Short survey

Challenges and opportunities in implementing allelopathy for natural weed management

Prasanta C. Bhowmik[a], Inderjit[b],*

[a] *Department of Plant and Soil Sciences, University of Massachusetts, Amherst, MA 01003, USA*
[b] *Department of Botany, University of Delhi, Delhi 110007, India*

Abstract

Plants may favorably or adversely affect other plants through allelochemicals, which may be released directly or indirectly from live or dead plants (including microorganisms). Due to increase in the number of herbicide-resistant weeds and environmental concerns in the use of synthetic herbicides, there have been considerable efforts in designing alternative weed management strategies. The conventional synthetic herbicides are becoming less and less effective against the resistant weed biotypes. The objective of this article is to examine the role of allelopathic cover crops/crop residues, natural compounds, and allelopathic crop cultivars in natural weed management. Numerous examples of employing crop residues, cover crops and allelopathic crop cultivars in weed management are provided. Although we cannot eliminate the use of herbicides, their use can be reduced by exploiting allelopathy as an alternate weed management tool for crop production against weeds and other pests.
ⓒ 2003 Elsevier Science Ltd. All rights reserved.

1. Introduction

Austrian plant physiologist, Hans Molísch (1937), coined the term allelopathy in 1937. Rice (1984) defined allelopathy as the effect(s) of one plant (including microorganisms) on another plant(s) through the release of a chemical compound(s) into the environment. This definition includes both stimulatory and inhibitory effects, depending on the concentration of the compound(s). Rice (1995) discussed the applied aspect of allelopathy i.e. employing allelopathy in natural weed management. The objectives of this article are to examine: (i) the role of cover crops and crop residues in natural weed management, (ii) allelochemicals as natural herbicides, and (iii) the use of allelopathic crop cultivars in natural weed control.

2. Cover crops and crop residues

Rotational or smoother crops such as rye (*Secale cereale* L.), wheat (*Triticum aestivum* L.), buckwheat

(*Fagopyrum esculentum* Moench.), black mustard (*Brassica nigra* (L.) Koch), sorghum-sudangrass hybrid (*Sorghum bicolor* (L.) Moench x *S. sudanense* (Piper) Stapf) are used in weed management (Weston, 1996). Allelopathic compounds that are reported to play a role in weed management are: allyl isothiocyanate (black mustard), fatty acids (buck wheat), isoflavonoids and phenolics (clovers, *Trifolium* spp.; sweet clover, *Melilotus* spp.), phenolic acids and scopoletin (oat, *Avena sativa* L.), hydroxamic acids (cereals), phenolic acids, dhurrin, sorgoleone (sorghum, sudangrass) (Weston, 1996). Crop residues can provide selective weed control through their physical presence on the soil surface and through the release of allelochemicals (Weston, 1996; Inderjit and Keating, 1999). Duration of cover crops residue on the soil surface often determines the extent of an effective weed control period. Yenish et al. (1995) studied the disappearance of rye residue and allelochemicals, DIBOA (2,4-dihydroxy-1,4-benzoxazin-3-one), DIBOA-glucoside and BOA from rye residues. These authors found that 50% of the initial content of rye residue disappeared by 105 days after clipping. However, the combined active compound concentrations of DIBOA-glucoside, DIBOA, and BOA disappeared 168 days after clipping. Barnes and Putnam

---

*Corresponding author. Department of Botany, University of Delhi, Delhi 110007, India. Tel.: +011-27662402; fax: +011-27662402.
E-mail address: allelopathy@satyam.net.in (Inderjit).

(1983) reported that rye residue used as mulch reduced total weed biomass by 63%. It was found that disappearance of rye allelochemicals was more closely related to weed suppression than to the disappearance of rye residues. Some part of weed suppression, however, could be due to the physical impeding of seed germination or to shading (Cardina, 1995). In addition to physical effects, mulching contributed to weed control through allelopathic interference. Successful weed control could be achieved by growing cover crop of rye, barley, wheat or sorghum to a height of 40–50 cm, then desiccating the crop by either contact herbicides or freezing, and allowing their residues to remain on the soil surface (Putnam et al., 1983). Up to 95% control of some weed species for a 30–60 day period was achieved by the cover crop. Bewick et al. (1994) investigated the effect of root residues of celery (*Apium graveolens* L.) on growth of several weed and crop species. *Amaranthus spinosus* L. (Spiny amaranth) was found to be the most sensitive to celery root residues followed by *Echinochloa crus-galli* (L.) Beauv. (barnyardgrass), *Brassica kaber* (DC.) L.C. Wheeler (wild mustard), *Solanum nigrum* L. (black nightshade), *Digitaria sanguinalis* [L.] Scop. (large crabgrass), *Setaria viridis* var. *major* [Gaudin] Pospichel (giant green foxtail) and *Portulaca oleracea* L. (common purslane). *Cyperus iria* L. (rice flatsedge) was as equally affected as giant green foxtail. The effect of allelochemicals contributed from crop residues also depends on the soil texture and substratum ecology (Inderjit, 2001; Inderjit and Weiner, 2001). It is also desirable to investigate if crop residues are influencing microbial population and/or nutrient dynamics.

Allelopathy can play a beneficial role in various cropping systems such as mixed cropping, multiple cropping, cover cropping, crop rotations, and minimum and no–tillage systems. In a 5–yr field study with sunflower (*Helianthus annuus* L.)–oat rotation, the weed density increase was significantly less in sunflower plots than in control plots (Leather, 1983a, b; 1987). It was found that sunflower plants possess chemicals, which inhibit the growth of common weed species. Macias et al., (1999) reported some sesquiterpene lactones with germacranolide and guaianolide skeletons and heliannuol from different cultivars of sunflower. These authors discussed their potential role as natural herbicides. Fujii et al. (1992) reported that velvetbean (*Mucuna prursens* (L.) DC. var. *utilis*) is a good candidate to smoother weeds. They identified L-DOPA (L-3,4-dihydroxyphenylalanine) as the chemical responsible for velvetbean phytotoxicity.

The suppression of broadleaf weeds by using sorghum as a cover crop was suggested by Einhellig and Leather (1988). However, grassy weeds were not affected. Forage, sorghum-sudangrass hybrid, can suppress weeds in no-till alfalfa (*Medicago sativa* L.) plantation (Forney and Foy, 1985). Other examples include:

suppressive effects of sweet potatoes (*Ipomoea batatas* [L.] Lam.) on *Cyperus esculentus* L. (yellow nutsedge) or soybean (*Glycine max* [L.] Merr.) on barnyardgrass (Harrison and Petersen, 1986; Inderjit and Keating, 1999). Environment (e.g. fertility) plays an important role in influencing rye phytotoxicity (Mwaja et al., 1995). Rye grown under low to moderate fertility had high levels of BOA and DIBOA when compared to that grown under high fertility. Hensley and Counselman (1979) studied allelochemical interaction between two biotypes, triazine-resistant and susceptible, of *Amaranthus retroflexus* L. (redroot pigweed). It was found that resistant biotypes were more influenced by allelochemicals when compared with susceptible biotypes. Resistant redroot pigweed biotypes were less vigorous and less competitive compared to susceptible biotypes. Such resistant weed biotypes can be controlled with allelopathic cover crops or residues. More research, however, is needed on this aspect. Przepiorkowski and Gorski (1994) investigated the effects of rye residues on germination and growth of triazine-resistant and susceptible biotypes of *Conyza canadensis* [L.] Cronq. (horseweed), *Epilobium cilatum* Rafin (willowherb) and barnyardgrass. These authors used rye root-incorporated soil to determine rye residue influence on two biotypes of selected weed species. Both biotypes of selected weed species were found to be sensitive to rye residues. Seed germination of both biotypes of willowherb and horseweed was adversely affected with increase in rye seeding rate. However, germination by none of the barnyardgrass biotypes was affected. The reduction in weed growth was, however, maximum in both biotypes of barnyardgrass compared to willowherb and horseweed (Table 1).

Cardina (1995) discussed some of the drawbacks of using cover crops in rotation systems. These include: delayed planting, delayed crop emergence, phytotoxic effects to major crop, and increased pest pressure. Moreover, cover crops are not much effective in containing perennial weed species. It is also believed that regrowth of certain perennial weeds may be favored due to far-red light environment under cover crops (Aldrich, 1984). Compared to desiccated hairy vetch (*Vicia villosa* Roth) treatment, total weed density and biomass were lower in live hairy vetch treatment (Teasdale and Daughtry, 1993). Red (660 nm) and far-red (730 nm) ratio of transmitted light was reduced by 70% in live hairy vetch and by 17% under hairy vetch desiccated by paraquat. Factors responsible for the weed suppression by hairy vetch include: light, soil moisture and temperature (Teasdale 1993). Birkett et al. (2001) discussed the significance of intercropping against problematic weeds, particularly those parasitic, such as *Striga asiatica* (L.) Ktze. (witchweed) and *S. hermonthica* (Del.) Benth (purple witchweed). Two intercrops, silverleaf (*Desmodium uncinatum* [Jacq.] DC.) and

Table 1
Effect of rye roots on relative dry weight of three triazine-resistant (R) and susceptible (S) weed species[a]

Rye seeding rate (kg)	Relative dry weight					
	Barnyardgrass (%)		Willowherb (%)		Horseweed(%)	
	R	S	R	S	R	S
	%					
0	100	100	100	100	100	100
100	26.7	33.5	74.8	69.1	70.8	58.7
160	20.2	29.9	70.9	71.0	66.1	55.8
220	22.7	27.1	65.3	74.0	58.5	55.8
280	19.4	28.7	62.6	70.6	57.7	52.2
LSD (0.05)	15.6	11.2	14.0	12.6	11.7	9.0

Source: Przepiorkowski and Gorski (1994). Reproduced after permission from Weed Science Society of America (WSSA).

[a] Percent based on comparison to the non-treated control (0 kg/ha seeding rate).

greenleaf (*D. intortum* [Miller] Urban) were effective in reducing infestation of *Striga hermonthica* to maize (*Zea mays* L.). This results in an increase of maize yield to 7–8 ton/ha compared to 4–5 ton/ha without intercrop (Khan et al., 1997). These authors identified allelopathy as the mechanism, however, they also recognized that nitrogen fixation by legumes can also help maize plants.

Inderjit and Keating (1999) discussed the question whether 100% weed control can be achieved by using cover crops or crop residues. In addition to using allelopathic cover crops or crop residues, post-emergence herbicides are still needed (Teasdale, 1998; Worsham, 1991). Cover crops should be killed to alleviate their phytotoxic effects to the following crop. In many situations, herbicides are needed to kill cover crops; however, natural elimination of cover crop can also happen. For example, severe frost can kill winter and spring oat and mustard (Parish, 1990; Putnam, 1983).

3. Allelochemicals as natural herbicides

Putnam (1983, 1988) termed allelochemicals as nature's own herbicides. Duke et al. (2000) discussed that natural compounds have several benefits over synthetic compounds. For example, natural compounds may have novel structure due to diversity of molecular structure. This diversity is because synthetic chemists have been biased toward certain types of chemistry. They have had almost no interest in water-soluble compounds (Steve Duke, personal communication). Unlike a high proportion of synthetic pesticides, natural compounds are mostly water-soluble and non-halogenated molecules. Natural products relatively have short half-life and therefore considered safe of environmental

toxicology standpoint (Duke et al., 2002). There is a need to discover new herbicides since the number of herbicide-resistant weeds is increasing and conventional synthetic herbicides are becoming less and less effective against the resistant weed biotypes (Heap, 1997; Itoh et al., 1999; Bhowmik 2000; Fischer et al., 2000a, b; Duke et al., 2002). Duke et al. (2000) discussed the approaches needed to select sources of natural products for the discovery of potential herbicides. These are: (1) obtain pure compounds from other laboratories, (ii) obtain previously unexploited biological material and (iii) employ ethnobiological and/or chemical ecology data to select material. Understanding the ecological and physiological aspects of a compound has two main approaches: (i) allelopathy, e.g. sorgoleone, and (ii) sequestering of a compound by a species to avoid autotoxicity, e.g. artemisinin (Duke et al., 2000; Tellez et al., 1999).

Some of the natural products exploited as commercial herbicides are triketone, cinmethylin, bialaphos, glufosinate and dicamba. Bialaphos, a microbially originated herbicide, has limited use in Japan. A natural fatty acid, pelargonic acid and maize gluten (a byproduct of the maize-milling process) are mainly used in organic farming and have limited use in USA (Bhowmik, 1992; Duke et al., 2000). Another microbially originated herbicide is tentoxin and has good residual soil activity, unique dual mode of action (i.e. inhibition of chloroplast CF, ATPase and post-translational processing of polyphenol oxidase) (Duke et al., 2000). Natural plant products may provide clues to new and safe herbicide chemistry (Duke, 1986; Nimbal et al., 1996b). Therefore, modifying these natural products could give more active and selective herbicides. One of the first phytotoxic compounds to be implicated in higher plants was 1,8-cineole (Muller and Muller, 1964). Cinmethylin was developed as a herbicide and commercially used for weed control for a short period of time. It controls many annual grasses and suppresses many broadleaf weed species (Bhowmik, 1988). Its structure is similar to the structure of 1,4-cineole. A second natural herbicide is AAL-toxin, a natural metabolite produced by *Alternaria alternate* f. sp. *lycopersici*, the pathogen that causes stem canker of tomato (*Lycopersicum esculentum* Mill.) (Abbas et al., 1995). The phytotoxic effects of AAL-toxin were tested on 86 crop and weed species (Abbas et al., 1995). Monocots were generally immune to its effects. Black nightshade, *Datura stramonium* L. (jimsonweed), all species of tomatoes tested, and several other broadleaf weed species were susceptible at low doses. Other broadleaf species were susceptible but only at higher doses. Differential selectivity of species to AAL-toxin should be exploited for selective weed control. Recently, mesotrione, a HPPD inhibitor, has been developed as a herbicide for selective weed control in corn (Bhowmik and Zhang, 2003). This herbicide

chemistry was discovered from a natural compound from lemon bottlebrush (*Callistemon citrinus* Splendens). There is not much success in discovering natural herbicides from higher plants (Heisey, 1999). Some examples of synthetically derivatized benzoic acid metabolites from plants are dicamba and chloramben. The compounds having potential herbicidal activity but not commercially used are artemisinin, sorgoleone and ailanthone.

Artemisinin, a sesquiterpenoid lactone, has been shown to inhibit the growth of redroot pigweed, *Ipomoea lacunosa* L. (pitted morning glory), *Artemisia annua* L. (annual wormwood) and common purslane (Duke et al., 1987). Artemisinin at $33\,\mu M$ marginally increases mitotic index of lettuce (*Lactuca sativa* L.) root tips, and chromosomes are less condensed during mitosis. Duke et al. (1987) concluded that artemisinin is a selective phytotoxin with herbicidal activity similar to cinmethylin (Bhowmik, 1988). Although the exact mode of action is still unknown, Dayan et al. (1999) suggested that it is somewhat selective and might have a novel mode of action. Attempts have been made to use artemisinin as the basis for discovering new herbicides (Duke et al., 2001). Lydon et al. (1997) reported that the phytotoxic activities of annual wormwood cannot be solely explained by artemisinin. The dichloromethane extracts of annual wormwood leaves, which contain artemisinin, inhibited seed germination and seedling growth of redroot pigweed more strongly than did similar amounts of artemisinin alone. Furthermore, aqueous extracts without artemisinin had a similar activity to that of artemisinin alone. This illustrates the significance of joint action of allelochemicals in mixtures (Inderjit et al., 2002). Einhellig (1995) suggested that most allelopathic activities are due to the presence of several compounds in a mixture. The concentration of each compound in a mixture might be significantly less than the concentration of individual compounds needed to cause growth inhibition.

Einhellig and his group first reported the phytotoxic activity of sorgoleone (Einhellig, 1995; Einhellig and Souza, 1992). Sorgoleone and its analogues are structurally similar to plastoquinone (Duke et al., 2001). Sorgoleone inhibited the evolution of O_2 during photosynthesis in potato (*Solanum tuberosum* L.) and in common groundsel (*Senecio vulgaris* L.) (Nimbal et al., 1996a). Nimbal et al. (1996b) carried out a study on sorgoleone using triazine-susceptible potato and redroot pigweed thylakoids. Sorgoleone was a competitive inhibitor of atrazine binding sites. Sorgoleone also inhibited the photosystem II electron transport reactions (Gonzalez et al., 1997). Gattas-Halak et al. (1999) reported that sorgoleone influences the cell multiplication cycle by inhibiting the number of cells in prophase, metaphase, and anaphase stages. In theory, sorgoleone is considered as an efficient herbicide because of its

potential to inhibit electron transfer between Q_A and Q_B at the reducing site of photosystem II (Czarnota et al., 2001). When applied at a rate of 0.6 kg ai/ha, sorgoleone significantly inhibited growth of several broadleaf and grass species (Table 2). The most affected weeds ($>80\%$ inhibition) were black nightshade, redroot pigweed and *Ambrosia artemisiifolia* L. (common ragweed). Comparatively, lesser affected ($>40\%$ inhibition) weeds were *Cassia obtusifolia* L. (sicklepod), large crabgrass and *Abutilon theophrasti* Medik. (velvetleaf). Sorgoleone was applied to 14-day-old seedlings and data were collected 10 days after treatment. Although, sorgoleone is more active in vitro in inhibiting PS II when compared to atrazine, it is considered a weak herbicide due to its physicochemical properties and short environmental half-life (Streibig et al., 1999; Duke et al., 2000).

Heisey (1996) isolated a quassinoid compound, ailanthone, from bark and foliage of tree-of-heaven (*Ailanthus altissima* (Mill.) Swingle). The compound reported to possess pre- and post-herbicidal activity in greenhouse trials. Ailanthone exhibited a strong herbicidal activity when sprayed on soil before the seed germination. It, however, also had dramatic effects when sprayed onto seedlings after their emergence from soil (Fig. 1). Although, not yet commercially exploited, Heisey (1996) advocated the use of ailanthone as potential herbicide due to its efficacy compared to widely used herbicides such as glyphosate and paraquat. Ailanthone is not commercially used as herbicide because of its rapid degradation in soil (Fig. 2). Although weed species present at the time of spray may get killed, others may emerge once ailanthone disappears from the soil (Heisey, 1999). Multiple applications throughout the growing season of the crop could be a solution, but certainly would not be cost-effective or feasible.

Allelochemicals from weed species have the potential to be explored as natural herbicides. However, prior to

Table 2
Response of selected weeds to a foliar application of sorgoleone at 0.6 kg ai/ha. Data were collected 10 days after treatment

Plant species	Shoot fresh weight (g)		
	Control	Treatment	Inhibition (%)
Nightshade	2.2 ± 0.11	0.2 ± 0.21	90
Pigweed	5.8 ± 2.1	1.1 ± 0.85	82
Lambsquaters	11.9 ± 1.12	8.8 ± 0.36	26
Common ragweed	5.5 ± 2.13	0.6 ± 0.68	88
Giant foxtail	5.7 ± 0.84	5.0 ± 0.61	12
Sicklepod	1.4 ± 0.4	0.5 ± 0.23	60
Common purslane	2.3 ± 0.59	1.1 ± 0.19	53
Large crabgrass	2.1 ± 0.12	1.2 ± 0.36	43
Velvetleaf	0.5 ± 0.05	0.3 ± 0.04	40

Source: Czarnota et al. (2001). Reproduced after permission from Weed Science Society of America (WSSA).

Fig. 1. Effect of post-emergence application of ailanthone (0.5–8.0 kg/ha) and the control (0 kg/ha, far left). Plant species (front to back) are redroot pigweed, garden cress, velvetleaf, foxtail, barnyardgrass, corn, and *Ailanthus altissima*. Essentially all seedlings in treated flats are dead except velvetleaf and *A. altissima*. Some velvetleaf are still alive at lower doses. *A. altissima* shows no injury whatsoever, even at the highest dose. Source: Heisey (1996). Reproduced after permission from Botanical Society of America.
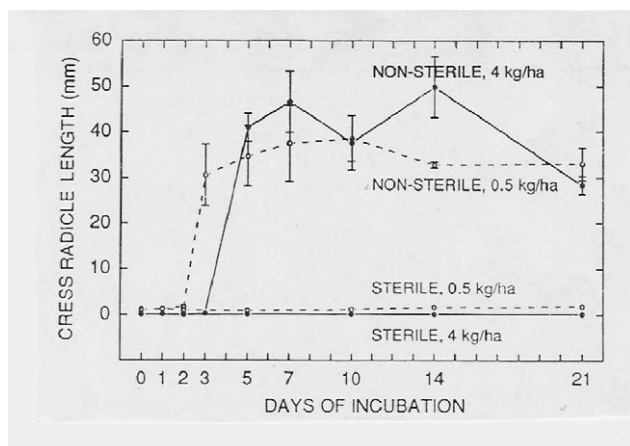

Fig 2. Effect of sterile or non-sterile soil treated with 0.5 or 4.0 kg ailanthone/ha and incubated 0–21 days on radicle growth of garden cress. Bars show ±SE, where bars are absent, ±SE is less than or equal to the height of symbol. Source: Heisey (1996). Reproduced after permission from the Botanical Society of America.

using them as herbicides, the following questions should be considered:

1. At what minimum concentration does each compound have phytotoxic activity?
2. Whether the compound is accurately separated and correctly identified?
3. What is the residence time and fate of the compound in the soil environment?
4. Does the compound influence microbial ecology and physicochemical properties of the soil?
5. What is the mode of action of the compound?
6. Has the compound any adverse effect on desired crops?
7. Whether the compounds are safe from health standpoint?
8. Whether the large production of the compound at commercial scale is economical?

4. Allelopathic crop cultivars

Researchers have screened crop cultivars for their differential allelopathic activity (Wu et al., 1999; Olofsdotter, 2001). Putnam and Duke (1974) tested 526 accessions of cucumber (*Cucumis sativus* L.) and 12 accessions of eight related *Cucumis* species, representing 41 nations of origin, for their allelopathic activity on white mustard (*Brassica hirta* Moench.) and wild proso millet (*Panicum miliaceum* L.). One accession inhibited growth of test species by 87%, and 25 accessions inhibited growth by 50% or more. These authors concluded that the incorporation of an allelopathic character into a crop cultivar could provide the crop with a competitive advantage over certain weeds. Fay and Duke (1977) screened 3000 accessions of the USDA world collection of *Avena* sp. germplasm for their ability to exude scopoletin. Twenty-five accessions exuded more scopoletin from their roots than a standard oat cultivar, 'Garry'. They found that four accessions exuded up to three times as much scopoletin as 'Garry' oats. One of these accessions grown in sand culture for 16 days with wild mustard significantly reduced mustard growth more than that obtained when the weed was grown with 'Garry' oats. The plant exhibited severe chlorosis, stunting, and twisting, indicating allelopathic effects rather than simple competition. Twenty soybean cultivars of varying competitive ability were tested for their allelopathic potential on velvetleaf and *Setaria italica* (L.) Beauv. (foxtail millet). On an average, these cultivars decreased the dry weights of velvetleaf by 46% and that of foxtail millet by 65% (Rose et al., 1984).

Sunflower varieties have the ability to inhibit the growth of certain weeds (Leather, 1983a; Leather and Forrence, 1979). Responses to weed seed germination were inhibition, stimulation or no effect depending on sunflower variety, weed species, and extract concentration. Root exudates of 100 sorghum cultivars were evaluated for their potency to affect the seed germination and growth of redroot pigweed (Alsaadawi et al., 1986). Some cultivars were more toxic than others. While the concentration of gramine (*N,N*-dimethyl-3-aminomethylindole) was reported to vary between 2 and 10 mg/g in barley (*Hordeum vulgare* L.) cultivars such as 'Arimer', 'Maraini', CI 12020, and four *H. spontaneum* Koch races, the genotype such as Proctor had an undetectable amount of gramine i.e. $< 30\,\mu$g/g dry weight (Hanson et al., 1981).

Baghestani et al. (1999) investigated the phytotoxic effects of root exudates of highly competitive (HC) and less competitive (LC) cultivars of wheat, oat and two- and six-rowed barley on germination and seedling growth of wild mustard. HC wheat cultivars were found to be more phytotoxic compared to LC cultivars. Root exudates of cereal cultivars mainly contained phenolic acids. These authors concluded that vanillic and *o*-coumaric acids and scopoletin are likely to be responsible for phytotoxic effects of wheat, barley and oat, and should be considered for use when monitoring the breeding potential for allelopathic crop cultivars.

Inderjit et al. (2001) studied the interaction between wheat and *Lolium perenne* L. (perennial ryegrass). These authors observed root inhibition of perennial ryegrass when grown with wheat. The observed growth suppression of perennial ryegrass was dependent on the density of wheat seeds. Lemerle et al. (2001) investigated the competitive advantage of 12 wheat varieties against *Lolium rigidum* Gaudin (rigid ryegrass). It was found that variation in crop grain yield was mainly due to variety and environmental effects. These authors stressed the need of introducing greater genetic variability into wheat to enhance competitiveness.

Hydroxamic acids (4-hydroxy-1,4-benzoxazin-3-ones) are present in wild and cultivated members of the family *Poaceae* (tribe *Triticeae*) (Niemeyer et al., 1992). Significant amount of literature is available on the differential production of hydroxamic acids in cereals. The main hydroxamic acids reported from cereals are DIBOA and DIMBOA (2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one); their distribution with cultivated *Poaceae*, however, is uneven (Niemeyer, 1988). While wheat has both DIMBOA and DIBOA, rye contains only DIBOA. The significant variation in the amount of DIBOA and DIMBOA in seedlings of wild Poaceae was reported by Gianoli and Niemeyer (1998) (Table 3). These authors reported the correlation between the amount of hydroxamic acid and resistance to Russian wheat aphid (*Diuraphis noxia*) and the greenbug

Table 3
DIBOA (2,4-dihydroxy-1,4-benzoxazin-3-one) and DIMBOA (2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one) content (mmol/kg fresh weight, mean $\pm$ SE) in wild *Poaceae*)

Species	Accession	N	DIBOA	DIMBOA
Deschampsia caepistosa	PI 223364	9	0.33 ± 0.50	2.23 ± 0.41
D. flexuosa	PI 253191	9	6.05 ± 0.65	2.31 ± 0.25
Elymus agropyroides	PI 269646	9	5.97 ± 1.22	2.79 ± 1.31
E. arizonicus	PI 531558	8	28.01 ± 8.72	1.01 ± 0.58
E. breviaristatus	PI 504445	12	1.68 ± 0.39	1.35 ± 0.21
E. magellanicus	PI 531634	10	1.56 ± 0.18	5.28 ± 2.19
E. sibiricus	PI 406465	10	6.69 ± 2.79	0.03 ± 0.01
E. vaillantianus	PI 531549	8	5.0 ± 1.47	3.94 ± 0.47
E. virginicus	PI 531706	9	3.76 ± 1.50	4.16 ± 1.27
Hordeum brevisubulatum subsp. *Violaceum*				
	PI 401380	5	3.93 ± 0.47	ND
	PI 401381	5	3.50 ± 0.33	ND
	PI 401389	4	0.56 ± 0.09	ND
Hordeum bulbosum				
	PI 204579	5	0.52 ± 0.09	ND
	PI 207770	4	1.51 ± 0.18	ND
	PI 240161	5	3.43 ± 0.31	ND
	PI 249747	5	0.57 ± 0.11	ND
	PI 250930	4	2.47 ± 0.28	ND
Hordeum chilense				
	H8	5	1.65 ± 0.41	ND
	H13	4	1.38 ± 0.22	ND
	H16	4	0.55 ± 0.08	ND
	H39	5	0.99 ± 0.08	ND
	H46	5	0.58 ± 0.07	ND
	H55	4	0.43 ± 0.07	ND
	H60	5	0.77 ± 0.11	ND
	H93	5	0.97 ± 0.15	ND
Phalaris amethystine	PI 286171	10	0.63 ± 0.24	0.84 ± 0.05
P. angusta	PI 310292	6	0.95 ± 0.30	0.88 ± 0.24
P. minor	PI 231045	10	0.51 ± 0.09	0.73 ± 0.13

ND, not detected.
Source: Gianoli and Niemeyer (1998). Reproduced after permission from Kluwer Academic Publishers.

(*Schizaphis graminum*). High levels of DIBOA (28 mmol/kg fresh weight) were reported in *Elymus arizonicus* (Scribner & Smith) Gould (Arizona wheatgrass). Arizona wheatgrass is suggested to be the most promising genus for breeding programs. Hydroxamic acids are non-volatile compounds and released into the environment by root exudation (Niemeyer and Perez, 1995). Barnes and Putnam (1983, 1986) reported that spring-sown rye suppressed the weed biomass by 93% when compared to rye-free plots. Interestingly, suppression of weeds such as wild oat was observed with rye cultivars and not with wheat or oat cultivars (Niemeyer and Perez, 1995). Niemeyer and Perez (1995) concluded that high amounts of hydroxamic acids in the roots should not be the criterion for the selection of allelopathic varieties. Root exudates are key to crop allelopathy. Root content is of little value as exudation

is an active metabolic process dependent upon cultivar genetics (Terry Haig, personal communication). Copaja et al. (1991) screened 52 Chilean cultivars of *T. aestivum* and *T. durum*, and found that DIMBOA amount varied from 1.4 to 10.9 mmol/kg fresh weight. DIMBOA amount was found to be maximum in *T. speltoides* (16 mmol/kg fresh weight) and least in *T. tauschii* (Coss.) Schmalh (0.21 mmol/kg fresh weight). While both monogenic and polygenic controls were suggested for the accumulation of DIMBOA in maize, the allelochemical gramine is suggested to be synthesized in the presence of double-recessive genes (*mmtt*).

Dilday and his colleagues (1998) evaluated the phytotoxic effects of 12,000 rice accessions against ducksalad (*Heteranthera limosa* (Sw.) willd.) and 5000 against redstem (*Ammannia coccinea* Rottb.). It was found that 412 rice accessions developed an allelopathic zone around rice plants for ducksalad and 145 for redstem. A hybrid (stg 94L42-130) between p1 338046 (allelopathic) and Katy (non-allelopathic) was reported to increase the yield by almost 2000 kg/ha compared to the yield of Katy. In greenhouse trials, stg 94L42-130 had less ducksalad plants compared to non-allelopathic cultivar Rexmont (Dilday et al., 1998). Hassan et al. (1998) reported that out of 1000 rice varieties screened for allelopathic activities against barnyardgrass and *Cyperus difformis* L. (small flower umbrella sedge), more than 30 varieties (e.g., RP 2269-424, LD 183-3, LDS 183-7, IET-1444, Dular, CI-selection 63, UPR 82-1-7, GZ 1368-5-2 and OR-131-58) had 50–90% control of barnyardgrass in a field situation. More than 10 varieties (e.g. RP 2271-433-231, IET 11754, Dular, OR 131-5-8) suppressed the growth of small flower umbrella sedge by 50–75%.

There has been significant progress in isolating rice allelochemicals (Rimando et al., 2001) and locating genes controlling allelopathic effects of rice (Jensen et al., 2001). Using a relay seeding technique, cultivar IAC 165 was shown to possess strong allelopathic activity compared to CO 39 having weak allelopathic activity (Jensen et al., 2001). These same workers identified quantitative trait loci (QTL) associated with the rice allelochemicals against barnyardgrass. This is an important step toward breeding allelopathic rice varieties. It was found that 35% of the total phenotypic variation of allelopathic activity of population was explained by four main effect QTLs situated on three chromosomes. There are, however, some questions yet to be answered. For example: Do allelopathic rice varieties have auto-toxic effects? (Jensen et al., 2001). Does the allelopathic potential of rice cultivars adversely influence cyanobacteria population of the paddy field? Cyanobacteria are known to fix nitrogen in paddy fields (Brady, 1996). Any adverse effect of allelopathic rice cultivars on nitrogen-fixing potential of cyanobacteria may not be desirable.

Wu et al. (1999) discussed several difficulties in investigating the inheritance of allelochemicals, for example, phytochemical analysis of plant material from genetically diverse genotypes. To have qualitative and quantitative data on allelochemicals, sophisticated techniques of natural product chemistry are needed. The nature of inheritance of allelochemicals may be complex. There may be more than two genes responsible for the production of an allelochemical. Furthermore, there are chances that allelopathic activity, due to several genes, is not/weakly correlated to yield of the crop (Olofsdotter et al., 1995). Another problem is the isolation of chemicals from the substratum. Even if a crop cultivar has high allelochemical levels and releases allelochemicals in large quantities, substratum ecology plays an important role by influencing the qualitative and quantitative availability of allelochemicals (Inderjit and Weiner, 2001).

As can be seen from the above discussion, there are now numerous examples of allelopathic effects that have been established decades ago. Today we are still looking for other allelopathic plants or weed species. Realistically, we have made a significant advances in this direction over the last three decades. We still have a long way to go in terms of using or developing plant species that would be used for weed management or can be used as companion crop.

5. Challenges in implementing allelopathic concepts

Demonstrating allelopathy as a strategy of interference in competitive crop cultivars might be a difficult process because different mechanisms of interference such as resource competition, allelopathy, nutrient immobilization and microbial influence all operate in parallel. Furthermore, allelochemicals are interwoven with environmental stresses (Einhellig, 1999). Therefore, demonstrating allelopathy as the sole mechanism of interference may prove to be a difficult task (Inderjit and Del Moral, 1997). A series of laboratory experiments involving modification of adverse effects of cultivars with N-fertilization, activated charcoal and abiotic soil might give some information on involvement of allelochemicals.

5.1. Limitations

There are certain limitations for using allelochemicals as natural herbicides. High cost, limited activity and selectivity restrict the use of natural herbicides e.g., maize gluten (Bhowmik, 1992) and pelargonic acid (Duke et al., 2001). Natural herbicide may also be toxic to non-target organisms. For example, a natural compound, alpha-terthienyl, isolated from the roots of the common marigold (*Tagetes erecta* L.) was originally

patented as a herbicide (Inderjit and Bhowmik, 2002). In addition to its herbicidal activity, alpha-terthienyl was also toxic to non-target species. Toxicity to non-target species is one of the main reasons which limit the use of natural compounds as herbicides. Duke et al. (2000) discussed some shortcomings of employing natural products as herbicides. These are: (i) many natural compounds are extremely expensive to synthesize, e.g. in spite of the excellent herbicidal activity of tentoxin, it is too expensive to manufacture, (ii) natural products have generally short environmental half-lives, and (iii) some natural compounds have potential mammalian toxicity and are carcinogenic; for example, AAL-toxin and fumonisin are toxic to mammalian cells. Some natural products may have other problems, like allergy. Sorgoleone, for example, is reported to cause dermatitis (Inderjit and Bhowmik, 2002).

Several phenolic acids (e.g., *p*-hydroxybenzoic, *trans-p*-coumaric, *cis-p*-coumaric, syringic, vanillic, *trans-* and *cis-*ferulic acids and 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one) are identified from wheat seedlings (Wu et al. 2000). Allelopathic wheat cultivars are reported to possess higher amounts of these compounds (Wu et al., 1998). Although these compounds are reported to be good candidates for herbicidal activity, weed-suppressing wheat cultivars can be used to naturally suppress weeds.

One important question is, which class of organic compounds (i.e. phenolics, terpenoids, alkaloids, etc.) is a better candidate for natural plant herbicides. Are there any steps that can be used to exploit the classes of natural compounds that can be used in weed management systems? Generally, concentrations used to test the activities of allelochemicals range from 10^{-4} to 10^{-7} M (Macias, 1995). From the environmental safety standpoint, good candidates for natural herbicide should have activity between 10^{-5} and 10^{-7} M (Macias 1995). Many phenolic compounds, alkaloids and quinones, however, have an activity range of $10^{-2} – 10^{-5}$ M, and thus are poor candidates for natural herbicides (Macias, 1995).

In general, the number of problems to be considered in discovery and development of a natural product as a herbicide is known to be larger and more complex when compared to a synthetic herbicide. In addition, molecular complexity, limited environmental stability, and the low herbicidal activity of many natural toxins are not encouraging at this time. Therefore, these characteristics of allelopathic compounds limit the scope of any developmental process by industries.

Although most of the simple phenolic acids and flavonoids are known to possess phytotoxicity, they seem to present as weak phytotoxins when in soil, and have little selectivity. Many of the phenolic compounds (e.g. salicylic acid and *p*-hydroxybenzoic acid), at very high rates, are effective against weeds and are relatively non-selective (Duke and Lydon 1987). Synthetic struc-

tural modifications of these compounds, however, may increase their activity and selectivity against weed species.

5.2. Interactions of allelochemicals and herbicides

Various ecological factors such as habitat, climate, edaphic factors, and agricultural practices greatly influence the fate, persistence, and quantitative and qualitative availability of allelochemicals in the rhizosphere. These factors along with crop management factors play an integral part in allelopathic expression in the field.

Foliar-applied herbicides may be exuded through roots of weed species and then be absorbed by nearby crop plants. Nicosulfuron is an effective herbicide against *Sorghum halepense* (L.) Pers. (johnsongrass) and *Elytrigia repens* (L.) Nevski (quackgrass) (Bhowmik et al. 1992). It is considered a good herbicide because corn is tolerant to the normal field use rate of nicosulfuron (18 – 105 g active ingredient/ha) (Bhowmik et al., 1992; Kapusta and Krausz, 1992; Camacho et al., 1991). Gubbiga et al. (1996) investigated the root exudation of nicosulfuron from nicosulfuron-treated johnsongrass. Johnsongrass was foliar treated with 50 or 100 μg ^{14}C-nicosulfuron/plant. The 23% of ^{14}C-nicosulfuron absorbed by the johnsongrass was found in the medium by 30 days after treatment. The subsequent uptake of exuded ^{14}C-nicosulfuron by corn roots was also shown. In subsequent experiments, these authors found that 10^{-8} M nicosulfuron can cause growth reduction in corn. Therefore, the sensitivity of a crop to a herbicide is an important factor in determining its use as a commercial herbicide.

The interaction between allelochemicals and herbicides is an area that might be exploited for weed management. A herbicide applied along with allelopathic conditions (crops or weeds) could have a complimentary action in weed management. This concept may lead to a reduced level of synthetic herbicide being used for a specific management program. The manipulation of formulation, timing, and rate of application of a herbicide may influence the nature of weed control.

6. Conclusion

In spite of several challenges in implementing the allelopathy concept in weed management, there is tremendous scope for exploring allelopathy phenomena for natural weed management. More research is needed on natural product chemistry and breeding of allelopathic crop varieties. Although chemicals have been identified from several plant varieties, it is not yet demonstrated beyond doubt that isolated chemicals are

actually responsible for allelopathic activity under field conditions. Furthermore, possible joint action of chemicals in determining allelopathic activity is an area of study that largely remains neglected. We can employ molecular and biotechnological tools to study the genetic control of quantitative trait and mapping of genes (Olofsdotter, 2001). Duke et al. (2000) state "We speculate that biotechnology may eventually allow for the production of highly allelopathic crops through the use of transgenes to increase allelochemical production to levels that effectively manage weeds without herbicides or with reduced herbicides input". Fischer et al. (1997) suggested that a little compromise with the crop yield in favor of better competitiveness is a profitable deal, particularly in view of the high cost of weed control and environmental hazards associated with the overuse of herbicides. We need to pay more attention to employ allelopathy as an alternate weed management strategy. With recent sophisticated molecular and biotechnological tools, the importance of allelopathy can be better explored and understood in weed management.

Acknowledgements

References

Abbas, H.K., Tanaka, T.K., Duke, S.O., Boyette, C.D., 1995. Susceptibility of various crop and weed species to AAL-toxin, a natural herbicide. Weed Technol. 9, 125–130.

Aldrich, R.J., 1984. Weed Crop Ecology: Principles in Weed Management. Breton Publishers, North Scituate, MA.

Alsaadawi, I.S., Al-Uqaili, J.K., Alrabeaa, A.J., Al-Hadithy, M., 1986. Allelopathic suppression of weed and nitrification by selected cultivars of *Sorghum bicolor* (L.) Moench. J. Chem. Ecol. 12, 209–219.

Baghestani, A., Lemieux, C., Lerour, G.D., Baziramakenga, R., Simard, R.R., 1999. Determination of allelochemicals in spring cereal cultivars of different competitiveness. Weed Sci. 47, 498–504.

Barnes, J.P., Putnam, A.R., 1983. Rye residues contribute to weed suppression in no–tillage cropping systems. J. Chem. Ecol. 9, 1045–1057.

Barnes, J.P., Putnam, A.R., 1986. Evidence of allelopathy by residues and aqueous extracts of rye (*Secale cereale*). Weed Sci. 34, 384–390.

Bewick, T.A., Shilling, D.G., Dusky, J.A., Williams, D., 1994. Effects of celery (*Apium graveolens*) root residues on growth of various crops and weeds. Weed Technol. 8, 625–629.

Bhowmik, P.C., 1988. Cinmethylin for weed control in soybeans, *Glycine max*. Weed Sci. 36, 678–682.

Bhowmik, P.C., 1992. Annual grass weed control. Mass Weed Sci. Res. Results 11, 77–80.

Bhowmik, P.C., 2000. Herbicide resistance: a global concern. Med. Fac. Landbouww. Univ. Gent. 65/2a, 19–30.

Bhowmik, P.C. Zhang, C.X. 2003. Potential use of mesotrione in controlling annual weed species in maize (*Zea mays*). The 19th Proceedings of the Asian-Pacific Weed Science Society Conference in press.

Bhowmik, P.C., O'Toole, B.M., Andaloro, J., 1992. Effects of nicosulfuron on quackgrass (*Elytrigia repens*) control in corn. Weed Sci. 6, 52–56.

Birkett, M.A., Chamberlain, K., Hooper, A.M., Pickett, J.A., 2001. Does allelopathy offer real promise for practical weed management and for explaining rhizosphere interactions involving higher plants? Plant Soil 232, 31–39.

Brady, N.C., 1996. The Nature and Properties of Soils. Prentice-Hall of India, New Delhi.

Camacho, R.F., Moshier, L.J., Morishta, D.W., Devlin, D.L., 1991. Rhizome johnsongrass (*Sorghum halepense*) control in corn (*Zea mays*) with primisulfuron and nicosulfuron. Weed Technol. 5, 789–794.

Cardina, J., 1995. Biological weed management. In: Smith, .A.E. (Ed.), Handbook of Weed Management Systems. Marcel Dekker, New York, pp. 279–341.

Copaja, S.V., Barria, B.N., Niemeyer, H.M., 1991. Hydroxamic acid content of perennial *triticeae*. Phytochemistry 30, 1531–1534.

Czarnota, M.A., Paul, R.N., Dayan, F.E., Weston, L.A., 2001. Further studies on the mode of action, localization of production, chemical nature, and activity of sorgoleone: a potent PS II inhibitor produced in *Sorghum* spp. root exudates. Weed Technol. 15, 813–825.

Dayan, F.E., Hernandez, A., Allen, S.N., Moraces, R.M., Vroman, J.A., Avery, M.A., Duke, S.O., 1999. Comparative phytotoxicity of artimisinin and several sesquiterpene analogues. Phytochemistry 50, 607–614.

Dilday, R.H., Yan, W.G., Moldenhauer, K.A.K., Gravois, K.A., 1998. Allelopathic activity in rice for controlling major aquatic weeds. In: Olofsdotter, M. (Ed.), Allelopathy in Rice. IRRI Press, Manila, pp. 7–26.

Duke, S.O., 1986. Naturally occurring chemical compounds as herbicides. Rev. Weed Sci. 2, 15–44.

Duke, S.O., Lydon, J., 1987. Herbicides from natural compounds. Weed Technol. 1, 122–128.

Duke, S.O., Vaughn, K.C., Croom, E.M., Elsohly, H.N., 1987. Artemisinin, a constituent of annual wormwood (*Artemisia annua*) is a selective phytotoxin. Weed Sci. 35, 499–505.

Duke, S.O., Dayan, F.E., Ramagni, J.G., Rimando, A.M., 2000. Natural products as sources of herbicides: current status and future trends. Weed Res. 40, 90–111.

Duke, S.O., Scheffler, B.E., Dayan, F.E., 2001. Allelochemicals as herbicides. In: Bonjoch, N.P., Reigosa, M.J. (Eds.), First European OECD Allelopathy Symposium: Physiological Aspects of Allelopathy. GAMESAL, SA, pp. 47–59.

Duke, S.O., Dayan, F.E., Rimando, R.M., Schrader, K.K., Aliotta, G., Oliva, A., Romagni, J.G., 2002. Chemicals from nature for weed management. Weed Sci. 50, 138–151.

Einhellig, F.A., 1995. Allelopathy: current status and future goals. In: Inderjit, Dakshini, K.M.M., Einhellig, F.A. (Eds.), Allelopathy: Organisms, Processes and Applications. American Chemical Society, Washington, DC, pp. 1–24.

Einhellig, F.A., 1999. An integrated view of allelochemicals amid multiple stresses. In: Inderjit, Dakshini, K.M.M., Foy, C.L. (Eds.), Principles and Practices in Plant Ecology: Allelochemical Interactions. CRC Press, Boca Raton, FL, pp. 479–494.

Einhellig, F.A., Leather, G.R., 1988. Potentials for exploiting allelopathy to enhance crop production. J. Chem. Ecol. 14, 1829–1844.

Einhellig, F.A., Souza, I.F., 1992. Phytotoxicity of sorgoleone found in grain sorghum root exudates. J. Chem. Ecol. 18, 1–11.

Fay, P.K., Duke, W.B., 1977. An assessment of allelopathic potential of *avena* germplasm. Weed Sci. 25, 224–228.

Fischer, A., Ramirez, H.V., Lozano, J., 1997. Suppression of junglerice (*Echnochloa colona* (L.) Link.) by irrigated rice cultivars in central America. Agron. J. 89, 516–521.

Fischer, A.J., Ateh, C.M., Bayer, D.E., Hill J ,E., 2000a. Herbicide-resistant *Echinochloa oryzoides* and *E. phyllopogon* in California *Oryza sativa* fields. Weed Sci. 48, 225–230.

Fischer, A.J., Beyer D ,E., Carriere, M.D., Ateh, C.M., Yim, K.O., 2000b. Mechanisms of resistance to bispyribac-sodium in an *Echinochloa phyllopogon* accession. Pestic. Biochem. Physiol. 68, 156–165.

Forney, D.R., Foy, C.L., 1985. Phytotoxicity of products from rhizosphere of a sorghum–sudangrass hybrid (*Sorghum bicolor* X *Sorghum sudanense*). Weed Sci. 33, 597–604.

Fujii, Y., Shibuya, T., Yasuda, T., 1992. Allelopathy of velvetbean: its discrimination and identification of L-DOPA as a candidate of allelopathic substances. Jpn. Agric. Res. Q. 25, 238–247.

Gattas-Hallak, A.M., Davide, L.C., Souza, I.F., 1999. Effect of sorghum (*Sorghum bicolor* L.) root exudates on the cell cycle of the bean plant (*Phaseolus vulgaris* L.) roots. Gen. Mol. Biol. 22, 95–99.

Gianoli, E., Niemeyer, H.M., 1998. DIBOA in wild *poaceae*: sources of resistance to the russian wheat aphid (*Diuraphis noxia*) and the greenbug (*Schizaphis graminum*). Euphytica 102, 317–321.

Gonzalez, V.M., Kazimir, J., Nimbal, C., Weston, L.A., Cheniae, G.M., 1997. Inhibition of a photosystem II electron transfer reaction by the natural product sorgoleone. J. Agric. Food Chem. 45, 1415–1421.

Gubbiga, N.G., Worsham, A.D., Corbin, F.T., 1996. Root/rhizome exudation of nicosulfuron from treated johnsongrass (*Sorghum halepense*) and possible implication for corn (*Zea mays*). Weed Sci. 44, 455–460.

Hanson, A.D., Trayner, P.L., Dittz, K.M., Reicosky, D.A., 1981. Gramine in barley forage—effects of genotypes and environment. Crop Sci. 21, 726–730.

Harrison Jr, H.F., Petersen, J.K., 1986. Allelopathic effects of sweet potato (*Ipomoea batatas*) on yellow nutsedge (*Cyperus esculentus*) and alfalfa (*Medicago sativa*). Weed Sci. 34, 623–627.

Hassan, S.M., Aidy, I.R., Bastawisi, A.O., Draz, A.E., 1998. Weed management using allelopathic rice varieties in Egypt. In: Olofsdotter, M. (Ed.), Allelopathy in Rice. IRRI Press, Manila, pp. 27–37.

Heap, I.M., 1997. The occurrence of herbicide-resistant weed worldwide. Pestic Sci. 51, 235–243.

Heisey, R.M., 1996. Identification of an allelopathic compound from *Ailanthus altissima* (simaroubaceae) and characterization of its herbicidal activity. Am. J. Bot. 83, 192–200.

Heisey, R.M., 1999. Development of an allelopathic compound from tree-of-heaven (*Ailanthus altissima*) as a natural product herbicide. In: Cutler, H.G., Cutler, S.J. (Eds.), Biologically Active Natural Products: Agrochemicals. CRC Press, Boca Raton, FL, pp. 57–68.

Hensley, J.R., Counselman, C.J., 1979. Allelopathic interaction between triazine resistant and susceptible strains of redroot pigweed. Weed Sci. Soc. Am. Abstr. 19, 110.

Inderjit, 2001. Soils: environmental effect on allelochemical activity. Agron. J. 93, 79–84.

Inderjit, Bhowmik, P.C., 2002. The importance of allelochemicals in weed invasiveness and the natural suppression. In: Inderjit, Mallik, A.U. (Eds.), Chemical Ecology of Plant: Allelopathy of Aquatic and Terrestrial Ecosystems. Birkhauser Verlag AG, Basal, pp. 187–192.

Inderjit, Del Moral, R., 1997. Is separating resource competition from allelopathy realistic? Bot. Rev. 63, 221–230.

Inderjit, Keating, K.I., 1999. Allelopathy: principles, procedures, processes, and promises for biological control. Adv. Agron. 67, 141–231.

Inderjit, Weiner, J., 2001. Plant allelochemical interference or soil chemical ecology? Perspec. Plant Ecol. Evol. System 4, 3–12.

Inderjit, Olofsdotter, M., Striebig, J.C., 2001. Wheat (*Triticum aestivum*) interference with seedling growth of perennial ryegrass

(*Lolium perenne*): influence of density and age. Weed Technol. 15, 807–812.

Inderjit, Striebig, J., Olofsdotter, M., 2002. olofsdotter, m. Joint action of phenolic acid mixtures and its significance in allelopathy research. Physiol. Plant 114, 422–428.

Itoh, K., Wang, G.X., Ohba, S., 1999. Sulfonylurea resistance in *Lindernia micrantha*, an annual paddy weed in japan. Weed Res. 39, 413–423.

Jensen, L.B., Courtois, B., Shen, L., Li, Z., Olofsdotter, M., Mouleon, R.D., 2001. Locating genes controlling allelopathy effect against barnyardgrass in upland rice. Agron. J. 89, 21–26.

Kapusta, G., Krausz, .R.F., 1992. Interaction of terbufos and nicosulfuron on corn (*Zea mays*). Weed Technol. 6, 999–1003.

Khan, Z.R., Ampong-Nyarko, K., Chiliswa, P., Hassanali, A., Kimani, S.I., Wande, .W., Overholt, W.A., Pickett, J.A., Smart, I.E., Wadhams, I.J., Woodcock, C.M., 1997. Intercropping increase parasitism in pest. Nature 388, 631–632.

Leather, G.R., 1983a. Sunflowers (*Helianthus annuus*) are allelopathic to weeds. Weed Sci. 31, 37–42.

Leather, G.R., 1983b. Weed control using allelopathic crop plants. J. Chem. Ecol. 9, 983–990.

Leather, G.R., 1987. Weed control using allelopathic sunflowers and herbicide. Plant Soil 98, 17–23.

Leather, G.R., Forrence, L.E., 1979. Allelopathic potential of thirteen varieties of sunflower. Abstr. Weed Sci. Soc. Am. 19, 172.

Lemerle, D., Verbeek, B., Orchard, B., 2001. Ranking the ability of wheat varieties to compete with *Lolium rigidum*. Weed Res. 41, 197–209.

Lydon, J., Teasdale, J.R., Chen, P.K., 1997. Allelopathic activity of annual wormwood (*Artemisia annua*) and its role of artemisinin. Weed Sci. 45, 807–811.

Macias, F.A., 1995. Allelopathy in search for natural herbicide models. In: Inderjit, Dakshini, K.M.M., Einhellig, F.A. (Eds.), Allelopathy: Organisms, Processes, and Applications. American Chemical Society, Washington, DC, pp. 310–329.

Macias, F.A., Varela, R.M., Torres, A., Molinillo, J.M.G., 1999. Potential of cultivar sunflowers (*Helianthus annuus* L.) as a source of natural herbicide template. In: Inderjit, Dakshini, K.M.M., Foy, C.L. (Eds.), Principles and Practices in Plant Ecology: Allelochemical Interactions. CRC Press, Boca Raton, FL, pp. 531–550.

Molisch, H. 1937. Der Einfluss einer Pflanz auf die andere–Allelopathige. Fischer, Jena, Germany.

Muller, W.H., Muller, C.H., 1964. Volatile growth inhibitors produced by *Salvia* species. Bull. Torrey Bot. Club 91, 327–330.

Mwaja, V.N., Masiunar, J.B., Weston, L.A., 1995. Effect of fertility on biomass, phytotoxicity and allelochemical content of cereal rye. J. Chem. Ecol. 21, 81–96.

Niemeyer, H.M., 1988. Hydroxamic acids (4-hydroxy-1,4-benzoxazin–ones) defense chemicals in the gramineae. Phytochemistry 27, 267–292.

Niemeyer, H.M., Perez, F.J., 1995. Potential of hydroxamic acids in the control of cereal pests and diseases and weeds. In: Inderjit, Dakshini, K.M.M., Einhellig, F.A. (Eds.), Allelopathy: Organisms, Processes, and Applications. American Chemical Society, Washington, DC, pp. 260–270.

Niemeyer, H.M., Coapaja, S.V., Barria, B.N., 1992. The triticeae as sources of hydroxamic acids, secondary metabolites in wheat conferring resistance against aphids. Hereditas 116, 295–299.

Nimbal, C.I., Pedersen, J.F., Yerkes, C.N., Weston, L.A., Weller, S.C., 1996a. Phytotoxicity and distribution of sorgoleone in grain sorghum germplasm. J. Agric. Food Chem. 44, 1343–1347.

Nimbal, C.I., Yerkes, C.N., Weston, L.A., Weller, S.C., 1996b. Herbicidal activity and site of action of the natural product sorgoleone. Pest Chem. Physiol. 54, 73–83.

Olofsdotter, M., 2001. Rice — a step toward use of allelopathy. Agron. J. 93, 3–8.

Olofsdotter, M., Navarej, D.C., Moody, K., 1995. Allelopathic potential of rice (*Oryza sativa* L.) germplasm. Ann. Appl. Biol. 127, 543–560.

Parish, S., 1990. A review of non-chemical control technologies. Biol. Agric. Hortic. 7, 117–137.

Przepiorkowski, T., Gorski, S.F., 1994. Influence of rye (*Secale cereale*) plant residues on germination and growth of three triazine-resistant and susceptible weeds. Weed Technol. 8, 744–747.

Putnam, A.R., 1983. Allelopathic chemicals: nature's herbicide in action. Chem. Eng. News 4, 34–45.

Putnam, A.R., 1988. Allelochemicals from plants as herbicides. Weed Technol. 2, 510–518.

Putnam, A.R., Duke, W.D., 1974. Biological suppression of weeds: evidence for allelopathy in accessions of cucumber. Science 185, 370–372.

Putnam, A.R., DeFrank, J., Barnes, J.P., 1983. Exploitation of allelopathy for weed control in annual and perennial cropping systems. J. Chem. Ecol. 9, 1001–1010.

Rice, E.L., 1984. Allelopathy. Academic Press, Orlando, FL.

Rice, E.L., 1995. Biological Control of Weeds and Plant Diseases: advances in applied allelopathy. University of Oklahoma Press, Norman, OK.

Rimando, A.M., Olofsdotter, M., Dayan, F.E., Duke, S.O., 2001. Searching for rice allelochemicals: an example of bioassay-guided isolation. Agron. J. 93, 16–20.

Rose, S.J., Burnside, O.C., Specht, J.E., Swisher, B.A., 1984. Competition and allelopathy between soybeans and weeds. Agron. J. 76, 523–528.

Streibig, J.C., Dayan, F.E., Rimando, A.M., Duke, S.O., 1999. Joint action of natural and synthetic photosystem II inhibitors. Pestic. Sci. 55, 137–146.

Teasdale, J.R., 1993. Interaction of light, soil moisture, and temperature with weed suppression by hairy vetch residue. Weed Sci. 41, 46–51.

Teasdale, J.R., 1998. Cover crops, smoother plants, and weed management. In: Hatfield, J.L., Buhler, D.D, Stewart, B.A. (Eds.), Integrated Weed and Soil Management. Ann Arbor Press, Chelsea, MI, pp. 247–270.

Teasdale, J.R., Daughtry, C.S.T., 1993. Weed suppression by live and desiccated hairy vetch (*Vicia villosa*). Weed Sci. 41, 207–212.

Tellez, M.R., Canel, C., Rimando, A.M., Duke, S.O., 1999. Differential accumulation of fumonisins and related compounds in a ducksalad bioassay. Phytochemistry 33, 779–785.

Weston, L.A., 1996. Utilization of allelopathy for weed management in agroecosystems. Agron. J. 88, 860–866.

Worsham, A.D., 1991. Allelopathic cover crops to reduce herbicide input. Proc. South West Sci. Soc. 44, 58–69.

Wu, H., Pratley, J., Lemerle, D., Haig, T., Verbeek, B., 1998. Differential allelopathic potential among wheat accessions to annual ryegrass. In: Michalk, D.L., Prately, J.E. (Eds.), Proceedings, of the Ninth Australian Agronomy Conference. Wagga Wagga, Australia, pp. 567–571.

Wu, H., Pratley, J., Lemerle, D., Haig, T., 1999. Crop cultivation with allelopathic activity. Weed Res. 39, 171–180.

Wu, H., Haig, T., Pratley, J., Lemerle, D., An, M., 2000. Distribution and exudation of allelochemicals in wheat *Triticum aestivum*. J. Chem. Ecol. 26, 2141–2154.

Yenish, J.P., Worsham, A.D., Chilton, W.S., 1995. Disappearance of DIBOA-glucoside, DIBOA, and BOA from rye (*Secale cereal* L.) cover crop residue. Weed Sci. 43, 18–20.