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Allelopathic effects of three plant invaders on germination of native species: a field study

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Abstract The ability of some invasive plant species to produce biochemical compounds toxic to native species, called allelopathy, is thought to be one of the reasons for their success when introduced to a novel range, an idea known as the Novel Weapons Hypothesis. However, support for this hypothesis mainly comes from bioassays and experiments conducted under controlled environments, whereas field evidence is rare. In a field experiment, we investigated whether three plant species invasive in Europe, *Solidago gigantea*, *Impatiens glandulifera* and *Erigeron annuus*, inhibit the germination of native species through allelopathy more than an adjacent native plant community. At three sites for each invasive species, we compared the germination of native species that were sown on invaded and non-invaded plots. Half of these plots were amended with activated carbon to reduce the influence of potential allelopathic compounds. The germination of sown seeds and of seeds from the seedbank was monitored over a period of 9 weeks. Activated carbon generally enhanced seed germination. This effect was equally pronounced in invaded and adjacent non-invaded plots, indicating

that invasive species do not suppress germination more than a native plant community. In addition, more seeds germinated from the seedbank on invaded than on non-invaded soil, probably due to previous suppression of germination by the invasive species. Our field study does not provide evidence for the Novel Weapons Hypothesis with respect to the germination success of natives. Instead, our results suggest that if invasive species release allelopathic compounds that suppress germination, they do so to a similar degree as the native plant community.

Keywords Activated carbon · Allelopathy · *Erigeron* · Field experiment · *Impatiens* · Novel weapons hypothesis · *Solidago*

Introduction

The distribution and abundance of plant species is determined by their ability to compete for resources (Casper and Jackson 1997; Grime 2001; Huston and Smith 1987; Tilman 1988) and by other types of biotic interactions (Callaway 2007). Some plant species suppress the growth or establishment of their competitors by releasing toxic compounds, a mechanism referred to as allelopathy (Inderjit et al. 2011). Allelopathic compounds can directly harm other species by decreasing their germination or growth (e.g. Callaway and Aschehoug 2000; Prati and

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Bossdorf 2004). Alternatively, these compounds can act indirectly through effects on the soil microbial community, i.e. by suppressing mutualists or by promoting antagonists of other plant species (Mangla and Inderjit 2008; Stinson et al. 2006). Thus, allelopathic compounds can play a major role in plant–plant interactions (Inderjit et al. 2011; Muller 1966; Wardle et al. 1998). Moreover, allelopathic compounds can be persistent in soils. The resulting legacy effects of allelopathic species can affect future plant species and potentially entire ecosystems in the long term (Prati and Bossdorf 2004; Stinson et al. 2006).

During the last decade, the concept of allelopathy has received increased attention in the context of plant invasions. Some plant species are so successful in their novel range that resource competition alone seems an unlikely explanation for their success. Hence, other mechanisms, such as allelopathy, might be involved (Rabotnov 1981). The Novel Weapons Hypothesis proposes that invasive plant species possess biochemical compounds with a strong allelopathic effect on native plant species due to an evolutionary mismatch (Callaway and Ridenour 2004). Indeed, invasive plant species often differ from native species in their prominent secondary compounds (Barto et al. 2010; Cappuccino and Arnason 2006), but the relevance of these differences for the success of invasive plant species remains controversial (Kim and Lee 2011; Lind and Parker 2010; Scharfy et al. 2010; Stowe 1979). Previous studies provided evidence for both direct and indirect allelopathic effects of invasive plant species (Callaway and Aschehoug 2000; Callaway et al. 2008; Jarchow and Cook 2009; Murrell et al. 2011; Ridenour and Callaway 2001; Stinson et al. 2006). However, this evidence mainly relies on bioassays and pot experiments carried out under controlled conditions. Only few studies have tested the Novel Weapons Hypothesis under field conditions. Most of them focused on allelopathic effects of plant invaders and did not compare these effects to those of native species (Cipollini et al. 2008; Cipollini and Schradin 2011; Perry et al. 2005; Siemens and Blossey 2007; Tian et al. 2007; but see Gomez-Aparicio and Canham 2008). Since the Novel Weapons Hypothesis implies that allelopathic effects of invasive species must be stronger than those of native species (otherwise this would not explain the invasive behavior), the comparison of invasive and native species is a crucial next step.

Thus, our study aims to evaluate the ecological relevance of the Novel Weapons Hypothesis for three invasive plant species by testing whether invasive species have stronger allelopathic effects than native species in the field. We used activated carbon, an efficient adsorbent of biochemical compounds, to test for potential allelopathic effects on seed germination. Activated carbon can affect other soil properties (Lau et al. 2008; Weisshuhn and Prati 2009; Wurst et al. 2010), but these side effects are likely to be similar in invaded and non-invaded plots within the same site (i.e. similar soil conditions), so that they would not bias a comparison of allelopathic effects between invasive and native species based on activated carbon. We therefore compared the effect of activated carbon on plots dominated by one of the invasive species to effects on adjacent plots dominated by native plant species. If invasive species suppress seed germination more than native species through allelopathy, we expect that activated carbon enhances germination stronger in invaded compared with adjacent non-invaded plots. Conversely, if invasive and native species exert the same allelopathic effect, activated carbon should have the same effect on germination in both invaded and adjacent non-invaded plots.

Materials and methods

Invasive plant species and site selection

To study potential allelopathic effects of invasive plant species in the field, we selected three of the most invasive species in Central Europe: *Solidago gigantea*, *Impatiens glandulifera* and *Erigeron annuus*. *S. gigantea* is a clonal perennial species producing annual shoots and a large number of wind-dispersed seeds. Once established, *Solidago* further spreads through rhizomes (Weber and Jakobs 2005). In contrast, both *I. glandulifera* and *E. annuus* are annuals without clonal growth (Beerling and Perrins 1993; Stratton 1992). The native range of both *S. gigantea* and *E. annuus* is North America whereas *I. glandulifera* is native to the Himalayan region (Beerling and Perrins 1993; Stratton 1992; Weber and Jakobs 2005).

For each invasive species, we selected three sites in northern Switzerland at 400–500 m a.s.l. (Table 1). Mean annual temperature ranged from 9.5 to 10 °C and mean annual precipitation from 950 to 1,050 mm at all sites. All sites were densely populated by one of the

Table 1 Study site characteristics and test species set used at each site

Invasive species	Site	CH coordinates	Test species set ^a
<i>Solidago gigantea</i>	Chablais forest	576990 200487	Forest
	Sugiez	575993 200985	Forest
	Chablais reed	576310 200320	Wet grassland
<i>Impatiens glandulifera</i>	Buchs Wyne-Rus	650617 249098	Forest
	Buchs Ruppertswil	651105 250075	Forest
	Mühleberg	587449 200614	Forest
<i>Erigeron annuus</i>	Müntschemier	579033 204815	Dry grassland
	Lenzburg banquette	656833 249352	Dry grassland
	Gümmenen-Saanespitz	586195 203032	Wet grassland

^a Forest: *Festuca rubra*, *Geranium sylvaticum*, *Silene dioica*, *Lythrum salicaria*, *Stachys sylvatica*; Wet grassland: *Festuca arundinacea*, *Geranium pyrenaicum*, *Silene dioica*, *Geum urbanum*, *Ranunculus repens*; Dry grassland: *Festuca rubra*, *Geranium robertianum*, *Echium vulgare*, *Sanguisorba minor*, *Salvia pratensis*

invasive species, covering 80–100 % of the soil in midsummer. According to the managers of the areas, sites did not have any history of invasion control, nor did population size of the invasive species decrease naturally over the past decades. Thus, adjacent non-invaded areas were likely never colonized by any of the invasive species in the past. The habitat types of the sites ranged from dry grassland (*Erigeron*) and wet grassland (*Erigeron*, *Solidago*) to forest (*Impatiens*, *Solidago*).

Native test species selection

We used three sets of native species to test for allelopathic effects of plant invaders on species that are typical for each habitat type. Thus, the effect of one plant invader was not necessarily tested on the same set of native species at all sites (Table 1). Each test species set consisted of five native species: one grass and four herb species commonly found in one habitat type: *Festuca arundinacea*, *Geranium pyrenaicum*, *Silene dioica*, *Geum urbanum*, *Ranunculus repens* (wet grassland), *Festuca rubra*, *Geranium robertianum*, *Echium vulgare*, *Sanguisorba minor*, *Salvia pratensis* (dry grassland), *Festuca rubra*, *Geranium sylvaticum*, *Silene dioica*, *Lythrum salicaria*, *Stachys sylvatica* (forest). These species differ in seed size, but none of them is known to have special germination requirements (Royal Botanic Gardens Kew 2008).

Experimental design

The experiment was set up between 25 April and 15 May 2011 in a split-split-plot design. At each of the nine sites,

four plots were set up on invaded and adjacent non-invaded soil, respectively. Plots on invaded soil were randomly placed within a stand densely populated by one of the invasive species. Adjacent non-invaded plots were placed as close as possible to the invaded stands (2–5 m), but where the invasive species was absent. Care was taken that no litter of invasive species was covering the soil and that species richness was similar between invaded and adjacent non-invaded plots ($F_{1,6} = 0.08$, $p = 0.78$). However, invaded plots differed from non-invaded plots with respect to plant cover ($F_{1,60} = 19.46$, $p < 0.001$) and biomass ($F_{1,60} = 27.05$, $p < 0.001$) due to the high productivity of the invasive species. Each plot was divided into two subplots of 20×20 cm, 5 cm apart from each other. Subplots did not differ in plant cover, biomass, and species richness (all $p > 0.18$). For each subplot, species composition was recorded; then the biomass of invasive and native species was removed, separately dried at 80 °C, and weighed.

To remove potential allelopathic compounds from one of the two subplots, we added pure activated carbon (Charcoal Activated, Merck KGA, Darmstadt, Germany; Zn < 200 ppm, Fe < 1,000 ppm, no detectable P). Activated carbon is an efficient adsorbent of biochemical compounds and often used in allelopathy studies both in greenhouse and field experiments (e.g. Callaway and Aschehoug 2000; Gomez-Aparicio and Canham 2008; Lau et al. 2008; Murrell et al. 2011; Prati and Bossdorf 2004). Activated carbon can alter soil nutrient availability, water retention, pH or plant mycorrhization (Lau et al. 2008; Kabouw et al. 2010; Weissshuhn and Prati 2009; Wurst et al. 2010), but these possible artifacts are likely to be similar in invaded and

non-invaded plots. Thus, different effects of activated carbon in invaded and non-invaded soils can be attributed to different allelopathic effects of invasive and native species. We collected 2,000 ml of top soil from each subplot, removed large roots and rhizomes, and added activated carbon at a concentration of 25 ml/L. We thoroughly mixed soil and carbon and returned the mixture to the subplot. To control for the effect of disturbance, the second subplot was treated identically, but without addition of carbon. After soil was returned to the subplots, we evenly added 20 seeds from each of the five test species to each subplot. For this we subdivided the subplot into 100 squares of $2 \times 2 \text{ cm}^2$ using a grid, each receiving one seed of one of the five test species. To protect subplots from herbivores, we covered each subplot with a fence of 1 cm mesh size and 2 cm height. Each invaded/non-invaded plot was replicated four times per site, resulting in 16 subplots per site and 144 subplots across all sites.

Measurements and data analysis

We recorded the germination of sown seeds and the number of seedlings spontaneously emerging from the seed bank in each subplot three times at intervals of three weeks, starting in late May. For these records, we placed the $2 \times 2 \text{ cm}^2$ grid on the subplot and recorded seedlings found in each grid cell. The germination of sown species could potentially be overestimated by spontaneous germination from the seed bank, but because single test species were sown into known squares, this effect is likely to be negligible.

We analyzed treatment effects on the number of seedlings (only sown species or total) using a mixed model with the identity of invasive species, stand type (invaded/non-invaded), activated carbon treatment and the three record dates as fixed effects, while sites, plots (nested in sites) and subplots (nested in plots) were included as random effects to account for the experimental design and repeated measures.

To analyze the germination of single test species, the model was reduced by excluding invasive species identity, given that test species were not full-factorially combined with invasive species. The co-variables total plant cover, total biomass, native biomass prior to the experiment and the set of test species were not included in the final model as they were not significant, except for a weak significance of native biomass on number of seedlings from sown seeds ($t_{67} = -2.205$,

$p = 0.03$). However, this relationship was only weakly negative (slope = -0.03) and did not affect the outcome for other factors qualitatively. In all models, only two-way interactions were included as higher interactions were never significant. Response variables were $\log(Y + 1)$ -transformed to meet model assumptions; back-transformed mean values are presented in figures and text. All analyses were performed in R 2.14.0 (R Development Core Team 2011) using the function 'lme' in the package 'nlme'.

Results

Germination of sown seeds did not differ between invaded and adjacent non-invaded soils (Table 2). In contrast, the mean number of seedlings from the seedbank was 89 % higher on invaded than on non-invaded soil (Table 2; Fig. 1). Activated carbon increased the germination of sown seeds by 16 % and the number of seedlings from the seedbank by 20 % (Table 2). The effect of activated carbon on sown seeds was due to the enhanced germination of herb species, while sown grasses were not affected (Table 2). The increase in germination with activated carbon was similar in both invaded and adjacent non-invaded soil (Fig. 1), as indicated by the absence of any activated carbon \times soil-interaction for all response variables (Table 2). The positive effect of activated carbon was consistent for all record times (no significant interactions of activated carbon with record time in Table 2).

The above patterns were consistent for all three invasive species; their identity did not influence germination success and did not interact with activated carbon or soil (Table 2; Fig. 1). However, at *Solidago* sites, sown and total seedling numbers decreased with time, indicating mortality, whereas for *Erigeron* and *Impatiens*, they increased with time.

Analyzing single test species did not show any effect of activated carbon and soil type (data not shown), mostly because these tests included fewer sites, reducing their power.

Discussion

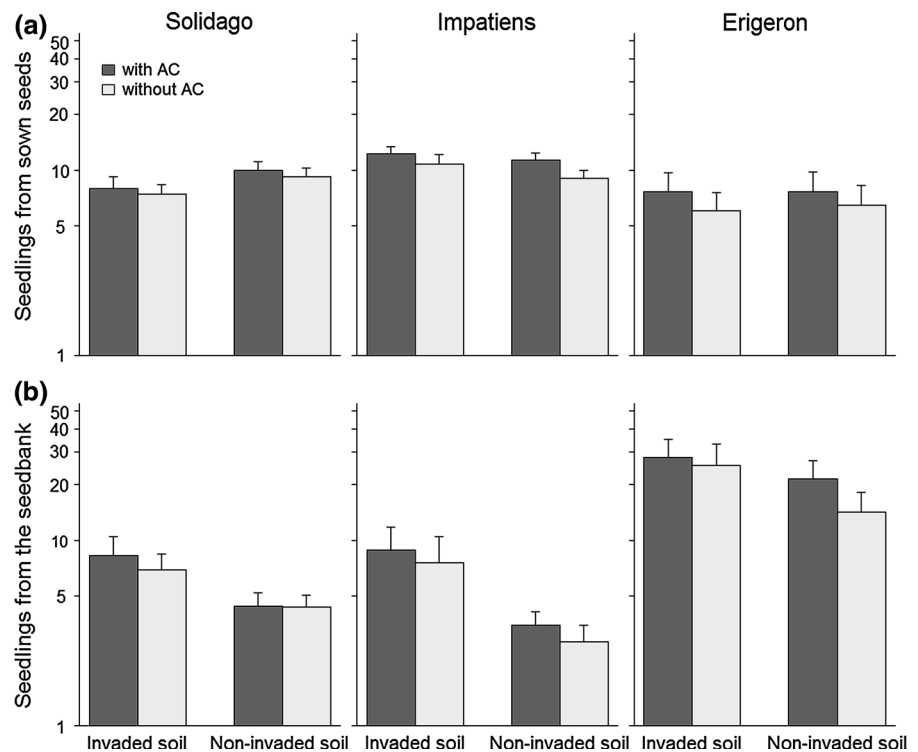
Our most prominent finding was that the germination of native plant species increased with the addition of

Table 2 Effects of invasive species identity, soil colonization history, activated carbon, time of germination record and two-way interactions of these factors on the number of germinated seedlings from sown seeds and from the seedbank at the end of the experiment

Factors	df1	df2	Seedlings from sown seeds			Seedlings from seedbank	All seedlings
			All	Grasses	Herbs		
Invasive species (Sp)	2	6	0.24	1.50	1.95	1.87	1.36
Invaded/non-invaded (I)	1	60	0.19	1.02	0.50	13.17***	7.12**
Activated carbon (AC)	1	68	7.23**	1.33	8.96**	5.74*	4.94*
Record time (RT)	2	278	20.30***	4.30*	78.97***	20.20***	44.91***
Sp × I	2	60	0.96	1.07	0.06	0.84	0.91
Sp × AC	2	68	0.51	0.33	0.93	0.38	0.14
Sp × RT	4	278	23.34***	8.81***	13.76***	27.91***	41.52***
I × AC	1	68	0.01	0.08	0.47	0.27	0.75
I × RT	2	278	0.22	1.06	1.28	3.53*	2.74
AC × RT	2	278	0.79	1.44	0.04	1.51	2.29

Shown are F values and level of significances (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$)

Fig. 1 Effect of soil type and activated carbon (AC) on the number of seedlings from sown seeds (a) and from the seedbank (b) at the end of the experiment for the three invasive species separately. Shown are means and standard errors on a logarithmic scale



activated carbon whether or not the plot was invaded by any of the three invasive species (Fig. 1; Table 2). This result suggests that under field conditions, invasive plant species do not possess allelopathic compounds that are more powerful in reducing the

germination success of natives compared with the resident plant community as predicted by the Novel Weapons Hypothesis (Callaway and Ridenour 2004).

There are two alternatives to explain why invaded and non-invaded soil showed equal increase of germination

with activated carbon. First, the distance between invaded and non-invaded plots may have been not large enough such that allelopathic compounds of invasive species diffused to the plots on non-invaded soil. However, even in a tree species, *Ailanthus altissima*, allelopathic effects were undetectable after five meters from the trunk (Gomez-Aparicio and Canham 2008). It is therefore unlikely that allelopathic compounds of our herbaceous invasive species were transported to adjacent non-invaded soil over a distance of more than two meters. Second, activated carbon potentially alters soil properties like plant available phosphorus and other nutrients, water retention, pH or the degree of mycorrhization of test species (Lau et al. 2008; Kabouw et al. 2010; Weissshuhn and Prati 2009; Wurst et al. 2010). However, these effects are likely the same in both invaded and non-invaded soils. The plots were selected as close by as possible to minimize environmental differences. Furthermore, plant species richness was similar between invaded and non-invaded plots, except for the presence of the invasive species. Therefore, the main conclusion that allelopathic compounds of invasive and native species exert similar effects on germination of other natives still holds true.

Evidence for the Novel Weapons Hypothesis mainly stems from controlled pot experiments. The three test species we used in our field experiment do not support this hypothesis. This partly concurs with findings from Scharfy et al. (2011) showing that in a pot experiment *Solidago gigantea* and *Erigeron annuus* exerted allelopathic effects on growth of a grass species, which were similar to the ones of native species. However, the allelopathic effect of *Impatiens glandulifera* was twice as strong as the effect of any native species whereas in our study the allelopathic effect of *I. glandulifera* was the same as effects of the non-invaded plant community. This contrast shows the need of conducting field experiments to study the ecological relevance of allelopathic effects, but also of looking at allelopathic effects on different life stages, as allelopathic compounds may act on growth rather than germination.

In other field experiments, invasive plant species exerted both negative and no allelopathic effects on other plant species (Cipollini et al. 2008; Cipollini and Schradin 2011; Perry et al. 2005; Siemsen and Blossey 2007; Tian et al. 2007). Only few studies compared effects of invasive species with those of natives. In a transplant experiment, Gomez-Aparicio

and Canham (2008) found that allelopathic effects of the invasive tree species *Ailanthus altissima* quickly decreased with distance from the trunk, dropping to zero within five meters. In another transplant experiment, Wixted and McGraw (2010) showed that an invasive and a native species can both exert allelopathic effects on another species. In concurrence with these surveys, our results show the need of a comparative approach to study allelopathic effects of invasive species, as these may be similar to allelopathic effects of native species, and hence not explain the invasiveness.

The second major and rather surprising finding was that the number of spontaneously emerging seedlings from the seed bank was higher in invaded than in non-invaded plots. One explanation for this finding could be that invasive species have been suppressing seed germination, so that seeds could accumulate in the seed bank before the start of the experiment. Indeed, *Solidago gigantea* has been found to suppress its own seedlings (Weber and Jakobs 2005), while seedlings have been observed after disturbance (Hartmann et al. 1995). Thus, disturbing soil during the set-up of the experiment may have activated the seed bank of invaded soil, leading to germination in high numbers. Alternatively, seed rain may have been higher on invaded than non-invaded plots. However, species richness was similar in both plot types, and the small distance between them (2–5 m) renders it unlikely that differences in seed rain could account for the different germination. Another explanation for our finding could be that invasive species have altered soil conditions in a way that promotes native species' seed germination, or that favorable environmental conditions promoted the invasion initially. This explanation, however, is unlikely as the number of seedlings from sown seeds would also have been affected by such general differences between invaded and non-invaded plots.

In conclusion, our results suggest that allelopathic effects of our three invasive species on the germination success of native species do not explain their overwhelming success in the invaded range. Our experiment also shows the importance of comparing allelopathic effects of invasive and native species, because allelopathic effects of invaders must be stronger than those of the resident community to effectively contribute to invasion success. Our experiment only considered seed germination. As

allelopathic compounds of invaders may act on other life stages like growth or reproduction, future field experiments should compare allelopathic effects of invasive and native species on later life stages.

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