

Allelochemicals: sources, toxicity and microbial transformation in soil - a review

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Abstract - Soil microorganisms interact with plants in diversified manner ranging from mobilising nutrients and enhancing their growth, to inducing diseases. They also produce allelochemicals directly or indirectly through conversion from other compounds. In order to hamper plant growth, allelochemicals must accumulate and persist at phytotoxic levels in the rhizosphere soil. However, after their entry into environment, persistence, availability and biological activities of allelochemicals are influenced by microorganisms. Transformation of allelochemicals by soil microbes may result into the compounds with modified biological properties. Such bio-transformations affect the overall allelopathic capability of the producer plant in a direct manner. Several reports describe the allelopathic significance of microbial metabolism products. For instance, a bacterium *Actinobacter calcoaceticus*, can convert 2(3H)-benzoxazolinone (BOA) to 2,2'-oxo-1,1'-azobenzene (AZOB) which is more inhibitory to some plants. On the contrary, bacterium *Pseudomonas putida* catabolises juglone in soils beneath walnut trees; otherwise, juglone accumulates at phytotoxic levels. This review article describes the nature of microbially produced allelochemicals, and the ways to mediate microbial degradation of putative allelochemicals. The given information develops an understanding of persistence, fate and phytotoxicity of allelochemicals in the natural environment, and also points out the possible solution of the problems due to microbial interventions in the soil.

Key words: weed control, toxicity dynamics, microorganisms, phenols, quinones, degradation.

INTRODUCTION

The environmental and health hazards from the use of herbicide have led to find the alternative methods of weed management. Among such alternatives, one is the use of allelopathic crops. They release chemicals into the soil that can contribute to weed management through suppression of weed seed germination, seedling emergence and establishment, and seedling growth (Haramoto, 2004). Although, the main mechanism of weed dissemination is through natural propagation, however, the un-composted crop residues and animal excreta may also cause weed infestation when applied as soil amendment (Ahmad *et al.*, 2007). Biological control and integrated management of plant diseases and weeds are considered a part of sustainable farming system.

Numerous crops and weeds have been investigated for their allelopathic characteristics. Alfalfa has long been thought to be autotoxic (allelopathy due to plants of the same species). Grain sorghum, rye, oats, wheat, and many weed species are suspected of heterotoxicity (allelopathy from plants of different species). Hong *et al.* (2004) achieved 90% weed control in paddy fields by incorporating *Datura stramonium*, *Desmodium triflorum* and *Melia azedarach* each at 1 t ha⁻¹ separately, and 70% weed reduction at 2 t ha⁻¹ of *Clerodendrum trichotomum* biomass. The organic amendments hold great promise as a

source of multiple nutrients and ability to improve soil characteristics (Jilani *et al.*, 2007), but if applied injudiciously they may also cause some tribulations. Biochemical compounds resulting from the mineralisation of organic residues or litter also render great impact on soil microorganisms. Recently, Kara and Asan (2007) found that fungal community composition was altered by the organic compounds entering the forest soil from plant litter. The organic wastes like from olive milling industry dispersed as fertilizer are also suspected to have potential toxic effects on soil microflora (Giuntini *et al.*, 2006).

Allelochemicals present in the soil and being released by plants may interact synergistically with each other, resulting into higher reductions of plant growth. Combined application of ferulic and *p*-coumaric acid exerted enhanced effects on seedling growth and germination of sorghum than each compound did alone (Rasmussen and Einhellig, 1977). While in the soil, allelochemicals are exposed for various physicochemical and biological processes, and they may be detoxified, made more toxic, or may serve as a carbon skeleton for the production of new toxins by soil organisms (Blum *et al.*, 1999).

Reduced diffusion rates of allelochemicals in soil and various complexation/sorptive reactions diminish their toxicity. Basically, the phytotoxicity is caused by reactive oxygen species (ROS) generated during redox cycling between the oxidised and reduced states of allelochemical. Living organisms encode enzymes that detoxify the ROS (Testa, 1995). So, the biological activities of new compounds would differ from the original ones (Morimoto and Komai, 2005). First allelochemical

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naphthoquinone juglone, isolated from black walnut tree was in fact an artefact obtained during the isolation procedure from the plant (Williamson and Weidenhamer, 1990). Precursor of juglone released from the plant as a glucoside, is converted to juglone and degraded into other derivatives by microorganisms. Two allelochemicals cyperotundone and α -cyperone and their derivatives isolated from tubers of purple nutsedge were modified after released into the rhizosphere, and their allelopathic effects were also rendered on lettuce seed germination and seedlings (Morimoto and Komai, 2005).

For establishing allelopathy at larger scale as a practice for weed eradication, therefore, needs comprehensive knowledge and monitoring of allelochemical dynamics in the soil. This review essay presents the current understanding about various allelochemicals and their derivatives for their activity in soil and effects on weeds. It will provide first-hand information to the agronomists to formulate recommendations for crop rotations and cropping systems to have better weed management and higher crop production with reduced use of herbicides.

PERSPECTIVE

Over the centuries, it has been known that walnut trees poison the soil to underlying vegetation (Gries, 1942). The Greek botanist Theophrastus (300 BC) documented the allelopathic properties of plants first time with the observation that chickpea plants extinguished the weeds. Afterwards, a Roman scholar, Pliny the Elder, found that preceding chickpea and barley crops deteriorated the soil for maize, and that walnut trees had toxic residual effects on neighbouring plants (Weir et al., 2004).

The term 'allelopathy' coined by Austrian plant physiologist Molisch Hans (1937) from two Greek words 'allelon' meaning 'of each other or mutual' and 'pathos' meaning 'to suffer or harm', refers to the chemical inhibition of one organism by another. Although the term allelopathy is most commonly used to describe the chemical interaction between two plants, but it has also been used to describe microbe-microbe, plant-microbe and plant-insect or plant-herbivore chemical communication (Weir et al., 2004). The crop plants may affect themselves, other crop plants and weeds, and weeds may affect crop plants and other weeds as well.

As defined by the International Allelopathy Society, allelopathy is any process involving secondary metabolites (allelochemicals) produced by plants, microorganisms, viruses and fungi that influence the growth and development of agricultural and biological systems (excluding animals) including positive and negative effects (Elijarrat and Barcelo, 2001). According to Rice (1984) "allelopathy are direct or indirect (harmful or beneficial) effects of a plant including microbes, on another plant through the release of compounds that escape into the environment".

SOURCES

Organic compounds that mostly inhibit the plant growth (allelochemicals) exist in almost all plants and their tissues (roots, stem, bark, leave, flowers, fruits or seeds) as secondary or waste products of metabolism. However, their concentration varies from one part to another (Qasem and Foy, 2001). Root exudates represent the largest source of allelochemical inputs into the rhizosphere soil. Naturally, these chemicals come to the rhizosphere through exudation from roots, wash down from stems and leaves, volatile emissions from leaves, or degradation of plant biomass in soil (Bertin et al., 2003). Decomposition of plant residues release secondary metabolites that exhibit phytotoxic effects on other plants (Inderjit et al., 1995; Kohli et al., 2001). The synthesis and exudation of allelochemicals are enhanced by the stress conditions that plant encounters such as extreme temperature, drought and UV exposure (Rice, 1984; Pramanik et al., 2000; Inderjit and Weston, 2003).

There is also a big share of microbially produced and transformed allelochemicals. Soil microorganisms produce secondary metabolites either directly from their metabolic activities or indirectly from the decomposition of organic residues. Like, a bacterium strain B-916 of *Bacillus subtilis* induced disease resistance and caused growth promotion in rice (Ren et al., 2006) by producing beneficial allelochemicals.

CHEMICAL FORMS

The secondary metabolites such as 2-benzoxazolinone (BOA) and 6-methoxy-benzoxazolinone (MBOA) from wheat, rye, and corn are known to have allelopathic activity. The benzoxazinones are a class of phytoanticipins occurring in the Gramineae, Acanthaceae, Ranunculaceae, and Scrophulariaceae families (Niemeyer, 1988). In *Aphelandra* sp. plants, the lactams [2-hydroxy-1,4-benzoxazin-3(2H)-one (HBOA) and 2-hydroxy-7-methoxy-1,4-benzoxazin-3(2H)-one (HMBOA)], the hydroxamic acids [2,4-dihydroxy-1,4-benzoxazin-3(4H)-one (DIBOA) and 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3(4H)-one (DIMBOA)], and the corresponding glucosides are accumulated (Baumeler et al., 2000). As soon as the integrity of the cells is ruptured, rapid deglycosylation leads to the aglucosins. While the hydroxamic acids are chemically transformed into toxic benzoxazolinone (BOA or MBOA), the less-toxic lactams stay intact as HBOA and HMBOA (Virtanen and Hietala, 1960).

The field crops such as wheat (*Triticum aestivum*) and rye (*Secale cereale*) produce BOA and MBOA, respectively, from their corresponding hydroxamic acids DIBOA and DIMBOA. The hydroxamic acids are bound as glucosides in plant vacuoles and released by α -glucosidases upon disruption of cellular integrity (Yue et al., 1998). Further degradation products have

Name of allelochemical	Acronym	Source
Benzoxazolin-2-one	BOA	DIBOA
6-methoxybenzoxazolin-2-one	MBOA	DIMBOA
2,4-dihydroxy-1,4-(2H)-benzoxazin-3-one	DIBOA	
2,4-dihydroxy-7-methoxy-1,4-(2H)-benzoxazin-3-one	DIMBOA	
2-amino-3H-phenoxazin-3-one	APO	BOA
2-amino-7-methoxy-3H-phenoxazin-3-one	AMPO	DIMBOA, MBOA
2-acetylamino-7-methoxyphenoxazin-3-one	AAMPO	MBOA
N-(2-hydroxyphenyl) malonic acid	HPMA	

been identified as 2-amino-3H-phenoxazin-3-one (APO) and 2-amino-7-methoxy-3H-phenoxazin-3-one (AMPO) from BOA and MBOA, respectively (Kumar *et al.*, 1993; Fomsgaard *et al.*, 2004; Macías *et al.*, 2004; Gents *et al.*, 2005; Understrup *et al.*, 2005).

Formation of APO from BOA has been found to occur through the intermediate 2-aminophenol, both as a chemical process and as a microbial process (Gagliardo and Chilton, 1992). Endophytic fungi were found to produce N-(2-hydroxyphenyl) malonic acid (HPMA) and N-(2-hydroxy-4-methoxyphenyl) malonic acid (HMPMA) besides APO and AMPO (Friebe *et al.*, 1998; Yue *et al.*, 1998; Zikmundová *et al.*, 2002a). Gallic acid and hydroquinone which occur as glycosides in the foliage of *Polygonella myriophylla* are its major allelochemicals (Weidenhamer and Romeo, 2004).

BIOCHEMICAL NATURE

The allelochemicals range from simple compounds of hydrocarbons to complicated polycyclic aromatics e.g. phenols, terpenes, flavonoids, polyacetylenes, fatty acids, steroids, etc. Quinones and phenolics are among the most commonly described classes of allelopathic phytotoxins (Inderjit, 1996). Quinones are oxidised phenols, and phenols are reduced quinones, and transformations between these states have biological significance (Harborne, 1989). The best-known is sorgoleone, a lipophilic benzoquinone produced by *Sorghum bicolor*, which acts as an allelochemical by inhibition of photosystem II (Weir *et al.*, 2004). A highly toxic quinone responsible for walnut allelopathy is juglone (5-hydroxyl-1,4-naphthoquinone), which is also used in pharmacological studies (Gries, 1942; Kamei *et al.*, 1998; Inbaraj and Chignell, 2004).

Fomsgaard *et al.* (2006) reported that cereals contain biologically active secondary metabolites such as the benzoxazinones [2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA) and 2,4-dihydroxy-1,4-benzoxazin-3-one (DIBOA)] and the benzoxazolinones [6-methoxy-2-benzoxazolinone (MBOA) and 2-benzoxazolinone (BOA)]. The benzoxazolinones are found as degradation products of DIMBOA and DIBOA both in plants and in soil, respectively.

Several allelochemicals identified in alfalfa include: medicarpin, 4-methoxymedicarpin, sativan, 5-methoxysativan, saponins, salicylic acid (Dornbos *et al.*, 1990; Nakahisa *et al.*, 1994), gallic acid, p-coumaric acid, protocatechuic acid, p-hydroxybenzoic acid, catechin, vanillic acid, vanillin, syringic acid and ferulic acid (Xuan *et al.*, 2003b). Tsuzuki (2001) reported that buckwheat contains fatty acids (palmitic, stearic, arachidic, behenic) and phenolic acids (ferulic, caffeic, chlorogenic). The phenolics detected in kava root extracts are: protocatechuic acid, p-hydroxybenzoic acid, p-coumaric acid, ferulic acid, salicylic acid, trans-o-coumaric acid and trans-cinnamic acid (Xuan *et al.*, 2003c).

Flavonoids are the polyphenolic secondary metabolites which occur widely in plants. Their role in plant defence is less popular, except the catechins and proanthocyanidins (Feucht and Treutter, 1999). They are polyaromatic compounds with a 15-carbon skeleton and can be divided into subclasses depending on their structure (Shaw *et al.*, 2006). The (+) and (-) isomers of catechin and 7,8-benzoflavone have allelopathic roles (Bais *et al.*, 2002).

TOXICITY DYNAMICS

The decomposition of plant residues releases secondary metabolites that exhibit phytotoxic effects on other plants (Inderjit *et al.*, 1995; Kohli *et al.*, 2001). Factors on which phytotoxicity of allelochemicals is dependent have been classified into three main categories by An *et al.* (2002) as: amount and composition of plant residues (type and quantity), the environment of decomposition (temperature, moisture, aeration, soil texture, inorganic ions, and pH), and management practices (decomposition time, residue placement, and weathering).

The phenolic acid reactivity in soils may hinder the expression of allelopathy in the field through abiotic reactions such as oxidation of the allelochemicals and through biotic mineralisation of the allelochemicals prior to interacting with the target species (Lehmann *et al.*, 1987; Schmidt and Ley, 1999). The oxidative reactivity of phenolic acids may limit the potential of allelopathy. It suggests that reaction with soil ameliorates the toxicity of the released compounds (Ohno *et al.*, 2000). Xuan *et al.* (2005) found that the variations in electrical conductivity (EC) and osmotic pressure (OP) were strongly related to chemicals and toxins exuded into the soil during decomposition, and were proportional to the magnitude of inhibition observed, whereas pH did not correlate with inhibition.

Included in the mechanisms of quinone cytotoxicity, the most significant are those associated with free-radical formation during quinone reduction. Single electron reductions catalysed by enzymes such as quinone oxidoreductase or xanthine oxidase produce highly reactive semiquinone intermediates that directly bind to and inactivate nucleic acids, proteins, lipids and carbohydrates (Testa, 1995). Semiquinone radicals also react with molecular oxygen leading to generate superoxide anions and hydroxyl radicals. These highly toxic radicals inactivate enzymes, break DNA strands, and cause membrane-lipid peroxidation (Hammond-Kosack and Jones, 1996).

Phytotoxicity of juglone also results from similar mechanisms. Juglone is not synthesized by walnut trees, which rather synthesize the non-toxic reduced form 1,4,5-trihydroxynaphthalene (hydrojuglone) (Lee and Campbell, 1969). Hydrojuglone is abundantly produced by roots, leaves and nuts and becomes oxidised to toxic juglone upon exposure to air or oxidising agents from other organisms, including roots of other plants (Gries, 1942). Cytotoxicity of phenolic allelotoxins is largely associated with free radicals produced during redox cycling.

Phytotoxicity dynamics is likely that decaying plant residues exhibit the most severe inhibition at the early stages of decomposition, as it proceeded, phytotoxicity is declined (Patrick *et al.*, 1963; Chou and Lin, 1976; Mason-Sedun and Jessop, 1988). Stimulation is obvious only at the later stages of decomposition (Mason-Sedun and Jessop, 1988; An *et al.*, 1996). Concentration changes of allelochemicals in decomposing plant residues are related to phytotoxicity dynamics (Chou and Patrick, 1976; Tang and Weiss, 1978). An *et al.* (1996) also demonstrated such a correlation theoretically through mathematical modelling.

Findings of Kong *et al.* (2004) revealed that transformation between ageratochromene and its two dimers in the *Ageratum conyzoides* intercropped citrus orchard soil was reversible. However, this dynamic transformation did not occur in the soil with low organic matter and fertility. The dimerization was not correlated with microorganisms in the soil. The reversible transformation between ageratochromene and its dimers could be an important mechanism maintaining bioactive allelochemicals at an effective concentration.

Dynamics of 20 identified allelochemicals in *Vulpia myuros* residues were monitored, and their kinetic phytotoxicity was assessed by An *et al.* (2000). Total content of allelochemicals and phenolics in decaying *Vulpia* residues were increased over a 21 day decomposition period. Phytotoxicity was increased from 42 to 82% of radical inhibition. Allelochemicals changed in composition and quantity over the duration of the residue decomposition. Addition of soil to the residues reduced the total allelochemical contents, and only 14 against the 20 identified allelochemicals were detected in the mixture of soil and residues.

The effects of allelopathic plant residues on weed growth last for a short time, and later the weeds re-emerge (Xuan *et al.*, 2003a). Sorgoleone from the root exudate of sorghum (*Sorghum bicolor* L.) persisted in soil for 8 weeks in detectable limits but its concentration was decreased drastically within 1 week (Weston *et al.*, 1999). Xuan and Tsuzuki (2002) observed a maximum weed control of 91.5% when alfalfa (*Medicago sativa* L.) pellets were applied immediately after watering the soil, but after 20 days, only 55.3% weeds were controlled. Kava (*Piper methysticum* L.) exhibited the strongest inhibition (80%) on barnyard grass and monochoria growth 1 day after application but at 9 days, the weed control was reduced to 25% (Xuan *et al.*, 2003a). Xuan *et al.* (2005) reported that both alfalfa and kava strongly inhibited barnyard grass and monochoria weed growth until 10 days (80-100% control), and after 20-25 days, weed control was reduced to 50%. Under such dynamics of allelochemicals in soil, there may be a possibility that periodic application of allelopathic amendments would result in maximum weed control.

PHYTOTOXIC EFFECTS

Impact of allelochemicals on plants is stimulatory at low concentrations, turns to inhibitory as the concentration increases, and finally ends in total inhibition of growth (Carballeira *et al.*, 1988). Decomposing tissues of *Argemone mexicana* weed in soil at 10 g kg⁻¹ enhanced the growth of tomato plants; at 30 g kg⁻¹ growth was substantially retarded, while at 50 g kg⁻¹ there was 80% mortality. Further, the decomposing plant material caused greater phytotoxicity compared to the aqueous extract (Shaukat *et al.*, 2002). Sampietro and Vattuone (2006) showed that sugarcane straw leachate (having water-soluble phenolics) interfered with seedling growth of beggarticks and wild mustard.

The weeds may be eradicated either by growing a crop that can exude allelochemicals or by incorporating plant residues in soil that would release a high content of allelochemicals (Elijarrat and Barcelo, 2001). The BOA applied at 1023 M was found to reduce the radish germination by 50% and caused a delay in radicle elongation (Chiapusio *et al.*, 2004). Alfalfa pellets applied at 1-2 t ha⁻¹ in the paddy field reduced the weeds significantly without any harmful effect on rice crop (Xuan and Tsuzuki, 2002). Incorporation of buckwheat pellets at 2 t ha⁻¹ also resulted in strong paddy weed reduction. Kava controlled weeds in paddy remarkably at 1 t ha⁻¹ and increased tillering and root count of rice plant (Xuan *et al.*, 2003a).

The flavonoids play a multifunctional role in plant defence and in allelopathic interactions. The (+/-)-catechin is secreted by *Centaurea maculosa* (spotted knapweed) roots, but (-)-catechin specifically inhibits seed germination and is a potent herbicide (Bais *et al.*, 2002). The (-)-catechin inhibits seed germination by disrupting mitochondrial respiration (Weir *et al.*, 2004). Flavanol triggers the generation of reactive oxygen species (ROS) which leads to a Ca²⁺ signalling cascade and to the death of cells in root system (Bais *et al.*, 2003).

Numerous mechanisms exist in plants to overcome herbivory and microbial diseases, including the production of toxic metabolites. These are either constitutive secondary compounds present already in healthy plants (phytoanticipins) or synthesized in response to the attack of pathogens (phytoalexins). Many plant pathogens have the ability of detoxifying these bioactive defence compounds (Osborn, 1999; Van Etten *et al.*, 1995).

FATE IN SOIL

Activity of allelochemical in the soil is altered or influenced by soil factors such as organic matter, inorganic ions, reactive mineral surfaces, ion-exchange capacity and biotic barriers (Inderjit, 2001). As the changing environmental conditions over time modify the composition and quantity of allelochemicals substantially (Dalton, 1999; Okumura *et al.*, 1999), therefore, there is a need to consider soil processes explicitly to make allelopathy research relevant to agricultural systems (Dalton, 1999; Inderjit and Dakshini, 1999).

The phenolic acids react abiotically with soils, possibly involving ligand exchange reactions, soil surface catalyzed oxidation, and/or incorporation into soil organic matter (Dalton *et al.*, 1989). It is also reported that phenolic acids are rapidly sorbed and subsequently oxidised by soil (Makino *et al.*, 1996; Lehmann *et al.*, 1987). Ohno and First (1998) found that sorption of phenolic acids was related to both organic matter and manganese oxide content of soils. The increased concentration of Mn²⁺ in the soil-phenolic acid suspension suggests that phenolic acids are oxidised upon sorption to the soil.

Initial concentrations of allelochemical in soil influence its transformation pathway and degradation rate. During ecotoxicological tests, Fomsgaard *et al.* (2006) found that DIMBOA was degraded and partly transformed to MBOA. Testing of MBOA on *Poecilus cupreus* media showed that at the initial concentrations of 2 and 10 mg kg⁻¹ no MBOA was left after 45 days, but AMPO was formed, and on both *Folsomia candida* and *Poecilus cupreus* test media BOA was transformed to a biologically more active compound APO.

Microbial and nonmicrobial oxidative transformations of soil allelochemicals mediate the allelopathic effects of *Polygonella myriophylla* (Weidenhamer and Romeo, 2004). Soil sterilisation stabilised the arbutin, hydroquinone and gallic acid effectively, but benzoquinone was degraded rapidly under this nonmicrobial oxidative condition. Degradation of MBOA and its isotopomer 6-trideuteriomethoxybenzoxazolin-2-one ([D3]-MBOA) in soil yielded AMPO and AAMPO, and several novel compounds were also detected (Etzerodt *et al.*, 2006).

BIO-TRANSFORMATION

Parallel to the abiotic reactions of allelochemicals in soils, biotic processes are also involved in determining the fate of these compounds. Microorganisms produce enzymes which catalyze the oxidation and polymerization reactions of phenolic acids (Huang *et al.*, 1999). Myrosinase enzyme found in some microorganisms and released to soils via root exudation and decomposition, hydrolyzes glucosinolates to D-glucose and allelochemicals (Al-Turki and Dick, 2003). Microorganisms also carry out reversible enzymatic reactions including oxidation/reduction and acetylation/hydrolysis (Zikmundová *et al.*, 2002b).

The ecotoxicological testing of allelochemicals is influenced by the fact that the compounds are subject to microbial transfor-

mation during the test period (Fomsgaard *et al.*, 2006). Schmidt and Ley (1999) suggested that carbon-limited soil organisms would rapidly mineralise phenolic compounds due to their higher energy content on a per weight basis than simple sugars. Blum *et al.* (1999) demonstrated that microbial activity will alter phenolic compounds in soil and subsequently alter the expressed level of phytotoxicity.

Zikmundová *et al.* (2002a) studied the biotransformation of the phytoanticipins BOA and HBOA by four endophytic fungi isolated from *Aphelandra tetragona*. It was shown that the metabolic pathway for HBOA and BOA degradation leads to *o*-aminophenol as a key intermediate. Phenolic acids are readily converted from one structure to another with different phytotoxicities (e.g., ferulic acid to vanillic acid) by soil-borne microbes (Blum, 1998). For instance, the contents of *p*-hydroxybenzoic acid were increased simultaneously upon a rapid decrease in *p*-coumaric acid during the incubation of rice straw (Shindo and Kuwatsuka, 1975a, 1975b).

Phytopathogenic fungi can detoxify BOA and MBOA to *N*-(2-hydroxyphenyl)malonamic acid and *N*-(2-hydroxy-4-methoxyphenyl) malonamic acid, respectively (Friebe *et al.*, 1998; Vilich *et al.*, 1999; Glenn *et al.*, 2001). Additionally, 2-amino-3*H*-phenoxazin-3-one was detected as the transformation product of BOA by the fungal pathogen *Gaeumannomyces graminis* var. *tritici* (Friebe *et al.*, 1998) and by soil- and root-colonizing bacteria (Gagliardo and Chilton, 1992; Friebe *et al.*, 1996). It was also found that the metabolism of BOA and MBOA by endophytic fungus of corn *Fusarium moniliforme*, was identical to that of pathogenic fungi (Yue *et al.*, 1998).

The biotransformation of phytoanticipins BOA and HBOA by endophytes living inside the roots and shoots of *A. tetragona* could yield several new products through oxidation, reduction, hydrolysis, acetylation, and nitration processes (Zikmundová *et al.*, 2002a). Such biotransformations by soil microorganisms could yield compounds with modified biological properties, affecting the overall allelopathic capability of the producer plant in a direct manner. It was reported that DIMBOA degraded rapidly, yielding MBOA, and the MBOA, an intermediate in the degradation pathway from DIMBOA to AMPO, was more resistant to biodegradation (Macías *et al.*, 2004).

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