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RESEARCH PAPER

Assessment of the allelopathic potential of 17 Iranian barley cultivars in different development stages and their variations over 60 years of selection

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Laboratory experiments were conducted to determine the allelopathic potential of 17 Iranian barley cultivars in four development stages and their variations over the last 60 years of collection. Imbibed seeds and water leachates that were extracted from the barley plants at the seedling, tillering, stem elongation, and heading stages were used for the bioassays, including filter paper, neighboring barley seeds in soil, and soil mixed with dried barley residues. The experiments were conducted with the use of wild mustard (*Sinapis arvensis*) as the test plant. The Germination Rate Index (GRI) and emergence of *S. arvensis* were inhibited on both the filter paper and soil. The highest inhibitory effect was seen with the tillering stage's water leachate on filter paper. The GRI decreased in response to the increased density of barley imbibed seeds. The germination was less affected by the presence of barley seeds from the soil than those from the filter paper. The GRI of *S. arvensis* seeds was lower in the older than in the recently developed cultivars. Although there were some fluctuations in the GRI value with time, the germination inhibitory effect has decreased as new, higher-yielding cultivars have been released.

Keywords: allelopathy, barley cultivars, Germination Rate Index, *Sinapis arvensis*.

INTRODUCTION

Allelopathy arises from the release of chemicals by one plant species that affects other species in its vicinity, usually to their detriment (Nilsen *et al*. 1999; Tapaswi & Mukhopadhaya 1999; An *et al*. 2003). Molicsh (1937) coined the term "allelopathy" to include both harmful and beneficial biochemical interactions between all types of plants, including microorganisms. Baker (1965) and Rice (1984) reinforced this definition in the first monograph on allelopathy. The allelopathic characteristic of an allelochemical is defined as the biological property of the allelochemical, as opposed to its physical property, in virtually all plant tissues, including leaves, flowers, fruits, stems, roots, rhizomes, seeds, and pollens. They can be released from plants into the environment by means of volatilization, leaching, root exudation, and decomposition of plant residue (Putnam & Tang 1986; An *et al*. 2003). Each plant species can produce a toxicant that reaches another species through a diffusive process and affects its growth. It is well documented that the production of secondary metabolites in a plant's tissue is determined by the plant's genetic make-up in combination with its interaction with environmental conditions during its growth (Quader *et al*. 2001). Much research has shown that the amount of allelopathic production is different in crop cultivars. In an evaluation of 52 accessions of cucumber (*Cucumis sativus*) from 41 nations, one accession inhibited the growth of the receiver plants by 87%, whereas 25 other accessions caused growth inhibition of >50% (Putnam & Duke 1974). All cereals have been reported to be allelopathic (Baghestani *et al*. 1999; Fujii 2001). Rice (*Oryza sativa* L.) has been assessed extensively for allelopathic activity during the last decade

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(Fujii 1992; Dilday *et al.* 1994). Some accessions had a weed-free radius from the base of the rice plant. The plants of more strongly allelopathic accession were able to suppress 72–95% of the weed population using allelopathy alone, compared with 100% control by the herbicide, bensulfuron (Lin *et al.* 1992a). Wheat (*Triticum aestivum* L.) has been examined for differential allelopathic potential among accessions. Spruell (1984) reported that five accessions produced root exudates significantly more inhibitory to the root growth of the two receiver plant species than a commercial cultivar, T64. Barley germplasm contained higher allelopathic substances, such as phenolic acids, than wheat germplasm (Baghestani *et al.* 1999; Ma *et al.* 1999). Also in barley, there are some differences among the cultivars. Hanson *et al.* (1981) reported that the gramine concentration varied significantly between the modern cultivars of barley (*Hordeum vulgare* L.) and races of *Hordeum spontaneum* koch. The wild progenitors and four *H. spontaneum* races always contained high levels of gramine, whereas some other genotypes contained no detectable gramine. In another direct screen for gramine with 43 lines of barley, Lovett and Hoult (1992) claimed that a higher gramine content was found in ancestral barley or *H. vulgare* landraces (i.e. primitive and undeveloped cultivars that come from the wild species) than in bred cultivars. It has been postulated that the wild types of existing crops once might have possessed high allelopathic activity and that this characteristic was advertently alternated through continuous selection of crop plants for other desirable characteristics (Putnam & Duke 1974). Bertholdsson (2004) assessed the variation in allelopathic activity over 100 years of European barley selection and breeding. He found that the old cultivars and landraces had higher allelopathic activity than the newly released cultivars. A similar report was presented in relation to wheat cultivars (Escobar & Niemeyer 1993). In order to crop with increasing weed problems, herbicide use is increasing rapidly all over Asia. Concerns about human health, environmental contamination, and the development of herbicide-resistant weeds make the development of weed management methods with a minimal use of chemicals an area of interest. The genetic enhancement of the secondary compounds of crop plants offers potential implications for weed management. It should not be expected that allelopathy alone can control all the weeds in a typical agricultural setting. However, it could be a component of the overall weed management strategy. The present study was conducted to investigate the allelopathic properties of barley cultivars with different bioassay substrates and to compare the variation of this useful effect with the age of the plant. Our final goal was to examine whether there had been a similar change, as that reported for wheat and European barley cultivars, in the allelopathic properties of Persian barley cultivars over time in historical germplasm collections.

MATERIALS AND METHODS

Plant materials

The seeds of 17 barley (*H. vulgare* L.) cultivars, including both old cultivars and advanced breeding lines that have been introduced in Iran over the last 60 years, from 1949 to 2003 (Table 1), were obtained from the Cereals Research Department, Seed and Plant Improvement Institute, Karaj, Iran. In 2006, in order to prepare the plant materials for the experiments, the seeds of the barley cultivars were grown in four replicated pots (40 cm diameter and 25 cm height), each pot comprising 60 plants (~450 plants m^{-2}) arranged in a randomized complete block design. The samples were taken from four different phonological stages of barley (seedling, tillering, stem elongation, and heading stages). At each sampling stage, 10 plants were harvested and dried at 60°C for 24 h. For the treatments, the plant materials from four replications were mixed and those complexes were used as the plant materials for the next experiments. Wild mustard (*S. arvense* L.) is a Brassicaceae plant possessing competitive potential against main crops, like wheat, barley, and canola. It is a widespread and problematic weed of Iranian agriculture. Thus, *S. arvense* seeds were used for the bioassays. The weed seeds were collected from barley fields in fall 2005.

Influence of the neighboring barley seeds in the *in vitro* experiment

An experiment was conducted to evaluate the effect of neighboring barley seeds on the germination and early root length of *S. arvensis* seeds that were incubated with 0, 18, and 36 adjacent seeds of barley. The experiment was set up as a factorial design with four replications. The experimental units consisted of *S. arvensis* seeds uniformly placed within a sterilized system, which consisted of two layers of filter paper (No. 2; Whatman International, Maidstone, UK) in a Petri dish moistened with 1.5 mL of distilled water and the dish border sealed with a plastic film. A treatment without *S. arvensis* seeds, but with 30 barely seeds, was included to provide a control for the effects of the *S. arvensis* seeds on barley germination. The distance between the adjacent *S. arvensis* seeds was 1 cm, forming a grid of six rows by six rows of *S. arvensis* seeds. The Petri dishes were randomly placed within a germinator with day/night temperatures of 22/14°C and a 14 h photoperiod. To avoid competition

Table 1. Pedigree of the Iranian barley cultivars used for allelopathic effect assessments

Cultivar	Year	Planting area	Origin	Pedigree
Zarjoe	1949	Temperate and cold areas	Hamedan	1-28-9963
Gouharjoe	1959	Temperate areas	Choobak, Hamedan	1-30-14267
Californi	1959	Tropical areas	Africa	–
Eram	1962	Fars province	Bojnourd, Iran	1-32-5136
Gorgan 4	1962	Gorgan, Mazenderan, Moghan	Sweden	Herta
Sina	1966	Khouzestan	FAO	–
Kavir	1979	Tropical areas	USDA	Arivat
Karoun	1980	Southern areas	USDA	Strain-205
Valfajr	1985	Cold climate	Barley International Collection	CI-108985
Aras	1988	Moghan	Europe	Arumir
Makoui	1991	Azarbaijan	FAO	Star
Moghan	1993	Moghan	France	Probestdwarf
Torkman	1993	Gorgan	ICARDA	Rihane04
Rihane	1994	Temperate and tropical areas	ICARDA	Rihane
Afzal	1996	Areas under salinity stress	Yazd landraces	Chah afzal
Jonoub	1997	Tropical areas	CYMMIT	Gloria "s"/Copal "s"
Sahra	2003	Caspian Beach areas	CYMMIT	L.B.LRAN/Una 8271/Gloria"s"Com

CYMMIT, International Maize and Wheat Improvement Center; FAO, Food and Agriculture Organization; ICARDA, International Center for Agricultural Research in Dry Areas; USDA, United States Department of Agriculture.

for water during germination, it was replenished as necessary (six-to-seven drops of distilled water per Petri dish) to maintain the filter papers so they were completely saturated. In this, and all subsequent experiments, the seedlings with radicles protruding at least 1 mm through the seed cover were considered to have germinated. The germinated seeds of both species were recorded every day. No seed germinated after 12 days. The root length of five randomly chosen *S. arvensis* seedlings was measured twice for each Petri dish. The experiment was repeated twice.

Influence of the water leachate in the *in vitro* test

To assess the influence of the water leachate on germination, the germination and root elongation of the *S. arvensis* seedlings were evaluated in response to the water leachate of the barley stems and leaves. The plant materials used for preparing the water leachate included the stems and leaves of the barley plants of all the cultivars. These materials were harvested in four different phonological stages, that is, the seedling, tillering, stem elongation, and heading stages.

To obtain potentially diffusive inhibitors, 10 g samples of the dried leaves and stems were soaked in 250 mL flasks containing 200 mL distilled water for 22 h in a rotary shaker (85 r.p.m.) (Stuart Scientific, Stone, UK) at laboratory temperature (22°C). The solution was filtered through a filter paper and then sterilized by autoclaving the solution for 15 min at 0.1 MPa. Thirty-six surface-sterilized (3 min with sodium hypochloride 0.5%) *S. arvensis* seeds were uniformly placed in a sterilized system as a seed-to-seed bioassay. The filter papers in each Petri dish were moistened with 2 mL of test solution or distilled water. The experiment was set up as a factorial design and each treatment was replicated four times. All the Petri dishes were incubated under the same conditions that were described for the previous assay. The germinated seeds were recorded every day. After 12 days in the germinator, the ungerminated seeds were tested for viability using the tetrazolium test (Lakon 1949).

Influence of the barley seeds and plant materials incorporated into the soil

The germination and growth of the *S. arvensis* seedlings in response to the barley seeds and dried barley plant materials were evaluated in the soil as substrata. In one series of treatments, 36 *S. arvensis* seeds were sown with neighboring barley seed cultivars in each pot. Another series of treatments consisted of pots that were filled with

0.1 m^2 of soil that was mixed with 100 g dried plant materials (~10 t ha^{-1}; ~0.0038 g per pot). Regarding the results of the water leachate experiment, the plant materials of the tillering stage were mixed into the soil. The pots were plastic cylinders of 7 cm diameter by 6 cm height and were filled with soil to 1 cm from the top. A constant weight of soil was used for each pot and its final bulk density was set at 0.7 g cm^{-3}.

The seeds of *S. arvensis* were arranged in a grid of six rows by six columns with 1 cm between the adjacent seeds. Then, the barley seeds were distributed as a grid of 6×6 seeds over the *S. arvensis* grid and covered with a 2 mm layer of sieved soil. The experimental design was completely randomized with a factorial arrangement of the treatments. Each treatment was replicated four times. After the sowing of all the treatments, water was uniformly dropped on to the soil. The emerged seedlings of both species (i.e. those with completely expanded cotyledons) were counted every day and the barley seedlings were removed after each count. After 14 days, the seeds of *S. arvensis* that failed to emerge were retrieved by soil washing over sieves and their viability was tested by the tetrazolium test (Lakon 1949).

Data analysis

The Germination Rate Index (GRI) (Maguire 1962) was calculated using the formula:

$$\mathrm{GRI}(\%/\mathrm{day}) = \sum[(\mathrm{Gi} - \mathrm{Gi} - 1)/\mathrm{i}], \quad (1)$$

where i is the germination count day, Gi is the percentage of seeds germinated by day i, and Gi-1 is the percentage of seeds germinated by the previous count day.

The treatment effects in the different bioassays were evaluated by analysis of variance and linear and nonlinear regressions. The data were analyzed by SAS software ver. 9 (SAS Institute, Cary, NC, USA) using a general linear model and orthogonal comparisons were used to compare the effect of the treatments on seed germination and seedling emergence. The data were arcsin square root transformed before the analysis (Laterra & Bazzalo 1999). A Gompertz model was best fit to the data of cumulative seed germination and seedling emergence. The nomenclature used for the Gompertz equation was:

$$Y = a \exp(-b \exp[-cx]), \quad (2)$$

where Y is the cumulative proportion of seeds that germinated or emerged, a is the asymptotic value of Y, b and c are parameters, and x is the time measured as days after sowing, using SigmaPlot ver. 6 (SPSS, Chicago, IL, USA). The parameters were independently estimated for each experimental unit and compared among the treatments using orthogonal comparisons. Finally, a multivariate technique, that is, principal components analysis (PCA) was used to better explore the allelopathic variations among the barley cultivars, using the PRINCOMP procedure of SAS (SAS Institute 2001).

RESULTS AND DISCUSSION

The seed germination rate, total germination rate, and early seedling root length of *S. arvensis* were similarly affected by all the barley cultivar seeds for both repetitions of the bioassay, so the results of only one of them are presented. No significant effect was detected on the final cumulative germination rate of *S. arvensis,* which ranged from 93–96%. All those seeds that failed to germinate were shown to be rotten by the pressure of a forceps. Both the germination rate of *S. arvensis*, which was measured as the GRI, and the root length of the seedlings at the seventh day after sowing declined with barley seed density (Figs 1,2).

The results showed that the diffusing of allelopathic substances during barley imbibitions had inhibitory effects on *S. arvensis* germination. Increasing the density of barley seeds decreased the rate of *S. arvensis* seed germination, maybe because of the increased concentration of allelopathic inhibitors.

Influence of the water leachate of the barley seeds

All the water leachates of the barley cultivars reduced the final accumulated germination and root elongation of

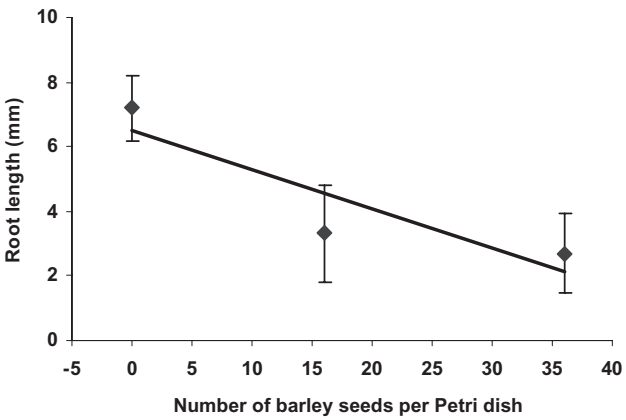

Fig. 1. Variation in the root length of *Sinapis arvensis* in response to different densities of barley seeds 7 days after sowing. Fitted line: $y = -0.1211x + 6.5066$, $R^2 = 0.81$. Bar = ±SE, $P < 0.05$.

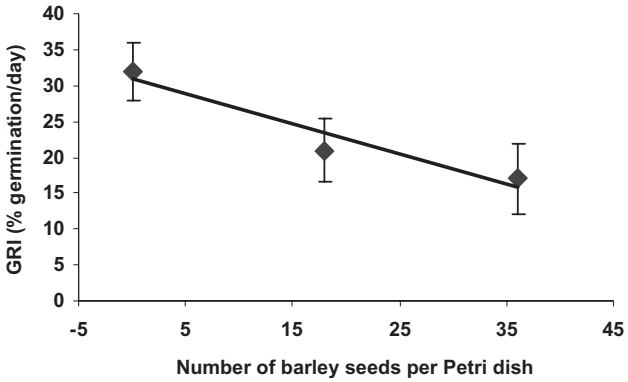

Fig. 2. Variation in the Germination Rate Index (GRI) of *Sinapis arvensis* in response to different densities of barley seeds. Fitted line: $y = -0.4167x + 30.833$, $R^2 = 0.93$. Bar = ±SE, $P < 0.05$.

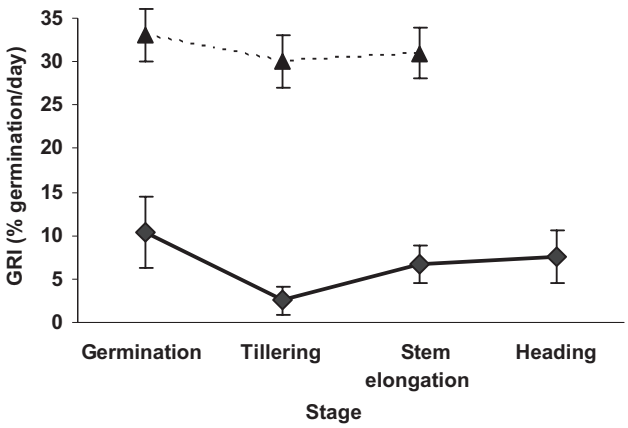

Fig. 3. Comparison of the Germination Rate Index (GRI) of *Sinapis arvensis* seeds in response to the water leachate of four growing stages of the barley plants. Bar = ±SE, $P < 0.05$. (▲), control.

S. arvensis significantly. The inhibitory activity of the solutions differed with the age of the plant materials used for the preparation of the water leachates. But, the cultivars and growing stages had no significant interaction effects. The inhibitory effect increased over the seedling to the tillering stages, but decreased at later stages (Fig. 3). Possibly, at the early stage, the allelochemical concentrations are low, increasing to a peak value at the tillering stage, then gradually declining with plant age. It is well documented that allelochemicals decrease with the age of the plant (Koeppe *et al*. 1970; Woodhead & Berbays 1978; Wolfson & Murdoil 1990; An *et al*. 2003). Much research shows the possibility of initial allelochemical content and accounts for its change in living

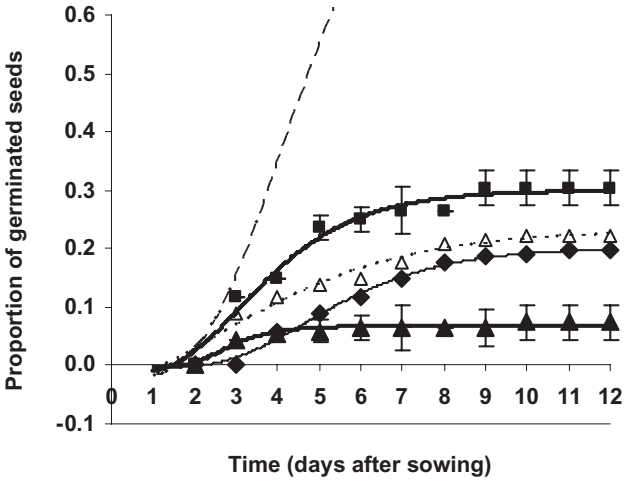

Fig. 4. Accumulated germination of the *Sinapis arvensis* seeds, incubated on filter paper with water leachate from barley plants at the tillering stage. (▲), seedling stage, $R^2_{adj} = 0.94$; (■), Stem elongation, $R^2_{adj} = 0.97$; (◆), heading, $R^2_{adj} = 0.99$; (△), $R^2_{adj} = 0.96$ of the barley plants and distilled water; ( ), $R^2_{adj} = 0.99$, bar = ±SE, $P < 0.01$.

plants. As a plant becomes mature, the ability to produce allelochemicals declines in the same way as the other characteristics of a plant. Corresponding to the decreasing concentration of allelochemicals with the increasing age of the plant, the dynamics of allelochemicals were simulated by the model (An *et al*. 2003).

The asymptotic germination value (parameter a in the Gompertz model), the maximum germination rate ($GR_{max} = a\ c\ e^{-1}$), and the inflection time (ln [b] c^{-1} days after sowing) tended to be reduced with the age of the plants from the seedling to the tillering stages. At the later stages of stem elongation and heading, parameter a and the GR_{max} increased, whereas the inflection time was constant (Fig. 4).

Overland (1966) pointed out that there was a possible periodical production of the inhibitors in barley plants. In all the barley cultivars, the allelopathic concentration decreased with age. The results indicated that the inhibition of radicle growth by the water leachate with the barley leaf and stem extracts generally decreased with the growing stages, from the early stages to heading. The model simulation showed that such fluctuation might result from the periodic production of alkaloids (Nicollier *et al*. 1985; An *et al*. 2003). Chemical studies indicated that some allelochemicals occurred at a certain stage. For example, the inhibitory compounds, coumarin, hydroxycinnamic acid, and their derivatives, as well as vanillic acid, have been shown to occur in

barley husks and gramine (N,N-dimethyl-3-aminomethylindole) as well-known constituents of the young shoots of certain *Hordeum* spp., but not in the seeds (Overland 1966). If considering that allelopathy acts as a defense system in a plant (Lovett & Ryuntyn 1992), then the idea that the overall concentration of allelochemicals in a plant declines with the increasing age of a plant is logical. A defense system is an inherent characteristic: as the age of a plant increases, its defense capability inevitably experiences weak, strong, and then decreasing stages (Rice 1984).

Assessment of the allelopathic effect in the soil used as a bioassay substrate

The rate of germination and the emergence of *S. arvensis* varied when the soil was used as a bioassay substrate. Both the neighboring barley seeds and incorporated dried leaves and stems in the soil significantly reduced the final proportion of the germinated seeds. But, the soil-dried plant materials mix exhibited a greater inhibitory effect on the emergence rate (Fig. 5). It is possible that incorporating the plant materials into the soil provides uniform distribution of the allelochemicals and, subsequently, puts the *S. arvensis* seeds in touch with these substances more so than the neighboring seed condition. Returning the plant materials of higher allelopathic plants to the soil could become an important tool in integrated weed management strategies with a minimal use of herbicides. Maybe, the increasing problem with herbicide-resistant weeds could be alleviated by highly allelopathic cultivars (Lemerle *et al*. 2001). Although the maximum emergence rate was significantly reduced in both the neighboring barley seeds and soil–barley residue bioassays, the inhibitory effect was lower for the latter (Fig. 6). The spatial and temporal variations in the concentrations of allelochemicals in the soil might have represented opportunities for the escape of *S. arvensis* from critical concentrations, which could not have happened when the allelochemicals were added through the leachates or neighboring seed *in vitro* bioassay. Moreover, in the soil environment, toxins are less available as they might be bound to the organic matter and clays (Dalton *et al*. 1983). The main part of the allelochemical release and dissipation happen in the soil substrate. Allelochemicals are released into the soil from living plants and are degraded into non-allelopathic substances or dissipated by the second process. Therefore, maybe the soil substrate bioassay can simulate the allelopathic effect better than the other methods. Allelopathic effects can be altered by the reaction of the responsible allelochemical compound with other chemical substrates in the soil, its leaching, microbial breakdown, binding with soil particles, and plant uptake (Laterra & Bazzalo 1999).

Variation in the allelopathic potential among the barley cultivars

The results showed that, except for two cultivars, Jonoub and Moghan, the GRI of *S. arvensis* was lower in the older rather than the recently developed cultivars

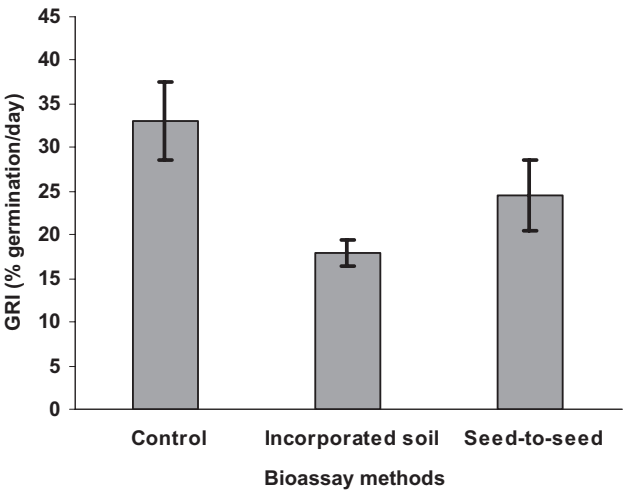

Fig. 5. Comparison of the Germination Rate Index (GRI) of *Sinapis arvensis* seeds in response to neighboring barley seeds and soil-dried barley plant materials mixed in soil substrate bioassays. Bar = ±SE, $P < 0.05$.

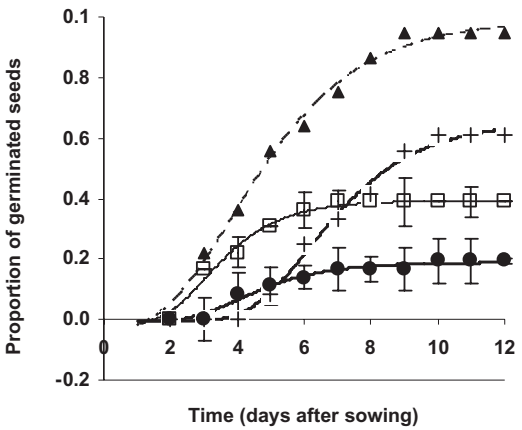

Fig. 6. Accumulated germination of *Sinapis arvensis* seeds, under different substrates, used for the allelopathic activity bioassay. (●), *In vitro* water leachate, $R^2_{adj} = 0.99$; (□), *in vitro* seed-to-seed, $R^2_{adj} = 0.98$; (+), soil, $R^2_{adj} = 0.99$; (▲), *in vitro* distilled water, $R^2_{adj} = 0.97$. Bar = ±SE.

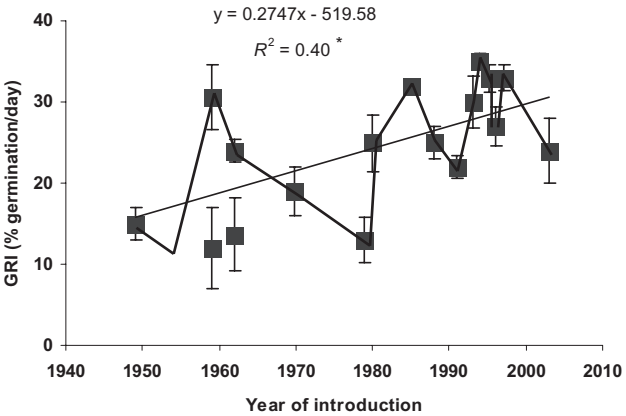

Fig. 7. Variation in the Germination Rate Index (GRI) of *Sinapis arvensis* seeds in response to the dried plant materials water leachate of 17 Iranian barley cultivars that have been introduced over the last 60 years. Bar = ±SE, ⋆$P < 0.05$.

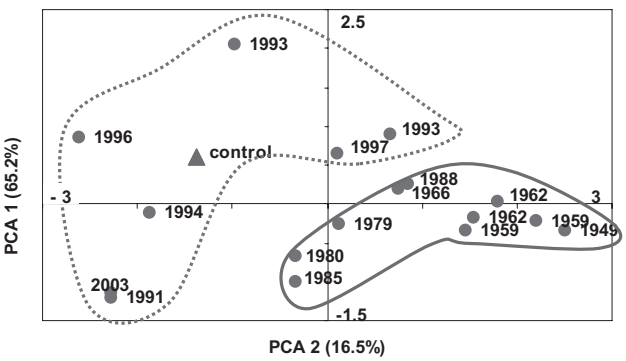

Fig. 8. Biplot illustrating the allelopathic potential variations of Iranian barley cultivars. The numbers show the year of the cultivar's release. Old and modern cultivars are separated by solid and dashed circles, respectively.

(Fig. 7). The two cultivars that exhibited the highest inhibitory effects, Gouharjoe and Kavir, were located in an old cultivars collection and the years of their introduction were 1959 and 1979, respectively.

The variation trend showed that the inhibitory activity of the plant materials has decreased over the years. Although there are some fluctuations in the GRI value with time, the germination inhibitory effect of the cultivars has obviously decreased as new, higher-yielding cultivars were released. Regarding the differences that were observed in the allelopathic effects of the different cultivars in the diagram of the PCA, the old cultivars were located closer together in one group and the newly released cultivars were classified in one segregated group. As depicted in Fig. 8, most of the newly released cultivars were located on the negative side of PCA1. On the contrary, almost all of the old cultivars clumped separately on the positive side of the PCA. There are a number of possible reasons for a change in the ability to produce and secrete allelochemicals. One of them is that the physiological costs of a high content of allelochemicals in the root exudate potentially counteracts high yields. Another reason could be that the original genes coding for exudation from high allelopathic landraces have become more and more diluted during a breeding process, only selecting for higher yields at high resource availability (Bertholdsson 2004). Also, autotoxicity at high expression levels decreases the plant's yielding ability and overall plant growth (Chung & Miller 1995; Ben-Hammouda *et al.* 2002). The ability to interfere with weed growth is a characteristic that has gradually been lost in the breeding process of barley, as most yield improvements have occurred at the expense of enhanced vegetative growth (Austin *et al.* 1980; Lednet & Stoy 1988). In breeding for competitive ability in crops, plant traits traditionally considered to determine competitive ability, such as a longer duration of the crop, early seedling emergence and vigor, faster growing rates, higher tillering capacity, taller plants, and greater root volume (Khush 1996). But, several of these characteristics (e.g. high tillering capacity and taller plants) oppose current breeding efforts for a new, high-yielding plant type. Another reason for the lack of results in breeding for competitive ability could be the complexity of competition as a result of adding up a still unknown number of influencing factors: chemical interference among plants (allelopathy) could be one of them. Thus, it seems that if no direct selections for allelopathic activity will be done, these useful traits will continue to decrease in barley germplasm in the future. Undoubtedly, there is a need for cultivars with such traits, especially in organic farming production systems. The incorporation of allelopathic traits together with other plant interference potential (e.g. early vigor, leaf size, plant height, and tillering) into commercial cultivars could be a major step towards the further development of sustainable crop production systems with less reliance on herbicides.

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