

Plant-microbe-herbivore interactions in invasive and non-invasive alien plant species

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Summary

1. Plants interact with many organisms, such as microbes and herbivores, and these interactions are likely to affect the establishment and spread of plants. In the context of plant invasions, mycorrhizal fungi and constitutive and induced resistance of plants against herbivores have received attention independently of each other. However, plants are frequently involved in complex multi-trophic interactions, which might differ between invasive and non-invasive alien plants.

2. In a multi-species comparative experiment, we aimed to improve our understanding of plant traits associated with invasiveness. We tested whether eight invasive alien plant species use the mycorrhizal symbiosis in a more beneficial way, and have higher levels of constitutive or induced resistance against two generalist bioassay herbivores, than nine non-invasive alien species. We further assessed whether the presence of mycorrhizal fungi altered the resistance of the plant species, and whether this differed between invasive and non-invasive alien species.

3. While invasive species produced more biomass, they did not differ in their biomass response to mycorrhizal fungi from non-invasive alien species. Invasive species also did not have higher levels of constitutive or induced resistance against the two generalist herbivores. Mycorrhizal fungi greatly affected the resistance of our plant species, however, this was also unrelated to whether the alien species were invasive or not.

4. Our study confirms the previous findings that invasive species generally grow faster and produce more biomass than non-invasive alien species. We further show that alien plant species used a variety of defence strategies, and also varied in their interactions with mycorrhizal fungi. These multi-trophic interactions were not consistently related to invasiveness of the alien plant species.

5. We suggest that awareness of the fact that alien plant species are involved in multi-trophic interactions might lead to a more complete understanding of the factors contributing to a plant's success.

Key-words: herbivore resistance, induced and constitutive resistance, invasive plant species, mycorrhizal dependency, phenotypic plasticity, plant defence, plant defence strategies, plant dominance, plant invasions, plant-microbe-herbivore interaction

Introduction

Growing in both the above and below ground compartments, plants interact with a variety of different organisms that may affect their establishment and spread. The response of plants to one group of organisms might also affect their response to another group. Such multi-trophic interactions can have substantial consequences for the functioning of all parties involved. One such example is the multi-trophic interaction of below ground

microbes, plants and above ground herbivores. To defend themselves against enemies, plants evolved a variety of resistance strategies, which can be constitutively expressed or induced following damage (Karban & Baldwin 1997). Recently, there has been growing evidence that symbiotic microbes (e.g. N fixing bacteria, mycorrhizal fungi) associated with plants might influence constitutive (Kempel, Brandl & Schädler 2009; Pineda *et al.* 2010) and induced resistance to herbivores (Bennett, Bever & Bowers 2009; Kempel *et al.* 2010), and thus may both directly and indirectly affect a plant's success.

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Although it has frequently been suggested that alien plants are released from enemies (Keane & Crawley 2002), herbivores contribute to the biotic resistance of native communities against invaders (Levine, Adler & Yelenik 2004). This might imply that alien species with high levels of constitutive resistance should have a higher chance to become invasive. However, alien species most likely interact with generalist rather than with specialist herbivores (Parker, Burkepile & Hay 2006). Therefore, plastic induction of resistance in the presence of enemies which has been suggested to be particularly effective against generalist herbivores (Agrawal 1999a) has recently attracted theoretical attention as a potentially useful strategy for dominant invasive plants (Richards *et al.* 2006; van Zandt 2007; Verhoeven *et al.* 2009; Berg & Ellers 2010; Orians & Ward 2010). Moreover, induced resistance is suggested to be less costly than permanent constitutive resistance (Harms & Mattson 1992). This adaptive plastic response (Baldwin 1998; Agrawal 1999b, 2001) would allow plants to allocate more resources to growth and competitive strength in the absence of enemies but would still provide resistance in the presence of enemies. Indeed, Kempel *et al.* (2011) recently found a positive association between induced resistance and competitive ability of plant species.

So far, only a handful of experimental studies addressed the roles of constitutive and induced resistance in invasion success of alien species. This was done by comparing either patterns of resistance between the native and introduced range of an invasive plant species (Cipollini *et al.* 2005; Eigenbrode *et al.* 2008; Carrillo *et al.* 2012) or between native and invasive plant or animal species (Engelkes *et al.* 2008; Engel & Tollrian 2009; Zas, Moreira & Sampedro 2011). Although these approaches can reveal whether there has been evolutionary change, and whether invasive alien species have strategies that differ from the ones of natives, they cannot reveal why some alien species became invasive and others did not (Strauss, Webb & Salamin 2006; van Kleunen *et al.* 2010). Moreover, most previous studies were restricted to one or a few species, which makes it difficult to draw more general conclusions on the importance of a certain trait for invasiveness.

The role of interactions between plants and soil microbes in general (e.g. van Grunsven *et al.* 2007), and especially mycorrhiza, has received increased attention in the context of plant invasions (Reinhart & Callaway 2006; van der Putten, Klironomos & Wardle 2007; Pringle *et al.* 2009). Although associations between plants and mycorrhizal fungi are frequently assumed to be mutualistic, plant responses to mycorrhizal fungi can range across the whole spectrum from negative to positive, depending on environmental variables and the identities of the plants and fungi (Johnson, Graham & Smith 1997; van der Heijden, Wiemken & Sanders 2003; Klironomos 2003; Hoeksema *et al.* 2010). Many invasive plant species can form associations with mycorrhizal fungi (Fumanal *et al.* 2006; Smith *et al.* 2008; Štajerová, Smilauerová & Smilauer 2009), most likely generalistic ones (Moora *et al.* 2011). However,

being not obligatorily dependent on mycorrhizal fungi might be more advantageous for a plant in a new range (Richardson, Williams & Hobbs 1994; Reinhart & Callaway 2006; van der Putten, Klironomos & Wardle 2007; Pringle *et al.* 2009). Concordantly, several studies showed that mycorrhizal dependency was lower in alien than in native species (Reeves 1979; Allen & Allen 1980; Pendleton & Smith 1983; Vogelsang & Bever 2009). However, the weaker positive response to mycorrhizal fungi of alien species does not explain why some aliens become invasive and others do not, unless the dominant invasive aliens use the mycorrhizal symbiosis in a more beneficial or less detrimental way than non invasive alien species do.

Most, if not all, studies on invasive plants and mycorrhizal fungi are focused on biotrophic interactions (Harvey, Bukovinszky & van der Putten 2010). However, mycorrhizas can also affect the herbivore community by changing plant quality, thereby affecting plant fitness. A meta analysis showed that mycorrhizal fungi usually increase plant resistance against generalist chewing herbivores, but reduce resistance against specialist chewing herbivores (Koricheva, Gange & Jones 2009). The net effect of mycorrhizal fungi on herbivores might depend on altered nutrient uptake by plants and changes in the constitutive production of secondary defence metabolites. Much less is known about the effects of mycorrhizal fungi on induced resistance of plants to herbivores. In one study, induced resistance was decreased by mycorrhizal fungi (Bennett, Bever & Bowers 2009), while in another study it was increased (Kempel *et al.* 2010). In addition, a growing body of evidence suggests that mycorrhizal fungi themselves may induce plant resistance, possibly involving cross talk between the salicylic acid and jasmonate dependent defence pathways (Pozo & Azcon Aguilar 2007). Given that the effect of mycorrhizal fungi on plant resistance differs between species and is ecologically relevant, one might expect that species whose resistance is increased by an association with mycorrhizal fungi might be more successful than species whose resistance is decreased or not affected.

In this study, we therefore address questions on multitrophic interactions between arbuscular mycorrhizal fungi (AMF), plants and two generalist herbivores in the framework of biological invasions. Using a multispecies approach, we assessed the biomass response of eight dominant invasive alien and nine non invasive alien plant species to a short period of herbivory and to a mixture of common mycorrhizal fungi. We also assessed, in the presence and in the absence of mycorrhizal fungi, constitutive and induced resistance of the 17 plant species to the generalist bioassay caterpillars *Spodoptera littoralis* and *Mamestra brassicae*. Specifically, we addressed the following questions. (i) Are dominant invasive alien plant species more able to induce resistance against generalist herbivores than non invasive alien species are, and do they generally differ in their constitutive level of resistance? (ii) Do invasive species utilize mycorrhizal fungi in a more beneficial

way than non invasive alien species do? (iii) Do mycorrhizal fungi affect constitutive and induced resistance of alien plant species, and if yes, do mycorrhizal fungi strengthen the resistance of dominant invasive species more than the resistance of non invasive alien species?

Materials and methods

PLANT SPECIES

We used 17 herbaceous plant species that are alien to Switzerland, from three different plant families (Table 1). We considered eight of the alien plant species to be invasive and the remaining nine alien species to be non invasive in Switzerland. We compared invasive alien species with non invasive alien species because this is the most direct test of determinants of invasiveness, and allows us to contribute to answering why some alien species became invasive while others did not (van Kleunen *et al.* 2010). We categorized plant species as invasive if they are on the Black List or the Watch List for invasive plant species in Switzerland (http://www.cps.skew.ch/fileadmin/template/pdf/deutsch/Empf_Liste_IV_d.pdf, assessed January 2012), and are widespread in Switzerland (Table 1). The alien species categorized as non invasive are not on the Black List or Watch List, and are naturalized at only a few locations in Switzerland. The non invasive alien species are not known to outcompete native plant species, and are always less dominant than their invasive counterparts (Landolt *et al.* 2010). The invasive and non invasive alien plant species were chosen in such a way that they belonged to the same genus and had similar life forms, to avoid confounding effects of invasiveness status of the species with taxonomy and growth form (Table 1). For the analyses, we considered the confamilial species pair *Polygonum orientale* and *Fallopia japonica* (synonym: *Polygonum Reynoutria* MAKINO, *Polygonum cus-*

pidatum SIEBOLD & ZUCC.) as a congeneric pair. Due to a lack of historical introduction data, we cannot exclude the possibility that invasive and non invasive alien plant species were introduced at different times. However, among the 12 species for which we could find the exact year of first recorded naturalization in Germany, there was hardly any difference (mean for seven invasive alien species: 1867; mean for five non invasive alien species: 1876; Table 1).

We collected the seeds from wild populations in Switzerland, obtained them from botanical gardens, or ordered them from a commercial seed supplier (B & T World Seeds, Aigues Vives, France, Table 1). Congeneric pairs were mostly obtained from the same seed source. Because *F. japonica* in Europe does not reproduce by seeds but by rhizomes, we collected rhizome pieces for this species.

HERBIVORE SPECIES

Direct measurements of the production of plant defensive compounds and their effectiveness against herbivores for many different plant species are very laborious, especially when chemicals are not yet identified for certain species. Therefore, we used the growth response of generalist herbivores as integral indicator of constitutive and induced plant resistance (e.g. Joshi & Vrieling 2005; van Zandt 2007; Kempel *et al.* 2011). To assess constitutive resistance and the ability to induce resistance of our plant species, we used larvae of two generalist herbivores, the native cabbage armyworm *M. brassicae* (L.) (Lepidoptera: Noctuidae), and the non native Egyptian cotton leafworm *S. littoralis* (Boisduval) (Lepidoptera: Noctuidae). Larvae of both species are known to feed on a wide range of plant species of more than 20 (Rojas, Wyatt & Birch 2000) and 40 plant families (Brown & Dewhurst 1975), respectively. The extreme polyphagy of both species has led to their frequent use in bioassays (Joshi & Vrieling 2005; van Zandt 2007; Kempel *et al.* 2010, 2011). Their feeding response and

Table 1. List of the 17 plant species used in the experiment. LF Life form (t therophyte, h hemicryptophyte, g geophytes), F frequency of occurrence in Switzerland [%], D dominance in the wild (numbers from 1 to 5 with 5 being the most dominant category), List species listed in the Black List (B) or Watch list (W) (SKEW 2009), or not listed (). Time Time of first naturalization in Germany. Data were obtained from Landolt *et al.* (2010), and the Bioflora database (Kuhn, Durka & Klotz 2004)

Invasive	LF	F	D	List	Time	Seed source	Not invasive	LF	F	D	List	Time	Seed source
Asteraceae							Asteraceae						
<i>Solidago canadensis</i> L.	h	46	5	B	1853	Bot. Gard. Gottingen	<i>Solidago rugosa</i> MILL.	h	0.2	4			Bot. Gard. Gottingen
<i>Solidago gigantea</i> AITON	h	42	5	B	1859	B&T	* <i>Solidago graminifolia</i> (L.) SALISB.	h	2	4		1848	B&T
<i>Senecio inaequidens</i> DC.	h	8	4	B	1889	Wild collections	<i>Senecio vernalis</i> WALDST. & KIT.	h,t	2	2		1850	Bot. Gard. Gottingen
<i>Bidens frondosa</i> L.	t	5	4	B	1891	Wild collections	<i>Bidens bipinnata</i> L.	t	0.7	3			Wild collections
<i>Erigeron annuus</i> (L.) DESF.	h,t	44	2	W	18th c.	Wild collections	<i>Erigeron karvinskianus</i> DC.	h	5	2			Bot. Gard. Gottingen
<i>Artemisia verlotiorum</i> LAMOTTE	h	24	5	B	1920	Bot. Gard. Salzburg	<i>Artemisia biennis</i> WILLD.	h,t	0.5	2		1894	Bot. Gard. Konstanz
							<i>Artemisia annua</i> L.	t	1	3		1890	Bot. Gard. Gottingen
Brassicaceae							Brassicaceae						
<i>Lepidium virginicum</i> L.	h,t	31	2		1786	Wild collections	<i>Lepidium neglectum</i> THELL	h,t	3	2		1900	Wild collections
Polygonaceae							Polygonaceae						
<i>Fallopia japonica</i> (HOULT.) RONSE DECR.	g	43	5	B	1872	Bot. Gard. Bern (Rhizomes)	<i>Polygonum orientale</i> L.	t	0.7	3			Bot. Gard. Gottingen

*Note that *S. graminifolia* is a Synonym of *Euthamia graminifolia* (L.) NUTT.

performance although possibly not representative for all herbivores are used as integrative and functionally relevant measures of plant resistance against generalist herbivores (Joshi & Vrieling 2005; van Zandt 2007). *Mamestra brassicae* and *S. littoralis* are both known to induce plant resistance (Anderson, Jonsson & Morte 2001; Gomez, van Dijk & Stuefer 2010; Kempel *et al.* 2011). *Spodoptera littoralis* larvae originated from a lab stock at the University of Bern (Switzerland), and *M. brassicae* egg batches were obtained from the Entomology Laboratory of Wageningen University (the Netherlands). Caterpillars were bred on an artificial diet to avoid adaptation of the insects to specific plant species.

Experiment

DESIGN

In August 2009, we surface sterilized seeds of 16 plant species with 1% H₂O₂, and germinated them in trays filled with potting soil ('Aussaart und Pikiererde 191', Ricoter, Switzerland). This soil had first been steam sterilized at 100 °C for a minimum of 4 h to eliminate AMF. For *F. japonica*, we cut the rhizomes into pieces of 5 cm, washed them carefully and placed them on moist filter paper. We filled 1.36 L pots with a steam sterilized 1:1 mixture of sand and plain field soil from an agricultural field in the Bern region ('Landerde', Ricoter, Switzerland, N content: 0-17%), and placed them in a greenhouse (14 30 °C, a constant day length of 14 h, and additional light). We irrigated the pots twice prior to the start of the experiment to leach excess nutrients from the soil, which might have become available during the steaming process (Endlweber & Scheu 2006). The experiment was set up in a nearly full factorial design (Fig. 1) using mycorrhizal fungi, induction of resistance and herbivore species as treatments, with the restriction that each *M. brassicae* larva fed only on *M. brassicae* induced plants, and each *S. littoralis* larva fed only on *S. littoralis* induced plants. All 14 treatment combinations were replicated five times resulting in 70 pots per plant species. We randomly assigned pots to five blocks in the greenhouse and randomized pots within each block several times during the experiment. We watered all plants when needed.

MYCORRHIZAL FUNGI TREATMENT

Two weeks after germination, we transplanted if possible 70 plants of each species into the experimental pots. Before planting,

we added 10 g of a multi species AMF inoculum, consisting of spores and hyphae of five common AMF species: *Rhizophagus intraradices* (*Glomus intraradices*), *Funneliformis mosseae* (*Glomus mosseae*), *F. geosporum* (*Glomus geosporum*), *Claroideoglomus claroideum* (*Glomus claroideum*), and *C. etunicatum* (*Glomus etunicatum*) (Symbiom, Lanskrone, Czech Republic), in a layer 4 cm below the soil surface in half of the pots. We used a multi strain inoculum rather than a single fungus, since AMF generally occur as assemblages in ecosystems and in individual plant roots (Vandenkoornhuys *et al.* 2002). Although all fungal species have a global distribution, the fungal strains used originate from Europe. Control plants received 10 g of a sterilized mycorrhizal inoculum to control for the substrate component of the inoculum, and 10 mL of a microbial wash, to return a portion of the potential non mycorrhizal microbial community of the mycorrhizal inoculum to the control plants (Koide & Li 1989). The microbial wash was created by mixing 150 g of the live mycorrhizal inoculum with 7 L of water and decanting the mixture three times through 20 µm filter paper (AMF spores are bigger than 20 µm and cannot pass the filter).

We did not quantify the degree of mycorrhization, but at the end of the experiment, we checked whether mycorrhizal fungal colonization occurred in the mycorrhizal fungal treatment, and was prevented in the non mycorrhizal fungal treatment. For this purpose, we randomly selected one plant per species of the non mycorrhizal fungal treatment and two plants per species of the mycorrhizal fungal treatment. Root samples of these plants were washed, cleared in 10% KOH (80 °C for 15 35 min, depending on the plant species), stained in 5% black ink (Parker Quink, black) in vinegar solution (80 °C, 5 min), and destained in 50% glycerol. We assessed the presence or absence of mycorrhizal structures (hyphae, arbuscules and vesicles) under a microscope. This examination showed AMF structures in the mycorrhizal fungal treatment for all species except *Artemisia annua*, while we found no such structures in plants of the non mycorrhizal fungal treatment.

INDUCTION AND BIOASSAY OF RESISTANCE

Induced plant resistance is defined as a reduced preference or performance of herbivores in response to previous stress or injury of the plant (Karban & Myers 1989). Therefore, we used the performance response of the caterpillars to quantify the effects of induction on plant resistance. Because AMF may need up to several weeks to colonize roots, and it may require another several weeks

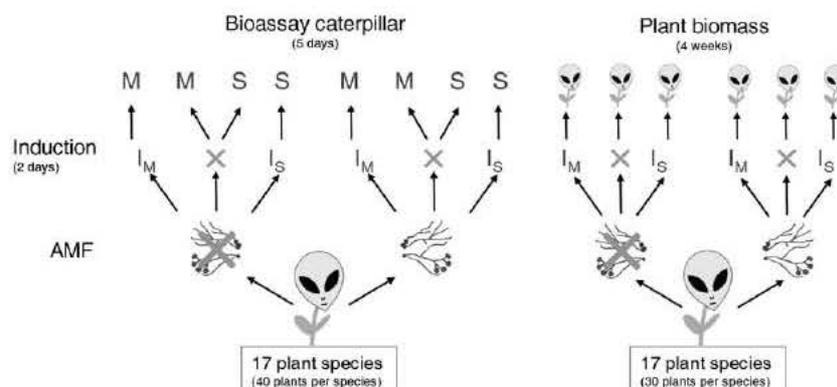


Fig. 1. Experimental design. Plants grew with or without a mixture of mycorrhizal fungi (AMF treatment) and were exposed for 2 days to herbivory (induction) by either *Mamestra brassicae* (I_M) or *Spodoptera littoralis* (I_S), or not induced at all (X). To assess the constitutive and induced resistance, we added the two generalist herbivores as bioassay caterpillars to a set of those plants and determined their growth. To assess the growth response of plants to induction and arbuscular mycorrhizal fungi, we grew a second set of those plants for four more weeks after the induction treatment.

of root colonization to have an effect on plant growth and herbivores, we started the induction treatment to assess herbivore performance on undamaged and damaged (induced) plants after 10 weeks of growth.

We enclosed all plants with a nylon gauze. To induce possible resistance mechanisms, we added two third to fourth instar larvae of *M. brassicae* and *S. littoralis* (hereafter called induction caterpillars) to each of 10 plants per species and mycorrhizal fungal treatment, and let them feed for 2 days. The remaining plants were used as non induced control plants. One day after removal of the induction caterpillars, we added one third instar *M. brassicae* larva as a bioassay caterpillar to each of the five *M. brassicae* induced and five non induced plants of each mycorrhizal fungal treatment. Similarly, we added one third instar *S. littoralis* larva to each of five *S. littoralis* induced and five non induced plants per species and mycorrhizal fungal treatment. We allowed the larvae to feed on the plants for 5 days (Fig. 1). We assessed the increase in biomass of the bioassay caterpillars by recording fresh mass of the caterpillars before and after feeding. We calculated their relative growth rate as $\ln(\text{larval mass after feeding}/\text{larval mass before feeding})$ (Kogan & Cope 1974). The remaining plants per species (five *M. brassicae* induced, five *S. littoralis* induced and five undamaged plants per species and mycorrhizal fungal treatment) were allowed to grow for four more weeks without herbivores to investigate their growth responses to induction and mycorrhizal fungi (Fig. 1). For those plants above and below ground biomass was harvested, dried at 70 °C for at least 3 days and weighed.

For some non invasive alien plant species, we had low germination rates, and as a consequence, we did not have enough plants for both mycorrhizal fungal treatments. In those cases, we used most plants for the mycorrhizal fungal treatment because this treatment is more likely to reflect natural field conditions. In some analyses, we therefore had to exclude those species for which we did not have data on all treatment combinations (*A. annua*, *Erigeron karvinskianus*, *P. orientale*, *Solidago graminifolia* and *Senecio vernalis*) as well as their congeneric counterparts.

STATISTICAL ANALYSIS

We used linear mixed effects models with the function *lmer* of the *lme4* package (Bates & Maechler 2009) in R (R Development Core Team 2010). For the analysis of total plant biomass, we used mycorrhizal fungal treatment (yes, no), induction treatment (not induced, induced by *M. brassicae*, induced by *S. littoralis*), invasive status (non invasive, invasive) and their interactions as fixed factors. We included block, genus and species nested within genus (and invasive status) as random factors. We also ran models with random slopes for genus and species with respect to mycorrhizal fungi, and induction, but because this increased the AIC values (i.e. decreased model fit), we did not further consider these models. We simplified the full model by removing non significant terms to produce a minimum adequate model. Significance was assessed using likelihood ratio tests comparing models with and without the terms of interest (Zuur *et al.* 2009). In this analysis, we had to exclude the plant species for which we had too few replicates in the non mycorrhizal fungal treatment, as well as their congeneric invasive counterparts. To be better able to test for the effect of invasive status and its interaction with induction of resistance, we also did a separate analysis for the mycorrhizal fungal treatment only, where we only had missing data for the two non invasive alien plant species *P. orientale* and *Senecio vernalis*.

We calculated the biomass response to the presence of mycorrhizal fungi for each plant species as $\ln(\text{mean dry biomass growing with mycorrhizal fungi}/\text{mean dry biomass growing without mycorrhizal fungi})$. A positive value would indicate that mycorrhizal fungi acted mutualistically, and a negative value would indicate that mycorrhizal fungi acted parasitically on the plants. We

also tested whether invasive or non invasive alien plant species responded more or less strongly to mycorrhizal fungi, comparing their absolute (i.e. unsigned) values of response to mycorrhizal fungi by means of an ANOVA.

For the analysis of the relative growth rate of the bioassay caterpillars, we used induction treatment (yes, no), herbivore (*M. brassicae*, *S. littoralis*), invasive status, mycorrhizal fungi and their interactions as fixed factors, and block, genus and plant species nested within genus (and invasive status) as random factors. Again, this analysis missed several plant species, and we therefore did a separate analysis for plants in the mycorrhizal fungal treatment only, for which we had complete data. We also ran models with random slopes for genus and species with respect to induction, herbivore, invasive status and mycorrhizal fungi, and kept the random slopes when the model had a lower AIC value (i.e. when there was an increased model fit).

Results

PLANT BIOMASS

In all congeneric species pairs, invasive alien plants produced more biomass than non invasive alien plants (Fig. 2). This effect was only marginally significant in the overall analysis, but was significant when we did the analysis for a larger number of species by analysing mycorrhized plants only (Table 2). Overall, inoculation with mycorrhizal fungi tended to reduce total plant biomass (marginally significant mycorrhiza effect in Table 2), both for invasive and non invasive alien plant species (Fig. 3, no significant invasive status \times mycorrhizal fungal interaction in Table 2). However, invasive species tended to have less extreme positive and negative responses to mycorrhizal fungi (unsigned values differed marginally significantly between non invasive and invasive plant species, estimate of invasives \pm SE: -0.311 ± 0.165 , $P = 0.084$, Fig. 3) suggesting lower sensitivities of invasive species to mycorrhizal fungi. Potential induction of resistance by the two bioassay caterpillars had no effect on total plant biomass, and did neither differ between mycorrhized and non mycorrhized plants nor between invasive and non invasive alien species (no significant induction effect and induction \times invasive status interaction in Table 2).

HERBIVORE PERFORMANCE

Overall, herbivore performance did not differ significantly between invasive and non invasive alien plant species ($P = 0.49$, see Table S1 in Supporting information, Fig. 4). Caterpillars feeding on previously induced plants had a lower growth rate than caterpillars feeding on non induced plants ($P = 0.018$, Table S1, Supporting information), indicating that overall, our plant species were able to induce resistance. However, induced resistance did not differ between invasive and non invasive alien plant species (no significant induction \times invasive status interaction) and also not between mycorrhized and non mycorrhized plants (no significant induction \times mycorrhizal fungi interaction in Table S1, Supporting information). Furthermore, the effect of mycorrhizal fungi on the ability to induce

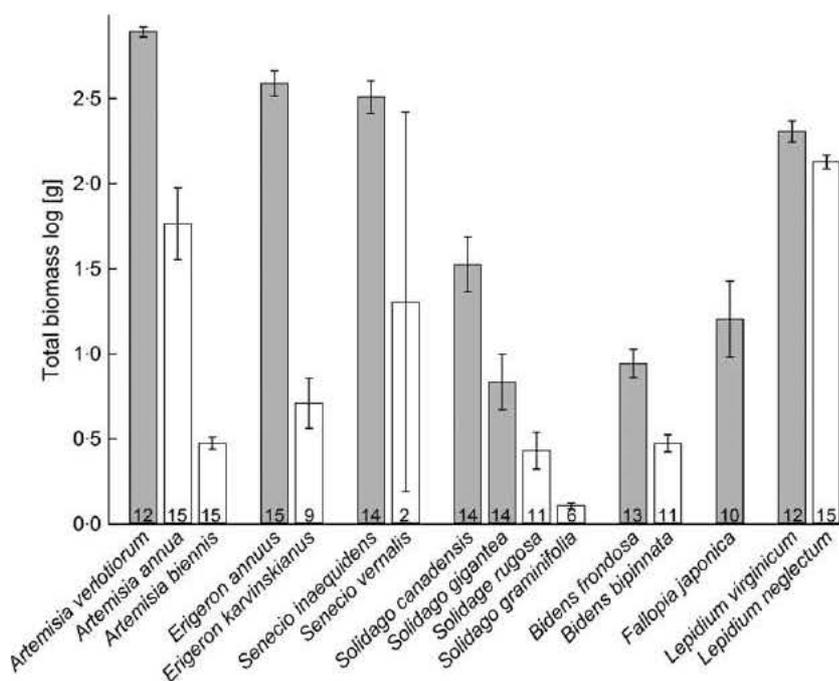


Fig. 2. Total plant biomass \pm SE of mycorrhizal invasive (grey) and non invasive (white) alien plant species. We indicated the numbers of replicates in each bar.

Table 2. Results of a linear mixed effect model using total plant biomass of invasive and non invasive alien plant species as dependent variable for plants of both mycorrhizal fungal treatments (here we had to remove eight of the 17 plant species) and of the mycorrhizal fungal treatment only (here we had to remove four of the 17 plant species)

	Both AMF treatments			AMF treatment only		
	χ^2	d.f.	P value	χ^2	d.f.	P value
<i>Fixed factors</i>						
Mycorrhiza (M)	3.356	1	0.067			
Induction (I)	2.857	2	0.240	1.760	2	0.416
Status (S)	2.931	1	0.087	6.768	1	0.009
M \times S	0.233	1	0.629			
S \times I	1.379	2	0.502	1.218	2	0.544
M \times I	1.053	2	0.591			
S \times I \times M	0.185	2	0.912			
<i>Random factors</i>						
Block	1.366	1	0.242	2.497	1	0.114
Genus	150.410	1	<0.0001	97.347	1	<0.0001
Genus /species	224.630	1	<0.0001	101.230	1	<0.0001

resistance did not generally differ between invasive and non invasive alien species (no significant induction \times mycorrhizal fungi \times invasive status interaction, Table S1, Supporting information). Thus, herbivore performance and the effects of induction, mycorrhizal fungi and their interaction on herbivore performance varied without any consistent pattern among species (Fig. 4, Data S1 and Table S2, Supporting information).

Analysis of the subset of plants in the mycorrhizal treatment confirmed the negative effect of induction on the relative growth rate of the caterpillars (P 0.048, Table S1, Supporting information). Furthermore, *S. littoralis* caterpillars had a higher growth rate than *M. brassicae* caterpillars (P 0.048). *Spodoptera littoralis* caterpillars tended to have lower growth rates on invasive species (invasive status \times herbivore interaction: P 0.062). However, herbivore performance as well as the ability to induce resistance did not differ significantly between invasive and non invasive alien plant species, and thus varied without consistent pattern among species (Tables S1 and S2, Supporting information; Fig. 4). This was confirmed when analysing species pairs separately. In some species pairs, the invasive alien species was significantly more able to induce resistance than the non invasive alien one, whereas in other species pairs the opposite was the case, and in yet others, the induction response did not differ between the invasive and non invasive alien species (Table S3 and Fig. S1, Supporting information).

Discussion

CONSTITUTIVE AND INDUCED RESISTANCE VALUABLE FOR SOME BUT NOT FOR ALL

In recent years, general strategies and traits associated with plant invasiveness have gained more and more research attention, and results from database and experimental studies suggest that invasions are not just random events. For instance, several studies report a higher performance and fecundity of invasive alien compared with native or non invasive alien species (Pyšek & Richardson 2007; van

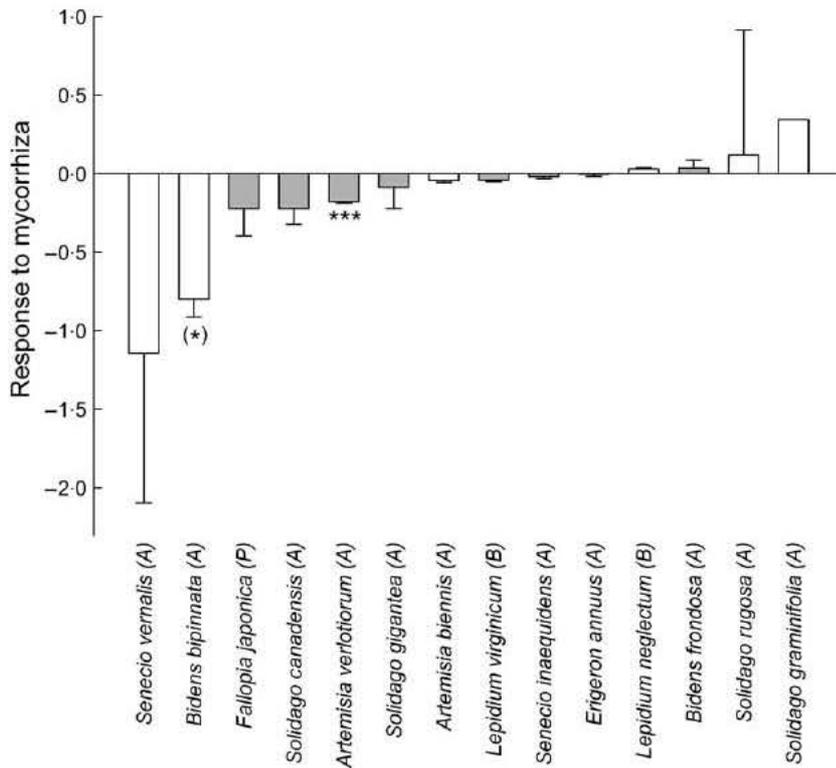


Fig. 3. Biomass response to mycorrhiza of invasive (grey) and non invasive (white) alien plant species in increasing order. Response to mycorrhiza is calculated as the log response ratio of total plant biomass growing with and without mycorrhiza, separately for each species. Error bars are based on the variance of the log response ratio (Hedges *et al.* 1999). Due to low numbers of replication we have no error bars for *Solidago graminifolia*. We had no complete data for *Polygonum orientale*, *Erigeron karvinskianus* and *Artemisia annua*. (a) Asteraceae, (b) Brassicaceae, (p) Polygonaceae.

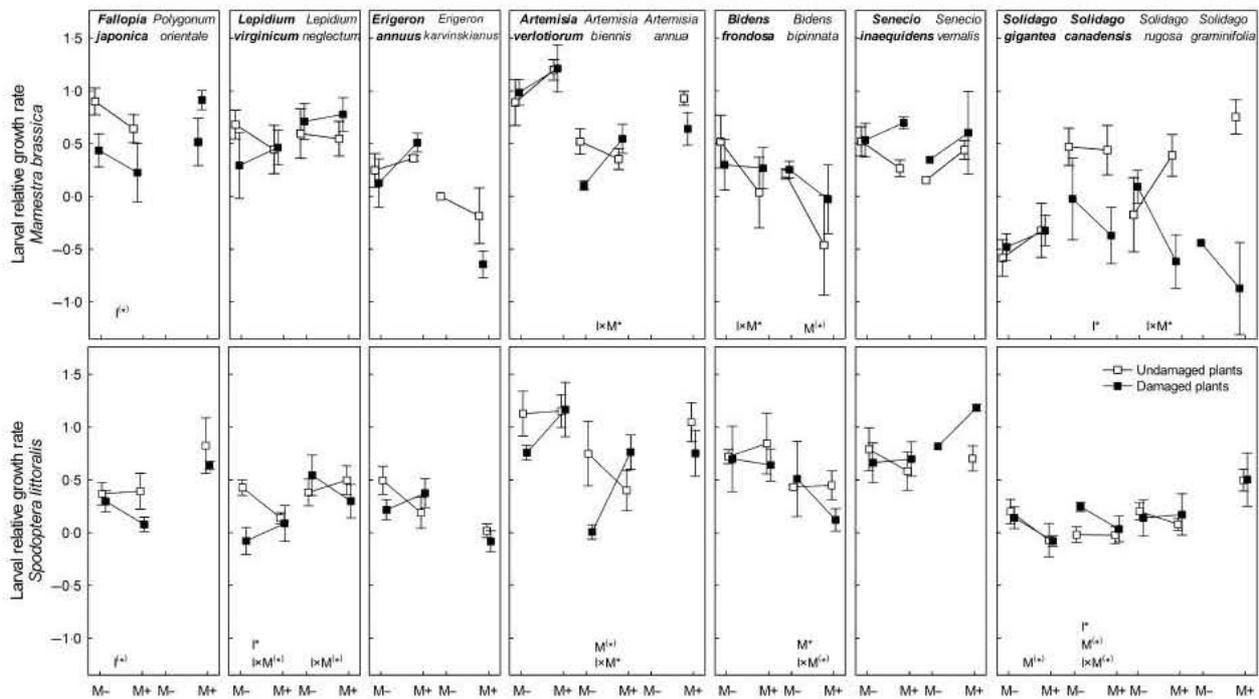


Fig. 4. The interacting effects of arbuscular mycorrhizal fungi (without AMF: M–, with AMF: M+) and induction on larval relative growth rates of *Spodoptera littoralis* and *Mamestra brassicae* feeding on the eight invasive (species name in bold) and the nine non invasive alien plant species. Values are means \pm standard errors. Significant effects of induction (I), mycorrhizal fungi (M) and their interactions (I \times M) on larval growth are indicated (see also Supporting Information Table S3).

Kleunen, Weber & Fischer 2010; Schlaepfer *et al.* 2010; Godoy, Valladares & Castro Díez 2011; van Kleunen *et al.* 2011). However, for many other traits that are thought to

promote invasions, no consistent pattern arose (Pyšek & Richardson 2007). Especially, when experimentally testing for differences between traits of not just one or two, but

multiple pairs of related invasive and non invasive alien or native species, complex results are quite common (e.g. Dostál 2011).

Our results are in line with recent findings that species capable of high biomass production appear to be pre adapted for invasion (van Kleunen *et al.* 2010; Schlaepfer *et al.* 2010; Godoy, Valladares & Castro Díez 2011). However, our results indicate that different invaders use different sets of defence related traits, and a trait being advantageous for a particular alien species might not be so for another. For instance, one of the world's most noxious invaders, the Japanese knotweed *F. japonica*, strongly induced resistance against both generalist herbivores (Table S2, Supporting information), and this was stronger than in the non invasive alien confamilial species *P. orientale* (Table S3, Supporting information). As *F. japonica* is a strong competitor, it is indeed likely that the ability to plastically increase the defence against herbivores represents a key adaptation for invasion success in this particular species. On the other hand, *Solidago gigantea*, another dominant and successful invader, showed no induction response at all to any of the two herbivore species (Table S2, Supporting information), whereas its non invasive alien congeners did (Table S3, Supporting information). However, herbivores generally performed very poorly on *S. gigantea*, and a further increase of resistance would probably not add any further benefit to the already high level of constitutive resistance (Fig. S1, Supporting information; Herms & Mattson 1992; Kempel *et al.* 2011). Herbivores performed best on the invasive *Artemisia verlotiorum*, which also had the highest biomass production. This could indicate that tolerance, investment in growth rather than resistance, may play a role in the invasion success of this alien species. Future studies should test explicitly, whether invasive and non invasive alien species differ consistently in their tolerance to herbivory.

Our results thus suggest that different species have different solutions to the same problem, and that consequently, no general pattern appeared. From our multi species study, we therefore conclude that the ability to plastically increase defences upon herbivore attack could be valuable for certain plant species, but is not a general key trait associated with invasion success. Invasive species are also not generally less or more defended against generalist herbivores than non invasive alien species are, and show as the non invasive alien species do the whole spectrum of different levels of constitutive and induced resistance.

LOW MYCORRHIZAL DEPENDENCY OF BOTH INVASIVE AND NON INVASIVE ALIEN SPECIES

Mycorrhizal fungi have been suggested to play an important role in plant invasions (Richardson *et al.* 2000; Pringle *et al.* 2009; Štajerová, Smilauerova & Smilauer 2009). One might thus expect that invasive species use the mycorrhizal symbiosis in a more beneficial way than

non invasive alien species or that they are less dependent on them. In our study, plant growth responses to arbuscular mycorrhizal fungi ranged from mainly negative to slightly positive, indicating that mycorrhizal fungi mainly acted parasitically. Such negative effects of mycorrhizal fungi are not rare, and are more common when nutrient rich instead of nutrient poor soil is used (Smith & Read 2008).

Although there are examples of invasive plant species that are obligately mycorrhizal (Richardson, Williams & Hobbs 1994; Fumanal *et al.* 2006; Smith *et al.* 2008), low mycorrhizal dependency has been suggested to be advantageous for species colonizing a new range (Reinhart & Callaway 2006; van der Putten, Klironomos & Wardle 2007). Our results showed that the invasive and non invasive alien plant species did not differ consistently in their average response to mycorrhizal fungi. A glance at the response to mycorrhizal fungi of all species, however, suggests that the range of positive and negative responses to mycorrhizal fungi was greatest for non invasive alien species, and that invasive species were not or only slightly negatively affected by mycorrhizal fungi. Although this difference was only marginally significant, a reduced response of invasive species to mycorrhizal fungi would not only reduce the potentially beneficial, but also the detrimental parasitic aspects of the symbiosis. The latter are usually strongest in nutrient rich conditions (van der Putten, Klironomos & Wardle 2007; Smith *et al.* 2008), which are also the type of conditions preferred by many invasive plant species (Dostál *et al.* 2012). If this difference in sensitivity holds true, future studies should address the question whether this reflects pre adaptation or evolutionary change in the new range. Our results only allow us to conclude that, although a mismatch of the local mycorrhizal community with an exotic plant might in some cases be a barrier to invasion (Richardson, Williams & Hobbs 1994), a more beneficial use of the mycorrhizal symbiosis does not appear to necessarily lead to invasion success of alien species.

MYCORRHIZAL FUNGI AFFECT INTERACTIONS BETWEEN ALIEN PLANT SPECIES AND HERBIVORES BUT NOT IN A CONSISTENT WAY

It has been frequently suggested that generalizations in invasion biology are rare due to context dependency and interactions among traits (Pyšek & Richardson 2007), but surprisingly few studies have tested for such interactions (but see Küster *et al.* 2008). Mycorrhizal fungi are known to affect levels of constitutive and induced resistance in plants (Bennett, Bever & Bowers 2009; Koricheva, Gange & Jones 2009; Kempel *et al.* 2010). We found that the way in which mycorrhizal fungi affected the outcome of the plant herbivore interactions did not differ consistently between invasive and non invasive alien plant species. Our results are thus in line with the current literature exhibiting the whole spectrum from positive to negative effects of

mycorrhizal fungi on constitutive resistance and the ability to induce resistance against generalist herbivores, but with out an emerging general pattern.

Eight of the 13 alien plant species altered their constitutive or induced resistance significantly in the presence of mycorrhizal fungi (Fig. 3, Table S2, Supporting information), with some being more resistant or more able to induce resistance in the presence of mycorrhizal fungi, and others in their absence. The effect of mycorrhizal fungi on resistance against herbivores does not appear to be related to their effect on plant biomass. For instance, *Lepidium virginicum*, showed as expected among the Brassicaceae almost no change in plant biomass to the presence of the fungi, but its ability to induce resistance was significantly reduced. Although we cannot exclude that this significant result is a type I error due to multiple testing, a biological explanation could be that upon recognition of the mycorrhizal fungi, cross talk between defence related pathways has modulated the plant's defence system (Pozo & Azcon Aguilar 2007). So, even when direct effects of mycorrhizal fungi on plant performance are absent, mycorrhizal fungi can have far reaching consequences for herbivores, and possibly, also for other community members such as pollinators and natural enemies of herbivores, and thereby ultimately on the performance of plants. The diversity of our results illustrates the spectrum of such multi trophic interactions, and demonstrates their presence even within alien plant species that have no or only a short sympatric evolutionary history with these fungi.

Conclusions

Our study demonstrates that high biomass production is a general characteristic of invasive alien plants, whereas induced resistance and constitutive resistance are not. Invasive and non invasive alien species both exhibited a variety of strategies to cope with herbivores. In addition, invasive alien species neither used the mycorrhizal symbiosis in a more beneficial nor in a less detrimental way than non invasive alien species did. However, a reduced sensitivity of invasive species to the local AMF community appears to be common, and might be a potential mechanism to avoid the parasitic nature of the fungi in nutrient rich habitats. Generally, it appears as if 'simple traits', such as biomass production, show more consistent differences between invasive and non invasive alien species than do 'complex' traits such as resistance and mycorrhization.

The great variability of mycorrhizal effects on constitutive and induced resistance of our species illustrates that mycorrhizal fungi can have substantial effects on non co evolved plant species and their associated herbivores although its contribution to a plant's performance is less clear. Nevertheless, bearing in mind the multi trophic nature of biotic interactions of alien plant species might help us to better understand their effect on the composition and functioning of recipient communities and ecosystems.

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References

- Agrawal, A.A. (1999a) Induced responses to herbivory in wild radish: effects on several herbivores and plant fitness. *Ecology*, **80**, 1713–1723.
- Agrawal, A.A. (1999b) Induced plant defense: evolution of induction and adaptive phenotypic plasticity. *Inducible Plant Defenses against Pathogens and Herbivores: Biochemistry, Ecology, and Agriculture* (eds A.A. Agrawal, S. Tuzun & E. Bent), pp. 251–268. American Phytopathological Society Press, St. Paul, MN.
- Agrawal, A.A. (2001) Ecology phenotypic plasticity in the interactions and evolution of species. *Science*, **294**, 321–326.
- Allen, E.B. & Allen, M.F. (1980) Natural re-establishment of vesicular-arbuscular mycorrhizae following stripmine reclamation in Wyoming. *Journal of Applied Ecology*, **17**, 139–147.
- Anderson, P., Jönsson, M. & Mörte, U. (2001) Variation in the intensity and temporal changes in the induced defence of cotton: effects on *Spodoptera littoralis* larval feeding preference. *Entomologia Experimentalis et Applicata*, **101**, 191–198.
- Baldwin, I.T. (1998) Jasmonate-induced responses are costly but benefit plants under attack in native populations. *Proceedings of the National Academy of Science USA*, **95**, 8113–8118.
- Bates, D. & Maechler, M. (2009) lme4: Linear mixed-effects models using Eigen and Eigen. R package version 0.999375-32. Available at: <http://CRAN.R-project.org/package=lme4>.
- Bennett, A.E., Bever, J.D. & Bowers, M.D. (2009) Arbuscular mycorrhizal fungal species suppress inducible plant responses and alter defensive strategies following herbivory. *Oecologia*, **160**, 771–779.
- Berg, M.P. & Ellers, J. (2010) Trait plasticity in species interactions: a driving force of community dynamics. *Evolutionary Ecology*, **24**, 617–629.
- Brown, E.S. & Dewhurst, C.F. (1975) The genus *Spodoptera* (Lepidoptera, Noctuidae) in Africa and the Near East. *Bulletin of Entomological Research*, **65**, 221–262.
- Carrillo, J., Wang, Y., Ding, J., Klootwyk, K. & Siemann, E. (2012) Decreased indirect defense in the invasive tree, *Triadica sebifera*. *Plant Ecology*, **213**, 945–954.
- Cipollini, D., Mbagwu, J., Barto, K., Hillstrom, C. & Enright, S. (2005) Expression of constitutive and inducible chemical defenses in native and invasive populations of *Alliaria petiolata*. *Journal of Chemical Ecology*, **31**, 1255–1267.
- Dostál, P. (2011) Plant competitive interactions and invasiveness: searching for the effects of phylogenetic relatedness and origin on competition intensity. *The American Naturalist*, **177**, 655–667.
- Dostál, P., Dawson, W., van Kleunen, M., Keser, L.H. & Fischer, M. (2012) Central European plant species from more productive habitats are more invasive at a global scale. *Global Ecology and Biogeography*, **22**, 64–72.
- Eigenbrode, S.D., Andreas, J.E., Cripps, M.G., Ding, H., Biggam, R.C. & Schwarzländer, M. (2008) Induced chemical defenses in invasive plants: a case study with *Cynoglossum officinale* L. *Biological Invasions*, **10**, 1373–1379.
- Endlweber, K. & Scheu, S. (2006) Establishing arbuscular mycorrhiza-free soil: a comparison of six methods and their effects on nutrient mobilization. *Applied Soil Ecology*, **34**, 276–279.
- Engel, K. & Tollrian, R. (2009) Inducible defences as key adaptations for the successful invasion of *Daphnia lumholzi* in North America? *Proceedings of the Royal Society B: Biological Sciences*, **276**, 1865–1873.

- Engelkes, T., Morriën, E., Verhoeven, K.J.F., Bezemer, T.M., Biere, A., Harvey, J.A., McIntyre, L.M., Tamis, W.L.M. & van der Putten, W.H. (2008) Successful range-expanding plants experience less above-ground and below-ground enemy impact. *Nature*, **456**, 946–948.
- Fumanal, B., Plenchette, C., Chauvel, B. & Bretagnolle, F. (2006) Which role can arbuscular mycorrhizal fungi play in the facilitation of *Ambrosia artemisiifolia* L. invasion in France? *Mycorrhiza*, **17**, 25–35.
- Godoy, O., Valladares, F. & Castro-Díez, P. (2011) Multispecies comparison reveals that invasive and native plants differ in their traits but not in their plasticity. *Functional Ecology*, **25**, 1248–1259.
- Gomez, S., van Dijk, W. & Stuefer, J.F. (2010) Timing of induced resistance in a clonal plant network. *Plant Biology*, **12**, 512–517.
- van Grunsven, R.H.A., van der Putten, W.H., Bezemer, M., Tamis, W.L.M., Berendse, F. & Veenendaal, E.M. (2007) Reduced plant-soil feedback of plant species expanding their range as compared to natives. *Journal of Ecology*, **95**, 1050–1057.
- Harvey, J.A., Bukovinsky, T. & van der Putten, W.H. (2010) Interactions between invasive plants and insect herbivores: a plea for a multitrophic perspective. *Biological Conservation*, **143**, 2251–2259.
- van der Heijden, M.G., Wiemken, A. & Sanders, I.R. (2003) Different arbuscular mycorrhizal fungi alter coexistence and resource distribution between co-occurring plants. *New Phytologist*, **157**, 569–578.
- Hedges, L.V., Gurevitch, J. & Curtis, P. (1999) The meta-analysis using response ratios in experimental ecology. *Ecology*, **80**, 1150–1156.
- Herms, D.A. & Mattson, W.J. (1992) The dilemma of plants to grow or defend. *Quarterly Review of Biology*, **67**, 283–335.
- Hoeksema, J.D., Chaudhary, V.B., Gehring, C.A., Johnson, N.C., Karst, J., Koide, R.T., Pringle, A., Zabinski, C., Bever, J.D., Moore, J.C., Wilson, G.W.T., Klironomos, J.N. & Umbanhowar, J. (2010) A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. *Ecology Letters*, **13**, 394–407.
- Johnson, N.C., Graham, J.H. & Smith, F.A. (1997) Functioning of mycorrhizal associations along the mutualism-parasitism continuum. *New Phytologist*, **135**, 575–586.
- Joshi, J. & Vrieling, K. (2005) The enemy release and EICA hypothesis revisited: incorporating the fundamental difference between specialist and generalist herbivores. *Ecology Letters*, **8**, 704–714.
- Karban, R. & Baldwin, I.T. (1997) *Induced Responses to Herbivory*. University of Chicago Press, Chicago, IL.
- Karban, R. & Myers, J.H. (1989) Induced plant responses to herbivory. *Annual Review of Ecology and Systematics*, **20**, 331–348.
- Keane, R.M. & Crawley, M.J. (2002) Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution*, **17**, 164–170.
- Kempel, A., Brandl, R. & Schädler, M. (2009) Symbiotic soil microorganisms as players in aboveground plant-herbivore interactions – the role of rhizobia. *Oikos*, **118**, 634–640.
- Kempel, A., Schmidt, A.K., Brandl, R. & Schädler, M. (2010) Support from the underground: Induced plant resistance depends on arbuscular mycorrhizal fungi. *Functional Ecology*, **24**, 293–300.
- Kempel, A., Schädler, M., Chroboczek, T., Fischer, M. & van Kleunen, M. (2011) Tradeoffs associated with constitutive and induced plant resistance against herbivory. *Proceedings of the National Academy of Sciences USA*, **108**, 5685–5689.
- van Kleunen, M., Weber, E. & Fischer, M. (2010) A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters*, **13**, 235–245.
- van Kleunen, M., Dawson, W., Schlaepfer, D., Jeschke, J.M. & Fischer, M. (2010) Are invaders different? A conceptual framework of comparative approaches for assessing determinants of invasiveness. *Ecology Letters*, **13**, 947–958.
- van Kleunen, M., Schlaepfer, D., Glättli, M. & Fischer, M. (2011) Pre-adapted for invasiveness: do species traits or their plastic response to shading differ between invasive and non-invasive plant species in their native range? *Journal of Biogeography*, **38**, 1294–1304.
- Klironomos, J.N. (2003) Variation in plant response to native and exotic arbuscular mycorrhizal fungi. *Ecology*, **84**, 2292–2301.
- Kogan, M. & Cope, D. (1974) Feeding and nutrition of insects associated with soybeans. 3. Food intake, utilization, and growth in the soybean looper, *Pseudoplusia includens*. *Annals of the Entomological Society of America*, **67**, 66–72.
- Koide, R.T. & Li, M. (1989) Appropriate controls for vesicular-arbuscular mycorrhiza research. *New Phytologist*, **111**, 35–44.
- Koricheva, J., Gange, A.C. & Jones, T. (2009) Effects of mycorrhizal fungi on insect herbivores: a meta-analysis. *Ecology*, **90**, 2088–2097.
- Kühn, I., Durka, W. & Klotz, S. (2004) BiolFlor – a new plant-trait database as a tool for plant invasion ecology. *Diversity & Distributions*, **10**, 363–365.
- Küster, E.C., Kühn, I., Bruehlheide, H. & Klotz, S. (2008) Trait interactions help explain plant invasion success in the German flora. *Journal of Ecology*, **96**, 860–868.
- Landolt, E., Bäumler, B., Erhardt, A., Hegg, O., Klötzli, F., Lämmler, W., Nobis, M., Rudmann-Maurer, K., Schweingruber, F.H., Theurillat, J.-P., Urmi, E., Vust, M. & Wohlgenutz, T. (2010) *Flora indicativa Ökologische Zeigerwerte und biologische Kennzeichen zur Flora der Schweiz und der Alpen*. Haupt Verlag, Bern.
- Levine, J.M., Adler, P.B. & Yelenik, S.G. (2004) A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters*, **7**, 975–989.
- Moor, M., Berger, S., Davison, J., Öpik, M., Bommarco, R., Bruehlheide, H., Kühn, I., Kunin, W.E., Metsis, M., Rortais, A., Vanatoa, A., Vanatoa, E., Stout, J.C., Truusa, M., Westphal, C., Zobel, M. & Walthert, G.-R. (2011) Alien plants associate with widespread generalist arbuscular mycorrhizal fungal taxa: evidence from a continental-scale study using massively parallel 454 sequencing. *Journal of Biogeography*, **38**, 1305–1317.
- Orians, C.M. & Ward, D. (2010) Evolution of plant defenses in nonindigenous environments. *Annual Review of Entomology*, **55**, 439–459.
- Parker, J.D., Burkepile, D.E. & Hay, M.E. (2006) Opposing effects of native and exotic herbivores on plant invasions. *Science*, **311**, 1459–1461.
- Pendleton, R.L. & Smith, B.N. (1983) Vesicular-arbuscular mycorrhizae of weedy and colonizer plant species at disturbed sites in Utah. *Oecologia*, **59**, 296–301.
- Pineda, A., Zheng, S.-J., van Loon, J.J., Pieterse, C.M. & Dicke, M. (2010) Helping plants to deal with insects: the role of beneficial soil-borne microbes. *Trends in Plant Science*, **15**, 507–514.
- Pozo, M.J. & Azcon-Aguilar, C. (2007) Unraveling mycorrhizal-induced resistance. *Current Opinion in Plant Biology*, **10**, 393–398.
- Pringle, A., Bever, J.D., Gardes, M., Parrent, J.L., Rillig, M.C. & Klironomos, J.N. (2009) Mycorrhizal symbioses and plant invasions. *Annual Review of Ecology, Evolution and Systematics*, **40**, 699–715.
- van der Putten, W.H., Klironomos, J.N. & Wardle, D.A. (2007) Microbial ecology of biological invasions. *The ISME Journal*, **1**, 28–37.
- Pysek, P. & Richardson, D.M. (2007) Traits associated with invasiveness in alien plants: where do we stand? *Biological Invasions* (eds W. Nentwig), pp. 97–125. Springer Verlag, Berlin.
- R Development Core Team (2010) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.
- Reeves, F. (1979) Role of endomycorrhizae in revegetation practices in the semi-arid west. A comparison of incidence of mycorrhizae in severely disturbed vs. natural environments. *American Journal of Botany*, **66**, 6–13.
- Reinhart, K.O. & Callaway, R.M. (2006) Soil biota and invasive plants. *New Phytologist*, **170**, 445–457.
- Richards, C.L., Bossdorf, O., Muth, N.Z., Gurevitch, J. & Pigliucci, M. (2006) Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecology Letters*, **9**, 981–993.
- Richardson, D.M., Williams, P.A. & Hobbs, R.J. (1994) Pine invasions in the southern-hemisphere – determinants of spread and invadability. *Journal of Biogeography*, **21**, 511–527.
- Richardson, D.M., Allsopp, N., D'Antonio, C.M., Milton, S.J. & Rejmanek, M. (2000) Plant invasions – the role of mutualisms. *Biological Reviews*, **75**, 65–93.
- Rojas, J.C., Wyatt, T.D. & Birch, M.C. (2000) Flight and oviposition behavior toward different host plant species by the cabbage moth, *Mamestra brassicae* (L.) (Lepidoptera, Noctuidae). *Journal of Insect Behaviour*, **13**, 247–254.
- Schlaepfer, D.R., Glättli, M., Fischer, M. & van Kleunen, M. (2010) A multi-species experiment in their native range indicates pre-adaptation of invasive alien plant species. *New Phytologist*, **185**, 1087–1099.
- SKew (2009) Liste der unerwünschten Arten. Available at: http://www.cps-skew.ch/fileadmin/template/pdf/deutsch/Empf_Liste_IV_d.pdf (assessed January 2012).
- Smith, L.L., DiTommasso, A., Lehmann, J. & Greipsson, S. (2008) Effects of arbuscular mycorrhizal fungi on the exotic invasive vine Pale Swallow-Wort (*Vincetoxicum rossicum*). *Invasive Plant Science and Management*, **1**, 142–152.
- Smith, S.E. & Read, D.J. (2008) *Mycorrhizal Symbiosis*. Academic Press, London.

- Stajerová, K., Smilauerova, M. & Smilauer, P. (2009) Arbuscular mycorrhizal symbiosis of herbaceous invasive neophytes in the Czech Republic. *Preslia*, **81**, 341–355.
- Strauss, S.Y., Webb, C.O. & Salamin, N. (2006) Exotic taxa less related to native species are more invasive. *Proceedings of the National Academy of Sciences USA*, **103**, 5841–5845.
- Vandenkoornhuyse, P., Husband, R., Daniell, T.J., Watson, I.J., Duck, J. M., Fitter, A.H. & Young, J.P. (2002) Arbuscular mycorrhizal community composition associated with two plant species in a grassland ecosystem. *Molecular Ecology*, **11**, 1555–1564.
- Verhoeven, K.J.F., Biere, A., Harvey, J.A. & van der Putten, W.H. (2009) Plant invaders and their novel natural enemies: who is naïve? *Ecology Letters*, **12**, 107–117.
- Vogelsang, K.M. & Bever, J.D. (2009) Mycorrhizal densities decline in association with nonnative plants and contribute to plant invasion. *Ecology*, **90**, 399–407.
- van Zandt, P.A. (2007) Plant defense, growth, and habitat: a comparative assessment of constitutive and induced resistance. *Ecology*, **88**, 1984–1993.
- Zas, R., Moreira, X. & Sampedro, L. (2011) Tolerance and induced resistance in a native and an exotic pine species: relevant traits for invasion ecology. *Journal of Ecology*, **99**, 1316–1326.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009) *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York.

Supporting Information

Fig. S1. Relative growth rate of *Spodoptera littoralis* and *Mamestra brassicae* feeding on undamaged and damaged plants (mycorrhized plants only).

Table S1. Results of a linear mixed effects model using larval growth rate as dependent variable.

Table S2. Results of an ANOVA using either the mean larval growth rate of both herbivore species, of *Spodoptera littoralis* only and of *Mamestra brassicae* only, as dependent variable.

Table S3. Results of linear mixed effect models using the relative growth rate of the caterpillars as dependent variable.

Data S1 Details on the effects on herbivore growth rate, separately for each plant species.