

Chapter 14

Allelopathy and Crop Nutrition

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Abstract Allelopathy, the natural phenomenon of production and release of secondary metabolites and interaction(s) among organisms, is a subject of diverse significance and applications in plant sciences. Other than their role in plant defense against biotic and abiotic stresses, plant secondary metabolites or allelochemicals play a significant role in plant nutrition. These allelochemicals regulate solubilization, mobilization, release, and chelation of mineral nutrients, upon release into the rhizosphere. Arresting nitrification could be a key strategy to improve nitrogen (N) recovery and agronomic N use efficiency (NUE) in situations where loss of N is significant. Allelopathy can help to improve NUE by

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suppressing the rate of nitrification. In this chapter, the role of allelopathy in nutrient release and acquisition by crop plants is discussed.

14.1 Introduction

The word allelopathy has been derived from two Latin words ‘*allos*’ and ‘*pathos*’ meaning ‘each other’ and ‘harm’, respectively. According to Farooq et al. (2011), ‘allelopathy is a phenomenon whereby secondary metabolites synthesized by fungi, viruses, microorganisms and plants influence biological and agricultural systems, which may be either stimulatory or inhibitory’. The ancient Greek and Roman scientists were familiar with the concept of ‘plants interfering the plants’; however, the phenomenon was first defined by a plant physiologist Hans Molish in 1937. Rice (1984) defined allelopathy as ‘the influence of one plant on the growth of another one, including microorganisms, through release of chemical compounds into the environment’. These chemical compounds released by plants are known as secondary metabolites or allelochemicals, produced in all parts of plants, i.e., roots, shoots, leaves, seeds, and flowers (Weston 1996), and released into the environment through processes such as volatilization, leaching from decomposing plant residues, and root exudation. Allelopathy is thus a chemical warfare among plants.

Allelochemicals, upon release into the rhizosphere, may influence nutrient movement, availability, and uptake by plants. Changes in microbial activities and nutrient dynamics on addition of allelochemicals to the soil have been reported (Karmarkar and Tabatabai 1991). Usually, allelochemicals are first perceived by the receiver plant’s roots, which may then affect nutrient uptake (Yu and Matsui 1997). These compounds may restrict or improve the nutrient’s mobility to plants (Yu and Matsui 1997). Nutrient supply to plants and status in soil also governs the release of allelochemicals into the rhizosphere. For instance, some plant species release allelochemicals (Haynes 1990; Jones and Darrah 1994) when grown under zinc (Zn), iron (Fe), and/or phosphorus (P) deficiency, to improve the available form of respective nutrients. In addition, microorganisms present in the rhizosphere also promote production and release of allelopathic compounds (Gardner et al. 1983) thereby controlling the release, mobilization, chelation, and uptake of nutrient(s).

In this chapter, the roles of allelopathy in nutrient dynamics in the rhizosphere, and their release, mobilization, and uptake by plants are discussed.

14.2 Improving Nitrogen Use Efficiency Through Biological Nitrification Inhibition

Much of the nitrogen (N) applied to agricultural soils is lost to the environment, increasing serious concerns on environmental pollution. Moreover, escalating fertilizer costs are increasing production costs of crops thus reducing profit

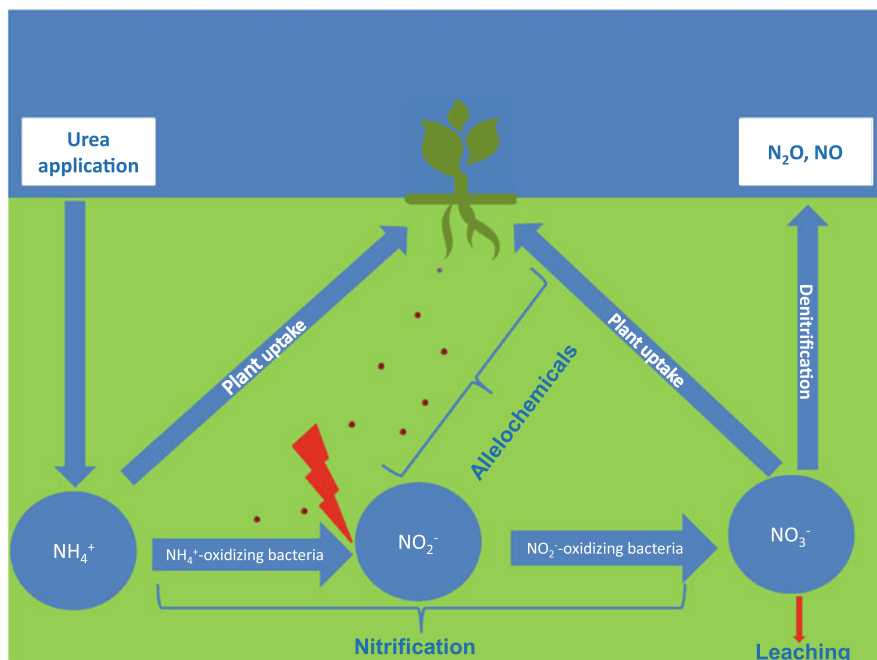


Fig. 14.1 Influence of allelopathy on biological nitrification inhibition and nitrogen dynamics

margins. The nitrate form of N is lost through NO_3^- leaching in groundwater leading to decreased soil fertility and increased water pollution. The release of N_2O during denitrification contributes to global warming. Nitrogen (ammoniacal form) when added to soil is readily converted into highly mobile nitrate (NO_3^-) form by soil microorganism, *Nitrosomonas europaea*, a ubiquitous component of the microbial population in the soil (Leninger et al. 2006).

According to recent estimates, 61.5 Tg N is lost per year through leaching (Schlesinger 2009). To improve N use efficiency (NUE) in agricultural systems, the nitrification rate in soil should be decreased, which is an important strategy to minimize N losses (Prasad and Power 1995; Subbarao et al. 2006a).

Allelopathy offers an attractive and natural option to decrease nitrification for improving NUE in agricultural systems. Incorporating various crop residues into soil and release of allelochemicals from plant roots may help suppress the nitrification process in soil; the phenomenon known as biological nitrification inhibition (BNI) (Subbarao et al. 2006a, b). The process is accomplished by exudation of allelochemicals which reduce the activity of *Nitrosomonas* and *Nitrobacter* (Subbarao et al. 2006b). Allelochemicals released in the rhizosphere inhibit the activities of vital enzymes of ammonium-oxidizing bacteria involved in the nitrification process including ammonium mono-oxygenase and hydroxylamine oxidoreductase (Fig. 14.1 Subbarao et al. 2009). It is well known that phenolics released from plants in the rhizosphere can inhibit oxidation of NH_4^+ to NO_3^-

by inhibiting activity of nitrifying bacteria (Rice 1984). However, in addition to root exudates plant water extracts can also suppress the process of nitrification in soil (Alsaadawi 2001). Allelochemicals such as methyl 3-(4-hydroxyphenyl) propionate (Zakir et al. 2008), linoleic acid, α -linolenic acid, methyl-*p*-coumarate, and methyl ferulate are responsible for BNI (Subbarao et al. 2009).

A variety of field crops such as sorghum (*Sorghum bicolor* L.) and sunflower (*Helianthus annuus*) have been evaluated for BNI capacity. For instance, Alsaadawi (1988) evaluated the allelopathic potential of sunflower cultivars to inhibit the process of nitrification and found that both sunflower residues (root and shoot) incorporated in the soil and sunflower water extracts of all tested cultivars reduced the process of nitrification. However, cultivars differed in their capacity for nitrification inhibition. In an initial screening experiment, BNI activity in the exudates of 36 different rice (*Oryza sativa*) genotypes was evaluated using a bioassay based on a recombinant *Nitrosomonas* strain. Significant genotypic variation was detected with upland cultivar IAC25 demonstrating consistently high BNI activity, while modern lowland varieties such as Nipponbare or IR64 exhibited lower activity (Tanaka et al. 2010). Subsequent experiments ruled out the possibility that BNI activity is simply due to non-specific (solute) leakage from roots. Roots of some rice cultivars also had excretions responsible for reducing the pace of nitrification in soil (Tanaka et al. 2010). In another study, four cultivars of sorghum (two allelopathic and two non-allelopathic) inhibited the nitrification process when their residues were incorporated in soil and, compared with the control with no residue incorporation, nitrification inhibition in soil was higher for allelopathic cultivars than non-allelopathic cultivars. In addition, water extracts of 100 sorghum cultivars inhibited the process of nitrification (Alsaadawi et al. 1986b).

Some tropical grassland species, including false creeping paspalum (*Brachiaria humidicola*), exude allelochemicals in the rhizosphere, with the potential to suppress soil nitrification (Subbarao et al. 2006b). However, this natural phenomenon has not been exploited to improve NUE in agricultural production systems (Subbarao et al. 2006a). Root exudates of mammoth wild rye (*Leymus racemosus*), a wild relative of wheat (*Triticum aestivum*), can suppress NO_3^- formation and keep more than 90 % of the soil's inorganic N in the NH_4^+ form for about 60 days (Table 14.1 in Subbarao et al. 2007).

Although allelopathy entails tremendous scope for improving NUE by reducing N losses, most studies have been conducted under laboratory conditions; little information is available regarding field appraisal and application of this phenomenon for improving NUE.

14.3 Nutrients Solubilization and Release

In addition to support and anchorage, soil provides nutrition to plants and contains microorganisms such as bacteria, fungi, algae, nematodes, etc., which interact to facilitate nutrient acquisition (Richardson et al. 2009). Mineral nutrients are present

Table 14.1 Nitrification inhibition by allelochemicals released by various plant species

Treatment	Incubation period (days)	Inhibition (%) on nitrate formation	Reference
Root exudate from <i>Leymus racemosus</i>	30	74.7	Subbarao et al. (2007)
Root exudate from cultivated wheat cv. Chinese Spring	30	24.9	Subbarao et al. (2007)
Root exudate from <i>Leymus racemosus</i>	60	91.5	Subbarao et al. (2007)
Root exudate from cultivated wheat cv. Chinese Spring	60	-5.2	Subbarao et al. (2007)
Root exudates of <i>Brachiaria humidicola</i> in barren soil	30	28	Gopalakrishnan et al. (2009)
Root exudates of <i>Brachiaria humidicola</i> in Rhizosphere soil	30	08	Gopalakrishnan et al. (2009)
Root exudates of <i>Brachiaria humidicola</i> in barren soil	60	56	Gopalakrishnan et al. (2009)
Root exudates of <i>Brachiaria humidicola</i> in rhizosphere soil	60	12	Gopalakrishnan et al. (2009)
Wheat extract (10 %, w/v)	5	14.3	Zwain (1996)
	10	48.9	
	15	39.0	
	20	20.8	
Soil incorporation of wheat residues	5	81.7	Zwain (1996)
	10	88.7	
	15	87.6	
	20	70.1	

in the soil in various forms with varying solubilities. Hence availability to higher plants is highly dependent on the concentration of nutrients either dissolved or adsorbed, which can easily be taken up by plants (Marschner 1995). In highly acid or alkaline soils, nutrients are present in precipitated forms with either Al, Fe (acid soils), or Ca (alkaline soils). Soil microorganisms, especially bacteria, promote plant growth in these soils directly by fixation of atmospheric N, solubilization, and mobilization of nutrients such as P, Zn, and Fe in the soil, and excretion of some substances with plant growth-promoting activity (Franche et al. 2009).

Free-living plant growth-promoting rhizobacteria (PGPR) belonging to genera such as *Pseudomonas*, *Enterobacter*, *Bacillus*, *Alcaligenes*, *Azospirillum*, and *Azotobacter* can mobilize some micronutrients such as Zn and Fe, but a small proportion of these bacteria fix N₂. The most important trait of these free-living PGPR is solubilization of insoluble organic and inorganic phosphates present in soil which is correlated with their ability to produce organic acids. These organic acids chelate cations bound to insoluble phosphates and convert them to a soluble form (Pérez et al. 2007).

Allelochemicals play a pivotal role in nutrient acquisition by plants grown in nutrient-limited environments. Under these situations, plants interact with soil microorganisms and release allelochemicals, which facilitate nutrient solubilization

and release (Gardner et al. 1983; Jones and Darrah 1994). In P-deficient soils, for instance, production of extracellular enzymes phosphatases (Duff et al. 1994) and their release to the rhizosphere are very important (Goldstein et al. 1988; Lee 1988; Dinkelaker and Marschner 1992). These phosphatases mediate hydrolysis and mobilization of inorganic P from monoester soil organic phosphates (Duff et al. 1994). These monoester soil organic phosphates account for ~30–80 % of total P in agricultural soils (Gilbert et al. 1999). Release of more acid phosphatase from roots of crops grown on P-deficient soil, compared with those with sufficient P, has been reported in a number of crops (Tadano and Sakai 1991; Duff et al. 1994). Low tissue P concentration in plants triggers production and release of phosphatase into the rhizosphere (Lung et al. 2005; Wang et al. 2009), which hydrolyzes P and improves its availability to plant (Duff et al. 1994; Gilbert et al. 1999).

Phenolics are an important group of root-exuded allelochemicals (D'Arcy-Lameta 1982, 1986), which trigger solubilization and release of Fe, P, and other nutrients in the soil solution. This helps plants to improve uptake of respective nutrients. For instance, alfalfa (*Medicago sativa*) plants grown under Fe deficiency release isoflavonoid phytoalexin [2-(3,5-dihydroxyphenyl)-5,6-dihydroxy benzo-furan] in the rhizosphere, which solubilize ferric phosphate upon release making both P and Fe plant available (Masaoka et al. 1993). Similarly, Fe-deficient tomato (*Solanum lycopersicum*) plants also secrete allelochemicals such as caffeic acid, which improve Fe release from insoluble sources (Olsen et al. 1981). Likewise, dicotyledonous plants, if raised with Fe and P deficiencies exude phenolics/organic acids in the rhizosphere, which improve solubilization and mobility of P and Fe (Römheld 1987; Marschner 1995; Aziz et al. 2011). Upon release, phenolic substances improve solubilization and availability of P and Fe by forming iron chelates with aluminum (Al) present in insoluble phosphates of Fe and Al.

Certain grasses and cereals exude phytosiderophores, a group of hydroxy- and amino-substituted amino-carboxylic acids, which improve solubility and release of Fe (Römheld 1987), Zn, manganese (Mn), and copper (Cu) (Treeby et al. 1989) in soil solution. Crop species and even cultivars differ widely in the release of these compounds to the rhizosphere under nutrient deficiencies; and hence differ for tolerance to their dearth in soils. Breeding for these characters may help to improve nutrient use efficiency in crop plants.

14.4 Nutrient Uptake

Allelochemicals may reduce the uptake of nutrients, which can be exhibited in the form of nutrient deficiency symptoms in growing plants and reduced plant growth (Booker et al. 1992; Tharayil et al. 2009). Reduced nutrient uptake by neighboring plants of allelochemical-exuding plants will reduce growth, fresh weight, root size, dry mass, etc., of the affected plants. For example, according to Walker et al. (1989), soil amendment with sweet potato (*Ipomoea batatas*) root or vine by 1.67 % w/v not only reduced shoot dry weight of sweet potato but also decreased

Table 14.2 Influence of allelochemicals on nutrient uptake in various plant species

Allelochemical	Plant species	Role/action	Reference
Galic acid	<i>Phalaris minor</i>	Decreased P and Zn uptake in wheat	Chakraverty et al. (2005)
Protocatechuic acid			
<i>p</i> -Hydroxy benzoic acid			
Caffeic acid			
Galic acid	<i>Chenopodium album</i>	Decreased P and Zn uptake in wheat	
Protocatechuic acid			
<i>p</i> -Hydroxybenzoic acid			
Vanillic acid			
Galic acid	<i>Polygonum hydropiper</i>	Decreased P and Zn uptake in wheat	
Protocatechuic acid			
<i>p</i> -Hydroxybenzoic acid			
Protocatechuic	<i>Chenopodium murale</i>	Suppressed nodulation in chickpea	Batish et al. (2007)
Ferulic acid			
<i>p</i> -Coumaric acid			
Syringic acid		Suppressed nodulation in pea	
Protocatechuic			
Ferulic acid			
<i>p</i> -Coumaric acid			
Syringic acid			
Ferulic acid	–	Decreased N, P, K and S uptake in cucumber	Booker et al. (1992); Lyu and Blum (1990)
Ferulic acid	–	Decreased P, K, Mg, Ca, Fe and Zn uptake in sorghum	Kobza and Einhellig (1987)
Ferulic acid	–	Decreased Fe, Mo, N, P and K in cowpea	Alsaadawi et al. (1986a)
Syringic acid			
Caffeic acid		No effect on autotrophic nitrifying microorganisms	McCarty et al. (1991)
Protocatechuic acid			
Caffeic acid	<i>Ipomoea batatas</i>	Reduced uptake of P, K, Ca, Mg, S, Zn, B and Cu by sweet potato	Walker et al. (1989)
<i>p</i> -Coumaric acid			
–	<i>Cucurbita pepo</i>	Improved uptake of K, Mg, Fe, Zn by summer squash	Gent et al. (2005)
Citric acid	<i>Vigna mungo</i>	Improved P uptake by blackgram	Jakkeral and Kajjidoni (2011)
Citric acid			
Oxalic acid			

its nutrient (Ca, Mg, S, P, K, Zn, Cu) uptake (Table 14.2). These authors suggested that reduced shoot dry weight and nutrient uptake of sweet potato was due to the allelopathic effect of decaying sweet potato residues. Cinnamic acid is an allelochemical exuded by a number of plant species. Yu and Matsui (1997) evaluated the role of cucumber-exuded allelochemicals on the uptake of several nutrients (N, P, S, K, Ca, Mg) by intact seedlings of cucumber, while cinnamic acid inhibited the uptake of nearly all nutrients.

Ferulic acid is another allelochemical found in many plants such as sorghum and rice, which is also exuded into soil by these plants. Booker et al. (1992) used intact cucumber (*Cucumis sativus*) seedlings to evaluate the effect of ferulic acid on mineral uptake and water relations of cucumber. Ferulic acid inhibited mineral uptake, especially N, and also reduced leaf turgor pressure and water potential. Wacker et al. (1990) evaluated the influence of asparagus-produced ferulic acid on hyphal elongation and colonization of asparagus by *Glomus fasciculatum*. Ferulic acid decreased hyphal elongation, mycorrhizal colonization, and growth while P in plant tissues was not affected. The authors concluded that asparagus-produced ferulic acid decreases plant growth by reducing symbiotic effectiveness of the fungus. Kobza and Einhellig (1987) treated sorghum seedlings with ferulic acid (0.25 and 0.5 mM) to evaluate its effects on tissue concentration of nutrients (K, Mg, P, Zn, Fe, Ca). Roots and shoots of treated plants had lower concentrations of K, Mg, Fe, and P than the control. The nutrient imbalance reduced tissue weights of the plants. Alsaadawi et al. (1986a) tested the influence of various concentrations of phenolic acids (syringic acid, caffeic acid, protocatechuic acid) on nutrient uptake by cowpea (*Vigna unguiculata*) seedlings. All concentrations of phenolic acids reduced uptake of Fe, molybdenum (Mo), N, P, and K; however, Mg uptake was not affected. The reduction in ion uptake by phenolic acids in chickpeas reduced the dry weight of these plants.

Water extracts of weeds—little seed canary grass (*Phalaris minor* Retz.), water pepper (*Polygonum hydropiper*), and lambs quarters (*Chenopodium album*)—reduced uptake of P and Zn in wheat roots and shoots with little seed canary grass having the greatest effect (Chakraverty et al. 2005).

Allelochemicals have been reported to decrease uptake of mineral elements by altering the functions of plasma membranes in plant roots, depolarizing the electrochemical potential gradient across membranes—a primary driving force for ion uptake—and decreasing ATP content of cells by inhibiting electron transport and oxidative phosphorylation, and by changing the permeability of membranes to mineral ions (Balke 1985).

However, Gent et al. (2005) reported that subspecies of summer squash (*Cucurbita pepo*), which can release more citric acid to the rhizosphere, are better able to acquire K, Mg, Fe, Zn than subspecies lacking this ability. Likewise, in black gram [*V. mungo*], the response of genotypes grown with P deficiency differed. Genotypes producing and releasing allelochemicals (citric acid and oxalic acid) were superior in both acquisition and utilization of under P stress conditions due to enhanced root production and shoot expansion (Jakkeral and Kajjidoni 2011). Improvement in exudation of allelochemicals, coupled with increased

proliferation of the root system, enhances the ability of plants to acquire more P under conditions of P deficiency (Jakkeral and Kajjidoni 2011).

The mechanism involved in allelopathic-induced decrease in mineral uptake depends on soil moisture and nutrient status, type and concentration of allelochemicals, and prevailing environmental conditions. Further investigation is required to elucidate the mechanism of allelopathic-induced decrease in mineral uptake to improve mineral uptake and use efficiency in crop plants.

14.5 Chelation and Nutrient Transformation

Chelation is the formation or presence of two or more separate coordinate bonds between a polydentate (multiple bonded) ligand and a single central atom. Usually these ligands are organic compounds, and are called chelates, chelators, chelating agents, or sequestering agents (Anonymous 2011). Artificial metal chelators are used to hold nutrients in the soil for improving nutrient retention (Baret et al. 1995). Root exudates or allelochemicals from plants may also act as natural chelators. Organic acids such as malate, oxalate, citrate etc., excreted from roots of different plants (e.g., chickpea, cowpea, and soybean) chelate Fe, Al, and Ca from their phosphates and hence solubilize P, which lead to improved P availability in soil.

Organic anions released by plant roots in the rhizosphere increase plant availability of Mn and Fe (Marschner 1995). In a similar manner, these acid anions can make chelates with Al and Fe in the form of insoluble phosphates; P is thus available for plant uptake (Marschner 1995). Moreover, P can be desorbed from sesquioxide surfaces by anion exchange with these acids (Bolan et al. 1994; Jones and Darrah 1994; Jones 1998). Through competitive displacement from adsorption sites, these organic acids also help to maintain sulfate mobility in the rhizosphere (Evans and Anderson 1990).

Chelation of metal cations in the rhizosphere may also increase plant's resistance to high concentrations of Al and other such elements. For instance, Al-resistant wheat genotypes released 5–10 folds more malic acid than Al-sensitive genotypes (Delhaize et al. 1993); however, Al-resistant genotypes released substantially higher amounts of citric acid in the rhizosphere than Al-sensitive genotypes in snap bean (*Phaseolus vulgaris*) (Miyasaka et al. 1991), buckwheat (*Fagopyrum esculentum*) (Zheng et al. 1998), and maize (*Zea mays*) (Pellet et al. 1995).

14.6 Conclusions

Through diverse mechanisms, allelopathy plays a fundamental role in crop nutrition. Allelochemicals, upon release to the rhizosphere, help in the solubilization, release, and uptake of mineral nutrients. However, reduced nutrient uptake

after release of allelochemicals to the rhizosphere has been reported, indicating that the type and concentration of allelochemical and prevailing conditions drive the direction of allelochemical–nutrient interaction. In addition, allelochemicals detoxify heavy metals by chelation and improve nutrient use efficiency through reduced nutrient losses. There is great scope for improvement in nutrient acquisition and use efficiency of crop plants by exploiting the phenomenon of allelopathy, which should be exploited to harvest better yields on sustainable basis.

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