

Allelopathic effects of *Ambrosia artemisiifolia* L. in the invasive process



Francesco Vidotto^a, Franco Tesio^{b,*}, Aldo Ferrero^a

^a Department of Agricultural, Forestry, and Food Sciences, Università degli Studi di Torino, Via L. da Vinci, 44, 10095 Grugliasco, Italy

^b ValOryza, Corso Gastaldi, 55, 13100 Vercelli, Italy

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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 hay fever and interferes with several important crops. We investigated if common ragweed invasiveness could be explained by its leaf tissue and root exudate allelopathic potential on indicator crops (alfalfa, barley, maize, lettuce, tomato, and wheat), weeds (*Echinochloa crus-galli*, *Solanum nigrum*, *Portulaca oleracea*, and *Digitaria sanguinalis*), and common ragweed itself in laboratory and greenhouse conditions. Different residue substrates were prepared for soil incorporation 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 grow *A. artemisiifolia*. 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 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. If common ragweed occurred as weed in a field, the cultivation of a less sensitive crop such as winter wheat should be considered before the cultivation of a more susceptible crop.

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1. 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 and Canada. 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), as well as in horticultural crops 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 botanical gardens in Europe during the latter half of the 1800s, common ragweed spread 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 highly allergenic pollen (Wayne et al., 2002). The plant main flowering time is in the northern hemisphere from mid-August until mid-September and each plant can produce large quantities of pollen

grains (Rogers et al., 2006). The high allergenic potential coupled with its broad distribution has caused health organizations to list common ragweed one of the most problematic invasive plants in Europe (Wayne et al., 2002).

Studies have been carried out on *A. artemisiifolia* as non-indigenous to several European plant communities such as its abiotic-limiting factors, the potential activity of its competitors, and its natural enemies (Rabitsch and Essl, 2006). The theory “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 Ridenour, 2004), suggests that plant community evolution is accelerated when subjected to allelochemicals 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 (Beres et al., 2002). In particular, the sensitivity of cereals seeded after crop species belonging to this family (*Helianthus annuus* L., common sunflower and *Helianthus tuberosus* L., Jerusalem artichoke) 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

* Corresponding author.

E-mail address: franco.tesio@valoryza.it (F. Tesio).

environmental effect and is often practiced by producers interested in reducing chemical inputs (Tesio et al., 2012).

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 (Baležentienė, 2012). In this latter case, native plants may be 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 (Patraccchini et al., 2011). Recently, this species has been reported to occur after winter cereal field harvest, even if common ragweed seedlings have already emerged in the cereal crop. After crop harvest, when light conditions and resource availability are favorable for growth, plants are able to grow rapidly, flower, and produce seeds (Patraccchini et al., 2011).

This study evaluated the potential phytotoxic effects of common ragweed upon succeeding crops which are common in Italian field rotations. Experiments were performed under both laboratory and greenhouse studies conducted in Italy. Using controlled laboratory and greenhouse conditions. We assessed the impact of *A. artemisiifolia* on the germination and growth 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 to elucidate the effects of root exudates upon plant growth.

2. Materials and methods

2.1. Plant material

The study was conducted during 2007–2008 in the laboratory and greenhouse of the Department of Agricultural, Forestry, and Food Sciences at Grugliasco (Turin, Italy – 45°03'53"N 7°35'38"E). *A. artemisiifolia* shoots and seeds were harvested during 2007 from a heavily infested field in the experimental site of the university campus at Grugliasco. 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 in September and dried in open trays in the laboratory at room temperature (22–25 °C) for two weeks. Dried seeds were stored until needed in a refrigerator at 4 °C.

Indicator crops included in the experiment were alfalfa (*Medicago sativa* L.), barley (*Hordeum 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 *A. artemisiifolia*, *Digitaria sanguinalis*, *Echinochloa crus-galli* (L.) Beauv., *Portulaca oleracea* L. and *Solanum nigrum* L., that commonly infest both horticultural and cereal crops in the experimental area. With the exception of *A. artemisiifolia*, all weed seeds were purchased from the Herbiseed Company (Twyford, UK).

2.2. Laboratory – experiment 1

The potential inhibition of dried *A. artemisiifolia* leaf tissue was studied by assessing its impact on indicator species seed

germination and radicle 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 (Tesio et al., 2010). Preparation of the experimental substrate 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 × 100 × 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 (Whatman No. 1, Whatman International Ltd., Maidstone, UK) 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 mm² pieces combined to the soil mixture.

A. artemisiifolia, *D. sanguinalis*, *E. crus-galli*, *P. oleracea*, and *S. nigrum* 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 subjected 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 measurement after six days. The experiment was arranged as a completely randomized design with four replicates, and the study was replicated twice.

2.3. Greenhouse – experiment 2

Greenhouse experiments were conducted from June through September 2008 at temperatures varying between 15 and 25 °C. Pots (8 × 8 cm, 8 cm height) were filled with 600 g of the same soil used for Experiment 1. To each pot was added 1.28 g (equivalent to 2 t/ha) of powdered common ragweed dried tissue residue and then thoroughly mixed. The amount used is similar to that used in other allelopathy experiments reported in the literature for the Asteraceae (Dongzhi et al., 2004; Hong et al., 2004; Khanh et al., 2005). 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 at 0.5 cm 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 had saucers to prevent contamination of leachates from other treatments. Pots were arranged in a completely randomized design, with four replicates and 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 m². Emergence percentage, seedling height, and shoot dry weight were determined 20 days after seeding.

2.4. Greenhouse – 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 plants reached the 3-leaf stage pots were thinned to three similar sized plants per pot. Pots were left in an open field on the campus of the University of Torino – Grugliasco, watered as needed in post saucer and weeded weekly by hand. After five months, the *A. artemisiifolia* 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 maintaining 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 a greenhouse at temperatures that varied between 18 and 28 °C. Containers (8 × 8 cm, 8 cm height) were filled with soil from Experiment 3 pots used to grow *A. artemisiifolia* 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 *A. artemisiifolia* 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 *D. sanguinalis* and *E. crus-galli*. Weed species were chosen because reported as the most and the least sensitive to allelochemicals in studies evaluating the inhibitory effects of other Asteraceae species (Tesio et al., 2010). The number of seeds per pot varied between 4 (maize), 6 (alfalfa, barley, and winter wheat), 9 (*E. crus-galli*), and 12 (*D. sanguinalis*, lettuce, and tomato). Only a single indicator species was seeded per pot. Seeded pots were maintained as indicated in Experiment 2. Pots were arranged 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. Emergence percentage and shoot dry weight were determined 30 days after seeding.

2.5. Statistical analysis

For each experiment (1, 2, and 3), the mixed model available in the package lme4 of the R software was used separately to test the effect of the two sets of replicates, considering them as a random effect. Then, for the laboratory experiment data, an analysis of variance (ANOVA) was performed separately by species using statistical software SPSS (version 16), pooling together the two sets of replicates. In the few cases lacking variance homogeneity, a *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).

3. Results

3.1. Laboratory – experiment 1

The effect of *A. artemisiifolia* residues on indicator species seed germination and early seedling growth varied according to indicator species. Results ranged from stimulation to inhibition, especially when the highest rates of dried residue were used.

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

Effect of different dried leaf tissue concentrations of *A. artemisiifolia* on total emergence (TE), shoot and root length of the weeds: *A. artemisiifolia*, *D. sanguinalis*, *E. crus-galli*, *P. oleracea*, and *S. nigrum*.

	Indicator species	Control ^a	Dried leaf tissue amounts (g Parker dish ⁻¹) ^a		
			1.0	2.0	3.0
TE (%)	<i>A. artemisiifolia</i>	50.0 a	40.0 a	42.5 a	32.5 a
	<i>D. sanguinalis</i>	48.8 a	42.5 a	30.0 ab	5.0 b
	<i>E. crus-galli</i>	42.5 a	62.5 a	45.0 a	50.0 a
	<i>P. oleracea</i>	55.0 a	60.0 a	77.5 a	60.0 a
	<i>S. nigrum</i>	12.5 a	10.0 a	30.0 b	45.0 b
Shoot (mm)	<i>A. artemisiifolia</i>	17.7 a	16.9 a	17.9 a	12.5 a
	<i>D. sanguinalis</i>	16.8 a	15.8 a	17.1 a	19.5 a
	<i>E. crus-galli</i>	26.5 a	16.7 a	27.2 a	19.9 a
	<i>P. oleracea</i>	6.7 a	9.9 a	8.45 a	6.8 a
	<i>S. nigrum</i>	10.0 a	6.5 a	5.9 a	10.8 a
Root (mm)	<i>A. artemisiifolia</i>	40.3 a	37.6 a	32.6 ab	21.9 b
	<i>D. sanguinalis</i>	16.4 a	17.2 a	16.3 a	20.5 a
	<i>E. crus-galli</i>	21.3 a	13.7 a	21.1 a	13.8 a
	<i>P. oleracea</i>	9.2 a	8.1 ab	7.3 ab	4.34 b
	<i>S. nigrum</i>	35.4 a	8.2 b	5.5 b	13.0 b

^a Mean values sharing the same letter are not significantly different (Tukey – b test, *p* <= 0.05).

(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 stimulation 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.

3.2. Greenhouse – experiment 2

Across the seeded crops, total emergence (TE) differences relative to the control were observed only for winter wheat (Fig. 1), with an emergence inhibition of about 30%. The presence of common ragweed residues did not, however, result in a winter wheat

Table 2

Effect of different dried leaf tissue concentrations of *A. artemisiifolia* on total emergence (TE), shoot and root length of the crops: winter wheat (*T. estivum*), lettuce (*L. sativa*), alfalfa (*M. sativa*), tomato (*L. esculentum*).

	Indicator species	Control ^a	Dried leaf tissues amount (g Parker dish ⁻¹) ^a		
			1.0	2.0	3.0
TE (%)	Winter wheat	87.5 a	97.5 a	87.5 a	95.0 a
	Lettuce	97.5 a	93.7 a	90.0 a	85.0 a
	Alfalfa	84.4 a	92.5 a	92.5	87.5 a
	Tomato	93.7	97.5	100.0*	85.0
Shoot (mm)	Winter wheat	41.6 a	35.2 a	34.7a	35.2 a
	Lettuce	24.5 a	10.0 b	12.0 b	10.2 b
	Alfalfa	20.2 a	20.4 a	17.5 a	20.2 a
	Tomato	22.4 a	15.9 a	13.9 a	6.2 b
Root (mm)	Winter wheat	48.1 a	38.2 a	40.4a	38.2 a
	Lettuce	26.2 a	13.5 a	12.4 b	9.8 b
	Alfalfa	28.6 a	27.1 a	23.9 a	24.6 a
	Tomato	29.6 a	26.4 a	24.2 a	8.06 b

^a Mean values sharing the same letter are not significantly different (Tukey – b test, *p* <= 0.05).

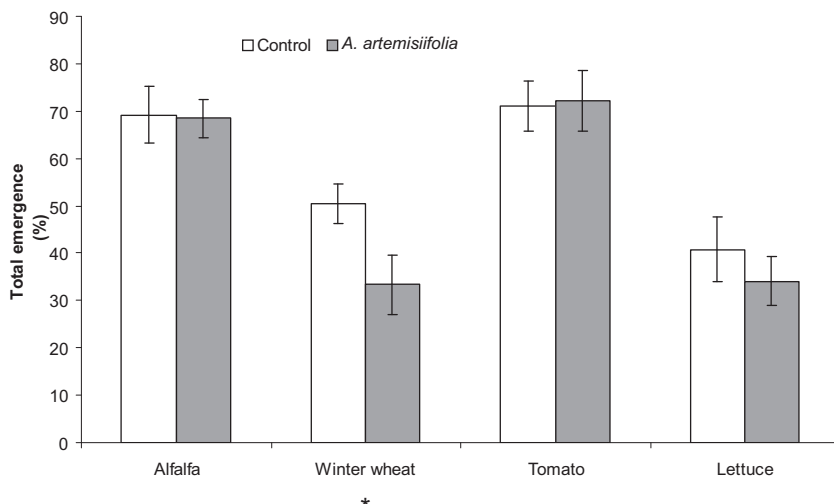


Fig. 1. Greenhouse experiment: emergence response of crop species to the presence of 2 t/ha of *A. artemisiifolia* dried residues. Bars indicate standard error. *Refers to significant differences from the control with $p \leq 0.05$.

plant height reduction (Fig. 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 emergence, plant height, and plant weight, plant weight displayed the least effect from incorporating *A. artemisiifolia* residues into the substrate (Fig. 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%).

3.3. Greenhouse – experiment 3

Emergence was not significantly affected if seeds were placed in pots in which *A. artemisiifolia* was grown (Fig. 4). No weed species plant weight was depressed compared to the control treatment, nor were crops lettuce and alfalfa (Fig. 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.

4. Discussion and conclusions

Our findings showed that varying the amount of *A. artemisiifolia* dried residue in soil affected the seed emergence and seedling growth variation of differing indicator crop and weed species. Even though some stimulation effects were observed on emergence, 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 (Tesio et al., 2008; Tesio and Ferrero, 2010). 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

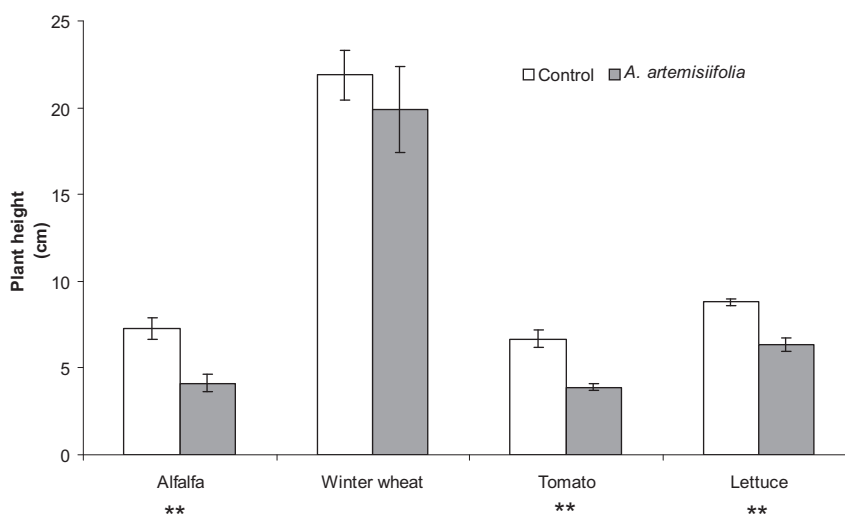


Fig. 2. Greenhouse experiment: plant height response of crop species to the presence of 2 t/ha of *A. artemisiifolia* dried residues. Bars indicate standard error. *Refers to significant differences from the control with $p \leq 0.05$ or ** with $p \leq 0.01$.

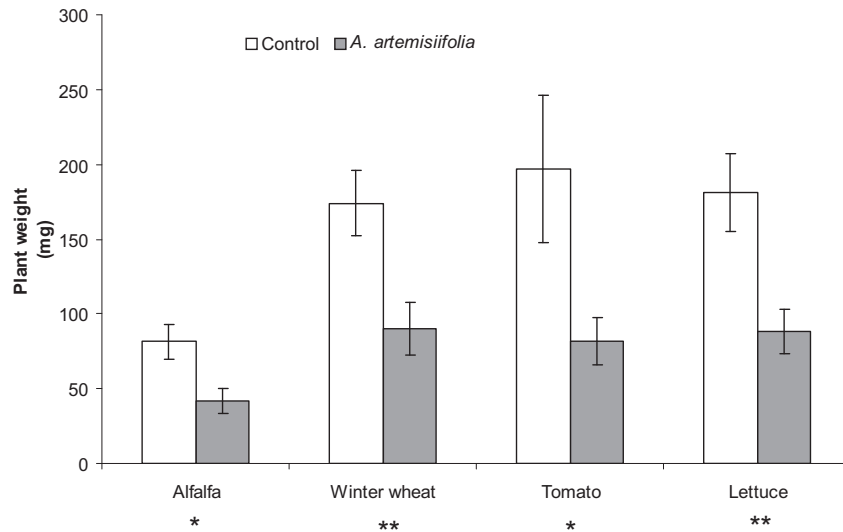


Fig. 3. Greenhouse experiment: plant weight response of crop species to the presence of 2 t/ha of *A. artemisiifolia* dried residues. Bars indicate standard error. *Refers to significant differences from the control with $p \leq 0.05$ or ** with $p \leq 0.01$.

of more realistic conditions, similar to the natural environment because toxic compound release occurred 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. These findings may be helpful to discourage tomato cultivation if heavy *A. artemisiifolia* infestations occur in the previous year. 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 displayed 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. Further studies are therefore needed to clarify the diverse sensitivity to the allelopathic activity caused by different plant parts on the same indicator species.

E. crus-galli was not affected by common ragweed, neither in terms of emergence nor early seedling growth. Conversely, *D. sanguinalis* suffered an important germination reduction. From an overall review of the weed species, *P. oleracea* and *S. nigrum* were 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 is strongly related to seed size of the crop (Belz et al., 2005; Tesio et al., 2011). Even in the case of crops, a similar seed size effect could be ascribed as the inhibition effect roughly followed the same rank order as that of seed (tomato > lettuce > winter wheat). In practice, if common

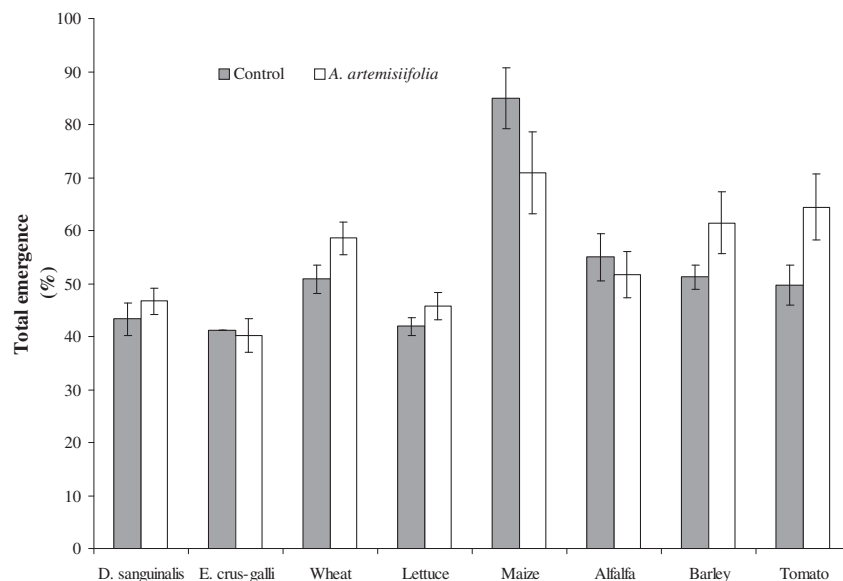


Fig. 4. Greenhouse experiment: emergence response to root exudates of *A. artemisiifolia*. Bars indicate standard error.

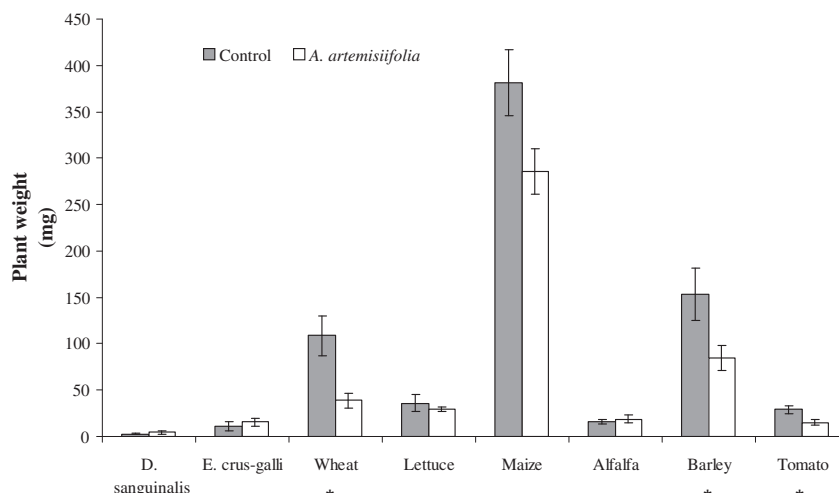


Fig. 5. Greenhouse experiment: plant weight response to root exudates of *A. artemisiifolia*. Bars indicate standard error. *Refers to significant differences from the control with $p \leq 0.05$.

ragweed occurred as weed, the growth of a less sensitive crop such as maize may be planned before the growing of a more susceptible horticultural species.

Less 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 in natural or disturbed settings, common ragweed is a widespread and noxious weed of several crops. It has also 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 (Mutch et al., 2003). 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 investigating the role allelopathy might play in the invasive process. Our studies highlighted the crucial 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 and the chemicals responsible of this phenomenon.

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