



Importance of allelopathy in agriculture: Bioavailability and functions of allelochemicals in soil environment

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ABSTRACT

Weed invasion and subsequent infestation represents a major problem in crop production. Chemical weed control is the major management tactic used in conventional agriculture. Complementary strategies to herbicides are increasingly being investigated. The importance of allelopathy has been considered for weed management over the years. However, the relevance of allelopathy has been highly discussed due to the lack of phytotoxic concentrations of allelochemicals under field conditions. *Avena fatua*, *Brassica nigra*, *Fagopyrum esculentum*, *Secale cereale*, *Sorghum bicolor*, *Triticum aestivum* and other cover crops have been used in weed management on a limited basis. Crop residues from existing crop or rotational crops can provide selective weed suppression through their physical presence on the soil surface and/or through the release of allelochemicals. Some of the allelochemicals have been reported to play a role in weed management, including phenolic acids, DIBOA, DIBOA-glycoside, and BOA, dhurrin, fatty acids, hydroxamic acids, isoflavonoids, isothiocyanate, juglone, momilactone, scopoletin, and sorgoleone. The soil system, a living and dynamic, influences the fate and functions of allelochemicals in time and space. The bioavailability of allelochemicals in the soil is dependent on processes such as adsorption, leaching and degradations by abiotic and biotic factors. The clay types, organic matter, and soil pH can affect the bioavailability of allelochemicals in the soil. Thus, the allelopathic potential of many compounds may not be expressed in some soils because of the chemical adsorption to soil colloids. The resulting concentrations (sub-toxic) of any of these allelochemicals in soil matrix may have a variety of functions that influence seed germination, seedling emergence, plant growth suppression, nutrient acquisition or soil microbial activity. Examples of such compounds are benzoic acid, catechin, coumaric acid, dihydroxyphenylalanine, ferulic acid, hydroxybenzoic acid, sorgoleone, vanillic acid, and others.

In my view, future allelopathic research should be focused on mechanisms facilitating persistence of allelochemicals in soil environment and characterization of complementary roles of these compounds in plant growth and development. The bioavailability of allelochemicals under field conditions must be established for its effective role in weed management. Currently, we face challenges and opportunities in using allelopathy as a part of weed management strategies in today's production agriculture.

INTRODUCTION

An Austrian plant physiologist, Hans Molisch coined term allelopathy in 1937. Later, allelopathy was defined as the effect(s) of one plant (including microorganisms) on another plant through the release of a chemical compound(s) into the environment (Rice 1984). This definition includes both inhibitory and stimulatory effects, depending on the

concentration of the compound(s). However, inhibitory effects of plants or crop residues are of great importance in relation to weed management. Allelopathic research through the last several decades has demonstrated many aspects of allelopathy, including the applied nature of allelopathy in weed management. To demonstrate allelopathy, one must identify one or more phytotoxins produced by the

putative allelopathic plant or identify a compound(s) produced by the donor plant that is converted to a phytotoxin in the soil complex. The compound(s) must be present in sufficient quantity (in time and space) in the soil for allelopathic effects in controlling weeds. Allelochemicals are generally weak phytotoxins. Most of the allelochemicals are present at low concentrations, and undergo rapid chemical and biological degradation in the soil. The focus of this presentation is to discuss (i) the importance of cover crops residues in weed management, (ii) the nature of allelochemicals, and (iii) the role of soil factors in allelopathic activity, and iv) challenges in implementing allelopathy in weed management.

Cover crops residues

Cover crop residues such as *Avena fatua*, *Brassica nigra*, *Fagopyrum esculentum*, *Secale cereale*, *Sorghum bicolor*, *Triticum aestivum*, *Vicia villosa* and others have been used in weed management on a limited basis. Crop residues from existing crop or rotational crops can provide selective weed control through their physical presence on the soil surface and through the release of allelochemicals (Fay and Duke 1977, Bhowmik and Doll 1982, Alsaadawi *et al.* 1986, Teasdale 1993, Weston 1996, Barker and Bhowmik 2001, Jabran *et al.* 2015). The allelochemicals are concentrated and exuded through roots or are released during decomposition of plant litter (Siqueira *et al.* 1919, Bonanomi *et al.* 2006).

Earlier reports have shown that 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 winter freezing, and allowing their residues to remain on the soil surface (Putnam *et al.* 1983, Barker and Bhowmik, 2001). Barnes and Putnam (1983) reported that *Secale cereale* 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. 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 *Secale cereale* residue and allelochemicals, DIBOA (2,4-dihydroxy-1,4-benzoxazin-3-one), DIBOA-glycoside and BOA from *Secale cereale* residues. These authors found that 50% of the initial content of *Secale cereale* residue disappeared by 105 days after clipping. However, the combined active compound concentrations of DIBOA-glycoside, DIBOA, and BOA disappeared 168 days after clipping.

Allelopathy can play a beneficial role in various cropping systems (Haramoto and Gallandt 2005, Macias *et al.* 2014, Jabran *et al.* 2015). In a 5-yr field study with *Helianthus annuus* and *Avena fatua* rotation, the weed density increase was significantly less in sunflower plots than in control plots (Leather, 1983). It was found that sunflower plants possess chemicals, which inhibit the growth of common weed species.

Allelochemicals for weed management

Thousands of allelopathic substances have been isolated from plants and their chemical structure has been determined. However, the mode-of-action (MOA) has only been elucidated for a limited number of allelochemicals (Vyvyan 2002). Some of the allelochemicals such as allyl isothiocyanate (*Brassica* sp., black mustard), fatty acids (*Polygonum spp.*), isoflavonoids and phenolics (*Trifolium spp.*, *Melilotus spp.*), phenolic acids and scopoletin (*Avena sativa*), hydroxamic acids (*Triticum* sp.), phenolic acids, dhurrin, and sorgoleone (*Sorghum bicolor*) have been reported for weed control (Duke *et al.* 2002). Artemisinin, a sesquiterpenoid lactone, has been shown to inhibit the growth of *Amarantus retroflexus*, *Ipomoea lacunosa*, *Artemisia annua* and *Portulaca oleracea* (Duke *et al.* 1987). The phytotoxic activity of sorgoleone against weed species was first reported by Einhellig and Souza (1992). Mushtaq and Siddiqui (2010) reported that plants belonging to Asteraceae family are the most studied species for allelopathic potential to control weeds in India. Some of the species including *Parthenium hysterophorus*, *Ageratum conyzoides* and others received more attention.

Allelopathic activity in soil environment

The soil system, a living and dynamic, influences the fate and functions of allelochemicals in time and space. The bioavailability of allelochemicals in the soil is dependent on processes such as adsorption, leaching and degradations by abiotic and biotic factors. The clay types, organic matter, and soil pH can affect the bioavailability of allelochemicals in the soil. An excellent review in this area has been published by Kobayashi (2004).

The allelopathic activity of many compounds is not expressed in some soils because of the chemical adsorption to soil colloids. For instance, sorgoleone binds strongly to soil colloids because it is a highly lipophilic allelochemical, with a logP (log octanol-water partition coefficient) of 6.1 (Trezzi *et al.* 2016). The allelopathic compounds 1-3,4dihydrox

phenylalanine and catechin are also strongly adsorbed by soil colloids, possibly due to the catechol group present in these molecules (Furubayashi *et al.* 2007). Reduced allelopathic potential of benzoxazinoid compounds 2-aminophenoxazin-3-one and DIBOA (2,4-dihydroxy-(2H)-1,4-benzoxazin-3(4H)-one) have been reported due to their adsorption by soil colloids (Teasdale *et al.* 2012). The chemical compounds that are not adsorbed onto colloids or minerals are usually in the soil solution. Thus, they can be absorbed by plants or leached (Kobayashi 2004, Kong *et al.* 2007, Li *et al.* 2013). Kong *et al.* (2007) reported that flavonoids with a high mobility in the soil profile were less phytotoxic than those with reduced soil mobility with rice plants. Similarly, an analysis of ten potential allelochemicals revealed an inverse relationship between soil mobility and their toxic effect on target plants (Li *et al.* 2013).

Preferential absorption allelochemicals in soil

Use of allelopathy is gaining its application in current agricultural science. However, the role of sorption to soil in modifying the bioavailability of components in complex allelochemical mixtures is still not well understood. Soils are capable of altering the phytotoxicity of plant secondary metabolites by changing their bioavailability, persistence, and fate under field conditions. Sorption is one of the prominent factors affecting the phytoavailability of allelochemicals in soil.

In one of our studies, the role of preferential sorption to soil in altering the chemical composition of plant exudates was studied in a silt loam soil using representative mixtures of plant phenolic acids, namely, hydroxybenzoic acid, vanillic acid, coumaric acid, and ferulic acid Tharayil *et al.* (2006). Removal of organic matter substantially decreased the sorption affinity of all phenolic acids. Direct competition for sorption sites was observed even at low concentrations of phenolic acids. The K_d value of hydroxybenzoic acid was decreased more than 90% in the presence of coumaric acid. About 95% of sorbed vanillic acid was displaced into the soil solution in the presence of ferulic acid. Hydroxybenzoic acid did not affect the sorption affinity of other phenolic acids significantly, whereas ferulic acid showed low displacement by other phenolic acids. The displacement pattern indicated directional sorption of phenolic acids with -OH and -COOH groups. Soil organic matter was associated with preferential sorption. The preferential sorption to soil can alter the availability of plant exudates in mixtures and thus may mediate their phytotoxic effects (Tharayil *et al.* 2006).

Soil sorption can also protect compounds from microbial degradation and thus indirectly alter their phytotoxic effects (Dalton, 1989, Wauchope *et al.* 2002). The soil sorption properties of some individual allelochemicals have previously been studied. Various soil components such as organic matter, sesquioxides, and clay minerals have been found to affect the phytoavailable concentration of allelochemicals (Dalton *et al.* 1989, Ohno, 2001, Wang *et al.* 1978). Considering the fact that compounds in the soil solution are more phytoavailable than those sorbed to the soil matrix (Lehman and Blum, 1999, Ito *et al.* 1998), the varied sorption affinity of compounds in a mixture will change the composition of plant exudates that become bioavailable. Different compounds in plant exudates differ widely in their phytotoxicity (Wu *et al.* 2002, Uren, 2001) and therefore preferential sorption to soil could in turn alter the phytotoxicity of these exudates.

Microbial degradation in soil

Biotic processes are involved in determining the fate of allelopathic compounds in soil. Microorganisms produce enzymes which catalyze the oxidation and polymerization reactions of phenolic acids (Huang *et al.* 1999, Lou *et al.* 2016). Microbial activity will alter phenolic compounds in soil and subsequently alter the expressed level of phytotoxicity (Blum 1998).

Phenolic acids are readily converted from one structure to another with different phytotoxicities (e.g., ferulic acid to vanillic acid) by soil-borne microbes (Blum 1998). Schmidt and Ley (1999) suggested that carbon-limited soil organisms would rapidly mineralize phenolic compounds due to their higher energy content on a per weight basis than simple sugars. Zikmundová *et al.* (2002) studied the biotransformation of the phytoanticipins BOA and HBOA by four endophytic fungi isolated from *Aphelandra tetragona*. It was shown that the metabolic pathway for HBOA and BOA degradation leads to o-aminophenol as a key intermediate.

Microorganisms play important roles in releasing additional allelochemicals bound up in the recalcitrant fractions of cover crop residues (Barnes *et al.* 1987). These insoluble allelochemicals can constitute a significant fraction of total allelopathic potential of a cover crop residue (Harper and Lynch 1982), so microbes may slowly release residue-derived allelochemicals, extending the longevity of a cover crop's effectiveness. Microbes can deactivate water soluble allelochemicals released soon after

cover crop residue incorporation (Jilani *et al.* 2008). As agricultural soils are not sterile, it is important to understand how microbial activity moderates allelopathic potential of cover crop residues (Blum 1998, Inderjit 2005). Mohler *et al.* (2012) recently showed that unsterilized live soil (*i.e.*, with a natural microbial community) reduces seedling germination rates when cover crop residues are incorporated, and the combined effect of residues and live microorganisms is greater than the effect of either of these components alone.

The degradation of allelochemicals in the soil may be altered, reducing their efficacy. In non-sterilized soil, for instance, DIBOA showed a half-life of 43h. However, 2-aminophenoxazin-3-one (APO), the final degradation product of DIBOA, has a low mineralization rate and therefore, a half-life greater than 90 days (Macías *et al.* 2005). In addition, some flavonoid glycoside molecules exuded by rice plants can suffer high mineralization by soil microorganisms, resulting in a glycosylated compounds. Flavonoid glycosides and a glycoside have a half-life of 2 h and 30 h, respectively, suggesting a higher allelopathic activity for the second group (Kong *et al.* 2007). The biodegradation of the sorgoleone quinone ring is relatively slow, with only 21% being mineralized 77 d after incubation in soil. However, the sorgoleone methoxy group was biodegraded within a few days, particularly in soils with a low colloid content (Gimsing *et al.* 2009).

Bioavailability of allelochemicals

Soils may also influence the relative activity of allelochemicals in combination(s). Because allelochemicals are generally exuded in mixtures of metabolites that often include other allelochemicals (Wu *et al.* 1999, Uren *et al.* 2001), preferential sorption of compounds onto the soil matrix could further alter availability.

The persistence of allelochemical mixtures may be enhanced in soil environment. In one of our studies, we found that one compound in combination can make the bioavailability and half-life of others greater in soil, because of competitive sorption and preferential degradation. Allelochemicals may also help plants to acquire nutrients in infertile soils which give competitive advantage to the donor plant over its neighbors.

The interaction of allelochemicals in the soil matrix remains as one of the least understood areas in the research on allelopathy (Tharayil *et al.* 2006). Most of the allelopathic interactions take place in the soil, where allelochemicals are concentrated and

exuded through roots (Bias *et al.* 2003) or are released during decomposition of plant litter (Bonanomi *et al.* 2006, Siqueira *et al.*, 1991). Thus, soil matrix forms the primary medium for the transport of allelochemicals from a donor to a receiver plant. During this transportation, the soil matrix is capable of altering the bioavailability of allelochemicals by various processes including sorption and chemical and microbial degradation (Tharayil *et al.* 2006, Ohno 2001). Because allelochemicals are secreted in quantities far less than needed to overwhelm the soil processes, at the field level, the soil matrix becomes the governing factor in the allelopathic activity. Thus, in many cases allelochemicals are not found in phytotoxic quantities under field conditions (Perry *et al.* 2007, Blum 1992).

A less attention has been made in the fact that the allelochemicals may be released as mixtures with other compounds (Wu *et al.* 2002). The degradation pattern of individual allelochemicals in soil matrices has been studied before (Dalton 1989, Ohno 2001). The disappearance of allelochemicals was delayed when present in a multi-solute mixture from both soils. This slow disappearance of allelochemicals in a mixture could be due to the combined effect of preferential degradation, where compounds with a stable ring structure and without a 3-C (acrylic) side chain are less susceptible to degradation, and competitive sorption, where less hydrophobic molecules are displaced into soil solution (Tharayil *et al.* 2006).

Microbial degradation of substrate in soil matrix is related to biological activity of the compound, where toxic compounds are degraded slowly (Kurt-Karakus *et al.* 2007). Addition of a more soluble and energy-efficient carbon source has been shown to reduce the microbial decomposition accompanying complex substrates (Pue *et al.* 1995). Competition for sorption sites arises if the same sites can be occupied by more than one non identical molecule (Xing *et al.* 1996, Tharayil *et al.* 2006). This competition for sorption sites in a soil matrix could increase the effective concentration of phenolic acids in soil solution (Tharayil *et al.* 2006).

Litter decomposition of *Centauria maculosa* in sandy loam soil yielded five phenolic acids, namely, hydroxybenzoic, vanillic, protocatechuic, p-coumaric, and ferulic acids (Tharayil *et al.* 2008). The degradation studies were conducted by exogenous application of catechin, the primary allelochemical exuded by *C. maculosa*, and the phenolic acid co-solutes in a sandy loam and silt loam soil. Compared to a single-solute system, in a multi-

solute system the persistence of individual allelochemicals was significantly increased in both soils. Oxidation and sorption were primarily involved in the disappearance of allelochemicals. Catechin rapidly underwent polymerization to form procyanidin dimer both in soil and in bioassay medium, resulting in reduced persistence and phytotoxicity. Hence, catechin phytotoxicity could occur only under conditions that would inhibit these condensation reactions. This study clearly demonstrates that various soil mechanisms including competitive sorption and preferential degradation would increase the persistence of allelochemical mixtures in a soil matrix (Tharayil *et al.* 2008).

Allelopathic crop cultivars

Researchers have screened crop cultivars for their differential allelopathic activity for the last three decades (Gealy *et al.* 2000, Wu *et al.* 1998, Kato-Noguchi *et al.* 2010, Mahmood *et al.* 2013, Mahajan and Chauhan 2013, Masum *et al.* 2018). In general, more monocot crop species have been searched for allelopathy compared to broadleaf species. Several members of the family Poaceae have been identified as allelopathic. 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-1,4benzoxazin-3-one); their distribution with cultivated Poaceae, however, is uneven (Niemeyer 1988). While wheat has both DIMBOA and DIBOA, *Secale cereale* contains only DIBOA.

The allelopathic activity of *Avena* species has been established by Fay and Duke (1977). They examined 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 *Brassica caber* significantly reduced Brassica plant growth more than that obtained when the weed was grown with 'Garry' oats.

Over the last decade, *Oryza spp.* accessions or cultivars have been examined for their allelopathic activity in suppressing weed species (Dilday *et al.* 1998, Hassan *et al.* 1998, Gealy *et al.* 2000, Olofsdotter 2001, Olofsdotter *et al.* 1995). Dilday and his colleagues (1998) evaluated the phytotoxic effects of 12,000 rice accessions against *Heteranthera limosa* and 5000 against *Ammannia*

coccinea. They found that 412 rice accessions developed an allelopathic zone around rice plants for *Heteranthera limosa* and 145 for *Ammannia coccinea*. 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.

Eight cultivars of *Oryza sativa* inhibited shoot and root growth of *Echinochloa crus-galli* when co-cultured with rice seedlings in a bioassay medium (Koto-Noguchi *et al.* 2010). They identified momolactone A and B in the bioassay medium of all rice cultivars. The concentrations of momolactone A and B varied from 0.21-1.5 and 0.66-3.8 $\mu\text{mol/L}$, respectively demonstrating the evidence of secretion of these two compounds from all rice cultivars into the medium.

Allelopathic activity of rice species has been reported by screening 50 rice cultivars from Bangladesh against *Echinochloa crus-galli* (barnyardgrass) and *Echinochloa colona* (jungle rice) by using Equal Compartment Agar Method (Masum *et al.* 2016). They reported 7 to 37% suppression of *Lactuca sativa*, *Lepidium sativum*, and *Raphanus sativus*. Recently, Masum and his group (2018) identified four potential allelochemicals from four indigenous rice cultivars. Aqueous methanol extracts of the Bangladesh indigenous rice (*Oryza sativa* L.ssp. *indica*) variety 'Boterswar' inhibited the germination and seedling growth of *Lepidium sativum* and *Echinochloa crus-galli* which suggested that this variety may contain phytotoxic substance(s). Four biologically active compounds, syringaldehyde (4-hydroxy-3,5-dimethoxybenzaldehyde), (-) loliolide, 3 α -hydroxy-5 α ,6 α -epoxy-7-megastigmen-9-one and 3-hydroxy- α -ionone, were isolated. The biological activity of these compounds showed that concentration > 10 μM significantly inhibited the root and shoot growth of *E. crus-galli* seedlings, and the *I50* (50% growth inhibition) values ranged from 16.03 to 27.23 μM and 23.94 to 75.49 μM for root and shoot growth, respectively (Masum *et al.* 2018).

Sorghum plants have been demonstrated for allelopathic effects on weed species (Nimbal *et al.* 1996, Czarnota *et al.* 2003, Weston *et al.* 2013). Root exudates of 100 cultivars of *Sorghum bicolor* were evaluated for their potency to affect the seed germination and growth of *Amaranthus retroflexus* (Alsaadawi *et al.* 1986). Some cultivars were more toxic than others.

Allelopathic activity of 526 accessions of *Cucumis sativus* and 12 accessions of eight related *Cucumis* species, representing 41 nations of origin,

was evaluated on *Brassica hirta* and *Panicum miliaceum* (Putnam and Duke 1974). One accession inhibited growth of test species by 87%, and 25 accessions inhibited growth by 50% or more. *Helianthus annuus* has been studied over the years for allelopathic effects (Leather 1983, Macias *et al.* 1999). Some sesquiterpene lactones with germacranolide and guaianolide skeletons and helianuol from different cultivars of *Helianthus annuus* were reported (Macias *et al.* 1999). These authors discussed their potential role as natural herbicides. *Mucuna prursens* has been reported to be a candidate to smother weed species (Fujii *et al.* 1992). They identified L-DOPA (L-3,4-dihydroxyphenylalanine) in *Mucuna prursens*.

Use of allelopathic plant extracts for weed management

Use of allelochemicals from plant extracts has been searched for weed management in agriculture. In Pakistan, for example, an aqueous extract deriving from sorghum shoots with a 10% concentration is left to ferment for several weeks and is subsequently sprayed post-emergence for weed control. This fermented water extract, known as "Sorgaab", reduced weed density and weed dry weight up to 50% in field trials, depending on the weed species (Cheema and Khaliq 2000, Cheema *et al.* 2002).

Limitations of allelopathic cover crop uses in agriculture

Using residues of cover or rotational crops for weed management in the field is challenging. There are limitations in using cover crops for various cropping systems. Delayed planting, delayed crop emergence, phytotoxic effects to major crops, and increased pest pressure are some of the limitations. In addition, cover crops are not much effective in managing 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. *Vicia villosa* has been used as a cover crop and has been demonstrated potential use in weed management. Total weed density and biomass were lower in live *Vicia villosa* treatment compared to desiccated *Vicia villosa* plots (Teasdale and Daughtry 1993). Red (660 nm) and far-red (730 nm) light ratio of transmitted light was reduced by 70% in live *Vicia villosa* and by 17% under *Vicia villosa* desiccated by paraquat. They concluded that factors such as light, soil moisture and temperature are responsible for the weed suppression by *Vicia villosa*.

The question remains whether residues from crops or cover crops can provide successful weed management (100%) in the field. Under the best management practices, it is possible to integrate allelopathic crop residues and other chemical control strategies (such as pre- or post-emergence herbicides).

Challenges in implementing allelopathic concepts

In nature, plant products represent a vast diversity of compounds with a variety of biological activity (Duke *et al.* 2002, Bhowmik and Inderjit 2003, Weston and Duke 2003, Duke 2015). The natural products represent a diverse class of chemical compounds. These allelochemicals will have impact on different species of plants.

There are limitations for using allelochemicals for successful weed management. Some of these factors in implementing natural products for effective weed management include (i) compounds are present in very low concentration, (ii) allelochemicals have generally short half-lives, (iii) narrow spectrum weed selectivity, and (v) high cost of production.

Conclusion

Numerous examples of allelopathic effects have been established decades ago. Today, we are still looking for other allelopathic plants or weed species. We have made significant advances in this direction over the last three decades. However, we still have a long way to go in terms of using allelochemicals or developing plant cultivars that would be used for complete weed management. The environmental fate of allelochemicals is a complex issue that is affected by the donor and receiver target plant species, as well as soil and environmental variables that affect the fate of the chemicals in the soil complex. Knowledge concerning the variation in these factors is essential to use the allelopathic relationship among plants in agroecosystems to promote weed control.

In spite of many challenges in implementing the allelopathic concept in weed management, there is tremendous scope for exploring allelopathy phenomena for successful weed management. Biotechnology may eventually allow for the production of highly allelopathic crop cultivars that may effectively suppress many weeds. The bioavailability of allelochemicals under field conditions must be established for its effective role in weed management. Continued research on these areas is important and we must invest our resources in exploring allelopathy as a complimentary component in successful weed management.

REFERENCES

- Alsaadawi IS, Al-Uqaili JK, Alrabeaa AJ and Al-Hadithy M. 1986. Allelopathic suppression of weed and nitrification by selected cultivars of *Sorghum bicolor* (L.) Moench. *Journal of Chemical Ecology* **12**: 209.
- Barker AV and Bhowmik PC. 2001. Weed control with crop residues in vegetable cropping systems. *Journal of Crop Production* **4**(2): 163–183.
- Barnes JP and Putnam AR. 1983. Rye residues contribute to weed suppression in no-tillage cropping systems. *Journal of Chemical Ecology* **9**: 1045–1057.
- Barnes JP, Putnam AR, Burke BA and Aasen AJ. 1987. Isolation and characterization of allelochemicals in Rye Herbage. *Phytochemistry* **26**: 1385–1390.
- Bhowmik PC and Doll JD. 1982. Corn and soybean response to allelopathic effects of weed and crop residues. *Agronomy Journal* **74**: 601–606.
- Bhowmik PC and Inderjit. 2003. Challenges and opportunities in implementing allelopathy for natural weed management. *Crop Protection* **22**(4): 661–671.
- Bias HP, R. Vapachedu R, Gilroy S, Callaway R and Vivanco J. 2003. Allelopathy and exotic plant invasion: from molecules and genes to species interactions. *Science* **301**: 1377–1380.
- Blum U. 1992. Allelopathic interactions involving phenolic acids. *Journal of Nematology* **28**: 259–267.
- Blum U. 1998. Effects of microbial utilization of phenolic acids and their phenolic acid breakdown products on allelopathic interactions. *Journal of Chemical Ecology* **24**: 685–708.
- Bonanomi G, Sicurezza MG, Caporaso S, Esposito A, and Mazzoleni S. 2006. Phytotoxicity dynamics of decaying plant materials. *New Phytology* **169**: 571–578.
- Cheema ZA and Khaliq A. 2000. Use of sorghum allelopathic properties to control weeds in irrigated wheat in a semi-arid region of Punjab. *Agricultural Ecosystem Environment* **79**: 105–112.
- Cheema ZA, Khaliq A and Ali K. 2002. Efficacy of sorghum for weed control in wheat grown at different fertility levels. *Pakistan Journal of Weed Science Research* **8**: 33–38.
- Czarnota MA, Rimando AM and Weston LA. 2003. Evaluation of root exudates of seven sorghum accessions. *Journal of Chemical Ecology* **29**: 2073–2083.
- Dalton BR. 1989. Physiochemical and biological processes affecting the recovery of exogenously applied ferulic acids from tropical forest soil. *Plant Soil* **115**: 13–22.
- Dilday RH, Yan WG, Moldenhauer KAK and Gravois KA. 1998. Allelopathic activity in rice for controlling major aquatic weeds. pp. 7–26. In: *Allelopathy in Rice*. (Ed. Olofsson M), IRRI Press, Manila.
- Duke S. 2015. Proving allelopathy in crop-weed interactions. *Weed Science* **63**(spl): 121–132.
- Duke S, Vaughn KC, Croom EM and Elsohly HN. 1987. Artemisinin, a constituent of annual wormwood (*Artemisia annua*) is a selective phytotoxin. *Weed Science* **35**: 499–505.
- Duke S, Dayan FE, Rimando RM, Schrader KK, Aliotta G, Oliva A and Romagni JG. 2002. Chemicals from nature for weed management. *Weed Science* **50**: 138–151.
- Einhellig FA and Souza IF. 1992. Phytotoxicity of sorgoleone found in grain sorghum root exudates. *Journal of Chemical Ecology* **18**: 1–11.
- Fay PK and Duke WB. 1977. An assessment of allelopathic potential of *Avena* germplasm. *Weed Science* **25**: 224–228.
- Fujii Y. 1992. The potential biological control of paddy weeds with allelopathy – Allelopathic effect of some rice cultivars. pp. 305–320. In: *Proceedings of the International Symposium on Biological Control and Integrated Management of Paddy and Aquatic Weeds* (Tsukuba, Japan). National Agriculture Research Center.
- Furubayash A, Hiradate S and Fujii Y. 2007. Role of catechol structure in the adsorption and transformation reactions of L-DOPA in soils. *Journal of Chemical Ecology* **33**: 239–250.
- Gealy DR, J.D. Mattice JD, Moldenhauer KA and Dilday RH. 2000. Allelopathy in rice as a weed control strategy. Proceedings of the International Weed Science Congress, Foz do Iguassu, Brazil **3**: 33–34.
- Gimsing AL, J. Baelum J, Dayan FE, Locke MA, Sejero LH and Jacobsen CS. 2009. Mineralization of the allelochemical sorgoleone in soil. *Chemosphere* **76**: 1041–1047.
- Haramoto ER and Gallandt ER. 2005. Brassica cover cropping-I. Effects of weed and crop establishment. *Weed Science* **53**: 695–701.
- Harper SHT and Lynch JM. 1982. The role of water-soluble components in phytotoxicity from decomposing straw. *Plant and Soil* **65**: 11–17.
- Hassan SM, Aidy IR, Bastawisi AO and Draz AE. 1998. Weed management using allelopathic rice varieties in Egypt. pp. 27–37. In: *Allelopathy in Rice*. (Ed. Olofsson M), IRRI Press, Manila.
- Huang PM, Wang WC and Wang MK. 1999. Catalytic transformation of phenolic compounds in the soils. pp. 287–306 In: *Principles and Practices in Plant Ecology: Allelochemical Interactions*, (Eds. Inderjit, Dakshini KMM and Foy CL), CRC Press, Boca Raton, FL.
- Inderjit. 2005. Soil microorganisms: an important determinant of allelopathic activity. *Plant and Soil* **274**: 227–236.
- Ito I., Kobayashi K and Yoneyama T. 1998. Fate of dehydromatricaria ester added to soil and its implications for the allelopathic effect of *Solidago altissima* L. *Annals of Botany, London* **82**: 625–630.
- Jabran K, Mahajan G, Sardana V and Chauhan BS. 2015. Allelopathy for weed control in agricultural systems. *Crop Protection* **72**: 57–65.
- Jilani G, Mahmood S, Chaudhry AN, Hassan I and Akram M. 2008. Allelochemicals: sources, toxicity and microbial transformation in soil – a review. *Annals of Microbiology* **58**(3): 351–357.
- Kato-Noguchi H, Hasegawa M, Ino T, Ota K and Kujime H. 2010. Contribution of momilactone A and B to rice allelopathy. *Journal of Plant Physiology* **167**: 787–791.
- Kobayashi K. 2004. Factors affecting phytotoxic activity of allelochemicals in soil. *Weed Biology and Management* **4**: 1–7.

- Kong CH, Zhao H, Xu XH, Wang P and Gu Y. 2007. Activity and allelopathy of soil of flavone O-glycosides from rice. *Journal of Agriculture and Food Chemistry* **55**: 6007–6012.
- Kurt-Karakus PB, Stroud JL, Bidleman T, Semple KT, Jantunen L and Jones KC. 2007. Enantio selective degradation of organochlorine pesticides in background soils: variability in field and laboratory studies. *Environmental Science & Technology* **41**: 4965–4971.
- Leather GR. 1983. Sunflowers (*Helianthus annuus*) are allelopathic to weeds. *Weed Science* **31**: 37–42.
- Lehman ME and Blum U. 1999. Evaluation of ferulic acid uptake as a measurement of allelochemical dose: Effective concentration. *Journal of Chemical Ecology* **25**: 2585–2600.
- Li XJ, Xia ZC, Kong CH and Xu XH. 2013. Mobility and microbial activity of allelochemicals in soil. *Journal of Agricultural and Food Chemistry* **61**: 5072–5079.
- Luo Yi, Davis AS and Yannarell AC. 2016. Interactions between allelochemicals and the microbial community affect weed suppression following cover crop residue incorporation into soil. *Plant Soil* **399**: 357–371.
- Macías FA, Varela RM, Torres A and Molinillo JMG. 1999. Potential of cultivar sunflowers (*Helianthus annuus* L) as a source of natural herbicide template. pp. 531–550. In: *Principles and Practices in Plant Ecology: Allelochemical Interactions*. (Eds. Inderjit, Dakshini KMM and Foy CL), CRC Press, Boca Raton, FL.
- Macías FA, Oliveros-Bastidas A, Marín D, Castellano D, Simonet AM and Molinillo JMG. 2005. Degradation studies on benzoxazinoids: soil degradation dynamics of (2R)-2-O-beta-D-glucopyranosyl-4hydroxy-(2H)-1,4-benzoxazin-3(4H)-one (DIBOA-Glc) and its degradation products, phytotoxic allelochemicals from gramineae. *Journal of Agricultural and Food Chemistry* **53**: 554–561.
- Macías FA, Oliveros-Bastidas A, Marín D, Chinchilla N, Castellano D and Molinillo JMG. 2014. Evidence for an allelopathic interaction between rye and wild oats. *Journal of Agricultural and Food Chemistry* **62**: 9450–9457.
- Mahajan G and Chauhan BS. 2013. The role of cultivars in managing weeds in dry seeded rice production systems. *Crop Protection* **49**: 52–57.
- Mahmood K., Khaliq A, Cheema ZA and Arshad M. 2013. Allelopathic activity of Pakistani wheat genotypes against wild oat (*Avena fatua* L.). *Pakistan Journal of Agricultural Science* **50**: 169–176.
- Masum S, Hossain A, Akamine H, Sakagami Jun-Ichi and Bhowmik PC. 2016. Allelopathic potential of indigenous Bangladeshi rice varieties. *Weed Biology and Management* **16**: 119–131.
- Masum S, Hossain A, Akamine H, Sakagami Jun-Ichi, Ishii T, Gima S, Kensaku T and Bhowmik PC. 2018. Isolation and characterization of allelopathic compounds from the indigenous rice variety ‘Boterswar’ and their biological activity against *Eichornia crus-galli* L. *Allelopathy Journal* **43**(1): 31–42.
- Mohler CL, Dykeman C, Nelson EB and Ditommaso A. 2012. Reduction in weed seedling emergence by pathogens following the incorporation of green crop residue. *Weed Research* **52**: 467–477.
- Molisch H. 1937. *Der Einfluss einer Pflanze auf die andere- Allelopathie*; Fischer: Jena
- Mushtaq W and Siddiqui MB. 2017. Allelopathy studies in weed science in India – A review. *International Journal of Natural Research Ecology and Management* **2**(6): 99–103.
- Niemeyer HM. 1988. Hydroxamic acids (4-hydroxy-1,4-benzoxazin-ones) defense chemicals in the gramineae. *Phytochemistry* **27**: 267–292.
- Nimbal CI, Pedersen JF, Yerkes CN, Weston LA and Weller SC. 1996. Phytotoxicity and distribution of sorgoleone in grain sorghum germplasm. *Journal of Agricultural and Food Chemistry* **44**: 1343–1347.
- Olofsdotter M. 2001. Rice - a step toward use of allelopathy. *Agronomy Journal* **93**: 3–8.
- Olofsdotter M, Navarej DC and Moody K. 1995. Allelopathic potential of rice (*Oryza sativa* L.) germplasm. *Annals of Applied Biology* **127**: 543–560.
- Ohno T. 2001. Oxidation of phenolic acid derivatives by soil and its relevance in allelopathic activity. *Journal of Environmental Quality* **30**: 1631–1635.
- Perry LG, Thelen GC, Ridenour WM, Callaway RM, Paschke MW and Vivanco JM. 2007. Concentration of allelochemical (–)-catechin in *Centaurea maculosa* soils. *Journal of Chemical Ecology* **33**: 1573–1561.
- Pue KJ, Blum U, Gerig M and Shafer SR. 1995. Mechanisms by which non-inhibitory concentrations of glucose increase inhibitory activity of p-coumaric acid on morning glory seedling biomass accumulation. *Journal of Chemical Ecology* **21**: 833–847.
- Putnam AR and Duke WD. 1974. Biological suppression of weeds: evidence for allelopathy in accessions of cucumber. *Science* **185**: 370–372.
- Putnam AR, DeFrank J and Barnes JP. 1983. Exploitation of allelopathy for weed control in annual and perennial cropping systems. *Journal of Chemical Ecology* **9**: 1001–1010.
- Rice EL. 1984. *Allelopathy*. 2nd. Edn., Academic Press, New York, USA.
- Schmidt SK and Ley RE. 1999. Microbial competition and soil structure limit the expression of allelochemicals in nature. pp. 339–351. In: *Principles and Practices in Plant Ecology: Allelochemical Interactions*, (Eds. Inderjit, Dakshini KMM and Foy CL), CRC Press, Boca Raton, FL.
- Siqueira J, Nair MG, Hammerschmidt R and Saúr GR. 1991. Significance of phenolic compounds in plant-soil-microbial systems. *Critical Review Plant Science* **10**: 63–121.
- Teasdale JR. 1993. Interaction of light, soil moisture, and temperature with weed suppression by hairy vetch residue. *Weed Science* **41**: 46–51.
- Teasdale JR and Daughtry CST. 1993. Weed suppression by live and desiccated hairy vetch (*Vicia villosa*). *Weed Science* **41**: 207–212.
- Teasdale JR, Rice CP, Cai GM and Mangum RW. 2012. Expression of allelopathy in the soil environment: soil concentration and activity of benzoxazinoid compounds released by rye cover crop residue. *Plant Ecology* **213**: 1893–1905.

- Tharayil N, Bhowmik PC and Xing B . 2006. Preferential sorption of phenolic phytotoxins to soil: implications for altering the availability of allelochemicals. *Journal of Agricultural and Food Chemistry* **54**: 3033–3040.
- Tharayil N, Bhowmik PC and Xing B. 2008. Bioavailability of allelochemicals as affected by companion compounds in soil matrices. *Journal of Agricultural and Food Chemistry* **5**: 3706–3713.
- Trezza M, Vidal RA, Babinot Junir AA, Bittencourt H.vonH and da Silva Souza Fihó AP. 2016. Allelopathy: driving mechanisms governing its activity in agriculture. *Journal of Plant Interactions* **11**(1): 53–60.
- Uren NC 2001. Types, amount and possible functions of compounds released into the rhizosphere by soil-grown plants. In *The Rhizosphere: Biochemistry and Organic Substances at the Soil Plant Interface*; Pinto, R., Varanini, Z., Nannipieri, P., Eds.; Marcel Dekker: New York, pp 19–40.
- Vyvyan J. 2002. Allelochemicals as leads for new herbicides and agrochemicals. *Tetrahedron* **58**:1631–1646.
- Wauchope D, Yeh S, Linders J, Kloskowski R, Tanaka K, Rubin B, Katayama A, Kordel W, Gerstl Z, Lane M and Unsworth J. 2002. Pesticide soil sorption parameters: Theory, measurement, uses, limitations and reliability. *Pest Management Science* **58**, 419–445.
- Wang TSC, Li SW, and Feng YL. 1978. Catalytic polymerization of phenolic compounds by clay minerals. *Soil Science* **126**: 15–20.
- Weston LA. 1996. Utilization of allelopathy for weed management in agroecosystems. *Agronomy Journal* **88**: 860–866.
- Weston LA and Duke SO. 2003. Weed and crop allelopathy. Critical Review. *Plant Science* **22**: 367–389.
- Weston LA, Alsaadawi IS and Baerson SR. 2013. Sorghum allelopathy from ecosystem to molecule. *Journal of Chemical Ecology* **39**: 142–153.
- Wu H, Pratley J, Lemerle D, Haig T and Verbeek B. 1998. Differential allelopathic potential among wheat accessions to annual ryegrass. pp. 567–571. In: *Proceedings, of the Ninth Australian Agronomy Conference*. (Eds. Michalk, DL and Pratley JE), Wagga Wagga, Australia.
- Wu H, Pratley J, Lemerle D, Haig T and Verbeek B. 1999. Crop cultivars with allelopathic capability. *Weed Research* **39**: 171–180.
- Wu H, Haig T, Pratley J, Lemerle D and An M. 2002. Biochemical basis of wheat seedling allelopathy on the suppression of annual ryegrass (*Lolium rigidum*). *Journal of Agricultural and Food Chemistry* **50**: 4567–4571.
- Xing B, Pignatello JJ and Gigliotti B. 1996. Competitive sorption between atrazine and other organic compounds in soils and model sorbents. *Environmental Science & Technology* **30**: 2432–2440.
- Yenish JP, Worsham AD and Chilton WS. 1995. Disappearance of DIBOA- glucoside, DIBOA, BOA from rye (*Secale cereal* L.) cover crop residue. *Weed Science* **43**: 18–20.
- Zikmundová M, Drandarov K, Bigler L, Hesse M and Werner C. 2002. Biotransformation of 2-benzoxazolinone and 2-hydroxy-1,4-benzoxazin-3-one by endophytic fungi isolated from *Aphelandra tetragona*. *Applied Environmental Microbiology* **68**(10): 4863–4870.