

Review

Allelopathy in weed management: A critical review

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Allelopathy is defined as both beneficial and deleterious biochemical interaction between plant and weeds, and / or plants and microorganisms through the production of chemical compounds that escape into the environment and subsequently influence the growth and development of neighboring plants. Allelochemicals are present in all types of tissues and are released into the rhizosphere by a variety of mechanism, including decomposition of residues, volatilization and root exudation. Allelochemical its structure and mode of action are different and may offer a potential for future development of herbicide. This paper describes the variety of weeds and crop species that exhibit allelopathic interface either with crop or weeds.

Key words: Allelopathy, allelochemicals, agriculture, crop, weed.

INTRODUCTION

The capability of some plant species to affect surrounding plants has been well documented since antiquity. The earliest writings on this topic are attributed to Theophrastus (ca. 300 B.C), a successor of Aristotle who noticed the harmful effects of cabbage on a vine and suggested that such effects were caused by “odours” from the cabbage plants (Willis, 1985). This phenomenon is known as allelopathy (from the Greek *allelon* = of each other, *pathós* = to suffer). The term was coined in 1937 by German plant physiologist Hans Molisch to define “the harmful effect of one plant upon another”. Currently, a more complete definition includes the positive and negative effects of chemical compounds produced mainly from the secondary metabolism of plants, microorganisms, viruses and fungi that have an influence upon the growth and development of agricultural and biological ecosystems (excluding mammals) (Kruse et al., 2000;

Olofsdotter et al., 2002; Weston, 2005).

Although allelopathy has been observed for over 200 years and the phenomenon reports as early as 300BC document that many crop plants inhibited the growth of other plants and destroyed its field weeds (Rice, 1984). In 1974, after the publication of first book of allelopathy by Elory L. Rice the phenomenon got a new attention in science community, who later reinforced this definition of allelopathy (Olofsdotter et al., 2002). The effects of one plant to another plant may be either both stimulatory and inhibitory that depends on the concentration of the released compounds (Bhowmik and Inderjit, 2003). From a practical point of view, such effects are achieved due to the release of active biomolecules, commonly called “allelochemicals”, into the environment by the “allelopathic” plants (Kruse et al., 2000; Bertin et al., 2003). Chemicals, at lower concentration that inhibit the

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growth of some species where at higher concentration that may be stimulate the growth of different species (Ahmed et al., 2007). Allelochemicals may be involved in plant-plant, plant insect or plant-herbivore chemical communication (Weir et al., 2004) as well as micro-organism-derived allelochemicals that may be involved in microbe-microbe or microbe-plant interactions (e.g., colonisation process of a new environment) (Singh et al., 2003).

The occurrence of natural allelopathic activity in crops has important positive and negative implications for cropping systems. The application of the allelopathic properties of some crops has been suggested for weed management due to the possibility of reducing the application of expensive, pollutant synthetic herbicides (Belz, 2007; Kruse et al., 2000). On the other hand, agricultural practices such as crop rotation, use of green manure, minimal tillage, covering crop, etc., require previous knowledge on the part of farmers regarding the allelopathic interactions that can occur between the plant species involved. Changes in the distribution pattern of crops, difficulties in replanting crops and fruit trees in orchards or low yield could be an indication of negative allelopathic activity (Chon et al., 2006; Kruse et al., 2000). When a given species produces and releases allelochemicals that can cause damage to a different plant species, this phenomenon is called *heterotoxicity*, whereas, when its own germination and development is affected, this allelopathic effect is called *autotoxicity* (Chon et al., 2006; Kruse et al., 2000).

Autotoxicity is thought to be the result of natural selection, in which an older plant avoids competing with younger individuals for resources (light, water, nutrients, etc.) by maintaining them at a certain distance. Thus, in harsh natural habitats, it is possible to see somewhat uniform spatial patterns within populations, such as in desert plant populations, in which plants tend to be evenly spaced. From the agronomic point of view, the interest in autotoxicity resides in the possible problems for reseeding or overseeding crops (Chon et al., 2006). Autotoxicity has been studied in members of the Cucurbitaceae family, revealing considerable genetic variations, mainly in cucumber, watermelon and melon. Benzoic and cinnamic acid are among the allelochemicals exudated from the roots of these plants (Ding et al., 2007). The authors cited suggest that there is a specific recognition of these allelochemicals. The addition of cinnamic acid, an autotoxin exudated by cucumber roots, to a nutritive solution was found to cause oxidative stress followed by the death of cucumber root tissues, but did not cause the same damage to the roots of *Cucurbita ficifolia* Bouché, which is a member of the same family. A number of important crops have recognised allelopathic activity that can be either greater or lesser depending on the cultivar, climatic conditions, soil fertility, water availability and competing weeds.

The current worldwide demand for cheaper, more

environmentally-friendly weed management technologies has motivated a number of studies on the allelopathic interaction between crops and weeds (Dudai et al., 1999; Om et al., 2002). Agricultural practices such as reseeding, overseeding, cover crops and crop rotation must take into account the allelopathic activity of the crops involved, at the risk of obtaining low yields (Chon et al., 2006; Oueslati, 2003). Allelopathic plants may also be considered a potential source of new molecules with herbicidal action for the chemical industry, the necessity of which is due to the emergence of resistant weeds to older synthetic molecules (Bhowmik and Inderjit, 2003; Duke et al., 2000; Einhellig, 1996; Kruse et al., 2000). Another potential application is in the development of genetically modified crops that can be used as allelopathic plants (Duke, 2003; Duke et al., 2001; Taiz and Zeiger, 2006). From an ecological perspective allelopathy may play an important role in the process of biological invasion. It has been observed that some exotic invaders succeed in obtaining high densities in the invaded ranges, but exhibit low densities in their native ranges. To try to explain this phenomenon, the "novel weapons" theory was proposed, which holds that some exotic plants release into the new invaded ecosystem a set of biochemical compounds with inhibitory effects on local plant and soil microbes, but with relative inefficacy against their natural neighbourhood that had been adapted over time (Callaway and Ridenour, 2004; Vivanco et al., 2004). Seen as the Achilles' heel in the beginning of allelopathic research due to the lack of chemical evidence to corroborate this phenomenon, currently the isolation and identification of allelochemicals is well established.

Modern techniques and equipment are available and an increasing number of bioactive molecules are isolated and identified every year from crops, weeds and forest trees. A number of chemical separation methods combined with spectroscopic techniques, such as multinuclear/ multidimensional nuclear magnetic resonance (NMR), have proven useful for isolating, quantifying and identifying known or new molecules with potential allelopathic activity (D'Abrosca et al., 2001). Bioassays using target species with an isolated substance or mixture of substances at increasing concentrations are carried out to confirm their allelopathic activities. A large number of biological molecules throughout diverse chemical groups can exhibit allelopathic activity. It is notorious that in their majority allelochemicals are products of secondary metabolism, with a few exceptions of primary metabolism. However, even with this diversity, these metabolites have basically four precursors: acetyl coenzyme A, shikimic acid, mevalonic acid and deoxyxylulose phosphate. Based on these precursors, secondary metabolites can be grouped into three main chemical classes: terpenoids, N-containing compounds and phenolic compounds. There is some consensus that a simple compound in a field

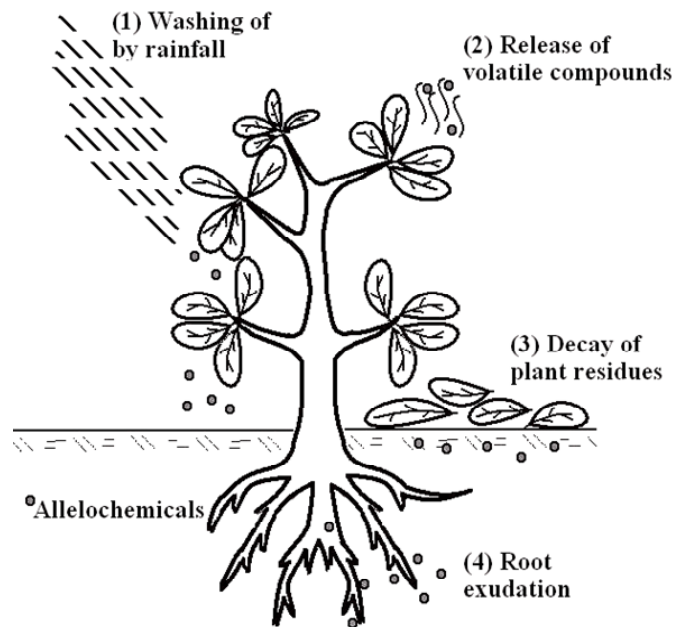


Figure 1. Possible pathways for release of allelochemicals into the environment.

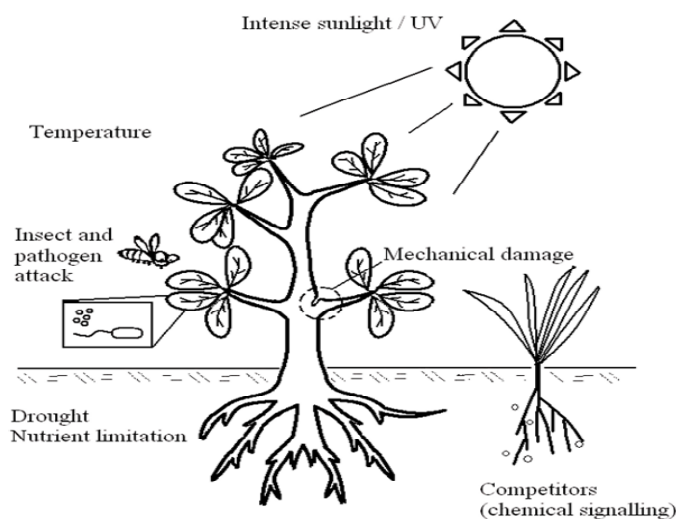


Figure 2. Induction of allelochemical production by biotic and abiotic factors.

situation may not be enough to affect the growth of the receiving plant and it is likely that different allelochemicals act additively or synergistically to inhibit growth (Belz, 2007; Kruse et al., 2000; Tabaglio et al., 2008). The present literature review covers aspects of the current knowledge on the allelopathic interaction between crops and weeds. Examples of crops and weeds with recognized allelopathic activity and their importance for weed management are presented.

RELEASING ALLELOPATHIC COMPOUNDS INTO THE ENVIRONMENT

Allelochemicals can be found in different concentrations in several parts of plants (leaves, stems, roots, rhizomes, seeds, flowers and even pollen) (Bertin et al., 2003; Gatti et al., 2004; Kruse et al., 2000) and their pathway of release into the environment varies among species. The following are known pathways: (1) Exudation and deposition on the leaf surface with subsequent washing off by rainfall; (2) Exudation of volatile compounds from living green parts of the plant; (3) Decay of plant residues (e.g., litterfall or dead roots); and (4) Root exudation (Chon et al., 2006; Olofsdotter et al., 2002) (Figure 1). Different types of abiotic and biotic stress can alter the production and release of allelochemicals during the vital cycle of plants. Drought, irradiation, temperature, nutrient limitation, competitors, disease and damage from insects have been pointed out as factors that can cause an increased release of allelochemicals from allelopathic plants (Figure 2) (Cseke and Kaufman, 2006; Einhellig, 1996)

Studying the effects of varietal and seasonal variations in the expression of autotoxicity of field-harvested barley on germination and seedling growth under laboratory conditions, Oueslati et al. (2005) found barley autotoxicity to be enhanced under severe drought conditions. Ben-Hammouda et al. (2001) observed that the inhibitory effects of barley extracts can oscillate depending on the plant part and growth plant stage. Furness et al. (2008) found that Houndstongue (*Cynoglossum officinale* L.) plants grown with increasing degrees of ultraviolet-B radiation increased their allelopathic influence on some forage grasses. Debris from *Helianthus annuus* L. plants grown under nutrient deficiency was found to be more effective at depressing *Amaranthus retroflexus* L. germination than debris from control plants (Hall et al., 1982). Volatiles from *Ageratum conyzoides* L. plants under nutrientdeficient conditions or in competition with *Bidens pilosa* L. were found to increase their allelopathic effects on the peanut (*Arachis hypogaea* L.), redroot amaranth (*A. retroflexus*), cucumber (*Cucumis sativus* L.) and ryegrass (*Lolium multiflorum* Lam.) (Kong et al., 2002). Mwaja et al. (1995), evaluating the effects of three fertility regimes (low, medium or high) *Sorghum* sp. after exposure to water-soluble root leachates from *Abutilon theophrasti* Medik., thereby suggesting that chemical-mediated crop/weed interactions may include biochemical signalling for the induction of plant defence against weeds.

FATE OF ALLELOCHEMICALS IN SOIL

Once released into the soil by the donor plant, allelochemicals enter a complex plant-soil system in which diverse factors affect their availability, and

consequently their effective influence on target plants (Kruse et al., 2000). Processes such as those mentioned above are responsible for the addition of allelochemicals to the system, for which the amount added depends on donor plant biomass and density, and phenologic stage as well as the concentration and solubility of specific allelochemicals (Seigler, 1996; Weidenhamer, 1996). On the other hand, leaching, physiochemical processes, microbial breakdown and uptake by plants are factors that can reduce the soil concentration of allelochemicals (Inderjit, 2001; Inderjit et al., 2001; Vidal and Bauman, 1997). Weidenhamer (1996) argues that, similar to herbicides, allelochemicals can be made unavailable due to their binding to organic matter and clays in the soil. Studying the degradation of catechin, a supposed allelochemical exuded by *Centaurea maculosa* Lam., and phenolic acid cosolutes in a sandy loam and silt loam soil. Tharayil et al. (2008) found that oxidation and sorption are the primary factors involved in the disappearance of these allelochemicals. Soil texture can also have a direct influence on the leaching of allelochemicals. Studying the influence of soil texture on the flow of alfalfa extracts in columns, Jennings and Nelson (1998) found that allelopathic chemicals moved through the Sarpy fine sandy loam (mixed, mesic Typic Udipsamments) soil faster than through the Carlow silty clay loam (fine, smectitic, mesic Vertic Endoaqualls). Soil microbes take up the compounds released from plants and degrade them through the action of extra-cellular and intercellular microbial enzymes for their own energy-building processes. Such microbiological transformations can either detoxify the soil of these compounds or produce other more phytotoxic allelochemicals (Bhinu et al., 2006). A typical example is the occurrence of AZOB (2,2 - oxo-1,1 -azobenzene), an azoperoxide – in non-sterilised soils after addition of BOA (benzoxazolin-2(3H)-one) or DBOA (2,4-dihydroxy-2H-1,4-benzoxazin-3(4H)-one), which are hydroxamic acids with allelopathic properties produced by rye residues (Nair et al., 1990). These allelochemicals are found almost exclusively in Gramineae (Frey et al., 1997).

Physiochemical degradation of plant residues (e.g., oxidation) can also detoxify or produce additional allelochemicals (Weidenhamer, 1996). Sorgoleone (2-hydroxy-5-methoxy-3-[(8Z,11Z)-8,11,14-pentadecatriene]-p-hydroquinone), a potent PSII inhibitor produced from *Sorghum* plants – is apparently exuded as a reduced inactive form and, after its secretion, is oxidised into an active benzoquinone (Dayan et al., 2003). However, the studies of Czarnota et al. (2001) on the soil persistence of sorgoleone suggest that the soil microflora have a minimal role in sorgoleone degradation. Weston and Czarnota (2001), studying the soil persistence of sorgoleone, verified that its recovery from an artificially impregnated soil declined during a period of 42 days, being detectable even after 7 weeks. Contradictory results were found by Gimsing et al. (2009)

when studying the mineralisation of sorgoleone in four soils (two from North America and two from Denmark). These authors verified a complete degradation into CO₂ in all soils tested, and the mineralisation kinetics indicated that microorganisms in American soils use sorgoleone as a source of energy.

Rice

Chung et al. (2003) described the effect of allelopathic potential of rice (*Oryza sativa* L.) residues against *Echinochloa crusgalli* P. Beauv. var. *oryzi-cola* Ohwi (barnyardgrass), an associated weed of paddy. It was found that average inhibition by the variety Duchungjong on *Echinochloa crusgalli* was 77.7% higher than other 113 tested varieties. Early and late maturing varieties showed less inhibitory effect of 50.2 and 56.1% respectively and intermediate rice varieties with 59.3% inhibition, although the difference between the intermediate and late-maturing groups was not significant. Microscope studies revealed that allelopathic rice cultivars seem to inhibit secondary growth in barnyard grass roots besides reducing root elongation (Figure 1) (Olofsdotter et al., 2002). Numerous phytotoxins such as cytokinins, diterpenoids, fatty acids, flavones, glucopyranosides, indoles, momilactones (A and B), oryzalexins, phenols, phenolic acids, resorcinols and stigmastanols have been identified as growth inhibitors in rice. However, the actual modes of action of these compounds as well as other potential rice phytotoxins in nature are not well understood (Khanh et al., 2007).

More than ten phytotoxic compounds from several chemical classes (e.g., fatty acids, benzoxazinoids, indoles, phenolic acids, phenylalkanoic acids and terpenoids) have been identified in rice extracts and exudates, as listed by Belz (2007). Momilactone B diterpenoid (3,20-epoxy-3 α -hydroxy-9 β -primara-7,15-dien-16,6 β -olide) has been suggested as an important allelochemical for weed suppression (Kato-Noguchi and Ino, 2005), as have a flavone (5,7,4'-trihydroxy-3', 5'-dimethoxyflavone) and cyclohexenone (3- isopropyl-5-acetoxycyclohexene-2-one-1) (Kong et al., 2004). Moreover, momilactone A and B may be involved in physiological defence strategies in the rice rhizosphere, preventing competition from neighbouring plant roots (Kato-Noguchi et al., 2008)

According to the authors cited above, at low concentrations, these three compounds can inhibit the growth of the weeds *Echinochloa crus-galli* (L.) Beauv. and *Cyperus difformis* L., which are associated with rice. The mixture of these compounds exhibited stronger inhibitory activity than the individual compounds. Furthermore, allelopathic rice can detect the presence of other plants and modify microorganisms in the soil through the release of allelochemicals. A study on the

interaction of allelochemicals from rice roots with micro-organisms in the soil found that some micro-organisms either increase or decrease in number depending on the type of allelochemicals released, suggesting that allelopathic rice could modify the microbial community (Gu et al., 2008). Testing three rice cultivars (one non-allelopathic and two allelopathic) under hydroponic conditions, Kim et al. (2005) concluded that the allelopathic activity of rice was species-specific and depended on the source and concentration. Antifungal activity has also been found in rice allelochemicals.

Wheat (*Triticum aestivum* L.)

Considered the second most produced food among the cereal crops, wheat is another member of the Triticeae tribe and has allelopathic potential for the management of weeds, pests and diseases. Its allelopathic activity is due to the release of a broad set of allelochemicals, including phenolic acids (p-hydroxybenzoic, vanillic, p-coumaric, syringic and ferulic acids), hydroxamic acids and short-chain fatty acids. Both wheat residue allelopathy and wheat seedling allelopathy can be used for managing weeds, including resistant biotypes. Wheat varieties differ in allelopathic potential against weeds, indicating that the selection of allelopathic varieties may be a useful strategy in integrated weed management (Wu et al., 2001). Oueslati (2003) evaluated the allelopathic effects of diluted extracts from the roots, leaves and stems of two varieties (Karim and Om rabii) of durum wheat (*Triticum durum* L.) on germination rate and radicle length of one barley (*Hordeum vulgare* L. cultivar Manel) and one bread wheat (*T. aestivum* cultivar Ariana). The leaf extract was more effective at depressing radicle length in both crops. Based on the results, the author suggests that durum wheat heterotoxicity could be depressive to crops in a sequence. Krogh et al. (2006) incorporated wheat and rye sprouts into the soil in order to follow the fate of the allelochemicals. In the wheat experiments, the authors report 6-methoxybenzoxazolin-2-one (MBOA) as the main compound; 2-hydroxy-7-methoxy-1,4-benzoxazin-3-one (HMBOA) and 2-hydroxy-1,4-benzoxazin-3-one (HBOA) were detected as well and no phenoxazinones were detected. Macías et al. (2004a), analysing the fate of benzoxazinoids in two soils cultivated with two wheat varieties, verified that DIMBOA degraded rapidly, yielding MBOA in both studied soils at different doses and that MBOA, an intermediate in the degradation pathway from DIMBOA to 2-amino-7-methoxy-3Hphenoxazin-3-one (AMPO), was more resistant toward biodegradation. Recently the European Commission funded the FATEALLCHEM project, a multi-country ecological effort that aims at an environmental and human risk assessment of exploiting the allelopathic properties of winter wheat in conventional and organic farming, and developing a framework for future assessments of other

allelopathic crops (Duke et al., 2007). Oueslati (2003) examined the allelopathic effect of diluted extracts of roots, leaves and stems of two durum wheat varieties viz., Karim and Om rabii on barley (variety Manel) and bread wheat (variety Ariana).

Buckwheat

Buckwheat (*Fagopyrum* spp.) is not only an important crop in many countries, but is also useful for soil improvement and reduction of pests and weeds (Xuan and Tsuzuki, 2004). The allelopathic potential of buckwheat species follows the order: Perennial > tartary > annual (Tsuzuki et al., 1975). In upland fields, buckwheat (cv. Hruszowska) markedly suppressed growth of quack grass (*Agropyron repens* L.) (Golisz et al., 2002). In another trial, buckwheat, weed alone, and buckwheat–weed incorporation were established (Tominaga and Uezu, 1995). Among 13 weed species found, the biomass of *Digitaria ciliaris* and *Galinsoga ciliata* was drastically reduced by buckwheat. The biomass of *E. crus-galli*, *Portulaca oleracea*, *C. album* and *Amaranthus lividus* was 32.8, 31.9, 13.1, and 10.3% of that in the weed plot respectively (Tominaga and Uezu, 1995). In paddy fields, application of buckwheat pellets at 2 tons ha⁻¹ significantly reduced weed density (75-80%) and dry weight (60%). The pellets completely controlled the growth of *C. difformis*, *Dopatrium junceum*, and reduced the growth of *E. crus-galli*, *E. acicularis* and *M. vaginalis* (Xuan and Tsuzuki, 2004).

Barley (*Hordeum vulgare* L.)

Barley is an annual cereal grain that serves as a major animal feed crop, with smaller amounts used for malting and in health food. It is also known as a “smother crop”, initially due to its competitive ability for nutrients and water and later due to the release of allelochemicals (Overland, 1966). Dhima et al. (2008), investigating the phytotoxic activity of 10 winter barley varieties on barnyard grass in the laboratory, found varietal differences in the level of germination, root length and total fresh weight inhibition. Linking these results with the data obtained from a two-year field experiment, these authors suggest that the increased competitiveness of the variety Lignee 640 was possibly higher due to its phytotoxic ability. Bertholdsson (2005) suggests that for barley and wheat the early crop biomass and potential allelopathic activity are the only parameters that significantly contribute to their competitiveness. Little information has been produced in the last ten years on the identification of barley allelochemicals (Belz, 2007).

Phytotoxic phenolic compounds, including ferulic, vanillic and p-hydroxybenzoic acids, have been identified in the cold-water extract of barley straw as well as in

methanol extract from living barley roots. The allelopathic action of the alkaloids gramine (N,N-dimethyl-1H-indole-3-methanamine) and hordenine (p-[2-(dimethylamino)ethyl]phenol) has been confirmed.

Rye (*Secale cereale* L.)

Rye is a member of the wheat tribe (Triticeae), closely related to barley and wheat, and grows extensively as a grain and forage crop. Its allelopathic activity has mainly been investigated in relation to its ability to suppress weeds when used as green manure or as a cover crop (due to its massive biomass production) and root exudate release of allelochemicals (Barnes and Putnam, 1983; Kruse et al., 2000; Its known effective allelochemicals include phenolic acids [beta-phenyl-lactic acid (PLA) and beta-hydroxybutyric acid (HBA)], hydroxamic acids [2,4-dihydroxy-1,4(2H)-benzoxazin-3-one (DIBOA), 2(3H)-benzoxazolinone (BOA) and 2,2'-oxo-1,1'-azobenzene (AZOB, which is a compound formed by the microbial transformation of rye residues)]. Hence, a variety of natural products can contribute to the herbicidal activity of rye residues Kruse et al., 2000; Reberg-Horton et al., 2005). Reberg-Horton et al. (2005) identified seasonal changes in the production of allelochemicals that varied depending on the cultivar and harvesting time, with lesser production at the end of the harvest. Chlorosis was a symptom of damage from rye residues on several indicators and may be related to the effect of DIBOA and BOA on photophosphorylation and electron transport (Barnes and Putnam, 1987). Structural changes such as a delay in cell differentiation and reduction in the number of lateral roots were observed in cucumbers after exposure to DIBOA and BOA, respectively (Burgos et al., 2004). The study cited also found that the roots of seedlings cultivated in vitro in the presence of allelochemicals increased in diameter and decreased in length. Moreover, tissue changes were observed after treatment with BOA (increase in size and decrease in number of meristematic cells) and DIBOA (more numerous and smaller cortical cells).

Sorghum

Cheema (1988) reports at least nine water-soluble allelochemicals from mature sorghum plants that are phytotoxic to weeds, such as *Phalaris minor* Retz., *Chenopodium album* L., *Rumex dentatus* L. and *Convolvulus arvensis* L. However, the most studied metabolites exudated by the living roots of sorghum are a group of hydrophobic benzoquinones called sorgoleone – 2-hydroxy-5-methoxy-3-[(Z,Z)-8',11',14'-pentadecatriene]-pbenzoquinone and its 1,4-hydroquinone (Czarnota et al., 2001, 2003a). Ultrastructure analysis has revealed that the production of exudates occurs in the root hairs,

deposited between the plasmalemma and cell wall. In *Sorghum*, the root hairs are glandular and can produce and release high quantities of an oil-like substance containing 80 to 95% sorgoleone (Dayan et al., 2007). Sorgoleone was revealed to be a potent inhibitor of the oxygen evolution of plants (Einhellig and Souza, 1992), with a similar effect to the so-called diuron-type herbicides, such as s-triazines, phenylureas, triazinones, ureas, uracils and biscarbamates (Streibig et al., 1999). Nimbal et al. (1996) showed that sorgoleone was a potent competitive inhibitor of electron transport in photosystem II (PSII). However, Czarnota et al. (2001) provided conclusive evidence when these authors observed that sorgoleone required about half the amount of free energy to dock at the plastoquinone QB-binding site of PSII, compared with plastoquinone. In addition, other effects can be detected in higher plants treated with sorgoleone. Sorgoleone also inhibits hydroxyphenyl-pyruvate dioxygenase (HPPD), which disrupts the biosynthesis of carotenoids, resulting in foliar bleaching (Weir et al., 2004). Anatomical changes in the stem occur in bean (*Phaseolus vulgaris* L.) seedlings exposed to sorgoleone. This tissue undergoes changes in the cellulose wall, inhibition of cell division and an increase in the number of metaphases, the latter of which is mainly related to changes in the division of spindle fibres (Hallak et al., 1999). Currently, sorgoleone biosynthesis is nearly completely elucidated and several key enzymes have been identified and characterised (Baerson et al., 2008; Dayan et al., 2007). Netzly and Butler (1986) isolated sorgoleone {2-hydroxy-5-methoxy-3-[(8'Z, 11'Z)-8',11',14'-pentadecatriene]-p-benzoquinone} from hydrophobic root exudates of sorghum. Sorgoleone, the major p-benzoquinone, and three other structurally related minor p-benzoquinones together constitute 90% or more of the root exudates (Netzly et al., 1988). Cheema and Khaliq (2000) tested the allelopathic effect of sorghum to control weeds of irrigated wheat under semiarid region of Punjab (Table 1). These authors found that soil incorporation of sorghum stalks at 2, 4 and 6 Mg ha⁻¹ reduced weed dry weight by 42, 48 and 56%, respectively. Sorgaab spray reduced weed dry weight by 35 to 38%. They also studied the effect of concentration and frequency of sorgaab application. They found that one, two or three sorgaab spray at 1:10 gave the same result as three sprays at 1:20 ratio at 90 DAS, although one or two sprays showed less weed suppression.

Black mustard (*Brassica nigra* L.)

Brassica spp. contains high amounts of glucosinolates (Fenwick et al., 1983). According to Petersen et al. (2001) Isothiocyanates were strong suppressants of germination on tested species-spiny sowthistle (*Sonchus asper* L. Hill), scentless mayweed (*Matricaria inodora* L.), smooth pigweed (*Amaranthus hybridus* L.), barnyard

Table 1. Effect of various weed control methods on density and dry weight of weeds.

Treatment	Weed density (Number of plants per m ²)	Weed dry weight (g m ⁻²)
Control	63.7 ^{aa}	19.6 ^a
Sorghum stalks (soil incorporation) at 2 Mg ha ⁻¹	50.9 ^b (20.2 ^b)	11.3 ^{bcd} (42.0)
Sorghum stalks (soil incorporation) at 4 Mg ha ⁻¹	45.0 ^c (29.2)	10.0 ^{cd} (48.0)
Sorghum stalks (soil incorporation) at 6 Mg ha ⁻¹	37.7 ^d (40.8)	8.6e(56.0)
Sorgaab spray (1:20) 30 DAS	50.0 ^b (21.6)	12.6 ^b (35.4)
Sorgaab spray (1:20) 30 and 60 DAS	49.0 ^{bc} (23.1)	12.0 ^{bc} (38.7)
Chlorotoluron CMCPA AND 2.50 kg ha ⁻¹	11.6e(81.8)	2.3f(88.0)
Hand weeding	32.6 ^d (48.9)	6.6 ^{dc} (51.0)
LSD (0.05)	4.9	2.12

^a Means with different letters in a column differed significantly (5% level); ^b In parenthesis % decrease compared with control; DAS, days after sowing; Major weed flora of the experimental field: *Fumaria indica*, *Phalaris minor* Retz., *Rumex dentatus* L. and *Chenopodium album* L. Source: Cheema and Khaliq (2000)

Table 2. Influence of various concentrations of different aqueous extracts made from *Brassica nigra* L. plant parts on the germination of *Avena fatua* L. seeds.

Extracting plant part	Germination by extract concentration (g kg ⁻¹)					LSD (0.05)
	4	8	12	16	20	
Leaf	73	70	62	55	43	3.0
Stem	90	86	82	77	71	4.0
Flower	80	75	69	65	61	4.0
Root	85	80	75	69	65	3.2
Mixture	76	71	65	59	48	2.3
Control			98			
LSD (0.05)	3.0	3.0	2.8	4.0	3.0	

Leaf, stem, root extracts obtained from vegetative parts; flower extract obtained from reproductive parts. The mixing equal parts from Leaf, stem, flower root extracts prepared from the mixture. Source: Turk and Tawaha (2003).

grass (*Echinochloa crusgalli* L. Beauv.), blackgrass (*Alopecurus myosuroides* Huds.) and wheat (*Triticum aestivum* L.). Turk and Tawaha (2003) studied the allelopathic effect of black mustard (*Brassica nigra* L.) on germination and seedling growth of wild oat (*Avena fatua* L.). Allelopathic effect of extracts of different plant parts like leaf, stem, flower and root of black mustard was experimented. These authors found that germination and radicle length were affected by extract solutions and the inhibitory effect on germination increased with increasing concentration of extract solution of the fresh plant parts (Table 2). They also observed that the protease enzyme activity was suppressed causing reduced water uptake, which led to poor seed germination of wild oat. They found that residue incorporation affected the germination, plant height and dry matter accumulation per plant and the effect was greater for both root and shoot incorporation than only root incorporation.

Legumes

Allelopathic effect of aqueous extracts of perennial

legume *Pueraria thunbergiana* leaves on the germination and growth of lettuce was reported by Fujii (1994). Noguchi (2002) reported that xanthoxins may be responsible for the allelopathic effect of this plant. Kato-Noguchi (2003) isolated pisatin (32.7 nmol g⁻¹ fresh weight) from methanol extract of pea shoots and showed its inhibitory effect on the root and hypocotyl growth of cress at concentrations greater than 10 mM, and those of lettuce at concentrations greater than 30 mM. Akemo et al. (2000) used mulch of dead pea plants to control weeds with an aim to utilize its allelopathic potentiality in place of man-made chemicals. They found that growth of several weeds was affected. Caamal-Maldonado et al. (2001) examined the toxic effect of four legumes velvetbean (*Mucuna deeringiana* (Bort) Merr.), jackbean (*Canavalia ensiformis* (L.) DC.), jumbiebean (*Leucaena leucocephala* (Lam.) de Wit), and wild tamarind (*Lysiloma latisiliquum* (L.) Benth.) on growth of three weeds viz., barnyardgrass (*Echinochloa crusgalli* L. P. Beauv.), alegría and amaranth (*Amaranthus hypochondriacus* L.). The aqueous leachates (1%) of all four legumes exhibited strong phytotoxic effect on the radical growth of the weeds.

Sunflower

The sunflower is an annual oleaginous plant native to the Americas that also has allelopathic activity against weeds (Bogatek et al., 2006). Its use as a natural herbicide for some broadleaf weeds has been suggested (Anjum and Bajwa, 2007a, b). In this species several substances with allelopathic properties such as phenolic compounds, diterpenes and triterpenes have been isolated and chemically characterised (Macías et al., 2004b). Om et al. (2002) found that the use of sunflowers as green manure promoted a reduction in the population of *Phalaris minor* Retz., by 42 and 100% under field and laboratory conditions, respectively.

Trees

A member of the Juglandaceae family, the black walnut (*Juglans nigra* L.) is one of the oldest known examples of allelopathic activity among woody species. The members of this family produce *juglone* (5-hydroxy-1,4-naphthoquinone), which is a potent allelochemical that can inhibit the growth of a large number of plants at concentrations as low as 1 µM. Sensitive plants include both herbaceous and woody species (e.g., tomato, potato, apple, cucumber, watermelon, alfalfa, wheat and corn) that can exhibit wilting, browning of vascular tissues, necrosis and eventually death when cultivated close to established black walnut trees (Bertin et al., 2003; Willis, 2000). An elegant series of studies were carried out by von Kiparski et al. (2007), to verify the occurrence and fate of juglone in Alley soils under black walnut trees (juglone's release, accumulation and decline in greenhouse pot and laboratory sorption/degradation studies). These authors found that juglone is both microbially and abiotically degraded, and is particularly short-lived in soils supporting microbial activity. *Leucaena leucocephala* (Lam.) de Wit is a tree used for revegetation, soil and water conservation, and animal improvement in India. It contains mimosine, a toxic, non-proteinamino acid in its leaves and foliage that exhibits allelopathic activity (Xuan et al., 2006). Studying the allelopathic potential of aqueous extracts from the aerial part of *L. leucocephala* on the weeds *Desmodium purpureum* Hook. and Arn., *B. pilosa* and *Amaranthus hybridus* L., Pires et al. (2001) found that *B. pilosa* and *A. hybridus* were the most sensitive species to the extract in the bioassays. The same authors found a correlation between mimosine and extract concentrations, and suggest this allelochemical as possibly responsible for the effects on weed germination and development. *Eucalyptus* is another interesting genus with evidence of allelopathic activity. Studies conducted by May and Ash (1990) mimicking the typical daily rainfall rates upon quantities of foliage, leaf litter and bark litter as well as root leachates, soil leaching and volatiles from leaves on the germination of *Lolium* and growth of *Lolium*, *Lemna*,

Eucalyptus and *Acacia* concluded that the allelopathic activity of the *Eucalyptus* genus is probably the cause of understorey suppression, especially in drier climates. Babu and Kandasamy (1997), investigating the effects of fresh and dried leaf leachates of *Eucalyptus globulus* Labill. on *Cyperus rotundus* L. and *Cynodon dactylon* L., verified significant suppression of the establishment of propagules and early growth of these two species. El-Rokiek and Eid (2009), evaluating the effects of aqueous extracts of *E. citriodora* Hook. on *Avena fatua* and associated grassy weeds, found that the inhibitory effects on weeds were correlated with accumulation of the internal contents of total phenols. Investigating the allelopathic potential of leaf powder and ethanolic extracts from 15 arboreal species found in the exclusive Brazilian biome known as the *cerrado*, Silva et al. (2006) found that at least four species had an inhibitory effect: *Ouratea spectabilis* (Mart.) Spreng., *Pouteria ramiflora* (Mart.) Radlk., *Qualea grandiflora* Mart. and *Stryphnodendron adstringens* (Mart.) Coville. Among these species, *S. adstringens* was selected for detailed phytochemical and biological studies, in which four active fractions (one in ethyl acetate and three in chloroform) exhibited positive reactions to terpenoids. Evaluating the allelopathic activity of aqueous leaf extracts from four native Brazilian species [*Erythroxylum argentinum* O. E. Schulz, *Luehea divaricata* Mart., *Myrsine guianensis* (Aubl.) Kuntze and *Ocotea puberula* (Rich.) Nees], Maraschin-Silva and Aquila (2006) detected a slight alteration in lettuce germination by the *E. argentinum* and *L. divaricata* extracts, while all the species inhibited the growth of the target plant.

Allelopathic potentiality of weeds

Many weeds are now achieving importance as an agent of weed control for having special types of allelochemicals. These allelochemicals are capable of suppressing germination and growth of several other weeds, some of which are herbicide resistant.

Congress grass (*Parthenium hysterophorus* L.)

Parthenium hysterophorus L. is an obnoxious weed of present day, which is creating problem by its huge proliferation in any place. It exerts negative effects on agriculture, animal husbandry, ecology and the environment (Kohli and Rani, 1994). The allelopathic effect of this weed is mainly due to the presence of parthenin, a sesquiterpene lactone of pseudoguanolide nature in various parts of the plant (Kanchan and Jayachandra, 1980b; Kohli et al., 1993; de la Fuente et al., 2000), having greatest concentration in the leaves followed by inflorescence, fruits, roots and stems (Kanchan, 1975). Parthenin is known to have specific inhibitory effects on root and shoot growth of *Crotalaria mucronata* L., *Cassia tora* L., *Oscimum basilicum* L.,

Table 3. Allelopathic effect of different weeds on germination and growth of *Phalaris minor*.

Treatment		Germination of <i>P. minor</i> (%)	% inhibition over control	Length of plumule	Length of radicle
Weeds					
1	<i>C. arvense</i>	34.33(34.66)	47.85	2.25(1.78)	2.75(2.03)
2	<i>A. arvensis</i>	59.16(50.53)	10.13	3.78(2.17)	4.03(2.25)
3	<i>C. album</i>	0.00(0.57)	100.0	0.00(1.00)	0.00(1.00)
4	<i>R. acetosella</i>	59.67(50.69)	9.36	3.58(2.12)	3.82(2.18)
5	<i>L. aphaca</i>	40.83(39.22)	37.98	3.95(2.22)	4.11(2.25)
6	<i>M. denticulata</i>	0.00(0.57)	100.0	0.00(1.00)	0.00(1.00)
7	<i>M. indica</i>	0.00(0.57)	100.0	0.00(1.00)	0.00(1.00)
8	<i>V. hirsuta</i>	9.00(12.87)	86.33	0.80(1.28)	1.27(1.43)
9	<i>C. arvensis</i>	0.0(0.57)	100.0	0.00(1.00)	0.00(1.00)
10	<i>C. didymus</i>	68.00(55.73)	-3.30	4.12(2.23)	4.90(2.72)
11	<i>C. dactylon</i>	71.00(57.76)	-7.85	3.90(2.20)	4.60(2.37)
12	Control	65.83(54.38)	-	3.73(2.17)	4.97(2.40)
CD at 5%		(4.59)	-	(0.13)	(0.12)
Extract concentration					
1:4		30.19(26.94)		2.17(1.67)	2.48(1.76)
1:8		37.78(32.74)		2.18 (1.69)	2.60(1.79)
CD at 5%		(1.87)		(NS)	(NS)

Oscimum americanum L. and barley (*Hordeum vulgare* L.) (Khosla and Sobti. 1979, 1981). Various phenolic compounds identified in *Parthenium* (caffeic, vanillic, ferulic, chlorogenic and anisic acid) (Kanchan, 1975; Kanchan and Jayachandra, 1980a, b) may be responsible for growth reduction of test crops in amended soils. There was a 30-40% reduction in yield of crop plants when grown on soil containing dried root and leaf material of *Parthenium*. Parthenin enters the soil through the decomposing leaf litter (Kanchan and Jayachandra, 1976).

Chenopodiacea species

Jefferson and Pennacchio (2003) tested the allelopathic potentiality of the aqueous and methanol extracts of the leaves of four Chenopodiacea species viz., *Atriplex bunburyana* F. Muell., *Atriplex codonocarpa* Paul G. Wilson., *Maireana georgei* (Diels) Paul G. Wilson and *Enchylaena tomentosa* R. Br. at 0.006, 0.06, 0.63, 1.55, 3.12, 6.25 g l⁻¹ and 0.025, 0.25, 2.5, 6.25, 12.5, 25 g l⁻¹ respectively, for allelopathy on lettuce seeds as well as on the chenopod species themselves. They found that germination of lettuce seed was inhibited at concentrations ranging from 3.12 and 6.26 g l⁻¹. The root and shoot growth of lettuce was also inhibited. These authors also observed the inhibitory effect of the extracts of the leaves of *Atriplex bunburyana* and *Atriplex codonocarpa* on the seed of the chenopods, *Enchylaena tomentosa* and *Maireana georgei*. However, *A. codonocarpa* was not, in contrast, affected by extracts

derived from the leaves of *E. tomentosa* and *M. georgei*. At the same time all four species were susceptible to allelopathy by extracts isolated from leaves of their own respective species. These results indicated that allelopathy could be considered as a possible mechanism controlling the timing of chenopod germination and seedling establishment.

Canary grass (*Phalaris minor* Retz.)

Om et al. (2002) listed the allelopathic effect of different weeds on *Phalaris minor* (Table 3). It is clear from the data that the allelopathic potentiality is in the following order: *Chenopodium album* L. < *Medicago denticulate* L. < *Melilotus indica* L. < *Convolvulus arvensis* L. (inhibiting 100% germination over control) < *Vicia hirsute* L. (inhibited 86.33% germination) < *Cirsium arvense* L. (47.85% inhibition) < *Lathyrus aphaca* L. (37.98%) < *Rumex acetosella* L. (9.36%). Two weeds, that is, one grassy (*Cynodon dactylon* L.) and one broad leaf (*Coronopus didymus* L.) had stimulating effect by 7.85 and 3.30% increase in germination. The length of radicle and plumule was affected in the similar order as that of germination. Higher concentration of weed extract (1:4) had more inhibiting effect by about 20 to that of lower concentration (1:8) (Table 3).

Russian knapweed (*Acroptilon repens* L.)

A. repens is a widely distributed and problematic weed of

the western US (Maddox et al., 1985). Stevens (1986) found that the roots of *A. repens* inhibited the root growth of many plants including some weed species also such as *Lactuca sativa*, *Medicago sativa*, *Echinochloa crusgalli* and *Panicum miliaceum* by 30% at concentrations comparable to those found in the soil surrounding *A. repens* plants.

The germination of *Agropyron smithii* and *Bromus marginatus* was inhibited by aqueous leaf extracts of *A. repens* at high levels, however, according to Beck and Hanson (1989), germination was induced by lower concentrations.

Morning glory (*Ipomoea tricolor* Cav.)

Similarly, some species of *Ipomoea* are used as green manures and as a weed controller in some tropical regions of Mexico. In sugarcane (*Saccharum officinarum* L.) fields of the state of Morelos, Mexico, farmers promote *Ipomoea tricolor* (Cav.) growth before sugarcane cultivation. The allelopathic potential of *Ipomoea* was described by Anaya et al. (1990). Pereda-Miranda et al. (1993) identified Tricolorin A as the major phytochemical inhibitor from the resin glycoside mixture of the plants.

Croton bonplandianum

Sisodia and Siddiqui (2010) conducted a study to investigate the allelopathic effects of *Croton bonplandianum* weed on seed germination and seedling growth of crop plants (*Triticum aestivum* L., *Brassica oleracea* var. botrytis L. and *Brassica rapa* L.) and weed plants (*Melilotus alba* Medik., *Vicia sativa* L. and *Medicago hispida* Gaertn). Aqueous extracts of root, stem and leaf of *Croton* at 0.5, 1.0, 2.0 and 4.0% concentrations were applied to find out their effect on seed germination and seedling growth of test plants under laboratory conditions. The root, stem and leaf extracts had no effect on seed germination. The stem extracts had a stimulatory effect on the shoot length at all concentration levels, as against an inhibitory effect of leaf extracts.

Among the different parts, leaves were the most allelopathic and stems were least allelopathic. The inhibition effect was found to increase with increasing concentrations of different aqueous extracts (Sisodia and Siddiqui, 2008, 2009). Stem extracts at low concentration generally promoted root length but leaf and root extracts inhibited root length and dry weight. Root length, shoot length of weed species decreased progressively when plants were exposed to increasing concentration (0.5, 1, 2 and 4%). It was also found that with increasing concentrations of aqueous extracts of different parts of *C. bonplandianum*, the osmotic potential and phenolic content increased while pH does not have any major change.

Conflict of Interest

The authors have not declared any conflict of interest.

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