Allelopathy, an alternative tool to improve cropping systems. A review

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Review article

Allelopathy, an alternative tool to improve cropping systems. A review

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Abstract – Known since ancient times, the phenomenon of allelopathy has recently received greater attention from researchers and farmers worldwide. Crop failures and low yields caused by the reseeding, overseeding, crop rotation and replanting of fruit trees in orchards are believed to be caused by allelopathic activity. Moreover, the expensive and environmentally impacting herbicides for weed control have motivated studies directed at developing cheaper, environmentally-friendly alternatives. Despite the difficulties in separating chemical interference from other mechanisms, more modern approaches have produced consistent and conclusive data on this topic. The release and dynamics of allelochemicals in the soil are discussed herein. Examples of allelopathic crops, the allelochemicals produced and their uses in cropping systems are also presented along with current research trends regarding allelopathy.

allelopathy / chemical interference / agriculture / potential use

1. 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 [an]other". Currently, a more complete definition includes the positive and negative effects of chemical compounds produced mainly from the secondary metabolism of plants, micro-organisms, 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; Rice, 1984; Seigler, 1996). 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; Seigler, 1996; Bertin et al., 2003). 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 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; Rabotnov, 1982; 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; Macías et al., 1999a). 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 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; Einhellig, 1996; Kruse et al., 2000; Seigler, 1996; 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 recognised allelopathic activity and their importance for weed management are presented. Moreover, laboratory, greenhouse and field approaches for the detection of allelopathic activity and their application to agricultural systems are discussed.

2. RELEASING ALLELOPATHIC COMPOUNDS INTO THE ENVIRONMENT

Allelochemicals can be found in different concentrations in several parts of plants (leaves, stems, roots, rhizomes, seeds,
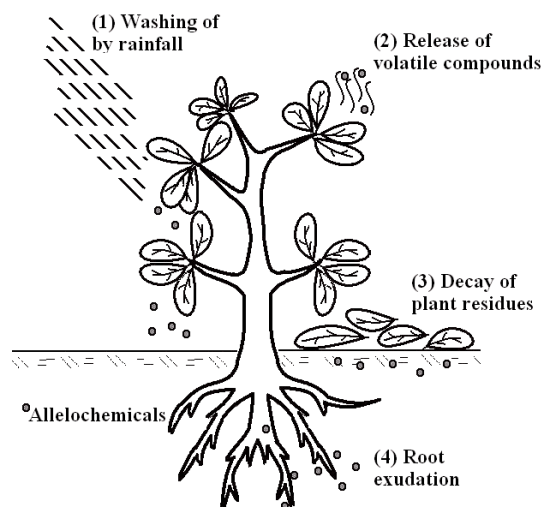

Figure 1. Possible pathways for release of allelochemicals into the environment.

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; Qasem, 2001) (Fig. 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 (Fig. 2) (Cseke and Kaufman, 2006; Einhellig, 1996; Vidal and Bauman, 1997).

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 nutrient-deficient 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)
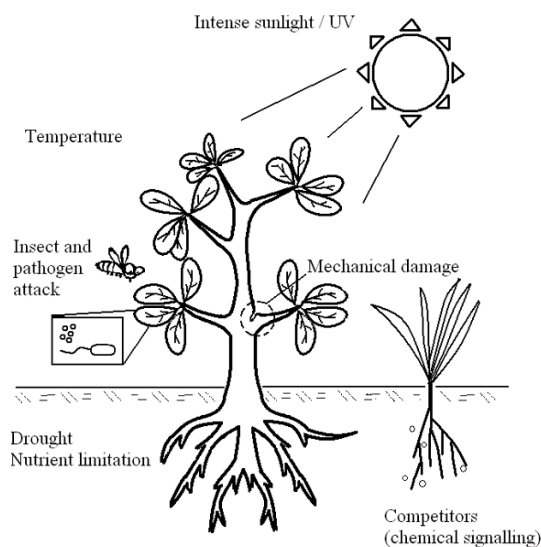
Figure 2. Induction of allelochemical production by biotic and abiotic factors.

on biomass production, tissue phytotoxicity and allelochemical content in rye (*Secale cereale* L.), suggested that despite the larger amounts of rye biomass, low fertilisation favours the phytotoxicity residue and/or allelochemical content.

When under insect or pathogen attack, plants undergo complex biochemical changes in response to herbivores and disease, including an increased release of allelochemicals (Mattner, 2006). Soil in which rusted ryegrass (*Lolium perenne* L.) attacked by *Puccinia coronata* Corda f.sp. *lolii* Brown was grown suppressed clover (*Trifolium repens* L.) biomass by 36% more in comparison with the direct effect of soil in which healthy ryegrass was grown in the greater rainfall areas of south-eastern Australia (Mattner and Parbery, 2001).

A number of recent studies have reported cellular and molecular processes involved in the production of allelochemicals and the response of target plants (Baerson et al., 2005; Dayan, 2006; Ding et al., 2007; Golisz et al., 2008; Song et al., 2008). During the molecular oxygen reduction process, intermediate molecules known as Reactive Oxygen Species (ROS) [e.g., superoxide (O_2^-), hydrogen peroxide (H_2O_2) and hydroxyl radical ($OH\cdot$)] are produced. These molecules are very toxic to cells and their excessive production may be triggered during biotic and abiotic stress (Resende et al., 2003; Veronese et al., 2003). Allelochemicals can also trigger the formation of ROS. Treatment with the allelochemical gallic acid produced by *Phragmites australis* (Cav.) Trin. ex Steud., in susceptible *Arabidopsis thaliana* (L.) Heynh. plants caused an increase in ROS levels on the root surface, causing damage to the formation of microtubules and collapse in the cellular architecture of this tissue (Rudrappa et al., 2007).

Belz (2007) argues that weeds may elicit allelochemical biosynthesis in competing crops, as occurs in plant defence induced by disease and insect attack. The author cites the examples of the exudation of three important allelochemicals from rice allelopathic cultivars in the presence of *Echinochloa crus-galli* (P) Beauv. (barnyardgrass) and sorgoleone from

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.

3. 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 (Blum et al., 1999; 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) (Fig. 3).

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 Endoaquulls).

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; Nair et al., 1990). 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 DIBOA (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-[(8′Z,11′Z)-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
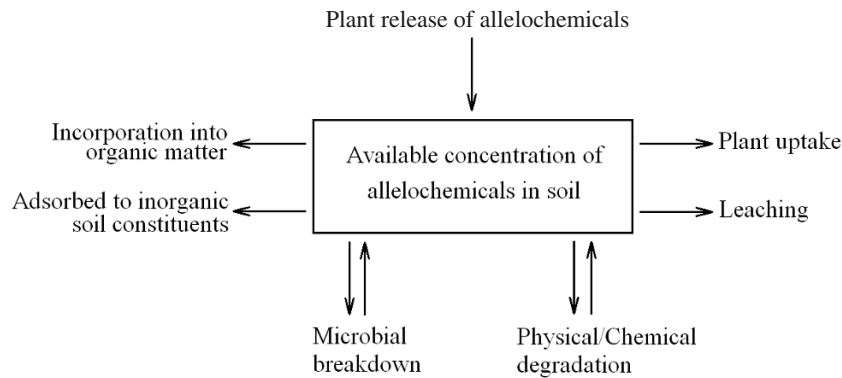
Figure 3. Input and output dynamics of allelochemicals in soil.

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 CO_2 in all soils tested, and the mineralisation kinetics indicated that microorganisms in American soils use sorgoleone as a source of energy.

4. ALLELOPATHIC ACTIVITY IN CROPPING SYSTEMS

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; Miller, 1996). 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 exuded 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 exuded 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. Examples of allelopathic crops and their respective allelochemicals are presented below.

4.1. Alfalfa (*Medicago sativa* L.)

Alfalfa is a Fabaceae forage crop cultivated worldwide as forage for cattle, and is most often harvested as hay or silage, grazed, or fed as greenchop. The autotoxic chemical substances from alfalfa are known to be (i) water-soluble, (ii) extractable from fresh alfalfa herbage, (iii) not produced from microbial activity, and (iv) more concentrated in shoots than in roots. Although the exact number of allelochemicals involved in alfalfa autotoxicity is not fully known, there are indications of the involvement of saponins, chlorogenic acid, medicarpin and other phenol-like compounds (Hall and Henderlong, 1989; Dornbos et al., 1990). However, there is no unequivocal proof of which chemical compound is the primary cause of autotoxicity in alfalfa. Replanting on an old alfalfa stand is discouraged due to autotoxic effects (low germination, poor establishment, dwarfed plants, reduced development of taproot and low productivity) (Jensen et al., 1981; Seguin et al., 2002). According to Chon et al. (2006), the most common intervals recommended for the reseeding of alfalfa in the USA are between

six and 12 months, with as many as 24 months in some cases. Interseeding alfalfa to re-establish old stands in declining productivity is infrequently successful also due to the autotoxicity. Jennings and Nelson (2002) after a series of field studies found an influence zone of 20–25 cm around established alfalfa plants. These authors also suggest that the density of established alfalfa would have to be less than 8 plants.m^{-2} before new seedlings could be productive.

4.2. 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; Pérez and Ormeno-Nunez, 1993; Wójcik-Wojtkowiak et al., 1990). 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 (Chase et al., 1991; 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).

4.3. 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).

4.4. 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. Gramine in barley leaves is located in the

mesophyll, parenchyma and epidermis and is mainly released into the environment by rain (Yoshida et al., 1993), but is not present in barley seeds or roots. Hordenine is not found in seeds, but has been found in roots from the first day of germination up to 60 days when cultured in a hydroponic system (Liu and Lovett, 1993).

4.5. Rice (*Oryza sativa* L.)

Rice is a member of the family Poaceae and is considered the most important crop worldwide for human consumption. Its weed management is currently completely dependent on chemical herbicides (Kim et al., 2005). However, rice can also be considered the most screened crop species for allelopathic activity. Rice screening started in the early 1970s and has been widely studied in the USA, Europe, Japan, Korea, India and China (Khanh et al., 2007). Field experiments in 1988 and 1989 identified rice accessions from the USDA-ARS rice germplasm collection for allelopathic effects on ducksalad [*Heteranthera limosa* (Sw.) Willd.] (Dilday et al., 1994). Several authors have screened the activity of a large number of rice allelochemicals (Kato-Noguchi et al., 2008; Olofsdotter et al., 1995). 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-3α-hydroxy-9β-primara-7,15-dien-16,6β-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. A study on three rice varieties revealed that the presence of aqueous and n-hexane extracts suppressed the in vitro growth of two phytopathogenic fungi (Bawja et al., 2008).

4.6. Sorghum [*Sorghum bicolor* (L.) Moench. and *Sorghum sudanense* (Piper) Stapf]

An annual or short-term perennial, with culms of 1–4 m, sweet except in grain types, sorghum is considered the fifth most important crop in the world. Its use as green manure or a cover crop for the suppression of weeds in nursery crops, alfalfa and crop rotations is common in the U.S. (Weston, 1996). To test the allelopathic activity of sorghum on wheat weeds, two field experiments were carried out in Faisalabad, Pakistan, through either the incorporation of sorghum stalks in the soil or the application of a filtered mixture of water and sorghum herbage (sorgaab) in a foliar spray (Cheema and Khaliq, 2000). According to the authors, the incorporation of 6 Mg.ha^{-1} of sorghum stalks reduced weed density and dry weight by 40.8% and 56.0%, respectively, whereas one application of sorgaab 30 days after sowing was sufficient to reduce weed density and dry weight by 23.1% and 35.4%, respectively. Several allelochemicals are found in sorghum, distributed in leaves, stems, roots, flowers and fruit (Santos, 1996). These include the chlorogenic acids p-coumaric and p-hydroxybenzaldehyde, found in *S. halepense* Pers., (Abdoul-Wahab and Rice, 1967); dhurrin, found in *S. halepense* (Nicolieur et al., 1983), *S. sudanense* and *S. bicolor* (Gorz et al., 1977); sorgoleone, found in *S. bicolor* and *S. sudanense* (Netzly et al., 1988); as well as strigol and sorgolactane, both present in *S. bicolor* (Hauck et al., 1992). According to Rice (1984), the effects of sorghum allelochemicals are concentration-dependent and selective. 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 exuded 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]-p-benzoquinone and its 1,4-hydroquinone (Czarnota et al., 2001, 2003a). It was discovered in roots of *S. bicolor* by Netzly and Butler (1986) when these authors were investigating seed stimulants of *Striga asiatica* (L.) Ktze. This benzoquinone has received more attention due to its larger production in roots and its potent allelopathic activity even at low concentrations (inhibitory activity against broadleaves and grass weeds has been achieved at concentrations as low as 10 μM in hydroponic assays) (Einhellig and Souza, 1992; Nimbal et al., 1996). 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 hydroxyphenylpyruvate 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). Varietal differences in the allelopathic activity of sorghum have been detected and quantitative variation in sorgoleone exudation has been suggested as the possible cause of such differences (Czarnota et al., 2003b; Trezzi et al., 2005). Moreover, age and environmental factors, such as luminosity, temperature, soil moisture and the presence of certain chemical compounds in the ground, are pointed out as possible causes of the variability in sorgoleone exudation (Hess et al., 1992). Although sorgoleone is the main molecule exudated in the roots, other analogue substances have also been identified. These compounds differ either in the aromatic ring substituents or in the number of carbons and double bonds in the aliphatic side chain. Studies have demonstrated that all have a similar inhibitory effect on PSII and probably contribute to *Sorghum* phytotoxicity to other plants (Kagan et al., 2003).

4.7. Sunflower (*Helianthus annuus* L.)

The sunflower is an annual oleaginous plant native to the Americas that also has allelopathic activity against weeds (Bogatek et al., 2006; Wilson and Rice, 1968; Ohno et al., 2001). 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). Heliannuol sesquiterpenoids have been isolated from the extract of cultivated sunflowers (*Helianthus annuus* L. SH-222) and are believed to be involved in the allelopathic action of sunflowers against dicotyledons (Macías et al., 1999b). Macías et al. (1999a) report the isolation, structural elucidation and allelopathic bioassays of 13 compounds from the sunflower cultivar Peredovick. Two new sesquiterpene lactones – helivypolide D and helivypolide E – and the bisnorsesquiterpene annuionone D (first reported as a natural product) have been described. The effects of a series of aqueous solutions (10^{-4} to 10^{-9} M) of these compounds on the root and shoot lengths of *Lactuca sativa* L., *Lepidium sativum* L., *H. vulgare* and *Allium cepa* L., seedlings have been studied. 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.

4.8. Kenaf (*Hibiscus cannabinus* L.)

Kenaf originated on the African continent and is used in the paper industry due to its light-coloured fibre which reduces the use of clarifying acids. It is also employed as raw material for handicrafts due to its highly durable fibre (Webber and Bledsoe, 2002). Russo et al. (1997) tested its potential use for allelopathic purposes using frost-killed kenaf that was chipped and either immediately frozen (weathered 0 months) or weathered in mats in the soil for two or four months. Extractions with distilled water were applied to the seeds of cucumber (*C. sativus*), green bean (*Phaseolus vulgaris* L.), tomato (*Lycopersicon esculentum* Mill.), redroot pigweed (*A. retroflexus*) and annual Italian ryegrass at different concentrations. According to the authors, extracts from kenaf weathered up to four months reduced germination in pigweed by 50 to 70%, especially at the highest concentration. The highest concentration of non-weathered kenaf was able to reduce germination in tomato and ryegrass by 30%. As the increase in the length of weathering time led to an increase in the degree of germination and size of most plants, the authors suggest the use of non-weathered kenaf or its extracts to suppress weeds. Analysing the chemical composition of the essential oil of kenaf using GC-MS, Kobaisy et al. (2001) found fifty-eight components, the most abundant of which were (E)-phytol (28.16%), (Z)-phytol (8.02%), n-nonanal (5.70%), benzene acetaldehyde (4.39%), (E)-2-hexenal (3.10%) and 5-methylfurfural (3.00%). Phytotoxic studies have demonstrated the effects of kenaf on lettuce and bentgrass as well as antifungal activity against *Colletotrichum fragariae* Brooks, *Colletotrichum gloeosporioides* Penz. and Sacc., and *Colletotrichum accutatum* Simmonds. However, little or no algicidal activity has been observed.

4.9. 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-napthoquinone), 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; Crist and Sherf, 1973; 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-protein

amino 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 *Avenua 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 Áquila (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.

4.10. Weeds

Weed species with allelopathic activity can play an important role in weed-weed and weed-crop interactions. Such interactions are believed to be the reason for the success of invasive weeds. Examples of known allelopathic weed species are described below.

Centaurea maculosa Lam. is one of the most aggressive invaders in North America, that renewed the interest in allelopathy after the discovery that its roots release a racemic mixture of (±) catechin that in determined concentrations can inhibit the growth and germination of North American plant species. (–)-catechin is considered a potent phytotoxin, whereas (+)-catechin is a weaker phytotoxin with some antimicrobial activity (Bais et al. 2002, 2003; Ridenour and Callaway, 2001). However, its role has recently been criticised due to the low concentration of (–)-catechin found in soils with *C. maculosa,* that exhibit values considered very low to cause significant damage (Duke et al., 2009; Perry et al., 2007). These last authors also report this phytotoxin cannot cause oxidative damage because this molecule can be quickly degraded by extracellular root enzymes.

Barnyardgrass (*E. crus-galli*) is considered the worst weed affecting rice cultivations around the world. Investigating allelochemicals in barnyardgrass-infested soil and their activity on crops and weeds, Khanh et al. (2008) found 18 compounds belonging to terpenes, derivatives of cinnamic acid and ferulic acid, long-chain fatty acids, and steroids.

Sambucus nigra L. is a shrub that is widely found throughout Italy that causes considerable crop loss. Using a sequential series of solvents and eluents as well as different isolation methods (including thin-layer chromatography, column chromatography, flash column chromatography, reverse-phase high-pressure liquid chromatography, etc.), D'Abrosca et al. (2001) found at least twenty-four aromatic metabolites in this species, belonging to cyanogenins, lignans, flavonoids and phenolic glycosides. Structures were determined on the basis of their spectroscopic features, with two new compounds isolated and identified as (2S)-2-O-b-d-glucopyranosyl-2-hydroxyphenylacetic acid and benzyl 2-O-b-d-glucopyranosyl-2,6-dihydroxybenzoate. All compounds were assayed on the dicotyledons *L. sativa* (lettuce) and *Raphanus sativus* L. (radish) and monocotyledon *A. cepa* (onion) to test their stimulatory or inhibitory effects on seed germination and radicle elongation. Cyanogenins had a mainly inhibiting effect, whereas lignans stimulated growth.

Leonurus sibiricus L. is a perennial roadside weed that grows vigorously in all seasons in West Bengal, India. In order to evaluate the allelopathic activity of its root exudates, Mandal (2001) found a stimulatory effect that increased with the increase in concentration of root exudates, peaking at a ten-fold increase and decreasing thereafter; at fifty-, seventy-five- and one hundred-fold concentrated root exudates, there was an inhibitory effect (nearly 100% at seventy-five- and one hundred-fold). Paper chromatography and staining suggested the presence of phenolics in root exudates, including caffeic acid. In *Mikania micrantha* Kunth ex H.B.K. – a herbaceous vine that smothers trees and crops, suppressing vigour and eventually killing the affected plants – Shao et al. (2005) isolated and identified three sesquiterpenoids: dihydromikanolide, deoxymikanolide and 2,3-epoxy-1-hydroxy-4,9-germacradiene-12,8:15,6-diolide, which demonstrated allelopathic activity against lettuce, *L. multiflorum*, *Acacia mangium* Willd, *Eucalyptus robusta* Sm. and *Pinus massoniana* Lamb. Aqueous extracts from *Conyza canadensis* (L.) Cronquist were found to reduce the germination and early growth of six target plants (tomato, radish, wheat, corn, bulrush millet and mungbean) (Shaukat et al., 2003). According

to the authors cited, the addition of decaying shoots in sandy loam with 5, 10 and 20 g. 400 g^{-1} of soil inhibited the germination and growth of bulrush millet at all dosages. Chromatographic analyses for phenolics revealed gallic acid, vanillic acid, cathecol and syringic acid.

Artemisia vulgaris L. is a North American invasive perennial that produces and releases a series of volatile compounds with an allelopathic effect. Barney et al. (2005) isolated and identified *via* gas chromatography coupled with mass spectrometry a set of terpenes from fresh leaves (camphor, eucalyptol, α-pinene and β-pinene). Comparing three plant populations, these authors verified that none of the individual monoterpenes could account for the observed phytotoxicity imparted by total leaf volatiles, suggesting a synergistic effect or activity of a component not tested.

Garlic mustard [*Alliaria petiolata* (M.Bieb.) Cavara & Grande] is another North American invasive herbaceous biennial that releases a series of glucosinolates and flavonoid glycosides (Vaughn and Berhow, 1999). Barto and Cipollini (2009), evaluating the half-lives of several flavonoid glycosides produced by *A. petiolata* in sterile and non-sterile soil at two temperatures, found that the flavonoid glycosides had half-lives in non-sterile soil ranging from 3 h to 12 h (the longest half-life was only 45.5 h in sterile soil). Based on these very low field levels and short half-lives the authors suggest that the allelopathic effects of *A. petiolata* are probably either due to the degradation of the produced compounds, or to other unknown mechanisms.

5. TECHNIQUES USED IN ALLELOPATHIC STUDIES

As mentioned above, plant age, type of plant organ, cultivar and diverse environmental factors can either increase or reduce the release of allelochemicals. Given such a scenario, in which many agents can affect allelopathic activity, the choice of an adequate methodology for identifying allelopathic plants and/or allelochemicals is important. Some laboratory and greenhouse routine protocols are presented below:

5.1. Bioassay using Petri dishes

Bioassays with Petri dishes constitute the commonest technique and are, at times, part of a more elaborate study in allelopathy research. A bioassay consists of evaluating the effects of plant extracts (aqueous, hydroalcoholic, fractions from different solvents, etc.), volatile essential oils, and isolated or commercial chemicals on the germination and initial growth of a given target plant. The extracts are commonly made from leaves from the donor plant, but it is possible to test extracts from virtually any part of a plant (stems, roots, flowers, fruit and seeds). To carry out a bioassay, the bottom of the Petri plate is normally lined with filter paper and the seeds of the target plant are deposited to receive the solutions, often in different concentrations. The dishes may be kept in a Biochemical Oxygen Demand (BOD) chamber either in the dark or with a programmed photoperiod depending on the photoblastism of the seed tested. A small variation in this protocol is the use of solid agar medium amended with the extracts or isolated substances. Germination velocity and percentage as well as shoot and root length are the variables commonly evaluated in these bioassays.

An et al. (1997) evaluated the phytotoxic properties of *Vulpia myuros* (L.) C.C. Gmel. residue extracts on wheat (*T. aestivum* L. cv. *Vulcan*) in the laboratory and found germination delay and inhibition as well as a reduction in coleoptile and root growth. Pérez-Leal et al. (2005), through Petri dish bioassays, verified that organic extracts (methanol and dichlorometane) of *Petiveria alliacea* L. were more phytotoxic on germination and initial development of lettuce and amaranth than water extracts.

5.2. Competition tests

Academically speaking, competition can be seen as the withdrawal from the environment of shared resources, whereas allelopathy consists of the addition of chemicals with phytotoxic potential (Olofsdotter et al., 2002). Despite this clear conceptual division, these same authors call attention to the fact that in field experiments this separation is almost impossible to detect. Thus, how to separate the effects of pure competition from allelopathy has been a dilemma among researchers when they are using pot experiments to confirm a plant species as allelopathic.

There are several methods to study competition effects that can be classified into four general types: additive, substitutive, systematic and neighbourhood (for more details see Radosevich et al., 1997). Among them, the additive type (that consists of keeping the density of one plant species constant while the other is changed) can be adapted to help identify allelopathic species. Based on the assumption that the response of the target plant is dependent on the concentration of allelochemicals available in the environment, in this type of experiment (also known as density-response) the number of donor species is maintained while the number of target plants is reduced. Thus, a constant number of donor species ensures that the volume of allelochemicals released into the environment is constant, and a smaller number of target plants ensures a larger volume of allelochemicals available for each target plant (Kruse et al., 2000; Weidenhamer, 1996). So, if the negative effects observed are due to competition, a lower density of plants would be better for the target species. With allelopathic action, however, a decrease in the number of target species leads to a higher dose of allelochemicals for each plant. Another variation of this technique consists of the use of plant residues or extracts, with a variation in the number of the target plants. This type of test can be performed in bioassays, in greenhouse or field experiments.

Tseng et al. (2003) performed a density-response phytotoxicity analysis of lettuce seedlings growing in soil mixed with powder from *Macaranga tanarius* (L.) Müll.Arg. leaves and found that the growth of the seedlings was most suppressed in the experiment with low seed density, suggesting that the

phytotoxins produced during leaf decomposition inhibited the growth. Through a series of extraction procedures, the authors identified at least ten chemical compounds in *M. tanarius* leaves (nymphaeol-A, nymphaeol-B, nymphaeol-C, quercetin, abscisic acid, blumenol A, blumenol B, roseoside II, tanariflavanone A and tanariflavanone B). Among these compounds, quercetin, abscisic acid, blumenol A, blumenol B, tanariflavanone A and tanariflavaone B exhibited inhibitory effects on radicle growth in lettuce and weeds, among which abscisic acid was the greatest growth inhibitor.

Once a species is confirmed as allelopathic, the other types of competition experiments can be used to select from among genotypes/cultivars the one with major allelopathic potential, given that the rate of allelochemical release can differ within a given species (Kruse et al., 2000). A screening test with 102 Bangladesh rice cultivars and four target species [*L. sativum*, *L. sativa*, *E. crus-galli* and *Echinochloa colonum* (L.) Link. revealed at least one high-yielding cultivar – BR17, which inhibited shoot and root growth in the four species by approximately 59% (Kato-Noguchi et al., 2009).

5.3. Residual toxicity in the soil

Soil samples are collected in the rhizosphere of alleged allelopathic species and are used as substrate for the germination and growth of target species (Kruse et al., 2000). Soil samples from nearby areas, but without the alleged allelopathic species, are used as control. Aqueous extracts of these soils can also be used in Petri dish bioassays.

Growing six target species in soil collected from a field where Mexican sunflowers [*Tithonia diversifolia* (Hemsl.) A. Gray] had been grown for 5 years, Tongma et al. (2001) found a decrease in seed germination, shoot growth and root growth in all plant species tested when compared with those grown in soil from an area without the sunflower. Analysing the phytotoxicity of allelochemicals in soil on crops and weeds, Khanh et al. (2008) found that paddy soil infested with barnyardgrass exerted a strong inhibitory effect on growth. The authors used different water and EtOH solutions from resin-retained compounds that demonstrated strong phytotoxic action against the growth of rice and barnyardgrass, of which the water solutions were more inhibitive than the EtOH solutions. Using the resin separation method, the authors identified at least 18 chemical compounds. Kong et al. (2006) analysed soil samples surrounding the first root of different rice cultivars and found that only momilactone B, 3-isopropyl-5-acetoxycyclohexene-2-one-1 and 5,7,4'-trihydroxy-3',5'-dimethoxyflavone were released into the soil at phytotoxic levels from allelopathic rice cultivars in early growth stages. On the other hand, the concentration of phenolic acids released by living roots of allelopathic rice seedlings never reaches phytotoxic levels in the soil.

5.4. Detoxification of the substrate

Activated carbon has the ability to adsorb a wide range of organic compounds when mixed into the soil and such an effect can be used to evaluate allelopathic activity. Activated carbon indirectly reduces the action of phytotoxins, which may be absorbed and retained in the activated carbon, thus reducing their availability, particularly those with large structures. Therefore, it is assumed that if any substance can cause allelopathic activity, its effect is diminished or eliminated by the presence of activated carbon (Kruse et al., 2000). Activated carbon can be placed directly on the soil surface, incorporated into the soil, and mixed with plant extracts or in a hydroponic solution. The assessment of allelopathic activity is made by a comparison of treatments with a control (without the addition of activated carbon), in which inferior development is expected. Studying the effects of activated carbon on autotoxicity in *C. maculosa*, Perry et al. (2005) found a positive response in the seedling establishment of this weed with the addition of activated carbon to the soil. On the other hand, Ridenour and Callaway (2001) investigated allelopathic interactions between *C. maculosa* and *Festuca idahoensis* Elmer (the latter of which is a native American bunchgrass) in a competition experiment and found that the addition of activated carbon promoted a lesser production of leaf, stem and root biomass in *C. maculosa*. The authors suggest that the activated carbon reduced the effectiveness of *C. maculosa* root exudates, thereby competitively favouring *F. idahoensis*. Despite these interesting experiments, the use of activated carbon in field experiments may produce ambiguous results. As activated carbon indiscriminately absorbs organic exudates from crops and weeds, its addition to the soil does not necessarily offer benefits to crop plants. Activated carbon may bind molecules that act as a microbial growth factor, affecting the growth of the microbiota and indirectly affecting crop growth. Moreover, there is the as-yet unproven possibility that activated carbon amendment could sequester molecules released from the roots that inhibit the growth of pathogenic fungi and bacteria. Activated carbon may also sequester organic nitrogen and phosphorus from the soil, thereby reducing the mineralisation rate of these nutrients and their availability (Kulmatiski and Beard, 2006; Lau et al., 2008).

5.5. Hydroponic experiments

Hydroponics has been used as an interesting tool for investigations into allelopathy. A hydroponic apparatus can be used for two general purposes: (1) to serve as a medium for the diffusion and delivery of allelochemicals to target plants (the allelochemical source can be from crude plant extracts, isolated or commercial chemicals, etc.); and (2) for collection of root-exuded compounds that can be recovered for subsequent allelopathic bioassays and/or chemical identification.

Jose and Gillespie (1998) added juglone at three different concentrations (10^{-6} M, 10^{-5} M and 10^{-4} M) to hydroponically grown corn and soybean seedlings. Within three days, this allelochemical significantly inhibited shoot and root growth rates, leaf photosynthesis, transpiration, stomatal conductance, and leaf and root respiration when compared with control (without juglone addition). The authors also concluded that soybean was more sensitive to juglone than corn, although

both crops proved sensitive. A similar study was carried out by Nimbal et al. (1996) to evaluate the effects of sorgoleone on the growth of velvetleaf (*Abutilon theophrasti* Medic.), ivyleaf morningglory [*Ipomea hederacea* (L.) Jacq.], large crabgrass [*Digitaria sanguinalis* (L.) Scop.] and barnyardgrass (*E. crusgalli*).

The Continuous Root Exudates Trapping System (CRETS), which is an adaptation of the Nutrient Flow Technique (NFT), is an interesting hydroponic system for collecting and studying root-exudated compounds (Tang and Young, 1982). In this system, a thin film of nutrient solution flows continually through plastic channels or tanks, in which the roots are partially in the shallow stream of re-circulating solution and partially above it. The nutrient solution then drains back into the tank and is re-circulated to the plants. Before being pumped into the first tank, the solution passes through a column filled with adsorbent material (e.g., C-8, C-18 silica, XAD-4 resin or activated charcoal), in which the exudated organic solutes are trapped. The solutes are then recovered and their allelopathic activity is evaluated, following separation and identification through current analytical procedures.

Evaluating the allelopathic potential of watermelon root exudates recovered from a CRETS, Hao et al. (2007) found that the seedling growth of both watermelon and lettuce was significantly inhibited by watermelon root exudates and the degree of inhibition increased with the increase in the concentration of exudates, with inhibition most pronounced 41 to 50 days after transplanting. Ferulic acid and ρ-hydrobenzoic acid were the dominant phenolic compounds found in the root exudates using HPLC. Tsanuo et al. (2003) used the same method on the root exudates of the cattle forage legume *Desmodium uncinatum* (Jacq.) DC. The authors obtained three isoflavanones [5,7,2',4'-tetrahydroxy-6-(3-methylbut-2-enyl)isoflavanone (1), 4'',5''-dihydro-5,2',4'-trihydroxy-5''-isopropenylfurano-(2'',3'';7,6)-isoflavanone (2) and 4'',5''-dihydro-2''-methoxy-5,4''-dihydroxy-5''-isopropenylfurano-(2'',3'';7,6)-isoflavanone (3)] as well as a previously known isoflavone: 5,7,4'-trihydroxyisoflavone [genistein (4)]. These substances induced germination, but negatively affected the growth of *Striga hermonthica* (Del.) Benth, which is a parasitic plant of cereals. The authors hypothesise that such an occurrence may have prevented the normal attachment of *S. hermonthica* to the host plants as part of a protection mechanism.

5.6. Amendment of plant residues

The amendment of plant residues consists of the addition of different amounts of plant material to the substrate in order to test the allelopathic effect of its decay and the release of allelochemicals on the target species. However, given the possibility of an increase in microbial activity that could result in a depletion of nutrients, fertilisation or sterilisation of the substrate is recommended. This technique has been used in greenhouse and field experiments with relative success to exhibit allelopathic effects. Testing the effects of soil amendment with residues from an invasive weed, *Parthenium hys-*

terophorus L., Singh et al. (2005) found that the addition of residues at 40 g.kg^{-1} of soil reduced the size and dry mass of *Brassica oleracea* L., *B. campestris* L. and *B. rapa* L. The authors credit these results to the release of water-soluble phenolics into the soil by *P. hysterophorus* residues. Batish et al. (2006), set up a similar experiment to verify the effect of *A. conyzoides* residues added to soil on the growth and nodulation of *Cicer arietinum* L., and verified that 10 g.kg^{-1} residues incorporated into the soil were sufficient to cause significant reductions in all analysed variables. Soil amendment with *Chenopodium murale* L. residues reduced the growth, nodulation and macromolecule content of two legume crops (*C. arietinum* and *Pisum sativum* L.) (Batish et al., 2007). The amendment of soil by leaf residues from *Croton bonplandianum* Baill. was found to affect seedling height, size and number of leaves, and number of branches, capitula and seeds/plant of the weed *P. hysterophorus* (Thapar and Singh, 2006). The authors cited attribute the growth inhibition to a decrease in chlorophyll, sugars, protein and lipid content, whereas organic and amino acids were increased.

5.7. Plant box method

The plant box method is based on the principle of dose response, the intention of which is to link growth inhibition with the concentration of root exudates in the media. This is achieved by the use of agar as a diffusion medium, allowing the dispersion of allelochemicals exudated from roots of the donor plant to the target plant (Fujii, 1994; Nishihara et al., 2005), the latter of which is increasingly affected as it gets closer to the donor plant. The procedure consists of putting a donor plant in a cellulose (or nylon) tube and placing it in one corner of a plant box. The box is kept in ice and filled with autoclaved and cooled agar (40° C). After gelatinising the agar, seeds from the target plant are concentrically placed in the area around the donor plant and the container is sealed with clear wrap to prevent evaporation. The boxes are placed in a black vinyl pot to darken the roots of the target seedlings and kept in a Biochemical Oxygen Demand (BOD) chamber. A plant box without the donor plant is used as an untreated control. The expectation is that the allelopathic effects will be viewed gradually, correlating the effects with the distance of the target plants from the donor plant.

Parvez et al. (2003) used the plant box method to identify allelopathic activity in *Tamarindus indica* L. seedlings. Shiraishi et al. (2002) used the method to identify seven other ground-cover plant species. Nishihara et al. (2005) confirmed the influence of L-DOPA [L-3-(3,4-dihydroxyphenyl)alanine] as an allelochemical exudated from *Mucuna pruriens* (L.) D.C. roots using this method.

5.8. The sandwich method

The sandwich method consists of the use of a special six-well multidish (Nalge Nunc International K.K.), in which dry

leaves from the donor plant are placed at the bottom and autoclaved agar cooled to 40 °C to 45 °C is added. After gelatinising, the same volume of agar is added again, forming a double-layer medium, on which seeds from the target plant are placed vertically at the surface. The system is then sealed and kept in a BOD chamber. Agar substrates alone are used as untreated controls (Fujii, 1994). Shiraishi et al. (2002) used this method to screen the allelopathic activity of leachates from seventy-one plant leaf residues and found at least seven species that inhibited the growth of lettuce seedlings by more than 50%. Fujii et al. (2003) also used this method to screen 239 medicinal plant species and, based on the lettuce growth inhibition, highlighted species with strong activity [e.g., *Artabotrys odoratissimus* R. Br. ex Ker Gawl, *Annona cherimola* Mill. (both Annonaceae), *Dialium guineensis* Wild., *T. indica* (both Leguminosae), *Emblica pectinata* (Hook.f.) Ridley and *Hevea brasiliensis* L. (both Euphorbiaceae)].

6. GENETIC IMPROVEMENT OF ALLELOPATHIC ACTIVITY IN CROPS

The enhancement of the weed-suppressing ability of allelopathic crops through an increase in the amount released and/or the prolongation of the release of allelochemicals and the overcoming of the problem of autotoxicity in some crops through genetic improvement have been suggested as possibilities to be explored (Kruse et al., 2000; Weston 1996). However, breeding to improve competitive or weed-suppressive ability in crops using traditional plant breeding has received less attention than for plant resistance to insects and diseases, probably due to the relative lack of understanding of the mechanisms of plant interference and the absence of a means of reliably selecting for enhanced weed-suppressive traits (Bertin et al., 2008).

Commonly, a major emphasis in breeding programmes has been placed on yield and disease resistance in edible crops, while for non-edible crops such as turfgrass, selection for turf quality and ability to compete effectively with surrounding vegetation has been important for low-maintenance cultivars. As a consequence, most edible crops possess low allelopathic capability, as detected by Bertholdsson (2004). This author, assessing the allelopathic potential of 127 landraces and cultivars of barley from four countries (that covered most of the gene pool resulting from 100 years of breeding), verified a decreasing trend in allelopathic activity as a possible consequence of the dilution of the genes from landraces.

Techniques such as traditional or molecular breeding and transgenics could be used to transfer allelopathic traits between cultivars of the same species or between species (Belz, 2007; Rice 1984). Genetically modified plants may be widely used in the future to reduce pesticides, such as organophosphates and organocarbonates, in agriculture as well as to remove the residue of agrochemicals and industrial or accidental contamination from the environment (Macek et al., 2008). However, studies designed for the accomplishment of these goals cannot be carried out in a single laboratory, which makes the collaboration of professionals from a wide range of research fields necessary, such as biologists, ecologists, agronomists, natural product chemists, plant physiologists and geneticists (Olofsdotter, 2001).

Rice is the crop at the most advanced research stage regarding this subject due to the screening work that has been carried out since the late 1980s (Dilday et al., 1994; Jensen et al., 2001). According to Jensen et al. (2001), 12 000 accessions from USDA-ARS have been screened in field experiments for their potential regarding ducksalad [*Heteranthera limosa* (Sw.) Willd.], redstem (*Ammannia coccinea* Rottb.), broadleaf signalgrass [*Brachiaria platyphylla* (Griseb.) Nash], rice flatsedge (*Cyperus iria* L.), sprangletop (*Leptochloa* spp.) and barnyardgrass (*E. crus-galli*). Allelopathic genes could be transferred to rice; weeds could be inhibited; and the use of herbicides could be decreased (Yongjun et al., 2008). The use of marker-assisted selection through quantitative trait loci (QTL) to improve allelopathy in recombinant inbred line populations of rice has been suggested (Olofsdotter et al., 2002). Wheat, barley and oats (*Avena* ssp.) are examples of other crops that are currently under genetic investigation for the identification of encoding genes associated with allelopathic traits. However, current knowledge on allelopathic QTL remains incomplete (Belz, 2007).

Song et al. (2008) demonstrated the intensification of allelochemical biosynthesis in rice grown under stress nutrition (i.e., low levels of nitrogen). This experiment revealed the overexpression of genes that encode for PAL (phenylalanine ammonia-lyase), O-methyltransferase, triosephosphate isomerase and P450 – all related to the synthesis of phenolic compounds and detoxification. Moreover, a proteomic analysis of rice grown in the presence of barnyardgrass weeds (*E. crus-galli*) has revealed the induction of the following proteins: PAL, a thioredoxin and 3-hydroxy-3-methilglutaril-coenzyme A reductase 3 (HMGR) (Lin et al., 2004). The identification of these genes and proteins demonstrates different signs, plant-environment interactions or plant-plant communication triggering the biosynthesis of phenolic compounds that are also known to be involved in defence processes.

An analysis of *A. thaliana* transcripts after exposure to the allelochemical BOA has revealed the expression of oxidoreductases, aldo-ketoreductases, peroxidases, cytochrome P450-like proteins, glutathione S-transferases, glucosyltransferase and members of several families of efflux transporters for drugs; all these genes are involved in detoxification through the modification, conjugation or elimination of xenobiotics (Baerson et al., 2005). More recently, an analysis of the gene expression of *A. thaliana* though a micro-array following exposure to fagomine, gallic acid and rutin has revealed that genes expressed in response to allelochemicals share the same pathways triggered during the response to abiotic and biotic stress (Golisz et al., 2008).

The use of biotechnological tools for the enhancement of the allelopathic potential of some crops encounters difficulties, especially when the genes involved belong to very well-defined metabolic pathways and have seasonal, tissue and genotype variations in the production of their metabolics (Cambier et al., 2000; Reberg-Horton et al., 2005; Wu et al., 2000). For example, five genes are required for the

biosynthesis of DIBOA in maize: *Bx1* to *Bx5*. *Bx1* encodes a trytophan synthase α homolog and *Bx2* to *Bx5* encode cytochrome P-450-dependent monooxygenases involved in the formation of oxidised DIBOA (Frey et al., 1997).

7. CONCLUSION

Studies on allelopathy in crops and weeds have been developed in the past few decades and the use of allelopathic crops in crop rotation, cover crops, green manure, intercropping, etc., has become a reality. However, allelopathy must be recognised as a dynamic process that involves more than just donor and target plants. Variations in the type of soil, water and nutrient availability, previous or companion crops, climate conditions, etc. are determinants of the occurrence of effective allelopathic activity. Modern methods and new approaches have helped identify potential allelochemicals and have led to a better understanding of the biosynthesis, release and dynamics of these allelochemicals in the soil. Genetic studies are just getting underway and gene identification and manipulation are currently seen as the next step in the establishment of allelopathic traits as important tools in weed management programmes.

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