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REVIEW ARTICLE

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ABSTRACT

Allelopathy determines the dynamics of plant species in different environments. Understanding this biological phenomenon could help to develop applications in both natural and agricultural systems. This review summarizes the genetic and environmental characteristics that control the production and release of allelochemicals in agroecosystems. This study highlights the current understanding of the environmental changes caused by allelochemicals and summarizes the knowledge about the mechanisms of action of these compounds. Finally, it reviews novel applications of allelopathy in agricultural production systems, including the role of allelochemicals in consortia and their potential use in no-tillage cropping systems through cover crops or mulches.

1. Introduction

Allelopathy is a form of positive and negative interaction among organisms that is caused by the action of chemical compounds referred to as allelochemicals (Rice 1984). These compounds are produced mainly as a result of the secondary metabolism of plants and microorganisms (bacteria, viruses and fungi) and can influence several processes in ecosystems and agroecosystems (Rizvi et al. 1992; Seigler 1996; Olofsdotter et al. 2002). Allelochemicals can lead to different mechanisms of action in plants. An allelopathic effect is mainly referred to as a type of negative interaction (Radosevich et al. 2007; De Albuquerque et al. 2011), but positive interactions have also been reported, depending on the allelochemical considered, the target plant and the concentration tested (Eichenberg et al. 2014).

The plant kingdom consists of about 300,000 species (Bold et al. 1980), which have the ability to produce several secondary compounds and it has been estimated that only a limited proportion of these chemicals has been investigated (Wink 2010). The substances produced by plant secondary metabolism are essential for the interaction of plants with the biotic part of the environment and help to attract pollinators or seed dispersers and also act as a defense against natural enemies and as allelochemicals against potential competitors (Kroymann 2011). The ability to produce and release allelopathic compounds into the environment, or even to tolerate the presence of allelochemicals released by other plants, can determine the ability of a species to survive and reproduce. The ecological approach to allelopathy can become very complex because it can occur in a wide range of plant species with different survival and propagation strategies. In an agricultural context, allelochemicals can be produced by crops, or by uncultivated plants, many of which are considered weeds.

In agroecosystems, allelopathy can affect weed management, plant reproduction, species consortia, the mulching effect on crops and the succession and rotation of cultivated species (Chon et al. 2006). Additionally, allelochemicals have the potential to be used for herbicide synthesis, enabling the discovery of new mechanisms of action. From a genetic point of view, molecular biology techniques (especially transgeny), or even classical breeding, can hasten the goal of increasing the production of desirable allelochemicals by crops. Genetic studies are extremely useful to understand better the true role of allelochemicals in plant–plant interactions and to evaluate their limitations and effects on the environment. However, the production of these compounds requires energy investment by the plant, which might theoretically limit their biological production. In the context of genetic improvement, the balance between allelopathy and yield potential is a recurring challenge (Wink 2010).

Weed infestation represents a major constraint to agricultural production. Chemical weed control is the major management tactic used in conventional agriculture. However, complementary strategies to herbicides are increasing in importance, to reduce the dependence on chemical control and to mitigate the negative impacts that these compounds impose on the environment. Knowledge of allelopathy might constitute an important asset to increase the acceptance of agricultural products in today's demanding consumer markets.

The objective of this study was to discuss the recent advances in scientific knowledge about allelopathy in agroecosystems. It highlights the major factors and mechanisms involved in the production of allelochemicals, as well as their potential use in the production of food, fiber and bioenergy.

2. The production and composition of allelochemicals

Allelopathy can be considered to be a form of communication among plants (Bais et al. 2004; Weir et al. 2004; Yoneya &

Takabayashi 2014). Plants synthesize a multitude of compounds via secondary metabolism. The production of these compounds depends on the existence of precursor molecules and the activation of specialized genes. The activation of genes required for biosynthesis of allelochemicals is often dependent on environmental stimuli (Croteau et al. 2000).

2.1. Genetic factors

The production of compounds via secondary metabolism in plants (including allelochemicals) is dependent on the appropriate genetic components. For example, a rice (*Oryza sativa* L.) breeding program that pursued the development of cultivars with increased allelochemical production has benefited from the elucidation of the enzymes and genes involved in momilactone B synthesis (Toyomasu et al. 2008). Momilactone B is a rice allelochemical that has one of the highest activity levels against weeds. It is a diterpene compound biosynthesized from geranylgeranyl pyrophosphate by diterpene synthase enzymes using the methylerythritol phosphate (MEP) pathway (Dudareva et al. 2013). Using reverse genetic tools, it was possible to elucidate the two genes encoding diterpene synthases responsible for its production: 4-copalyl-diphosphate synthetase and kaurene synthase-like 4 (Xu et al. 2012).

Another study with rice used an RNA interference technique (RNAi) to establish a cause–effect relationship between the expression of the phenylalanine ammonia-lyase (PAL) gene and the biosynthesis of phenols. Gene-silenced plants showed reduced amounts of PAL enzyme, a low phenol concentration in the tissues and a limited amount of root exudates compared to wild plants. Thus, the results of these experiments provide strong evidence for the allelochemical potential of wild plants associated with the synthesis of phenols (Fang et al. 2013). Phenols have at least six distinct mechanisms of action within plants, which are outlined in the review by Li et al. (2010). Nevertheless, the occurrence of other substances together with phenols, or a combination of different phenolic compounds, might also result in synergistic effects, increasing their phytotoxicity even at low concentrations (Rasmussen & Enhellig 1979; Blum 1996).

Advances in technological and research methods have allowed the identification of several factors that control the gene expression of the enzymes involved in the synthesis of plant allelopathic compounds. For example, the importance of many jasmonates (methyl jasmonate and jasmonic acid) in the regulation of expression of the gene encoding the enzyme o-methyltransferase (Uddin et al. 2013) has been understood following the elucidation of the biosynthetic pathway of sorgoleone in epidermal cells of the sorghum root system. The progress in this area is likely to increase the identification of other biosynthetic pathways, enzymes and genes responsible for producing several other allelochemicals.

2.2. Environmental factors

Environmental conditions can directly or indirectly affect the allelopathic performance of a plant. The most important environmental factors that influence allelopathy include UV radiation, temperature, water and nutrient availability and competition stress (Croteau et al. 2000; Marchese & Figueira 2005; Meiners et al. 2012). The environment can affect allelopathy in at least three ways: the production of compounds (through gene interaction), their bioavailability and their effect on target species.

There is strong evidence to support the hypothesis that environmental stress can increase the production of allelochemicals. For example, stresses from UV radiation, nutrient shortage, plant pathogen infection and wounding are reported to stimulate the activity of PAL, which is the first committed step in the biosynthesis of phenolic compounds (Dixon & Paiva 1995; Croteau et al. 2000). The phenol cinnamic acid is produced by some plant species, such as cucumber (*Cucumis sativus* L.), and is a precursor of several phenylpropanoids that cause peroxidation and a reduction of the cell membrane H^+-ATPase activity, consequently decreasing the root viability of target plants (Ding et al. 2007). Jasmonate synthesis is also stimulated by environmental stress. As a consequence, these hormones can trigger the expression of genes related to secondary metabolism in several plant species (Wasternack & Parthier 1997).

The presence of other plants surrounding sorghum can exacerbate the impact of the environmental stress on the production of sorgoleone (Dayan 2006). Similarly, the environmental stresses arising from the interaction among plants are also important for the production of other allelochemicals (Rivoal et al. 2011). For example, rice seedlings cultivated with *Echinochloa crus-galli* L. Beauv. (barnyardgrass) showed a concentration of momilactone B almost seven times higher than that in rice seedlings grown alone (Kato-Noguchi 2011). The momilactone B concentration in some rice cultivars can reduce the number of *E. crus-galli* shoots by 81% (Kato-Noguchi et al. 2010).

The bioavailability of allelochemicals in the soil is dependent on processes of transference (mainly adsorption and leaching) and degradation (abiotic and biotic) (as reviewed by Kobayashi 2004). Several factors can affect the bioavailability of allelochemicals in the soil, including the clay and organic matter content, water availability, soil pH, and biological activity. Thus, the allelopathic potential of many compounds is not expressed in some soils because of the chemical adsorption to soil colloids. For instance, sorgoleone binds strongly to soil colloids because it is a highly lipophilic allelochemical, with a log P (log octanol-water partition coefficient) of 6.1 (Trezzi et al. 2006). The allelopathic compounds l-3,4-dihydroxyphenylalanine and catechin are also strongly adsorbed by soil colloids, possibly due to the catechol group present in these molecules (Furubayashi et al. 2007). The benzoxazinoid compounds 2-aminophenoxazin-3-one and DIBOA (2,4-dihydroxy-(2H)-1,4-benzoxazin-3(4H)-one) are other examples of compounds that have a reduced allelopathic potential due to their adsorption by soil colloids (Teasdale et al. 2012).

The chemical compounds that are not adsorbed onto colloids or minerals are usually in the soil solution. Thus, they can be absorbed by plants or leached (Kobayashi 2004; Kong et al. 2007; Li et al. 2013). A study with rice plants has shown that flavonoids with a high mobility in the soil profile were less phytotoxic than those with a reduced soil mobility (Kong et al. 2007). Similarly, an analysis of ten potential allelochemicals revealed an inverse relationship between soil mobility and their toxic effect on target plants (Li et al. 2013).

Environmental factors can affect the degradation of allelochemicals in the soil, reducing their efficacy. In non-sterilized soil, for instance, DIBOA showed a half-life of 43 h. However,

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

In summary, the environmental fate of allelochemicals is a complex issue that is affected by the donor and target plant species, as well as environmental variables and other processes that affect the fate of the chemicals in the environment. Knowledge concerning the variation in these factors is essential to use the allelopathic relationship among plants in agroecosystems to promote weed control.

3. Environmental changes caused by allelochemicals

Allelochemicals can trigger various ecological processes that alter several environmental conditions and indirectly affect other plants (Inderjit & Del Moral 1997; Inderjit & Weiner 2001). These modifications can be best observed in locations where the producer of the allelochemical is considered an invasive species. The increased magnitude of the effect occurs because the environment changes become more evident when the new plant species does not have a history of interaction with other organisms in the new habitat (Inderjit et al. 2011).

The environmental changes can include modifications at the plant community level, with species inclusion and exclusion (Batish et al. 2001) and also, at the ecosystem level, via influences on abiotic factors (Inderjit & Weiner 2001; Buehler & Rodgers 2012).

Some soil modifications, especially those related to nutrient concentration, can be explained by allelochemical action. It is known, for example, that allelochemicals such as phenolic monomers and phenolic acids can form complexes with nutrients and toxic substances in the soil, which alters their availability to plants. Thus, phenolic acids can increase the availability of phosphorus to plants by competing with the sites of immobilization of this nutrient in the soil organic matter, clay particles, soluble aluminum, iron or manganese (Appel 1993). In addition, allelochemicals such as sorgoleone, which are produced and released by the roots of sorghum plants, can influence the biogeochemical cycles of nutrients, such as nitrogen. Indeed, sorgoleone reduced the activity of the nitrifying bacterium *Nitrosomonas* and consequently, increased the NH_4^+ content in the soil, improving its efficiency as a nitrogen fertilizer (Tesfamariam et al. 2014).

Allelochemical-producing plants can also affect the presence of mycorrhizal fungi, nitrogen-fixing bacteria and pathogens in the soil. In consequence, these chemicals can impact the associations among plants or between plants and microorganisms (Weston & Mathesius 2013). Plants of the Brassicaceae, Chenopodiaceae, Caryophyllaceae and Cyperaceae families are tolerant to some fungal pathogens and show no symbiotic associations with mycorrhizal fungi,

due to the allelochemicals released by their roots (Schreiner & Koide 1993). When released into the soil, these allelochemicals can also inhibit the germination of spores, as well as the symbiotic association between mycorrhizal fungi and surrounding host plants (Stinson et al. 2006; Javaid 2007; Cipollini et al. 2012).

The association between the microorganisms responsible for biological nitrogen fixation with their host plants is stimulated by some flavonoids produced by legume plant species. These flavonoids are responsible for bacterial attraction to the rhizosphere and for increasing the expression of specific nodulation (*Nod*) genes (Bertin et al. 2003). In contrast, phenolic substances produced by rice plants had a negative effect on three strains of *Rhizobium* spp. As a consequence, there was a reduction in the hemoglobin content in the root nodes in two bean (*Phaseolus vulgaris* L.) varieties, thus impairing the N_2 fixation capacity of the plants (Rice et al. 1981).

Allelochemicals can also have an impact on populations of species that are potentially harmful to crop plants. Exudates from the rice root system, with a high concentration of *p*-coumaric acid, led to decreased fusarium attack (*Fusarium oxysporum* f. sp. *niveum*) in melon grown in rotation (Hao et al. 2010). Rape plants (*Brassica napus* L.), used as green manure incorporated into the soil, decreased the population of nematodes (*Xiphinema americanum*) in orchards due to production of isothiocyanates, thiocyanates, and nitriles after glucosinolate hydrolysis (Halbrendt 1996). Moreover, allelochemicals can also reduce the populations of various species of phytophagous arthropods (Farooq et al. 2011). These results reveal the potential of using some allelochemicals as a basis for generating new fungicides, insecticides and nematicides. Similarly, this knowledge can assist in planning improved crop rotations to reduce the use of pesticides.

4. Mechanisms of allelochemical action

There are two main reasons to identify the mechanisms of action (MeA) of allelochemicals: to understand and explore their ecological role and to serve as leads in herbicide discovery programs. To date, some commercial herbicides derived from plants or microorganisms that have already been introduced onto the market belong to different chemical groups, with entirely novel MeA (Duke et al. 2002; Dayan et al. 2012). The need for new herbicide MeA should be emphasized for at least three important reasons: (a) no new herbicide MeA were released onto the market within the past two decades; (b) the number of herbicides launched onto the market is decreasing steadily, especially due to registration issues; and (c) limitations of current herbicides due to herbicide-resistant weeds are increasing (Duke 2012). Allelochemicals can improve the potential to discover innovative MeA and can enable the discovery of different chemical moieties. Compared to chemical-based herbicide discovery, further benefits of allelochemical-based herbicide discovery include: reduced environmental impact, higher consumer acceptance and easier registration (Dayan et al. 2012).

Thousands of allelopathic substances have been isolated from plants and their chemical structure has been determined; however, the MeA has only been elucidated for a limited number of allelochemicals (Vyvyan 2002). In a review that highlighted 30 phytotoxins produced by microorganisms and plants, 23 different MeA were identified

(Duke et al. 2002). Additionally, twelve new MeA were documented within 14 compounds isolated from microorganisms and four new mechanisms were discovered in compounds from four different plants species (Dayan et al. 2012). The main MeA of herbicides include: (a) inhibition of photosystem II electron transport; (b) interruption of respiration and adenosine triphosphate synthesis; (c) mediation by reactive oxygen species (ROS); (d) alternative mechanisms, mainly the action on amino acid synthesis and plant growth regulators (auxins and gibberellins); (e) indirect allelopathic effects (Weir et al. 2004); (f) inhibition of photosystem I; (g) inhibition of tubulin polymerization; and (g) action on RNA polymerase (Duke et al. 2002), among others.

Among the allelochemicals isolated from plants, some have been used as leads for herbicide discovery and have yielded successful compounds. The triketone herbicides (mesotrione, tembotrione, sulcotrione) are chemical analogues of the allelochemicals leptospermone, grandiflorone and flavesone. These compounds are inhibitors of the hydroxyphenylpyruvate dioxygenase (HPPD) enzyme (Dayan et al. 2012). The cinmethylin herbicide is an inhibitor of the tyrosine aminotransferase enzyme and was obtained through the incorporation of benzyl ether to the 1,4-cineole (a common essential oil of many aromatic plants) structure, with the intention of reducing its volatility (El-Deek & Hess 1986; Grossmann et al. 2012).

Derivatives of plant allelochemicals with the potential to serve as sources for new substances that allow the discovery of new herbicides and/or new MeA include benzoxazinones (benzoxazolinone and others), sarmentine, citral, momilactones, and sorgoleone. Benzoxazolinone (BOA) is a benzoxazinone that is exuded from the roots of various cultivated grasses and exerts multiple physiological effects on plants. The generation of ROS and oxidative stress are key events in the mode of action of BOA in plants (Schulz et al. 2013). Sarmentine and other fatty acids, such as pelargonic acid, can increase the fluidity of leaf cuticles and increase peroxidase activity, which has potential use as a desiccant (Huang et al. 2010). Citral is a well-known essential oil, which can disrupt microtubule polymerization and also offers potential for use as a desiccant herbicide (Dayan et al. 2012). Sorgoleone is a known inhibitor of photosystem II and 4-hydroxyphenyl-pyruvate dioxygenase (HPPD). Because of the high lipophilicity of this compound, it is strongly adsorbed by soil colloids (Trezzi et al. 2006) and undergoes limited translocation in plants (Dayan et al. 2009), which limits its herbicide action. The momilactones A and B are two allelochemicals secreted by rice roots that show promising results in controlling several weed species (Kato-Noguchi 2011), but their MeA have also not yet been fully elucidated.

Indirect mechanisms can explain plant–plant interactions that are not directly driven by allelochemicals released by a species. For example, the secretion of glucose and phenyl-alanine by plants reduces the sorption and biodegradation of the allelochemical *p*-coumaric acid, thus, synergistically inhibiting *Ipomoea violacea* L. growth (Blum et al. 1993; Pue et al. 1995). Additionally, indirect action is attributed to substances that indicate the presence of neighboring plants, inducing an adaptive advantage. Ethylene and methanol are examples of substances that can act as signals of the competitive process (Kegge & Pierik 2009). Similarly, mixtures of volatile compounds produced by different species or cultivars might signal the presence of neighboring plants (Ninkovik 2003; Runyon et al. 2006).

5. The use of allelopathy in cropping systems

The impact of allelochemicals on crops and weeds is dependent on the behavior of these compounds in the soil. Upon release from a source organism, the soil is the main vehicle that mediates the contact between allelochemicals and their target plants. Even highly volatile oily compounds, such as terpenoids, that lose their efficacy in high-temperature environments can be effective within the soil. Indeed, some volatile oils are released from the roots or rhizomes and their effects are magnified within the soil because they are less susceptible to volatilization (Vilhena et al. 2014).

After being released into the soil, allelochemicals need to reach the target plant to perform their ecological function. This movement involves a series of complex processes in the soil, and in general, occurs via mass flow, diffusion and root interception. During this movement, allelochemicals undergo various processes, such as retention and transformation/degradation. The retention process involves the attraction of allelochemicals to soil colloids, which restricts their mobility (Kah & Brown 2006). Low mobility is not a permanent condition, due to changes in soil properties, such as pH, organic matter content, the levels of ions, microbial growth, and other factors, which might promote the desorption and release of the substance from the soil.

After the degradation or transformation process, the new compound can have a simpler or more complex structure, which alters its biological activity (Cheng 1992). The inactivation of allelochemicals in the soil can be associated with the presence of certain microorganisms, such as the fungal genera *Gloeophyllum*, *Chaetomium*, *Preussia* and *Pseudomonas* bacteria (Hess et al. 1992).

The characteristics of allelochemicals play an important role in their fate in the environment. For instance, the water solubility of the compounds might affect their mobility within the soil; the vapor pressure can impact their volatilization; and the chemical structure can influence their affinity with the soil surface (Souza Filho & Alves 2002). The net result of all these complex events results in the allelopathic effect and potential agronomic use.

One of the great challenges to the use of allelopathy as a tool for weed management is probably the skepticism caused by the difficulty in accessing information and the lack of information on the topic. The use of appropriate methodologies to analyze field trials remains a challenge. Recently, scientific progress and new equipment and experimental protocols have helped to reveal parts of this complex problem. Some allelochemicals, such as benzoxazinones and their derivatives, which can cause weed suppression, have been already characterized from their production in the donor plant (*Secale cereale* L.) to their action on the target plant (*Avena fatua* L.) (Macías et al. 2014). Up to 20 kg ha^{-1} benzoxazinones can be released from rye residues and after degradation, up to 5 kg ha^{-1} was recovered from the soil (Schulz et al. 2013). Unfortunately, this is an exception, since the complete pathway for most allelochemicals remains unknown. Advances in this area will provide the knowledge required to better exploit allelopathy in the weed management of production systems (Gronle et al. 2015).

In addition, many techniques and knowledge that appears to take advantage of allelopathy have already been used empirically in agriculture to exploit the suppressive effect on weeds by some crop species. Current agriculture is

strongly associated with conventional tillage CT) and intensive use of inputs (such as synthetic fertilizers and pesticides, energy, water, mechanization). As an alternative, Conservation Agriculture (CA) is based on minimal soil disturbance (no-till, NT) and permanent soil cover (mulch), combined with rotation and is becoming a common approach in rainfed areas for water and soil conservation (Tabaglio, Gavazzi, Menta et al. 2008; Bajwa 2014). Tillage systems can influence both the emergence and the development of annual and perennial weed species (Arif et al. 2007). Understanding allelopathy is helpful for planning and managing cropping systems (Gronle et al. 2015). Reduced weed infestation in CA can be achieved with proper weed-suppressive cover crops (Altieri et al. 2011; Jabran et al. 2015; Nichols et al. 2015), or via the use of allelopathic crop cultivars (Balbinot Junior et al. 2003; Nichols et al. 2015) or consortium systems that involve potential allelopathic species. Highly productive crop rotations should consider crop species that are tolerant to the allelochemicals released from previous crops.

Knowledge concerning allelopathy can also be a key component in supporting organic farming, for which weed management is a major problem. The use of cover crops is probably the most common form of allelopathy knowledge used for weed suppression in organic agroecosystems (Wortman et al. 2013). Organic farming can involve reduced weed infestation by intercropping plant species with an allelopathic potential or using plant extracts (Wortman et al. 2013; Bajwa et al. 2015).

Cover crops provide many benefits to cropping systems in organic and conventional systems. For instance, *Vicia* spp. and other species from the Fabaceae family can promote nitrogen fixation in the soil and release some allelochemicals that inhibit weed emergence. Similarly, plants from the Poaceae family, such as oats (*Avena strigosa* Schreb. and *Avena sativa* L.) and rye (*Secale cereale* L.), are useful cover crops in the NT system because they can reduce the weed population (Tabaglio, Gavazzi, Schulz et al. 2008; Gavazzi et al. 2010; Bittencourt et al. 2013; Schulz et al. 2013). However, the straw of ryegrass (*Lolium multiflorum* Lam.) releases allelochemicals that can inhibit 34% corn root growth (Martin et al. 1990). Therefore, in NT systems, ryegrass plants should be controlled 15 days before the sowing of maize, but the control of summer weeds should still be maintained (Altieri et al. 2011).

Crop species that produce beneficial allelochemicals in agroecosystems include sorghum (*Sorghum bicolor* L.), which exudes sorgoleone from its roots and inhibits the emergence and growth of various weed species (Trezzi and Vidal 2004). Mucuna species (*Mucuna* spp.) are very useful to reduce the infestation of the world's worst weed, nutsedge (*Cyperus rotundus* L.) (Zanuncio et al. 2013). Several other annual crop species are known for their allelochemical production, including alfalfa (*Medicago sativa* L.), rye (*Secale cereale* L.), wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L.), rice (*Oryza sativa* L.) and sunflower (*Helianthus annus* L.) (De Albuquerque et al. 2011). NT cropping systems appear to be more likely to benefit from scientific research on the allelopathic effects of cover crops or forage mulching. The special impact of this knowledge can be foreseen on reduced weed emergence and growth and the potential decline in herbicide use (Tabaglio, Gavazzi, Schulz et al. 2008; Altieri et al. 2011; Pudelko et al. 2015).

Crop cultivars with an increased production of allelochemicals might be another technological application to reduce weed infestation (Balbinot Junior et al. 2003). However, in some instances, there is no correlation between the production of allelopathic compounds and the competitive ability of the crop (Worthington et al. 2015). The variation in allelopathic effects can depend on the cultivar used, as shown with rice (Chung et al. 2001), alfalfa (Xuan & Tsuzuki 2002) and rye (Tabaglio et al. 2013), among others.

Allelopathic cultivars can be obtained by classical breeding or genetic engineering. Usually, the development of allelopathic cultivars has not been a target for the majority of conventional crop breeding programs. Rather, the focus of attention has been directed to increasing the crop yield; thus, there is a tendency to reduce the allelopathic potential in modern cultivars (Bertholdsson 2004). Indeed, there is a hypothesis that the energy required for allelochemical biosynthesis can reduce the amount available for plant primary metabolism, including plant development and reproduction. Rice is a promising allelopathic crop because screening programs were conducted on thousands of cultivars in search of allelopathic effects. Some cultivars possessed a high ability to reduce weed infestation, and subsequently, allowed the identification of some genes involved in rice allelopathy (Jensen et al. 2001). An alternative to this approach is the use of molecular markers associated with allelopathic traits, such as genes encoding the synthesis of allelochemicals (Macías et al. 2007). Advances have been made in identifying quantitative trait loci (QTL) in wheat and rice, although our knowledge remains incomplete. Advances have also been made in identifying genes encoding momilactones in rice (Xu et al. 2004). The discovery of the association between allelochemicals and their respective QTLs indicates that breeding assisted by molecular markers can lead to the development of elite cultivars with allelopathic traits (Rector 2008). However, the genes involved in the synthesis of hydroxamic acids in wheat have not been identified to date.

Recent molecular investigations have attempted to identify the genes and corresponding enzymes associated with sorgoleone biosynthesis, which are considered to be the main allelochemicals of sorghum plants. Sorgoleone production depends on the action of alquilresorcinol synthase enzymes (ARS1 and ARS2). Evidence that ARS1 and ARS2 are involved in sorgoleone synthesis was uncovered using RNAi techniques, yielding silenced transgenic sorghum plants with no sorgoleone production (Cook et al. 2010). The determination of the key biosynthetic enzymes allows the major transcriptional and post-transcriptional mechanisms involved in allelochemical production to be elucidated. Nevertheless, genetically modified sorghum plants that differ in sorgoleone production allow sorgoleone function in plant–plant interactions to be studied, as well as its effect on soil microorganisms or its function as a nematode repellent (Weston et al. 2013).

Plant extracts are another way of using allelochemicals for weed management in agroecosystems, as they have been already used as post-emergence natural herbicides in some countries. In Pakistan, for example, an aqueous extract deriving from sorghum shoots with a 10% concentration is left to ferment for several weeks and is subsequently sprayed post-emergence for weed control. This fermented water extract, known as "Sorgaab", reduced weed density and weed dry weight up to 50% in field trials, depending on the weed species (Cheema & Khaliq 2000; Cheema et al. 2002).

Another use of allelopathic effects occurs when some crop species that exude allelochemicals are intercropped. For instance, intercropping corn and *Urochloa* spp. (*Brachiaria* spp.) increases the crop and forage yield, improves the soil quality and reduces the weed infestation in the area (Borges et al. 2015). Allelopathic effects explain the reduced infestation by the parasitic weed *Striga hermonthica* (Del.) Benth. when *Desmodium* spp. is intercropped with corn (Khan et al. 2002). Additionally, natural compounds have been identified as potent weapons against certain insects and diseases, improving the degree of crop protection in agroecosystems (Farooq et al. 2013).

6. Concluding remarks

Allelopathy is a form of plant interference that can significantly influence ecosystem and agroecosystem dynamics. Allelochemical biosynthesis, release, environmental fate and action on other plant species can depend on genetic factors, or on the environment and their interaction. Because of these interactions, allelopathy is a complex phenomenon with limited field repeatability. Associated with this, the existence of other types of positive or negative plant interactions obscures the identification of allelopathic phenomena in the field. Studies on the genetic and environmental factors and the direct and indirect interactions that determine the allelopathic phenomenon have evolved slowly compared to other areas of science. The development of multidisciplinary studies in this area will broaden the understanding of the role of allelochemicals in agroecosystems, as well as in natural ecosystems. Furthermore, it will provide a greater understanding of the communication networks that are allelochemically mediated between different organisms.

The knowledge of allelopathic relationships is also important for defining weed management strategies, especially those that relate to the suppressive effect of cover crop mulching on weeds in NT cropping systems. Crop rotation and intercropping or crop succession should take into account the absence of negative allelopathic effects among crop species. Apparently, this is a currently underexplored line of research that might be useful to improve crop production systems. The MeA of allelochemicals on target plants are very specific. However, the majority of allelochemical research has focused on the isolation and identification of chemical structures, whereas the MeA have not been sufficiently elucidated. Scientific efforts in this area might support the development of new products to target plants and other organisms.

Other lines of research that are useful for a better understanding of the action of allelochemicals include the association of chemicals and their possible synergistic, additive and antagonistic effects and their environmental fate. Mostly, allelopathic effects depend on the joint action of allelochemicals and therefore, an increase in the study of these interactions might lead to advances in the understanding of their action on target organisms. Studies on the fate of allelochemicals in the environment are required, to identify the retention, degradation and transport mechanisms of the compounds in the environment, which are determinants of their persistence in the soil and their efficacy on target organisms. The wished expansion of allelopathic knowledge is likely to improve crop management systems that integrate weed and pest management, with plants that offer allelopathic potential, and chemical options. As a result, increased agricultural efficiency would boost food, fiber and bioenergy production and help to address the world's food demand.

Disclosure statement

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