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Does allelopathy increase the invasion of *Diplotaxis erucoides* in disturbed arid land?

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ABSTRACT

Diplotaxis erucoides has invaded the arid land in Zarqa, Jordan. A field study indicated a gradual and significant increase in *D. erucoides* accompanied with significant decrease in *E. sativa* and other weed species. Aqueous and ethanolic extracts of *D. erucoides* caused significant decrease in seed germination of *E. sativa*, *Sonchus oleraceus*, *Tragopogon coelesyriacus*, *Launea nudicaulis*, *Salsola baryosma* and *Taraxacum officinale*. Laboratory experiments showed that foliage and root aqueous extracts of *D. erucoides* at 6 mg ml^{-1} and 5 mg ml^{-1} concentrations respectively decreased the seed germination of *E. sativa*. Similarly ethanolic extracts of *D. erucoides* reduced the germination of *E. sativa* seeds at lower concentrations of 3 mg ml^{-1} and 2 mg $ml^{-1}$of foliage and roots, respectively. Reciprocal allelopathic effects of aqueous extracts of *D. erucoides* and *E. sativa* were significant. Autotoxicity of foliage aqueous extract was also significant on the germination of *D. erucoides* seeds. Soil amended with full strength or 1:1 diluted solutions of leaf leachates of *D. erucoides* decresed the shoot growth of *E. sativa* seedlings. The inhibitory effects were similar in autoclaved or not autoclaved soils. These field and laboratory results indicated that *D. erucoides* use its allelopathic activity to shift the balance of competition in its favour and consequently it dominated the dry land habitat.

Keywords: Allelopathy, arid land, *Diplotaxis erucoides*, *Eruca sativa*, extract, germination, leachate, plant interactions, seedling growth, weeds invasion

INTRODUCTION

Weeds are the main constraints to plant production and biodiversity in all agro-ecosystems worldwide. The extent of negative effects of weeds on crops is known, but those of environmental weeds in natural ecosystems are rarely studied (50). Invasive plant species threaten the integrity of natural systems by establishing monocultures in new habitats and displacing native plant communities. Disturbance is precursor to invasions as it provides an opportunity for weeds invasion (11,22,23). Disturbances due to human activities can change or remove the filters acting on a plant community and consequently alter habitat characteristics that favour the proliferation of weeds (15). The type, frequency and extent of disturbance will create different invasion opportunities for weedy species (12,30,35,40). Some species are more invasive than others (6). A leading theory for the

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success of invasive species is their escape from their natural enemies that hold them in check, freeing them to utilize their full potential for resource competition (29). The negative interactions of allelopathy, due to the release of phytotoxins by plants, have been proposed as an alternative theory for the success of some invasive plants (7,21). The production of secondary metabolites by the invasive species induces important effects on other organisms and key processes, which help determine how the ecosystem functions and ultimately the structure of plant community (50).

Diplotaxis erucoides (white rocket) is native annual plant in Mediterranean zone of Jordan and is spreading as weed in semi-desert and desert areas. The transfer of fertile red top soil to areas with poor soil, to establish agricultural plots in the Hashemite University Campus (Zarqa), has aided in the spread of *D. erucoides*. This disturbance of natural semi-desert ecosystem provided opportunities for not only native but also non-native weeds to flourish and becoming naturalized (19). Thus, *D. erucoides* became a naturalized species in Zarqa area and flourishes in spring (February-April). Aided by periodic irrigation, it has become invasive and dominates our campus agro-ecosystems. *Diplotaxis erucoides* has spread as weed in many field crops, fruit orchards and in rangelands in Jordan. It has spread progressively showing strong competitiveness over other common weeds like *Eruca sativa* (sub-dominant herbaceous weed). *D. erucoides* exerts allelopathic effects on certain vegetable crops (38). It is hypothesized that allelopathic interactions favour the abundance of *D. erucoides* and enhance its invasiveness in disturbed environment. In this study, we investigated the allelopathic plant-plant interactions between *D. erucoides* and co-existing weed species in field surveys and in *in- vitro* studies. This study aimed to answer the following questions: (i). Does *D. erucoides* have allelopathic effects on seed germination of *Eruca sativa* and other weed species at study site? (ii). Is there a reciprocal allelopathic effect of *E. sativa* on seed germination of *D. erucoides*? (iii) Does the change in population dynamics of weeds under field conditions match the results of *in vitro* laboratory studies?

MATERIALS AND METHODS

Study site: The study was conducted at Hashemite University Campus, Zarqa [(32^{o}04 N, 36^{o}12 E; altitude: 550-650 m), Mean annual rainfall 115 mm (October and April), the lowest minimum temperature (0^{o}C) in December - January and the highest (40^{o}C) in July/August]. Mean minimum temperature in winter is 2.7^{o}C and the mean maximum temperature in summer is 34.3^{o}C. Zarqa is 40 km east of Amman, (Jordan), typically in arid Mediterranean with Irano-Turanian steppe region (1,54). The natural vegetation is mainly bushes [*Salsola baryosmo*, *Noaea mucronata*, *Hamada scoparia*, *Anabasis syriaca*, and *Artemisia herba-alba*]. Since past 8-15 years, olive trees have been planted in plains and low slopes and ornamental shrubs/trees (*Pinus*, *Casuarina*, *Cupressus*, *Eucalyptus* and *Ceratonia*) on the hill slopes, along the roads and near the buildings. The dominant weed species in order of dominance were: *Diplotaxis erucoides*, *Eruca sativa*, *Sonchus oleraceus, Malva neglicta, Launea nudicaulis* and *Chenopodium album*..

Seeds of *D. erucoides* and other plant species (except *Taraxacum officinale*) were harvested from the experimental field and those of *T. officinale* were collected from Amman area (40 km away).

Field population of *Diplotaxis erucoides, Eruca sativa* and other plants

A 10-years old plantation of pine trees (30 x 20 m) was selected for this study. At planting, 10 cm depth of red topsoil (transported from Amman) was applied over the entire area. Prior to the experimental work, periodic irrigation and hand weeding was done (without fertilizer or herbicide). In pine plantation, 20 *Pinus* tree basins (100-120 cm dia. and 20-50 cm depth) were selected randomly in December 2009 (before weed emergence) to investigate the vegetative and reproductive features of *D. erucoides* and *E. sativa* plants present at study site. The basins were permanently marked using wooden sticks and no further management (except irrigation) was applied to the basins. In April 2009, species-wise weed populations were counted in each tree basin. About 100 plants of each test species (10 from each basin) were randomly chosen to determine their shoot height, tap root length, number of leaves per plants and number of shoots (stems) per plants were measured and/or counted. These plants of each species were carefully removed from the soil, the roots were thoroughly washed and plants were partitioned in above- and below-ground components. These biomasses were separately kept in paper bags, oven-dried at 80°C for 72 h and weighed. The number of fruits per shoot and the number of seeds per fruit were counted using a total of 100 shoots belonging to 20 different plants, including five mature shoots of each plant.

In December 2007, before the weeds emergence, to assess the weeds population, 20 *Pinus* tree basins were selected randomly. The basins were permanently marked using wooden sticks. Botanical surveys (number of individuals of each weed species) were conducted in these basins at the end of each month from January to June in 2007, 2008 and 2009. As *D. erucoides* is not common in natural undisturbed habitat of study sites, no control plots (undisturbed) were examined in this study. The surveys included counting the number of *D. erucoides* and *E. sativa* plants present in each marked tree basins. Individuals of other weed species found in basins, were collated as ‘other weeds’.

Preparation of plant extracts

Plants of *D. erucoides*, were collected in April 2008 from our campus. Aboveground portions (stem, leaves and flowers) were separated from the belowground parts (roots). Roots were thoroughly washed with tap water to remove soil particles. Plant materials were air-dried in a greenhouse environment (25-35°C) and then grinded using a grinder to a powder state.

The aqueous extract was prepared by soaking, air dried plant materials 100 g/l in almost boiling (95-98 °C) distilled water for 30 min with continuous stirring. The resultant solution was filtered through Whatman filter paper. The filtrate (pH = 6) was collected and identified as full-strength solution (10 mg/ml). Dilutions of 1, 2, 3 and up to 9 mg/ml were prepared using sterile distilled water and then their effects on seed germination were immediately assessed. For ethanol extracts, 100 g ground, air-dried plant material were kept in cotton cloth bag and then dipped into 250 ml diethyl ether and kept for 6 days (exchanged twice). The bags with plant materials were removed, completely air-dried and then placed into 250 ml ethanol (exchanged twice) and kept for 6 days. Filtrates were collected, evaporated using an evaporator and then the extracts were transferred to Eppendorf tubes and kept in the refrigerator (4°C) for future testing.

Effects of *D. erucoides* extracts on *E. sativa* and other plant seeds germination

I. Petri plate bioassay

Germination of *Eruca sativa* seeds: Aqueous extract concentrations (1, 2, 3, 4, 5, 6, 7, 8, 9 and 10 mg/ml) of *D. erucoides* were tested on germination of *E. sativa* seeds. Two Whatman No. 1 filter papers were placed in Petri plates (9-cm dia). These filter papers were saturated with 3 ml of respective extract concentration. Distilled water was used as control. Ten *E. sativa* seeds were placed on the moistened filter paper of each plate and then plates were sealed with parafilm. The treatments were replicated five times. The experiment was done in completely randomized design and was repeated twice. Plates were incubated at 26-/28°C under two 34-W cool white fluorescent lights on a 16-h day: 8-h night cycle. Germinated seeds were counted and removed every day for 14 days. Accumulative germination (%) was recorded for each treatment.

Germination of other plant seeds: The effects of *D. erucoides* concentration (5 mg ml^{-1} aqueous extract) were determined on germination of other weed and native species (*Sonchus oleraceus*, *Tragopogon coelesyriacus*, *Launea nudicaulis*, *Salsola baryosma* and *Taraxacum officinale*). Ten seeds of each plant species were used as per the above mentioned procedure and repeated in similar conditions. Germinated seeds were counted and removed daily. The experiment was terminated when there was no further germination in treatments for 3-consecutive days. Thus, the experimental duration was 1-2 weeks based on the species. Accumulative germination (%) was recorded for each treatment.

Autotoxicity and reciprocal effects of aqueous extracts of *Diplotaxis erucoides* and *Eruca sativa*

Aqueous leaf extracts of *D. erucoides* and *E. sativa* were assayed at four concentrations (0,1,5 and 10 mg ml^{-1}) on seeds of test plants. For each plant species, 10 seeds in five replicates were used. The experiments were repeated twice in similar conditions. Germinated seeds were counted and removed daily for 2-weeks and the cumulative germination (%) was recorded.

To study autotoxicity of *D. erucoides*, the aqueous extract of foliage parts at 1,5,10 mg ml^{-1} were applied to *D. erucoides* seeds. Ten seeds in five replicates were used. The experiment of each plant species was repeated twice under similar conditions.

The germination inhibition (%) was calculated as below:

$$\text{Inhibition } \% = (Cg - Tg/Cg)\ 100,$$

Where, Cg: Cumulative germination in control, Tg: Cumulative germination in treatments

2. Pot culture

The allelopathic potential of *D. erucoides* was evaluated in natural local soil according to Inderjit (25), with some modifications. Leaves of *D. erucoides* were collected from the study site. After air-drying, leaves were used for preparing leachates. one hundred g dried leaves were soaked in 2 L double-distilled water for 72 h and then the leachate was filtered using two layers of cheese cloth. The collected filtrate was labelled as full-strength leaf leachate and then diluted in ratio of 1:1, 1:3, 1:7, 1:10 with distilled water (v/v). A natural soil (Sandy soil: 85% sand; 9% silt; 6% clay) was used to fill plastic pots (5-cm diameter). The pots were labelled according to leachate dilution from T1 (full strength) to T5 (the most diluted) and then each irrigated with 50 ml of assigned leachate. Control pots were irrigated with 50 ml water each. Ten *E. sativa* seeds were sown in each pot and dealt with as one experimental unit. The pots were arranged randomly on a greenhouse bench and maintained under greenhouse conditions (24 ± 2^{o}C with 15 hr of light/day at photon flux density minimum of 350 ± 50 µmol m^{-2} s^{-1}). The experiment was with one factor and five replications in a completely randomized design and repeated once. To evaluate the interaction of soil microorganisms (if any) with allelopathic effect of *D. erucoides*, another trial was conducted at the same time and with similar experimental conditions except that the soil was autoclaved 3 times at 120 ^{o}C and 103 KPa pressure for 30 min. 15-days post sowing, the shoot height of each plant in each experimental trial was measured and recorded.

Statistical Analysis

The seed germination (%) were arcsine transformed and analysed using One-way ANOVA and significant differences among means were evaluated by Tukey's test at p = 0.05. Means were then converted back to original scale for presentation of results. According to Bartlett test, data from the two experimental trials were homogeneous, thus the two experiment data were pooled and analysed with 10 replications. The significant difference between the control and treatments on seed germination was accomplished using a paired *t*-test at p =0.05 (SAS Institute Inc. 2005).

RESULTS AND DISCUSSION

Botanical surveys conducted from 2007-2009 showed significant increase in *D. erucoides* population accompanied by significant decrease in *E. sativa* and "other weeds" densities. During 2007 to 2009, a significant 2- fold increase in the mean monthly density of *D. erucoides* was reported, while *E. sativa* population was significantly decreased to about 40%. More over population densities of other weeds were significantly declined to about 50% (Data not shown). The significant differences during 2007-2009 in weed densities were mainly in January (emergence time) and April (peak of growing season. Our results also showed greater mean values for all measured vegetative and reproductive parameters (Data not shown) of *D. erucoides* than *E. sativa.* The above results indicate higher growth vigour and density for *D. erucoides* than *E. sativa* in the study site.

Bioassays

Foliage and root aqueous extracts of *D. erucoides* caused significant decrease in seed germination of *E. sativa* starting from a concentration of 6 mg ml^{-1}, and 5 mg ml^{-1}, respectively (Fig. 1). Interestingly, above and below-ground ethanolic extracts of *D. erucoides* were stronger than aqueous extracts and were able to significantly reduce the germination of *E. sativa* from a concentration of 3 mg ml^{-1} for the foliage and of 2 mg ml^{-1} for the root extracts (Figure 1). Ethanol extracts of *D. erucoides* showed significant differences between aboveground and belowground parts, favoured the latter, on decreasing seed germination of *E. sativa*, however higher extract concentrations (8, 9 and 10 mg ml^{-1}) of both parts had similar inhibitory effects. In opposite to that, the same concentration of above and belowground aqueous extracts had no such significant differences.

Increasing the concentrations of any of the above and below-ground extracts of *D. erucoides* resulted in a significant gradual decrease in germination of *E. sativa.* Concentration of 10 mg ml^{-1} reduced the germination of *E. sativa* to about 90 to 100% over the control (Figure 1). Applying 5 mg ml^{-1} of foliage aqueous extract of *D. erucoides* resulted in a significant decrease of seed germination of all plants tested (*S. oleraceus*, *T. coelesyriacus*, *L. nudicaulis*, *S. baryosma* and *T. officinale*). The significant inhibitory effects of seed germination over the control were ranged between 74% for *T. coelesyriacus* and 95% for *T. officinale* (Figure 2).

Pot culture

To demonstrate the allelopathic interactions, soil from the geographical area of the allelopathic plant should be used in laboratory bioassays (25,27,43). Natural soil collected from the study site and amended with either full strength or 1:1 dilution of leaf leachates of *D. erucoides* inhibited the shoot growth of *E. sativa* seedlings (Fig. 3). The significant inhibition of shoot growth occurred in both autoclaved and not autoclaved soil without significant differences due to the presence or absence of soil microbes. The inhibitory effects compared to control were 57% and 43% in the presence of biotic (not autoclaved soil) and 65% and 50% in the presence of abiotic (autoclaved soil) for full strength and diluted 1:1 leaf leachates, respectively (Fig. 3). In addition to that, 10%, 25% and 30% reduction in seed germination of *E. sativa* occurred due to 1:3 dilution, 1:1 dilution and full strength treatments, respectively, without significant difference between autoclaved and not autoclaved soils (data not shown). Soil microbes may manipulate the allelopathic compounds contributed to soil through leaf leachate and in consequence affect the allelopathic interaction (25).

Our results agree with Qasem (38) who reported concentration dependent effects of *D. erucoides* extracts on seed germination of many vegetable and cereal crops, especially cucumber and wheat. Qasem (38) suggested that allelochemicals might be released from residues of *D. erucoides* on the soil or due to the substantial increase in concentration of plant leachates through time. In the present study, allelopathic effects of root extract were stronger than foliage extracts which may boost the significant role of soil in plant-plant interaction and the substantial gradual increase of allelochemicals in soil may explain the progressive decrease of *E. sativa* and other weed densities.

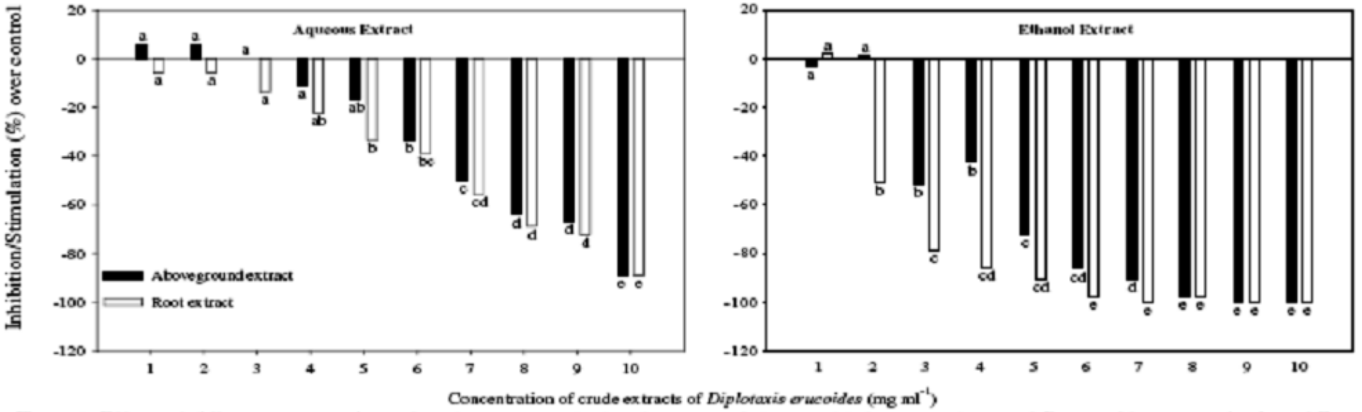

Figure 1. Effects of different concentrations of crude aqueous and ethanol extracts of above and below-ground parts of *D. erucoides* on germination of *E. sativa* seeds. Within each graph, bars with common letters for root and shoot extracts are not significantly different at $p \leq 0.05$ (Tukey's test).

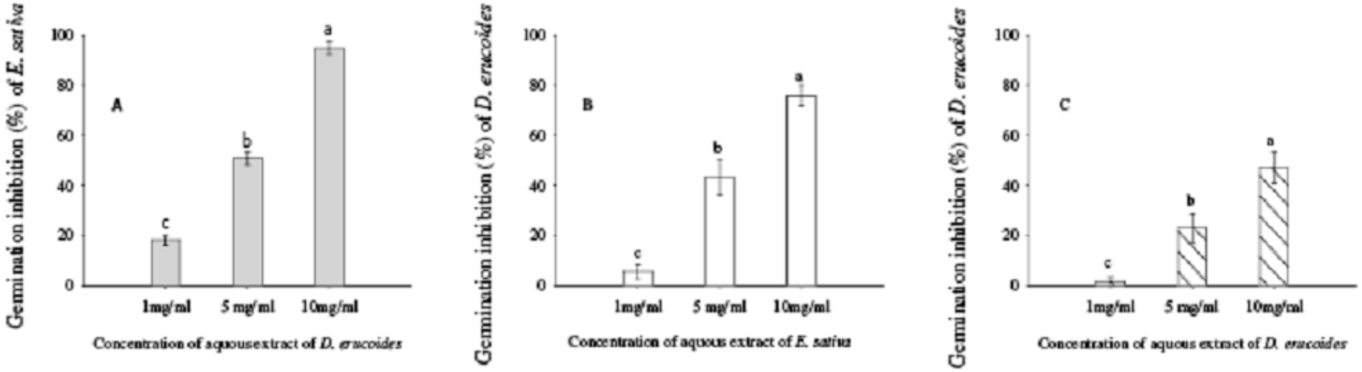

Figure 4. Inhibitory effects of crude aqueous extract of above-ground parts of (A). *D. erucoides* on seed germination of *E. sativa*, (B). *E. sativa* on seed germination of *D. erucoides* and (C). *D. erucides* on seed germination of *D. erucoides*. Error bars represent the standard errors of means. Within each graph, bars with common letters are not significantly different at $p \leq 0.05$ (Tukey's test).

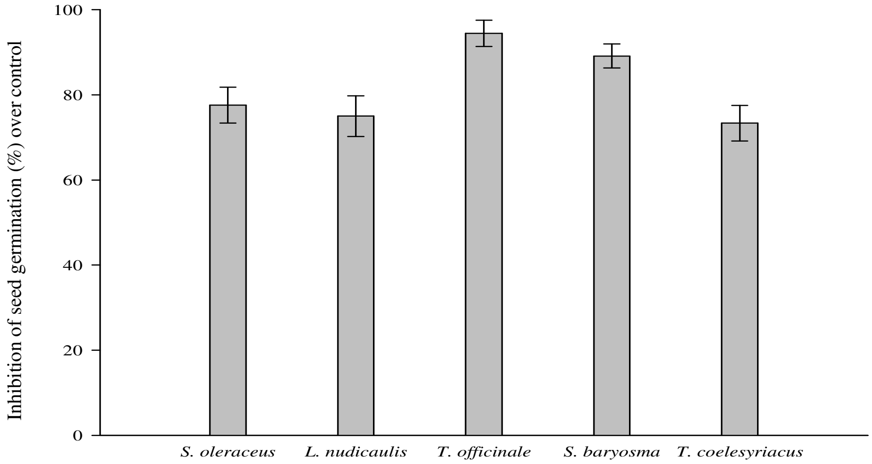

Figure 2. Effects of crude aqueous extract (5mg ml^{-1}) of aboveground parts of *D. erucoides* on seed germination of selected plants. Error bars represent the standard errors of the means. All treatments were significant at $p \leq 0.01$ compared to control.

In vitro allelopathic effects of wild rocket, *Diplotaxis tenuifolia* on radish, lettuce, barley, purslane, lambsquarter and trees of heaven were reported by Giordano *et al.* (18). The authors attributed the allelopathic effect of wild rocket to the bioactive compound S-glucopyranosyl thiohydroximate. Brassicaceae are known to contain glucosinolates, a group of b-d-thioglucosides that are characteristic of all species in the family (13,18). In addition to the allelopathic effect of the glucosinolates (18) their potential for the control of some soil borne diseases and pests has been explored (5,31,33,53). *Diplotaxis tenuifolia* extract decreased imbibition and distension of seed cells (13) which are basics for the radicle to rupture the seed coat and achieve germination without cell division that begins later (36). Unfortunately, in this study, isolation and investigation of the effects of *D. erucoides* glucosinolates on *E. sativa* were not conducted, but similar observations on seed germination were noticed as no radicles from non-germinated seeds were usually formed.

The three years survey of weed populations encountered in the area indicated a progressive decrease in their densities (excluding the two abundant species: *D. erucoides, E. sativa*). These results were supported by significant ($P \leq 0.01$) allelopathic effects from *D. erucoides* on three species that were frequently encountered in the studied plots, *S. oleraceus*, *L. nudicaulis* and *T. coelesyriacus.* The above mentioned results may support the role of allelopathy of *D. erucoides* on the weed community in the area. *D. erucoides* seemed to possess a broad active spectrum on many weed species. Several allelochemicals have been shown to have a broad spectrum action by being toxic or inhibitory to more than one group of organisms including plants and animals (17,51). Despite the multiple activity of allelopathy of certain species, the dosage factor can create a degree of specificity in terms of differences in the magnitude of impact on target species under different concentration levels (34).

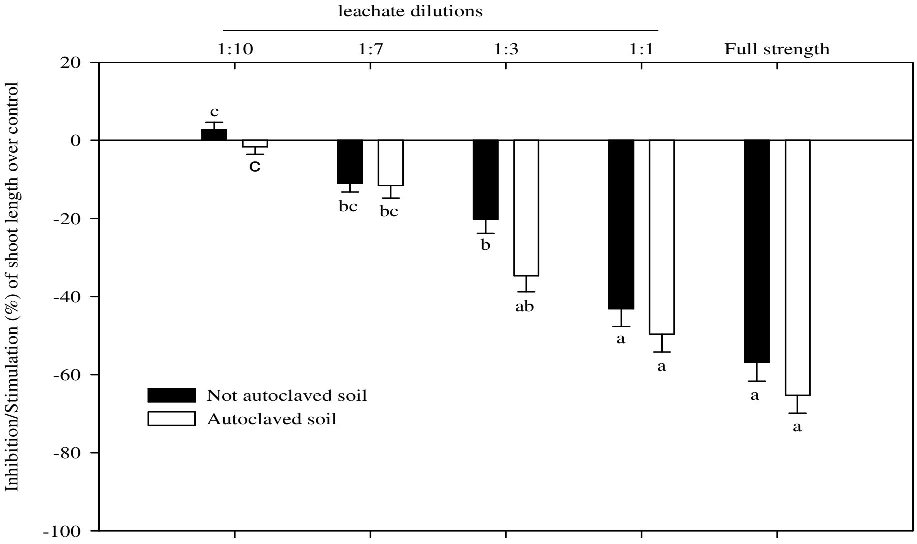

Figure 3. Effect of autoclaved and not autoclaved soil amended with full strength and diluted leaf leachates of *D. erucoides* on shoot growth of *E. sativa*. Bars with common letters are not significantly different at $P = 0.05$ according to Tukey's test. Error bars represent the standard errors of the means.

Many studies highlighted the role of allelopathy in determining associations in plant communities (37,41,50). *Diplotaxis* and *Eruca* are phylogenetically close to the economically important genus *Brassica* (20,28) and the order Brassicales is characterised by the presence of glucosinolates (13). Our results indicated reciprocal allelopathic effects of *E. sativa* aqueous extract on seed germination of *D. erucoides* (Figure 4). These results might be explained by the presence of glucosinolates in both *Diplotaxis and Eruca* (13). The size and weight of *E. sativa* seeds are about 5-folds greater than *D. erucoides* seeds; however our bioassays were standardized for both species. The application of the same volume of the extract on the same number of seeds in each treatment of the two species may have been a mistake. As a result, the laboratory bioassays for the allelopathic effect of *E. sativa* on *D. erucoides* may be overestimated compared to field conditions. Small seeded species have been shown to be more inhibited than larger seeded species at a given concentration of allelochemicals (3,9,39). Plant ecologists criticized the use of laboratory bioassays to explain plant association under field conditions (41). In the present study, under field conditions the net outcomes favoured the dominance of *D. erucoides* over *E. sativa* and other weeds. The relative density between the donor and the receiver species under field conditions has been considered to be an important factor in the level of expression of allelopathy and it has been suggested as a method to distinguish between allelopathy and resource competition (32). The confusion of competition and allelopathy in plant-plant interactions has been argued and debated in the literature (8,21,32,41,50).

Our results indicated autotoxicity of *D. erucoides* and seed germination was inhibited to about 50% under the highest concentration used (10 mg ml^{-1}) (Figure 4). Such regulation could reduce the intensity of intraspecific competition and maximize the fitness of the dominant members of a population (42).

For annual species, allelopathic activity has been suggested to be part of their success as weeds (26) and allelopathy is more likely to occur in species poor communities than in species rich (49). The simultaneous presence of several age-class plants in the same population may also be important due to the critical life stage that releases the allelochemicals (26). More over, in stressed situations allelopathy may be the factor that tips the outcome of competition to the advantage of the allelopathic species (32,46). All of the above might be used to support the role of allelopathy in dominance of the annual weed *D. erucoides* which has shown to possess several age-class plants in the same population at any time during its growing season (from January to June) in a stressed and poorly diversified arid land environment. Similarly phytotoxic effects of *D. erucoides* residues may be important in arid and semi arid conditions under which cereal crops are grown in Jordan (38). However, and as many authors mentioned, allelopathy should be seen as part of the strategy of a species, rather than being the main determinant of interaction in natural systems (8,21,32,41,50). Our results, indicated that *D. erucoides* possesses more vigorous vegetative and reproductive features than *E. sativa*. This is likely to be important to add more competitive features for *D. erucoides* in the field and in consequence to add more competitive pressure on *E. sativa* through resource competition.

Allelopathy has also been suggested as a mechanism for the success of invasive plants in a certain area through the establishment of monoculture and decreasing species richness (16,21,41). Although no field experiments were conducted to study the allelopathic effects of *D. erucoides* on native species, our laboratory bioassays indicated a significant ($P \leq 0.01$) inhibition in seed germination of *Salsola baryosma*, a native annual bush dominant in the area (Figure 2). Our field observations have indicated the emergence of *S. baryosma* in May, the end of the growing season of most annuals including *D. erucoides,* which allow *S. baryosma* to grow and spread in most tree basins through summer season. Although the allelopathic effects can be obtained in seed germination tests, the release of allelochemicals under field conditions may not be a substantial factor in weed invasion (10,14).

Researchers discussed the applied aspects of allelopathy i.e. employing allelopathy in natural weed management (4,45,47,52). Various species of Brassicaceae were examined for their potential as allelopathic green manure crops and found to be with impressive results (2, 51). Dandelion has been reported in over 60 countries worldwide (24). In North America, dandelion is a common weed that infests terrestrial habitats with widely variable environments (44). It is a noxious weed in pastures, forages, orchards, lawns, golf courses, municipal parks, and road sides (24). The present study demonstrated the highly significant effect ($p \leq 0.01$) of aqueous foliage extract of *D. erucoides* on dandelion seeds (Figure 2) which in turn might be important for future management of weedy dandelions. In order to understand the allelopathic effect of *D. erucoides* on population changes of other weeds, further work on isolation of *D. erucoides* glucosinolates and their effects on weed's seedling establishments and survival is needed.

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