Allelopathic effects of Ambrosia artemisiifolia L. in the invasive process

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Short title: Allelopathy of *Ambrosia artemisiifolia*

Potential allelopathic effects of Common ragweed (*Ambrosia artemisiifolia* L.)

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Abstract

Ambrosia artemisiifolia (common ragweed), an annual native to North America, is now present in many European countries where it causes summer hayfever and disturbs several important crops. We investigated if common ragweed invasiveness could be explained by its leaf tissue and root exudate alleopathic potential on indicator crops (alfalfa, barley, corn, lettuce, tomato, and wheat), weeds (barnyardgrass, black nightshade, common purslane, large crabgrass), and common ragweed itself. Different residue substrates were prepared for soil incorpration and trials were conducted under both laboratory (1, 2, and 3 g residues /Parker dish) and greenhouse conditions (1.28 g residues / pot). The effect of the preparations on the germination and growth of the indicator crops and weeds were evaluated relative to soil previously used to cultivate common ragweed.

Results showed tomato was the most sensitive indicator crop species as growth was reduced by more than 50% in both laboratory and greenhouse experiments. Lettuce crop root and shoot growth were also inhibited, but only when common ragweed residues, and not root exudates, were added to the substrate. Among the weeds, *E. crus-galli* was not affected by common ragweed while *D. sanguinalis* suffered a large germination reduction (90%) after incorporation of 3 g of residues.

Nomenclature: alfalfa, *Medicago sativa* L.; barley, *Hordeum vulgare* L.; barnyardgrass, *Echinochloa crus-galli* (L.) Beauv. ECHCG; black nightshade, *Solanum nigrum* L. SOLNI; common purslane, *Portulaca oleracea* POROL; corn, *Zea mays* L.; Common ragweed, *Ambrosia artemisiifolia* L.; large crabgrass, *Digitaria sanguinalis* (L.) Scop. DIGSA; lettuce, *Lactuca sativa* L.; pea, *Pisum sativum* L.; redroot pigweed,; tomato, *Lycopersicon esculentum* Mill.; wheat, *Triticum aestivum* L.;

Key words: Phitotoxicity; residue degradation; crop rotation, plant invasion, root exudates.

Introduction

Common ragweed (*Ambrosia artemisiifolia* L.) is a herbaceous, annual plant that is native to North America and a pioneer dominant in abandoned croplands in several areas of the United States. This species is often present as a weed in field crops such as maize, soybean, and wheat (Bassett and Crompton 1979; Fumanal et al. 2008) and may grow exceptionally dense in fields plowed during the spring and subsequently abandoned (Raynal and Bazzaz 1975). It is also a common weed found along roadsides, in urban empty lots, and in other disturbed habitats (Lavoie et al. 2007). First reported in botantical gardens in Europe during the latter half of the 1800s, common ragweed spead to several European countries by the beginning of the 1900s (Chauvel et al. 2006; Vogl et al. 2008).

Many current objections to *A. artemisiifolia* center on its powerful provocation of pollen allergies (Wayne et al. 2002). The plant flowers in the northern hemisphere from mid-August until cooler weather arrives during with each plant can produce a great number of pollen grains (Rogers et al. 2006). The high allergenic potential coupled with its broad spread has caused health organizations to name common ragweed one of the most problematic invasive plants (Wayne et al. 2002).

Even though *Ambrosia artemisiifolia* is non-indigenous to several European plant communities, little is known about the factors that characterize its invasive processes: (Rabitsch and Essl 2006) its abiotic-limiting factors, the potential activity of its competitors, and its natural enemies. One such theory, the “enemy release hypothesis” (Keane and Crawley 2002), postulates that invasiveness can result from a loss of natural enemies during the invasion process while another, known as the “novel weapon allelopathy” theory (Callaway and Ashehoug 2000), suggests that plant community evolution is speeded when subjected to allelo-chemicals produced by species that have not co-evolved (Warwick 1991). Fortunately, the allelopathic potential, defined as the suppressive activity of one plant species on its neighbor plant(s) by toxic compound release, of the Asteraceae family has been widely studied. In particular, the sensitivity of cereals seeded after crop species belonging to this family (common sunflower) has largely been documented (Leather 1983). Agricultural management programs that incorporate allelopathic plant residues through rotational or cover crops is reported to have a positive environmental effect and is often practiced by producers interested in reducing chemical usage (Tesio and Ferrero 2010).

A potential negative consequence of allelopathy is the production of toxic compounds by non-native invasive species that unfavorably affect native communities (Vivanco et al. 2004). Noxious weeds may have an effect on other species through competition or the release of growth inhibitors. In this situation, native plants are unable to tolerate compounds released by a non-native plant that has not co-evolved in the same environment (Hua et al. 2005). This process of environmental modification causes continual change to the relationship and composition among the species in an area until a new equilibrium and a stable community is established.

Common ragweed is present throughout the northern part of Italy, where it is considered an annual summer crop weed after existing for decades in urban or disturbed areas and at field edges (Patracchini et al. 2011). Recently, this species has been reported to occur after winter cereal field harvest, even if common ragweed seedlings have already emerged into the cereal crop. After crop harvest, when light conditions and resource availability are favorable for growth, plants are able to effect large amount of canopy, flower, and produce seeds (Patracchini et al. 2011).

This study was designed to evaluate the potential phytotoxic effects of common ragweed upon succeeding crops which are common in Italian field rotations. Experiments were performed in both laboratory and greenhouse studies conducted in Italy. Using controlled laboratory and greenhouse conditions, we assessed the impact of *A. artemisiifolia* upon the germination and growth behavior of several crop and weed species after incorporating common ragweed dried residues into the soil. We also attempted to simulate common field conditions by performing greenhouse studies in a controlled environment to elucidate the effects of root exudates upon plant growth.

Materials and Methods

Plant material

The study was conducted during 2007 – 2008 in the laboratory and greenhouse of the Dipartimento di Agronomia Selvicoltura e Gestione del Territorio at Grugliasco (Turin, Italy – 45°03’53’’N 7°35’38’’E). *Ambrosia artemisiifolia* shoots and seeds were harvested during 2007 from a field heavily infested by the weed within the experimental site. Aboveground tissues were collected in June 2007 from healthy individuals by cutting plants 10 cm above the soil surface. The leaves were immediately separated from the stalks and dried in open trays in the laboratory oven at 60°C. The resulting dried material was stored in tightly closed plastic bags until needed in the experiment. Seeds were harvested by hand the during the subsequent September and dried in open trays in the laboratory at room temperature (22-25°C). Dried seeds were stored until needed in the refrigerator at +4°C.

The indicator crops included in the experiment were alfalfa (*Medicago sativa* L.), barley (*Ordeum vulgare* L.), lettuce (*Lactuca sativa* L.), maize (*Zea mays* L.), tomato (*Lycopersicon esculentum* Mill.), and winter wheat (*Triticum aestivum* L.). The weeds considered as indicator species in this study were common ragweed (*A. artemisiifolia* L.), large crabgrass (*Digitaria sanguinalis* (L.) Scop.), barnyardgrass (*Echinochloa crus-galli* (L.) Beauv.), common purslane (*Portulaca oleracea* L.) and black nightshade (*Solanum nigrum* L.). With the exception of *A. artemisiifolia*, all weed seeds were purchased from Herbiseed[1] .

Laboratory Experiment

Experiment 1

The potential to inhibit potential of dried common ragweed leaf tissue was studied by assessing its impact on indicator species seed germination and radical and hypocotyl elongation. The experiment was conducted using square plastic “Petri” dishes that contained soil and plant residue mixtures as well as indicator seedlings in a modified Parker bioassay (Weston 2005). Preparation of the experimental sbustrate began with collection of sandy-loam, textured alluvium soil (Typic Udifluvents) from the Tetto Frati research station located in Carmagnola, Italy. Next, the soil was air dried, sifted, and combined with fine silica sand (1:1 v/v) to allow increased water permeability during bioassay preparation. Initially, 100 g of the soil mixture was placed in 100 x 100 x 15 mm Parker dishes. The soil was then topped with varying amounts of chopped common ragweed plant residues (1, 2, or 3 g), after which an additional 50 g of the soil mixture was layered over the residues. Dishes were moistened with 35 ml of deionized water and a square piece of filter paper[3] was placed on the soil surface of each dish. The control treatment consisted of an inert, prewashed paper towel (1.0 g) cut into about 1.5 mm^2 pieces combined to the soil mixture.

Common ragweed, large crabgrass, barnyardgrass, common purslane, and black nightshade were all used as weed indicator species while alfalfa (cv. Prosementi), lettuce (cv. Meraviglia d'inverno), tomato (cv. San marzano) and winter wheat (cv. Isengrain) were used as crop indicator species. All weed and crop species were exposed to all treatments. Ten seeds of each indicator species were placed uniformly in two separate but parallel rows on the filter paper surface. The dishes were taped shut to maintain moisture and encourage seed residue contact and were stacked and stored at an ambient temperature of 26°C for 6 days in a germination box to promote downward root growth.

Total germination was assessed in two ways: a daily count of germinated seeds throughout the experiment and hypocotyl and radical length meaurement after six days. The experiment was arranged as a completely randomized design with four replicates, and the study was replicated twice. While experimental results were analyzed separately for each species, results were combined over runs.

Greenhouse Experiment

Experiment 2

Greenhouse experiments were conducted from June through September 2008 in the department experimental greenhouse at temperatures varying between 15 and 25°C. Pots (8 x 8 cm, 8 cm height) were filled with the same soil used for Experiment 1 that was collected at experimental research station Tetto Frati located at Carmagnola, Italy. To each pot was added 1.28 g (equivalent to 2 t /ha) of powdered common ragweed dried tissue residue and then it was thoroughly mixed. The amount used is similar to that used in other allelopathic speicies experiments reported in the literature for Asteraceae (DongZhi et al. 2004a; DongZhi et al. 2004b; Hong et al. 2004; Khanh et al. 2005; Tesio et al. 2010; Vidotto et al. 2008). The controls were pots filled with soil only.

The impact of common ragweed residues was evaluated based on the germination and growth of several crops: alfalfa, lettuce, tomato, and winter wheat. The seeds were planted in pots devoted to a single indicator species at a rate of 9 seeds for alfalfa and winter wheat and 12 seeds for lettuce and tomato. Immediately after seeding, the pots were watered with a soluble fertilizer (NPK 21-10-20) solution. There after, the pots were watered daily with deionized water to maintain field capacity. The pots were supported by individual flower pot saucers beneath them to prevent contamination from the leaching of other treatments, and arranged on greenhouse benches in a completely randomized design, with four replicates. They were rotated weekly to minimize spatial variation. The experimental unit was the pot, and the experiment was repeated twice. Metal halide lamps supplemented natural light to produce a 14 h day length, which delivered about 55 µmol/s m^2. Germination percentage, seedling height, and shoot dry weight were determined 20 days after seeding.

Experiment 3

In early April 2009, pre-germinated seedlings of *A. artemisiifolia* were transplanted in plastic pots (30 cm height and 27 cm diameter) with a total capacity of about 12 L. Before transplanting, pots were filled with the same soil used in the previous greenhouse experiment. When a 3-leaf stge was reached, the common ragweed pots were thinned to obtain three healthy and uniform plants per pot. Pots were left in an open field in the area of the Dipartimento di Agronomia Selvicoltura e Gestione del Territorio – Grugliasco where they were irrigated twice each week by adding water to the post saucer and weeded weekly by hand. After five months, the common ragweed plants had reached an average fresh weight of 80 g $plant^{-1}$ (aboveground part) and were carefully removed from the pots with close attention paid to maintain intact roots. Pot soil was then mixed and used as substrate for a greenhouse assay, prepared as described below. This experiment was conducted during September 2009 in the experimental glasshouse, under temperatures that varied between 18 and 28°C. Containers (8 x 8 cm, 8 cm height) were filled with soil from Experiment 3 pots used to grow *A. artemisifolia* during the summer. Control pots were filled with soil maintained under identical conditions as those that contained common ragweed, but where no plants were grown.

The potential impact of common ragweed root tissue and exudate was investigated by evaluating the germination and growth of several indicator crop and weed species. The indicator crop species were alfalfa, barley, corn, lettuce, tomato, and winter wheat while the weeds included large crabgrass and barnyardgrass. The number of seeds per pot varied between 4 (maize), 6 (alfalfa, barley, and winter wheat), 9 (barnyardgarss), and 12 (large crabgrass, lettuce, and tomato). Only a single indicator species was seeded per pot. Seeded pots were maintained as indicated in Experiment 2. Pots were arranged on greenhouse benches in a completely randomized design with seven replicates, and rotated weekly to reduce spatial variation. The experimental unit was the pot and the experiment was repeated twice. Germination percentage and shoot dry weight were determined 30 days after seeding.

Statistical Analysis

Both laboratory and greenhouse experiments were analyzed. In the case of the laboratory experiement data, an analysis of variance (ANOVA) was performed separately by species using statistical software SPSS (version 16). In the few cases lacking variance homogenity, a paired samples *t*-test was conducted to detect differences from the control treatment. After an ANOVA analysis, means were separated using the post-hoc Tukey – b test ($p >= 0.05$). In the greenhouse studies (Experiments 2 and 3), differences to the control were identified with the independent sample t-test (SPSS software, version 16).

Results

Laboratory Experiment.

Experiment 1

The effect of common ragweed residues on indicator species seed germination and first seedling growth varied according to indicator species. Results ranged from stimulation to inhibition, especially when the highest rates of dried residue were utilized.

Among the weed species*, D. sanguinalis* seed germination was reduced when common ragweed residues were added at the highest rate (3 g/plate); a 90% reduction in total germination (Table 1) resulted compared to the control. By contrast, the germination percentage of *S. nigrum* was more than 3 times that of the control when high levels (3 g/plate) of residue was used. The root growth of *S. nigrum* germinated seedlings was reduced by 75% with even the lower amount of residues. Residue addition had neither a simulation nor inhibition effect on weed species shoot growth. The root growth of both *A. artemisiifolia* and *P. oleracea* were inhibited about 50% at the highest residue quantities.

Among the crops, tomato behaved similar to *S. nigrum* and showed a germination percentage increase compared to the control (Table 2), even when both shoot and root elongations were depressed by more than 70%. Lettuce suffered growth depression of more than 50% when the highest residue quantities were added to the plate.

Table 1. Effect of different dried leaf tissue concentrations of *A. artemisiifolia* on total germination (GT), shoot and root length of the weeds: *A. artemisiifolia* (AMBAR), *D. sanguinalis* (DIGSA), *E. crus-galli* (ECHCG), *P. oleracea* (POROL) and *S. nigrum* (SOLNI). Mean ± standard error. Values sharing the same letter are not significantly different (Tukey – b test, P<= 0.05).

	Indicator species	**Control**	**Dried leaf tissue amounts** (g Parker dish $^{-1}$)		
			1.0	**2.0**	**3.0**
GT	AMBAR	50.0± 7.07a	40.0± 6.41a	42.5± 6.29a	32.5± 2.50a
(%)	DIGSA	48.8± 0.00a	42.5± 0.15a	30.0± 0.37ab	5.0± 1.34b
	ECHCG	42.5± 0.00a	62.5± 0.13a	45.0± 0.30a	50.0± 0.42a
	POROL	55.0± 0.00a	60.0± 0.13a	77.5± 0.23a	60.0± 0.39a
	SOLNI	12.5± 0.00a	10.0± 0.32a	30.0± 0.37b	45.0± 0.45b
Shoot	AMBAR	17.7± 0.26a	16.9± 0.67a	17.9± 1.19a	12.5± 1.04a
(mm)	DIGSA	16.8± 0.42a	15.8± 0.75a	17.1± 0.35a	19.5± 0.02a
	ECHCG	26.5± 1.14a	16.7± 0.59a	27.2± 1.13a	19.9± 0.54a
	POROL	6.7± 0.47a	9.9± 0.25a	8.45± 0.39a	6.8± 0.26a
	SOLNI	10.0± 0.83a	6.5± 1.99a	5.9± 0.53a	10.8± 0.63a
Root	AMBAR	40.3± 1.10a	37.6± 2.77a	32.6± 5.02ab	21.9± 3.67b
(mm)	DIGSA	16.4± 1.73a	17.2± 2.97a	16.3± 1.44a	20.5± 0.02a
	ECHCG	21.3± 5.85a	13.7± 2.43a	21.1± 5.88a	13.8± 2.39a
	POROL	9.2± 1.23a	8.1± 0.78ab	7.3± 1.14ab	4.34± 0.68b
	SOLNI	35.4± 2.62a	8.2± 5.08b	5.5± 1.29b	13.0± 2.08b

Table 2. Effect of different dried leaf tissue concentrations of *A. artemisifolia* on total germination (GT), shoot and root length of the crops: *T. estivum* (WHEAT), *L. sativa* (LETTUCE), *M. sativa* (ALFALFA), *L. esculentum* (TOMATO). Mean ± standard error. Values sharing the same letter are not significantly different (Tukey – b test, P<= 0.05). Values marked with * or **are statistically different from the control with p<=0.05 or 0.01.

	Indicator species	**Control**	**Dried leaf tissues amount** (g Parker dish $^{-1}$)		
			1.0	**2.0**	**3.0**
GT	WHEAT	87.5± 0.00a	97.5± 0.10a	87.5± 0.21a	95.0± 0.00a
(%)	LETTUCE	97.5± 0.00a	93.7± 0.10a	90.0± 0.21a	85.0± 0.33a
	ALFALFA	84.4± 0.00a	92.5± 0.10a	92.5± 0.21a	87.5± 0.32a
	TOMATO	93.7± 0.00	97.5± 0.10	100.0± 0.20*	85.0± 0.33
Shoot	WHEAT	41.6± 0.33a	35.2± 0.55a	34.7± 0.23a	35.2± 0.55a
(mm)	LETTUCE	24.5± 1.12	10.0± 0.30**	12.0± 0.25*	10.2± 0.35**
	ALFALFA	20.2± 0.73a	20.4± 0.51a	17.5± 0.44a	20.2± 0.36a
	TOMATO	22.4± 1.90	15.9± 1.60	13.9± 1.59	6.2± 0.51*
Root	WHEAT	48.1± 2.12a	38.2± 3.28a	40.4± 1.37a	38.2± 3.27a
(mm)	LETTUCE	26.2± 5.55	13.5± 0.95	12.4± 0.87*	9.8± 1.12*
	ALFALFA	28.6± 3.29a	27.1± 2.31a	23.9± 1.82a	24.6± 1.61a
	TOMATO	29.6± 9.00	26.4± 6.40	24.2± 5.92	8.06± 1.27*

Greenhouse Experiment.

Experiment 2

Across the seeded crops, total germination (GT) differences relative to the control were observed only for winter wheat (Figure 1), with a germination inhibition of about 30%. The presence of common ragweed residues did not, however, result in a winter wheat plant height reduction (Figure 2) as was true for alfalfa, tomato, and lettuce which showed height reductions of 43%, 41%, and 26%, respectively. All other species showed sensitivity as well. Among the three factors evaluated, total germination, plant height, and plant weight, plant weight displayed the least effect from incorporating *A. artemisiifolia* residues into the substrate (Figure 3). In fact, all crops showed plant weight values of roughly half compared to the control treatment. As in Experiment 1, tomato was reduced the most (58%).

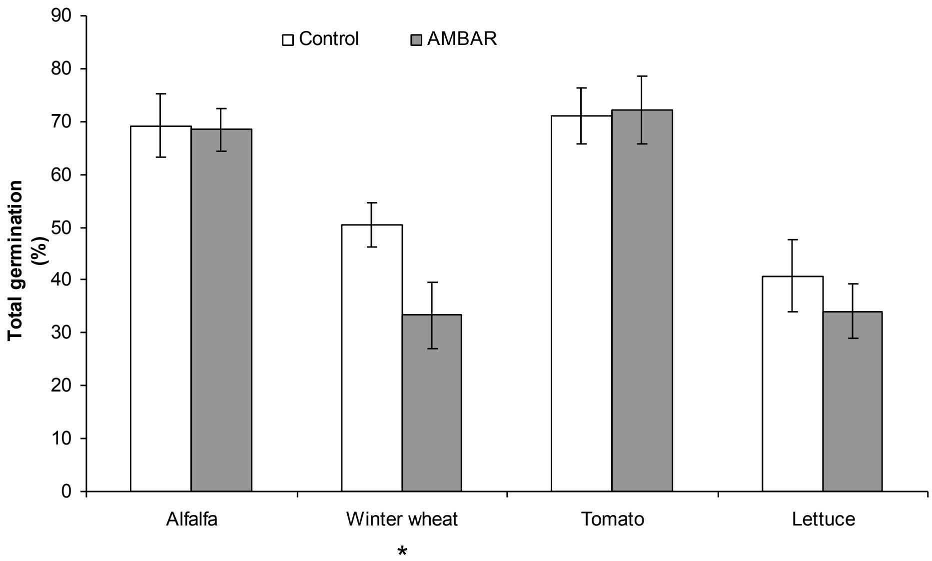

Figure 1. Greenhouse experiment: germination response of crop species to the presence of 2 t/ha of common ragweed (AMBAR) dried residues. Bars indicate standard error. * refers to significant differences from the control with p <= 0.05.

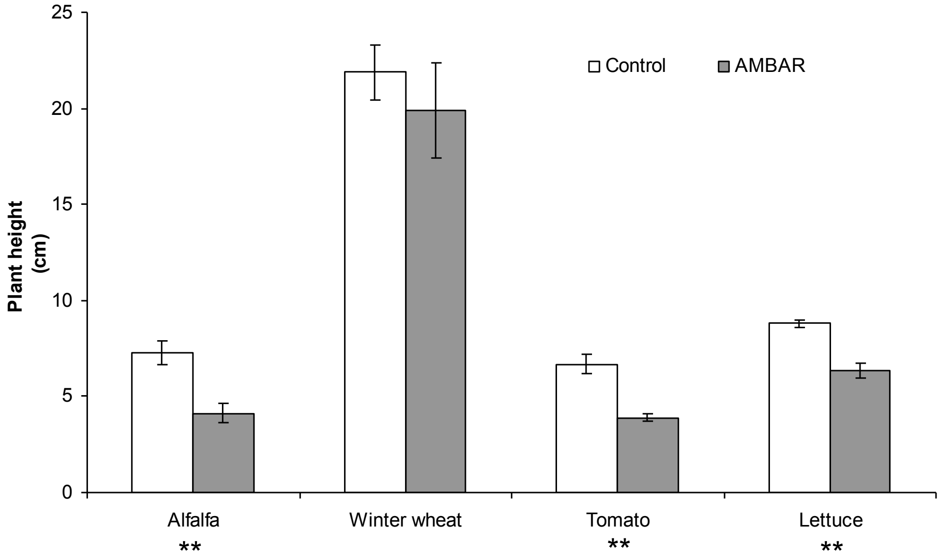

Figure 2. Greenhouse experiment: plant height response of crop species to the presence of 2 t/ha of common ragweed (AMBAR) dried residues. Bars indicate standard error. * refers to significant differences from the control with p <= 0.05 or ** with p <= 0.01.

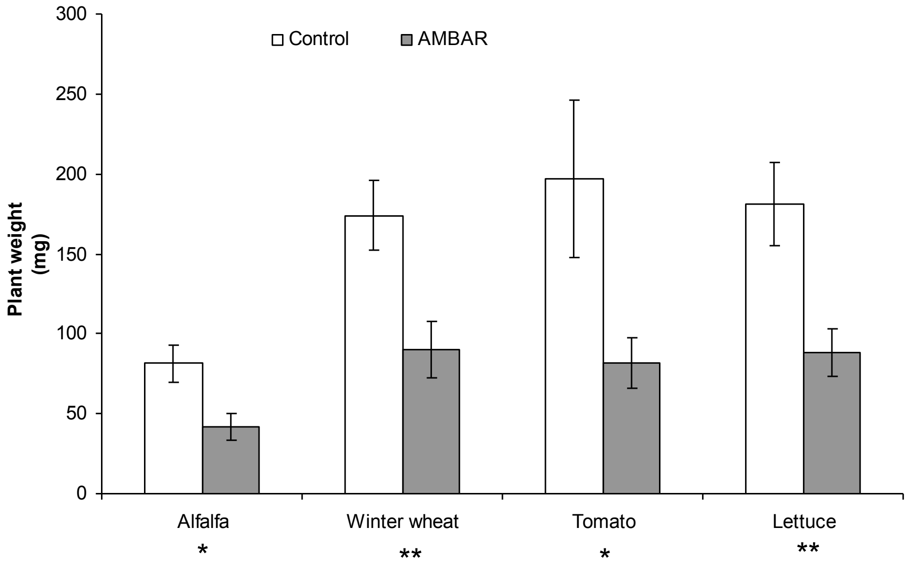

Figure 3. Greenhouse experiment: plant weight response of crop species to the presence of 2 t/ha of common ragweed (AMBAR) dried residues. Bars indicate standard error.
* refers to significant differences from the control with p <= 0.05 or ** with p <= 0.01.

Experiment 3

Germination was not significantly affected if seeds were placed in pots in which *A. artemisiifolia* was grown (Figure 4). No weed species plant weight was depressed compared to the control treatment, nor were crops lettuce and alfalfa (Figure 5). Conversely, the growth of winter wheat and barley was inhibited by about 60% and 45%, respectively. The high sensitivity of tomato to the allelopathic potential of common ragweed was also confirmed in this experiment; a growth reduction of about 50% was assessed on tomato seedling weight *versus* the control.

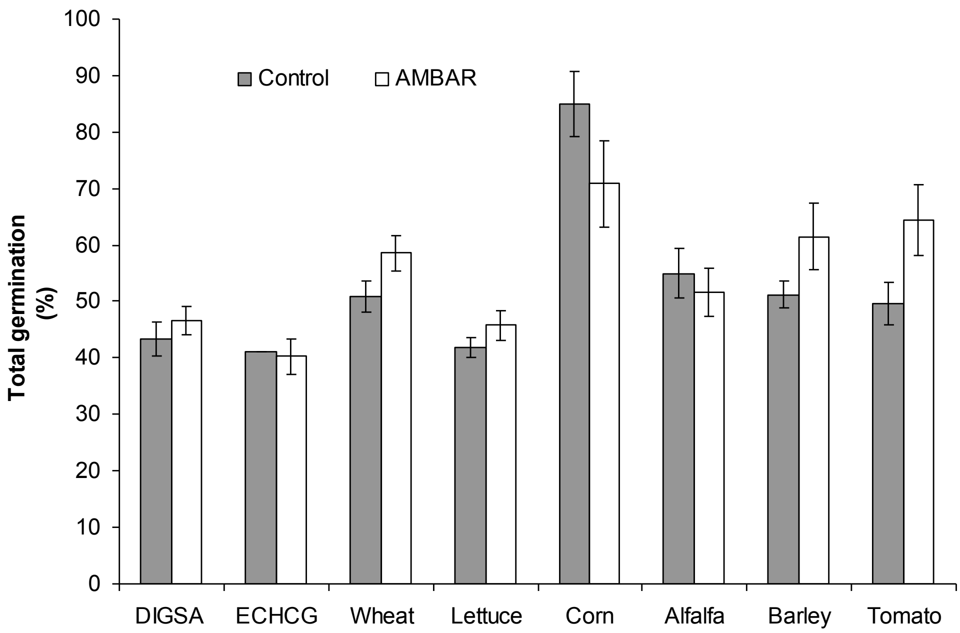

Figure 4. Greenhouse experiment: germination response to root exudates of common ragweed (AMBAR). Bars indicate standard error.

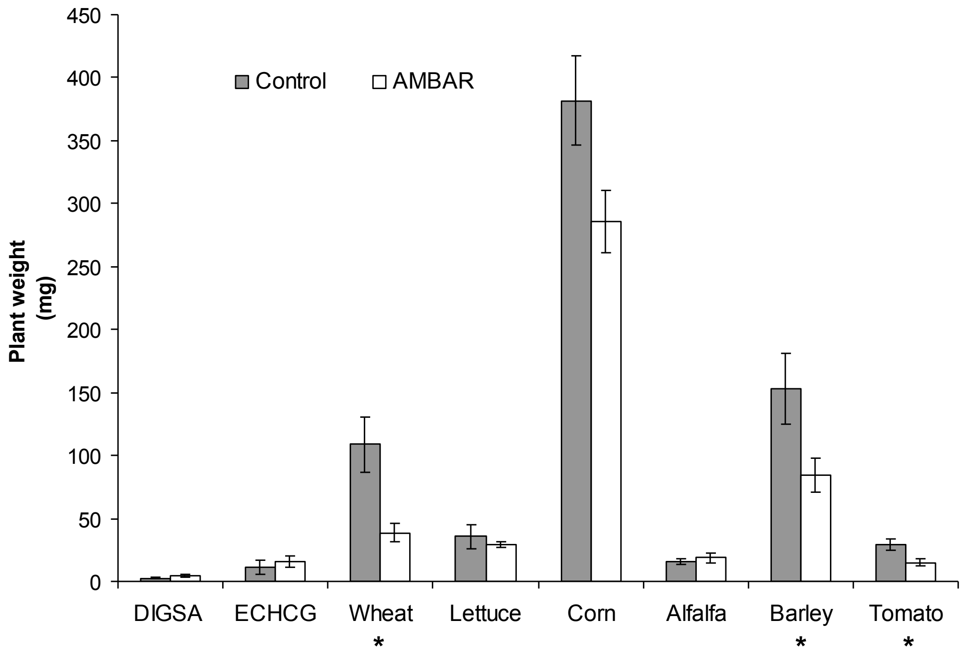

Figure 5. Greenhouse experiment: plant weight response to root exudates of common ragweed (AMBAR). Bars indicate standard error. * refers to significant differences from the control with p <= 0.05.

Discussion and conclusion

Our findings showed that varying the amount of *A. artemisiifolia* dried residue in soil affected the seed germination and seedling growth variation of differing indicator crop and weed species. Even though some stimulation effects were observed on germination, growth inhibition was observed more frequently, especially in root growth.

In allelopathic experiments, many factors play a role in the bioavailability of the toxic compounds in the rhizosphere, including organic matter adsorption, chemical inactivation and microbial degradation. The Parker dish bioassay used in the laboratory experiment was designed to simulate the allelochemical release into soil by tissue degradation over time after incorporation. This experiment allowed simulation of more realistic conditions than in the natural environment because toxic compound release occured gradually. Our experimental results can, therefore, be compared to those obtained in the greenhouse.

On average, among the crops, tomato was the most sensitive indicator species to common ragweed allelopathic residues; both in the laboratory and greenhouse experiments, more than 50% growth reduction occurred. The other crops tested showed a different sensitivity to common ragweed. Root exudates showed an inhibitory effect on winter wheat growth that was not observed in the residue degradation experiments. This species showed sensitivity only in the greenhouse experiment. Lettuce dispayed root and shoot growth inhibitory effects only if common ragweed residues were added to the substrate; there were no depressive effects associated with root exudates.

Weed species *E. crus-galli* was never affected by common ragweed, neither in terms of germination nor first seedling growth. Conversely, *D. sanguinalis* suffered an important germination reduction. From an overall review of the weed species, *P. oleracea* and *S. nigrum* showed themselves to be the most sensitive species, with more than a 50% root growth reduction. One explanation of sensitivity to common ragweed of the tested weed species might be related to water imbibition. Indeed, several studies have pointed out that the allelopathic activity of plant residue degradation upon a species that follows is strongly related to seed dimension of the crop (Tesio et al. 2011). The insensitivity observed by *E. crus-galli* might be explained by its very hard seed coat and associated reduced permeability (Tesio et al. 2008). Even in the case of crops, a similar seed dimension effect could be ascribed as the inhibition effect roughly followed the same rank order as that of seed dimension (tomato > lettuce > winter wheat).

No important autotoxic effects were observed as only the root growth of *A. artemisiifolia* was depressed by residue degradation.

The costs to limit the rapid expansion of *A. artemisiifolia* to Europe's crops and urban landscape, combined with the economics of pollinosis relief, demand a management response. Presently, eradication is impractical as whether in natural or disturbed settings, common ragweed has made clear that it is a widespread and noxious weed of several crops. It has also made evident, in some cases, its ability to colonize the soil rapidly after crop harvest (DiTommaso 2004) Several reports have related the consequence of its presence in the summer after winter wheat or barley cultivations when biomass and root exudates accumulate in the soil and potentially inhibit growth of the succeeding crop (DiTommaso 2004). Awareness of the relationships between this species and other crops and weeds, and knowing that rapid diffusion and expanded presence of the species across southern Europe might be linked to its allelopathic potential, its rapid growth rate, and its remarkable ability to recover from mulching interventions to produce, even after cutting, large amounts of seeds (Patracchini et al. 2011) is useful knowledge for both farmers and the scientific community.

Given the potential of common ragweed to reduce crop growth and yields, as well as its costly impact on human health, made a strong case for investigatting the role allelopathy might play in the invasive process. In our studies, germination and initial growth of lettuce and alfalfa were not affected, but winter wheat and tomato were quite sensitive to residue presence. Furthermore, our studies highlighted the cricial concern associated with the sensitivity of the succeeding crop, especially when establishment of a less competitive crop such as tomato is involved. Given these considerations, this work suggests that the management of common ragweed infestation, especially its impact on rotational crops, requires particular attention. In the greenhouse and laboratory experiments we attempted to recreate a possible field situation in which weed biomass is incorporated into the soil and a successive crop is planted.

Finally, it should be noted that the greenhouse and laboratory studies conducted here, the effects of residue incorporation and root exudates were evaluated separately. Further studies to consider the synergistic effects of residues and root exudates in greenhouse and field settings are necessary to fully determine the impact of this invasive species upon weed and crop establishment in successive cropping systems, as well as the invasion process in natural plant communities.

Source of material:

[1] Herbiseed, Twyford, UK.

[3] Whatman No. 1, Wathman International Ltd., Maidstone, UK.

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