

SHORT COMMUNICATION

Limited evidence for allelopathic effects of giant hogweed on germination of native herbs

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Abstract

Invasive alien plants often occur in monospecific stands with high density in the invaded range. Production of bioactive secondary metabolites in such stands could have allelopathic effects on germination of native species. We tested this component of the novel weapon hypothesis for *Heracleum mantegazzianum*, a prominent invader in Europe, using seeds of 11 native herbs exposed to soil or soil extracts from invaded stands, moist seeds or seed extracts of *H. mantegazzianum*. There was no effect of the various treatments on germination of most species, while germination was reduced in *Urtica dioica* on invaded soil, in *Poa trivialis* with *H. mantegazzianum* seed extract, and negative effects of the essential oil bergapten were found in three species. In *P. trivialis* the results of the seed extract were not supported by the experiment with added seeds of the invasive plant. Thus, there is limited evidence for allelopathic effects of the invasive *H. mantegazzianum* on germination of co-occurring native herbs.

Keywords: allelopathy, bergapten, *Heracleum mantegazzianum*, novel weapon, *Poa trivialis*, seed extract, *Urtica dioica*

Introduction

Invasive alien plant species have considerable effects on natural ecosystems and land use, because they displace native communities (Thiele *et al.*, 2010) and

change ecosystem processes (McNeish *et al.*, 2012). One of the current explanations for the exceptional success of invasive plants is the ‘novel weapon hypothesis’ (Callaway and Ridenour, 2004). It predicts plant invasions based on the ability to release novel phytochemicals into the invaded ecosystem. These allelopathic compounds have phytotoxic or fitness-reducing effects on the susceptible non-coevolved competitors; here ‘allelopathy’ is used in a broad sense (Inderjit and Weiner, 2001). The novel weapon hypothesis has been introduced to understand the invasion success of *Centaurea diffusa* (Callaway and Aschehoug, 2000; but see Blair *et al.*, 2006), *Alliaria petiolata* (Prati and Bossdorf, 2004) and *Solidago canadensis* (Abhilasha *et al.*, 2008). More recently, Yan *et al.* (2010) showed negative effects of phenolic compounds of the invasive alien *Merremia umbellata* on germination of *Arabidopsis thaliana*.

Thus, the novel weapon hypothesis might also help in understanding the success of the giant hogweed (*Heracleum mantegazzianum*) in Europe. However, despite numerous studies on population dynamics and management of this problematic plant (cf. Pyšek *et al.*, 2007), there are no published data on allelopathy. It is well known that species within the Apiaceae family produce a multitude of secondary metabolites, such as coumarins, essential oils, flavones, terpenes and acetylenic compounds (Bohlmann, 1971), and furanocoumarins are characteristic for the Peucedaneae tribe to which the genus *Heracleum* belongs (Molho *et al.*, 1971). These enzyme-inhibiting substances support plant defence against herbivorous insects and pathogens (Murray *et al.*, 1982), as also described for *H. mantegazzianum* (Hattendorf *et al.*, 2007). Seed germination can be negatively affected by plant leachates (Ruprecht *et al.*, 2008; Hassan *et al.*, 2012), and Baskin *et al.* (1967)

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showed that psoralen and furanocoumarins present in seeds of Apiaceae are responsible for inhibition of a competing species of *Psoralea subacaulis*. Junttila (1976) found inhibitory effects of the furanocoumarins of *Heracleum laciniatum* on the germination of lettuce, as also supported by Reynolds (1989). A recent study on coumarins as allelopathic agents comes from Razavi (2011). However, our study is the first attempt to investigate whether or not the furanocoumarins produced by *H. mantegazzianum* have negative effects on the germination of native species, and thus may act as a novel weapon facilitating invasion. Allelopathy could be due to leaf litter, seeds or root exudates of the species acting directly or mediated through the soil (P. Dostal, pers. comm.).

The focus of this study is on soil and seed effects on germination of co-occurring native herbs. Thus, a series of experiments was performed to investigate whether or not germination of these species is negatively affected by soil or soil extracts from *H. mantegazzianum* stands, or by seeds or seed extracts of the invasive alien species.

Materials and methods

Study species

Heracleum mantegazzianum Sommier and Levier (giant hogweed, Apiaceae) is a monocarpic, perennial, tall forb (Tiley *et al.*, 1996). It is native in the Western Greater Caucasus, where it occurs in tall-herb vegetation, abandoned grasslands, forest clearings and alluvial forests (Otte *et al.*, 2007). *H. mantegazzianum* has invaded most temperate regions of Europe and North America. It often grows along roads, rivers and forest margins, on abandoned grasslands, rubbish dumps and other urban habitats (Pyšek and Pyšek, 1995; Thiele and Otte, 2006).

Like other members of the Apiaceae, *H. mantegazzianum* is an aromatic plant producing essential oils. The fruits ('seeds') of *H. mantegazzianum* are 6–18 mm long and 4–10 mm wide, with four oil ducts on the outer and two on the inner surface. *H. mantegazzianum* is known to contain high concentrations of furanocoumarins in its roots, leaves and seeds (Molho *et al.*, 1971). The following furanocoumarins occur in seeds (Herde, 2005) in descending concentrations: angelicin, imperatorin, bergapten, pimpinellin, unknown hydroxycoumarin, isopimpinellin, unknown furanocoumarin, sphondin, psoralen and xanthotoxol. Glowniak *et al.* (2000) also found limettin and a derivative of anisocoumarin.

To investigate whether or not the invasive plant has allelopathic effects on germination of other plants, we selected 11 native species that co-occur

with *H. mantegazzianum* in the invaded range (NW Europe; Thiele and Otte, 2006). *H. mantegazzianum* seeds were collected in January and October 2008 from 25 plants within large populations in peatland near Hillerød (55.914943N, 12.3058E) and Ballerup, eastern Denmark (55.758017N, 12.282639E); seeds were stratified at 1–6°C until late March. Seeds of the native species were obtained from the Botanical Gardens, University of Copenhagen, except *Calystegia sepium* (L.) R.Br. (Botanical Garden Graz). For logistic reasons not all experiments could be performed with the full species set.

Germination experiments

In Experiment 1 seeds of *H. mantegazzianum*, *Rumex obtusifolius* L. and *Urtica dioica* L. were grown on soil sampled from invaded and un-invaded sites with otherwise similar conditions. In early March 2008 the soil was collected from 19 locations near Copenhagen (Ballerup-Knadrup, Faxe Bay, Hillerød), eastern Denmark. The soil was sieved and placed as a 2-cm layer in transparent plastic boxes with lids (11.5 × 7.7 × 4.5 cm). Within the boxes 40 seeds of one species were exposed on blotting paper (Munktell Filter Paper Grade 3 W) placed on top of c. 200 ml moist soil. The sample size was 111 boxes [(19 invaded soil + 18 un-invaded soil) × 3 species]; one sample of un-invaded soil was lost. The design was completely randomized, and boxes were rearranged at each date of counting. The experiment started in late March 2008 in a climate cabinet set to 10/20°C (12 h light). Germination was recorded over 8 weeks; seeds were considered germinated when the radicle had emerged, and seedlings were removed.

Experiment 2 investigated effects of aqueous extract of soil from *H. mantegazzianum* stands on germination of *Lapsana communis* L. and *R. obtusifolius*. Peat soil was collected at the above location near Hillerød from invaded and un-invaded sites in early March 2007. The soil samples were pooled, sieved, homogenized and stored in the greenhouse. Soil extracts were prepared by adding 5 litres of water to 5 litres of air-dried soil, stirring the mixture and letting it rest for 2 h. The standing water was transferred to other containers; the extract of the invaded soil had a pH 7.3 and a conductivity of 218 µS, compared with pH 6.5 and 174 µS for the un-invaded soil. About 50 ml of extract was poured into the plastic boxes, and seeds of the study species were placed on a plastic bridge covered with blotting paper inside the box. Samples comprised 20 seeds and were repeated eight times per species, on invaded and un-invaded soil, and as a control, the set-up was repeated with de-ionized water. The total number of samples was 48 (3 treatments × 2 species × 8 replications); one sample of *R. obtusifolius*

with invaded soil was excluded. Germination was recorded as above for 5 weeks.

Experiment 3 focused on the allelopathic effects of moist seeds of *H. mantegazzianum* on germination of *Brachypodium sylvaticum* (Huds.) P.B., *Calystegia sepium*, *Euphorbia helioscopia* L., *Festuca gigantea* L., *Mentha arvensis* L., *Poa trivialis* L., *R. obtusifolius* L., *Vicia hirsuta* (L.) Grey and *U. dioica*. The seeds of *C. sepium* and *V. hirsuta* were manually scarified by scratching the seed coat with sandpaper as suggested by Baskin and Baskin (1998). The experiments were conducted in Petri dishes (BD Falcon *Optilux*[™], 10 × 2 cm; Fisher Scientific, Slangerup, Denmark) on blotting paper (9 cm diameter), moistened with de-ionized water. Ten control dishes were prepared for each of the native species by placing 40 seeds per dish in a regular 8 × 8 mm grid pattern. In the mixed treatment 21 seeds of *H. mantegazzianum* were evenly distributed between the seeds of the native species. Sample size was 180 Petri dishes, i.e. 10 replicates per treatment and species. The dishes were cold stratified in a refrigerator set to 4°C for 3 weeks, after which they were transferred to a climate cabinet set to 10/20°C (12 h light). Germination was recorded as above for 18 weeks.

Experiment 4 tested the effects of *H. mantegazzianum* seed extracts on germination of *M. arvensis*, *P. trivialis*, *Sonchus oleraceus* L. and *U. dioica*. Seeds of these native species were exposed in five Petri dishes, respectively, to six treatments. In treatment 1, 40 seeds of each species were placed in a regular 8 × 8 mm grid pattern on blotting paper moistened with de-ionized water. In treatment 2, 21 seeds of *H. mantegazzianum* were added to the native seeds. For treatments 3 and 4, *H. mantegazzianum* seeds were frozen in liquid nitrogen, ground with a pestle and mortar, and two concentrations (0.02 and 0.2%, estimated after Herde, 2005) of aqueous solution of ground seeds were used to moisturize the blotting papers with native seeds. In treatment 5, the blotting paper was moistened with a 0.2% bergapten solution (Sigma-Aldrich, Brøndby, Denmark, 69 664, Fluka, 484-20-8) in 5% dimethyl sulphoxide (DMSO, Sigma-Aldrich, CAS67-68-5), and treatment 6 was a control with aqueous 5% DMSO solution. The furanocoumarin bergapten was chosen because it is common in seeds of the study species and was readily available. All Petri dishes were placed in a climate cabinet at 10/20°C and 12 h light, and seed germination was recorded as above for 14 weeks.

Statistical analyses

We calculated mean proportions of germinated seeds as the sum of all germinated seeds divided by the total number of exposed seeds within each combination of treatment and species. Standard errors (SE)

of the mean proportions were calculated using the equation

$$SE = \sqrt{\frac{p \times (1 - p)}{n}}$$

where p is the proportion of germinated seeds and n is the number of exposed seeds (Crossley, 2008). Effects of treatments were assessed with tests of equal proportions ('prop.test' from the 'binom' package; Dorai-Raj, 2009) conducted on all pairwise comparisons of treatments within species. Statistics were done in R 2.14.1 (R Development Core Team, 2011).

Results

Soil from stands of the invasive alien *H. mantegazzianum* significantly reduced germination in the co-occurring native herb *U. dioica* compared with similar soil from nearby vegetation (Table 1; test of equal proportions, $P < 0.001$). However, in Experiment 1 there was no significant difference in germination of *R. obtusifolius* and *H. mantegazzianum* on invaded and un-invaded soil ($P > 0.05$). Soil extracts from stands of *H. mantegazzianum* had no significant effects on germination of *L. communis* and *R. obtusifolius* (Experiment 2; $P > 0.05$). There was also no significant difference between un-invaded soil extract and de-ionized water as a control ($P > 0.05$). Of the nine native herbaceous species tested in Experiment 3 only *C. sepium* showed reduced germination with seeds of *H. mantegazzianum* present ($P < 0.01$). Hogweed seeds and weak seed extract did not have negative effects on the four species tested in Experiment 4, while strong seed extract negatively affected germination of *P. trivialis* ($P < 0.001$) and *U. dioica* ($P < 0.05$) compared with germination on blotting paper with de-ionized water. Bergapten in DMSO solution affected germination of *S. oleraceus* ($P < 0.01$) and *U. dioica* ($P < 0.05$) more strongly than DMSO solution without bergapten.

Discussion

The germination experiments conducted with soil, soil extracts, seeds or seed extracts of *H. mantegazzianum* showed only limited and partly inconsistent negative effects on 11 native plant species. Germination of *U. dioica* was reduced by 11–33% through strong seed extract, bergapten and soil from invaded stands (increasing order). *P. trivialis* was affected by strong seed extract, but not by bergapten, while *S. oleraceus* showed the opposite pattern (both were not tested in the soil experiment). *C. sepium* was the only species with reduced germination in the presence of *H. mantegazzianum* seeds. Negative effects of root exudates of *H. mantegazzianum* on germination of

Table 1. Germination percentages (means \pm SE) from four experiments on the effects of the invasive alien *H. mantegazzianum* on germination of native herbs in the invaded range. Treatments include soil and soil extracts from invaded sites versus un-invaded sites; mixtures of native seeds with 21 seeds of *H. mantegazzianum* per Petri dish; extracts of ground seeds of *H. mantegazzianum* at two concentrations (weak, strong); bergapten in DMSO solution and DMSO solution without bergapten. In the control treatments, seeds were exposed in Petri dishes with only de-ionized water. Values without common superscript letters are significantly different (test of equal proportions; $P < 0.05$). In rows without letters there were no significant differences

	Germination (%)					
	Invaded soil	Un-invaded soil				
<i>Heracleum mantegazzianum</i>	17.9 \pm 1.4	15.3 \pm 1.3				
<i>Rumex obtusifolius</i>	5.4 \pm 0.8	4.3 \pm 0.8				
<i>Urtica dioica</i>	14.5 \pm 1.3 ^B	21.7 \pm 1.5 ^A				
	Invaded soil	Un-invaded	Control			
	extract	soil extract				
<i>Lapsana communis</i>	18.1 \pm 3.0	21.3 \pm 3.2	13.1 \pm 2.7			
<i>Rumex obtusifolius</i>	77.5 \pm 3.8	79.4 \pm 3.2	76.9 \pm 3.3			
	Hogweed seeds		Control			
<i>Brachypodium sylvaticum</i>	6.3 \pm 1.2		8.5 \pm 1.4			
<i>Calystegia sepium</i>	39.0 \pm 2.4 ^B		48.8 \pm 2.5 ^A			
<i>Euphorbia helioscopia</i>	31.0 \pm 2.3		30.8 \pm 2.3			
<i>Festuca gigantea</i>	95.6 \pm 1.1		95.3 \pm 1.1			
<i>Mentha arvensis</i>	47.0 \pm 2.5		45.0 \pm 2.5			
<i>Poa trivialis</i>	69.8 \pm 2.3		70.8 \pm 2.3			
<i>Rumex obtusifolius</i>	42.5 \pm 2.5		47.0 \pm 2.5			
<i>Urtica dioica</i>	88.8 \pm 1.6		87.8 \pm 1.6			
<i>Vicia hirsuta</i>	63.8 \pm 2.4		66.5 \pm 2.4			
	Hogweed	Weak seed	Strong seed	Bergapten	DMSO	Control
	seeds	extract	extract	(DMSO)		
<i>Mentha arvensis</i>	31.0 \pm 3.3 ^{BC}	28.5 \pm 3.2 ^{BC}	38.0 \pm 3.4 ^{AB}	44.0 \pm 3.5 ^A	27.0 \pm 3.1 ^C	34.0 \pm 3.3 ^{ABC}
<i>Poa trivialis</i>	70.5 \pm 3.2 ^A	64.0 \pm 3.4 ^A	15.5 \pm 2.6 ^C	50.5 \pm 3.5 ^B	21.5 \pm 2.9 ^C	73.0 \pm 3.1 ^A
<i>Sonchus oleraceus</i>	98.0 \pm 1.0 ^A	95.5 \pm 1.5 ^{AB}	91.0 \pm 2.0 ^B	3.0 \pm 1.2 ^D	11.0 \pm 2.2 ^C	92.0 \pm 1.9 ^B
<i>Urtica dioica</i>	81.0 \pm 2.8 ^{AB}	88.5 \pm 2.3 ^A	76.0 \pm 3.0 ^B	24.5 \pm 3.0 ^D	35.5 \pm 3.4 ^C	86.0 \pm 2.5 ^A

Dactylis glomerata and *Plantago lanceolata* were found in a recent experiment conducted by P. Dostal *et al.* (pers. comm.). In their studies, soils from dominant stands of *H. mantegazzianum* showed variable patterns of allelopathic effects depending on target species and presence of soil biota. These findings indicate that allelopathic effects may be species-specific and depend on the source of the allelochemicals used in experiments.

The experiments with soil from *H. mantegazzianum* stands on *U. dioica* indicate that some compounds from this invasive species could have inhibitory effects on native plants from NW Europe. The apparent inconsistency with the results from the seed experiments could be due to indirect effects of these allelochemicals on native plants through changes in the chemical or microbial conditions of the soil (cf. Weir *et al.*, 2004), or due to different concentrations of potential allelochemicals in soil, aqueous solutions and extracts from seeds.

Another possible explanation could be the enrichment and accumulation of such inhibitory compounds in soil over time. Friedman *et al.* (1982) identified the coumarin xanthotoxin from the epicuticular waxes of

the seeds of *Ammi majus* as a major compound in aqueous leachates inhibiting germination. Though Friedman *et al.* (1982) found a slow rate of efflux, with the inhibitory potential of the leachate increasing after 4 d, in many cases the presence of potential allelochemicals in the soil seems to be ephemeral (Weidenhamer and Callaway, 2010). While the identification of potential inhibitory compounds is relatively easy (e.g. Glowniak *et al.*, 2000), it is a much more challenging task to measure the leaching and degradation of these compounds.

The difficulty in using realistic concentrations of potential allelochemicals in germination experiments can be a reason for the incongruent results on *P. trivialis* treated with concentrated aqueous solutions from ground seeds of *H. mantegazzianum* compared with the moist seed mixtures with this species. While solutions of ground seeds may contain concentrations of compounds that are too high, mixtures of seeds often underestimate the microbial degradation of plant material and the chemical reactions with other compounds in soil. The use of Petri dishes distorts further the time that these compounds remain in contact with the seeds, as they cannot leach out from

the dishes, and using distilled water as a medium has limitations for poorly water-soluble compounds. Finding natural or neutral solvents for such compounds is a methodological challenge, as many solvents have additional effects on the tested species. This can be seen in the overlapping results of the germination experiments conducted with bergapten and DMSO.

Furthermore, changes in soil pH or nutrient concentrations in stands invaded by *H. mantegazzianum* could explain differences in germination of other species. Rodgers *et al.* (2008) found that soils in North American temperate deciduous forest invaded by the European forb *Alliaria petiolata* were higher in nutrients and soil pH, in addition to the allelopathic effects observed by Prati and Bossdorf (2004). As seedling growth is often more sensitive to allelochemicals than germination (Araniti *et al.*, 2012), seed extracts of *H. mantegazzianum* could also directly inhibit the growth of native plants (J. Thiele, unpubl. data). Should *H. mantegazzianum* contain compounds that have negative effects on the plant performance of native species in its invasive range, it still remains to be seen if allelopathy facilitates the invasion of this species, acting as a novel weapon, as shown for other species (Ridenour and Callaway, 2001; Inderjit *et al.*, 2006).

We conclude that detection of allelopathic effects of invasive alien plant species depends on the experimental methods used and varies among the native species investigated. Despite high concentrations of potentially allelopathic furanocoumarins in the study species, there is only limited evidence that seeds or soil from *H. mantegazzianum* stands have negative effects on germination of co-occurring native herbs.

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