# Chapter 8: Non-trophic interactions: Allelopathy

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**Abstract** Plants use a variety of mechanisms to release allelopathic compounds into their surrounding and each of these processes may release chemicals that mediate allelopathic interactions between plants and other components of the ecosystem. In natural ecosystems, the most important influences of allelopathy occur through indirect effects rather than direct plant-plant interference, thus allelochemicals can influence abiotic components of the ecosystem, e.g., nutrient cycling, organic matter dynamics and soil nutrient availability, and can also alter biotic ecology by affecting soil microbes and plant pathogens. In managed ecosystems, allelopathy may be manifested to other crops when grown in various management systems, as autotoxic effects, soil sickness or as suppresors of various weed and pest species. Thus allelopathy plays a significant role in the agroecosystems, agroforestry systems and forest plantations leading to a wide array of interactions among crops, weeds and trees. These interactions are mostly deleterious to the receiver plants but may also provide a selective advantage to the donor.

The research and development of allelopathic research is of extreme importance for the improvement of agriculture, forestry and the global environment, because allelopathy majorly deals with invasive/exotic and native weeds, allelopathic crops that disturb agricultural practices and cause environmental degradation. This chapter reviews the latest development in our understanding of allelopathy in promoting and restricting plant growth and the ways in which our knowledge can be used in sustainable management of natural and managed ecosystems.

**Keywords** Allelopathic interactions, Promoting growth, Restricting growth, agroecosystems, forestry ecosystems

## Introduction

In the first part of 20 century, allelopathy research was focused mainly on agricultural productivity. However allelopathic patterns have been proved to occur in natural ecosystems, from boreal forests to tropical rain forests, from humid to desert ecosystems.In last few decades, research of allelopathy has spread in agriculture, forestry and ecology both in natural and the managed ecosystems throughout the world (Chou 1999; Kohli et al. 2000, 2006; Inderjit et al. 2011; Macías et al. 2004; Muscolo & Sidari 2010; Putnam 1985; Rice 1984; Zeng et al. 2008; Narwal et al. 2011). Recently, studies of allelopathy in terrestrial systems have experienced tremendous development as interest has risen in describing biochemical mechanisms responsible for structuring plant communities, determining agricultural and forest productivity, and explaining invasive behaviors in introduced organisms (Cippolini et al. 2012; Mitrović et al. 2012).

Allelopathy interactions are based primarily on the production of secondary chemicals by higher plants that induce a wide array of biological changes, many of which we are still trying to understand (Macías et al. 2004). Although plant secondary metabolites are generally associated with plant defense responses against herbivores and pathogens, these compounds can be involved in a broad array of ecological functions at the ecosystem level, by influencing the community structure, nutrient dynamics, soil and mycorrhizal ecology and resource competition (Inderjit & Weiner 2001; Inderjit & Mallik 2002; Inderjit et al. 2011). Although the reduction of biodiversity is primarily a result of human activities perhaps a small number of plant species extinction result from natural selection involving mechanism of plant interactions, such as allelopathy. In natural ecosystems, the most important influences of allelopathy occur through indirect effects rather than direct plant-plant interference (Inderjit & Weiner 2001), thus allelochemicals can influence abiotic components of the ecosystem, e.g., nutrient cycling, organic matter dynamics and soil nutrient availability. These chemicals can also alter biotic ecology by affecting soil microbes and plant pathogens. The environment (i.e. nutrient limitation, light regime and moisture deficiency) can in return influence the activities of the allelochemicals (Inderjit & Weiner 2001). In managed ecosystems, allelopathy may be manifested to other crops when grown in various management systems, as autotoxic effects, soil sickness or as suppresors of various weed and pest species (Kramer & Ben-Hammouda 2009). Recently, allelopathic research has focused on development of weed management strategies using allelopathic crop residues, with research interest in the mechanism of allelochemical action, and gene regulation of allelochemical production (Weston 2005). Likewise, allelopathic plants and their allelochemicals can be potentially utilized as an important part of pest management and control in agricultural ecosystems (Duke et al. 2000; Macías et al. 2004). In addition, recent studies have been recognized allelopathy as ecological mechanisms of exotic plant invasion on ecosystem level too (Callaway et al. 2005). Thus the development of allelopathic research is of extreme importance for the improvement of agriculture, forestry and the global environment (Zeng et al. 2008; Kohli et al. 2006). This chapter reviews the latest development in our understanding of allelopathy in promoting and restricting plant growth and the ways in which our knowledge can be used in sustainable management of natural and managed ecosystems.

## Negative effects of allelopathic chemicals

Allelochemicals production is genetically regulated, and their concentration varies with age, cultivar, and plant organ, and their amount is often enhanced by various biotic and abiotic stress factors. Pathogens, pests, parasites or herbivores can also stimulate allelochemical production. Thus any factor that induces stress can cause an increase in allelochemical production and release. Donor plants under stress often release a great variety and different concentration of allelochemicals, and stressed target plants may be more susceptible to allelochemicals (Reigosa et al. 2006). Plant phytotoxins vary considerably in chemical structure, mode of action and effects (Bais et al. 2006).

Allelopathy has been defined as the term covering both detrimental and beneficial biochemical interactions among all classes of plants through the production of chemical compounds that are released into the environment (Rice 1984). Plants use a variety of mechanisms to release allelopathic compounds into their surrounding environment by volatilization, root exudation, leaching and decomposition of residues and thus reach the soil underneath the canopy.

*The mode of action-* The mode of action of the allelopathic compounds is often very subtle and difficult to determine correctly due to the limited means a plant has to express stress and the symptoms that plants produce are often secondary in nature and are difficult to diagnose (Chou 1999). Allelopathy interacts with plant stress, because stressed source plants often release a great variety and different concentration of allelochemicals, and stressed target plants may be more susceptible to allelochemicals (Reigosa et al. 2006). To exert phytotoxic effects on other plant species, allelochemicals may have to move to the roots of the target plant through the soil. Once in the soil, they can affect soil chemistry i.e. nutrient cycling and organic matter dynamics and changes in soil nutrient availability by either increasing or decreasing microbial activity (Castells 2008). Allelochemicals can decrease N availability by complexation with proteins from litter or with extracellular enzymes from microorganisms thus delaying organic matter decomposition and mineralization (Hättenschwiler & Vitousek 2000; Wardle et al. 1998), by increasing microbial activity and N immobilization (Castells 2008) and by inhibiting fungal respiration and nitrification (Boufalis & Pellissier 1994). The resulting decrease in the inorganic N availability for plant uptake may potentially affect plant growth. Therefore, soil fertility is influenced by allelopathic compounds from plant or microbial sources not only because they are important precursors of soil stable humic substances, but also for their effects on soil nutrient dynamics (N, P, K, Mn, Fe, Cu, etc.), pH, ion-uptake, soil aggregation, etc.  (Muscolo et al. 2001, 2006; Djurdjević et al. 2010).

Allelopathy as chemical modification of the site by an individual to enhance interference effectiveness also involves ecological communications between species which can positively or negatively influence growth, behavior, reproduction, and survival of associated species (Narwal et al. 2000). Allelochemicals and other metabolites released by plant roots play important roles in rhizosphere signalling, plant defence and responses to abiotic stresses (Bais et al. 2006; Weston et al. 2012). Thus root exudates play a direct role in development of associations between parasitic plants and their hosts as well as indirect role in resource competition by altering the soil chemistry, soil processes and microbial populations (Bais et al. 2006). As a result, exudates can repel herbivores and microbes, stimulate symbiotic relationships, alter soil properties, and inhibit the growth of competing species (Mathesius & Watt 2011). Positive interactions between plants are sometimes controlled by root exudates due to the induction of defense responses in neighboring plants by reducing their susceptibility to pathogen infection or by initiating production and release of leaf volatiles that attract predators of plant enemies. In addition, effects of root exudates on soil processes and microbial populations can lead to some positive effects on neighboring plants e.g., Fe-mobilising phytosiderophores and phosphate-mobilising carboxylates that may lead to facilitation, i.e. amelioration of the environment of neighbouring plants (Lambers et al. 2008).

Allelopathic effects against higher plants are typically characterized as suppressing seed germination, root elongation and plant growth by inhibition of cell division. Several action modes have been observed, including direct inhibition of PSII components, reduction in chlorophyll content, the reduction in $CO_2$ assimilation, interruption of dark respiration and ATP synthesis, and reactive oxygen species (ROS)-mediated allelopathic mechanisms (Barkosky & Einhellig 2003; Inderjit & Duke 2003; Weir et al. 2004; Djurdjević et al. 2008; Hussain et al. 2011). Another mode of action is the allelopathic effect on membrane permeability that causes an alteration in water and ion permeability of the cytoplasmic membrane (Yu & Matsui 1997). Allelochemical toxic effects frequently resulted in decreased stomatal conductance together with loss of leaf turgor (Yu et al. 2003), reduced leaf water potential, shoot turgor pressure, and osmotic potential (Barkosky & Einhellig 2003; Sánchez-Moreiras & Reigosa 2005). Disruption of plant water relations as the primary mechanism of the growth inhibition and the chronic reduction in available $CO_2$ and water stress are the possible causes for the reduction in photosynthetic efficiency (Fv/Fm) of PSII caused by allelochemicals. Other modes of action include disruption of mineral uptake and transport, inhibition of enzymatic activity, inhibition of germination and inhibition of seedling growth (Muscolo & Sidari 2001; Weir et al. 2004).

Allelopathy not only affects neighbouring plants and influence plant community structuring, but can also induce a broader ecosystem level change when it coincides with disturbance (Wardle et al. 1998; Zackrisson et al. 1997). Allelopathic interactions are strongly related with microbial activity in the soil, because soil microorganisms are both producers and degraders of allelochemicals and, at the same time, they can be affected by plant secondary metabolites (Pellissier & Souto 1999; Reigosa et al. 1999; Muscolo & Sidari 2006). From an ecological and evolutionary perspective, allelopathic effects of plants on soil microbes may have indirect effects on competing plants that are just as important as direct effects. Thus effects on the microbial community on which competing plants rely for nutrient and water uptake, nutrient cycling, and other interactions could promote growth of an allelopathic plant as long as it does not harm the microbial community in the process (Callaway & Ridenour 2004). From this perspective, soil microorganisms can be considered as allelopathic interaction regulators. This fact, pointed out by Blum (1995), is particularly relevant in forest ecosystems.

*Role of allelopathy in promoting plant growth and ecosystem regeneration*- Allelopathy has been studied mostly in the context of its effects on agricultural systems (Weston 2005), and its effects can be positive or negative in terms of crop establishment and performance (Weston & Duke 2003). However, researchers often ignored the stimulatory effects, possibly because stimulatory effects are often not as spectacular as inhibitory effects. There is evidence that allelochemicals, at certain concentrations, may be inhibitory but at lower concentrations these allelochemicals might stimulate the growth of same or different species (Narwal et al. 2000).

Allelochemical compounds involved in allelopathic interactions are used by plants to counteract other plants, microorganisms, fungi, nematodes and insects (Michelsen et al. 1995). In earlier studies, in agriculture systems, numerous positive allelopathic effects were observed. For example, corn (*Zea mays* L.) residues increased grain yield of corn and soybean (*Glycine max* L. Merril) (Crookston 1991). Mughal (2000) found stimulatory allelopathic effect of leaf water extract of *Morus alba* L. on germination and seedling growth of peas (*Pisum sativum* L.), lentil (*Lens esculenta* Moench) and broad beans (*Vicia faba* L.), at concentration up to 50%. In lentil crop, leaf leachate at 25% water extract stimulated the germination and its seedling growth. Root exudates can have positive effects in plant-plant interactions, although these have been less frequently reported, by improving populations of certain soil microbes and reducing the others, resulting in a shift of nutrient accessibility and uptake by plants within the ecosystem (Inderjit & Weston 2003). Some root exudates induce defense responses in neighboring plants that reduce herbivore populations indirectly by attracting predators and parasites of the offending herbivore (Bais et al. 2006). For example, *V. faba* plants under attack release root exudates that induce green leaf volatile production in undamaged *V. faba* plants that in turn attracts aphid parasitoids (Du et al. 1998). Similarly, *Phaseolus lunatus* L. plants under attack by spider mites produce root exudates that induce volatile production in undamaged *P. lunatus* plants, attracting predatory mites (Guerrieri et al. 2002). Leaf volatiles produced by plants under herbivore attack have also been shown to induce volatile production in neighboring plants, increasing the predator attraction signal (Bruin & Sabelis 2001).

Forestry can also benefit from allelopathy in weed control on valuable tree species (Chou 1986; Birkett et al. 2001). For example, reduction of *Rubus idaeus* L. development in the *Picea mariana* (Mill.) B.S.P. forests using mulch of wheat, oat, barley or other donor plants is a good examples of a new management technique (Mallik 1991). A number of wild plants and weed species are also reported to have antifungal activity against phytopathogenic fungi (Qasem 1996). Therefore, allelochemicals are one of the best environmentally sustainable methods of plant disease control. For example, allelochemicals released from the residues of allelopathic vegetable crops can greatly reduce the incidence of soil-borne pathogens. In addition, some root exudates that act as metal chelators in the rhizosphere can increase the availability of metallic soil micronutrients, including iron, manganese, copper, and zinc (Dakora & Phillips 2002). Metal chelators form complexes with soil metals, thus releasing metals that are bound to soil particles and increasing metal solubility and mobility. Finally, the ecological consequences of fire could be related to allelopathy as well. Only wildfires are able to reduce the presence of ericaceous shrubs and the allelochemical content in forest soil to levels which allow the successful regeneration of the tree canopy (Mallik 2003).

Stimulatory allelopathic effects of any plant on other plants can be used to develop ecofriendly, cheap, and effective growth promoters because the overuse of synthetic agrochemicals during last few decades often causes environmental hazards, an imbalance of soil microorganisms, nutrient deficiency, and change of soil physicochemical properties, resulting in a decrease of crop productivity. Although it is not possible to exclude use of synthetic herbicides completely at the present time their use can be reduced to a certain extent by utilizing allelopathic interactions as an alternative weed management strategy for crop production as well as environmental protection.

*Role of allelopathy in restricting plant growth and ecosystem regeneration*- The allelopathy describes direct or indirect effect of plant chemical compounds on another plant or other organism, although it is most often used to refer to chemical-mediated negative interference between plants (Chou 1999; Rice 1984; Narwal et al. 2000). Thus phytotoxic root exudates are generally associated with the reduction in neighbouring plant growth, and resistance to or suppression of plant pathogens, soil microbes, and other herbivores (Mohney et al. 2009). The use of allelopathic substances could inhibit the germination and seedling growth of crops and weeds (Weston 2005), therefore, allelopathic crops may be used to effectively suppress common and invasive weeds acting as new herbicides (Duke et al. 2000). Selective activity of tree allelochemicals on crops and other plants has also been reported. For example, *Leucaena leucocephala* (Lam.) de Wit, a tree promoted for revegetation, soil and water conservation and animal improvements in India, have deleterious effects on a number of other trees and crops (Chou & Kuo 1986).

## Examples of Allelopathy in Managed and Natural ecosystems

Allelopathy is receiving increasing attention because allelochemicals cause a number of ecological and economic problems, such as declines in crop yield due to soil sickness, replanting problems and regeneration failure of natural forests (Rice 1984; Inderjit & Duke 2003). This negative feedback has been seldom considered in natural ecosystems despite some early demonstrations of its existence (Florence 1965).

There is a variety of crop and weed species that establish some form of potent allelopathic interference, either with other crops or weeds, in agricultural settings, in the managed landscape or in naturalized settings. Release of allelochemicals from leaving residues or decomposing plant material is often a cause of natural regeneration deficiency in forests, and problems of natural regeneration, reforestation, and management are often ascribed to the presence of phenolic substances that may influence the growth of plants and the activities of soil microorganisms involved in, or mediate interactions in a plant-soil system (Djurdjević et al. 2003, 2010; Mallik 2003).

Autoxicity is ubiquitous in both natural and managed ecosystems and may have important ecological implications (Zeng et al. 2008). In agroecosystems, soil sickness occurs when the same crop or its related species are cultivated on the same soil successively (monocropping systems) and it seems to be generated by many factors: build-up of pests in the soil and disorder of physico-chemical properties of the soil (Jacob et al. 2006; Zeng et al. 2008). In forest ecosystems, soil sickness cause delaying and/or reducing in germination and tree seedlings growth; autotoxicity; changes in soil microbial population structure and dynamics; reduced growth and respiration of mycorrhizal fungi; changes in soil nutrient dynamics; changes in decomposition process and forest regeneration failure (Dighton 2003).

Recent research suggests that allelopathic properties can render one species more invasive to native species and thus potentially detrimental to both managed and naturalized systems (Callaway et al. 2005; Weston 2005). Exotic plant invasions often cause high mortality in native populations and therefore have the potential to be a powerful selective force. In contrast, the allelopathic crops have strong potential for the development of cultivars that are more highly weed suppressive in managed systems. A new challenge for plant scientists is to generate additional information on allelochemical mechanisms of release, selectivity and persistence, mode of action and genetic regulation, in order to protect plant biodiversity and enhance weed management strategies in a variety of ecosystems (Weston 2005).

## Managed ecosystems

Allelopathy plays a significant role in the agroecosystems, agroforestry systems and forest plantations leading to a wide array of interactions among crops, weeds and trees (Kohli et al. 2006). Generally, these interactions are deleterious to the receiver plants but may also provide a selective advantage to the donor. In mostly managed systems, during monoculture, homogenous metabolites and plant residues are accumulated in the soil, very often in high threshold levels, thereby leading to soil sickness (Jacob et al. 2006; Kohli et al. 2006) or autotoxicity when a plant species releases chemical substances that inhibit or delay germination and growth of other species or the same plant species (Putnam 1985;

Singh et al. 1999). The principal causes of crop autotoxicity include the deliberate leaving of crop residues or old roots in soil releasing phytotoxins which may directly affect the succeeding crops, cause microbial imbalance, change organic matter of soil, increase ion leakage, disturb nutrient uptake and immobilization (Yu & Matsui 1997). Crop autotoxicity is particularly acute in croplands where tillage is not practiced. In the phenomenon of soil sickness, the release of substances during the decay of dead plant residues plays a role greater than the active secretion of allelochemicals by plants (Politycka 2005).

*Autotoxicity and soil sickness*- In both cereal and vegetable crops, it has been noted a significantly reduction of yield and quality due to natural soil sickness. Some of very important crops expressed autotoxicity including rice, wheat, maize, sugarcane, alfalfa and vegetable crops like, cucumber, tomato, pea, etc. (Table 8.1.). For example, flavonoids from sunflower have suppressive effect on root and shoot length of *Lactuca sativa var. nigra*, *Lepidium sativum* L., *Lycopersicon esculentum* Mill. and *Hordeum vulgare* L. seedlings (Maciás et al. 1996). Inhibitory effects of leaf extract and residues of sunflower to wheat, maize, sorghum, soybean, winter wheat and sunflower itself germination and seedlings growth were also observed (Batish et al. 2002; Kohli et al. 1998). Reduced germination and seedling establishment was observed in both sunflower and cotton crops planted after sunflower (Narwal 1999). It was also found that wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L.), oats (*Avena sativa* L.) and rice (*Oryza sativa* L.) extracts significantly reduced root growth of alfalfa (*Medicago sativa* L.), (Chon & Kim 2004). Rice inhibited root and seedlings growth of ducksalad *Heteranthera limosa* and *Lactuca sativa* L. (Ebana et al. 2001; Kato-Noguchi et al. 2008).

Legume, mungbean (*Vigna radiata* L.), monocropping for many years on same field causes up to 25% plant growth inhibition of lettuce (Chou 1995). Allelopathic inhibition of a number turnip species e.g., *Brassica nigra* L. on alfalfa, wheat and radish was also proved (Turk et al. 2003; Turk et al. 2005). Likewise, brassica species have harmful effects on crops by reducing seed germination and emergence of subsequent small-grain crops when grown in rotation (Bialy et al. 1990). Autotoxicity has been observed also in the garden asparagus (*Asparagus officinalis*) and garden cucumber (*Cucumis sativa*) (Yu et al. 2003). Mulberry (*Morus alba* L.) is an allelopathic plant where inhibitory effects of its fallen leaves on the understorey vegetation have also been noticed. Mughal (2000) found allelopathic effect of leaf water extract of *M. alba* on germination and seedling growth of peas, lentil and broad beans.

Allelochemicals have mostly negative effects on crop plants such as inhibition of nitrification and biological nitrogen fixation, (ii) predisposing the plants to diseases and (iii) inhibition or stimulation of germination, growth and yield (Hicks et al. 1988).

Table 8.1. Phytotoxic crop species (autotoxic and heterotoxic) and their allelochemicals

| Autotoxic species | Heterotoxic species | Allelochemicals |
|---|---|---|
| Rice<br>(*Oryza sativa* L.) | Rice<br>(*Oryza sativa*) | Phenolic acids:<br>*p*-hydroxybenzoic,<br>vanillic,<br>*p*-coumaric,<br>syringic,<br>ferulic |
| Wheat<br>(*Triticum aestivum* L.) | Wheat<br>(*Triticum aestivum* L.) | Hydroxamic acids:<br>2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA)<br><br>Phenolic acids:<br>*p*-coumaric,<br>syringic,<br>ferulic acids,<br>*p*-hydroxybenzoic,<br>vanillic,<br>cis-*p*-coumaric,<br>cis-ferulic,<br>trans-*p*-coumaric,<br>trans-ferulic |
| Sunflower<br>(*Helianthus annuus* L.) | Sunflower<br>(*Helianthus annuus* L.) | Sundiversifolide,<br>4, 15-dinor-3-hydroxy-1(5)-xanthene-12, 8-olide |
| Maize<br>(*Zea mays* L.) | Maize<br>(*Zea mays* L.) | Hydroxamic acids:<br>5-chloro-6-methoxy-2-benzoxazolinone (Cl18 MBOA),<br>6-methoxy-2-benzoxazolinone (MBOA) and 2, 4-dihydroxy-1, 4-benzoxazin-3-one (DIBOA)<br>Phenolic acids:<br>p-hydroxybenzoic, vanillic,<br>ferulic, o-coumarie,<br>o-hydroxyphenylacetic,<br>salicylic,<br>syringic,<br>p-coumaric, transcinnamic, |

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|---|---|---|
| | | caffeic acids |
| Cucumber<br>(*Cucumis sativa* L.) | | Phenolic acids:<br>Benzoic<br>Cinnamic |
| Mungbean<br>(*Vigna radiata* L.) | | |
| | Sugarcane (*Saccharum* officinarum L.) | |
| | Mustard (*Brassica nigra* L.) | |
| | Mulberry (*Morus alba* L.) | |
| | Barley (*Hordeum vulgare* L.) | |
| | Oats (*Avena sativa* L.) | |

*Allelopathic crops*- It was found that cover crop residues present on the soil surface suppress weeds physically and by allelochemicals released during decomposition of these residues also give selective weed control (Putnam 1985; Weston 1996). In recent studies, intercropping that provides better weed suppression through resource competition/or allelochemcal exudation into rhizoshere has been addressed as an option for integrated weed management (Iqbal et al. 2009). The most frequent allelopathic crops and their effects in suppressing growth of weeds are listed in Table 8.2.

In earlier studies, it was found that growing wheat or mulching with wheat straw can effectively control weeds in fields and orchards. Thus growing allelopathic wheat varieties significantly decreased weed infestation in the field and reduced the weed biomass in the following crops (Kong et al. 2007). Similarly, rice is an allelopathic plant and many studies on rice cultivars as a means of ecological weed control strategy have been presented (Rimando et al. 2001). For example, rice inhibited germination, seedling growth and root length of weeds *Parthenium hysterophorus* L. (Javaid et al. 2006) and Chinese milk vetch (*Astragalus sinicus* L.), (Pramanik et al. 2001). Allelopathic effect of rice was also proved on arrowhead (*Sagittaria montevidensis* Cham. & Schltdl.) root growth (Seal et al. 2004), barnyardgrass (*Echinochloa crus-galli* (L.) P. Beauv.) and ducksalad (*Heteranthera limosa* (Sw.) wild.), (Kato-Noguchi 2011; Ebana et al. 2001). Soil incorporation of rice residues reduced the population of both broadleaved and grassy weeds (Narwal et al. 2000). Straw and hulls of some rice cultivars suppressed the germination of *Echinochloa crus-galli* and mustard (Ahn & Chung 2000). Therefore, allelopathic rice plants through inhibitory effects on weeds as developed with genetic alterations in rice cultivars can lower production costs by reducing herbicide application and could benefit farmers, consumers as well as the environment (Rimando et al. 2001). Although maize (*Zea mays* L.) is allelopathic plant but it gained less attention than allelopathy in rice or wheat. Allelopathic compounds from rice were found inhibitory to the roots growth of following weed seedlings such as *Lepidium sativum* L. (Kato-Noguchi et al. 2008). Likewise, the cultivated sunflower (*Helianthus annuus* L.) is economically important oil seed crop, and some studies indicate that sunflower root, stem and leaf extracts caused significant reduction in dry weight of weeds *Phalaris minor, Chenopodium album* L., *Coronopis didymus* L. Smith, *Rumex dentatus* L., *Parthenium hysterophorus* L. and *Medicago polymorpha* L. (Javaid et al. 2006).

Sorghum (*Sorghum bicolor* L.) plant also contains a number of allelochemicals that possess phytotoxic effect against weeds. Previously, Panasiuk et al. (1986) revealed that weeds such as barnyard grass [*Echinochloa crus-galli* (L.) Beauv.], redroot pigweed (*Amaranthus retroflexus* L.) and red sorrel (*Rumex acetosella* L. when interplanted with sorghum showed a significant reduction in their germination, growth and dry weight. Later, Cheema & Khaliq (2000) revealed that water extracts of mature sorghum plants reduced the weed density and weed biomass by 35-49%. For example, seed germination and root length of weed *P. hysterophorus* L. was significantly reduced by extracts of sorghum (Javaid et al. 2006). Cultivated or naturally occurring *Brassica* spp. has been reported as weed suppressive for many years (Siemens et al. 2002). Narwal et al. (1994**)** found that some accessions of *B. juncea* and *B. nigra* caused significant reduction of 75-98% in the density of winter weeds *Phalaris minor* Retz., *Avena ludoviciana* Durand., *Cirsium arvense* (L.) Scop., *Chenopodium album*, *Melilotus alba* and *Rumex retroflexus*, respectively. Allelopathic effect of aqueous extracts of perennial legumes (*Mucuna deeringiana* (Bort) Merr., *Canavalia ensiformis* (L.) DC., *Leucaena leucocephala* (Lam.) de Wit) and *Lysiloma latisiliquum* (L.) Benth.) was proved to be efficient in suppression for growth of *Echinochloa crusgalli* L. P. Beauv., and *Amaranthus hypochondriacus* L. (John & Narwal 2003). The use of mulberry (*Morus alba* L.) might be useful option for biological weed control and for the reduction of herbicides use in paddy field due to suppression of weed population in rice by 72.7% and promotion of rice paddy yield by 23.3% (Hong et al. 2003).

Table 8.2. Allelopathic crops with potential for weed supresion

| Allelopathic crop | Weed | Allelochemicals |
|---|---|---|
| Wheat<br>(*Triticum aestivum* L.) | *Echinochloa crusgalli* L. Beauv<br>*Ipomoea hederacea* Jacq | Hydroxamic acid:<br>2,4-dihydroxy- 7- methoxy -1, 4-benzoxazin-3-one (DIMBOA) |
| Rice<br>(*Oryza sativa* L.) | *Parthenium hysterophorus* L.<br>*Astragalus sinicus* L.<br>*Sagittaria montevidensis* Cham. & Schl.<br>*Heteranthera limosa* (Sw.) wild.)<br>*Lactuca sativa* L.<br>*Echinochloa oryzicola* Vasing.<br>*Monochoria vaginalis* Presl var. *plantaginea* Solms-Laub. | Phenolic acids:<br>*p*-hydroxybenzoic,<br>vanillic,<br>*p*-coumaric,<br>syringic,<br>ferulic acid |
| Maize<br>(*Zea mays* L.) | *Lepidium sativum* L.<br>*Avena sativa* L.<br>*Phleum pretense* L.<br>*Digitaria sanguinalis* L.<br>*Lolium multiflorum* Lam.<br>*Amaranthus caudatus* L.<br>*Chenopodium album* L.<br>*Amaranthus retroflexus* L. | Hydroxamic acids:<br>-chloro-6-methoxy-2-benzoxazolinone (Cl18 MBOA), 6-methoxy-2-benzoxazolinone (MBOA), 2, 4-dihydroxy-1, 4-benzoxazin-3-one (DIBOA) |
| Sunflower<br>(*Helianthus annuus* L.) | *Synapis arvensis* L.<br>*Abutilon theophrasti* L.<br>*Datura stramonium* L.<br>*Ipomoea hederacea* Jacq<br>*Amaranthus retroflexus* L.<br>*Phalaris minor* Retz.<br>*Chenopodium album* L.<br>*Coronopis didymus* (L.) Sm.<br>*Rumex dentatus* L.<br>*Medicago polymorpha* L.<br>*Parthenium hysterophorus* L.<br>*Orobanche cernua* L.<br>*Chenopodium album* L.<br>*Rumex dentatus* L. | Phenolic acids:<br>chlorogenic,<br>caffeic,<br>vanillic,<br>syringic,<br>ferulic |
| Sorghum<br>(*Sorghum bicolor* L.) | *Echinochloa crus-galli* (L.) Beauv.<br>*Amaranthus retroflexus* L.<br>*Rumex acetosella* L.<br>*Parthenium hysterophorus* L. | Phenolic acids:<br>benzoic acid,<br>*p*-hydroxybenozoic,<br>vanillic,<br>*m*-coumaric, |

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|---|---|---|
| | | *p*-coumaric,<br>gallic<br>caffeic acid,<br>ferulic and<br>chlorogenic acid,<br>sorgoleone |
| *Brassica* spp. | *Physalis angulata* L.<br>*Phalaris minor* Retz.<br>*Avena ludoviciana* Durieu<br>*Cirsium arvense* (L.) Scop.<br>*Chenopodium album* L.<br>*Melilotus alba* Medik.<br>*Rumex retroflexus* L. | benzoyl,<br>o-tolyl,<br>m-tolyl,<br>tert-octyl,<br>3- fluorophenyl |

Putnam and Duke (1974) first introduced the concept of using allelopathic crops to suppress weed growth in agriculture, as they mentioned the weed-suppressive crops and their effectiveness for use in weed management. Later research efforts have made it possible to use allelopathy for increasing crop production with quality food, to reduce reliance on synthetic pesticides and improve the ecological environment (Qasem & Foy 2001; Rice 1984; Weston 1996). Therefore, the current trends in agriculture production are to find a biological solution to reduce the apparent harmful impacts from herbicides and pesticides.

*Agroforestry systems*- In addition to crops, trees are also an integral part of the agriculture under various intensive and extensive agroforestry systems. Agroforestry is a modern tool to develop sustainable land use and to increase food production by growing woody species with agricultural crops and/or animals however negative allelopathic effects have also been recognized (Kohli et al. 2000). Because three species coexist with the agricultural crops, and mostly have negative allelopathic effects, their allelopathic compatibility may be crucial to determine the success of an agroforestry system. As species remain a part of the agroecosystem for a longer period, and most of them produce a large amount of leaves and litter, their allelochemicals may play an important role in developing an eco-friendly pest management strategy.

A significant reduction in crop density, root and shoot length and biomass were observed due to allelopathic effect of *Eucalyptus* spp. Trees, for example, *Eucalyptus camaldulensis* Dehnh. cause meristematic root tips and radical growth, and peroxidase activity in *Lepidium sativum*, *Rumex acetosella*, and *Avena fatua* L. in Iran (Moradshahi et al. 2003). *Eucalyptus citriodora* Hook. caused inhibition of *Avena fatua* and *Hippeastrum hubridum* Hort. in Egypt (El-Rokiek & Eid 2009). *Eucalyptus dundasii* Maiden. inhibited germination and growth of *Lolium rigidum* Gaudin and *Hordeum glaucum* L. in Australia too (Wu et al. 2011) while *Eucalyptus tereticornis* Sm. reduced seedling growth and photosynthesis metabolism of *Amaranthus viridis* (Kaur et al. 2011) in India. Effect of *Gliricidia sepium* litter on survival was negative on *Saccharum spontaneum* (Cummings et al. 2012). Likewise, various species of *Populus*, *P. deltoides* especially, are also known to exert allelopathic effect on other plants including crop plants (Kohli et al. 2000) due to the toxicity of allelochemicals including phenolics acid and salicin. *Leucaena leucocephala* is another fast growing nitrogen-fixing multipurpose tree that has been widely used for plantation under various agroforestry plantations. Its leaf and litter aqueous extracts have inhibitory effects on a number of plant species including crops like sorghum, cowpea and sunflower (Singh et al. 2001). *Albizia lebbeck* (L.) Benth. can also inhibit germination and growth of mungbean and soybean (Parvin et al. 2011). The most frequent allelopathic trees and their effects in suppressing growth of crops are listed in Table 8.3.

Table 8.3. Allelopathic trees and their effects on crops and other plants

| Tree species | Response species | Allelopathic effects on crops |
|---|---|---|
| *Acacia* spp. | *Hedera hibernica* G. Kirchn.<br>*Dactylis glomerata* L. | Affected net photosynthesis and respiration |
| *Albizzia lebbeck* (L.) Benth. | *Lactuca sativa* L. | Inhibition of germination and growth |
| *Eucalyptus* spp. | *Lepidium sativum* L.<br>*Rumex acetosella* L.<br>*Avena fatua* L.<br>*Lolium rigidum* Gaudin<br>*Hordeum murinum* L. *ssp. glaucum* (Steudel) Tzvelev | Reduction of crop density, root and shoot length and biomass<br>Inhibition of meristematic root tips and radical growth, and peroxidase activity |
| *Juglans* spp. | *Sinapis alba* L.<br>*Zea mays* L.<br>*Glicine max* (L.) Merr. | Inhibition of germination and growth |
| *Leucaena leucocephala* (Lam.) de Wit | *Sorghum* spp.<br>*Vigna unguiculata* (L.) Walp.<br>*Helianthus annuus* L. | Reduction of growth and development od crops |
| *Populus deltoides* W. Bartram ex Marshall | *Triticum aestivum* L.<br>*Lens culinaris* Medikus | Loss of yield |

| | | |
|---|---|---|
| | *Phaseolus mungo* (L.) Hepper<br>*Avena sativa* L.<br>*Trifolium alexandrinum* L.<br>*Brassica juncea* (L.) Czern.<br>*Helianthus annuus* L. | |

Studies with various tree and shrub plants can be used for further applications of allelopathy in weed control. Therefore, if properly understood and the nature of chemicals involved is elucidated, such mechanisms can be effectively exploited to enhance the crop productivity through management of weeds, nematodes, pathogens and insects. Agroforestry can, therefore, be manipulated to make agroecosystems sustainable through proper management and/or mulching of the litter of the trees growing in agroecosystems to improve the soil quality, conserve moisture and bring about the cooling effect (Kohli et al. 2006).

*Forest ecosystems*- Although the study of allelopathy involving plants in agricultural and horticultural systems has a long history of allelopathy research in forested ecosystems is rather recent (Mallik 2008). In such ecosystems, the soil plays an important role as the matrix through which potential allelochemicals pass, therefore, the influence of allelochemicals on different components of the soil ecosystem and their role in shaping community structure has been studied by numerous authors (Rice 1984; Einhellig 1995; Boufalis & Pellissier 1994; Inderjit & Mallik 1997; Djurdjević et al. 2004, 2010; Muscolo & Sidari 2010; Mitrović et al. 2012; Wardle et al. 1998). Allelopathic effects are directly related to forestry issues, for example the delay and reduction of germination, and/or stunted growth of conifer tree seedlings by allelopathic activity of the understory species (Mallik 2003; Pellissier & Souto 1999). Shrub species often quickly invade areas disturbed by removal of canopy trees by forest harvesting due to their stress tolerating strategies and form a dense understory that can alter natural regeneration of trees (Mallik & Prescott 2001). Therefore, one of the greatest challenges for plant ecophysiologists today is restoring natural and crop forests.

In forestry systems, allelopathy can affect many aspects of plant ecology including occurrence, growth and plant succession, the structure of plant communities, dominance, diversity and plant productivity. The allelochemicals released from forest trees affect the understory species, at least affect the donor species and may cause problems of natural regeneration in forest ecosystems (Reigosa et al. 2000; Djurdjević et al. 2003). Namely, in forest plantations, generally there are one or few dominant tree species, which would lead to accumulation of allelochemicals of these species. The intensive modern forestry has lead to serious changes in the physico-chemical and biological properties of soil. Effect of soil sickness can be observed better in ecosystems which are affected by anthropogenic activities, mainly in replacing natural mixed forests by monocultures. Thus forestry monoculture for long periods slowly intoxicates the soil, leading to the gradual changes in stand structure and tree species composition (Caboun 2005). In such case, soil sickness appears to be widespread. Allelopathic effects of certain canopy trees on tree seedlings and understory plants have direct effects on forest regeneration (Mallik 2008). In addition, introduction of exotic tree species in forest plantation may also increase accumulation of allelochemicals in soil due to very high requirements of such species for water and nutrients and consequently cause their deficit in soil, leading to increased production of allelochemicals. Beside this, the soil microflora, as important part in allelopathy, may not be adapted to such allelochemicals, which leads to its accumulation in toxic levels in soil.

Most forests are managed for timber production. In such forests the fate of natural understory plant communities, and thus of plant diversity in general, is a function of silvicultural practices, that promote rapid decomposition of plant material, designed with the primary intent of maximizing the value of the dominant tree crop (Roth et al. 2002). Silvicultural practices change the physico-chemical conditions of the soil or the biotic relations into the soil solution (Leckie et al. 2004) and therefore, change the allelopathic tree-understory relationships. However, the establishment and productivity decline of replanted tree ecosystems has remained a significant problem. Autotoxicity is a major reason for managed tree ecosystems regeneration failure, causing replant problems. Thus *Eucalyptus exserta* F. Muell. and *Eucalyptus urophylla* S.T. Blake were introduced in 1960's and become dominant species in man-made forest communities in South China as an important for the paper industry. However, aqueous leaf leachate and leaf volatile of *E. urophylla* expressed allelopathic effects on several native tree species including *Cinnamomum burmanni* (C. Nees & T. Nees) C. Nees ex Blume, *Cryptocarya concinna*

Hance, *Machilus chinensis* (Benth.) Hemsl., *Photinia benthamiana* Hance and *Pygeum topengii* Merr. (Fang et al. 2009).

In addition, in fire adapted boreal forests, particularly natural fires, the level and distribution of fire severity play a critical role in the manifestation of forest allelopathy. The high severity fires break down allelochemicals by thermal decomposition, create favorable seedbed by consuming forest floor humus and releasing nutrients and removing competing plants by killing underground regenerating organs. Clearcut harvesting and low-severity fires on the other hand, may promote vegetative regeneration of understory plants with competitive and allelopathic properties as their underground perennating structures remain unharmed. This may cause retrogressive succession by resisting tree colonization and inducing long-term habitat degradation (Mallik 2008).

Control of competing and allelopathic plants by herbicides after forest harvesting is a serious issue in forestry. Alternative methods such as use of allelopathic straw mulch, herbicides of biological origin, planting tree seedling pre-inoculated with mycorrhiza, and scarification and spot fertilization at planting have produced good results. It is possible to develop alternative methods of weed control in forestry by using allelopathy principle.

### Natural ecosystems

The idea of allelopathy as an ecological phenomenon structuring natural plant communities is rather recent (Mallik 2005). Unlike managed systems, allelopathic effects can result from interactive effects among multiple compounds (Inderjit et al. 2011) thus making it difficult to consistently demonstrate allelopathy in natural conditions and to identify the ecological relevance of particular chemicals. Belowground influences of ecosystem processes driven by soil biota, genetic effects on root interactions, and complex interactions among different root exudates seem to shape allelopathic interactions (Blair et al. 2006).

*Population and community structure changes by invasive species*- Research of allelopathic activity in natural ecosystems has often been initialised by field observations of changes in vegetation patterns in natural habitats such as reduced species richness. In Spanish scrublands, the floristic diversity of other species has been reduced by *Cistus* *ladanifer* L. allelochemicals that inhibited or delayed germination, and reduced seedling growth of species that are growing adjacent to *C. ladanifer* scrublands. Thus the distribution of these species is apparently limited by the allelopathic action of *C. ladanifer* (Chaves & Escudero 1997). The release of allelochemical compounds from *Ailanthus altissima* (P. Mill.) Swingle also has inhibitory effects on neighbouring plant species (Gómez-Aparicio & Canham 2008). Likewise, Mallik & Pellissier (2000) found that the Eurasian *Vaccinium myrtillus* L. generally showed stronger biochemical affects on the North American *Picea mariana* than on the Eurasian *Picea abies* (L.) Karst. Similarly, exotic invasive woody weed *Lantana camara* L. that form dominant components within various types of Australian forests was proved to interrupt the natural forest regeneration processes by decreasing germination, reducing early growth rates, and reducing survival of natural species (Gentle & Duggin 1997). Another example is the allelopathic tree *Acacia dealbata* Link, an Australian woody legume, that has become a serious environmental problem in Northwest Spain, where its expansion is assumed to reduce populations of native species and threaten local plant biodiversity (Lorenzo et al. 2011).

Exotic plant invasions often cause high mortality in native populations. A few examples demonstrate the importance of allelopathy for successful invasion e.g. two of North America's most destructive invaders, *Centaurea maculosa* auct. Amer., and *C. diffusa* Lam. that establish virtual monocultures and both species have powerful antiplant and antimicrobial root exudates (Callaway et al. 2005). *Alliaria peteolata* (M. Bieb.) Cavara & Grande, a devastating invader of North American temperate forests, also has strong allelopathic effects on *Geum laciniatum* Murray and *Geum urbanum* L. (Prati & Bosdorf 2004). The release of allelochemicals from plants known as aggressive colonisers *Elytrigia repens* (L.) Gould and *Vulpia myuros* (L.) C.C. Gmel., suggests that allelopathy is often involved in successful invasions (An et al. 1997). In New Zealand, allelochemicals from decomposing leaves of *Carduus nutans* L. have been reported to be involved in the establishment of this species in pastures of *Lolium perenne* L. and *Trifolium repens* L. (Wardle et al. 1998). Authors also reported that the decline in soil nitrogen input may benefit the subsequent *C. nutans* cohorts as this species tolerate low nitrogen conditions better than most forage species that illustrates how the allelopathic activity of a plant species may contribute to changes in ecosystem functioning.

Weidenhamer et al. (1989) suggested that the allelopathic effect might be intensified in natural communities where overall plant densities are lower for example because of stressful environmental conditions e.g. communities such as the Florida scrub, the California coastal chaparral and dry tropical scrub communities. Allelopathy is also more intensive in poor soils (Inderjit & Callaway 2003) supporting the hypothesis that allelopathy increases the invasive potential of exotic plants in environments with low resource availability (Hierro & Callaway 2003). Such statement partially explains how some plants become invasive monotypes in the area of introduction (Ridenour & Callaway 2001).

Allelopathy is a natural process also present in forest ecosystems that strongly influences forest development. Namely, stress or exotic species invasion could increase allelopathic importance in many forests. There are reports about allelochemical production in many woody species, from *Eucalyptus* sp. forests in Australia (Lovett 1986), to boreal conifer forests (Mallik 2003), tropical forests (McKey et al. 1978), temperate forests (Willianson et al. 1992) and sub-desert communities (Van Rooyen et al. 2004). Conifer forests with ericaceous understory or *Eucalyptus* sp. forests are ecosystems with a strong allelopathic influence. Most studies dealing with allelopathy were focused on the allelochemical influence on conifer forest regeneration following disturbances such as wildfires, windstorms or clearcuts (Pellissier & Souto 1999). In Canada and northern Europe, ericaceous shrubs proliferate during the period of higher resource availability after tree canopy removal and then allelochemical production and accumulation in forest soil increases (Mallik 2003). The conifer seedlings, the most allelochemical-susceptible stage, are not able to compete with ericaceous plants and their ability to develop mycorrhizae is inhibited (Inderjit & Mallik, 2002). Numerous negative allelopathic effects were reported understory phenolic-containing associated shrubs (*Ledum palustre* L. and *Empetrum hermaphroditum* L.) inhibitory effects on seed germination, rooting ability, seedling growth and regeneration of spruce species (*Picea glauca* (Moench) Voss and *Picea mariana* (Mill.) Britton, Sterns & Poggenb.) (Castells et al. 2005); inhibition of *Pinus sylvestris* L. regeneration post-fire in sites dominated by *E. hermaphroditum* (Zackrisson et al. 1997); and suppression of vascular plant growth in Sphagnum-dominated bogs. In another example, secondary metabolites from *E. hermaphroditum* inhibited symbiotic associations between *P. sylvestris* trees and mycorrhizal fungi, thus reducing *P. sylvestris* nitrogen uptake (Nilsson & Zackrisson 1992). Moreover, secondary metabolites in *E. hermaphroditum* litter inhibit soil microbial and macrofaunal activity, thus reducing decomposition rates and further reducing soil nutrient availability (Wardle & Lavelle 1997). The allelochemicals from ericaceous *Kalmia augustifolia* L. affect root growth of *P. mariana* (Inderjit & Mallik 2002). Only wildfires are able to reduce the presence of ericaceous shrubs and the allelochemical content in forest soil to levels which allow the successful regeneration of the tree canopy (Mallik 2003). Changes in the mineralization and decomposition rates, as the main factors responsible for the changes in humus characteristics following a *K. angustifolia* invasion, may be the cause of changes in soil fertility (Yamasaki et al. 1998). Similar relationships have been reported in *Cryptomeria japonica* (L. f.) D. Don forests in Taiwan (Chou 1986) and in *Eucalyptus* sp. forests in Australia (Lovett 1986).

In natural forest ecosystems the concentration of allelopathic compounds in the surrounding environment are variable and can be seasonally based. Allelochemicals released from the tree bark, needles, litter and root/mycorrhizal exudates remain in the soil and interfere with the germination of seeds or growth and development of young seedlings thus preventing their natural regeneration. Fernandez et al. (2006) and Monnier et al. (2011) reported an autotoxicity due to the allelopathy as the main reason for natural regeneration failure in the fire free *Pinus halepensis* Mill., forest in Mediterranean basin. Allelochemicals are released by trees for a long period and during time may accumulate in soil to toxic levels. Some examples of strong allelopathic effects can be found in the genus *Acacia*, *Ailanthus*, *Eucalyptus*, *Juglans*, *Leucaena* and some *Quercus* species (Cummings et al. 2012; Lorenzo et al. 2011; Hussain et al. 2011). Inhibition of germination and retardation of seedlings are the most common allelopathic effects in the natural ecosystems.

## Conclusion

Environmental implications of the allelochemical compounds are difficult to quantify and evaluate in both natural and managed ecosystems due to numerous confounding factors. In addition, the interactive nature of allelopathic compounds and occurrence of multi stresses under field conditions further complicates the problem. Beside natural environmental change, plants cope with a variety of increased human-induced environmental changes, during the last decades. Thus, allelopathy is receiving increasing attention because allelopathic interactions among crops, weeds, trees and microbes play an important role in the managed ecosystems thereby resulting in a decline in crop productivity, problem of soil sickness, increasing depletion of biodiversity and regeneration failure of natural forests. Therefore, there are two major challenges the researchers, to minimize the negative impacts of allelopathy on crop growth and yield, and to exploit allelopathic mechanisms as additional pest control or crop growth regulation strategies. Allelochemicals and/or their derivatives can directly be used as novel chemicals for sustainable management in an ecofriendly manner.

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