect of invasive plants in the invaded range. I was able to show this by examining reciprocal interactions between goldenrod and tansy and their insect herbivores.

7-1 Invader performance

7-1-1 Population level

To understand if invasive plants have the ability to increase their invaded range and exclude native plants, I compared the current distribution of native tansy and invasive goldenrod to their distribution 10 years ago in a field survey (chapter 2). I found that natural disturbances and human-made changes in site conditions increase the chance that safe sites for establishment of invasive plants appear over time (Pyšek and Jarošík 2005). I show that invasive goldenrod has the ability to successfully increase its invaded range and that the spread of goldenrod has not yet reached its limits. The rate and extent of this spread may be influenced by patterns of land use (e.g. urbanization and fragmentation) among different European countries and by the specific biological features (e.g. short life cycle, high seed production, efficiency in seed dispersal) of the invasive species. Weber (2001) suggests that with an increase in suitable habitats, goldenrod, besides increasing their population numbers, individuals may substantially increase their size as well. Yet only in few sites (3%), tansy was replaced by goldenrod and in most of the sites, tansy was still present (80%).

7-1-2 Individual plant level

After being introduced to a new area, many invasive plants appear to have higher performance in their invaded than in their native range. In chapter 3 I compared individual performance of native and invasive plants in both their invasive and native range. As expected our results showed that while both plant species are present in the habitat of the other species, they have a better performance in the invaded compared to the native range. Our results agree with other studies which showed that individual plant performance was higher in the introduced range compared to the native range (for overviews see Bossdorf et al. 2005).

7-2 Mechanisms of interaction between native and invasive species

Different mechanisms have been described to explain how invasive plants have the ability to increase their invaded range and have higher performance there compared to their native range. In the following, I will check some of the most important mechanisms and hypotheses that could explain the better performance of tansy and goldenrod in their invaded range.

7-2-1 Competition between invasive and native plants

Competition plays an important role in structuring plant communities and experimental evidence supports this view (Fowler 1986, Weiner 1990, Casper and Jackson 1997). High competitive ability of invasive species has been mentioned as a key factor promoting successful invasive potential, and competitive exclusion by native plant species seems to be a major force resisting invasive plants (Keane and Crawley 2002). I investigated the competitive interaction between native and invasive tansy and goldenrod in a field experiment (in both the native and invaded range; chapter 3), and under controlled conditions in a common greenhouse experiment (chapter 4). Our results from the field experiment (chapter 3) show that both of the plants studied exhibit higher competitive ability in the invaded range. Yet our greenhouse experiment results (chapter 4) suggest that the main effect of competition was the reduced size of competing plants. In our experiment, control plants without competition were bigger than plants in competition by a factor of about two. These results indicate that resource reduction and competition for soil nutrients which were in short supply might have occurred. The presence of competing plants in a given volume of soil can induce nutrient stress in a given plant as neighbors acquire limiting resources (Craine and Dybzinski 2013). Our experiments (chapter 3 & 4) yielded no evidence for the competitive exclusion of native species by invaders.

7-2-2 The Enemy Release Hypothesis

The success of invasive species in the invaded range and their high competitive ability have been explained by a lack of natural enemies (e.g. herbivores) in the invaded range as detailed in the Enemy Release Hypothesis (ERH; Jones and Lawton 1991, Keane and Crawley 2002, Colautti et al. 2004). To test if higher performance of invasive plants in the invaded range can be attributed to a release from herbivores, I investigated whether introduced species have less herbivory damage in their invaded compared to their native range (chapter 3). The proportion of herbivory damage found in the native range was much higher compared to damage in the invaded range for both species. This results was consistent with the ERH prediction and with results from prior studies (e.g. Torchin et al. 2003, Hierro et al. 2005, Liu et al. 2007, Bossdorf et al. 2009) but see also (Agrawal and Kotanen 2003). The results from our cross-continental comparison (chapter 3) are also in accordance with a recent database study across 473 herbaceous plant species, which showed that plant pathogens are often less diverse in introduced plant populations, and that the degree of this loss of pathogens is positively correlated with the invasion status of a species (Mitchell and Power 2003).

Overall, the data from field studies suggest that invasive plants indeed perform better and are less affected by herbivores in the introduced range. The ERH further predicts that invasive plants gain a competitive advantage over native plants due to the low attack rates by enemies in the invaded range. I tested this prediction, by manipulating herbivory on both native and invasive plants (chapter 3 and 4). If the absence of natural enemies on invasive plants strongly facilitates plant invasion, then the competitive advantage of invasive plants should be removed in mixed communities when we either remove herbivores from both native and invasive plants by using insecticide (chapter 3) or add herbivores to invasive plants (chapter 4). Our results suggest that a release from herbivores might contribute to a higher tansy performance in its invaded range, as tansy biomass increased with applying insecticide in the native range but did not change in the invaded range (chapter 3). This means that tansy is free from herbivory in the invaded range, hence applying insecticide did not further increase tansy performance. We also found that adding herbivory will remove the competitive advantage of tansy over goldenrod (chapter 3). These results indicate that especially when tansy was free from herbivory, in greenhouse experiment or had lower herbivory in the field, invasive tansy could be considered a threat for goldenrod, hence the ERH can explain the success of tansy in USA. In contrast our results for goldenrod did not agree with the ERH because adding or removing herbivory did not change goldenrod interaction with native tansy. That is the reason why the higher performance of goldenrod in the invaded range is unlikely to be explained by the Enemy Release Hypothesis, other mechanisms must play a role.

7-2-3 The Evolution of Increase Competitive Ability Hypothesis

While the Enemy Release Hypothesis has been widely accepted to explain the invasive success of many invasive plant species, an alternative hypothesis, the Evolution of Increased Competitive Ability (EICA; Blossey and Nötzold 1995), proposes that invasive plants evolve a reallocation of nutrients from defense to growth and/or reproduction because they are seldom attacked by enemies in their invaded range (Thompson 1988, Willis and Blossey 1999, Willis et al. 2000). To assess if such a reallocation of nutrients leads to increased performance in seeds of tansy and goldenrod plants from both native and invaded origins, I used reciprocal seed transplants in a common greenhouse study (chapter 3). For both species, plants derived from populations in the invaded range grew larger than plants from populations in the native range. Because allocation of nutrients to defense may be as costly as herbivore damage (Strauss and Agrawal 1999, Stastny et al. 2005), plants that escape their enemies in an introduced range would gain a selective benefit from decreasing their defensive investment (Wolfe et al. 2004). Differences between populations from native and invaded origins are believed to be based on genetically determined characteristics of invasive plants (Wolfe 2002, Bossdorf et al. 2005) and might contribute to their invasiveness in the novel habitat supporting the EICA hypothesis. Some studies confirm differences in growth and competitive ability of plant individuals from invasive and native origins (Blossey and Nötzold 1995, Willis and Blossey 1999, Leger and Rice 2003), while others are inconclusive (Willis and Blossey 1999, Willis et al. 2000, Thebaud and Simberloff 2001). As such, the EICA hypothesis could be suitable mechanisms to explain higher performance of tansy and goldenrod in the invaded range. According to the EICA hypothesis, the discrepancy in growth rates between native plants and invasive plants arises from the unique combination of low herbivory and low defense that native plants are unable to achieve and helps invasive plants have better performance (Rogers and Siemann 2004).

7-2-4 Allelopathy as a weapon of invasive species

Beyond direct competitive interactions, some invasive plants have the potential to compete indirectly with their neighbors through allelopathy. In chapter5 I checked the potential to use allelopathic interaction in goldenrod and tansy and assessed its importance in shaping the surrounding plant community. We investigated if invasive goldenrod has a competitive advantage over native tansy via allelopathy by adding activated carbon to the soil. Activated carbon binds allelopathic chemicals in the soil and will therefore decrease competitive ability of any plants which use allelochemicals for competition. However, we did not find any evidence for allelopathic competition in goldenrod, because competition with tansy was not alleviated with activated carbon. There are several potential explanations for this result. It may be that allelopathic effects of goldenrod are restricted to seed germination or seedling establishment. The few studies that examine allelopathy in the lab and the field, found conflicting results as the observed allelopathy in the laboratory was not always demonstrated in the field (Pisula and Meiners 2010). Concentrations of the allelopathic agents might be low in the field, show fluctuations in toxicity in time and space, or be a sign that chemical interactions are offset by other processes.

Main mechanisms determining the invasiveness of tansy and goldenrod

While we do not have direct evidence of performance of different goldenrod genotypes, the results from the greenhouse experiment indicate some genotypic differences between native and invaded range of goldenrod that could be explained by the appearance of more vigorous goldenrod genotypes that is consist with EICA hypothesis (Blossey and Nötzold 1995).

Invasive tansy shows an increased performance as a result of the reduced impact of natural enemies (especially herbivores) in the invaded range (chapter 3, 4). The possibility is, over time, invasive tansy plants show increased vigor due to less herbivory compared with plants from populations within the native range which is consist with EICA hypothesis.

7-3 Consequences of invasion

Invasive plants can alter both natural communities and their physical environments (Mack et al. 2000). They can change selective pressures on native plants by altering biotic and abiotic conditions in invaded habitats (Goergen et al. 2011). Yet we know remarkably little about the long-term consequences of the novel pressures invaders impose on the native species they encounter. In addition to being critical to the effective management of invaders, this information provides valuable insight into processes that structure communities and permit species coexistence (Langkilde 2009). Here I discuss how interactions between invaders and native species change across invasion time, and how these changes alter the consequences of invasion for native communities and their higher trophic levels.

7-3-1 Consequences of invasion on native vegetation

7-3-1-1 Inter vs. intraspecific competition between native and invasive plants

Invasive plants have to be competitively superior to native species to establish in a new habitat or increase their invaded range. Yet, there are a lot of other processes that can shape the competition between native and invasive plant species within a mixed community once the invasive plant is established. Such processes involve resources, different vigor and ability of plants species that compete for resource (Freckleton and Watkinson 2001). To check if invasive plants can still be outcompeted by native plants through competition for resources, I compared the outcome of interspecific competition between native and invasive plants with intraspecific competition in a greenhouse and field experiment (chapter 3 and 4). Results from both field and greenhouse experiments showed that for goldenrod, interspecific competition was stronger than intraspecific competition. In contrast, the opposite was true for tansy: plant performance was more strongly reduced by intraspecific competition.

Despite the higher performance and competitive ability observed for tansy which decreased goldenrod performance, we found no competitive exclusion of native plants (goldenrod) in the field experiment in USA or in the greenhouse. It could be that the two species in the experiment coexisted because the length of time over which the experiment took place was not long enough for competitive exclusion of goldenrod. Additional, long-term experiments are needed to investigate if a continuing reduced performance of goldenrod when in competition with tansy eventually leads to a suppression of goldenrod and dominance by tansy. In the field experiment in Europe (chapter 3), the reduced interspecific competition between tansy and goldenrod compared to intraspecific competition within tansy points towards effects of niche separation and implies the potential for stable coexistence of the two species. In fact we observed in our survey (chapter 2) that in most of the sites in which tansy and goldenrod co-occur, they coexist. This was also found in a prior study by Rebele (2000) who showed that these two plant species still coexist after five years of a field experiment. The possibility is weaker interspecific competitive effects than intraspecific effects, because of trade-offs among the competitors, give each species unique advantages for exploiting environmental resource requirements (reviewed by Chesson 2000, Moll and Brown 2008).

7-3-1-2 Evolution of native species after invasion of their habitat

Remaining native tansy in a community invaded by goldenrod may also be because of tansy tolerant to the impacts of invasive goldenrod. This represents an evolutionary change in native populations in response to invasive species (Leger and Espeland 2010). In chapter 4 I checked if exposure to the invader prior to a new invasion event changes the outcome of competition for the native plant (here tansy). Tansy plants were grown from seeds which were collected either from plants with or without a competition history and their biomass under intra-and interspecific competition was compared. Plants with an inherited competition history increased their biomass under competition with the invasive plant more than plants without inherited competition history. This indicates that exposure to competition with goldenrod increases the competitive ability of tansy through maternal effects. Prior studies which compared plants from native and invaded sites also suggested that native species can respond evolutionarily to the novel environmental conditions caused by the invasion of a new species (Callaway et al. 2005, Lau 2006, Mealor and Hild 2006, Leger 2008, Goergen et al. 2011). Goergen et al. (2011) suggests that native species respond to the presence of invasive plants by selection. This make a different in native and invasive individuals and their population in respond to present of invasive competitor. It is possible that an increase in competitive ability of native species over time and low impacts of competition on plant performance stabilize coexistence (Chesson 2000).

7-3-2 Consequences of invasion on herbivores in the invaded plant community

Invasive species have the capacity to disrupt native communities by bottom-up effects, affecting native plants and interfering with a wide range of associated trophic interactions (Simao et al. 2010). In chapter 5, I examined how competition with invasive goldenrod affects herbivore performance, in particular aphids, and their impact on native tansy. Interspecific competition had negative effects on the aphid performance, as aphid numbers were generally lower on tansy plants in competition with invasive goldenrod. This is in line with other studies which showed that the presence of neighboring plants can affect host plant insects associated with native plants (Schädler et al. 2007, Bezemer et al. 2014). Invasive plants compete with native plants for nutrients and light and thereby affect the growth of native plants, which can lead to altered performance of insects on those native plants. Our results suggest that invasive plants can greatly affect native insect communities by competing with native host plants. Hence, invasions by invasive plants can negatively influence the diversity or abundance of native insects (Bezemer et al. 2014).

7-3-2-1 Interactions between effects of invasive species and growth conditions on herbivores

Different plant growth condition can have effects on herbivores performance which was proven by studies that manipulate plant growth condition. For example, Rebele (2000) shows that selective herbivore pressure caused a switch in dominance in mixtures of native tansy and invasive goldenrod on fields with higher fertility. This result indicates that invasive plants can indirectly alter the abundance or performance of native insects on native plants depending on plant growth conditions. In chapter 5, I examined how different plant growth conditions affect aphid performance and the performance of native plants when they are in competition with invasive species. Plant and herbivore growth and the feedback effects of the herbivores on plants were affected by both the abiotic and biotic plant growth conditions, in our case fertilization and plant-plant competition. Competition decreased and fertilization increased aphid performance. While generally effects of growth condition on plant biomass and aphid numbers mirrored each other, our results emphasize the shifts in the plant-herbivore interactions that depend on the exact way in which plant and herbivore can exploit an increase in plant nutrient availability and react to competition. Consequently, aphid impacts can decrease under fertilization even when absolute aphid numbers increase. These results show that the ecological costs of an infestation of aphids depends on the balance of effects of growth conditions on plant and herbivore performance. The results of our greenhouse study in chapter 5 are relevant to the understanding of plant herbivore interactions under field conditions. Invasive plants not only decreased the quality of native plants but also significantly altered the structure of the landscape by increasing diversity. For herbivores or pollinators that do not utilize the invasive plant, the availability of suitable host plants decreases or becomes increasingly more fragmented over time (Bezemer et al. 2014). These changes in the distribution, abundance, and quality of native plant can highly affect herbivore population persistence as well as their interactions with natural enemies and community diversity and composition (Bezemer et al. 2014).

7-3-3 Consequences of invasion on higher trophic levels associated with the invaded plant community

Spatial variation in the competitive situation and nutrient availability of the host plant will generally create variation in the local growth rates of plants and herbivores and such spatial heterogeneity has been shown to have dynamical consequences for plant-herbivore systems and also the dynamics of predators and parasitoids feeding on the herbivores. Aphids are special herbivores in the sense that they produce many generations per year and may quickly build up large populations. Consequently the effects of host plant growth conditions might be especially apparent for aphids. Some predators have a broad prey range, but not all prey is equally suitable for a predator. In chapter 6, I show that the growth rate of predators is dependent on the prey they feed on. In this case growth rates of lace wing (*Chrysoperla carnea*) and ladybirds (*Coccinella septempunctata*) were affected by feeding on tansy aphids resulting in a change of their total developmental time, maximum fresh and dry weight. While we did not consider how plant growth conditions affect higher trophic levels and their feedback effects on the herbivores (and possibly the plant), such interactions have been shown to be affected by resource availability (Hartvigsen et al. 1995). The critical factors limiting aphid colony size in the field is predation by a large guild of predators. Because of high rates of predation in the field, aphid colony growth critically depends on the balance between reproduction that is influenced by host plant growth conditions and mortality due to predation. Thus, any small negative effect on aphid growth rates, due to plant-plant competition, and every positive effect on growth rates, due to higher nutrient availability in the soil, is likely to critically affect local aphid persistence. This in turn will affect the higher trophic level like predators.

7-4 Conclusion

Invasion is a serious threaten for biodiversity, studies with other problematic invasive species will help to determine the factors influencing successional dynamics, community structure and ecosystem stability (Rogers and Siemann 2004). With the growing awareness of the devastating impacts of biological invasions, it is critical that we understand the forces that cause a species to behave differently after its introduction to a novel environment (Wolfe et al. 2004). The findings of this thesis will contribute to a better understanding the mechanisms in charge for the effect plant invasion. Higher knowledge about the effect of invasive plants help to develop effective management strategies to lessen their effects on a variety of threatened species and imperiled ecosystems (Rogers and Siemann 2004). Our results did not confirm the general view that all invasive species are generally competitively superior and exclude native plant species. In contrast, the low impacts of competition by the invasive plants on native plant performance indicate the potential for at least temporary coexistence of tansy and goldenrod in USA and stable coexistence in Europe. Thus, while both plants are invasive and show patterns of herbivory and growth consistent with current hypotheses on plant invasion, they are more likely to displace other native plants than one another. Coexistence of this two competing species is possible when intraspecific competition over-rules interspecific competition. The other possibility is that invasion by invasive goldenrod change the environment for native tansy. Evolution may help native plants to adapt to the new environments which may contribute to the coexistence between native and invasive species. Our results showed that the main effect of competition was the reduced performance of competing plants which in turn affect the quality of native plants. Therefore native-invasive plant competition not only decreased the quality of native plants but also affected their herbivores, this can consequently have an effect on higher trophic levels and therefore the biodiversity of the habitat as well.

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A study statement

This thesis contains five papers and the authors' contribution is given below. All authors agreed to include the scientific papers as chapter in the thesis.

Chapter 2

Mahdavi-Arab, N., Meyer, T. S. & Weisser, W. W: Does invasive goldenrod replace tansy in Germany?

NMA and WWW conceived and designed the survey. NMA performed the survey. NMA and STM analyzed the data. NMA wrote the manuscript, which was edited by STM and WWW.

Chapter 3

Mahdavi-Arab, N., Meyer, S. T., Pal, R., Nagy, D. U., Fletcher, R., Weisser, W. W. & R. Callaway: The role of insect herbivores in the interaction between Solidago canadensis and Tanacetum vulgare in a cross continental experiment.

NMA, RP, RC, and WWW conceived and designed the experiments. NMA, RP, DUN, RF and RC performed the experiments. NMA and STM analyzed the data. NMA wrote the manuscript, which was edited by STM, WWW, RP, RC, and RF.

Chapter 4

Mahdavi-Arab, N., Weisser, W. W. & Meyer, T. S: Effects of herbivory and competition history on the competitive interactions between tansy and goldenrod.

NMA and STM conceived and designed the experiments. NMA performed the experiments. NMA and STM analyzed the data. NMA wrote the manuscript, which was edited by STM and WWW.

Chapter 5

Mahdavi Arab, N., Meyer, T. S., Mehrparvar, M. & Weisser, W. W: Published in PLoS ONE

NMA and WWW conceived and designed the experiments. NMA performed the experiments. NMA and STM analyzed the data. NMA and STM wrote the manuscript, which was edited by STM, MM and WWW.

Chapter 6

Mehrparvar, M., Mahdavi Arab, N. & Weisser, W. W. Published in Biological Control

MM and WWW conceived and designed the experiments. MM and NMA performed the experiments. MM analyzed the data. MM wrote the manuscript, which was edited by WWW.

Appendix A: Chapter 5

- **Mahdavi Arab**, N., Meyer, S. T., Mehrparvar, M., & Weisser, W. W. 2014. Complex effects of fertilization on plant and herbivore performance in the presence of a plant competitor and activated carbon. PloS ONE 9:e103731.

  http://www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0103731

Appendix B: Chapter 6

- Mehrparvar, M., **Mahdavi-Arab, N.** & Weisser, W. W. 2013. Diet–mediated effects of specialized tansy aphids on survival and development of their predators: Is there any benefit of dietary mixing? Biological Control. 65: 142-146.

  http://www.sciencedirect.com/science/article/pii/S1049964412002824

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Education

- **2010-Present** **PhD in Ecology**
  Technichal University of Munich

  Thesis: **Plant invasion, insect herbivores and competition: insights into the ecological interactions between invasive Goldenrod (*Solidago canadensis*) and native Tansy (*Tanacetum vulgare*)**

- **2003-2006** **M.Sc. in Agricultural Entomology**
  Isfahan University of Technology, Iran.

  Thesis: **Insecticidal effect of some plant extracts on *Callosobruchus maculatus* F. under laboratory condition and *Laphigma exigua* H. in greenhouse.**

- **1999-2003** **B.Sc. in Plant Protection**
  Shahid Bahonar University of Kerman, Iran.

  Senior Project: **Faunistic survey of Rosaceae aphids in Kerman**

Honors and awards

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Working experience

- **03/2011-06/2011** **Wissenschaftliche Hilfskraft**
  Institut für Ökologie, Friedrich-Schiller-Universität Jena
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Research experience

- Morphometric analysis of populations of black legume aphid , *Aphis craccivora* (Hemiptera: Aphididae) on different host plants from June 2007-June 2008 (Co-Researcher).
- Research assistant in Lehrstuhl für Terrestrische Ökologie from May 2012 until present.

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Teaching courses for undergratuate students in:

- Entomology, Pests of agricultural crops. In Shahid Bahonar University of Kerman from September 2006 until Jun 2008, Iran
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Organisational / managerial skills	▪ organisational skills gained through the self-reliant organisation of the fieldwork of my PhD thesis
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Publications and conferences

- **Mahdavi Arab**, N., Meyer, S. T., Mehrparvar, M., & Weisser, W. W. 2014. Complex effects of fertilization on plant and herbivore performance in the presence of a plant competitor and activated carbon. PloS ONE 9:e103731.

- **Mahdavi-Arab**, N., Weisser, W. W., & Meyer, T. S. 2014 Effects of herbivory and competition history on the competitive interactions between tansy and goldenrod. GFÖ Annual Meeting 2014, Hildesheim.

- **Mahdavi-Arab, N.,** Meyer, S. T., Pal, R., Nagy, D. U., Fletcher, R., Weisser, W. W., &R. Callaway. 2014. The role of insect herbivores in the interaction between Solidago canadensis and Tanacetum vulgare in a cross continental experiment. 99th ESA Annual Meeting (August 10 - 15, 2014), Sacramento, California.

- Mehrparvar, M., **Mahdavi-Arab, N.** & Weisser, W. W. 2013. Diet–mediated effects of specialized tansy aphids on survival and development of their predators: Is there any benefit of dietary mixing? Biological Control. 65: 142-146.

- **Mahdavi-Arab**, N., Meyer, T. S., Pal, R., Fletcher, R., Callaway, R. & Weisser, W. W. 2013. The role of insect herbivores in the interaction between *Tanacetum vulgare* and *Solidago canadensis* in a cross continental experiment. GFÖ Annual Meeting 2013, Potsdam.

- Mehrparvar, M., Majdzadeh, S. M., **Mahdavi Arab, N.,** Esmaeilbeigi, M., and Ebrahimpour, E. 2012. Morphometric discrimination of Black Legume Aphid, *Aphis craccivora* Koch (Hemiptera: Aphididae), populations associated with different host plants. North-Western Journal of Zoology. 8 (1): 172-180

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- Mehrparvar, M., Mehrparvar, M., Sayahi, S. & **Mahdavi Arab, N.** 2008. Population fluctuation of the pine aphid, *Eulachnus tuberculostommata* (Hemiptera: Lachnidae) in Kerman, Iran. Proceedings of the 15th National & 3rd International Conference of Biology. Tehran, Iran. pp 126 - 127.

- Mehrparvar, M., Madjdzadeh, S. M. & **Mahdavi Arab, N.** 2008. Morphological variation among the black legume aphid, *Aphis craccivora* (Hem.: Aphididae) populations feeding on different host plants. Proceedings of the 18th Iranian Plant Protection Congress. Hamedan, Iran. pp 67.

- Mehrparvar, M., Madjdzadeh, S.M. & **Mahdavi Arab, N.** 2007. A survey of aphid fauna on plant family Lamiaceae in Northern half of Kerman province and a new record, *Ovatus mentharius* (Hom.: Aphididae) for Iran. Proceedings of the 2nd National Conference of Animal Science. Rasht, Iran. pp 139-140.

- Mehrparvar, M., Madjdzadeh, S.M. & **Mahdavi Arab, N.** 2007. *Aphis pseudopulchella* Blanchard (Hom.: Aphididae): A new record for Iran. Proceedings of the 2nd National Conference of Animal Science. Rasht, Iran. pp 199-200.

Reserch interest

- Invasive plants
- Effect of competition between invasive and native plants
- The role of insect herbivores in the interaction between invasive and native plants

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