Zahid A. Cheema · Muhammad Farooq
Abdul Wahid *Editors*

Allelopathy

Current Trends and Future Applications

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Foreword

In nature, the survival through competitive environments for space, light, water, and nutrients, as well as defense against microorganisms, insects, and herbivores is accomplished through a variety of adaptive mechanisms that are multifarious in nature on the one hand and depict biochemical interaction among living systems, i.e., plants, algae, and microorganisms on the other. The latter phenomenon is termed as allelopathy. It has been considered as a particular form of ammensalism. Allelopathic hormesis, stimulation, or attraction at low concentrations of allelochemicals and inhibition or repellence as the concentration increases, is one of the most consistent features in the studies of allelopathy and has been well recognized. Allelochemicals can be present in any part of the plant. They can be found in leaves, flowers, roots, fruits, or stems and can also be found in the surrounding soil released by decomposing plant residues or by the action of microorganisms and direct exuded by plant roots or leached from plants or their residues. The production of these toxins depends on various factors such as stage of the plant growth, species, biotic and abiotic stresses. Target species are affected by these toxins in many different ways. The toxic chemicals may inhibit shoot/root growth, they may inhibit nutrient uptake, or they may attack a naturally occurring symbiotic relationship thereby destroying the plant's usable source of a nutrient.

The idea that plants affect neighboring plants by releasing chemicals in the environment has been known since about 370 BC. Reports as early as 300 BC documented that many crop plants (e.g. chickpea, barley, and bitter vetch, etc.) destroyed weeds and inhibited the growth of other crop plants. The soil sickness problem in agricultural lands was specifically related to exudates of crop plants. However, it is only during the recent past that intensive scientific research on understanding this phenomenon started.

An Austrian scientist Hans Molisch coined the term "Allelopathy" in 1937 in his book "Allelopathie" to include both harmful and beneficial biochemical interactions between all types of plants including microorganisms. Rice deviated from this definition excluding the beneficial effects in his first book, while reconsidered and accepted Molish's definition in his second monograph. Research on symptoms and severity of adverse effects of living plants or their residues upon growth of higher plants and crop yields, interactions among organisms, ecological significance of allelopathy in plant communities, replanting problems, autotoxicity, problems with crop rotations, and the production, isolation, and identification of allelochemicals in both natural and agro-ecosystems have been topics of interest during the last decades. Research efforts in this emerging discipline of science has shown that allelopathy has promising solutions to many of the problems in contemporary agricultural systems.

This book represents primarily a collection of papers presented at the International workshop “Allelopathy—current trends and future applications” held in Faisalabad, Pakistan during March 18–21, 2007. At that time, I was President of International Allelopathy Society, and attended the workshop upon invitation by Prof. Zahid Ata Cheema. That workshop also proved nursery for ‘Asian Allelopathy Society’, as many delegates from Asian countries joined and discussed about the establishment of Asian Allelopathy Society.

I hope that this volume will contribute toward escalating the vision about allelopathy and reinforce understanding for its utilization to develop eco-friendly agricultural technologies ensuring a peaceful living on the Earth to all of us and future generations.

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Preface

The idea of putting together this book stemmed from a successful International Workshop on Allelopathy at Faisalabad, Pakistan during March 18–21, 2007. The workshop was organized in collaboration with University of Agriculture, Faisalabad, Pakistan, International Allelopathy Society and Higher Education Commission, Pakistan. Prof. Yoshiharu Fujii, then President, International Allelopathy Society proposed to compile the selected papers in the form of a book. Selected papers presented at this workshop and some additional invited chapters constitute this volume.

Efforts on understanding mechanisms of production of allelochemicals, their release into environment, influence on the neighboring plant, the mechanisms of action of allelochemicals at molecular level, their influence on soil, and ultimately the application of all these in the management of natural and agricultural ecosystems are the subject of interest for those engaged in allelopathic research worldwide. This involves scientists from an array of disciplines as analytical chemistry, botany, plant physiology, ecology, soil chemistry, microbiology, molecular biology and scientists from agronomy, horticulture, genetics, breeding, plant protection, and many others. The techniques and tools employed are as diversified as the disciplines. Research efforts in this emerging discipline of science has shown that allelopathy has promising solutions to many of the problems in contemporary agricultural systems. We felt that it is timely to collect and synthesize the latest developments on allelopathy research with special emphasis on its application in agricultural systems. We divided the contents of the book into four parts: (1) allelopathy from ecological perspectives, (2) allelopathy in agricultural systems: some case studies, (3) allelopathy in pest management and crop production, and (4) allelopathy: some emerging concepts.

A total of 45 researchers from 17 countries contributed chapters on various aspects of allelopathy. We thank the authors who responded to our call and contributed. We thank Springer for accepting our proposal for this book, especially Dr. Christina Eckey and Dr. Andrea Schlitzberger for keeping faith in us despite the long delay in completing the task.

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Part I
Allelopathy from Ecological Perspectives

Chapter 1
Role of Allelopathy During Invasion Process by Alien Invasive Plants in Terrestrial Ecosystems

Paula Lorenzo, M. Iftikhar Hussain and Luís González

Abstract Biological invasion is causing serious current biodiversity loss in different parts of the world and involves different stages: introduction, establishment, naturalization, and fast dispersion outside the normal ranks. Invasion may cause a reduction in abundance of native species or the elimination of populations of a particular species. Exotic species have to surpass different biological filters to get to be invaded in a new habitat. Importance of allelopathy in the invasion process may include the release of secondary chemical metabolites into the surrounding environment to inhibit the seedling establishment and other ecophysiological attributes of native biota. Temperature, drought, cold, association, and feedback from soil microorganisms can also adversely affect the biological nutrient cycle, and other aspects that can favor the invading capacity of exotic species. Environmental problems generated by invading species can become serious in naturally protected and sensitive areas, where climatic circumstances may evolve in the shape of global warming. The purpose of this chapter is to highlight the role of allelopathy during the invasion process with special emphasis to ecophysiological relationships between exotic and native plants, and soil microorganisms.

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1.1 Introduction

In a simple way, the invading species are those, which came from other regions. This definition, merely biogeographically, implies exotic species in contrast to the native species (Rejmánek 1995). However, an exotic species would not have to be considered an invading if it does not settle successfully in the introduced area and it is not able to regenerate by itself or it is not, later, able to disperse without direct human support (Binggeli 1994). Theoretically, an alien species can be considered invading when it enters an exponential phase of dispersion (Pyšek 1995). On the other hand, biological invasion is not a localized phenomenon, but it is a dynamic process that occurs through years as the invading population crosses different stages: introduction, establishment, naturalization, and fast dispersal outside the normal ranks (Fig. 1.1).

The invasion of new territories by alien plant species threatens the biodiversity and the stability of the ecosystems (Davis 2003). This process is responsible for eliminating the presence of native and extinction of certain species (Richardson et al. 1989; Gaertner et al. 2009), changes in the relation between soil microorganisms population (Jacinthe et al. 2009), modifications in the availability of soil nitrogen (Chen et al. 2009) and other nutrients (Rodgers et al. 2008) and changes in the soil properties (Zhang et al. 2009). These results maintain the open debate on the paradox of invasion, depending on the space scale of the study of the existence of positive and negative relations between the biodiversity of exotic and native species (Fridley et al. 2007; Rout and Callaway 2009). On the other hand, Meisner et al. (2009) indicated that the paradox of invasion does not exist. They concluded that there are underlying mechanisms to explain species in the new habitats. Rout and Callaway (2009) pointed out that a general pattern of improvement of the cycle of nitrogen does not exist for the invading plants. Despite this controversy, the invasion would cause a reduction in the abundance of native species or the elimination of some populations that could reduce the genetic diversity (Davis 2009).

The characteristics which favor the capacity of a plant to become invaded are directly related to their ability to reproduce, grow quickly from germination to reproductive stage, and, particularly, of its phenotypic plasticity that will allow them to adapt to the environmental stress of the new habitat (Baker 1974; Shi and Ma 2006). Nevertheless, most of alien invasive species do not share all these characteristics (Roy 1990; Pyšek and Richardson 2007; Lorenzo et al. 2010a, b). There is sufficient scientific work to support the hypothesis that the success of invasion could be triggered by functional characteristics, which differ quantitatively from presence in the native flora (Lloret et al. 2005). A study conducted in Ireland (Milbau and Stout 2008), analyzing the importance of different historical factors (environment and species), taxonomic and ecophysiological, classified their importance in the preponderance of species' ability to transform itself into naturalized or invaded. The factors that differentiate the invading exotic species from non-invading ones were the introducing ornamental species, hermaphrodite

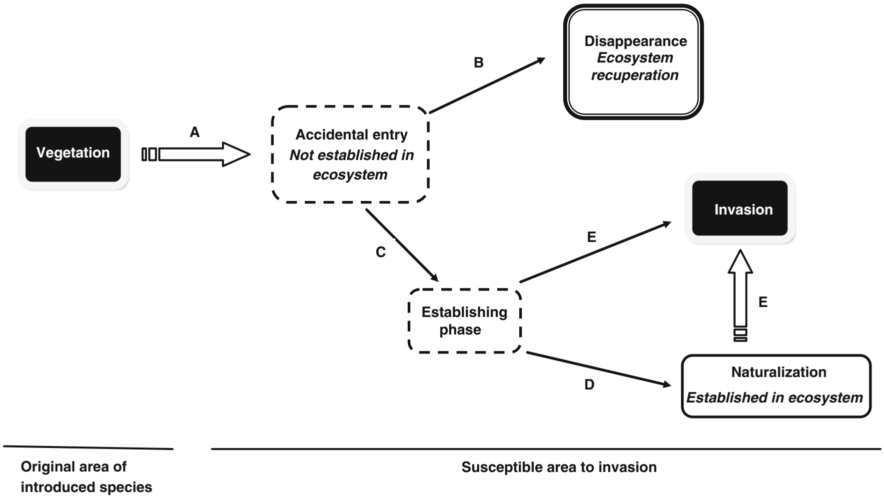

Fig. 1.1 Dynamic scheme of the invasion process. **A** introduction of propagules, **B** disappearance, **C** factors that influence in the establishment, **D** factors that influence the naturalization, **E** factors that influence the invasion

flowers, pollination types, time of flower initiation, indicating value of relative humidity, and the date of the first registry. The incorporation of phylogenetic information had little influence on the results, which suggested the capacity of exotic species to become naturalized and to become invading to evolve independently in different phylogenetic lineages. Jiang et al. (2007) suggested that different species that constitute the plant communities differ in their vital history, the biological and physiological characteristics, responsible for the existing relation between diversity, production of biomass, and capacity of invasion, are probably different. The invasive herb *Solidago canadensis* was introduced into Europe in the seventeenth century (Weber 2001). It is a perennial herb forming large clonal colonies that tend to reduce the abundance of native vegetation (Weber 1998). The taxon is highly variable and includes diploid, tetraploid, and hexaploid plants in the native range (Halverson et al. 2008), but only diploid cytotypes are found in Europe (van Kleunen and Schmid 2003).

It is well understood that the characteristics of the susceptible habitat to be invaded directly influence the invading capacity of the exotic species (Gaertner et al. 2009; Lorenzo and González 2010) and also that the abundance of the exotic species in the native range predicts the abundance in the colonized area (Firn et al. 2011). Without any doubt, a better knowledge of why some plants may act as invading could help us to identify species potentially detrimental and to control the present invading species, being a potentially useful criterion for the biosafety programs. This chapter covers the importance of allelopathy in the invasive process into the current context of exotic plant invasion, updating definitions and relationships with invasion, discussing the characteristics of exotics that make them invasive plants, reviewing allelopathic compounds that are involved in the invasion process, and revising ecophysiological aspects that could be affected by invasion process as physiological activity of native target species, soil microorganisms, and nutrient cycles.

1.2 Allelopathic Perspective

There are hundreds of thousands of plant species, but relatively few have the capacity to invade new habitats. We can understand the reason of this geographic specificity based on the different evolutionary filters (Lambers et al. 2008). The exotic plants would have to surpass these filters to get invaded (Lortie et al. 2004; Lorenzo and González 2010; Lorenzo et al. 2010a). The plant species are present in a determined area for historical reasons (plant evolution or derives continental) in spite of having appropriate environmental conditions in other regions, this one is the historical filter. Some species are absent from a certain area because they do not have the appropriate physiological characteristics to survive in that area (for example, they cannot tolerate conditions of extreme water deficit); this one would be the physiological filter. The interactions produced between exotic and native species in new atmosphere will determine the plant composition of the invaded area, being the biotic filter (Fig. 1.2). One of the components of this last filter is the allelopathic relations that can be produced between the plant species in the naturalized environment (Lorenzo et al. 2008), including alteration in soil microorganisms population (Zhang et al. 2009).

Within the framework of this text, the more accepted definition of allelopathy (Rice 1984) is “the effects (stimulatory and inhibitory) of a plant on other plants through the release of chemical compounds into the environment”. This definition also includes microorganisms. The allelopathic process, from the perspective of the competition between species, constitutes a passive element of interaction (Reigosa et al. 1999); neither the excess nor the less important ones. The hypothesis of Rabotnov (1974) indicates that the allelopathy is, probably, less significant in plant communities in which they have coevolved than in native versus invasive species, which have evolved in different biogeographical areas (Reigosa et al. 1999, 2002; Callaway and Hierro 2006). The allelochemicals of exotic species have manifold functions within the biotic framework in area of original distribution (allelopathic defense as opposed to herbivorous transporting metal agents or agents of symbiosis between soil microorganisms and the plant). In addition, in the new area, the allelopathic potential of the invasive species would be increased to escape from natural enemies and allelochemicals lose some of their original function (Sinkkonen 2006).

In the ecological frame generated by the filters of Lambers et al. (2008), different hypothesis are included to explain the invading success of some alien invasive species (Lorenzo and González 2010; Lorenzo et al. 2010a): the *propaguels pressure* hypothesis (PPH, di Castri 1989), *enemy release* hypothesis (ERH, Keane

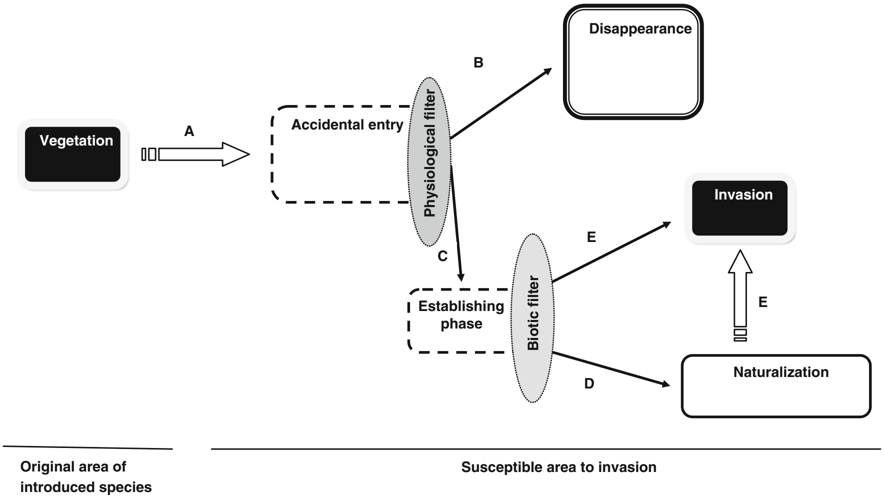

Fig. 1.2 Dynamic scheme of the invasion process including evolutionary filters like barriers. **A** introduction of propagules, **B** disappearance, **C** factors that influence the establishment, **D** factors that influence the naturalization, **E** factors that influence the invasion

and Crawley 2002), *superior competitor* hypothesis (SCH, Bakker and Wilson 2001), *Novel weapons' hypothesis* (NW, Callaway and Aschehoug 2000), *hypothesis of the evolution of the increased competitive capacity* (EICA, Blossey and Nötzold 1995), and *the hypothesis of resources fluctuation and disturb habitat* (FR & DHH, Davis et al. 2000). During the dynamic process of invasion, the exotic species use some of the mechanisms included in these hypotheses like expansion ways, being very probable, the participation of several of them throughout the invasive process (Jiang et al. 2007; Lorenzo et al. 2010a). From all these hypotheses, three of them, ERH, EICA, and NW, are most often suggested to explain the invasive ability of different plant species (Bais et al. 2003; Mitchell and Power 2003; Torchin et al. 2003; Callaway and Ridenour 2004; Callaway et al. 2005a, 2008; Gómez-Aparicio and Canham 2008; Handley et al. 2008; He et al. 2009; Hill and Kotanen 2009; Te Beest et al. 2009; Lind and Parker 2010; Lankau 2011).

According to ERH hypothesis the alien invasive species have the ability to increase its population density in the new geographical area because they are free of the predators that attack in their native range (Dostál 2010; Andonian and Hierro 2011; Vasquez and Meyer 2011). The EICA is based on the idea that when the invasive plants are released from their specific enemies, they can invest more resources in growing and less on defending (Herrera et al. 2011; Holzmueller and Jose 2011), which confers a competitive advantage forehead to the native species. Hypothesis NW asserts that the exotic species release allelochemicals that are relatively ineffective against their neighboring plants in the native range but highly inhibiting against the native plants in the new habitat. Factually, this phenomenon can be given mainly to the native species that are not adapted to the allelochemicals of the exotic species, being the evolutionary relations among the plant species to a key part of the hypothesis of the novel weapons (Inderjit et al. 2006). This theory is supported by biogeographical studies (He et al. 2009; Callaway et al. 2008; Thorpe et al. 2009) in which it was demonstrated that the invasive species produce more effects on the native communities of the invaded area than on the same types of native species in the original area. It seems, therefore, that the allelopathy plays an important role in the invasive success of these exotic plants that are able to dominate in the ecosystems where they are introduced. In fact, the allelopathy has been widely studied in the last decades within the context of the hypothesis of new weapons, because of the invasions of numerous plants originated by different reasons (Carballeira and Reigosa 1999; Callaway and Ridenour 2004; Callaway et al. 2005a; Lorenzo et al. 2008, 2010b; Ens et al. 2009a; Jarchow and Cook 2009; Lind and Parker 2010; Lankau 2011; Barto et al. 2010).

A large number of allelopathy experiments with exotic species evaluated the phytotoxic activity of the invasive species by means of bioassays in which the germination, seedling growth, and plant biomass are determined under laboratory or greenhouse condition (González et al. 1995; Carballeira and Reigosa 1999, Hoagland and Williams 2003; Lorenzo et al. 2008, 2010b; Hussain et al. 2011b). However, the study of the allelopathy in nature has been accompanied by great skepticism as a result of the inherent methodological difficulties to demonstrate this phenomenon under natural field conditions (Gómez-Aparicio and Canham 2008). To end this debate, it is necessary to design or carry out allelopathic experiments in natural conditions, which differentiate the resource competition from the allelopathic phenomenon. Although during the last years progress was made in the use of more realistic and sophisticated techniques, the studies of allelopathy in real conditions continued to be very small (Gómez-Aparicio and Canham 2008). One of the tools used in the allelopathic research, that separate allelopathy from resource competition, is the use of the activated charcoal. This element has the capacity to adsorb organic compounds released by the invading species (Inderjit and Callaway 2003). Nevertheless, recent investigations have found that the activated charcoal interferes with the availability of nutrients and growth of plants (Weißhuhn and Patri 2009; Lau et al. 2008) that represent an insecure methodology. Lorenzo et al. (2010a, b; 2012) has designed a new method maintaining the interaction of the donating and receiving species in an inclined plane that would allow detecting the allelopathic effect without the need to add external elements, which based on the capacity of the allelochemicals move in the soil solution. Although the preliminary results obtained with this method are promising, and we can suggest introducing improvements in the technique that will be effective tools for differentiating the allelopathy from other competitive mechanisms in the invasion processes.

Majority of compounds released by the plants are produced as off shoots of primary metabolic pathways (Hadacek 2002). Following the phytotoxic action, the bioactive concentration and its persistence and fate in the surrounding area in which they are released can act like allelopathic compounds (Inderjit and Duke 2003). In addition, in nature, the allelopathic activity is probably originated by the joint operation of several allelochemicals, as compared to action of single

Table 1.1 Effect of allelopathic compounds, which take part in the invasion process, on different receiving species

Allelopathic compounds	Invasive species	Inhibitory effects	Native species	Reference
Sesquiterpenes	*Chrysanthemoides monilifera* (L.) Norl. spp. *rotundata*	Inhibition in seedling growth	*Isolepis nodosa* (Rott.) R. Br *Acacia longifolia* var. *sophorae* (Labill.) F. (Muell.) *Banksia integrifolia* (L)	Ens et al. (2009b)
Soluble phenolics	*Typha angustifolia* L.	Reduction in germination	*Bolboschoenus fluviatilis* (Torr.) Soják	Jarchow and Cook (2009)
Glucosinolates and their hydrolysis products	Species from family *Brassicaceae*	Plant–plant, plant–microorganism and plant–insect interaction	Native species of invaded areas	Müller (2009)
7,8-benzoflavane	*Acroptilon repens* (L.) DC.	Effect on four plant species and their associate rhizosphere	*Astragalus cicer* L. *Hedysarum boreale* Nutt *Lupinus sericeus* Pursh *Medicago sativa* L.	Alford et al. (2009)
(±)-catechin	*Centaurea maculosa* Lam.	Effect on four plant species and their associate rhizosphere	*Astragalus cicer* L. *Hedysarum boreale* Nutt. *Lupinus sericeus* Pursh *Medicago sativa* L.	Alford et al. (2009)
(±)-catechin	*Centaurea maculosa* Lam.	Effect on seedling growth	Species that coexist with the invader in their native and invaded area	Thorpe et al. (2009)
Isopropilo and sec-butilo glucosinolatos and their degraded product Secondary butyl glucosinolates and their degraded products	*Sisymbrium loeselii* L.	Inhibition of germination and seedling growth	*Centaurea maculosa* Lam. *Pseudoroegneria spicata* (Pursh.) Love *Festuca idahoensis* Elmer. *Glomus intraradices* Schenck & Smith.	Bainard et al. (2009)

(continued)

Table 1.1 (continued)

Allelopathic compounds	Invasive species	Inhibitory effects	Native species	Reference
Cariofilone oxide, linoleic acid, germacrene B	*Centaurea diffusa* Lam.	Released into soil		Quintana et al. (2009)
(±)-catechin	*Centaurea maculosa* Lam.	Reduction of the biomass, reduction of the germination and increase of the mortality of the germinates	Native species of invaded area	He et al. (2009)
Monoterpenes	*Artemisia vulgaris* L.	Reduction of the above ground biomass	*Solidago canadensis* L.	Barney et al. (2009)
Poliacetilenes and diterpenes	*Solidago canadensis* L.	Effect on seedling growth	*Species nativas*	Abhilasha et al. (2008)
Cnicine	*Centaurea diffusa* Lam.	Reduction of germination, weight and inhibition of the growth of some gram (−) phytopathogenic bacteria	*Lycopersicum esculetum* L. *Lactuca sativa* L. *Triticum aestivum* L. *Leonorus sibiricus* L. *Pseudomonas syringae* Van Hall *Xanthomonas campestris (Pammel) Dowson* *Erwinia caratovora* Smith	Cabral et al. (2008)
Onopordopicrine	*Centaurea tweediei* Hook. & Arn.	Reduction of germination, weight and length of radical	*Lycopersicum esculetum* L. *Lactuca sativa* L. Disappearance *Ecosystem recuperation* *Triticum aestivum* L. *Leonorus sibiricus* L.	Cabral et al. (2008)

chemical (Inderjit et al. 2002; Inderjit and Duke 2003). Nowadays, there is a great debate in relation to the role of secondary metabolites such as allelochemicals in the natural ecosystems in general and invasion process in particular. The main problem is that low concentration of secondary metabolites under field conditions is insufficient to bring out a phytotoxic solution (Tharayil 2009).

In spite of controversial debates, considerable efforts have been used to demonstrate the mediation of compound released by invasive plants in the invasion processes (Carballeira and Reigosa 1999; Callaway and Ridenour 2004; Callaway et al. 2005b; Lorenzo et al. 2008, 2010b; Ens et al. 2009b; Jarchow and Cook 2009). Effects of different allelopathic compounds on native species and involved in invasion process are summarized in Table 1.1. Generally, allelopathic study of invasive species has been realized through bioassays in which extracts obtained of invasive species were applied on target species. The identification of chemical compounds of the extract and to determine which allelopathic compound is responsible for the invasion is a complicated and difficult task. Nevertheless, there are studies in which the allelopathic activity in the ecosystems is related to certain allelochemical groups, for example, simple phenols, flavonoids, terpenoids, alkaloids, fatty acids, poliacetilenos, sulfurated, oligopeptides, and glucosinolates (Müller 2009). There are few studies in which the allelopathic effect of an invasive species is associated to one or several identified molecules.

1.3 Ecophysiological Processes Affected by Allelochemicals During Invasion

In spite of its ecological relevance, as stated above the allelopathy is highly under debate these days (Fitter 2003; Fridley et al. 2007; Tharayil 2009). The ecological and physiological processes affected by the release of secondary metabolites from invasive species to soil solution are different. The plant invasions can not only disturb the diversity of plant species but also increase the plant productivity (Rout and Callaway 2009), and this phenomenon is the result of different interactions in the ecosystem that includes the soil microorganisms. The invasion processes often increase the deposits and flow of nitrogen through processes regulated by the soil microbial communities favoring the productivity (Rout and Callaway 2009) but, other times, inhibit the capacity of the native plants to take up nutrients through the suppression of associate mycorrhizae (Callaway et al. 2008). Under laboratory conditions, effects produced by the invasive species have been detected on physiological processes in the native species such as changes in the rate of germination or inhibition and stimulation in the growth of seedlings (Mei et al. 2005; Sun et al. 2006; Lorenzo et al. 2008, 2010b; Hussain et al. 2011a, b, c). In the last years, researchers have tried to know the mechanism of action of allelochemicals from invasive species and for this the strategy of investigators is to deepen the knowledge of primary effects in target plant (see Weir et al. 2004).

One of the better studied processes in allelopathy is the inhibition of the photosynthesis and the evolution of oxygen through interaction with components of the photosystem II (Martínez-Otero et al. 2005; Zhou and Yu 2006; Lorenzo et al. 2008, 2010b) and RuBisCO activity (Allen and Ort 2001). There are several reports regarding the effect of allelochemicals on respiration and ATP synthesis (Ishii-Iwamoto et al. 2006), carbon isotope discrimination (Hussain et al. 2008; Hussain et al. 2011a), photosynthetic efficiency, quantum yield, and heat energy dissipation (Hussain and Reigosa 2011), lipid and hydrogen peroxidation (Sánchez-Moreiras et al. 2011), on the respiration of native species (Lorenzo et al. 2008, 2010b). Gene expression studies have shown that Benzoxazolin-2(3H)-one (BOA) induces the transcription of a number of genes associated with cell detoxification and defense pathways (Baerson et al. 2005). Although the way of action of some allelochemicals has also been studied on redox system (reactive oxygen species), lignifications, stomatal conductance, foliar transpiration, metabolism of the amino acids, regulation of the concentration of hormones ,and cell cycle, these studies are not realized with extracts or allelochemicals derived from invasive species.

Invasive species also pose a significant threat to biodiversity. Moreover, compelling evidence exists, based on global trade and movement patterns, that the magnitude of this threat is increasing globally (Hulme 2009). Invasive species alter ecosystem processes (Raizada et al. 2008), decrease native species abundance and richness via competition, predation, hybridization, and indirect effects (Blackburn et al. 2004; Gaertner et al. 2009) change community structure (Hejda et al. 2009) and alter genetic diversity (Ellstrand and Schierenbeck 2000). For example, in Europe, the large majority of the most invasive species reduces diversity and change community structure, whereas a smaller percentage directly harms threatened species (Vilâ et al. 2009). Increases in the number and spread of alien species appear to be strongly associated with substantial increases in the extent and volume of trade and transport, particularly over the last 25 years (Levine and D'Antonio 2003; Ruiz and Carlton 2003; Hulme et al. 2009). Since global trends in trade and movement are clear, related patterns of the extent of biological invasion, their impacts on biodiversity, and societal responses to these impacts remain poorly quantified at a global scale. The Convention on Biological Diversity's (CBD) 2010 Biodiversity Target (UNEP 2002) and the associated Invasive Alien Species Indicator under the focal area 'Threats to Biodiversity' (Walpole et al. 2009) present one of the first concerted and globally coordinated efforts to do so.

In the small-scale experiments, the relation between the plant diversity of the community and the invasion by non-native species is negative (Maron and Marler 2007; Lorenzo and González 2010a); therefore, the resistance of the system to the invasion should increase with the diversity of species (Elton 1958). The arguments in favor of this old idea seems to reside in rich communities in species and offer few vacant niches (niche complementarily effect) or present a great probability that an invading plant is competitively excluded by a superior competitor (sampling effect) (Tilman 1999; Wardle 2001; Fargione and Tilman 2005). Although the studies realized in short periods of time indicate that the impact of invasive plants on ecosystems is relatively small, the future incidence on the native flora could be very high (van Wilgen et al. 2008) and the indications obtained until now suggests that the effect on biodiversity would have to be a reason for preoccupation.

During the process of invasion and its effect on the autochthonous diversity, the possibility of interaction with other environmental stress factors such as drought, more pronounced in a global warming context (van der Wal et al. 2008) that affect the native species, should be take into account (Maron and Marler 2007). Although wide scope exists in the field of ecophysiological interactions within the frame of the invasive species, the present data indicate that the plant communities do not respond similarly, which leads to significant changes in the composition and dominance of the species (Richardson et al. 1989; Gaertner et al. 2009; Matesanz et al. 2009). Black wood (*Acacia melanoxylon* R. Br.) has its origin in the temperate forests of southeast Australia and Tasmania currently considered as invasive in Galicia (Xunta de Galicia 2007) and currently covers a considerable area in the coastal zone of north-western Iberian Peninsula, both in monocultures and in mixed stands with *Eucalyptus globulus*. Upon invasion, it quickly establishes in the alien environment, thereby resulting in changes in structure and dynamics of native ecosystems. Recently, Hussain et al. (2011b, c) reported the inhibitory effects on seedling establishment and ecophysiological characteristics (leaf water contents, growth, photosynthetic efficiency, quantum yield, carbon isotope discrimination, and protein contents) of native species. The cause of inhibition was concluded to be the presence of growth inhibitory phenolic and flavonoid compounds present in flowers and phyllodes of *A. melanoxylon* R. Br. The differences in the ecophysiological characteristics also confirmed in lab tests where a positive relation has been elaborated between plant diversity and production and a negative relationship between plant diversity and invasion has also been verified. Nevertheless, the mechanisms that underlie in the invasion process are different according to the type of invaded community (Jiang et al. 2007).

The allelochemicals coming from invasive species have a strong impact on the dynamics of nutrient cycling in the soil of invaded area. The great diversity of invasive plant species and susceptible places for invasion showed that proposed patterns of differentiation between invaded areas by exotic species and free areas are inconsistent. Generally, the concentration of C, N, and P is increased with the growth of the invading species (Li et al. 2007). Studies realized with nitrogen-fixing invasive plants indicate that invaded areas showed a high content in N and a low C:N ratio. These variations with an increase in the contents of organic C, N, and interchangeable cations result in changes in the soil microorganisms (Marchante et al. 2008). These changes can be produced by different forms, for example, varying the entrance of organic matter in the invaded ecosystem (litter) or changing the radical system (Yan and Tong 2008). Some non-fixing invaders have also found to increase the total C, N, and net rate of nitrification (Chen et al. 2009). Although some non-invasive and invasive species have the same effect on the soil nutrients, we cannot affirm that a generalized phenomenon exists. In fact, other authors have published different results in the invaded areas where total N, P, N (NO_3^-) available P, and the stability of aggregates were decreased, while organic C and N (NH_4^+) were increased (Zhang et al. 2009).

The interactions between plants and their associated soil communities can result in dynamic feedbacks, where plants influence soil organisms and soil organisms in return influence plants (Bever et al. 1997; Wardle et al. 2004). The outcome of these interactions can range from negative to neutral or positive. Interactions are considered negative when the net effects of all soil pathogens, root herbivores, symbiotic mutualists, and decomposers reduce plant performance, whereas interactions are considered positive when the benefits brought about by symbionts and decomposers overwhelm the negative effects of soil pathogens and root herbivores and enhance plant performance (Wardle et al. 2004). Negative interactions enhance plant community diversity by exerting density-dependent control (Klironomos 2002; Reinhart et al. 2003) and speed up successional replacement (Van der Putten et al. 1993). The rate at which plants promote soil-borne pathogens differs among species (Klironomos 2002), functional groups (Kardol et al. 2007), and successional position (Kardol et al. 2006). As seen above, most of the effort to assess the invasion effect by alien plant has been done on the biodiversity of plants and animals species. However, attention has been devoted recently to the effects of plant invasion on soil microorganisms that could play a fundamental role in the invasion processes (e.g. Callaway et al. 2005a, b; Marchante et al. 2008; Rodríguez-Echeverría 2009).

Soil enzyme activities have been used as effective indicators of the capacity of the microbiota to mineralize carbon and mineral nutrients, and thus they can be used as measures of the functionality of the microbiota (Kourtev et al. 2003). Invasive plants can alter the microbial community surrounding the roots through root exudates (Bais et al. 2004). The obtained results indicate an increase in microbial biomass, increase in the density of the invasive species in invaded areas (Li et al. 2007; Jacinthe et al. 2009), metabolic activity (basal respiration) (Zhang et al. 2009, Jacinthe et al. 2009) and the functional diversity (Zhang et al. 2009).

Recent research has shown that some invasive species establish positive feedback cycles with the soil in which they invade and rhizosphere of the invasive species becomes rich in mutualistic organisms to get benefit from them (Rodríguez-Echeverría 2009). It has also been found that invaded soils have a high fungi/bacteria ratio, as compared to microbial communities in invaded soils or where native flora are different (Jacintheet al. 2009). Nevertheless, own results (Lorenzo et al. 2010b) obtained in different invaded ecosystems indicate that the ratio fungi/bacteria cannot be generalized, and probably it depends upon degree of time of the invasion and the floral typology of the invaded zone.

1.4 Conclusions

The invasions by alien species are responsible to a great extent for the current biodiversity loss and modification of the ecosystems. The invasive species use different mechanisms to invade new areas; among them the allelopathy seems to have an important role. During the invasion process, the invasive species release allelochemicals that seem to affect different primary and secondary physiological processes in the native species and soil microorganisms that are close to their rhizosphere altering the biodiversity. One more efficient use of resources and the competitive interaction by these resources based on allelopathic processes makes the exotic plants more invaders. A deeper knowledge of the underlying eco-physiological mechanisms to the invasion process will give a base to raise new control mechanisms and to avoid the loss of indigenous biodiversity of the threatened areas. Otherwise, the associated ecophysiological effects to this type of disturbance can be serious, mainly under the environmental conditions derived from the global warming (UNEP-WMO, 2001) and to show a new scene for the invaded areas.

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Chapter 2
Ecological Consequences of Allelopathy

A. Koocheki, B. Lalegani and S. A. Hosseini

Abstract Allelopathy refers to the effects of one plant on another plant through the release of chemical compounds into the environment. Chemicals released from plants, imposing allelopathic influences (allelochemicals) are classified as secondary metabolites and are produced as offshoots of the primary metabolic pathways in plants. Allelopathic compounds play important roles in the determination of nutrient dynamics, mycorrhizae, soil chemical characteristics, microbial ecology, plant diversity, dominance, invasion, succession, and climax of natural vegetation. Species richness and diversity are important indicators of ecosystem function, which are influenced by allelopathic plants thereby affecting invasion and dominance of plants within natural ecosystems. Moreover, allelochemicals may affect plant species by inhibiting their microbial symbionts such as mycorrhizae and nitrogen-fixing bacteria. Allelopathic potential of most invasive species is expressed as one of the most important factors in their successful establishment in new habitats. Also, allelopathy makes a significant contribution to the process of plant succession. This chapter is based on a literature review on allelopathy from a perspectives of allelopathic plants, including plant biodiversity, microbial symbiosis, invasion, and plant succession.

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2.1 Introduction

Allelopathy refers to the direct or indirect chemical effects of one plant on the germination, growth, or development of neighboring plants. Hans Molisch (1937) coined the term allelopathy, which is derived from the Greek words allelon (of each other) and pathos (to suffer) and mean the injurious effect of one upon the other (Rizvi et al. 1992). Rice (1984) defined allelopathy as the effect(s) of one plant (including microorganisms) on another plant(s) through the release of a chemical compound(s) into the environment. This definition includes both stimulatory and inhibitory effects, depending on the concentration of the compound(s). Some use the term in a wider sense, for instance entomologists, who include the effects of secondary compounds on plant–insect interactions. In 1996, the International Allelopathy Society defined allelopathy as follows: "Any process involving secondary metabolites produced by plants, micro-organisms, viruses, and fungi that influence the growth and development of agricultural and biological systems (excluding animals), including positive and negative effects" (Torres et al. 1996).

Chemicals released from plants, imposing allelopathic influences, are termed allelochemicals or allelochemics. Most allelochemicals are classified as secondary metabolites and are produced as offshoots of the primary metabolic pathways of the plant. Often, their functioning in the plant is unknown, but some allelochemicals are known also to have structural functions (e.g. as intermediates of lignification) or play a role in the general defense against herbivores and plant pathogens (Kruse et al. 2000). Allelochemicals can be present in several parts of plants including roots, rhizomes, leaves, stems, pollen, seeds, and flowers. Allelochemicals are released into the environment by root exudation, leaching from aboveground parts and volatilization and/or by decomposition of plant material (Fig. 2.1) and microorganisms may also play a role in the production of these chemical inhibitors (Rice 1984).

The most important allelochemicals include phenolic compounds, flavonoids, terpenoids, alkaloids, steroids, carbohydrates, and amino acids (Kruse et al. 2000). Phenolic compounds are some of the most widespread molecules among plant secondary metabolites, and are of great significance in plant development. They are involved in diverse processes including resistance to biotic and abiotic stress. Additionally, they serve as flower pigments, act as constitutive protection agents against invading organisms, function as signal molecules, act as allelopathic compounds, and affect cell and plant growth (Makoi and Ndakidemi 2007). Indeed, several allelopathic compounds may be released from a plant and may act together to cause an allelopathic effect. When susceptible plants are exposed to allelochemicals, germination, growth, and development may be affected. The most frequently reported gross morphological effects on plants are inhibited or retarded seed germination, effects on coleoptile elongation, and on radicle shoot and root development (Kruse et al. 2000).

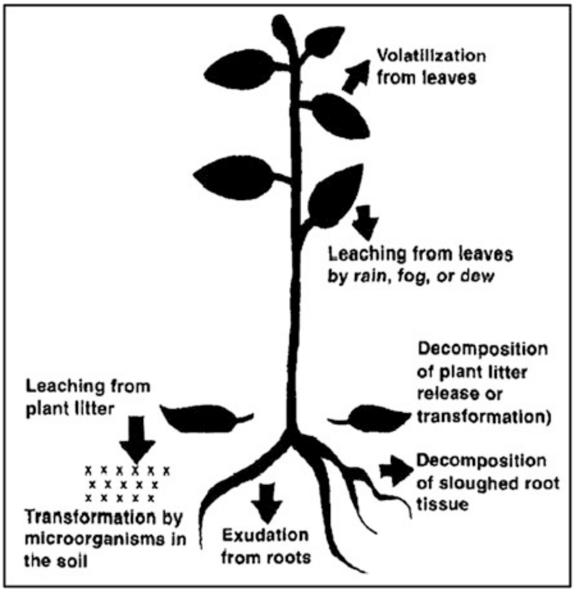

Fig. 2.1 Routes of allelochemicals release to the environment (Rice 1984)

Several researchers have suggested that allelopathic compounds play important roles in the determination of nutrient dynamics, mycorrhizae, soil chemical characteristics, microbial ecology, plant diversity, dominance, invasion, succession, and climax of natural vegetation (e.g., Rice 1984; Lawrence et al. 1991; Chou 1999; El-khatib et al. 2004; Nissanka et al. 2005). Wardle et al. (1998) stated that plants with allelopathic potential against other organisms apparently induce net changes in ecosystem properties, which may in turn affect the plant community in the long run.

Rice (1984), Wardle et al. (1998), Chou (1999), Kruse et al. (2000), and Hierro and Callaway (2003) have reviewed many ecological aspects of allelopathy, including allelochemical effects on plants, insects, animals, and on microbial symbioses, role of allelopathy in plant biodiversity, invasion, and plant succession, spread of allelopathic traits between species, allelopathy, and competition, environmental risk assessment of allelopathic plants, etc. This chapter is based on a literature review on allelopathy from an ecological impact point of view and aims to update and consolidate the previous allelopathy reviews. Moreover, some more important ecological consequences of allelopathic plants, including plant biodiversity, microbial symbiosis, invasion, and plant succession, are discussed. First, we consider role of allelopathy in plant biodiversity and dominance. Second, effects on microbial symbiosis (mycorrhizae and nitrogen fixing bacteria) are discussed briefly. We then have illustrated the role of allelopathy in plant invasion within natural ecosystems and finally significant contribution of allelopathy to the process of plant succession is illustrated.

2.2 Effects on Plant Biodiversity

Several experiments have been done on the role of allelopathy in biodiversity, including plants, bacteria, fungi, and other soil microorganisms, demonstrating the importance of allelopathy in changing biodiversity within various ecosystems (El-Khatib 2000; Lawrence et al. 1991; Chou 1999; Heisey 1996; Nissanka et al. 2005). Species richness and diversity are important indicators of ecosystem function and may be related to plant community resistance to invasion by non-indigenous species. It is suggested that the allelopathic activity of a plant may reduce both number and population size of other species by reducing their competitive ability (Chaves and Escudero 1997).

Chou (1999) reviewed the roles of allelopathy in plant biodiversity and noted many examples from this subject. For example, after the deforestation of coniferous or hardwood forests, a pasture grass, kikuyu grass (*Pennisetum clandestinum*) was transplanted onto the land. The grass was quickly established within 6 months. Significant suppression of weed growth by the kikuyu grass was found; however, the growth of coniferous or hardwood plants was not suppressed but stimulated (Chou 1999). Chester and Inderjit (2001) stated that in addition to their adverse effects on growth and yield of numerous crop species, many troublesome weeds such as mugwort (*Artemisia vulgaris*) and lantana (*Lantana camara*) influence biodiversity. In a field study, El-Khatib (2000) reported that *Alhagi graecorum* exhibited phytotoxic activity on the tested species. Accordingly, water-borne allelopathic compounds may be released from *A. graecorum* into the environment and suppress the growth of its associates where they were not able to compete with *A. graecorum* in the field, so the latter species become dominant. El-khatib et al. (2004) noted that allelopathy has a role in the ecology of *Chenopodium murale*. They studied the effects of shoot and root extracts of *C. murale* on seedling establishment, plant growth, and metabolite production of four target species (*Melilotus indicus*, *Trifolium alexandrinum*, *Triticum pyramidal*, *Lycopersicon esculentum*, and *Cucumis sativus*) and found that all studied traits were inhibited in these species. They concluded that allelopathic potential of *C. murale* plays significant role in its wide geographic distribution by inhibiting the growth of some target species.

Allelopathic plants may induce genetic changes within associated plant populations. *Ailanthus altissima*, tree of heaven, (Simaroubaceae), is located among top 25 alien invasive plants and poses an imminent threat to plant health and biodiversity in Britain. Heisey (1996) isolated a quassinoid compound, ailanthone, from bark and foliage of *A. altissima*. The compound is reported to possess pre- and post-herbicidal activity in greenhouse trials. Ailanthone exhibited a strong herbicidal activity when sprayed on soil before the seed germination. It, however, also had dramatic effects when sprayed onto seedlings after their emergence from soil.

Lawrence et al. (1991) studied allelopathic potential of *A. altissima*. They reported that release of allelochemicals from that seems to be responsible for altering the genetic pool of susceptible neighboring plant species. Both close

Table 2.1 Influence of *Pinus* and natural forests at Loolkandura on soil mycorrhizal, fungus, bacterial, earthworm populations, parasitic and non-parasitic nematodes, and microbial activity of soil

	Forest type Pine Forest	Natural Forest
Number of mycorrhizal spores/100 g soil	1450^a	
Population (Growth area g^{-1} soil)		
Fungus	62.33^a	151.67^b
Bactria	31.66^a	30.00^a
Number of earth worm (m^{-2})	44^a	200^b
Parasitic		
Pratylenchus loosi	ND	ND
Pin nematode	ND	ND
Non parasitic		
Free living	11.5^a	19.0^b
Microbial activity CO_2 (mg day^{-1})	105^a	410^b

Means with same letters are not significantly different at 5 % probability level, *ND* (not detected)
Source Nissanka et al. (2005)

(<1 m) and distant populations (>10 m) of *Tridens flavus* were inhibited by Ailanthus toxins, but the distal population includes a class of highly susceptible individuals not present in the proximal population. They opined that the genotypes sensitive to the allelochemicals have been removed from the gene pool of the proximal population by selection.

Nissanka et al. (2005) studied allelopathic influences of *Pinus caribea* on vegetation regeneration and soil biodiversity and stated that allelochemicals released by *Pinus* plants have considerable effects on floral and faunal species diversity. Number of plant species, families, total number of individuals per unit area, and canopy height and number of strata's in the canopy were greater in the natural/semi-natural forests at both locations than in *Pinus* forests. Also the soil microfloral density measured as mycorrhizal spore counts and fungus population was reduced by 54 % and 60 %, respectively, in the *Pinus* soil compared to natural forest. However, the soil bacterial population was similar in both forest types. Soil faunal diversity and density were also reduced significantly under *Pinus* vegetation compared to natural forests (Table 2.1). Earthworm and non-parasitic nematode populations in soil were also reduced by 78 % and 40 %, respectively, under *Pinus* forests. However, parasitic nematodes were suppressed under both forest types. Microbial activity was four times higher in the natural forest compared to *Pinus* forest, indicating very high biological diversity in the soil under the natural forest cover (Table 2.1).

Pinus root exudates can inhibit the mycorrhizal associations of other plant species and other type of mycorrhizal associations such as vesicular–arbuscular mycorrhizae (VAM). VAM associations were found in all ten under-storey plant species in both *Pinus* plantation and natural forests. However, mean percentage

Table 2.2 Plant species selected to study VAM associations, their important value index (IVI), and mean percentage of occurrence of VAM of dominant understorey species in *Pinus* and semi natural forests at Hantana range

Species	Family	IVI	Occurrence of VAM in forest understorey (%)	
			Pinus	Semi-natural
Panicum maximum	Poaceae	46.30	15.11	74.22
Psidium guineese	Myrtaceae	27.89	9.78	30.67
Eupatorium odoratum	Asteraceae	16.4	18.67	32.00
Hedyotis nitida	Rubiaceae	8.18	19.56	29.78
Axonopus compresses	Poaceae	8.12	12.00	26.68
Wikstroemia indica	Thymaliaceae	7.14	8.00	19.11
Eleutheranthera ruderalis	Poaceae	7.30	17.33	56.89
Mimosa pudica	Fabaceae	6.26	14.67	47.56
Vernonia cinerea	Asteraceae	6.06	24.44	84.89
Ageratum conyzoides	Asteraceae	5.42	17.78	44.89

Source Nissanka et al. (2005)

occurrences of VAM for all the ten species were significantly different and number of VAM present were lower in all species of *Pinus* plantations than the same species from natural forests (Table 2.2). Finally, Nissanka et al. (2005) concluded that very low diversity and population densities of floral and faunal species may be associated with the allelochemical released by *Pinus* plants.

Recently, Sheley et al. (2007) studied influence of herbicide application (clopyralid plus 2, 4-D, glyphosate, and fosamine) at different application rates and timings on richness and diversity of total species, total native species, and total non-native species within a Russian knapweed (*Acroptilon repens,* an allelopathic invasive species) infested plant community. They reported that only the glyphosphate treatment controlled Russian knapweed effectively, so total species richness (4.6 species m^{-2}) increased as decreasing Russian knapweed population.

In conclusion, allelopathy may have great influence on floral and faunal species diversity, thereby influencing invasion and dominance of plants within natural ecosystems. Studying effects of allelopathy on biological diversity can help to understand many common ecological phenomena such as succession and plant invasion.

2.3 Effects on Microbial Symbioses

Mycorrhizae, which result from a symbiosis between fungi and plant roots, are directly involved in plant mineral nutrition, the control of plant pathogens, and drought tolerance. Most horticultural and crop plants are symbiotic with arbuscular mycorrhizal fungi. Mycorrhizal fungi appear to be the most important telluric organisms to consider. One of the consequences of allelopathy in natural ecosystem is its effect on soil microbial population, their activity, and symbiosis with other plants. Allelochemicals may affect plant species by inhibiting their microbial symbionts such as mycorrhiza and nitrogen-fixing bacteria. Yamasaki et al. (1998) reported that under natural conditions, rate of mycorrhizal infection in seedlings of black spruce (*Picea mariana*) growing close to the allelopathic shrub *Kalmia angustifolia* was significantly lower than seedlings further away. Also, they noted that the presence of *K. angustifolia* reduced the growth of specific parts of the seedling (foliage, twigs and stem) as well as foliage concentrations of nitrogen and phosphorus. *K. angustifolia* invades many *P. mariana* plantations in central New Foundland and at many of these regions an increase in *K. angustifolia* cover is associated with chlorosis and decreased height of *P. mariana.*

In another study, Nilsson et al. (1993) reported that aqueous extracts of crowberry (*Empetrum hermaphroditum*) reduced the spread of mycorrhizal infection in seedlings of Scots pine (*Pinus sylvestris*). Also, the N uptake by Scot pine seedlings was reduced when extract of crowberry was added. The negative effect on N uptake was particularly evident on seedlings infested with mycorrhiza. They concluded that extract of crowberry reduced the ability of mycorrhiza to take up N. Similarly, decomposing leaves of nodding thistle (*Carduus nutans*) affect negatively the symbiotic nitrogen fixation of white clover; *T. repens*, in pastures dominated by white clover and perennial ryegrass, *Lolium perenne* (Wardle et al. 1998).

Weston and Putnam (1985) reported that compounds released from both living and herbicide-killed plant material of *Elytrigia repens* inhibit the symbiosis between *Rhizobium* and legume species. Both living and herbicide killed *E. repens* inhibited the nodulation and development of legume species. Their further laboratory studies indicated that compounds from *E. repens* are particularly inhibitory to root hair formation, which subsequently prevents the infection by *Rhizobium.* They found that compounds inhibiting root hair formation did not inhibit the growth of several species of *Rhizobium* and concluded that the morphological changes induced by allelochemicals can reduce nodulation in legume species.

2.4 Effects on Plant Invasion

Several studies have been done on the role of allelopathy in plant invasion in natural ecosystems (Bais et al. 2003; Callaway and Vivanco 2005a; Hierro and Callaway 2003; Zedler and Kercher 2004) demonstrating the importance of allelopathic potential in invasion and dominance of plants (especially exotic plants). Several examples are presented in this part.

International Union for Conservation of Nature and Natural Resources (IUCN) defines *alien invasive species* as an alien species, which becomes established in natural or seminatural ecosystems or habitat, an agent of change, and threatens native biological diversity.

Many of the world's most ecologically devastating exotic invaders are much more successful abroad than at home. Why many exotic plant species create virtual monocultures in invaded regions but not in their native regions remains one of the most important mysteries in ecology (Callaway et al. 2005b). In one of the most comprehensive reviews on allelopathy and invasion, Hierro and Callaway (2003) noted that the primary hypothesis for the astonishing success of many exotics as community invaders relative to their importance in their native communities is that they have escaped the natural enemies that control their population growth (the natural enemies hypothesis). However, the frequent failure of introduced biocontrol, weak consumer effects on the growth and reproduction of some invaders, and the lack of consistent strong top-down regulation in many natural ecological systems indicate that other mechanisms must be involved in the success of some exotic plants. One mechanism may be the release by the invader of chemical compounds that have harmful effects on the members of the recipient plant community (i.e., allelopathy). The primary rationale for considering allelopathy as a mechanism for the success of invaders is based on two premises. First, invaders often establish virtual monocultures where diverse communities once flourished, a phenomenon unusual in natural communities. Second, allelopathy may be more important in recipient than in origin communities because the former are more likely to be naive to the chemicals possessed by newly arrived species (Hierro and Callaway 2003). Also, Callaway et al. (2005b) noted that these allelopathic weapons may be relatively ineffective against their natural neighbors because of adaptation by natural neighbors, but the same biochemicals may be highly inhibitory to newly encountered plants in invaded communities because of a lack of adaptation. Resistance and adaptation in plants evolve rapidly in response to man-made chemical herbicides and particular chemical composition of neighboring plants.

Prati and Bosdorf (2004) reported that *Alliaria peteolata*, a devastating invader of North American temperate forests also had stronger chemical effects on *Geum laciniatum*, a new North American neighbor, than on *G. urbanum,* its natural European neighbor. In a related experiment, although not using invasive species, Mallik and Pellissier (2000) found that the Eurasian *Vaccinium myrtillus* generally had stronger biochemical effects on the North American *P. mariana* than on the Eurasian *P. abies*.

Most of the works on the role of allelopathy in plant invasions have been done on the invasive *Centaurea* species (*Centaurea maculosa* and *C. diffusa*). These invasive species produce chemicals in their root exudates with powerful toxic effects on other plants and soil microbes (Callaway and Vivanco 2005a). *C. maculosa* is a Eurasian species in the Asteraceae that invades North American grasslands. It reduces native biodiversity and rangeland forage quality (Perry et al. 2007). A possible role of allelopathy in *C. maculosa* invasion has received considerable attention. *C. maculosa* exudes large amounts of (±) catechin from its roots, whereas *C. diffusa* roots exude 8-hydroxyquinoline. Both species can establish virtual monocultures, but only in the regions where they invade. At home (Eurasia) they are far less abundant. In a fascinating twist, both *Centaurea* species and their allelochemicals have much stronger effects on species native to invaded regions in North America than related species in their communities of origin. These biogeographical differences in the effectiveness of root-exuded biochemicals

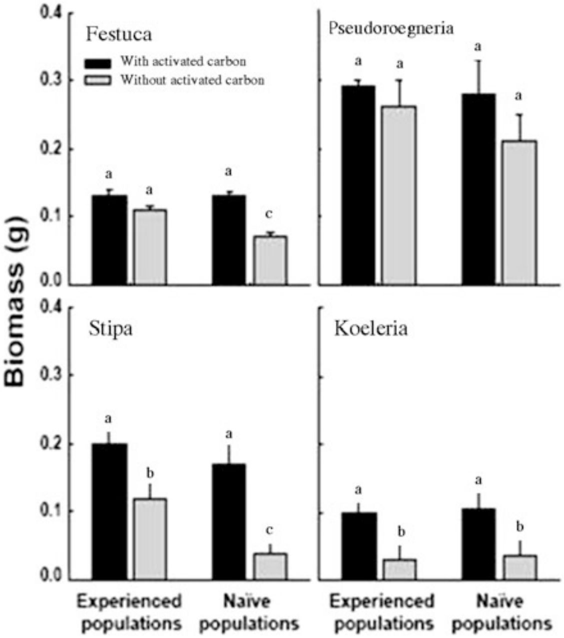

Fig. 2.2 Total biomass of grasses grown from seeds collected from North American native grasses that had either experienced and survived invasion by *C. maculosa* or had not experienced invasion by *C. maculosa*. These plants were grown in competition with *C. maculosa* in sand or in sand modified with activated carbon to ameliorate the allelopathic effects of *C. maculosa*. Error bars represent one standard error, and different letters above the bars designate significant differences for a one-way ANOVA conducted for that particular species. (Callaway and Vivanco 2005a)

suggest a new theory for the success of some invasive plants, "the novel weapons hypothesis" (Callaway and Vivanco 2005a).

Callaway and Vivanco (2005a) found that individuals of some North American species that had survived extensive invasion by *C. maculosa* had higher tolerances to the allelopathic effects of the invader than individuals from communities that had not experienced invasion. Some native species grown from the seed of individuals that survived *Centaurea* invasion were more resistant to general competitive effects of *Centaurea*, the root exudates from *Centaurea*, and to (±)-catechin. For *Festuca* and *Stipa*, plants grown from seed in competition with *C. maculosa* and without activated carbon in the soil were significantly smaller than those grown with activated carbon (Fig. 2.2).

More importantly, *Festuca* and *Stipa* grown from the seeds of naive maternal plants in competition with *C. maculosa* were smaller than those grown from the seed of experienced maternal plants, and activated carbon eliminated these differences, suggesting the possibility that selection for tolerance to *C. maculosa* may have occurred.

In another experiments, Callaway et al. (2005b) have found that not all North American natives are equally susceptible to the competitive effects of *C. maculosa. Gaillardia grandiflora and Lupinus argenteus* are good competitors against *C. maculosa*. Furthermore, native grasses are much more abundant near *Lupinus* in areas heavily invaded by *Centaurea*. In a field experiment native *Pseudoroegneria* and *Festuca* transplanted within 10 cm of a *Lupinus* plant grew significantly larger than those planted more than 1 m from *Lupinus* (Fig. 2.3).

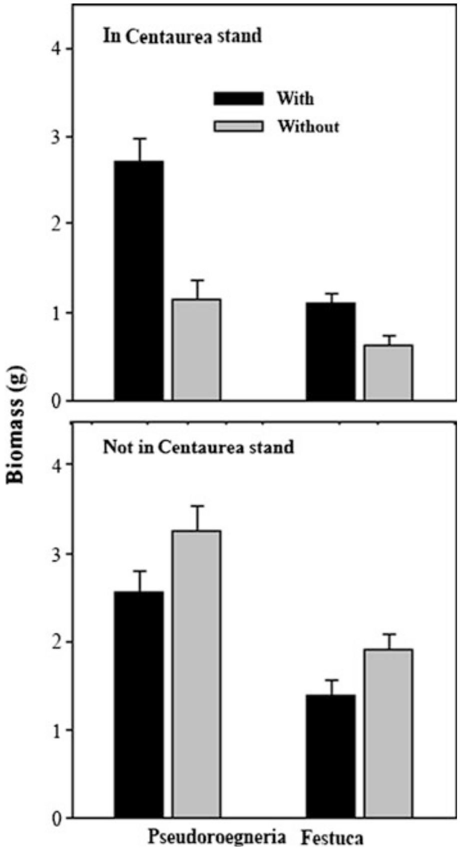

Fig. 2.3 Aboveground biomass of *P. spicata* and *Festuca idahoensis* transplanted either next to or far from *L. sericeus*, and either in intermountain grassland heavily invaded by *C. maculosa* or in grassland with ≈2 % cover of *Centaurea*. Error bars show 1 SE (Callaway et al. 2005b)

Recently, Perry et al. (2007) conducted extensive research on the measurements catechin concentrations in soil. They examined soil catechin in many sites and over one-year time course at one site (examining catechin in 402 samples from 11 *C. maculosa* sites) to better assess spatial and temporal variation in catechin concentrations in *C. maculosa* soils. They noted that the importance of (±)-catechin to *C. maculosa* ecology depends in part on whether sufficient catechin concentrations occur at appropriate times and locations within *C. maculosa* soil to influence neighboring plants.

Apart from *Centaurea* species, the role of allelopathy in invasion of other plant species has also been studied. In one of the most comprehensive reviews on allelopathy and plant invasion, Hierro and Callaway (2003) stated that the literature linking allelopathy to exotic invasion includes some of the best known plant invaders in the world, including *E. repens, Bromus tectorum,* several *Centaurea* species, *Cirsium arvense*, *Cyperus rotundus*, *Euphorbia esula*, *Parthenium hysterophorus, Setaria faberii*, and *Sorghum halepense*. Some examples of these invasive plants are described below.

The release of allelochemicals from plants known as aggressive colonizers (e.g. *E. repens* and *Vulpia myuros*) has led to suggest that allelopathy is involved in successful invasions. However, the actual importance of the release of allelochemicals by these colonizer plants has rarely been demonstrated under natural conditions (Kruse et al. 2000).

Lantana camara is another important species, and its allelopathic potential may be an important factor to invade, establish, and form dominant components within certain susceptible ecosystems. In an experiment, Gentle and Duggin (1997) attempted to distinguish between suppressed seedling growth caused by possible phytotoxins and density-dependent resource competition, respectively. Their results showed that *L. camara* is capable of interrupting the regeneration processes by decreasing germination, reducing early growth rates, and reducing survival of two indigenous species by allelopathy. These changes are expected to lead to disruption of community development because *L. camara* can also aggressively compete with indigenous seedlings.

Similarly, it has been reported that allelopathic potential of nodding thistle, one of the most noxious weed species, can be contributed to the establishment of this species in pastures (Wardle et al. 1998). The release of allelochemicals from decomposing leaves of nodding thistle has been reported to be involved in the establishment of this species in pastures of *L. perenne* and *T. repens* in New Zealand. Initially, bare patches in the pasture allowed seed of nodding thistle to germinate. The allelochemicals suppressed *T. repens* and thereby provided new bare patches where seeds of nodding thistle can germinate. Bioassays have indicated that the decomposing material of *C. nutans* is allelopathic and that the nature of this allelopathy is highly selective. Leguminous species appeared to be more sensitive than grass species. The suppression of *T. repens* seemed to be caused by a reduction in *T. repens* nodulation whereby the symbiotic nitrogen fixation became adversely affected.

Zedler and Kercher (2004) stated that although the case for allelopathy in wetland invasive species is weaker, phytotoxic compounds have been isolated in several *Typha* species and experiments with root tissue extracts of invasive *Typha domingensis* have revealed detrimental effects on the germination and growth of some species.

Clearly, understanding allelopathy may provide the potential for a new approach to combating exotic plant invasion, and development of native resistance to allelopathic chemicals. Although most of allelopathy-related studies from ecological point of view are related to plant invasion in natural ecosystems than other ecological subjects, allelopathy is worthy of more rigorous biochemical and ecological research regarding invasiveness.

2.5 Effects on Plant Succession

Allelopathy makes a significant contribution to the process of plant succession (Numata 1982). In the Swedish boreal forest, crowberry forms extensive clones in postfire successions on acid soils. Regeneration of Scots pine in such crowberry-dominated areas has often failed. Explanations have focused harsh climate, unfavorable soils and dense plant cover until it was suggested that chemical inhibition could be involved (Zackrisson and Nilsson 1992). In experiments it was shown that leaf exudates from crowberry strongly inhibited seed germination of Scots pine both in field experiments and under controlled conditions (Nilsson 1994). The toxin responsible for the inhibition was batatasin III, which in its purified form strongly inhibited seed germination of Scots pine. Batatasin III was produced in secretory gland cells in the leaves of crowberry (Wallstedt et al. 1997; 1998).

The effect of crowberry on Scot pine regeneration slows down the succession toward coniferous forest, which otherwise would be the natural climax vegetation in boreal areas. Under natural conditions this effect would be prevented by forest fires, which occur frequently enough to prevent the extensive dominance of the slow growing crowberry shrub. However, anthropogenic influence has decreased the natural fire frequency as well as the affected area in order to protect the wood production, with the consequence that crowberry shrubs become dominant and thereby a problem for forest establishment (Wallstedt et al. 1997).

Ragweed (*Ambrosia artemisiifolia*) is a dominant species in the first year of old field succession but rarely persists for more than 2 years. Jackson and Willemsen (1976) reported that ragweed and wild radish (*Raphanus raphanistrum*) failed to become reestablished in plots cleared of second stage perennial vegetations (dominated by *Aster pilosus*), despite the large number of seeds of these primary invaders in the soil. Their experiments showed that field soil from the second stage of succession inhibited the growth and germination of ragweed and wild radish, and concluded that the vegetation change from the first to the second stage of succession may be mediated at least partially by an allelopathic response.

Fernandez et al. (2006) tested extracts of *Pinus halepensis* against two target species (*Lactuca sativa* L. and *Linum strictum* L.) with aqueous extracts obtained from different organs (root and needle) taking into account the individual age (±10, ±30 and >60 years old). They reported that root and needle extracts affected differently germination and growth of the two target species, the responses varying with concentration of extracts, age, and organs tested. The strongest inhibitory effect was observed on the germination and growth of *L. strictum*, exposed to needle extracts of young *P. halepensis* (±10 years old), and root extracts of older *P. halepensis* (>30 years old). These extracts contained several phenolic acids (e.g. 4-hydroxybenzoic acid and p-coumaric acid), which are known as allelochemicals and their concentrations vary with age and organ tested. They concluded that *P. halepensis* could influence secondary succession through the release of potential allelochemicals in the environment by leaf leachates or root exudates.

Allelochemical inhibition of ectomycorrhiza forming fungi and other symbiotic fungi is another way to influence three stages in succession that relies on symbiosis (Nilsson et al. 1993; Wallstedt et al. 1997). Control of the succession can also take place in a more indirect manner through allelopathic inhibition of nitrogen-fixing microorganisms, e.g., *Rhizobium spp.* and many genera within the Cyanobacteria. Inhibition of nitrification and ammonification is another way of controlling the amount of plant available nitrogen. Such an inhibition can be advantageous to species tolerant to low nitrogen availability (Rice 1984). Such tolerance is typical for species belonging to early succession stages.

Another example of allelopathic plants having influence on succession has been hypothesized by Rice (1984) to explain why the first pioneer weed stage is so rapidly replaced by prairie threeawn (*Aristida oligantha*) in abandoned fields in Oklahoma and Kansas. Rice explained the observation with self-elimination due to production of toxins in the species belonging to the first pioneer stage. *A. oligantha,* being insensitive to these toxins, could replace the pioneer weed stage much faster than would be the case if this community level autotoxicity was not present (Kruse et al. 2000).

In the southern Appalachian Mountains, *Rhododendron maximum* L. is the dominant subcanopy evergreen species. Approximately 30 million hectares of the southern Appalachian Mountains are occupied by *R. maximum.* This subcanopy evergreen shrub forms extensive thickets, near streams and on north slopes, reaching a height of 3–6 m. On north-facing slopes these thickets form a mosaic of ~40 % cover. There is clear evidence that the coverage of *R. maximum* thickets has been increasing over the past 30 yrs. For example, the area occupied by *R. maximum* thickets in the Coweeta basin has increased from 14.8% in 1976 to 31.7% in 1993 (Dobbs 1995). The increase in abundance of this species is a concern for forest managers because recruitment of canopy tree seedlings under *R. maximum* thickets is substantially inhibited. One of the mechanisms by which seedlings could be inhibited is an allelopathic effect of decomposing litter or leachate from the canopy of *R. maximum* on seed germination, root elongation, or mycorrhizal colonization. Nilsen et al. (1999) tested the allelopathic potential of *R. maximum* establishment and survival of canopy tree seedlings. They concluded that *R. maximum* litter can have an allelopathic effect on seed germination and root elongation of bioassay species as well as some ectomycorrhizal species. However, this allelopathic effect is not manifested in field sites and is not likely to be an important cause for the inhibition of seedling survival within thickets of *R. maximum.* This study clearly indicated that direct allelopathic influences of *R. maximum* on seed germination, initial root growth, or ectomycorrhizal growth cannot be considered an important factor associated with the inhibition of seedling survival under *R. maximum.* Since a majority of native species require mycorrhizal synthesis for survival in the subcanopy, allelopathic inhibition of this colonization could reduce seedling survival. Also, the release of allelochemicals in *R. maximum* litter may inhibit the normal action of bacteria and invertebrates resulting in reduced soil nutrient availability. Lower soil nutrient availability is a characteristic of forests where *R. maximum* is present and may be an important process for seedling survival. In fact, the combination of resource limitation (nutrients and light) and inhibition of mycorrhizal synthesis may be the predominant process regulating canopy tree seedling survival in the southern Appalachian Mountains (Nilsen et al. 1999).

Although this study did not discern a significant allelopathic influence in the field, there are examples in other forest situations where allelopathy may be an important process for shrub inhibition of canopy tree seedlings. For example, there is strong evidence that allelopathy is an important mechanism by which black spruce seedlings are inhibited by *K. angustifolia* in Newfoundland (Mallik 1995). Moreover, toxicity *of K. angustifolia* may be manifested through an inhibition of ectomycorrhizae (Yamasaki et al. 1998). Other explanations for the reduced seedling success in the non-indigenous grasses could involve allelopathy (Callaway and Aschehoug 2000).

The importance of allelopathy in competition between species is not fully understood (Kruse et al. 2000). At least in a few cases it has been shown that the release of allelochemicals is important for the dominance of the donor species. This, apart from becoming dominant, also is able to control or at least to some degree slow down the natural succession rate. The control can be by direct inhibition of the germination of woody species, inhibition of symbiosis, or through control of available nitrogen by inhibition of nitrogen-fixing microorganisms. However, it is also possible that autotoxicity can speed up succession due to faster elimination of some succession stages (Kruse et al. 2000).

2.6 Conclusion

Several researchers have suggested that allelochemicals play important roles in the determination of nutrient dynamics, mycorrhizae, soil chemical characteristics, microbial ecology, plant diversity, dominance, invasion, plant succession, and climax of natural vegetation. Biodiversity (including plants, bacteria, fungi and other soil microorganisms), as one of the most important ecological index, may be influenced by allelopathy. Allelopathy may have great influence on flora and fauna species diversity, thereby influencing invasion and dominance of plants within natural ecosystems. Another consequence of allelopathy in natural ecosystem is its effect on soil microbial population, their activity, and symbiosis with other plants. Allelochemicals may affect plant species by inhibiting their microbial symbionts such as mycorrhiza and nitrogen-fixing bacteria. *Empetrum hermaphroditum*, *Carduus nutans*, *E. repens*, and *K. angustifolia* are among important plant species showing inhibitory effects on microbial symbiosis, thereby affecting the growth and development of other plant species.

Plant invasion is another important phenomena influenced by allelopathic plants. One mechanism of successful invasion is the release of chemical compounds by the invader that have harmful effects on the members of the recipient plant community. Most of the works on the role of allelopathy in plant invasions has been done on the invasive *Centaurea* species (*C. maculosa* and *C. diffusa*). Some of the best known allelopathic plant invaders in the world, include *E. repens,* several *Centaurea* species, *C. arvense*, *C. rotundus*, *Euphorbia esula*, *Parthenium hysterophorus, Setaria faberii*, *Sorghum halepense, V. myuros, L. camara*, and *C. nutans*.

Another ecological consequence of allelopathy is its effect on plant succession, which makes a significant contribution to it. The effect of *E. hermaphroditum* on

Scots pine regeneration, which slows down the succession toward coniferous forest, and replacing first pioneer weed stage so rapidly by *A. oligantha,* in abandoned fields in Oklahoma and Kansas, are among apparent examples regarding succession.

Finally, allelopathy may act directly on plants and other organisms and indirectly through alteration of soil properties, nutrient status and altered population, and/or activity of harmful or beneficial organisms such as microorganisms, insects, nematodes, etc. Therefore, allelopathic plants may have wideranging effects and consequences in ecosystems. Clearly, studying ecological effects of allelopathy in natural ecosystems help to understand complex relationships among plant communities and managing these communities as well as possible.

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Chapter 3
Evidences of Bryophyte Allelochemical Interactions: The Case of *Sphagnum*

Geneviève Chiapusio, Vincent E. J. Jassey, M. Iftikhar Hussain and Philippe Binet

Abstract In most terrestrial ecosystems, allelochemical interactions are involved in vascular plants. Nevertheless, bryophytes represent also a crucial group found in many ecosystems with a specific morphology and physiology (e.g. secondary metabolism). Among bryophytes, *Sphagnum* genus is of particular interest because they form a dense homogeneous carpet which is slowly decomposed (the peat) in peatlands. Such ecosystems represent a terrestrial sink of carbon and so are crucial to be studied, especially under a climate change. Objectives of this chapter were (1) to synthesize current bryophyte allelochemical interactions and (2) to illustrate recent research on *Sphagnum* with the case of *Sphagnum fallax* phenolics (production and degradation) recovered in a french peatland. The top layer of living *Sphagnum* represents the active allelopathic part where water-soluble phenolics were mostly recovered. Their concentrations were found to change along the seasons. The transformation of phenolic compounds is performed by an enzymatic system O_2 (phenoloxidases) or H_2O_2 (peroxidases) dependent. *Sphagnum*-peroxidases constituted the main oxidative system and fungal phenoloxidases were proposed to be regulated by phenolics. Moreover, *Sphagnum* was able to regulate its secondary metabolism under a climate forcing by decreasing its phenolic concentrations. Allelopathic potential of *Sphagnum* phenolics was stated with their role in the microdistribution of associated *Sphagnum* microorganisms. Finally, *Sphagnum* extracts also strongly delayed *Pine* and *Lolium* germination seeds and inhibited *Lolium* radicle growth and delayed *Raphanus* and *Pinus* radicles. Ecological and agronomic perspectives of *Sphagnum* extracts are discussed.

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3.1 Introduction

Since the early 1970s, research efforts on allelopathy have increased considerably. Because allelopathy meets current societal demands for environmentally sound approaches to agriculture, there is a growing interest in discovering, and understanding allelochemicals produced by plants. One way to identify allelopathic interactions is to study plants in their ecosystems. Numerous ecosystems have been studied through allelochemical interactions such as forests (Souto et al. 2000) or grasslands (Viard-Crétat et al. 2009). They involved mostly gymnosperms and angiosperms rather than nonvascular plants. Bryophytes represent one successful group of plants in terms of geographical distribution on all continents, habitat diversification, and number of species (Slack 2011). Even if bryophytes are known to produce chemicals which make mosses very unattractive for herbivores, little is known about the different roles of phenolics excreted by mosses in their surroundings. Allelopathy represents then one potential ecological interaction among all complex interactions involved in the functioning of ecosystems.

Among terrestrial ecosystems, peatlands are dominated by bryophytes of *Sphagnum* genus which forms a homogeneous carpet. The accumulated peat is mainly dominated by remnants of *Sphagnum*. Indeed, peatlands are characterized by the ability to store atmospheric carbon in the long-term accumulation of partially decomposed organic matter in form of decaying vegetation. The accumulation of organic matter in peatland is the result of production and decay of *Sphagnum* tissues with recalcitrant carbon such as polyphenols. The transformation of phenolic compounds is performed by an enzymatic system O_2 (phenoloxidases) or H_2O_2 (peroxydases) dependent. The interplay polyphenols/phenoloxidases is then a key process in peatland functioning. Recent research on the organo-chemical composition of *Sphagnum* clarified the ability of *Sphagnum* to outcompete other plants for light by creating acidic nutrient poor cold and anoxic conditions (Van Breemen 1995). The role of polyphenols on peatland functioning is mostly associated with the low decomposition of peat, which is of great importance for the peat storage function (Verhoeven and Liefveld 1997). Surprisingly, the exact role of phenolics remains understudy in growing *Sphagnum* plants. Moreover, a few studies focused on allelopathic interactions (Michel et al. 2011).

Recently, boreal peatland is of particularly interest, because it currently represents a terrestrial sink of carbon with approximately one-third of the world's organic carbon (390–455 Pg) (Gorham 1991; Moore 2002). The expected increase of air temperatures in boreal regions is predicted to lead to a destabilization of peatland carbon stores (Smith et al. 2004; Strack 2008). *Sphagnum* represents the crucial plants to study the effect of elevated temperature on peatlands. Most of the studies aim at understanding effects of temperature on the peat decomposition, but not on living *Sphagnum*. The study of *Sphagnum* phenolic metabolism under a climate forcing remains a challenge even if difficult and complex.

In this chapter, we present the main characteristics of bryophytes involved in allelochemical interactions. Then, the case of *Sphagnum* genus will fully illustrate why bryophytes is of interest to allelopathy based on their phenolic production, degradation, and variation.

3.2 Terrestrial Bryophytes

3.2.1 Morphology

Bryophytes represent an independent branch of the plant kingdom with more than 16,000 species, taking up a position between the algae and the pteridophytes (Slack 2011). From a taxonomic point of view they are divided into three classes namely hornworts (Anthoceratae), liverworts (Hepaticae), and mosses (Bryatae). Bryophytes lack the roots, the xylem, and the phloem of vascular plants. The dominant stage is the haploid green autotrophic gametophyte rather than the diploid sporophyte which remains parasite of the gametophyte. Bryophytes play a fundamental ecological role in many terrestrial ecosystems especially in rain forest and cold biomes where they are abundant (Tan and Pocs 2000). Many species are able to live in nutrient poor conditions and are adapted to respond physiologically to intermittent periods favorable to photosynthesis (Slack 2011).

3.2.2 Allelochemical Interactions

Studies in various plant communities as well as greenhouse experiments have demonstrated that germination and/or seedling emergence of vascular plants are affected by mosses (Asakawa 1990). The effect may be either positive or negative depending on the habitat and the species. The positive effects are generally explained by the moisture conditions favorable to germination and the negative ones by the low light intensity, the drier microhabitat and allelopathy (Zamfir 2000). Thus, interactions between bryophytes and vascular plants comprise a large spectrum of relations including resource competition, suppression, facilitation, and allelopathy. Among these effects allelopathy seems to be the most controversial mostly because sparse experiments were conducted and among them, differences were noticed between greenhouse and field experiments (Soudzilovskaia et al. 2011). Nevertheless, original allelochemical interactions were revealed either with native or laboratory test species (Table 3.1). In boreal ecosystems, Soudzilovskaia et al. (2011) assumed that bryophytes exclusively affect germination and very early establishment but do not influence the fitness of established seedlings. Nevertheless, nothing is much known about the importance of interspecific differences among bryophytes with respect to their effect on vascular plants or the functional traits responsible for such effects.

Table 3.1 Examples of laboratory experiments on allelochemical interactions between Bryophytes (donor plants) and vascular plants (target plants)

Bryophytes "donor plants"	Vascular plants "target plants"	Allelochemical effects	References
Hylocomium splendens, *Pleurozium schreberi,* *Dicranum scoparium,* *Polytrichum strictum,* *Barbilophozia lycopodioides,* *Ptilidium ciliare*	*Betula pubescens,* *Pinus sylvestris,* *Epilobium angustifolium,* *Solidago virgaurea,* *Festuca ovina*	Germination and growth inhibition	Soudzilovskaia et al. (2011)
Rhynchostegium pallidifolium	Cress, lettuce, alfafa	Growth Inhibition	Kato-Noguchi et al. (2010)
Sphagnum palustre, *Racomitrium japonicum,* *Dicranum japonicum,* *Hypnum plumaeforme*	Lettuce	Growth Inhibition	Tsubota et al. (2006)
Hypnum plumaeforme		Momilactone A and B (growth inhibitors)	Nosaki et al. (2007)
Dicranum scoparium, *Racomitrium canescens,* *Homalothecium lutescens,* *Hylocomium splendens,* *Hypnum cupressiforme,* *Rhytidiadelphus triquetrus,*	*Arenaria serpyllifolia* *Veronica spicata,* *Filipendula vulgaris* *Festuca ovina*	Seedling emergence inhibition/or not specific to each species	Zamfir (2000)
Campylopus introflexus	*Calluna vulgaris*	No effect on germination and growth	Equiha and Husher (1993)

3.2.3 Bryophyte Secondary Metabolites

Recent analytical techniques allow characterizing numerous natural products from bryophytes. Phenolics or polyphenolic compounds are known to represent a main class of secondary metabolites synthesized by plants (Grooss et al. 1999). They are involved in physiological plant processes (e.g. germination) but also in plant chemical interactions (Hattenschwiler and Vitousek 2000). Compared to other plants, the chemical investigation of bryophytes is a rather young discipline. There are several reasons for this: it is difficult to collect larger amounts of material, fields cultivation is not practicable and laborious procedure to have pure species (Becker 2000). Despite these difficulties, a large number of natural products, some of them with novel and unique skeletons, have been isolated from bryophytes during the past 30 years.

Because bryophytes are nonvascular plant, their secondary metabolism is limited/different compared to vascular plants. Even if flavonoids remain one of the most studied group, only a small percentage has been studied in details because most of the effort having been devoted to species of Marchantiales, Jungermanniales and Bryales (Markham 1990). Remarkable diversity of terpenoids has also been showed to be produce by liverworts (Geiger 1990). Nevertheless, investigations directed to the biosynthesis of such compounds in nonvascular plants are still rare compared to the numerous studies on terpenoid metabolism in vascular plants. Another example is the still controversial presence of lignin in bryophytes, because degradation's studies on bryophyte tissues did not recovered the usual lignin degradation products (Geiger 1990; Ligrone et al. 2008). In view of the limited sampling, any generalization on bryophyte secondary metabolite is then difficult to make.

3.3 The Case of *Sphagnum*

Among Bryophyte classes, *Sphagnum* genus takes a particular place because of its fundamental ecological role in peatlands especially for the global sequestering carbon. Even if *Sphagnum* is the dominant plant in peats in terms of biomass and productivity, sparse data are focused on *Sphagnum* chemical interaction.

3.3.1 Sphagnum Secondary Metabolites

The *Sphagnum* genus, consisting of around 300 species, is worldwide distributed and is a dominant component of peat bog vegetation (Opelt et al. 2007). *Sphagnum* is morphologically characterized by two distinct layers : (1) the living layer or top layer called "the capitulum" where the *Sphagnum* grow by around 1 mm/year and where the main physiological process occurred and (2) the decaying layer or bottom layer where the decay constitutes the accumulation of peat (Fig. 3.1). The limit between the two layers is generally considered as 0–3 or 0–6 cm for the

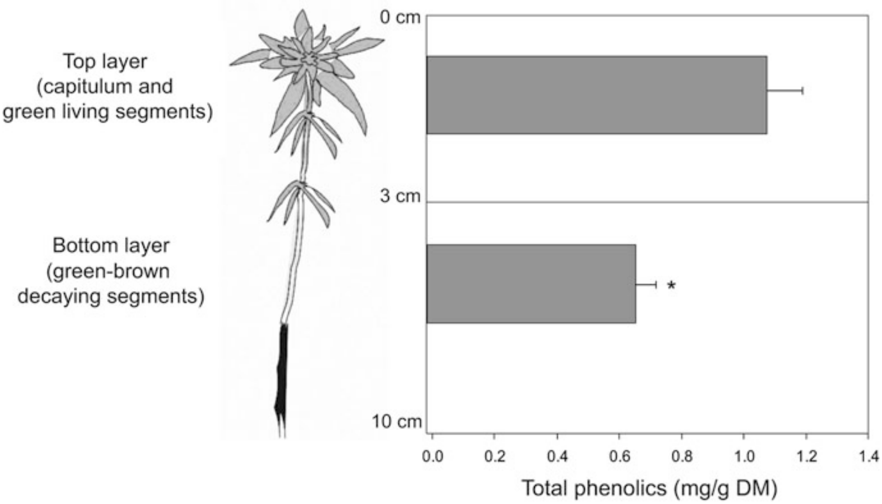


Fig. 3.1 Representation of *S. fallax* top and bottom layers with their respective total water-soluble phenolic concentrations expressed in mg g^{-1} DM. Mean ± S.E. ($n = 12$). *Asterisk* indicates significant differences between the two *Sphagnum* layers (Anova test $P < 0.05$) (adapted from Jassey et al. 2011a)

capitulum (0 from the top of the capitulum) and 3–10 or 6–10 cm for the bottom layer. The deepest layer (>10 cm) constitutes the peat soil itself.

All vascular plant organs contain varying amounts of chemicals with potential allelopathic effects. Nevertheless, here, only leaves represent the key living organ of *Sphagnum* because of their important biomass compared to stems. *Sphagnum* leaves are not fully protected from the surrounding environment because no cuticle is present. Moreover, *Sphagnum* leaves stored around 90 % of water in their hyaline cells. Thought that the exchange of water, from atmosphere, leachates and litter, a direct relation with *Sphagnum* surrounding environment occurs, and so ables easily chemical interactions.

The secondary metabolism of *Sphagnum* differs from vascular plants. For example, *Sphagnum* synthesizes specific polyphenolic compounds such as sphagnum acid (a cinnamic acid) synthesized via the Shikimate pathway (Rasmussen et al. 1995; Rudolph and Samland 1985). Another specific molecule is the flavonoid sphagnorubin, which is a red pigment which represents a natural constituent of cell wall of *S. magellanicum* (Tsutschek 1982).

3.3.2 Sphagnum Water Phenolic Production and Degradation

The first major group of secondary metabolite found in *Sphagnum* is the phenolics (Verhoeven and Liefveld 1997). To determine phenolic compounds produced by living sphagnum, the extraction method is crucial and depend on the goal of the

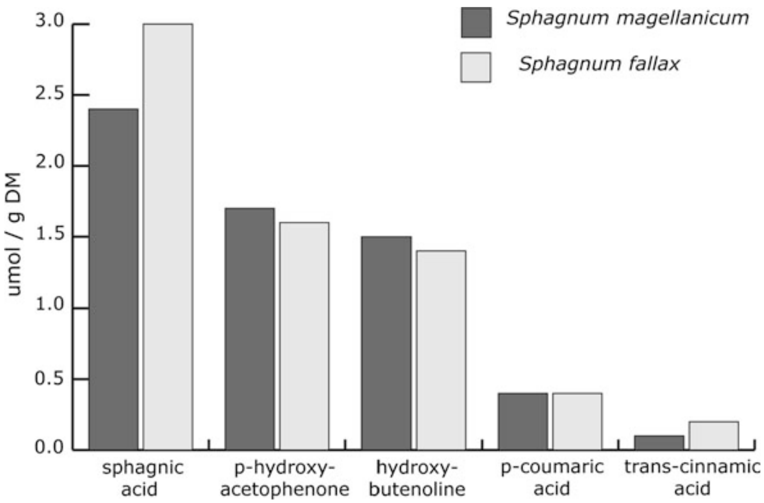


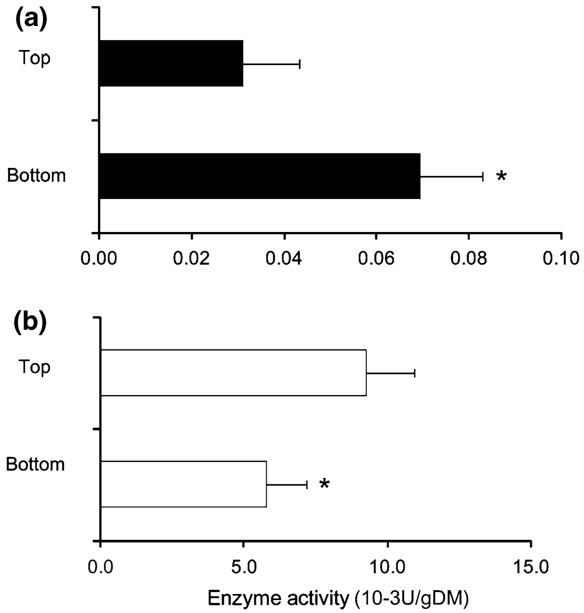
Fig. 3.2 Phenolic compounds quantified in *S. magellanicum* and *S. fallax* (adapted from Rasmussen et al. 1995)

study. Water to more polar solvents are commonly used and give different phenolic quantification recovery from the water extractable to the wall bound fractions. For example, *Sphagnum* species (*S. magellanicum, S. fallax, S. cuspidatum*) produced sphagnum acid, *p*-hydroxyacetophenone, hydroxy butenolide, *p*-hydroxybenzoic acid, *p*-coumaric acid, and trans cinnamic acid from 0.1 μmol g^{-1} DM up to 2.9 μmol g^{-1} DM (Fig. 3.2, Rasmussen et al. 1995). The phenolic profile was found to be species dependent (Opelt et al. 2007). To test allelopathic effect, the plant water extraction is commonly used.

In our work, *S. fallax* phenolics were extracted in cold water and quantified by using the Folin–ciocalteu reagent and gallic acid as standard (Jassey et al. 2011b). Phenolics were mainly recovered in the capitulum (1 mg g^{-1} DM) compared to the bottom layer (0.6 mg g^{-1} DM) (Fig. 3.1). These results clearly identified the active allelopathic part of *Sphagnum* as the top layer and the passive allelopathic part as the bottom layer. To conclude, the 0–10 cm *Sphagnum* layer gives a realistic allelopathic potential of *Sphagnum*.

The degradation of the recalcitrant polyphenolic plant residue represents a key process in the global carbon cycle of a peatland. A large diversity of extracellular enzymes, described as phenoloxidases, is involved in the degradation of polyphenolic compounds (Sinsabaugh 2010; Theuerl and Buscot 2010). Extracellular phenoloxidases are divided into phenoloxidases O_2 dependent (e.g. included laccases and tyrosinases; hereafter named phenoloxidases) and phenoloxidases H_2O_2 dependent (e.g. lignin and manganese peroxidases; hereafter named peroxidases). Generally, peroxidases are considered to be produced by basidiomycetes or ascomycetes but a recent work demonstrated that main peroxidase activities in an oak forest litter had a plant origin (Alarcón-Gutiérrez et al. 2009). According to

Fig. 3.3 Enzyme activities of two *S. fallax* layers 0–3 cm (*top*) and 3–10 cm (*bottom*) (October 2010): Phenoloxidases (**a**) and Peroxidases (**b**). Enzymatic activities were expressed in enzyme units (U) defined as one µmol of substrate oxidized per $\min^{-1}$ (peroxidase activities) or per h^{-1} (laccase activities) per gram of Dry Mass. Mean ± S.E. ($n = 6$). *Asterisks* indicate significant differences of enzyme activities among *Sphagnum* segments (Anova tests, $P < 0.05$) (adapted from Jassey et al. 2012)



Sinsabaugh (2010), peatlands represent a particular focus for studies of phenoloxidases and peroxidases activities because of their large role in oxidizing recalcitrant carbon such as polyphenolics.

In a recent study, we measured variations of phenoloxidase and peroxidase activities in the *Sphagnum* peatland of Frasnes (Jura mountains, France). Extracellular enzymes were extracted using a specific extraction reagent (0.1 M $CaCl_2$ with 0.05 % Tween 80 and 20 g PVPP). After centrifugation, the extracts were concentrated in a cellulose dialysis with a 10 kDa molecular mass cut-off covered with polyethylene glycol (Jassey et al. 2011c). Enzymes activities were quantified using diaminofluorene, which represents a relevant oxidative substrate to quantify both plant peroxidases and fungal phenoloxidases in an enzymatic extract (Criquet et al. 2001; Jassey et al. 2012).

A negative correlation between total phenolics and fungal phenoloxidase activities was found (respectively, $r = -0.42$ and $r = -0.38$, $P < 0.01$) (Jassey et al. 2011c). Phenolics at high concentration could inhibit the oxidation activity of fungal phenoloxidases. A regulation of the fungal phenoloxidases by phenolics is then suggested. Ultimately, our results also reinforce the point that phenoloxidase/ polyphenol interplay is especially critical to understanding peatland functioning.

Sphagnum peroxidases constituted the main oxidative system in *Sphagnum* peatlands, with values 1000-fold higher than fungal phenoloxidase activities. The highest level of peroxidase activities was measured in the top layer (0–3 cm), whereas fungal phenoloxidase activities were mainly detected in the deep layer (3–10 cm) (Fig. 3.3). Similar differences have been already recorded, but in the surface litter of forest with plant peroxidases 120-fold higher than fungal phenoloxidases (Alarcón-Gutiérrez et al. 2009).

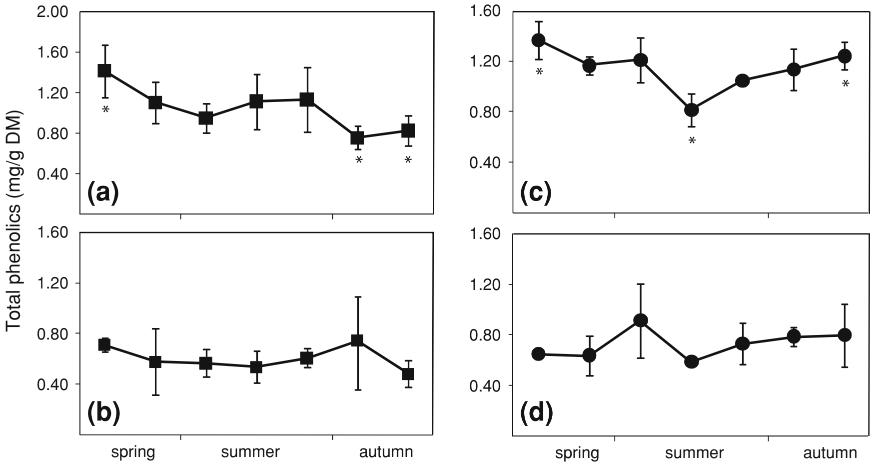


Fig. 3.4 Seasonal variations of water-soluble phenolic concentrations (expressed in mg g^{-1} DM) in two *S. fallax* layers (*top* **a**, **c** and bottom **b**, **d**) recovered in the bog (**a**, **b**) and fen (**c**, **d**) areas of the Frasne peatland. Mean ± S.E. ($n = 3$). *Asterisk* indicates significant difference among months (ANOVA tests, $P < 0.05$) (adapted from Jassey et al. 2011c)

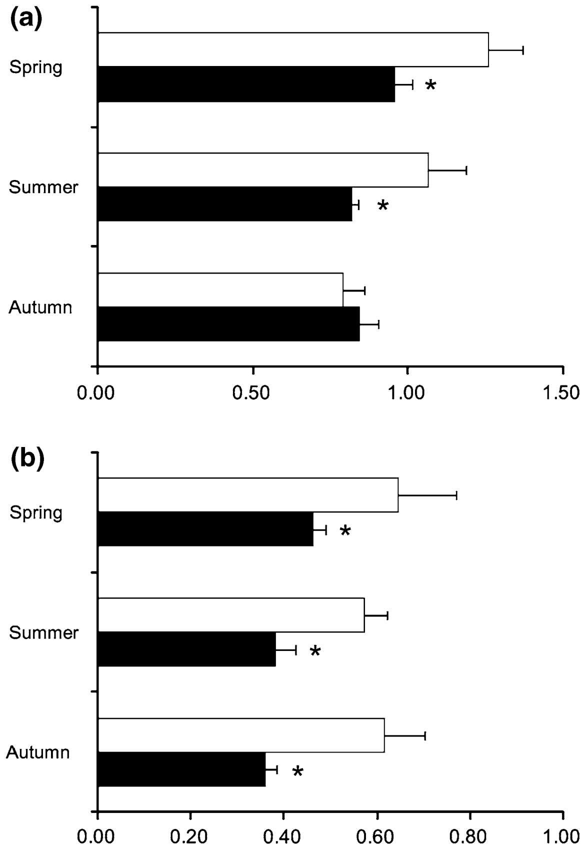
3.3.3 Seasonal Variations of Phenolics in Ambient and Warming Environment

In most ecosystems, seasonal variations of phenolics have been quantified to characterized allelochemical potential (Gallet and Lebreton 1995). Surprisingly, in peatlands, such data are scarce (Bonnett et al. 2006).

Seasonal variations of phenolics, fungal phenoloxidases involved in their degradation were quantified in the Frasne peatland (Jura mountains, France) in two ecological conditions. Briefly, the first ecological area was a transition *Sphagnum*-dominated poor fen characterized by a flat homogeneous carpet of *S. fallax* (hereafter called "Fen") and the second one was a *Sphagnum* bog characterized by lawns of *S. fallax* and hollows of *S. magellanicum* associated with vascular plants (such as *Eriophorum vaginatum*, *Vaccinium oxycoccos*) (hereafter called "Bog") (Jassey et al. 2011c). Recovered *Sphagnum* phenolic concentrations were found to depend on the season with a decrease in summer for the bog area and in autumn for the fen area (Fig. 3.4). *Sphagnum* was able to regulate its secondary metabolism by decreasing its phenolic concentration when environmental conditions changed. Indeed, in summer in the bog area the air temperature increased and the *Sphagnum* moisture decreased inducing a decrease of total phenolics (Jassey et al. 2011c).

Because the increased decomposition rates in peatlands with global warming might increase the release of atmospheric greenhouse gases (i.e. CO_2), *Sphagnum*s are ideal plants for climate change indication. Most of the literature focused on the effects of temperature on the decomposition of litter from boreal peatlands. Cautious conclusions suggest that not all peatlands may provide a positive

Fig. 3.5 Seasonal variations of water-soluble phenolic concentrations (expressed in mg g^{-1} DM) in two *S. fallax* layers (*top* **a** and *bottom* **b**) recovered in controls and OTC in the fen areas of the Frasne peatland. Mean ± S.E. ($n = 3$). *Asterisk* indicates significant difference between control and OTC (ANOVA tests, $P < 0.05$) (adapted from Jassey et al. 2011c)



feedback to global warming (i.e. differences between the fen and bog areas) (Weltzin et al. 2003). Anyway, sparse data are available on living *Sphagnum* and their response to a global warming.

In the Frasne peatland, an increase of air and soil temperatures was passively achieved by placing hexagonal ITEX open-top-chambers over the vegetation. In spring and summer (may to September), the OTC's significantly increased the daily maximum air temperature by an average of 3 °C and the average air temperature by 1 °C (Jassey et al. 2011c).

In response to the climate forcing, the phenolic concentrations decreased in the fen area irrespective of the seasons (Fig. 3.5) but not in the bog area. *Sphagnum* carbon allocation between primary and secondary metabolism changed. *Sphagnum* diminished its allocation to polyphenols to favor growth or crucial synthesis to better survive (Veteli et al. 2007). Indeed, biomass allocation is an important plant trait that responds plastically to environmental perturbations. Our results also highlighted different responses of *Sphagnum* phenolics along the fen-bog gradient (Jassey et al. 2011c). More studies with long-term conclusion with more than 1 year are needed to draw complete conclusion on the effect on global warming on *Sphagnum*.

3.4 *Sphagnum* Allelopathic Interactions

Sphagnum-dominated peatlands were at one time erroneously believed to be devoid of microbial life because of the acid pH. In reality, a high diversity of microbial communities lives in *Sphagnum* mosses, among which decomposers (bacteria and fungi), primary producers (microalgae, diatoms and cyanobacteria), protozoa, and micrometazoa (ciliates, testate amoebae, rotifers, and nematodes). These microorganisms are of greatest interest in peatland functioning because they act on nutrient cycling, mainly carbon and nitrogen, via the microbial loop (Gilbert et al. 1998; Gilbert and Mitchell 2006; Thormann 2006).

Because living *Sphagnum* has specific morphological, physiological, and ecological properties and are associated with a specific microbial loop, we proposed to use the original term "sphagnosphere" to represent such microecosystem. Thus, we define the "sphagnosphere" as a specific microecosystem between living S*phagnum* and its associated microorganisms. "Sphagnosphere" represents the first scale in peatlands allowing determining any relation with its surrounding environment.

3.4.1 Effect of Sphagnum Extract on Sphagnum Associated MicroOrganisms

The dynamic of *Sphagnum* associated microorganisms is usually explained by physical and chemical factors (e.g. water level, pH, redox potential). Unfortunately, the allelochemical interactions between *Sphagnum* and its associated microbial communities are rarely studied. Recently, Jassey et al. (2011a, b) suggested that phenolic compounds were involved in the structure of microbial assemblages in *Sphagnum* peatlands, especially on testate amoebae communities. Testate amoebae are abundant and diverse-shelled protozoa living in a wide range of habitats from soils to peatlands (Mitchell et al. 2008). They are an important group in microbial food web because they feed on a wide range of prey such as bacteria, algae, fungi, rotifers, nematodes, or other small testate amoebae. Owing to their role in microbial food web, they play a crucial role in the microbial loop and nutrient cycling (Gilbert et al. 2003; Wilkinson and Mitchell 2010). In *Sphagnum* peatlands, testate amoebae communities were strongly correlated to surface wetness conditions and water chemistry (Mitchell et al. 2008). Jassey et al. (2011a) demonstrated for the first time that phenolics explained a variance partitioning of 25.6% as physical factors (34.1%) and as chemical factors (16.8%) of their community composition along *Sphagnum* shoots. It strongly suggested the potential role of these compounds in their autecology. More precisely, a relationship between testate amoebae and polyphenols was confirmed. For example, the density of *Euglypha strigosa* was significantly correlated to the concentrations of *Sphagnum* water-soluble phenolics (Fig. 3.6). Although such result does not allow a conclusion to be strongly drawn on a possible direct positive effect

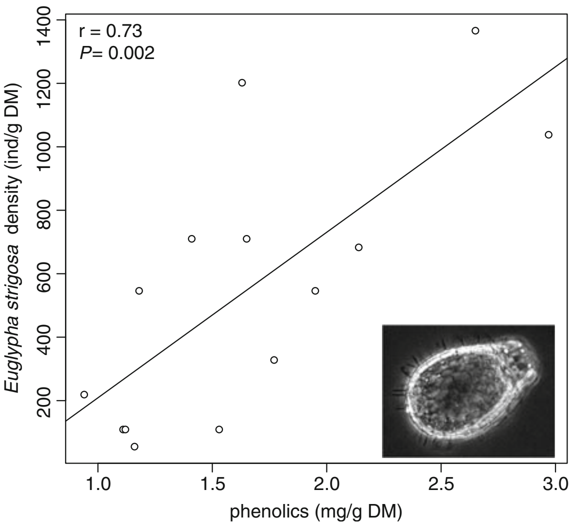


Fig. 3.6 *Euglypha strigosa* density (ind.g^{-1} DM) plotted against the concentrations of *S. fallax* water-soluble phenolics (mg g^{-1} DM) (ANOVA test, $P = 0.02$). *E. Strigosa* photo is reproducted, with kindly permission of E.A.D. Mitchell (adapted from Jassey et al. 2011c)

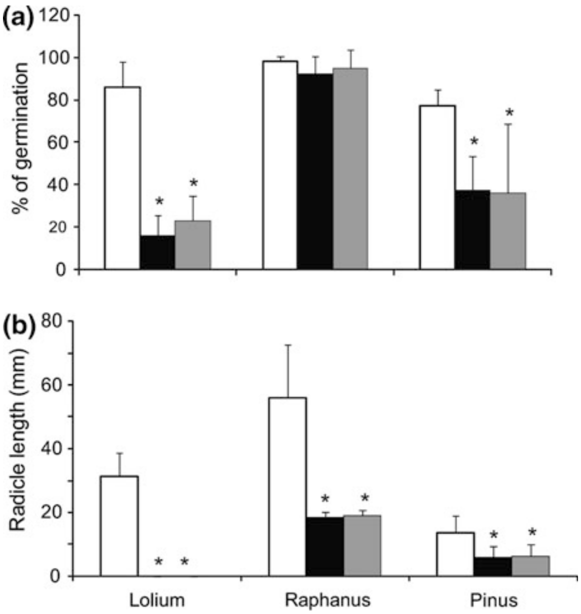
(or indirect effect on the food web) of phenol released by *Sphagnum* on *E. strigosa*, it raises the issue of the possible role of phenolics on microbial communities.

3.4.2 Effect of Sphagnum Extract on Germination and Early Growth of Vascular Plants

The bulk of research on allelopathy focuses on the visible effects of allelochemicals (secondary effects) particularly on germination and growth. These effects are tested with plant extract when the compounds have not been yet identified as it is the case for *Sphagnum* (Chiapusio et al. 1997).

The experimental procedure involved testing the effect of *S. fallax* extract on the germination and early growth of three vascular species a monocot *Lolium perenne,* a dicot *Raphanus sativa*, and a local gymnosperm peatland species *Pinus uncinata*. Extracts of *S. fallax* were realized by pressing by hands *Sphagnum* plants. The obtained extract was (1) directly used in the germination experiments and corresponded to the 100 % extract and (2) diluted in distilled water to obtain a 75 % extract. The pH of each *Sphagnum* extract was measured and other controls were also realized with the same pH. As no statistical difference between the "normal control" and the "buffered pH" was found, we concluded that the pH had no effect on the germination process. A 100 % *Sphagnum* extract and the 75 % extract had a drastic negative effect on *Lolium* germination (7- and 4-times, respectively less than the control) but also on *Pinus* germination (two times less than the control for both treatments) (Fig. 3.7a). On the contrary, no effect on germination of radish seeds was observed. Differences between monocot and dicot could explain such germination differences but need complementary experiments.

Fig. 3.7 Effect of *S. fallax* extract on **A** the germination (%) of *Lolium perenne*, *Raphanus sativus*, and *Pinus uncinata*. Mean ± S.D. ($n = 5$). (Mann–Whitney test, $P < 0.05$) and on **B** radicle length (mm) of *L. perenne, R. sativus,* and *P. uncinata.* Mean ± S.D. ($n = 5$). (Mann–Whitney test, $P < 0.05$) (Unpublished data)



Sphagnum extract on the radicle growth was drastic for all tested species (Fig. 3.7b). Indeed, inhibition of root was noticed for radish (30 %) and for *Pinus* (40 %) for both treatments. Moreover, when the *Lolium* seeds germinate they were then not able to develop their radicle in both *Sphagnum* extracts. The radicle growth was totally suppressed.

Living *Sphagnum* extracts offered interesting perspectives for allelochemical interactions in the functioning of peatlands to understand vegetation dynamics. Similar results, but with other bryophytic genus, were described (Zamfir 2000). Indeed, the homogeneous mat of *Sphagnum* is known to be due to low nutrient availability, anoxia, low temperatures, and high acidity (Van Breemen 1995). Along our results, *Sphagnum* ability to compete other plant species, especially vascular plants, could also be due to allelochemical production. The term interference, combining competition, and allelopathy becomes relevant then.

Moreover, the allelochemical *Sphagnum* extract could also be a good candidate as biopesticides (Chiapusio et al. 2005). Observed inhibitions of germination and growth are promising comparing with other allelochemicals (e.g. 2-benzoxazolinone, Chiapusio et al. 2004; Hussain et al. 2008). Such results constitute a crucial step for further experiments.

3.5 Conclusions

Water-soluble phenolics produced by living *Sphagnum* were found to be of great interest for the functioning of peatlands. First, they were concentrated in the top layer of Sphagnum and their concentrations varied along the seasons. *Sphagnum* peroxidases constituted the main oxidative system and fungal-phenoloxidases were proposed to be inhibited by phenolics. In such context, the polyphenolic phenoloxidase interplay is especially crucial to understand the mechanisms by which peatlands react under a climatic change. Indeed, peatlands could become weaker sinks of carbon but depends on their proper ecological conditions (e.g. ecological gradient).

Second, our hypothesis of allelopathic interactions in peatlands made sense with the evidence of original interactions between *Sphagnum* phenolics and its associated microorganisms, the “sphagnosphere.” Of course, allelopathy was not considered as the only factor explaining microbial dynamic and microbial food chain but was revealed to be fully considered and not neglected. Moreover, the drastic inhibition/delay of *Sphagnum* extract on germination and radicle growth of vascular plants could also explain the *Sphagnum* dominance under surrounding plants.

We still have a lot to learn from bryophyte secondary metabolite, not only to better understand their ecological role but also to discover original natural products that could be used as natural biopesticide. However, research is still needed on the identification and the biodegradability of bryophyte allelochemicals, which are largely unknown until now.

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Chapter 4
Plant-Mycorrhizae and Endophytic Fungi Interactions: Broad Spectrum of Allelopathy Studies

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Abstract Plants may compete with one another for resources and they could also release allelochemicals that inhibit or stimulate the development and survival of neighboring plants and microorganisms. Arbuscular mycorrhizal fungi (AMF) and fungal endophytes are part of the microbial community of almost every plant; the composition of a plant microbial community is thought to affect plant fitness and physiology as well as their interactions with other plants. Arbuscular mycorrhizal fungi and endophytes could affect the interactions between invasive and native plants or crops; this may be due to modifications in soil microbial communities mediated by allelochemicals produced by those fungi and plants. This chapter discusses the possible allelopathic interactions between maize and *Rottboellia cochinchinensis*, as well as the possible interactions with their associated AMF. Other group of microorganisms considered here are endophytic fungi. This type of fungi produces allelochemicals with a great chemical diversity and biological activities. Interactions between plants and their associated microbial communities are mediated by allelochemicals; direct or indirect effects of these compounds on plants and microorganisms are considered within the spectrum of allelopathy.

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4.1 Introduction

In nature, interactions between organisms include both direct and indirect interactions. Plants, for example, may compete with one another for resources, such as nutrients, water, light, and pollinators (resource competition). They may also release chemicals that inhibit or stimulate the germination, growth, development, and survival of neighboring plants and microorganisms, usually termed as allelopathy (Weidenhamer 2006).

Every plant in a natural or agricultural setting is colonized by a variety of microbes on both its outer and inner tissues, and each tissue represents a complex community of microorganisms, including fungi (Porras-Alfaro and Bayman 2011).

Interactions between plants and fungi are ancient, in fact it has been hypothesized that colonization of the land by eukaryotes was facilitated by the symbiotic relationships between a photosynthetic organism and fungi. Pirozynski et al. (1975) (cited by Singh et al. 2011) reasoned that the origin of land plants involved mycotrophism and that this type of association may have enabled various adaptations to life in a terrestrial environment (Selosse and Le Tacon 1998). Although the time of this colonization remains speculative, fossil, and molecular evidence of the extant plant *Nothia aphylla* have shown that the association between phototrophs and endophytes and arbuscular mycorrhiza fungi (AMF) has existed for at least 400 million years (Krings et al. 2007a, b).

Throughout evolutionary time, interactions among plants and fungi have continued. All plants in natural ecosystems are thought to be symbiotic with mycorrhizal and/or endophytic fungi (Petrini 1996; Brundrett 2006). AM fungi and fungal endophytes are part of the microbial community of almost every plant, and although their interactions with plants is not well understood, the composition of a plant microbial community is thought to affect its fitness and physiology as well as its interactions with other plants.

The interactions between plants include competition for resources, habitat alteration, and allelopathy (Cronk and Fuller 2001; Levine et al. 2003). Allelopathy is defined as "any process that involves secondary metabolites produced by plants, algae, bacteria, and fungi that influence the growth and development of biological systems" (IAS 1996). Bais et al. (2003) suggested that allelopathy might play an important role in the successful invasion of cultivated fields by certain alien plants. Invasive plants may influence other species through competition or by altering ecosystem processes, microbial communities, or the chemical properties of soils.

Orr et al. (2005) investigated the effects of the invasive plants *Lolium arundinaceum* (tall fescue) and *Elaeagnus umbellata* (autumn olive) on three common successional tree species: *Acer saccharinum* (silver maple), *Populus deltoides* (eastern cottonwood), and *Platanus occidentalis* (sycamore). Treatment with aqueous extracts of minced leaves from tall fescue reduced the probability of seedling emergence in native plants, and minced autumn olive leaves reduced the number of days of seedling emergence.

Microbes, such as AM fungi and endophytes, can be extremely important for, community composition, and ecosystem processes. The ability of a plant invader to use or change the existing soil microbial community could be a mechanism of invader species during their establishment on plant communities and ecosystems (Callaway et al. 2004). Alterations of the microbial and fungal communities in the soil caused by the invasion of exotic species may cause negative effects to native plants and their associated microorganisms, and provide invaders with a pathway to success. It has been demonstrated that invading plants are capable of altering AM fungal communities, both in terms of the fungi present in their own roots and those that colonize native plant roots after invasion (Hawkes et al. 2006).

Symbiotic and associative interactions may be important in the case of *Rottboellia cochinchinensis* (itchgrass) (Poaceae), a very competitive annual grass distributed throughout Asia, Africa, Australia, and America, particularly prevalent along the Gulf of Mexico and the Caribbean. *Rottboellia* invades agricultural fields, reducing crop growth and yields, and, for that reason, *Rottboellia* is considered a very aggressive invasive plant and one of the worst weeds in the world (Holm et al. 1977).

Ambrosia artemisiifolia L. (common ragweed) is an annual invasive plant in Europe. Approximately 94 % of *A. artemisiifolia* populations sampled in eastern France were mycorrhizal. In a greenhouse experiment, Fumanal et al. (2006) observed the positive effects of AMF on the growth and development of *A. artemisiifolia*. These authors proposed that the spread of this invasive plant species could be facilitated by AMF, underscoring the need to consider symbiotic interactions in future work on invasive plant processes.

Endophytes, as AM fungi, could affect the interactions between invasive and native plants. *L. rundina* (an invasive tall fescue) with endophyte *Neotyphodium coenophialum* is able to inhibit neighboring plants, including native tree seedlings (Orr et al. 2005; Rudgers and Clay 2007). This ability has been attributed to higher rates of seedling predation for native plants in plots that contain invasive tall fescue with the endophyte (Rudgers et al. 2007), and changes in soil microbial communities mediated by the endophyte, which could be the cause of reductions in tree establishment (Rudgers and Orr 2009). The great success of some grasses associated with endophytes could also be explained by their high concentrations of alkaloid toxins, combined with strong grazing pressure (Clay and Holah 1999).

Interactions of microbial communities with host plants reflect the complexity of biological systems. Investigations of plant-associated microbial communities are needed to understand the roles of allelochemicals produced or induced by AM fungi or by endophytes and to understand their effects on microbial and plant communities.

4.2 Plant–Mycorrhizae Interactions

AMF are the most common underground symbionts and are formed in the roots of a wide variety of host plants by aseptate, obligate symbiotic fungi of Phylum Glomeromycota (SchüBler and Walker 2010). The symbiosis is biotrophic and normally mutualistic, with long-term interactions based on bidirectional nutrient transfer between the symbionts (Smith and Read 1997). The AMF absorbs nutrients from the soil in inorganic and organic forms and translocate them to the roots to provide the plant with phosphorous (P) and nitrogen (N). Organic C derived from photosynthesis is also transferred from the plant to the fungus (Smith and Barker 2002). The effect of AMF on competition between plants is often attributed to the fact that it promotes the growth of mycorrhizal species rather than nonmycorrhizal species or those that have weak or facultative mutualisms (Hartnett et al. 1993).

The colonization of roots by AMF is characterized by the presence of fungal structures such as arbuscules. Arbuscules are the main sites of nutrient exchange between these fungi and the host plant (Parniske 2008). They grow until they reach their maximum size, after which degradation is induced (Javot et al. 2007), suggesting that their short lifetime is related to their ability to deliver phosphate and other nutrients to the plant. Additionally, this senescence allows for the constant renewal of the hyphal network (Parniske 2008). An AMF hyphal network can exceed 100 m of hyphae per cubic centimeter of soil, which makes AMF hyphae extremely adept at taking up water and plant nutrients, predominantly phosphate (Finlay 2008).

AMF root colonization decreases as nutrient availability increases in the soil, because greater nutrient content allows plants to more easily obtain nutrients on their own (Aerts and Chapin 2000). In general, AMF colonization is favored when nutrient content and plant density are low, and it typically decreases when nutrients are abundant and plant density increases (Koide 1991; Parniske 2008). High nutrient content and high density reduce the benefit/cost ratio and minimize the positive effects of AMF symbiosis (Schroeder-Moreno and Janos 2008).

4.2.1 Maize and **Rottboellia cochinchinensis***, Competition and Allelopathy*

Maize (*Zea mays* L.) is one of the main crops grown in several South American countries, with the largest quantities grown in Brazil, Argentina, and Mexico. Several weeds that affect maize are *Cynodon dactylon*, *Digitaria sanguinalis*, *Echinochloa crus-galli*, *Panicum fasciculatum* Swartz, *P. reptans*, Johnson *Sorghum halepense*, *Eragrostis cilianensis*, *Eleusine indica*, *Echinochloa colona*, *Ixophorus unisteus*, *Leptochloa filiformis*, and *R. cochinchinensis* (Espinosa-García and Sarukhán 1997).

Rottboellia cochinchinensis (*R. exaltata*) or “itchgrass” is listed as one of the worst invasive weeds in the world. It is an annual tropical grass found throughout Asia, Africa, Australia, America, along the Gulf of Mexico, and in the Caribbean (Holm et al. 1977). *R. cochinchinensis* invades agricultural fields, reducing crop growth, and lowering the yields of rice, sugar cane, beans, citrus, some tropical forest plantations, and maize, among other crops (Strahan et al. 2000; Esqueda-Esquivel 2005). Strahan et al. (2000) showed that *R. cochinchinensis* could reduce maize yields by 33 %. Other authors reported losses of 90 % and proposed that this effect could be caused by competition and/or allelopathy (Delgado et al. 2006; Kobayashi et al. 2008).

Several modes of action or physiological mechanisms might be involved in the inhibition and modification of plant development that occur when a weed interferes with a crop. Few studies have focused on the allelopathic potential of *R. cochinchinensis* or its ability to compete with crops for nutrients, light, and space (Bridgemohan and McDavid 1993; Strahan et al. 2000; Rivera et al. 2007; Kobayashi et al. 2008). There are no studies that have investigated the possible associations of AMF with *R. cochinchinensis*, although it can be hypothesized that AMF colonization would give *R. cochinchinensis* a competitive advantage against crops such as maize.

When plants grow together, the total yield increases linearly with density until it reaches the point that neighboring plants begin to compete with one another for resources. The mutual effects between crops and weeds may cause the inhibition and modification of plant growth and development that result from competition or interference (competition + allelopathy). The adaptive plasticity of plants allows them to change their morphological and/or physiological traits after exposure to different environmental conditions, e.g., competition or allelochemical stress (Thompson 1991). Phytotoxic compounds release by the weed *Sicyos deppei* delays germination and inhibit tomato root growth during in vitro bioassays. This phytotoxicity is caused by an oxidative imbalance that correlates to an inhibition or delay in the activity of some cell wall degrading enzymes, as well as a disturbed carbohydrate mobilization during germination (Romero-Romero et al. 2005; Lara-Núñez et al. 2006; Cruz-Ortega et al. 2007). The incorporation to soil of fresh and dry tissues of *S. deppei* releases compounds that negatively affect the growth of tomato and induce oxidative damage in their leaves (Cruz-Ortega et al. 2008). Bais et al. (2003) mention that allelopathy plays an important role in the successful invasion of cultivated fields by certain plants species (Bais et al. 2003). Different studies have been conducted to test the effects on growth and total yield of different plant densities and to discriminate allelopathy from resource competition (Weidenhamer et al. 1989; Nilsson 1994; Bednarz et al. 2000).

4.2.2 *Maize and* **Rottboellia cochinchinensis** *Growing Together: Interactions with Mycorrhizae*

Maize is an obligate or facultative mycotrophic plant, and when associated with AMF, it shows increased drought tolerance, higher yields, and improved P nutrition (Boomsma and Vyn 2008; Tanga et al. 2009). AMF can have a direct or indirect effect on crops and weeds and on their competitive ability. These fungi can confer a competitive advantage to their plant hosts, particularly if they depend on weeds rather than crops or if the fungi are less abundant in crops than in weeds. Many agricultural weeds are hosts for AMF, including *Digitaria sanguinalis*, *Setaria viridis*, and *Echinochloa crus-galli* (Rinaudo et al. 2010). Muthukumar and Udaiyan (2000) investigated the potential for association between AMF and *R. cochinchinensis,* and they found no AMF colonization occurring in their roots.

In a greenhouse experiment, Contreras-Ramos et al. (unpublished) analyzed the mutual effects of maize and *R. cochinchinensis* growing together at different densities in fertilized (F) and unfertilized (NF) conditions, particularly focusing on AMF colonization (percentage of arbuscules, vesicles, hyphae, and total colonization) and identification of spores of AM fungi isolates from the soil in each treatment. In this study, they found that in almost all treatments of plant densities and fertilization conditions, *R. cochinchinensis* and maize roots were colonized by AMF. In fertilized conditions, when maize grew without *R. cochinchinensis*, they displayed higher total colonization (TC) with AMF (84 %) in their roots; TC of fertilized *R. cochinchinensis* growing alone was lower (13.2 %). The maize root TC decreased sharply when the maize was grown with five or ten *R. cochinchinensis* plants (1.6 and 7.5 times, respectively). In contrast, when fertilized *R. cochinchinensis* grew with three or five maize plants, their roots displayed a great increase in TC (4.5 and 3.9 times, respectively). On the other hand, in unfertilized conditions, maize growing without this alien weed had a TC of 34.7 %. When grown with five or ten *R. cochinchinensis* plants, maize TC decreased two times and 4.2 times, respectively. Unfertilized *R. cochinchinensis* growing without maize had a TC of 23.4 % (an increase of 1.8 times compared with the same treatment in fertilized conditions). However, when it grew with three or five maize plants, its TC decreased only 1.2 times in both treatments (Table 4.1). In these experiments some *Glomus* species were identified in the soil of both species (maize and *R. cochinchinensis*) mainly *G. microaggregatum*, regardless of fertilization. *G. microaggregatum* is one of the *Glomus* species that proliferate in C_4 plant hosts and increase their spore production after N fertilization (Egerton-Warburton and Allen 2000; Johnson et al. 2003). *R. cochinchinensis* and maize are C_4 plants (Wang, 2006); thus, the results of Contreras-Ramos et al. (unpublished) in most cases are in accordance with the results of these authors with an exception, *G. microaggregatum* was not found in the soil of *R. cochinchinensis* this invader weed grew alone.

Contreras-Ramos et al. (unpublished) found that the roots of maize had a higher percentage of arbuscules than hyphae or vesicles in both fertilization conditions, but this percentage decreased when *R. cochinchinensis* density increased. In contrast, maize hyphae increased with the presence of *R. cochinchinensis,* regardless of fertilization. The increased number of hyphae of AMF in roots of maize growing with *R. cochinchinensis* suggests an effort by the fungus to acquire more nutrients, which could serve as a mechanism of competition when maize is affected by interspecific competition (Govindarajulu et al. 2005; Parniske 2008). On the other hand, when *R. cochinchinensis* plants grown alone, colonization of AMF was higher in unfertilized than in fertilized conditions. In general, low

Table 4.1 Hyphae, arbuscules, vesicles and total colonization percentages of arbuscular mycorrhizae fungi found in roots of maize and *Rottboellia* plants in fertilized and unfertilized conditions

	Fertilized (F)[a]						Unfertilized (NF)[a]					
	Maize roots			*Rottboellia* roots			Maize roots			*Rottboellia* roots		
AMF colonization	M1R0	M1R5	M1R10	R1M0	R1M3	R1M5	M1R0	M1R5	M1R10	R1M0	R1M3	R1M5
Hyphae (%)[b]	4.1	9.4	5.3	6.6	8.1	10.9	0.6	2.5	2.8	5.3	15.3	8.4
Arbuscules (%)[b]	69.4	24.1	5.0	4.1	46.6	27.8	34.1	9.4	3.4	5.3	0.9	7.2
Vesicles (%)[b]	10.9	7.5	0.9	2.5	5.3	12.8	0	5.6	2.8	12.8	3.7	4.4
Total colonization (%)[b]	84.4	41.0	11.2	13.2	60.0	51.5	34.7	17.5	9.0	23.4	19.9	20.0

[a] Means of four replicates ($n = 4$); [b] percentage of structures and colonization in the central plant; M1R0, M1R5 and M1R10 = one maize in the center of the pot and 0, 5, or 10 *Rottboellia* plants surrounding it; R1M0, R1M3 and R1M5 = one *Rottboellia* in the center of the pot and 0, 3, or 5 maize plants surrounding it

nutrient availability favored AMF colonization in host plants (Smith and Read 1997; Parniske 2008). In fertilized conditions, a significant increase in AMF TC in *R. cochinchinensis* roots was observed when the weeds grew with maize. Schroeder-Moreno and Janos (2008) postulated that this could occur because plant density enhances AMF colonization by multiplying the mycorrhizal structures that capture and transfer P. In a study by Contreras-Ramos et al. (unpublished), it appears that arbuscules and vesicles in *R. cochinchinensis* roots permit more efficient nutrient storage and provide the weed a best competitive advantage when it grows with maize (Table 4.1).

Maize growing alone in symbiosis with AMF species was favored by fertilization. However, the presence of *R. cochinchinensis* negatively affected this symbiosis, whether fertilization occurred or not. Bridgemohan and McDavid (1993) reported that maize had a greater competitive ability than *R. cochinchinensis* when the two were grown together. They suggested that a mutual antagonism or allelopathy could mediate the maize-*Rottboellia* interaction. This hypothesis could help explain certain observations about maize-*Rottboellia*-AMF interactions, specifically the fact that *Glomus sp.* provides a great competitive advantage at a low C cost when it is associated with *R. cochinchinensis*.

These experiments showed the importance of AMF fungi on the interactions between plants, and make evident the importance of studies of allelochemicals produced by microorganisms or those induced in plants by microorganisms' colonization that could influence the consequence of the interaction.

4.3 Plant–Endophytic Fungi Interactions

Endophytic fungi are organisms inhabiting plant organs during all or part of their life cycle, without causing apparent harm to the host (Petrini 1991; Wilson 1995). Endophytes are ubiquitous; they can be found in any organ in each of the four major groups of plants: non-vascular plants, seedless vascular plants, gymnosperms, and angiosperms (Arnold et al. 2001; Faeth and Fagan 2002). They inhabit a variety of habitats, from arctic tundra to tropical forests (Arnold and Lutzoni 2007).

In general, two groups of endophytic fungi are recognized based on the taxonomy of fungi, their plant hosts, and colonization (Rodriguez et al. 2009). The groups are the Clavicipitaceous endophytes (C-endophytes), which can be found in some grasses that exhibit systemic colonization; and the nonclavicipitaceous endophytes (NC-endophytes) that colonize all lineages of plants, forming localized infections within any organ of their host (Rodriguez et al. 2009). The C-endophytes are not considered here because they have unique properties distinct from other endophytes, their symbiosis, evolution, and functional significance are distinct from other groups of endophytes (Faeth and Fagan 2002; Rodriguez et al. 2009).

NC-endophytes display localized growth within particular tissues, and they accumulate as the tissues age (Espinosa-García and Langenheim 1990; Arnold and Herre 2003). These fungi are highly diverse, even within a host plant. For example, different leaves on the same tree may have distinctive assemblages of endophytic fungi, including species from each of the principal four phyla of fungi (Arnold et al. 2003, 2007). Individual plants may harbor hundreds of species of endophytic fungi, and those organisms could represent, both individually and collectively, a continuum of different associations, including mutualism, commensalism, latent pathogenicity, and exploitation (Schulz and Boyle 2006).

A single endophytic fungus could be a mutualist on one plant host and act as a pathogen on another plant species, and even within the same plant host, it could have different associations depending on biotic and abiotic factors (Saikkonen et al. 1998; Schulz et al. 1999; Redman et al. 2001; Kogel et al. 2006; Sieber 2007; Slippers and Wingfield 2007; Álvarez-Loayza et al. 2011; Porras-Alfaro and Bayman 2011). Symbiotic relationships between endophytic fungi and their hosts can be ambiguous; for example, the dark septate endophyte (DSE) *Phialocephala fortinii*, isolated from roots and aerial parts, can be a weak pathogen, a saprotroph on senescent root tissues, or a mutualist (Addy et al. 2005). Given this variability, the status "endophyte" describes an asymptomatic infection at one moment without specifying the role of the fungus in the host or its development at a later period (Petrini 1991; Schulz et al. 1999).

Studies of endophytic fungi frequently uncover novel species. The phyllosphere is a poorly explored habitat, and species found in that habitat are microscopic and inconspicuous. Thus, research on these microorganisms is very important for evaluating the diversity of fungi, their phylogenetic distribution and the complexity of the ecosystems they live in (McLaughlin et al. 2009). Moreover, these studies may show that fungal diversity is greater than previously suspected (Arnold et al. 2000, 2007; Stone et al. 2004).

Isolated allelochemicals from plant species and endophytic fungi of the El Eden Ecological Reserve, Quintana Roo, México, have been reported (Anaya et al. 2003a, b, 2005; Macías-Rubalcava et al. 2007). A great diversity of endophytic fungi was isolated from leaves of plants that produce allelochemicals. Cosmopolitan and tropical genera of endophytic fungi were frequently isolated from these plants, including *Guignardia*, *Phomopsis* and *Xylaria,* as well as other endophytes that did not sporulate, even under different culture conditions. From the leaves of *Callicarpa acuminata* (Verbenaceae), a novel species from a novel genus was isolated, i.e., *Edenia gomezpompae* (González et al. 2007). In the leaves of *Bursera simaruba* (Burseraceae), a novel species of *Muscodor* was found: *M. yucatanensis* (González et al. 2009). Both of these endophytes are members of the phylum Ascomycota.

4.3.1 Endophytes and Allelochemicals

Ever since the bioactive compound paclitaxel (taxol) was discovered in the endophytic fungus *Taxomyces andreanae* isolated from the yew *Taxus brevifolia*, there has been great interest in studying fungal endophytes (Stierle et al. 1993). In this case, the host plant (*T. brevifolia*) and the fungal endophyte (*T. andreanae*) produced the same compound, paclitaxel. This phenomenon could be the result of lateral gene transfer from host to fungus (Stierle et al. 1993). Other endophytic fungi (BT2) and the clone DA10, *Mucor rouxianus*, isolated from *T. chinensis* var. *mairei*, also produced taxol and the taxane baccatine III, an important intermediate of taxol in its industrial semi-synthesis (Guo et al. 2006). Isolation of these fungi constitutes a promising alternative for producing taxol. These are examples of microorganisms associated with plants that are capable of producing the same secondary metabolites as the plants. For example, the biosynthetic pathways for producing gibberellins in higher plants and fungi are very similar.

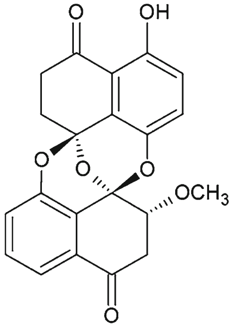
Numerous studies have shown that fungal endophytes are a promising source of biologically active compounds with medical or agricultural applications (Tan and Zou 2001; Zhang et al. 2006; Aly et al. 2010; Zhao et al. 2011). These secondary metabolites of endophytes are synthesized through various metabolic pathways (Tkacz 2000; Tan and Zou 2001). Classes of bioactive metabolites obtained from endophytes include alkaloids, benzopyranones, quinones, benzoquinones, flavonoids, phenols, steroids, terpenoids, tetralones, lactones, acids, xanthones, hexanones, peptides, aliphatic compounds, and others (Tan and Zou 2001; Strobel and Daisy 2003; Yu et al. 2010).

Studies on biologically active compounds isolated from endophytic fungi are performed mainly using medicinal plants (Huang et al. 2007; Yu et al. 2010) or plants that are known to produce bioactive compounds (Zhao et al. 2011), but endophytes isolated from these plants are not unique in producing interesting allelochemicals. Endophytic fungi isolated from plants in diverse environments are potential producers of novel and biologically active compounds (Strobel et al. 2004; Strobel 2006).

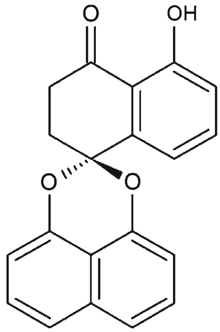
Macías-Rubalcava et al. (2008) isolated some novel compounds from the aforementioned fungus *E. gomezpompae*, which were collected from the host plant *C. acuminata* (Verbenaceae) that lives in the dry tropical forest at the El Eden Ecological Reserve. Four naphthoquinone spiroketals were isolated from this fungus and characterized (Fig. 4.1), palmarumycin CP2 as well as three novel compounds named preussomerin EG1, preussomerin EG2, and preussomerin EG3 (Macías-Rubalcava et al. 2008). Among the large number of novel bioactive metabolites that are known from various fungi, the preussomerins and palmarumycins (deoxypreussomerins) belong to a relatively new and rare family of bioactive natural products.

Muscodor yucatanensis, the novel fungal endophyte isolated from *B. simaruba*, similar to other *Muscodor* species (Ezra et al. 2004a, b; Strobel 2006), produces a mixture of volatile organic compounds (VOCs) when cultured under in vitro conditions. From *M. yucatanensis*, Macías-Rubalcava et al. (2010) isolated and identified different compounds from its VOCs and from the organic extracts of the culture medium and mycelium. The main VOCs produced by a 10-day-old *M. yucatanensis* culture comprised 38 compounds that were identified by Gas Chromatography–Mass Spectrometry GC/MS. This VOC mixture was selectively toxic to other endophytic and phytopathogenic fungi as well as to plant roots. In Fig. 4.2, the structures of three interesting compounds from *M. yucatanensis* VOCs are shown: 1-iodo-3-methyl-butane, 2-iodo-pentane, and *β*-elemene. It is

Fig. 4.1 Preussomerin EG_3 and Palmarumycin CP_2 two compounds isolated from the endophytic fungi *E. gomezpompae*

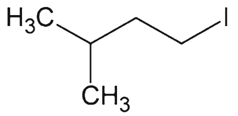


Preussomerin EG_3

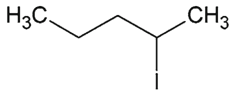


Palmarumycin CP_2

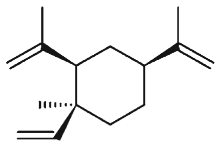
Fig. 4.2 Some volatile compounds, 1-iodo-3-methyl-butane, 2-iodo-pentane, and *β*-elemene, from the endophytic fungi *M. yucatanensis*



1-iodo-3-methyl-butane

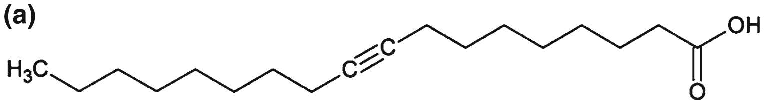


2-iodo-pentane

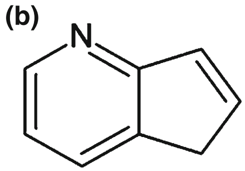


β-elemene

interesting that compounds produced by an endophytic fungus isolated from a dry tropical forest tree could contain iodine in their molecules. This element could be derived from the soils that cover the formerly marine parts of the Yucatan



Octadec-9-ynoic acid



5H-cyclopenta[b]pyridine

Fig. 4.3 **a** Octadec-9-ynoic acid identified from the organic extract of culture medium of *M. yucatanensis*. **b** 5H-cyclopenta[b]pyridine identified from the mycelium organic extract of *M. yucatanensis*

Peninsula that emerged from the sea in the Pliocene, 13 million of years ago. The sesquiterpene β-elemene is a potent antitumor agent that has a selective inhibitory effect on cerebrovascular endothelial cells and has given excellent results as an antitumor agent in the treatment of brain tumors (Barrero et al. 2011). The culture medium extract of *M. yucatanensis* contained 32 compounds, while the mycelium extract consisted of 23 compounds. In general, the compounds present in both extracts are alcohols, esters, and ketones of saturated and unsaturated compounds as well as benzene derivatives; two examples are shown in Fig. 4.3.

Endophytic fungi could be more than asymptomatic microorganisms living inside host plants. It is important to establish whether the plant allelochemicals are produced by the plants themselves or as a consequence of their symbiosis with fungal endophytes (Firáková et al. 2007). It is also important to determine if allelochemicals produced by endophytic fungi in their host plant are different from those produced in vitro.

Aly et al. (2008) reported that the fungal endophyte *Ampelomyces* sp isolated from the flower of the medicinal plant *Urospermum picroides*, exhibited considerable cytotoxic activity in vitro against L5178Y cells. Methanol and ethanol extracts of cultures grown in liquid or on solid rice media differed considerably in their secondary metabolites. The extract obtained from liquid cultures contained a pyrone and sulfated anthraquinones, along with other compounds. When grown on solid rice medium, the fungus yielded three main compounds with cytotoxic and antimicrobial activities. Two of the compounds, acrosporin and 3-O-methyl alaternin, were also identified as constituents of an extract derived from a healthy plant sample of *U. picroides* (Aly et al. 2008). These authors believed that the production of bioactive natural products by the endophyte also occurs within the host plant. This fact could contribute to the mutualistic interaction between the endophyte and its host plant, but it is also possible that ‘‘typical’’ fungal metabolites, reported previously from other plants, may likewise originate from endophytic fungi colonizing these plants. For example, bipendensin was originally isolated in very small amounts from wood samples of the African tree *Afzelia bipendensis* and was later obtained from an unidentified *Coniothyium fungus* (Connolly 1991; Krohn et al. 1994).

Endophytic fungi usually produce enzymes that enable the colonization of plant tissues. It has been demonstrated that endophytes are able to utilize, at least in vitro, nearly all plant cell components. Most of the investigated endophytes utilize xylan and pectin, show lipolytic activity and produce non-specific peroxidases and laccases (Sieber et al. 1991; Leuchtmann et al. 1992), chitinase (Li et al. 2004), glucanase (Moy et al. 2002), and xylanase (Suto et al. 2002). Furthermore, colonization by fungal endophytes stimulates the secretion of hydrolases from plant cells, which are able to limit or fragment the fungi. Fragments of endophytes, such as lipopolysaccharides, polysaccharides, and glycoproteins, can stimulate plant defenses and allelochemical production, which provides a way to suppress pathogen attacks efficiently (Gao et al. 2010).

4.3.2 Endophytic Fungi Allelochemicals: Interactions with Host Plants

In general, bioactive compounds are tested by looking for antimicrobial, insecticidal, cytotoxic, and anticancer activities (Porras-Alfaro and Bayman 2011), but little is known about the potential role of those allelochemicals in the host plant or in interactions with other members of the community, such as other endophytes, phytopathogens, plants, or herbivores. However, it is known that allelochemicals are secondary metabolites that transmit information between organisms and are a fundamental part of the regulatory systems of nature (Eisner and Meinwald 1995; Anaya and Espinosa-García 2006).

Allelochemicals produced by endophytes could have variable effects on the physiology of host plants. Negative effects on host plants could include the inhibition of photosynthesis (Costa Pinto et al. 2000), and positive effects could include the enhancement of plant growth (Lu et al. 2000; Schulz et al. 2002; Gao et al. 2010).

The endophytic fungi *Fusarium* spp. E4 and E5 can promote the growth of their host, *Euphorbia pekinensis*, and increase its terpenoid content (Gao et al. 2011). A similar situation was observed in suspension cultures of *T. cuspidate*, to which the addition of fungal endophyte culture supernatants led to the production of paclitaxel in amounts 1.8-fold greater than the controls (Li and Tao 2009). The endophyte PGP-HSF isolated and inoculated in vitro and in pot cultures of *Mentha piperita* had an effect on the emission of volatiles from the plant, such as the sesquiterpenoid cuparene (a novel compound of peppermint) (Mucciarelli et al. 2007). Terpenoids have roles in plant–fungus interactions as both constitutive and specifically induced chemical defenses.

Table 4.2 Percent inhibition of the root growth of three plant species by the organic extracts (CH_2Cl_2-Acoet 50:50) from the culture medium and mycelium of *P. medicaginis* an endophytic fungus isolated from *C. acuminata* leaves

Treatments	Incubated with constant agitation 100 μg/mL				Incubated in static conditions 100 μg/mL			
Plant species	Medium		Mycelium		Medium		Mycelium	
	CH_2Cl_2	Acoet	CH_2Cl_2	Acoet	CH_2Cl_2	Acoet	CH_2Cl_2	Acoet
Percentage of inhibition of root growth								
Amaranthus hypochondriacus	44.2*	48.8*	6.3	45.1*	75.8*	70.0*	78.1*	41.4*
Solanum licopersicum	30.1*	52.4*	11.1	38.7*	34.4*	72.1*	53.8*	44.4*
Ipomoea purpurea	20.7	7.5	14.0	40.5*	24.3*	22.8*	23.6*	12.6

* $p < 0.05$

Schulz et al. (1999) and Schulz and Boyle (2005) have proposed the hypothesis of balanced antagonism. According to this hypothesis, asymptomatic colonization is a balance of antagonisms between host and endophytic fungi or bacteria. Endophytes and pathogens can produce phytotoxic metabolites, and the host can defend itself with preformed or induced defense metabolites (Schulz et al. 2002; Schulz and Boyle 2005). If the fungal virulence and plant defense are balanced, the interaction remains asymptomatic, but if the host-endophyte interaction becomes imbalanced, a disease could occur in the host, or the fungus could be killed (Schulz et al. 2002; Schulz and Boyle 2005).

The type of interaction depends on the general status of the partners, the virulence of the fungus, the defenses of the host, environmental factors, nutritional status and the developmental stages of the partners (Saikkonen et al. 1998; Schulz et al. 2002; Schulz and Boyle 2005). Based on the hypothesis of balanced antagonism, fungal endophytes from previously reported plants with allelopathic potential inhabiting the El Eden Ecological Reserve were isolated and studied (Anaya et al. 2003a, b, 2005; Macías-Rubalcava et al. 2007). Considering the allelopathic properties of the hosts, endophytic fungi isolated from the plants were expected to have allelochemicals with phytotoxic activities. After several preliminary antagonism bioassays involving endophyte–plant, endophyte–endophyte, and endophyte–phytopathogen, the most antagonistic fungi were selected to investigate whether antagonism is related to the production of allelochemicals.

Organic extracts of the culture medium and mycelium of *P. medicaginis*, an endophytic fungus isolated from *C. acuminata* were tested for their effects on the root growth of three plant species. This endophytic fungus was cultivated in liquid potato-dextrose medium (PD) with constant agitation and in static conditions. Effects on the root growth were different depending on factors such as the test plant species, the extracted fungus material (culture medium or mycelium), the solvent used for extraction, and the incubation conditions. In general, *Amaranthus* and *Solanum* were the most inhibited plant species (Table 4.2).

Macías-Rubalcava et al. (2008) confirmed the phytotoxic effects of naphthoquinone spiroketals from *E. gomezpompae* on root growth; they hypothesized that these compounds could be involved in the antagonistic balance between plant and fungi defenses.

Plant hosts could have an effect on the ability of fungi to synthesize allelochemicals. A species of endophytic fungus could be isolated from distinct plants, and the allelochemical activities of the isolates could be different. Suryanarayanan et al. (2009) observed that the herbicidal activity of secondary metabolite(s) from the endophyte *Phyllosticta capitalensis* differed depending on the plant host from which the endophyte was isolated. It can be expected that morphologically indistinguishable strains of the same species will exhibit different physiological traits that may be host-related (Petrini 1991).

Plant defense compounds are common stressors encountered by endophytes, but some endophytes can tolerate the defense compounds produced by host plants. Maize (*Zea mays*) produces benzoxazinoids (BXs), compounds that have antifungal effects. Some *Fusarium* species can tolerate a toxic BX and those species are frequently isolated from maize that produces BXs (Saunders and Kohn 2009). Huang et al. (2007) studied endophytes of medicinal plants and found that endophytes that are isolated from tropical plants could coexist with some of the phenolic compounds produced by host medicinal plants, such as chlorogenic acid.

Allelochemicals produced by endophytic fungi could have an important role in biotic and abiotic stress tolerance in host plants, but this is not the only possible mechanism. Other compounds as antioxidants, produced by endophytic fungi could have the effect of enhancing stress tolerance in host plants (Schulz et al. 2002; Huang et al. 2007; White and Torres 2010).

Yuan et al. (2010) explain that plant nutrition acquisition, metabolism, and stress tolerance may be strengthened or modulated by fungal symbionts, because fungal endophytes effectively endow the host with an extended phenotype. They mention that *Piriformospora indica*, a member of the order Sebacinales, simultaneously confers host resistance to biotic and abiotic stress. The production of bioactive metabolites by fungi, the overexpression of stress-related enzymes, the induction of biochemical processes, and the induced resistance in hosts upon fungal colonization are responsible for direct or indirect beneficial effects to hosts.

To identify allelochemicals and other compounds produced by endophytes in vivo, as well as elucidate the induction of biochemical mechanisms in host are necessary for a better understanding of the endophytic symbiosis (Rodriguez et al. 2008; Rodriguez and Redman 2008).

4.3.3 Allelochemicals of Endophyyic Fungi: Effects on Other Fungi

Saucedo-García (2006); Macías-Rubalcava et al. (2008), and Macías-Rubalcava et al. (2010) observed that allelochemicals also have an important role in the interactions of endophytes with endophytes and endophytes with phytopathogens.

Table 4.3 Effect of the organic extracts (CH_2Cl_2-Acoet 50:50) from the culture medium and mycelium of the endophytic fungus *M. yucatanensis* on the growth of other endophytic fungi isolated from some plants of the dry tropical forest at El Eden Ecological Reserve

Fungi species Treatments	*Guignardia mangifera*	*Phomopsis* sp.	Isolate 120	*Xylaria* sp.	*Muscodor yucatanensis*
Culture medium extract (μg/mL)	Percentage of inhibition or stimulation				
250	+125.3*	25.08*	3.5	16.27	45.3*
500	+132.6*	29.1*	7.56	18.7	45.6*
1000	+138.9*	31.7*	10.03	32.9*	43.9*
Mycelium extract (μg/mL)					
250	+118.5*	44.7*	2.8	14.23	16.3
500	+121.6*	53.6*	11.45	21.5*	15.8
1000	+122.0*	55.2*	12.32	25.6*	17.0

+ percent of stimulation. $^* p < 0.05$

The effects of organic extracts and pure compounds of selected endophytic fungi on the growth of other endophytic fungi from the same host plant and on pathogenic fungi showed generally similar patterns of inhibition, as in the preliminary antagonism bioassays.

The effects of mixtures of allelochemicals produced and released to the environment by endophytic fungi on other endophytes could be very specific. Organic extracts of the culture media and mycelium of *M. yucatanensis* were tested at different concentrations for their effects on the growth of other endophytic and phytophatogenic fungi (Macías-Rubalcava et al. 2010). Both organic extracts had different effects depending on the receptor fungus. In general the endophytes, *Xylaria* sp. and the mycelia sterilia 120 grew similarly when they were exposed to both extracts. The phytopathogen *Phomopsis* sp. was more inhibited by the mycelium than by the culture media extract. In contrast, *M. yucatanensis* growth was more inhibited by the extract of its own culture medium than by extract of its mycelium. Interestingly, both extracts greatly stimulated the growth of the endophyte *G. mangiferae* isolated from the same host (*B. simaruba*). This last result could indicate a mutualistic interaction between *M. yucatanensis* and *G. mangiferae* (Macías-Rubalcava et al. 2010, Table 4.3). Furthermore, the effects of organic extracts from the culture medium and mycelium of *Phoma medicaginis,* the endophytic fungi isolated from *C. acuminata* leaves, were tested on the growth of two types of phytopathogenic fungi with economical importance (PEI) and isolated from the surface of *C. acuminata* (PCA). *P. medicaganis* was cultivated in static conditions and with constant agitation. Agitation could be considered a stress factor for this fungus and may produce more bioactive allelochemicals when agitated. The results suggest that organic extracts of culture medium and mycelium of *P. medicaginis* growing in constant agitation generally are more inhibitory than those produced in static conditions, and they show that extracts of the culture medium caused greater inhibition that those of the mycelium (Table 4.4).

Table 4.4 Effect of organic extracts (CH_2Cl_2-Acoet 50:50) from the culture medium and mycelium of *P. medicaginis,* an endophytic fungus isolated from *Callicarpa acuminata* leaves, on the growth of phytopathogenic fungi

Treatments	Incubated with constant agitation 200 μg/mL				Incubated in static conditions 200 μg/mL			
Phytopathogenic fungi	Culture medium		Mycelium		Medium		Mycelium	
	CH_2Cl_2	Acoet	CH_2Cl_2	Acoet	CH_2Cl_2	Acoet	CH_2Cl_2	Acoet
PEI	Percentage of inhibition of diameter growth							
Alternaria solani	69.8*	3.8	60.8*	23.6*	41.2*	14.4	16.5	13.4
Fusarium oxysporum	45.2*	48.8*	12.5	33.1*	35.6*	28.2*	9.5	18.2
Phytophthora capsici	71.7*	72.5*	67.4*	65.0*	49.2*	24.6*	12.8	13.6
Rhizoctonia sp.	79.8*	100*	40.5*	73.7*	50.8*	2.0	45.0*	27.3*
PCA								
Pestalotiopsis sp.	73.8*	77.8*	41.4*	70.2*	53.0*	37.0*	45.7*	25.8*
Fusarium sp.	33.4*	26.0*	103.9	35.8*	30.4*	1.8	6.7	22.8*

PEI = phytopathogens of economical importance; PCA = phytopathogens isolated from leaves surface of *Callicarpa acuminata.* * $p < 0.05$

The *Rhizoctonia* sp. and *Pestalotiopsis* sp. phytopatogens were the most inhibited by the extracts (Anaya et al., unpublished).

Antagonism bioassays were also performed to test whether the endophytes of the same plant showed lower antagonism or lower inhibition in their growth when interacting with each other rather than with endophytes isolated from different plants (Saucedo-García 2006). In general, it was observed that antagonism or growth inhibition did not differ significantly when endophytes interact with endophytes isolated from the same plant (same endophyte community) or with endophytes isolated from different plants (different endophyte community). This could mean that antagonism among endophytes is not dependent on the host plant. Because different fungi grow at different rates, an analysis of the correlation between the antagonism of endophytic fungi and their growth rates showed that fungi with lower growth rates had higher antagonism than fungi with high growth rates (Saucedo-García 2006). Fungal endophytes showing antibiotic effects tended to grow slower and were relatively less abundant than other fungi in the microbial communities. This could indicate a trade-off in endophytes between fast growth and the tendency to produce antibiotics (Mejía et al. 2008).

All these data are revelant because in a great number of the antagonism bioassays of endophytes versus phytopathogenic fungi, many endophytes reduced the growth of phytopathogens. That inhibition was also observed with organic extracts of those fungi. However, we cannot conclude that endophytes were "better competitors" than pathogens, because the bioassays were performed in vitro, and the growth rates of the pathogens and endophytes used on that bioassays were different. Host dependence could also be different between pathogens and those endophytes.

4.3.4 Endophytic Fungi: Bioassays In Vitro and In Vivo

Antagonism bioassays in vitro could show variable results depending on the culture medium used for the bioassays (Prada et al. 2009) or the use of leaf extracts from the host plant (Arnold et al. 2003). However, it is important to remember that allelochemicals from endophytic fungi that reduce growth of phytopathogen microorganisms in vitro could provide benefits to their host plants (Espinosa-García et al. 1996; Arnold et al. 2003).

The results of antagonism bioassays have been further corroborated in the greenhouse (Arnold et al. 2003; Rubini et al. 2005) and in the field (Mejía et al. 2008). Although in vitro results do not necessarily translate directly to what occurs in plants, all of these results are promising; endophytes have in many cases exhibited inhibition of important pathogenic organisms, even in cultures, and even when the inhibitory effect is lower than that of in vitro experiments or greenhouse experiments (Rubini et al. 2005; Mejía et al. 2008).

Endophytic fungi can reduce the plant damage caused by phytopathogenic microorganisms. *Theobroma cacao* endophytes significantly decrease oomycetes *Phytophthora* sp. (leaf necrosis and leaf mortality) (Arnold et al. 2003), and *Phytophthora palmivora* (black pod rot) (Mejía et al. 2008) and pathogen fungi *Moniliophthora roreri* (frosty pod rot), and *M. perniciosa* (witches broom) (Rubini et al. 2005; Mejía et al. 2008).

A reduction of foliar disease caused by *Puccinia* and *Pyrenophora* spp. in wheat has been reported when plants are initially inoculated with *Chaetomium* and *Phoma* endophytes (Dingle and Mcgee 2003; Istifadah and Mcgee 2006). This effect was attributed to allelochemicals produced by the endophytes because culture filtrates of these fungi also reduced the disease severity.

In their experiment, Lee et al. (2009) inoculated maize plants at different times with the endophyte *Fusarium verticillioides* and the phytopathogen *Ustilago maydis* and they obtained variable results. When endophytic fungi were simultaneously co-inoculated with the phytopathogen, the smut disease severity decreased significantly, and plant growth increased. However, this beneficial effect was not observed when the endophyte was inoculated before and after the phytopathogen. *F. verticillioides* interfered directly with the early infection process of *U. maydis*, limiting disease development. In this fungus–fungus interaction, *F. verticillioides* secretes allelochemicals such as fusaric acid (FA), which are passed to the phytopathogen and inhibit its growth. The role of FA and possibly other secondary metabolites in a mixture could be significant due to their allelopathic effects on *U. maydis*, because the addition of FA to liquid cultures of this phytopathogen decreased cell density by up to 99.8 % compared with the no-FA controls (Lee et al. 2009).

Endophyte−endophyte and endophyte–phytopathogen interactions have been studied in vivo indirectly. The co-occurrence of endophytes–endophytes and endophytes–pathogens has been analyzed to identify interspecific interactions (e.g., competition or facilitation) in the endophyte community assembly. With the objective of evaluating whether interspecific interactions in endophyte communities from a cultured plant are influenced for management culture, foliar endophytic fungi of *Coffea arabica* were isolated from four shaded coffee farms, with two distinct culture practices, from the central coffee region of Veracruz, Mexico. Facilitation is a kind of positive species interaction, in which a fungal endophyte community could occur if host infection by one species leads to the host becoming more vulnerable to infection by another species (Pan and May 2009). On the four coffee farms, facilitation between some co-occurring endophytes on each leaf was observed (Saucedo-García, unpublished).

In studies of endophytic fungi is evident a diverse assemblage of endophytes species in host plants. The diversity of those fungi could play an integral role in the resistance of hosts to pathogen damage. Endophytes might protect host plants via a "mosaic effect" (Carroll 1991), whereby endophytes create a heterogeneous chemical landscape within and among plant organs (Espinosa-García and Langenheim 1990). As a result, the tissues of plants would differ unpredictably for herbivores in terms of palatability and quality as well as infectivity for pathogens.

4.4 Conclusions

Plants live with a complex community of microorganisms that inhabit their surfaces or inside them. AMF and endophytes are part of that community and, as well as other microorganisms, have an important role in ecosystem processes and plant interactions.

Any alterations of their communities in the soil caused by the invasion of exotic species may modify competition and break out an allelopathic process. It has been demonstrated that invading plants are capable of altering AM fungal communities, both in terms of the fungi present in their own roots and those that colonize native plant roots after invasion, i.e., the interaction maize-*Rottboellia*. Maize grew without *R. cochinchinensis*, displayed the greater total colonization with AMF (84 %) in their roots; however, maize TC decreased sharply when the maize grew with *R. cochinchinensis* in fertilized and unfertilized conditions. On the other hand, fertilized *R. cochinchinensis* showed a very high increase in AMF colonization when it grew with maize. Nevertheless, in unfertilized conditions this invasive grass showed similar TC of AMF with and without the presence of maize. Some spores from *Glomus* species, mainly *G. microaggregatum,* were identified in the soils of both plants (*R. cochinchinensis* and maize) regardless fertilization, with an exception, *G. microaggregatum* was not found in soil of *R. cochinchinensis* growing alone.

Plants with allelochemical properties from Ecological Reserve El Eden Quintana Roo show a higher richness of endophytic fungi within their leaves. From the leaves of *C. acuminata* a new genus, species *E. gomezpompae* and from the leaves of *B. simaruba* the new species *M. yucatanensis* were isolated. These fungi and other endophytes isolated from plants of the dry tropical forest at the El Eden

Ecological Reserve and from leaves of *C. arabic*a from coffee plantations of Veracruz, produced allelochemicals with phytotoxic and/or fungitoxic activities. For example, from *E. gomezpompae* were isolated and characterized four novel naphthoquinone spiroketals with biological activities. Further investigations of plant-associated microbial communities are needed to understand the roles of allelochemicals produced or induced by AM fungi or by endophytes and to understand their effects on microbial and plant communities.

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Chapter 5
Allelopathic Dynamics in Resource Plants

Sang-Uk Chon and C. Jerry Nelson

Abstract Allelopathy plays a key role in both natural and managed ecosystems, especially agroecosystems such as weed control, crop protection, and crop re-establishment. Allelopathic chemical(s) are moved from the plant, mainly the leaves, to the soil by transfer mechanisms and their subsequent dissipation occurs in the soil. The allelopathic activity is confirmed through (a) bioassays with aqueous or various solvent extracts and residues, (b) fractionation, identification, and quantification of causative allelochemicals, and (c) mechanism studies on the allelochemicals. Most assessments of allelopathy involve bioassays of plant or soil extracts, leachates, fractions, and residues based on seed germination and seedling growth in laboratory and greenhouse experiments. Plant growth may be stimulated below the allelopathic threshold, but severe growth reductions may be observed above the threshold concentration depending upon the sensitivity of the receiving species. Petri dish bioassays with methanol extracts or fractions and causative phenolic allelochemicals showed significant phytotoxic activities in concentration-dependent manner. Delayed seed germination and slow root growth due to the extracts could be confounded with osmotic effects on rate of imbibition, delayed initiation of germination, and especially cell elongation; the main factor that affects root growth before and after the tip penetrates the seed coat. Microscopic approaches for extract evaluation at the ultrastructural level have been precisely investigated. Many wild plants have allelopathic potentials, and the activities and

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types and amount of causative compounds differ depending on the plant species. The incorporation of allelopathic substances into agricultural management may reduce the use of pesticides and lessen environmental deterioration.

5.1 Introduction

5.1.1 Allelopathy and Autotoxicity

Allelopathy was defined by Molisch (1937) as a chemical interaction between plants or sometimes between microbes and higher plants that includes stimulatory as well as inhibitory influences. Later, it was defined as any direct or indirect, harmful or beneficial effect of one plant as a donor plant on another as a recipient plant through the production of chemical compounds that escape into the environment (Rice 1984). When a plant produces allelopathic compounds that are detrimental to establishment of new seedlings of its own, the effect is called autotoxicity, which is a specialized intraspecific form of allelopathy. Allelopathy and autotoxicity can play significant roles under both natural and manipulated ecosystems (Rice 1984), mainly by adversely affecting seed germination and seedling growth. Allelopathic interactions among plants have been observed for centuries even though fewer specific allelochemicals have been identified.

Autotoxicity of alfalfa during and after alfalfa establishment was first described by Jensen et al. (1981). They concluded that autotoxicity exists, where alfalfa has low germination, poor establishment, and low productivity when grown after alfalfa, compared to that grown after another species or after fallow, but the mechanism was not understood. Potential problems could be due to (i) soil water depletion, (ii) plant diseases, and (iii) autotoxicity potential (Kehr et al. 1983; Martin and Leonard 1967; Tesar 1993) and each of these factors causing yield reductions. Of these, autotoxicity is now identified as the most frequent cause of reseeding failure (Tesar 1993; Miller 1996; Webster et al. 1967).

During the past few years, many general principles have been learnt about seedling responses to the toxins (Chon et al. 2000), their movement in soil (Jennings and Nelson 1998), and effect of management on autotoxicity (Tesar 1993; Miller 1996). The autotoxic chemicals are: (i) extractable from fresh alfalfa herbage (ii) not a product of microbial action (Hall and Henderlong 1989), (iii) water-soluble (Read and Jensen 1989), and (iv) more concentrated in alfalfa shoot than in roots (Miller 1996). These chemicals (i) delay germination (Dornbos et al. 1990), (ii) inhibit alfalfa root growth, (iii) cause swelling, curling, and discolouration of the root (Read and Jensen 1989), (iv) reduce alfalfa root growth more than seed germination (Read and Jensen 1989), and (v) cause lack of hairs in roots (Hegde and Miller 1992a).

Typical plant symptoms in autotoxic fields are dwarfed, spindly, yellowish-green seedlings with irregular brown-reddish to dark brown lesions on the tap and lateral roots and only few effective nodules (Webster et al. 1967). The microbial activity (Hall and Henderlong 1989; Barnes and Putnam 1986; Klein and Miller 1980; Weston and Putnam 1986) and macro- and micronutrient deficiencies (Webster et al. 1967; Webster and Dekock 1969) may also be the causes of growth inhibition. The main effect of alfalfa autotoxicity is reduced development of the taproot in seedlings.

Autotoxicity primarily causes stand failure, when alfalfa is planted too soon after old alfalfa. Often, autotoxicity is not considered a problem, if the new alfalfa stand becomes established as germination and plant development may appear normal. Yield reductions or poor persistence are attributed to other factors. However, evidence from recent research, shows that the negative effects of subtle autotoxicity may linger, causing unnoticed long-term reductions in plant stands and yield.

Autotoxic effects have been reported in coffee (*Coffea arabica*) (Friedman and Waller 1983), rice (*Oryza sativa*) (Chou and Lin 1976), grape (*Vitis* sp.) (Brinker and Creasy 1988), peach (*Prunus persica* L.) (Quiros and Bauchan (1988), apple (*Pyrus malus*), and asparagus (*Asparagus officinalis*) (Hartung et al. 1989). Autotoxicity has also been documented in certain ferns (*Osmunda cinnamomea*, *O. claytoniana*, and *Dennstaedtia punctilobula*) in New Jersey and Vermont (Munther and Fairbrothers 1980), ragweed parthenium (*Parthenium hysterophorus*) in India (Kumari and Kohli 1987), American pokeweed (*Phytolacca americana*) in Tennessee (Edwards et al. 1988), *Anastatica hierochunita*, a desert plant in Egypt (Hegazy et al. 1990) and in mesquite (*Prosopis juliflora*) in Saudi Arabia (Warrag 1994).

5.1.2 Role of Allelopathy in Agro-ecosystem

Suitable manipulation of allelopathy toward improvement of crop productivity and environmental protection through eco-friendly control of weeds, insect pests, crop diseases, conservation of nitrogen in crop land, and synthesis of novel agrochemicals based on natural products have gained prominent attention of scientists engaged in allelopathic research. The allelochemicals can affect physiological functions like respiration, photosynthesis, and ion uptake. More recently, however, attention has also been drawn to exploit the positive significant roles of allelopathy and what role this phenomenon can play in enhancing crop productivity. Allelopathy plays a significant role under both natural and managed ecosystems (Rice 1984), mainly by adverse effects on seed germination and seedling growth. Although allelopathic symptoms among plants have been observed for centuries, fewer specific allelochemicals have been identified. For example, the allelopathic plant black walnut (*Juglans nigra* L.) produces juglone, which is highly toxic to many plants (Scisciolo et al. 1990). Autotoxicity is specialized intraspecific form of allelopathy that involves one or more chemical compounds. In alfalfa (*Medicago sativa* L.), autotoxicity by the allelochemicals or their complex from the donor plant, adversely affects its own species more than other species. This raises interesting ecological situations for competitiveness and replant decisions.

5.1.3 Eco-friendly Weed Control Using Allelopathic Plants

A serious problem of modern agriculture is crop loss caused by weeds. Worldwide, weeds alone cause a 10 % loss in agriculture production (Altieri and Liebman 1988). Yet, allelopathic principles of crops can be used as an alternative mean of weed control based on natural products. Although allelopathy is often considered a problem for agriculture, there is now considerable evidence to suggest that it might be exploited to help manage weed problems in a variety of agroecosystems. In agroecosystems, several weeds, crops, agroforestry trees, and fruit trees have been shown to exert allelopathic influence on associated or subsequent crops, thus affecting their germination and growth adversely (Kohli et al. 1993). Most allelopathic evidence has been associated with the effect of weeds on crops, and crops on crops, and crops on weeds. Of these, an important economical potential of allelopathy may be the ability of crops to suppress weeds. Allelopathic weeds also can affect crops by a number of ways like delaying or preventing seed germination and reducing seedling growth. Approaches that have already been explored are selection for allelopathic types within the crop germplasm, use of allelopathic rotational or companion plants in cropping systems, and biosynthesis of useful natural herbicides from higher plants and microorganisms.

Alternatives to synthetic chemical herbicides need to be developed, especially for organic or eco-friendly farming operations, landscape management systems, home gardens, and for situations where public policies mandate reduced pesticide use. Most studies on allelopathy have focused on interference and allelopathic effects of several important weeds on crop yields. Several weeds have been shown to have allelopathic potentials and others are suspected to have allelopathic potential in agro-ecosystems (Rice 1984). Plant seedlings of various crops possess allelopathic potential or weed-suppressing activity, including cucumber (*Cucumber sativus*) (Putnam and Duke 1974), oat (*Avena spp.*) (Fay and Duke 1977), and rice (Dilday et al. 1994; Olofsdotter and Navarez 1996). A total of 538 accessions of cultivated and wild cucumber were screened in pot and field tests with several accessions causing inhibited growth of *Brassica hirt*a and *Panicum miliaceum* (Putnam and Duke 1974). Out of more than 3,000 accessions of oat, several exuded a large amount of an allelochemical, scopoletin (Fay and Duke 1977). Also oat suppressed the growth of *Erysimum cheiranthoides* in both laboratory and field tests due at least in part, to an allelopathic mechanism (Markova 1972).

Improving the competitive ability of crops also reduces dependency on herbicides. However, attempts to increase competitive ability while maintaining productivity have had limited success and no crop cultivar has been released with superior competing ability as a marketing argument. In crop competition including allelopathy, the importance of chemical interference has often been discussed (Rice 1995). The incorporation of an allelopathic character into a crop cultivar could provide the plant with a means of gaining a competitive advantage over certain important weeds (Putnam and Duke 1974). Wu et al. (1999) suggested that genetically improving crops with allelopathic potential and the allelopathy can play an important role in future management.

5.1.4 Growth Stimulation Effects of Allelochemicals

Einhellig and Rasmussen (1993) noted that biological activity of allelochemicals, including the autotoxic factors in alfalfa, was concentration dependent with a response threshold. Plant growth may be stimulated below the threshold, with mild to severe growth reductions observed above the threshold; each depending on the sensitivity of the receiving species, the plant process affected and the existing environmental conditions. Many instances of stimulatory effects of microorganisms on other organisms and of plants on microorganisms have been reported. Rice (1986) demonstrated growth stimulatory effects of volatile compounds, decaying leaves, and root exudates of parasitic and nonparasitic plants on several other species. He showed that decaying ground ivy leaves stimulated seedling growth of downy brome and radish. Chon et al. (2003a, b) evaluated aqueous extracts of 16 Compositae plants and found lettuce (*Lactuca sativa*), *Xanthium occidentale*, and *Cirsium japonicum* showed the highest inhibition on alfalfa seedlings. Conversely, extracts of *Chrysanthemum indicum, Youngia sonchifolia*, *Bidens frondosa*, and *Breea segeta* at concentrations below 20 g dry matter L^{-1} increased root length of alfalfa by 13–33 %. In another study, alfalfa root growth was stimulated by very low concentrations from alfalfa leaf extracts (Chon et al. 2000). We indicated that this stimulatory effect for a reputed autotoxic chemical was less than those reported by Einhellig and Rasmussen (1993) and Rice (1986) who evaluated stimulatory effects of allelochemicals. Chon et al. (2003a, b) reported stimulatory as well as inhibitory effects of Compositae plant species (Table 5.1).

5.2 From Petri Dish Bioassay to Field Trials

5.2.1 Bioassays for Improving Sensitivity

Sampling procedures of the donor material, conditions of the assay and selection of an appropriate test organism influence the sensitivity of a bioassay. A good bioassay gives precision of the measurement and consistency between experiments. To achieve this precision and consistency, studies on interference and sensitivity of

Table 5.1 Effects of aqueous extracts from several compositae plants on alfalfa root length (mm) 6 days after seeding. Root length of untreated control was 34.6 mm

Plant species	Extract concentration (g L^{-1})			
	10	20	30	40
Bidens frondosa	44.3(128)	39.7(115)	31.4(91)	7.1(20)
Breea segetum	42.1(122)	43.7(126)	28.2(81)	8.8(25)
Chrysanthemum indicum	41.2(119)	45.9(133)	35.3(102)	26.5(76)
Youngia sonchifolia	43.5(126)	40.1(116)	36.5(105)	27.4(79)
Eclipta prostrata	28.9(84)	19.5(56)	4.1(12)	1.7(5)
Cirsium japonicum	31.5(91)	22.0(63)	7.6(22)	0.0(0)
Xanthium occidentale	33.3(96)	2.9(8)	0.0(0)	0.0(0)
Lactuca sativa	34.3(99)	0.2(1)	0.0(0)	0.0(0)

Values in parentheses represent % of control
Source Chon et al. (2003a)

the bioassay are necessary. An appropriate bioassay to distinguish autotoxic factors from competition or inherent growth properties of alfalfa are needed to screen germplasm and to assess management practices. Autotoxic and allelopathic effects have been evaluated in petri plates with filter paper (Hall and Henderlong 1989; Chung and Miller 1995a; Cope 1982; Hegde and Miller 1990), but results can be inconsistent due to nonuniform moisture conditions or swelling of the paper in localized areas (Pederson 1986).

Bioassay techniques (Pederson 1986; Ben-Hammouda et al. 1995; Carlson et al. 1983; Dornbos and Spencer 1990) in which the extract is mixed into agar provide a more sensitive evaluation of allelopathic effects (Pederson 1986; Dornbos and Spencer 1990). Dornbos and Spencer (1990) reported that the modified agar bioassay required smaller quantities of compound per seed for comparable results compared to commonly used filter paper procedure. This was verified for autotoxicity of alfalfa (Chon et al. 2000).

Light had a stronger inhibitory effect on hypocotyl elongation of controls than did the autotoxic chemical(s). Root growth was sensitive to the autotoxin in both light and darkness (Chon et al. 2000). Arnim and Deng (1996) found that hypocotyl growth was inversely associated with light intensities and qualities. Reduction of hypocotyl length by light may have allowed allocation of more resources to root growth, thus longer roots are produced allowing a better estimate of growth rate. Hypocotyl growth was not very sensitive to the autotoxic chemical(s) on either agar or paper media, when the plate was flat, perhaps because the hypocotyl arched upward to escape contact with the extract. Hypocotyl growth was very sensitive when germination and seedling growth occurred in a rolled paper towel held vertically; likely because of the hypocotyl remained in continuous contact with the extract (Chon et al. 2000).

Root growth was stimulated at very low concentrations from leaf extracts (Chon et al. 2000). Einhellig (1986) noted that the biological activity of allelochemicals, including autotoxic factors in alfalfa, was concentration dependent with a response threshold in the experiment. Plant growth may be stimulated below the

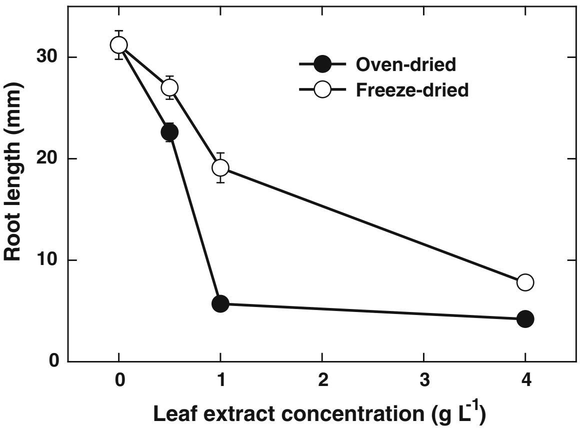


Fig. 5.1 Autotoxic effect of alfalfa leaf extract on alfalfa root growth as affected by different extract concentrations and drying methods. Each *bar* represents standard error of the mean (Chon and Nelson 2001)

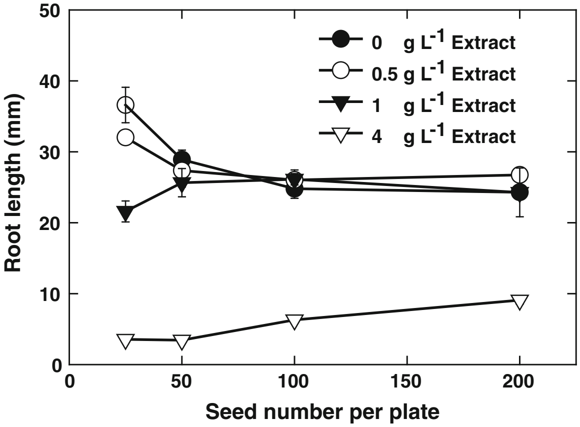
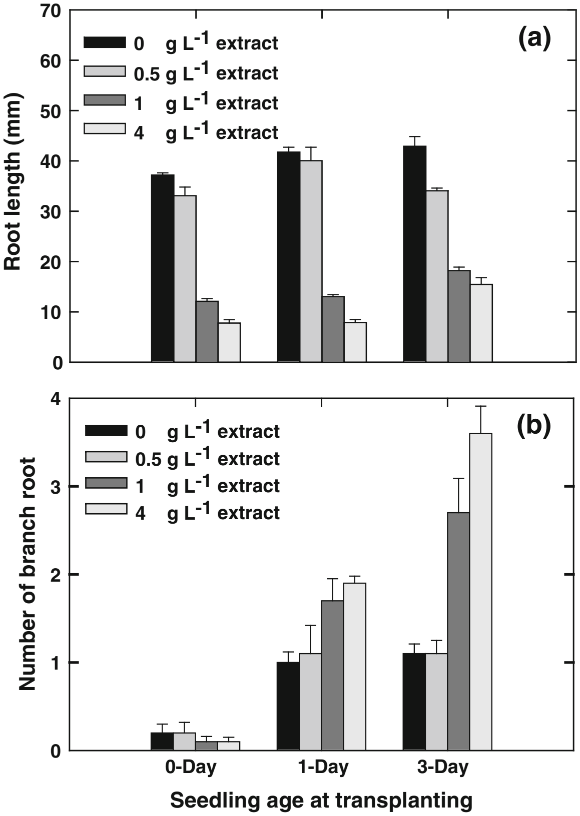


Fig. 5.2 Effect of seed number on the autotoxic responses of root length of alfalfa as affected by different extract–agar concentrations. Each *bar* represents standard error of the mean (Chon and Nelson 2001)

threshold, but mild to severe growth reductions may be observed above the threshold concentration depending upon the sensitivity of the receiving species, the plant process and environmental conditions. Many instances of stimulation effects of microorganisms on other organisms and of plants on microorganisms have been reported Chon et al. (2003a, b).

Extracts from oven-dried samples were stronger than those from freeze-dried samples (Chon and Nelson 2001) (Fig. 5.1). Chon and Nelson (2001) suggested that oven-drying and sterilizing by filtering or autoclaving can improve the consistency and precision of bioassay of leaf extracts (Fig. 5.2). The bioassay was suitable with 50 or fewer seed per 11-cm petri dish, which minimized interaction among seeds or interference (e.g., competition and autotoxicity from other seed in the test). The bioassay can be improved by using very young roots from imbibed seed, which are more sensitive to the autotoxin (Fig. 5.3). Chon et al. (2004) reported that release of autotoxic substances from seed during seed imbibition was

Fig. 5.3 Effect of seedling ages on the autotoxic responses of root length (**a**) and number of branch root (**b**) of alfalfa as affected by different extract–agar concentrations. Each *bar* represents standard error of the mean (Chon and Nelson 2001)

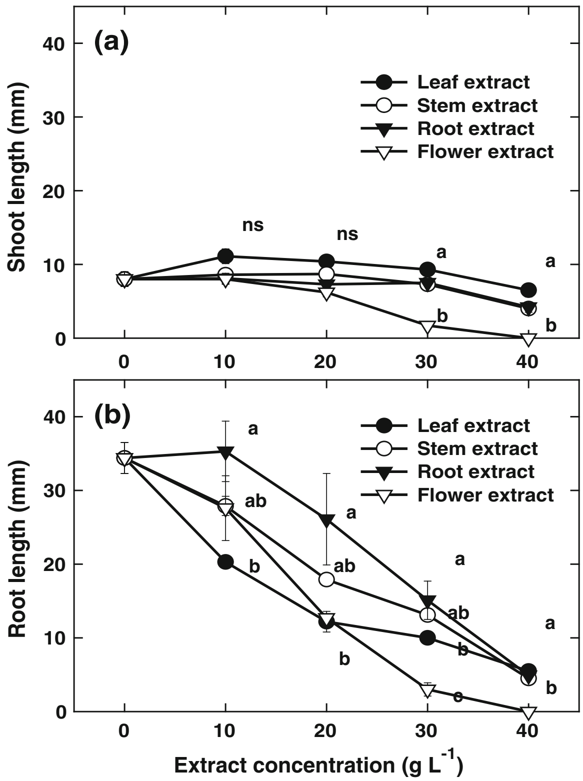


increased with increase of soaking time and seed amount and that autotoxicity was stronger in extract from ground seed than whole seed.

Most assessments of allelopathy, especially at early stages, involve bioassays of plant or soil extracts based on seed germination and seedling growth. A reliable bioassay that is sensitive is needed for more in-depth studies of the growth mechanisms involved and for developing initial analytical procedures to determine the chemical(s) responsible. Generally germination is less sensitive to the allelopathic chemical than is seedling growth, especially root growth (Miller 1996). Although many laboratory bioassays have proposed to demonstrate allelopathy, concerns have been raised that most of them have little relevance in terms of explaining behavior in the field (Connell 1990; Inderjit and Olofsdotter 1998; Inderjit and Dakshini 1995; Inderjit and Dakshini 1999).

Virtually all plant parts such as leaves (Kumari and Kohli 1987), roots (Horsley 1977), pollen (Cruz-Ortega et al. 1988), trichomes (Bansal 1990), bark (Kohli 1990) and seeds and fruits (Fredman et al. 1982) have allelopathic potential. It is generally accepted that water extracts of top growth (especially leaves) produce more allelopathy for seedlings than those from roots and crowns of alfalfa (Miller

Fig. 5.4 Effects of *C. japonicum* leaf, stem, root, and flower extracts on shoot (**a**) and root lengths (**b**) of alfalfa as affected by different concentrations. Within an extract concentration, means followed by the same letter are not significantly different at $p < 0.05$. Each *bar* represents standard error of the mean (Chon 2004)



1996), and that shoot extract from the reproductive stage was more inhibitory than from the vegetative stage under laboratory conditions (Chung and Miller 1995b; Hegde and Miller 1992b). Chung and Miller (1995b) ranked autotoxic effects of water extracts of plant parts of alfalfa as leaf (the greatest), seed, root, flower, and stem (the least). Chou and Leu (1992) reported that extracts from flowers of *Delonix regia* exhibited highest inhibition against three test plants, alfalfa, lettuce, and Chinese cabbage (*B. chinensis*). Chon (2004) reported that phytotoxic effects of a series of aqueous extracts from leaves, stems, roots and flowers of common thistle (*C. pendulum*) on alfalfa seedlings showed highest inhibition in the extracts from flowers and leaves, followed by stems, and roots (Fig. 5.4).

5.2.2 *Evaluating Methods on Allelopathy*

Two general approaches can be pursued for genetic solution to the autotoxicity problem, (i) to alter the production of the autotoxic chemical (s) in plants and (ii) to increase the tolerance of alfalfa seedlings to these chemical(s). Many questions arise regarding the former, especially if the autotoxic and heterotoxic chemical(s) is the same. If production of the chemical(s) is decreased, the range of compatibility with grasses would increase, but problems of weed control (during establishment and in thinning stands) may be increased. Conversely, the increased production of chemicals may lead to longer delays in reseeding alfalfa, but may be helpful for long-term weed control. There are many ecological issues to be seriously considered, but that should not delay feasibility studies on genetically altering plant productivity of the chemical(s).

Genetic tolerance of alfalfa seedlings to the chemical(s) has been evaluated in the field with minimal success. For example, there was little difference in tolerance to autotoxicity among alfalfa cultivars that differed in disease resistance (Goplen and Webster 1969; Hurd et al. 1996; Miller 1983) or phytophthora resistance (Cosgrove 1996). There have been few laboratory evaluations. Chung and Miller (1995a), (b) evaluated the extracts from several alfalfa cultivars on seed germination and early seedling growth from extracts of the same cultivar. Their data suggested genetic variation was occurring, but due to the nature of the experiment, it was not possible to determine if the difference is due to genetic variation in the production of the chemical, tolerance to the chemical, or a combination of both.

Evaluation of 20 alfalfa genotypes in the laboratory based on root length bioassay showed inherent genetic variation (Table 5.2). Nearly twofold range in response was found among genotypes to both 0.1 and 0.4 % water extract of ‘Cody’ leaf material (Chon et al. 2000). Path coefficient analysis revealed that genetic variation in root length was 7–17 times more important than hypocotyl length, for determining the total seedling length and that final root length for autotoxic effects of extracts was influenced more by variation in root growth rate than by variation in seed size (Chon et al. 2003a, b) or time to reach 50 % of final germination (GT_{50}) (Table 5.3). Next, we evaluated 18 progeny and parents (selected to show a range in response). Again we found similar twofold variation among the genotypes. This suggests genetic progress can be made in selection for tolerance to the autotoxic chemical(s) among broad-based entries. The problem is exacerbated, however, by needing to assess each germplasm in terms of the treatment relative to the control. Experimental errors for both measurements are included in the error for the final percentage.

We have discussed with several alfalfa breeders in the private sector and they report interest in increasing tolerance, but the early tests were not very effective. No significant trend was apparent among cultivars differing in fall dormancy, grazing tolerance, insect resistance, breeding company, method of prior selection, or area of origination of the cultivar. No specific reasons are known, although test-to-test variation in absolute root lengths was high but rankings among tests were very similar. Again, a deterrent to the rapid and accurate evaluation is slow bioassays that require control plants of each entry to calculate the relative tolerance. Breeders need rapid and accurate techniques to evaluate parents and progeny to make progress as quantitative traits may require several generations to make a difference. Thus the need to identify the chemical(s) involved is again emphasized so that better laboratory methods, including biotechnology, can be used to facilitate evaluations and improve selection progress.

Table 5.2 Percent of control in root length of 20 germplasms 5 days after seeding on agar containing leaf extracts of alfalfa 'Cody'[a]

Germplasm Entry number	Extract concentration	
	$1.0\ g\ L^{-1}$	$4.0\ g\ L^{-1}$
15	91.4 a	17.3 bc
16	81.0 ab	28.6 ab
7	80.0 ab	36.4 a
11	78.4 abc	17.6 bc
14	69.9 abcd	14.9 c
10	64.4 bcde	11.2 c
19[b]	64.2 bcde	18.5 bc
12	64.0 bcde	20.7 bc
6	61.1 bcdef	13.7 c
18[b]	58.3 bcdef	10.3 c
5	58.2 bcdef	18.4 bc
20[b]	57.2 bcdef	11.4 c
13	55.2 cdef	14.7 c
17	54.2 cdef	12.4 c
3	49.9 def	9.5 c
4	49.5 def	11.2 c
8	48.9 def	12.9 c
9	46.3 def	12.1 c
2	42.1 ef	9.6 c
1	37.2 f	8.5 c
Mean	60.6	15.5
LSD, 0.05	24.3	12.4

[a] Means with the same letter are not significantly different

[b] Cultivars were entries 18 = 'Innovator', 19 = 'Magnum IV', and 20 = 'WL252'

Source Chon et al. (2003b)

5.2.3 Residue Incorporation in Soil

Generally, residue inhibition of seedling growth was enhanced if crop residue was incorporated before planting, drastically reduced if residue remained on the surface (Cochran et al. 1980; Elliott et al. 1981). Crop residue toxicity to winter wheat seedlings was likely to be caused by either an allelopathic compound or N immobilization due to increased microbial populations. The allelopathic compound was either a water-soluble compound leached from residue or a compound produced during microbial decomposition of plant residue (Cochran et al. 1980; Elliott et al. 1981). Another study (Kadioglu 2000) showed that the inhibitory effect of ground heartleaf cocklebur (*X. strumarium*) on *Amaranthus retroflexus*, *A. sterilis*, and *Conium maculatum*. Chon and Kim (2005) reported that the effect of residue incorporation with *X. occidentale* plant samples into soil on seedling growth of barnyard grass was examined in the greenhouse, and results showed that the leaf residues at 100 g kg^{-1} inhibited shoot and root dry weights of test plants by 70–90 % (Fig. 5.5).

Table 5.3 Path coefficient analysis, for autotoxic effects of extracts, of hypocotyl length, and root length on total seedling length across 20 germplasm

Pathway	Extract concentration		
	$0.0\ g\ L^{-1}$	$1.0\ g\ L^{-1}$	$4.0\ g\ L^{-1}$
Hypocotyl length vs total length, r_{21}	−0.017	−0.087	0.688
Direct effect, P_{21}	0.061	0.059	0.125
Indirect effect via root length, $r_{23}P_{21}$	−0.078	−0.146	0.563
Root length vs total length, r_{31}	0.998	0.998	0.995
Direct effect, P_{31}	1.003	1.007	0.919
Indirect effect hypocotyl length, $r_{23}P_{31}$	−0.005	−0.009	0.076
Hypocotyl length vs root length, r_{23}	−0.078	−0.145	−0.613[a]
P_{31}/P_{21}^{b}	16.4	17.1	7.4

[a] The indirect effect of hypocotyl length on total length was 0.56 because the correlation (−0.61) between hypocotyl length and root length was inversely high at $4.0\ g\ L^{-1}$ extract concentration ($p < 0.05$)

[b] Variation in root length is 16.4–17.1 times more important at 0.0 and 1.0 extract concentrations than hypocotyls length, but only 7.4 times more important in defining at $4.0\ g\ L^{-1}$

Source Chon et al. (2003b)

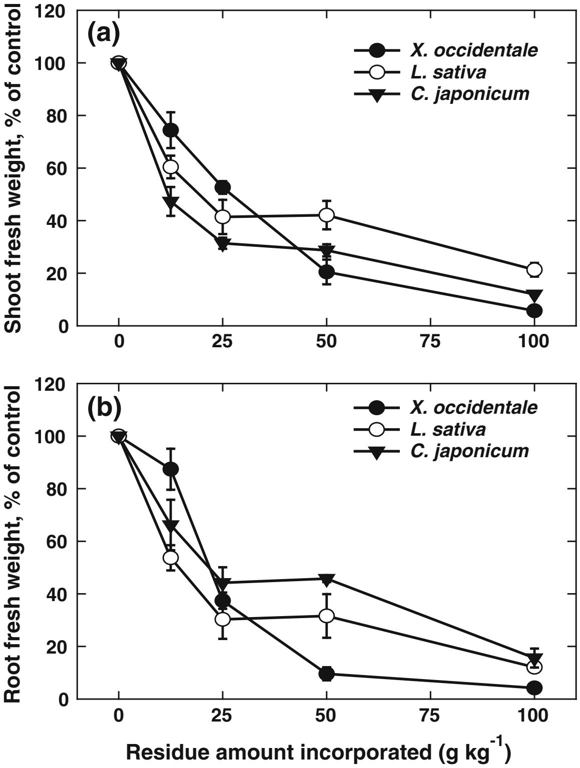


Fig. 5.5 Effects of dried leaf material incorporation of *X. occidentale*, *L. sativa*, and *C. japonicum* on shoot (**a**) and root (**b**) fresh weight of barnyard grass 15 days after seeding or treatment. Material was incorporated by mixing with soils. After incorporation, barnyard grass was seeded and immediately subirrigated. Shoot and root fresh weights were measured 15 days later (Chon and Kim 2005)

5.2.4 Field Experiments

A field research described that the early stage of grassland succession in Korea would be composed of *Plantago asiatica*, *Artemisia princeps* var. *orientalis*, *Oenothera odorata*, and *Zoysia japonica* was inhibited greatly by the *Artemisia* extracts. These contrasting views could result from differences between laboratory work and field observations (Park 1966). Yun and Kil (1992) reported that field soil collected under the *Artemisia* plants significantly reduced or somewhat promoted growth of the test plants. These results are in agreement or contrasted with following results: soil collected from some plant fields exhibited phytotoxicity by reducing growth (Al-Naib and Rice 1971; Al-Saadawi and Al-Rubeaa 1985; Inam et al. 1989) and soil from below some test plants did not inhibit germination and growth of the test species (Fadayomi and Oyebade 1984; Goel and Sareen 1986).

5.3 Discovery of Allelochemicals

5.3.1 Compounds Involved

Most important approach on allelopathy is to successfully isolate, identify, and quantify causative allelochemicals that present in plants or soils. It is essential that potential allelopathic compounds can also relate to the levels originally in the whole extracts. Natural products identified as allelopathic agents have been classed into the following (a) toxic gases, (b) organic acids from Krebs cycle and aldehydes, (c) aromatic acids, (d) simple unsaturated lactones, (e) coumarins, (f) quinones, (g) flavonoids, (h) tannins, (i) alkaloids, and (j) terpenoids and steroids, etc. Although many of these compounds are secondary products of plant metabolism, several are degradation products that occur in the presence of microbial enzymes. Several biosynthetic pathways lead to production of the various categories of allelopathic agents. The inhibitors usually arise through either the acetate or through the shikimic acid pathway. Several types of inhibitors, which originated from amino acids, come through the acetate pathway. Most of compounds that cause allelopathy were derived from amino acids, via the shikimic acid pathway (Rice 1984).

The source of the active agents may be living plants, litter, detritus, leachates, soil bacteria, fungi, mycorrhiza, root exudates, atmosphere, water, air-borne particles, or pathogenic organisms. Many organisms may be involved simultaneously in a particular interaction. Compounds isolated from plants or their leachates often do not reproduce the observed allelopathic effects without the associated factors. In many instances, these plant-derived compounds are modified by oxidation, reduction, photochemical activation (Fisher et al. 1994), detoxification, or biochemical activation by bacteria and fungi. Bioactive molecules may leave the system by being adsorbed onto inorganic particles or organic matter in the soil, or leached from the system.

5.3.2 Isolation, Identification, and Quantification

Causative allelochemicals reported from plants of family Compositae have not been fully identified. Identifying and quantifying the causative allelochemicals in plant and associated environments are the most important approaches for allelopathy study. Phenolic acids in the literature on allelopathy are often mentioned as putative allelochemicals and are perhaps the most commonly investigated compounds among potential allelochemicals. They are found in a wide range of soils or plants, and their phytotoxic potential against various plants has been demonstrated under controlled conditions. Phytotoxicity-based extraction and fractionation were employed to separate allelochemicals contained in each plant extracts. Chon et al. (2003a, b) reported that by means of high-performance liquid chromatography (HPLC) analysis, the responsible causative allelopathic substances present in *L. sativa, X. occidentale*, and *C. japonicum* were isolated from various fractions and identified as coumarin, *trans*-cinnamic acid, *o*-coumaric acid, *p*-coumaric acid, and chlorogenic acid.

5.3.3 Fractionation and Bioassay of Causative Allelochemicals

Methanol extracts from ground plant samples are used for the following bioassay and fractionation. Chon et al. (2003a, b) reported that these major phenolic compounds present in Compositae species were total phenol compounds of all fractions in *C. japonicum*, *L. sativa*, and *X. occidentale* by 60.3, 18.5, and 84.4 mg, 100 g^{-1}, respectively. They reported also, through the bioassay procedure, *X. occidentale* which had the highest total concentration, showed the most inhibitory effect on test plants in Compositae plant species (Table 5.4).

Chon et al. (2003a, b) reported that among 10 phenolic compounds assayed for their phytotoxicity on root growth of alfalfa, coumarin, *trans*-cinnamic acid, and *o*-coumaric acid were most inhibitory. Especially, coumarin at 10^{-3} M significantly inhibited root growth of alfalfa. Methanol extracts from BuOH, EtOAc, hexane, and water fractions were also assayed to confirm their phytotoxic effects. The results showed that methanol extracts of *X. occidentale* were most inhibitory on root growth of alfalfa, and that methanol extracts from BuOH and EtOAc fractions of *X. occidentale* reduced alfalfa root growth more than did those from hexane and water fractions. Methanol extracts from hexane and EtOAc fractions of *L. sativa* and *C. japonicum* reduced alfalfa root growth more than did those of BuOH and water

Table 5.4 Quantitative determination of HPLC analysis of some phenolic compounds (mg kg^{-1}) present in leaves of *X. occidentale*

Compound	Fractions				
	Hexane	EtOAc	BuOH	Water	Total
Coumarin	1.431	20.653	20.160	1.845	44.100
trans-cinnamic acid	83.932	201.550	42.026	2.001	329.500
o-coumaric acid	ND[a]	ND	ND	ND	ND
p-coumaric acid	ND	2.435	ND	ND	ND
Chlorogenic acid	22.418	2.406	35.899	333.314	394.000
Total	108.293	230.170	133.996	371.064	843.523

[a] Non-detected

Source Chon et al. (2003a)

fractions. Especially, methanol extracts from hexane and EtOAc fractions at 50 g L^{-1} reduced root growth by each 85 %, while treatment at same concentration of BuOH and water fractions reduced root growth by 40 and 15 %, respectively (Fig. 5.6).

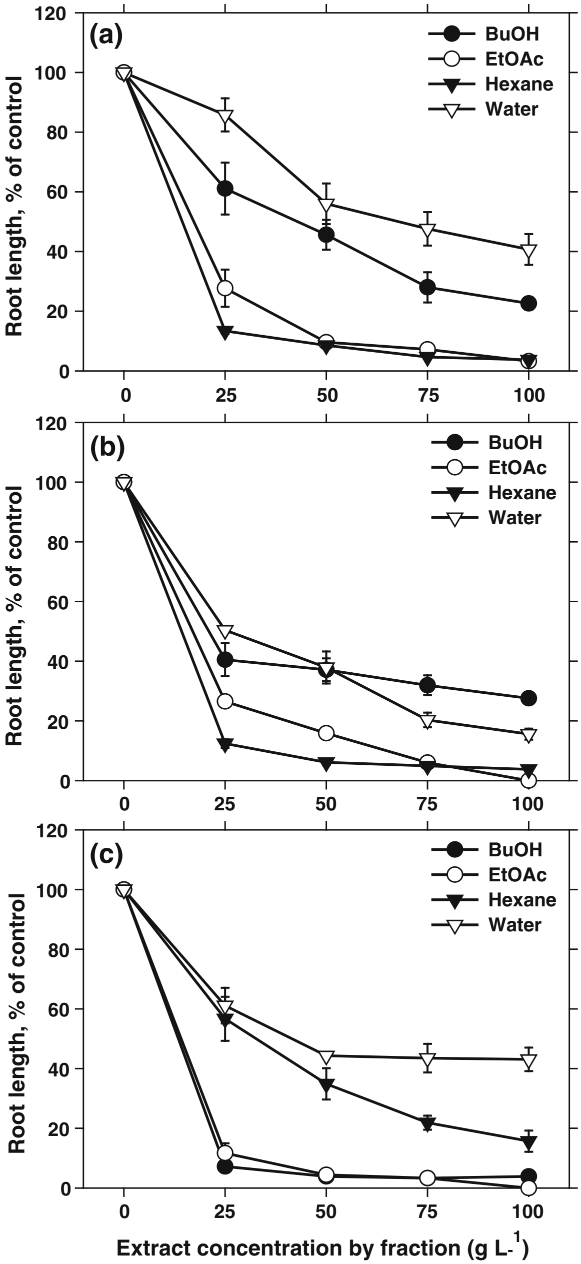
5.4 Mechanisms of Action of Allelochemicals

The allelochemicals act in a variety of ways, the major ones are described below.

5.4.1 Principal Modes of Action of Allelochemicals

This area of research has caused similar challenges for investigators working with either natural products or synthetic herbicides. The major difficulty is to separate secondary effects from primary causes. Although effects can be measured in isolated systems, there always remains the critical questions of whether the inhibitor reaches that site in the plant in sufficient concentration to specifically influence that reaction, and whether other processes may be affected more quickly. Some studies of the physiological events influenced by allelochemicals leading to the visible effects on target species are nutrient uptake (Rice 1984; Harper and Balke 1981; Fuerst and Putnam 1983), cell division (Rice 1984; Bukolova 1971), extension growth (Rice 1984; Lee and Skoog 1965), photosynthesis (Einhellig and Rasmussen 1979; Patterson 1981), respiration (Rice 1984; Koeppe 1972), protein synthesis (Zweig et al. 1972), membrane permeability (Harper and Balke 1981; Levitan and Barker 1972), and enzyme activity (Rice 1984; Lockerman and Putnam 1981; Lynch 1980; Williams and Hoagland 1982).

Fig. 5.6 Effects of various fractions from methanol extracts of *C. japonicum* (**a**), *L. sativa* (**b**), and *X. occidentale* (**c**) on alfalfa root length 6 days after seeding (Chon et al. 2003a)



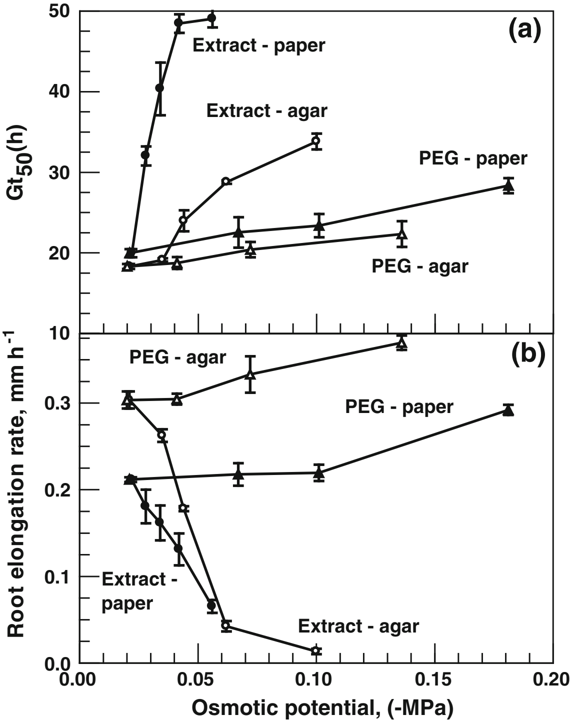


Fig. 5.7 Effect of osmotic potential of PEG 8000 and leaf extracts on (**a**) time to reach 50 % of final germination (Gt_{50}) and (**b**) root elongation rate. *Vertical bars* represent standard errors, some of which are hidden by the data symbol (Chon et al. 2004)

5.4.2 Allelopathy Versus Osmotic Effect

Osmotic solutions induce stress in plants, primarily due to tissue dehydration and reduced cell expansion (Bewley and Black 1994). Often the response of seed or seedlings to plant extracts in allelopathy assays is assumed to be due to chemical interference, but aqueous foliage extracts can also exert negative osmotic effects on test species (Bell 1974). Wardle et al. (1992) concluded from studies using aqueous leaf extracts of four pasture grasses that allelopathy bioassays are more realistic when the control treatments have been adjusted to the same osmotic potential as the plant extract being tested. Part of the autotoxic effect on alfalfa may be osmotic, as several osmotica are known to slow seed imbibition and time to emergence of alfalfa (Fick et al. 1988).

Delayed seed germination and slow root growth by an autotoxic extract could be confounded with osmotic effects on rate of imbibition, delayed initiation of germination, and especially cell elongation (Black 1989); the main factor that affects root growth before and after the tip penetrates the seed coat (Bewley and Black 1994). Root growth within the seed of germinating dicots is generally more sensitive to osmotic stress than after the tip is exposed beyond the seed coat (Hegarty and Ross 1978).

Alfalfa is autotoxic to seed germination and root growth of alfalfa seedlings. Transfer to polyethylene glycol (PEG 8000) at 10 h showed that delay in germination was due to osmotic properties. Root elongation rate was increased slightly by PEG solutions with greater than −0.20 MPa, which was lower osmotic potential than those of the strongest extracts, −0.10 MPa in agar, and −0.05 MPa on filter paper. These extracts reduced root elongation rate by up to 90 % due to the toxicity factors. Inhibition was slowed mainly by osmotic factors whereas delayed seed germination and, especially, reduced root elongation were due mainly to toxic factors of the leaf extract (Chon et al. 2004) (Fig. 5.7).

5.4.3 Transfer of Allelochemicals

Some consideration needs to be given to the mechanisms of autotoxic chemical (s) movement from plant to soil and their subsequent dissipation in soil (Chon et al. 2006) (Fig. 5.8). The leaves have the highest concentration, but the mechanisms of chemical movement from leaves to soil are unknown. Possibilities include (i) exudation of the chemical to the leaf surface, where it is washed off by rainfall and (ii) or release from the decay of leaves (dropped on soil due to disease or harvest). Most methods to prepare extracts do not use macerated tissue, yet the autotoxin is readily moved into solution (Chung and Miller 1995a, b) suggesting its deposition on leaf surface. After cutting of a leaf, the stomata close quickly and tightly, this suggests that the chemical has already moved to the surface leaf and being water soluble, was washed off. In some cases, e.g., alfalfa (Chung and Miller 1995a, b), the leaf surface of the donor seedlings was first sterilized (for an unknown period in 1:10 NaClO/water) which may have altered the amount of chemical on the leaf surface before the test extract was made. In this case the test leachate extracted with water, was not strong enough to affect alfalfa germination but it reduced root growth.

To date we do not know how the chemical is moved out of alfalfa leaves. For example, Guenzi et al. (1964) compared the amount of toxic chemical extracted from nonmacerated alfalfa shoot (presumably with stomata closed) and found differences due to season of year and stage of growth, but rainfall records were not given, hence we can not determine if the variation was due to physiological state of the plant or time elapsed after the most recent rainfall.

Most literature on forest allelopathy suggest that the allelochemicals are transferred by degradation of litter (Reigosa et al. 1999). The degradation process is closely associated with microbial activity, which is strongly influenced by temperature and soil water content. In alfalfa, leaf loss due to disease or harvesting may be major contributors to allelochemicals transport (Fig. 5.8). Addition of ground dry leaf material of alfalfa to soil can cause autotoxicity and is partly dependent on the amount added.

Rovira and Vallejo (2000), in a 2-year study, measured the rate of decomposition of alfalfa debris buried at different soil depths in September in a Mediterranean

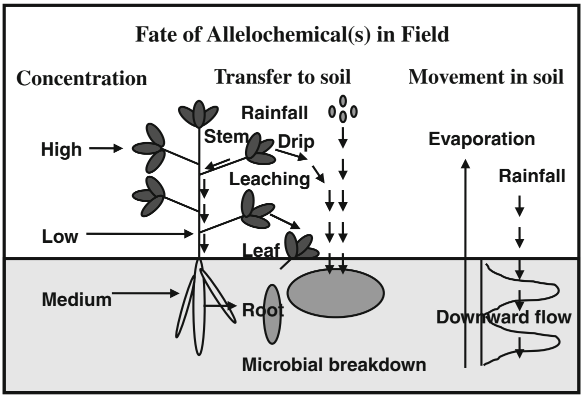


Fig. 5.8 Fate of allelochemical(s) in plant and fields. Concentration of allelochemical(s) is highest in leaves, intermediate in stems, and lowest in roots of alfalfa. The allelopathic chemical can be transferred to the soil by rainfall washing of the leaf and stem tissues and by dropping of old or diseased leaves (Chon et al. 2006)

climate. In all layers, the degradation was rapid in the first 4 months, then slowed down at 5-cm depth (where the soil water content was lower) than at 20- and 40-cm depths. In all cases, the nitrogen component disappeared faster than carbon component, with lignified tissue degrading slowest. At 5-cm depth, 28 % of the original C and 18 % of the original N remained in the debris after 2 years, whereas at 20- and 40-cm depths the amounts remaining were only about 19 and 12 %, respectively. No attempt was made to evaluate autotoxic potential. We expect more autotoxicity in spring seedlings than in fall seedlings in our continental climates, with higher summer rainfall. The high summer rainfall may facilitate faster microbial breakdown of residues and more downward flow in the soil to remove the chemical (Jennings and Nelson 1998).

There is some evidence for direct release of allelochemicals as root exudates (Hegde and Miller 1990). Root exudates may be less problematic for reseeding, as the chemical would be released about 1.5–2.0 cm below the zone of germination and early seedling development, unless the chemical(s) is moved upward by evaporation of soil water. In general, research shows that plowing the soil causes more rapid break down/decomposition of the autotoxin compared with minimum tillage that leaves the soil surface intact. The result is confounded, however, because the tillage increases the microbial activity and there is mechanical movement of the chemical away from the upper soil layers, where new seedlings would be exposed.

The chemical(s) moves with water in the soil and the movement is faster in sandy than in clay soils (Jennings and Nelson 1998). In addition to direct runoff of water from the leaves, there may be stem flow downward to the crown. This would affect lateral uniformity of deposition in the soil, with the highest concentration near the old plant for its protection against competitors. Moreover, the concentrated deposition of the autotoxin on the soil near the crown and root may confound interpretations that root exudation was involved. We are not aware of data for alfalfa documenting the comparative water movement off the canopy by leaf drip or by stem flow.

5.4.4 Inhibition of Nitrification

Conserving nitrogen in the soil is very important, and vital for sustaining crop productivity and management of natural resources. The inhibition of nitrification which converts ammonium (less leachable form) to nitrate (more leachable form) helps in conserving nitrogen as well as energy in the arable lands. Of late, the importance of its inhibition is realized so much that farmers have even started adding synthetic chemicals to achieve it. Nitropyrin is one such product, which is commercially available for this purpose. Some studies indicate that allelochemicals, particularly tannins, phenolic acids, and flavonoids, from living plants or their residues or exudates inhibit nitrification (Rice and Pancholy 1973, 1974). Mulches of barley, wheat, and oat when added to the pots having *Picea mariana* seedlings increased the ammonium content by reducing the number of ammonium oxidizers, thus, lowering the loss of nitrogen in soil. This effect was attributed to the presence of phenolic acids in the mulches (Jobodon et al. 1989). Likewise, improvement of degraded soils through stimulation of nitrogen conservation has been reported by leaf litter of *Elaeagnus angustifolia* (Llinares et al. 1993). The phenomenon of allelopathy can, therefore, be successfully exploited to conserve soil nitrogen. However, more needs to be done in this regard.

5.5 Ecological Approaches

5.5.1 Allelopathy Versus Competition

Under field conditions, alfalfa populations decline over time and follow the relationships described by competition models such as the "−3/2 thinning law" and the "law of constant yield" (Silvertown 1987; Watkinson 1986). An inverse relationship exists in normal populations in which plant density decreases naturally due to mortality, as individual plants become larger with age, leading to population decline. As the autotoxic chemical is more concentrated in top growth, negative impacts on new seedlings would be expected to be greatest near the existing plants. But the existing plant simultaneously competes with the seedlings for resources and sustains an autotoxic environment, making it difficult to separate effects of competition and autotoxicity. Few experiments have attempted to separate these effects. One approach has been to determine, how low doses of toxins cause plant populations to deviate from the established models by causing growth stimulation rather than growth reduction at higher toxin concentrations (Thijs et al. 1994; Weidenhamer 1996; Winkle et al. 1981).

This principle has been supported in alfalfa by both lab and field studies. Alfalfa seedlings exposed to low concentrations of the autotoxic chemical (Chon et al. 2000) showed stimulation of root growth under laboratory conditions.

Under field conditions, alfalfa seedlings planted within 1 m from existing alfalfa plants gave maximum yield per seedling, an effect not explained by competition alone (Jennings and Nelson 2002). Spatial patterns often occur in desert plant populations, in which plants tend to be evenly spaced. Perhaps, the severe soil toxicity on seedlings nearest to established plants, maintains distance between neighbors with the stimulation at increased distances away from the old plant improving establishment, thus maintaining somewhat uniform spatial patterns within populations.

5.5.2 Decomposition of Allelochemicals

Alfalfa has been successfully established after alfalfa by killing the old stand with herbicide and planting 2 or 3 weeks later (Tesar 1993; Mueller-Warrant and Koch 1981). Autotoxic effects were observed in both studies, if alfalfa was seeded less than 2 weeks after killing the old stand. By contrast, research in Illinois and Wisconsin showed that 1-year rotation with maize, gave higher stand density and forage yield of alfalfa following alfalfa compared to reseeding after shorter intervals (Klein and Miller 1980; Cosgrove 1996). In Wisconsin, Cosgrove (1996) observed that when an old alfalfa stand was plowed in the fall and reseeded in the following spring, plant density of the new stand was acceptable, but dry matter yield was less compared with alfalfa planted after a rotation with maize.

In Missouri, alfalfa was reseeded after old alfalfa in three experiments using rotation intervals of 2–18 months (Jennings and Nelson 1995). The old alfalfa was killed with herbicides in sequence so that all treatments could be planted the same day. Plant stands and dry matter yields were greatest for the 12- and 18-month rotations. Plant densities of the 2- and 3-week rotations were 13–20 % lower than in the 18-month treatment and yields were up to 8 % lower. An annual yield reduction of 8 % over the life of alfalfa stand is quite significant. The stand in the 6-month fallow treatment was similar to the 12- and 18-month treatments, but had lower yield. Plants dug 2 years later at bloom stage from the 2- and 3-weeks rotation plots had extensively branched roots with little taproot development, while the plants from 12- and 18-months plots had prominent taproots similar to normal alfalfa plants. Exposure to the autotoxic chemical may have inhibited the taproot growth, but plants survived by producing branch roots. The longest rotations had the greatest and the shortest rotations had the lowest plant density. Similar to the California study, plant density declined in all rotation treatments at a similar rate for 3 years.

Stands affected by autotoxicity have slower regrowth after each cutting. Thus, autotoxicity can cause modest reductions in stand or yield that may not be noticeable in the fields. In lower Midwest of the United States, alfalfa production becomes uneconomical when stands drop below 30 plants m^{-2} and stands affected by autotoxicity may decline below this critical plant density level sooner, thus reducing profitability. The affected stands do not overcome the

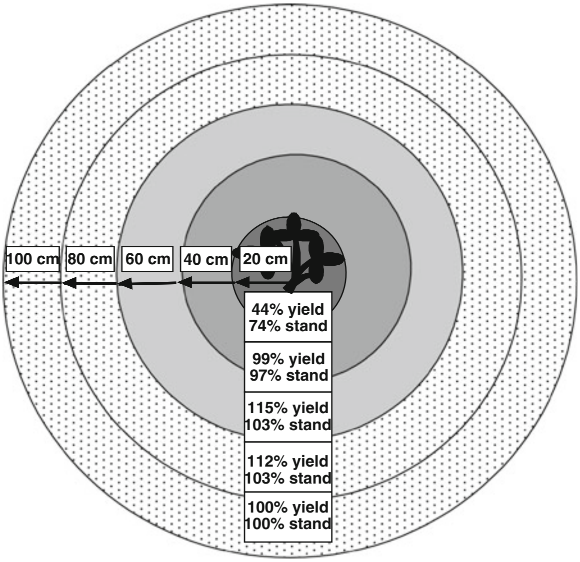


Fig. 5.9 Zone of influence effects within a 1-m radius of an old alfalfa plant. Percent yield and plant density of new alfalfas are based on data from three locations (Chon et al. 2006)

autotoxic effect and the modest reductions continue in plant density and yield. The term “auto-conditioning” has been coined to describe the long-term stunting effect caused by autotoxicity (Winkle et al. 1981).

5.5.3 Autotoxic Zone of Old Plants

Experiments were designed to determine the size of the autotoxic zone of influence around old alfalfa plants. Old plants were selected in production fields and protected, while all other surrounding plants were killed with herbicide 1 year before the new alfalfa was planted. Alfalfa was planted in the spring in spoke-like rows extending 1 m from the base of the plant crown of the old live plant. Both plant survival and dry matter yield of the new alfalfa plants were measured at intervals from the old plant for 2 years after planting to determine the zone of influence (Fig. 5.9). Density and yield of alfalfa were both strongly inhibited within a 20-cm radius of the old alfalfa plant (Jennings and Nelson 1994).

A zone of 40-cm diameter around alfalfa plants means stand density would be <8 plants m^{-2}, before new plants could establish between the autotoxic zones successfully. New seedlings emerging within the autotoxic zone of the old plant would likely contribute little to the yield. A stand density of 8 plants m^{-2} would be approximately 4 times thinner than the minimum level of 30 plants m^{-2} that is needed for economic alfalfa production. In practical terms, these results indicate that attempts at thickening the declining stand of alfalfa are not likely to be successful. In two Missouri studies, severe alfalfa seedling losses were observed, when alfalfa was interseeded into declining alfalfa stands. New seedlings came up between the old alfalfa plants, but either died soon after emergence or never reached sufficient size to contribute to yield. Good stands were established when alfalfa was sown after 1-year rotation with sorghum (*Sorghum bicolor*) (Jennings and Nelson 1991). Our studies on autotoxicity zone and thickening of old alfalfa stand indicate that seedling disease may not be the primary cause of stand failure, when attempting to thicken old alfalfa stands (Jennings and Nelson 1995). The soil sickness syndrome for alfalfa reseeding is more physiological than pathological.

5.5.4 Morphological Responses of Test Plants

Some plant genotypes are likely to escape the allelopathic chemical(s) by being hypersensitive. In this regard, the root tip may actually be strongly affected by allelochemical(s) and have its growth rate nearly stopped. But if the seedling quickly enables to produce several secondary roots, the number of apices per soil volume increases at higher position in soil profile. A study demonstrated microscopically that alfalfa extract reduced both root growth and root hair density of alfalfa (Hegde and Miller 1992a). Stimulation of lateral root growth to the detriment of the primary root also suggests disruption of hormonal balance (Dayan et al. 2000). Anatomical responses of tissue cells upon water-soluble substances or allelochemicals need to be elucidated. The morphology of seedlings grown in the presence of a phytotoxin may also yield important information. Stimulation of lateral root growth to the detriment of the primary root also suggests disruption of hormonal balance (Dayan et al. 2000). Benzoic and cinnamic acids-treated soybean plants showed fewer lateral roots and tended to grow more horizontally compared to the untreated plants. Their lateral roots were stunted and less flexible (Baziramakenga et al. 1994).

Not many microscopic approaches at ultrastructural level have been conducted on allelopathic effects of extracts or allelochemicals. Chon et al. (2002) suggested that the root systems, especially root tips of alfalfa, were stunted and swollen by the aqueous alfalfa leaf extracts at 30 g L^{-1} and coumarin at 10^{-3} M (Fig. 5.10). Duke et al. (1987) discovered artemisinin, a constituent of annual wormwood (*A. annua*), marginally increased the mitotic index of lettuce root tips at 33 μM. At the ultrastructural level by means of electron microscopic study, however, chromosomes were less condensed during mitosis in artemisinin-treated than control meristematic cells. Liu and Lovett (1993) demonstrated that barley allelochemicals, hordenine, and gramine affected damage of cell walls, increase in both size and number of vacuoles, autophagy, and disorganization of organelles. More recently, a study on allelopathic interference of benzoic acid against mustard (*B. juncea*) seedling growth showed irregular shaped cells arranged in a disorganized manner and disruption of cell organelles at cellular level (Kaur et al. 2005). Their

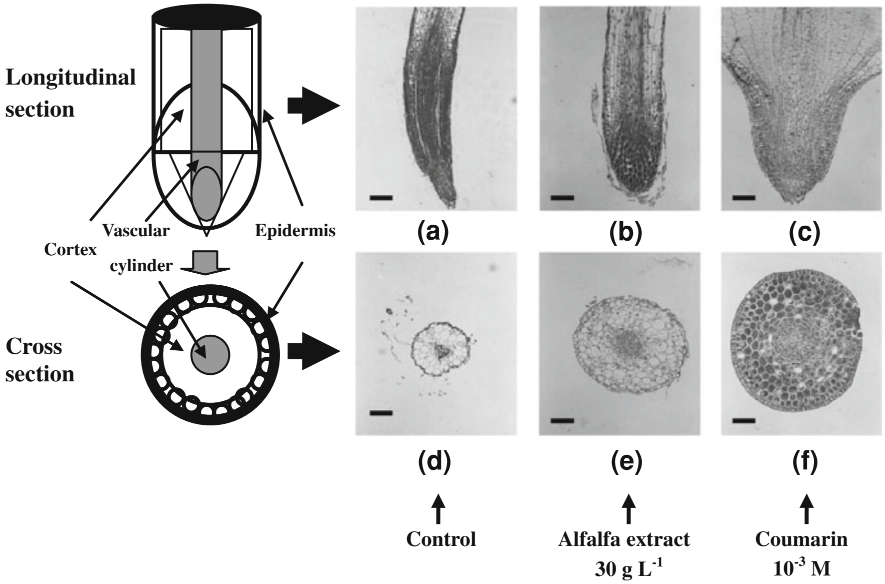


Fig. 5.10 Cross (**a**, **b**, and **c**) and longitudinal sections (**d**, **e**, and **f**) through the root tips of 'Vernal' alfalfa grown on distilled water (**a** and **d**), extracts at 30 g L^{-1} (**b** and **e**), and coumarin at 10^{-3} M (**c** and **f**). Assays were made using filter paper for 6 days. Photograph is about 100x. Cross-section was made at 1 mm distance from the root tip (Chon et al. 2002)

result indicated that damage to the mustard root at cellular level was clearly evidenced by the changes in cell morphology and internal organization.

5.6 Conclusions

Researchers must identify the chemical(s) involved and develop quantitative chemical assay. An accurate and consistent bioassay will verify the chemical(s) involved and to assist during isolation and purification of the chemical. Most scientists support a test similar to Koch's postulates for plant pathogens to verify the chemical(s) involved in autotoxicity or heterotoxicity. Only after a chemical(s) is proven to be involved, will researchers be able to conduct a chemical analysis for developing management and breeding strategies? These steps and potentials are critical for the advancement of the science of autotoxicity and allelopathy. The current environment of sustainability and environmental stewardship using natural products will help focus attention and resources on allelopathy as an ecological alternative to pesticides. This should help unravel the complex situation with autotoxicity of alfalfa.

Autotoxicity primarily affects the seed germination and early root growth, the latter is more sensitive than former. In severe cases, autotoxicity may cause stand failure, but sublethal exposure can alter root growth and development, thus reducing subsequent growth. This autoconditioning effect causes modest reductions in plant stands or yield that are difficult to be observed in field conditions. Currently, rotation intervals of >12 months have allowed natural decomposition of the chemicals in most soils and environments to avoid autotoxic effects. Irrigation in light-textured soils may dilute or leach the autotoxic chemical, to shorten the rotation interval. The autotoxic zone of influence around older plants appears to prevent the thickening of old stands. Continued research into production management and identification of the autotoxic compound may allow breeding of tolerant cultivars for reseeding for continuous alfalfa production. The soil sickness problem is not mitigated by fungicides or insecticides indicating an autotoxicity problem.

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Part II

Allelopathy in Agricultural Systems: Some Case Studies

Chapter 6
Application of Allelopathy in Crop Production: Success Story from Pakistan

Zahid A. Cheema, Muhammad Farooq and Abdul Khaliq

Abstract Allelopathy is an emerging field with its wider applications in agriculture and allied disciplines. In Pakistan, work on allelopathy was initiated in the early 1970s with screening of local flora for allelopathic potential in laboratory bioassays, while field studies were taken up during the early 1980s. Sorghum was found the most potent allelopathic plant in this regard, which was used as mulch material, intercrop, and plant water extracts for weed management. Application of sorghum plant water extracts proved more effective in controlling weeds than all other strategies. Several other plants including sunflower, canola, eucalyptus, rice, mulberry, etc. were also evaluated. Although each of the allelopathic sources provided some control, mixtures of allelopathic water extracts were more effective than the application of single plant extracts. To achieve effective weed control, allelopathic extracts were applied together with the lower herbicide dose. Mixed application of allelopathic extracts with one-third to half of the standard herbicide dose provided effective weed control as achieved from the standard herbicide dose in several field crops. Application of allelopathic mulches, soil incorporation of allelopathic residues, and intercropping with strong allelopathic crops also provided effective control of several weeds. In recent years, commercialization of allelopathic extracts for weed management is under way. Allelopathy has also been effective in controlling stored grain and field crop pests in addition to several

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pathogens which may also be controlled by allelopathy. Allelopathy is also being evaluated as growth promoter; foliar application of canola, sorghum, sunflower, and moringa extracts has been found effective in this regard. More recently, allelopathic extracts are being evaluated for their potential role in improving resistance against abiotic stresses in cereals.

6.1 Introduction

In the 1970s of the twentieth century, Prof. H. M. Naqvi started investigating allelopathic potential of certain grass species while working at the University of Peshawar in Pakistan. He and his graduate students conducted series of laboratory and greenhouse trials to screen local flora for possible allelopathic potential. Prof. Naqvi moved to the US in 1975 while, his then student but later colleague in the Department of Botany Dr. Farrukh Hussain continued the work and investigated certain other species and found promising results particularly from buffel grass (*Cenchrus ciliaris*); that buffel grass inhibited the germination and shoot growth of cattail millet (*Pennisetum americanum*), foxtail millet (*Setaria italic*), lettuce (*Lactuca sativa*), and mustard (*Brassica campestris*) (Hussain and Anjum 1981). It was the early 1980s when Cheema, initiated his PhD dissertation work at the University of Agriculture, Faisalabad, inspired by an article "killer pants" published in 'The Economist''. The article "killer plants" included the work done by Prof. Putman at University of Michigan, USA, which stated sorghum (*Sorghum bicolor*) as a potent allelopathic crop and he suggested that if fall planted sorghum is killed by frost and left in the field, its residues can kill weeds as common purslane (*Portulaca oleracea*) and smooth crab grass (*Digitaria ischaemum*) (Putnam and DeFrank 1983). With little information about the subject of allelopathy, a PhD dissertation for field application of allelopathy was taken up in 1984 by Cheema under the supervision of Prof Saeed Ahmad (Late).

Sorghum being a common fodder crop in rainfed and irrigated cropping systems of Pakistan and the indication by Putnam was the main reason to start investigations on this crop. The farmers were aware of adverse effects of sorghum on subsequent crops particularly wheat. The yellowing of wheat (*Triticum aestivum*) seedlings during the early growth stages was the common observation which was thought to be due to depletion of soil nutrients by the sorghum crop. Therefore, the findings of Putnam regarding sorghum and suppression of various weeds by its decomposing residues was not merely the physical smothering, rather phytotoxins released from sorghum were also involved. With this background information, the challenge was accepted and it is noteworthy that during the first year, laboratory trials showed prominent inhibitory effects in which fresh sorghum sap was used in petri plates. The sap trials were repeated and the sap exhibited selective inhibitory effects, although it delayed the initiation of germination in wheat and also restricted its seedling growth but the germination and seedling growth of common weeds of

Table 6.1 Effect of sorghum sap on germination of some weeds and wheat

Species	Inhibition in germination (%)
Lambsquarters (*Chenopodium album*)	100
Field bindweed (*Convolvulis arversis*)	100
Littleseed canarygrass (*Phalaris minor*)	100
Wild oat (*Avena fatua*)	77
Wheat (*Triticum aestivum*)	50

Source Cheema (1988)

Control without sorghum Whole sorghum incorporated at maturity

Fig. 6.1 Allelopathic effects of sorghum under field conditions

wheat as lambsquarters (*Chenopodium album*), field bindweed (*Convolvulus arversis*), little seed canary grass (*Phalaris minor*) and wild oat (*Avena fatua*) was much less than wheat (Table 6.1).

The second-year field experiments (1985) became a landmark in which sorghum (cv. JS 263) was planted and in the same plots its various parts as leaf, stem, roots, or whole plants were incorporated. Visible inhibitory effects on weed flora and the following wheat crop were noticed (Fig. 6.1; Cheema 1988).

Cheema and Saeed continued the work and various other aspects, appropriate fertilizer dose to wheat crop was found to mitigate toxic effects of sorghum while weeds density and biomass was considerably reduced under sorghum treatments. This work was expanded to other crops as pearl millet (*P. glaucum*), maize (*Zea mays*), and sunflower (*Helianthus annuus*) in addition to sorghum. The inhibitory allelopathic effects on weeds were in this order sorghum > pearl millet > maize. Sorghum and pearl millet also inhibited the wheat grain yield while, maize showed some promotive effect on wheat yield. Allelopathic effects of sorghum and pearl millet were modified by fertilizer and conventional tillage (Arshad 1995).

On similar patterns, Naseem (1997) investigated sunflower for its potential against weeds and wheat. His work further strengthened the findings of Cheema and Arshad. In continuation of his laboratory results (Cheema 1988), Cheema et al. (1990) investigated the subsequent inhibitory effects of wheat stubbles on cotton

(*Gossypium arboreum*) under field conditions. It was found that double irrigation before sowing wheat, improved cotton germination due to dilution of wheat allelochemicals. One application of fertilizer decreased inhibitory effects of wheat on cotton germination (unpublished work by Cheema).

A new era began in the history of allelopathy in 1995, when on the suggestion of Ahmad and Cheema, allelopathic water extracts of sorghum and sunflower as foliar spray in a field trial were used. The results were so encouraging that in future, Cheema focused most of his research activities on the use of allelopathic water extracts as natural herbicides. Cheema and his associates have completed two national projects at different locations in Punjab, Pakistan. They concluded that a combination of allelopathic crops extracts (sorghum, sunflower, brassica) can decrease the herbicides usage by 50 to 75 % in field crops such as wheat, maize, rice (*Oryza sativa*), and cotton (Cheema and Irshad 2004; Cheema et al. 2004; Iqbal and Cheema 2007; Jamil et al. 2009).

Further studies (Jamil et al. 2009; Razzaq et al. 2010; Mushtaq et al. 2010a) revealed that water extract of mulberry (*Morus alba*) combined with the sorghum and sunflower significantly inhibited weeds in wheat fields. In a wire house experiment, Haq et al. (2010) found 80 % inhibition of Bermuda grass (*Cynodon dactylon*) seedling and 41 % increase in wheat grain weight with two foliar sprays of mulberry leaf water extract. Perveen et al. (2009) identified allelochemicals as 3, 4-dihydroxy cinnamic acid, caffeic acid, and 4-hydroxybenzaldehyde that retarded the germination of little seed canary grass, with little inhibitory effects on wheat. In other field studies mulberry extract mixed with the previously mentioned extracts suppressed germination and growth of horse purslane (*Trianthema portulacastrum*), up to 76 % (Mushtaq 2007). It is hoped that allelopathic extracts either as water or dried powder, may possibly emerge as natural herbicides in the near future.

Although growth-enhancing effects of allelopathy are mentioned in the literature, very little attention is paid to this very vital aspect; since scanty information is available. Some indication of promotive effects of brassica pollen is available (Grove et al. 1979) and a compound as brassinolide is identified. However, several reports affirm that at lower concentrations the allelopathic extracts stimulate certain growth processes as germination of different test species (Cheema 1988; Randhawa et al. 2002; Anwar et al. 2003). Cheema and his student tested Brassica 2 % extract on wheat as foliar spray under field conditions and found 18 % increase in wheat yield (Cheema and Imran unpublished work). This work has been taken up as a regular feature of research activities by the research team of Cheema. Canola and moringa (*Moringa oleifera*) extracts were used as foliar sprays on maize. It was noted that with two sprays of moringa and canola mixture sprayed at 30 and 40 DAS increased maize grain yield by 83 % (Hussain 2010).

With this brief introduction and history of allelopathy in Pakistan, in this chapter the summary of the salient findings of allelopathic application in crop production in Pakistan has been discussed.

6.2 Allelopathy for Weed Management

Weeds are the aggressive, troublesome, competitive, and undesirable elements of crop lands that pose multidimensional problems in every cropping system, the most important of which is reduction in crop yields due to interference (competition, allelopathy or both). Modern agriculture is productivity oriented and relies predominantly on synthetic inputs to tackle weeds (Sadeghi et al. 2010). Intensive herbicide use over the past few decades for controlling weeds is posing serious ecological and environmental threats to the planet and its inhabitants. Herbicide residues in produce, soil and ground water, shifts in weed populations, evolution of resistant weed biotypes, and associated health hazards have diverted the research attention to discover and establish alternative weed management strategies. There is an ever-increasing thrust for organically produced commodities, the world over (Jamil et al. 2009). Reducing dependence upon traditional practices and synthetic herbicides and finding alternative strategies for weed management is the need of time (Farooq et al. 2011a). During last two decades, there has been a focus on plant-derived materials as an eco-friendly approach which can substitute herbicides for weed control (Cheema et al. 1997, 2001, 2002a–c; Jabran et al. 2010a, b; Farooq et al. 2011a). Allelopathic extracts have been exploited for weed control, and they have shown the potential as important tool for weed management in field crop production (Cheema et al. 1997, 2001, 2002a–c; Farooq et al. 2011a).

Utilization of allelopathic properties of native plant/crop species offers promising opportunities for this purpose. Allelopathic potentiality under field conditions can be utilized in different ways to manage weeds, i.e., surface mulch (Cheema et al. 2000a), incorporation into the soil (Ahmad et al. 1995; Matloob et al. 2010), aqueous extracts (Khaliq et al. 2002; Iqbal and Cheema 2007; Jabran et al. 2008, 2010a, b), combined application with lower herbicide doses (Khaliq et al. 2002; Iqbal and Cheema 2008; Razzaq et al. 2010) or mix cropping/intercropping (Iqbal et al. 2007). In the following lines, application of allelopathy for weed management in field crops has been discussed.

6.2.1 *Aqueous Allelopathic Extracts*

Most of the secondary compounds, possessing inhibitory activity are water soluble and after extraction in water can be used as “nature’s own herbicide”. In such aqueous extracts, water serves as the carrier and medium to express the allelopathic activity (Farooq et al. 2011a). Although several studies make use of organic solvents for extraction of allelochemicals besides water (Iqbal 2007), the use of aqueous allelopathic plant extracts offers a viable and pragmatic option for sustainable weed management. Aqueous allelopathic water extracts have shown promising results in many studies (Cheema et al. 1997, 2000a, b; Shahid et al. 2007; Iqbal and Cheema 2008; Jamil et al. 2009). In this section herbicidal potential of aqueous extracts of potential allelopathic crops and trees has been discussed.

6.2.1.1 Sorghum

Sorghum is the most extensively studied crop regarding its allelopathic potential (Weston and Duke 2003). Cheema and Khaliq (2000) prepared the aqueous extract after soaking mature sorghum plants in water for 24 h and recorded 35–49 % inhibition of weed density and biomass in wheat under semiarid conditions of Punjab (Table 6.2). Early research work in this context was focused on optimizing frequency, concentration and dose of sorghum water extract for weed management in a number of field crops with diversified weed flora (Cheema et al. 1997, 2000b; Khaliq et al. 1999; Cheema and Khaliq 2000). Simultaneously, susceptibility of various weed species to sorghum water extract was also evaluated in terms of their germination response and seedling growth in various bioassays (Iqbal 1997; Ahmad 1998; Randhawa et al. 2002). Shahid et al. (2006) from bioassay studies concluded that aqueous sorghum extract was inhibitory to germination and seedling growth of wheat and its associated weeds, although wheat was comparatively more tolerant to this extract. Sorghum extract also suppressed the germination of horse purslane (Randhawa et al. 2002) and sprouting of purple nutsedge (*Cyperus rotundus*) tubers (Iqbal 2007). Javaid et al. (2006) showed the susceptibility of parthenium (*Parthenium hysterophorus*) to allelochemicals contained in the shoot and root aqueous extracts of sorghum. Aqueous extract (10 %) of sorghum cultivars exhibited differential allelopathic effects eliciting purple nutsedge as more susceptible test species than horse purslane (Cheema et al. 2007).

In wheat, application of sorghum water extract at various rates and frequencies furnished reductions in weed density and biomass, with a simultaneous increase in grain yield (Cheema et al. 1997; Cheema and Khaliq 2000; Table 6.2). A single spray of 5 % sorghum water extract at 30 days after sowing (DAS) increased wheat yields by 14 % and suppressed weed biomass by 20–40 % (Cheema et al. 1997). In further investigations, Cheema et al. (2002b) showed that one foliar spray of sorghum water extract at 30 DAS or two sprays each at 30 and 60 DAS inhibited the density and biomass of weed species as lambsquarters by 26–32 and 39–48 %, little seed canary grass by 21–34 and 40–49 %, wild oat by 21–27 and 26–35 %, field bindweed by 26–36 and 35–40 %, toothed dock by 27–38 and 35–46 %, respectively. However, exception was observed regarding some species, as density and biomass of sweet clover (*Meliliotus albus*) was either increased or remained unchanged relative to control. Nevertheless, single and multiple applications resulted in similar weed suppression magnitude (Cheema and Khaliq 2000).

Besides as a potent natural weed inhibitor in wheat, sorghum water extract was also effective against weed flora of other field crops of both winter and summer seasons including soybean (*Glycine max*; Khaliq et al. 1999), rapeseed (*Brassica napus*; Bhatti et al. 2000), sunflower (Nawaz et al. 2001), cotton (Cheema et al. 2000a), rice (Irshad and Cheema 2004), maize (Cheema et al. 2004) and mungbean (*Vigna radiata*; Cheema et al. 2001). The extent of suppression in weed density and biomass in these crops was 27 and 16 %, 39–62 and 43–85 %, 16–19 and 21–27 %, 54 and 40 %, 0 and 41 %, 12–55 and 26–67 % and 11–32 and 14–44 %, respectively. Sorghum water extract at 12 and 15 L ha^{-1} as pre-emergence spray

Table 6.2 Allelopathic potential of water extracts for weed suppression in field crops

Allelopathic extract	Frequency[a]; time of application	Crop	Weed species	Weed control (%)	Yield increase (%)	Reference
Sorghum (*Sorghum bicolor* L.)	Three; 15, 30 and 45 DAS[b]	Cotton	*Trianthema portulacastrum*	Reduction in total weed density (47 %) and dry weight (DW) (29 %)	45	Cheema et al. (2002c)
	One; 30 DAS	Wheat	*Fumaria indica* *Phalaris minor* *Rumex dentatus* *Chenopodium album*	Reduction in total weed density (21.6 %) and DW (35.4 %)	11	Cheema and Khaliq (2000)
	Two; 30, 60 DAS			Reduction in total weed density (23.1 %) and DW (38.7 %)	15	
	Two; 30, 60 DAS			Reduction in total weed density (44.2 %) and DW (49 %)	20	
	Two; 30, 60 DAS			Reduction in total weed density (39.0 %) and DW (36.0 %)	14	
	One; 30 DAS	Mungbean	*Cyperus rotundus* *Chenopodium album* *Convolvulus arvensis*	Reduction in total weed density (17.54 %) and DW (23.73 %)	8.23	Cheema et al. (2001)
	Two; 30, 60 DAS			Reduction in total weed density (31.58 %) and DW (44.11 %)	17.75	
	One; 20 DAS	Cotton	*Trianthema portulacastrum* *Convolvulus arvensis* *Cynodon dactylon* *C. rotundus.*	Reduction in total weed DW (32.6 %)	17.7	Cheema et al. (2000a, 2000b)
	Two; 20, 40 DAS			Reduction in total weed DW (35.2 %)	59.0	
	Three; 20, 40, 60 DAS			Reduction in total weed DW (40.1 %)	23.0	
	One; 20 DAS	Sunflower	*Cyperus rotundus* *Trianthema portulacastrum*	Reduction in total weed density (19.3 %) and DW (27.2 %)	7.7	Nawaz et al. (2001)
	One; 40 DAS			Reduction in total weed density (15.8 %) and DW (19.12 %)	3.6	

(continued)

Table 6.2 (continued)

Allelopathic extract	Frequency[a]; time of application	Crop	Weed species	Weed control (%)	Yield increase (%)	Reference
Sorghum	Two, 15, 30 DAS)	Mungbean	*Cyperus rotundus* *Chenopodium album* *Convolvulus arvensis*	Reduction in total weed DW (59.62 %)	4.0	Khaliq et al. (2002)
Sunflower (*Helianthus annuus* L.)	Two, 30, 40 DAS	Wheat	*Phalaris minor* *Avena fatua*	Reduction in total weed density (16.53 %)	1.58	Cheema et al. (2003a)
	Two, 30, 40 DAS		*Melilotus officinalis* *Rumex obtusifolius*	Reduction in total weed density (33.59 %) and DW (2.22 %)	5.50	
Eucalyptus (*Eucalyptus camaldulensis* L.)	Two, 30, 40 DAS			Reduction in total weed density (15.86 %) and DW (22.75 %)	–	
Sorghum + Sunflower + Eucalyptus	One, 30 DAS			Reduction in total weed density (27.53 %) and DW (34.26 %)	3.47	
Sorghum	Two, 30, 40 DAS		*Phalaris minor* *Avena fatua*	DW reduction in *Phalaris minor* (23–41 %) and *Avena fatua* (21–41 %)	39	Jamil et al. (2009)
Sorghum + Eucalyptus	Two, 30, 40 DAS			DW reduction in *Phalaris minor* (13–28 %) and *Avena fatua* (28–32 %)	47.5	
[c]Sorghum + Sunflower	Two, 30, 40 DAS			DW reduction in *Phalaris minor* (30–35 %) and *Avena fatua* (24–39 %)	62	

Table 6.2 (continued)

Allelopathic extract	Frequency[a]; time of application	Crop	Weed species	Weed control (%)	Yield increase (%)	Reference
Sorghum + Sesame (*Sesamum indicum* L.)	Two, 30, 40 DAS			DW reduction in *Phalaris minor* (21–24 %) and *Avena fatua* (19–24 %)	44	
Sorghum + tobacco *Nicotiana tobaccum* L.)	Two, 30, 40 DAS			DW reduction in *Phalaris minor* (10–14 %) and *Avena fatua* (14 %)	18.5	
Sorghum + Brassica	Two, 30, 40 DAS			DW reduction in *Phalaris minor* (21–27 %) and *Avena fatua* (18–24 %)	19	
[d]Sorghum + Sunflower	Two, 30, 40 DAS			DW reduction in *Phalaris minor* (36–55 %) and *Avena fatua* (42–62 %)	53.5	
[e]Sorghum + Sunflower + rice (*Oryza sativa* L.)	One, 07 DAT[f]	Rice	*Echinocloa crusgalli* *Cyperus iria* *Dactyloctenum aegyptium*	Density reduction in *Echinocloa crusgalli* (18 %), *Cyperus iria* (10 %), and *Dactyloctenum aegyptium* (17 %)	29	Rehman et al. (2010)
[g]Sorghum	One, 15 DAT	Rice	*Echinocloa crusgalli* *Echinocloa colonum* *Cyperus rotundus* L. *Cyperus iria* *Dactyloctenum aegyptium*	Reduction in total weed DW (40.41 %)	12.52	Wazir et al. (2011)

(continued)

Table 6.2 (continued)

Allelopathic extract	Frequency[a]; time of application	Crop	Weed species	Weed control (%)	Yield increase (%)	Reference
Sunflower	One, Pre-emergence	Wheat	*Chenopoduim album* *Coronopus didymus* *Phalaris minor* *Avena fatua* *Convolvulus arvensis*	Reduction in total weed density (25.26 %) and DW (14.60 %)	12.38	Naseem et al. (2010)
	One, 25 DAS			Reduction in total weed density (10.63 %) and DW (11.24 %)	10.71	
	Two, Pre-emergence + 25 DAS			Reduction in total weed density (17.19 %) and DW (35.92 %)	17.38	
	Two, 25, 35 DAS			Reduction in total weed density (7.5 %) and DW (34.72 %)	15.71	
	Three, Pre-emergence + 25, 35 DAS			Reduction in total weed density (20.94 %) and DW (41.0 %)	7.28	
Mulberry	One, Pre-emergence- 25 % (v/v) extract	Wheat	*Cynodon dactylon*	Reduction in DW of weed shoot (29 %)	–	Haq et al. (2010)
	One, Pre-emergence- 50 % (v/v) extract			Reduction in DW of weed shoot (43 %)		
	One, Pre-emergence- 75 % (v/v) extract			Reduction in DW of weed shoot (64 %)		
	One, Pre-emergence- 100 % (v/v) extract			Reduction in DW of weed shoot (80 %)		

[*] Sorghum allelopathic water extract

[a] Number of sprays

[b] Days after sowing

[c] 6 L ha $^{-1}$ each

[d] 12 L ha $^{-1}$ each

[e] 15 L ha^{-1} each

[f] Days after transplanting [g] 15 L ha^{-1}

Extended from Farooq et al. (2011)

in cotton suppressed density of purple nutsedge by 31–56 and 35–52 %, respectively (Iqbal and Cheema 2008).

6.2.1.2 Sunflower

Sunflower (*Helianthus annuus*) is also a potent allelopathic crop (Anjum and Bajwa 2005). Chemical studies of sunflower have revealed its richness in phenolic compounds and terpenoids, particularly sesquiterpene lactones with a wide spectrum of biological activities including allelopathy (Macias et al. 1999, 2002, 2004; Ghafar et al. 2001; Anjum and Bajwa 2005). Higher phenolics content was detected in aqueous sunflower leaf extracts than aqueous stem extract. Five allelochemicals (chlorogenic, caffeic, syringic, vanillic and ferulic acid) in leaves, three in stem (chlorogenic, ferulic and vanillic acids) and only one (ferulic acid) in the roots were tentatively identified (Ghafar et al. 2001). Foliar application of aqueous sunflower extract was found to suppress total weed dry weight by 33–53 % (Cheema et al. 1997).

Anjum and Bajwa (2005) proposed the use of sunflower allelochemicals as a possible alternative for achieving sustainable weed management. Preliminary studies have shown the susceptibility of broad leaf weeds like lambsquarters to sunflower extracts (Anjum 2006). Later, herbicidal potential of aqueous sunflower water extracts was also demonstrated against noxious broad leaf weeds of wheat fields like toothed dock and lambsquarters. Although crude extract failed to score 100 % mortality of these weeds yet higher concentration accounted for substantial reduction in weed biomass and significant yield increase over control, leaf extracts showed greatest allelopathic potential than other plant parts (Anjum and Bajwa 2007a, b). Similarly, Shahid et al. (2006) reported that aqueous sunflower extract was the most-inhibitory to germination, shoot, and root length of wheat and to all species of weeds. Sunflower extract was also phytotoxic to grassy weeds like little seed canary grass (Naseem 1997). Pre-emergence application of sunflower water extract suppressed little seed canary grass density and dry weight by 50 and 65 %. Three foliar sprays of such extract as pre-emergence + 25 + 35 DAS suppressed the total weed biomass by 70 % in wheat fields (Naseem et al. 2010). Sunflower extract was also injurious to noxious invasive weed parthenium (Javaid et al. 2006).

In another study, Anjum and Bajwa (2008) while screening sunflower varieties for their suppressive allelopathic effects against weeds of wheat noticed highly significant interaction between sunflower varieties and tested weed species. Lambsquarters and toothed dock were the most sensitive to various treatments while little seed canary grass was the most resistant. Sunflower genotype Suncross-42 was the most allelopathic against selected weeds. Amelioration in suppression was enhanced with increase in concentration. Kamal and Bano (2008) mentioned the negative effects of aqueous sunflower extracts on germination and seedling growth of wheat. Adding further, Anjum and Bajwa (2010) pointed out that phytochemicals in aqueous extracts of sunflower are inhibitory to wheat, and such an inhibitory potential varied among sunflower genotypes. They proposed the use of sunflower allelochemicals for the management of weeds under field conditions that emerge 3–4 weeks after wheat seedlings.

6.2.1.3 Eucalyptus

Eucalyptus (*Eucalyptus camaldulensis*) is considered to be one of the most important allelopathic trees and possesses a number of allelochemicals. This tree is commonly planted in the command area of several canals as farm forestry in Pakistan. Khan et al. (1999) reported that aqueous extracts of eucalyptus leaves were inhibitory to germination and seedling growth of a number of crops viz. cotton, sorghum, sunflower, mungbean, and moth bean (*V. aconitifolia*). Aqueous extracts of eucalyptus leaves significantly inhibited seed germination, root and shoot length, fresh and dry weight of maize over control (Khan et al. 2004). Similar results were shown by Khan et al. (2007) when maize was grown in different soil series of Dera Ismail Khan, KPK. Marwat and Khan (2006) reported inhibition of wild oat germination and seedling growth by aqueous leaf extract of eucalyptus. Shahid et al. (2006) while evaluating the response of wheat and its associated weeds to aqueous allelopathic extracts showed that eucalyptus was inhibitory to root and shoot elongation as well as biomass accumulation in these parts of test species.

6.2.1.4 Mulberry

Inhibitory effects of mulberry against germination and seedling growth of pulses are known since last decade (Mughal 2000). Inspired from these interesting findings, Jabran et al. (2010b) conducted bioassays to evaluate the phytotoxicity of aqueous mulberry extracts against wild oat and canary grass, two pernicious weeds of wheat fields. Mulberry extract resulted in complete inhibition of germination of both the test species. In another study, Haq et al. (2010) concluded that aqueous mulberry extract suppressed the growth of Bermuda grass that was concentration-dependent, while growth of wheat was promoted. Extract concentrations of 75 and 100 % accounted for 100 % inhibition of the sprouting of Bermuda grass nodes, radicle length, plumule length, and radicle fresh weight as compared with the control.

6.2.1.5 Mixed Application of Allelopathic Aqueous Extracts

Use of allelopathic plant aqueous extracts is one way of employing allelopathy for managing weeds in agro-ecosystems (Cheema and Khaliq 2000; Jamil et al. 2009), and such extracts may be combined to enhance their efficacy. Cheema et al. (2003a) tested this idea with the application of sorghum mixed with sunflower and eucalyptus water extracts. Interestingly, mixed application of sorghum, sunflower, and eucalyptus water extracts gave >70 % weed control in wheat compared with the sole application of sorghum water extract. Adding further, Jamil et al. (2009) in a 2-year field study concluded that combination of sorghum and sunflower aqueous extracts each at 12 L ha^{-1} reduced density and dry matter of wild oat and canary grass by 42 and 62, and 36 and 55 %, respectively (Table 6.2). A combination of sorghum + sunflower + Brassica + mulberry water extracts caused complete failure of germination in horse purslane in laboratory bioassays and drastic reduction (96 %) in dry matter production (Table 6.2). In a recent study, Mahmood et al. (2010) showed 66 % reduction in shoot dry weight of horse purslane by combined application of sorghum and sunflower water extracts.

6.2.1.6 Combined Effect of Crop Water Extracts and Reduced Doses of Herbicides

Substantial scope exists to reduce the herbicide rate if applied together with allelopathic water extracts. For weed control in wheat, for example, when applied in combination with sorghum water extract (12 L ha^{-1}), rate of isoproturon application was decreased by 50–60 % (Table 6.3; Cheema et al. 2003b, c). In studies on weed management in cotton and maize, at sowing half-dose application of atrazine (150 g a.i. ha^{-1}) in combination with sorghum water extract (at 12 L ha^{-1}) controlled weeds paralleling full dose (Table 6.3; Cheema et al. 2003d; Iqbal et al. 2009). These authors further observed that combined application of sorghum water extract (at 12 L ha^{-1}) and pendimethalin at one-third (of the standard) dose produced more seed cotton yield than the full dose, even though weed suppression was relatively lesser. In another study on cotton, pre-emergence application of sorghum water extract (12 and 15 L ha^{-1}) in combination with half and one-third dose of herbicide (S. metolachlor), was more effective in controlling purple nutsedge than the standard dose (Iqbal and Cheema 2008).

In a field study on wheat, isoproturon application at standard rate provided 94.10 and 78.5 % reduction in total weed density and dry weight, respectively with a yield gain of 34 % over weedy check. However, mixed application of isoproturon at half rate with sorghum water extract provided 94.3 and 64.8 % reduction in total weed density and dry weight, respectively with 32.3 yield gain over weedy check (Table 6.3; Cheema et al. 2003b). Among the weeds, little seed canary grass was the main weed species and was followed by yellow sweet clover, swine cress, while a few plants of other weeds as toothed dock, wild oat, blue pimpernel (*Anagallis arvensis*), lambsquarters and purple nutsedge, wild medic (*Medicago denticulate* Wild) and field bindweed were also present (Cheema et al. 2003b). In a similar study on wheat, combined application of sorghum + sunflower water extracts with half dose of commercial herbicides was more effective in controlling weeds than the standard dose of respective herbicides (Table 6.3; Razzaq et al. 2010). Mushtaq et al. (2010b) proposed that herbicides use can be reduced by 75 % through integration with sorghum + sunflower extracts without

Table 6.3 Combined application of allelopathic water extracts and reduced herbicide doses for weed suppression in field crops

Allelopathic extract	Herbicide	Crop	Weed species	Weed control (%)		Yield increase (%)		Reference
				Standard herbicide	Herbicide (1/2 dose) + allelopathic extract	Standard herbicide	Herbicide (1/2 dose) + allelopathic extract(s)	
Sorghum (10 L ha^{-1})	S. metolachlor (2.3 kg a.i. ha^{-1} Dualgold 960 EC)	Mungbean	*Cyperus rotundus* *Chenopodium album* *Convolvulus arvensis*	Reduction in total weed dry weight (DW; 62.65 %)	Reduction in total weed DW (79.32 %)	25	40.3	Khaliq et al. (2002)
	Pendimethalin (330 g a.i. ha^{-1} Stomp 330 E)			Reduction in total weed DW (44.33 %)	Reduction in total weed DW (75.50 %)	14.00	24.6	
Sorghum + Brassica (15 L ha^{-1} each)	Pendimethalin (1.2 kg a.i.ha^{-1})	Canola	*Trianthema portulacastrum*	100 % reduction in density and DW	Reduction in density (91.3 %) and DW (94.18 %)	35.99	39.99	Jabran et al. (2008, 2010a)
			Cyperus rotundus	Reduction in density (32.2 %) and DW (6.34 %)	Reduction in density (42.82 %) and DW (37.46 %)			
			Chenopodium album	Reduction in density (78.37 %) and DW (83.07 %)	Reduction in density (74.27 %) and DW (62.2 %)			
			Coronopus didymus L.	Reduction in density (39.39 %) and DW (37.25 %)	Reduction in density (66.09 %) and DW (70.45 %)			
Sorghum (12 L ha^{-1})	Isoproturon (1 kg a.i. ha^{-1})	Wheat	*Phalaris minor* *Melilotus parviflora* Desf., *Coronopus didymus*	Reduction in total weed density (94.10 %) and DW (78.52 %)	Reduction in total weed density (94.25 %) and DW (64.82 %)	33.87	32.25	Cheema et al. (2003b)

(continued)

Table 6.3 (continued)

Allelopathic extract	Herbicide	Crop	Weed species	Weed control (%)		Yield increase (%)		Reference
				Standard herbicide	Herbicide (1/2 dose) + allelopathic extract	Standard herbicide	Herbicide (1/2 dose) + allelopathic extract(s)	
Sorghum + Sunflower (15 L ha^{-1} each)	Pendimethalin (825 mL a.i. ha^{-1}; $_{\text{Stomp330E}}$)	Sunflower	*Chenopodium album, Melitotus indica*	Reduction in total weed density (95 %) and DW (86 %)	Reduction in total weed density (84 %) and DW (67.26 %)	19	16.44	Awan et al. (2009).
Sorghum (12 L ha^{-1})	S. metolachlor (2.15 kg a.i. ha^{-1})	Cotton	*Cyperus rotundus*	Reduction in weed density (82 %) and DW (86 %)	77 % reduction in both weed density and DW	33.85	31.57	Iqbal and Cheema (2008)
Sorghum (10 L ha^{-1})	Pendimethalin (1 kg a.i. ha^{-1})	Cotton	*Cyperus* rotundus	Reduction in weed density (34.78) and DW (50.98 %)	Reduction in weed density (39.13 %) and DW (37.25 %)	19.96	7.97	Iqbal et al. (2009)
			Trianthema portulacastrum	Reduction in weed density (50.54 %) and DW (70.08 %)	Reduction in weed density (51.92 %) and DW (50.31 %)			
	S. metolachlor (2 kg a.i. ha^{-1})		*Cyperus rotundus*	Reduction in weed density (52.17 %) and DW (61.41 %)	Reduction in weed density (47.82 %) and DW (62.82 %)	18.14	3.52	
			Trianthema portulacastrum	Reduction in weed density (53.84 %) and DW (56.91 %)	Reduction in weed density (53.85 %) and DW (56.60 %)			
Sorghum + Sunflower + Rice (15 L ha^{-1} each)	Butachlor (1200 g a.i. ha^{-1})	Rice (*Oryza sativa* L.)	*Echinocloa crusgalli*	Reduction in weed density (80 %) and DW (79 %)	Reduction in weed density (75 %) and DW (66 %)	77	61	Rehman et al. (2010)
			Cyperus iria	Reduction in weed density (79 %) and DW (74 %)	Reduction in weed density (67 %) and DW (71 %)			
			Dactyloctenum aegyptium	Reduction in weed density (76 %) and DW (80 %)	Reduction in weed density (74 %) and DW (76 %)			

(continued)

Table 6.3 (continued)

Allelopathic extract	Herbicide	Crop	Weed species	Weed control (%)		Yield increase (%)		Reference
				Standard herbicide	Herbicide (1/2 dose) + allelopathic extract	Standard herbicide	Herbicide (1/2 dose) + allelopathic extract(s)	
Sorghum + Sunflower + Rice (15 L ha^{-1} each)	Pretilachlor (625 g a.i. ha^{-1})		*Echinocloa crusgalli*	Reduction in weed density (82 %) and DW (73 %)	Reduction in weed density (76 %) and DW (60 %)	74	59	
			Cyperus iria	Reduction in weed density (83 %) and DW (75 %)	Reduction in weed density (66 %) and DW (60 %)			
			Dactyloctenum aegyptium	Reduction in weed density (82 %) and DW (85 %)	Reduction in weed density (74 %) and DW (81 %)			
Sorghum + Sunflower + Rice (15 L ha^{-1} each)	Ethoxysulfuronethyl (30 g a.i. ha^{-1})		*Echinocloa crusgalli*	Reduction in weed density (81 %) and DW (73 %)	Reduction in weed density (72 %) and DW (62 %)	74	41	
			Cyperus iria	Reduction in weed density (79 %) and DW (75 %)	Reduction in weed density (69 %) and DW (64 %)			
			Dactyloctenum aegyptium	Reduction in weed density (85 %) and DW (82 %)	Reduction in weed density (75 %) and DW (69 %)			
Sorghum (15 L ha^{-1})	Penaxolam (30 mL a.i. ha^{-1})	Rice	*Echinocloa crusgalli* *Echinocloa colonum* *Cyperus rotundus* *Cyperus iria* *Dactyloctenum aegyptium*	Reduction in total weeds DW (26 %)	Reduction in total weeds DW (34.75 %)	10.84	4.18	Wazir et al. (2011)
Sorghum + Sunflower (18 L ha^{-1} each)	Bensulfuron + Isoproturon ((1,050 g a.i. ha^{-1} Cleaner 70 WP)	Wheat	*Phalaris minor*	Reduction in weed density (84.62 %) and DW (93.37 %)	Reduction in weed density (88.46 %) and DW (94.90 %)	15.24	23.81	Razzaq et al. (2010)
			Coronopus didymus	Reduction in weed density (81.87 %) and DW (64.29 %)	Reduction in weed density (88.24 %) and DW (87.14 %)			
	Metribuzin (175 g a.i. ha^{-1} Sencor 70 WP)		*Phalaris minor*	Reduction in weed density (92.31 %) and DW (46.43 %)	Reduction in weed density (69.23 %) and DW (82.86 %)	21.43	20.00	

(continued)

Table 6.3 (continued)

Allelopathic extract	Herbicide	Crop	Weed species	Weed control (%)		Yield increase (%)		Reference
				Standard herbicide	Herbicide (1/2 dose) + allelopathic extract	Standard herbicide	Herbicide (1/2 dose) + allelopathic extract(s)	
			Coronopus didymus	Reduction in weed density (90.60 %) and DW (77.14 %)	Reduction in weed density (88.33 %) and DW (97.96 %)			
	Metribuzin + fenoxaprop (190 g a.i. ha$^{-1\ \text{Bullet}}_{\text{38 SC}}$)		*Phalaris minor*	Reduction in weed density (88.46 %) and DW (92.35 %)	Reduction in weed density (82.31 %) and DW (96.94 %)	17.14	34.29	
			Coronopus didymus	Reduction in weed density (87.25 %) and DW (91.43 %)	Reduction in weed density (87.25 %) and DW (94.29 %)			
	Mesosulfuron + idosulfuron (120 g a.i. ha$^{-1}_{\text{Atlantis 12 EC}}$)		*Phalaris minor*	Reduction in weed density (42.31 %) and DW (85.21 %)	Reduction in weed density (88.46 %) and DW (97.96 %)	13.33	21.90	
			Coronopus didymus	Reduction in weed density (90.60 %) and DW (74.29 %)	Reduction in weed density (87.25 %) and DW (92.86 %)			

Extended from Farooq et al. (2011)

compromising yield and net benefits for cost-effective and eco-friendly management of wild oat and canary grass in wheat.

Likewise in rice, combined application of mixture of allelopathic water extracts with half dose of pre-emergence herbicides butachlor, pretilachlor, and ethoxysulfuron ethyl reduced barnyard grass, flat sedge, and crowfoot grass density by 75, 67, and 74 % and their dry weight by 66, 71, and 76 %, respectively (Table 6.3; Rehman et al. 2010).

Recent field studies evaluated allelopathic suppression of weeds in a canola field using crop water extracts—sorghum, sunflower, Brassica and rice—applied in combination with reduced doses of pendimethalin (one-third and half the recommended dose) (Jabran et al. 2008, 2010a). Crop water extracts at 15 L ha^{-1} each combined with pendimethalin at 400 and 600 g a.i. ha^{-1} were sprayed immediately after sowing, while the standard dose of pendimethalin was taken as control. Application of rice and sorghum water extracts in combination with half dose of pendimethalin suppressed the total weed population the most; by 67.58 and 66.21 % at 40 and 60 DAS, respectively. All treatments reduced total weed dry weight by more than 80 % at 40 DAS, while at 60 DAS reductions ranged from 44.93 to 63.99 %. Plots treated with sorghum and sunflower water extracts + 600 g a.i. ha^{-1} pendimethalin recorded maximum seed yields of 2.6 t ha^{-1}, which was 39.99 % more than the control. The authors concluded that 50–67 % less herbicide combined with allelopathic water extracts may be effective for weed control and increase yields in canola (Jabran et al. 2008, 2010a).

6.2.1.7 Powder Formulation

The powder made by hot air drying of sorghum water extract was investigated by Anwar (2011). The objective was to replace voluminous water extracts with a handy powder. The use of 18 g ha^{-1} of powder was as effective as 18 L ha^{-1} of boiled concentrated extract and 360 L ha^{-1} of water extract obtained after 24 h soaking in water. Sorghum powder reduced the population of two common weeds of wheat as lambsquarters and curly dock by 43 and 52 % respectively with 24.5 % increase in wheat grain yield. This was the first study of its type, which needs further validation. Costs involved in water extracts and powder formulation must be considered.

6.2.2 Mulching and Crop Residues

Mulch is spread over the soil surface to suppress weeds, among other strategies. Mulches obstruct seed germination of weeds and inhibit weed seedling growth through the release of allelochemicals. However, established weeds are difficult to control with mulches.

Residues of certain crops can pose a chemical (allelopathic) as well as a physical effect on the growth and development of subsequent crops and weeds (Matloob et al. 2010). In situ incorporation of whole sorghum plant or its various parts alone or mixed with each other suppressed weed growth in wheat field (Cheema and Khaliq 2000). Cheema et al. (2004) stated that sorghum mulch (10–15 t ha^{-1}) decreased the dry weight of purple nutsedge by 38–41 % compared to control (Table 6.4). Phytotoxicity of dried sorghum, sunflower and Brassica residues against purple nutsedge and horse purslane has been reported by Matloob et al. (2010) and Khaliq et al. (2011). These authors concluded that integration of different crop residues can provide satisfactory weed suppression than sole application of such residues. It was further confirmed by the field studies using maize as a test crop (Khaliq et al. 2010). In a dry seeded rice field, incorporation of sorghum residues at 8 t ha^{-1} scored over 50 % reduction weed density and dry weight (Riaz 2010). Incorporation of wheat straw also suppressed the germination dynamics, early seedling growth and photosynthetic pigments in horse purslane (Aslam 2010).

Soil incorporation of chopped sorghum mulch reduced the total weed dry weight from 26–56 % with yield increase of 6–17 % over weedy check in wheat (Table 6.4; Cheema and Khaliq 2000). In cotton however, application of sorghum surface mulch substantially reduced the weed density with significant yield increase (Table 6.4; Cheema et al. 2000a). In maize, however, 14–23 % mortality of purple nutsedge was observed when sorghum residue was applied at 10–15 t ha^{-1}(Cheema et al. 2001).

6.2.3 Intercropping

Intercropping is growing of two or more crops together. It can be used as an effective weed control strategy. Different plant species growing together enhance weed control by increasing shade and weed-crop competition through closer crop spacing and by releasing allelochemicals. It has high net returns, more biological diversity, less chance of total crop failure, reduced nutrient requirements, better use of resources, and suppressive effects on weeds, insect pests and diseases (Ali et al. 2000).

Allelopathy can be especially important for intercropping systems. Allelopathy is an intercropping benefit that can be exploited for managing weeds in agro-ecosystems. It is possible to utilize allelopathic interactions in farming as a cost effective alternative of synthetic chemical inputs for controlling weeds, thus contributing toward sustainable agriculture. In a study on cotton intercropping with single or double rows of sorghum, soybean and sesame (*Sesamum indicum*), all the intercropping systems significantly inhibited purple nutsedge density and dry matter production relative to control. However, cotton intercropping with two rows of sorghum and soybean were the most effective in controlling purple nutsedge (Iqbal et al. 2007; Table 6.5). In another study, sorghum intercropped with maize

Table 6.4 Effect of allelopathic mulches and crop residues on weed suppression in field crops

Allelopathic source	Application mode and rate	Crop	Weed species	Weed control (%)	Yield increase (%)	Reference
Sorghum	Soil incorporation (2 t ha^{-1})	Wheat	*Fumaria indica* Hauskn.,	Reduction in total weeds DW (26 %)	6	Cheema and Khaliq (2000)
	Soil incorporation (4 t ha^{-1})		*Phalaris minor* Retz., *Rumex dentatus* L.,	Reduction in total weeds DW (48 %)	16	
	Soil incorporation (6 t ha^{-1})		*Chenopodium album* L.	Reduction in total weeds DW (56 %)	17	
Sorghum	Surface mulch (3.5 t ha^{-1})	Cotton	*Trianthema portulacastrum* L.	Reduction in total weeds DW (53.2 %)	69.2	Cheema et al. (2000a)
			Convolvulus arvensis L.	Reduction in total weeds DW (80.9 %)		
			Cynodon dactylon (L.) Pers.	Reduction in total weeds DW (5 %)		
			Cyperus rotundus L.	Reduction in total weeds DW (16.5 %)		
	Surface mulch (7.0 t ha^{-1})		*Trianthema portulacastrum* L.	Reduction in total weeds DW (39.7 %)	53.3	
			Convolvulus arvensis L.	Reduction in total weeds DW (92.1 %)		
			Cynodon dactylon (L.) Pers.	Reduction in total weeds DW (63.6 %)		
			Cyperus rotundus L.	Reduction in total weeds DW (60.76 %)		
	Surface mulch (10.5 t ha^{-1})		*Trianthema portulacastrum* L.	Reduction in total weeds DW (49.8 %)	119.3	
			Convolvulus arvensis L.	Reduction in total weeds DW (96.6 %)		
			Cynodon dactylon (L.) Pers.	Reduction in total weeds DW (79.7 %)		
			Cyperus rotundus L.	Reduction in total weeds DW (35.4 %)		

(continued)

Table 6.4 (continued)

Allelopathic source	Application mode and rate	Crop	Weed species	Weed control (%)	Yield increase (%)	Reference
Sorghum	Surface mulch (10 t ha^{-1})	Mungbean	*Trianthema portulacastrum*	Reduction in weed density (14 %) and DW (35.2 %)	7.2	Cheema et al. (2000b)
	Surface mulch (15 t ha^{-1})			Reduction in weed density (19.7 %) and DW (44.8 %)	12	
Sorghum + Sunflower + Rice	Soil incorporation (5 t ha^{-1} each)	Maize	*Trianthema portulacastrum*	Reduction in weed density (76.47 %) and DW (67.86 %)	47	Khaliq et al. (2010)
			Cyperus rotundus	Reduction in weed density (47.78 %) and DW (61.89 %)		
	Soil incorporation (7.5 t ha^{-1} each)		*Trianthema portulacastrum*	Reduction in weed density (68.17 %) and DW (65.45 %)	45	
			Cyperus rotundus	Reduction in weed density (43.47 %) and DW (79.66 %)		
Sorghum + Rice + Brassica	Soil incorporation (5 t ha^{-1} each)		*Trianthema portulacastrum*	Reduction in weed density (68.17 %) and DW (65.45 %)	35	
			Cyperus rotundus	Reduction in weed density (61.65 %) and DW (62.67 %)		
	Soil incorporation (7.5 t ha^{-1} each)		*Trianthema portulacastrum*	Reduction in weed density (69.57 %) and DW (68.53 %)	47	
			Cyperus rotundus	Reduction in weed density (86.94 %) and DW (97.03 %)		
Sunflower + Rice + Brassica	Soil incorporation (5 t ha^{-1} each)		*Trianthema portulacastrum*	Reduction in weed density (60.53 %) and DW (60.14 %)	41	
			Cyperus rotundus	Reduction in weed density (78.32 %) and DW (91.80 %)		
	Soil incorporation (7.5 t ha^{-1} each)		*Trianthema portulacastrum*	Reduction in weed density (72.31 %) and DW (70.05 %)	38	

(continued)

Table 6.4 (continued)

Allelopathic source	Application mode and rate	Crop	Weed species	Weed control (%)	Yield increase (%)	Reference
			Cyperus rotundus	Reduction in weed density (60.83 %) and DW (76.70 %)		
Sorghum + Sunflower + Brassica	Soil incorporation (5 t ha^{-1} each)		*Trianthema portulacastrum*	Reduction in weed density (72.82 %) and DW (83.16 %)	39	
			Cyperus rotundus	Reduction in weed density (65.27 %) and DW (88.15 %)		
	Soil incorporation (7.5 t ha^{-1} each)		*Trianthema portulacastrum*	Reduction in weed density (79.91 %) and DW (88.83 %)	54	
			Cyperus rotundus	Reduction in weed density (86.94 %) and DW (97.21 %)		
Sorghum	Surface mulch (10 t ha^{-1})	–	*Cyperus rotundus*	Reduction in weed density (35.71 %) and DW (48.81 %)	–	Mahmood and Cheema (2004)
	Surface mulch (15 t ha^{-1})			Reduction in weed density (51.01 %) and DW (62.41 %)		
	Soil incorporation (10 t ha^{-1})			Reduction in weed density (30.31 %) and DW (47.16 %)		
	Soil incorporation (15 t ha^{-1})			Reduction in weed density (46.07 %) and DW (57.48 %)		

Table 6.5 Effect of allelopathic intercropping on weed dry weight and crop yields

Treatments	Reduction in weed dry weight (%)	Average yield of intercrops (kg ha^{-1})	Average seed cotton yield (kg ha^{-1})
Control (weedy check)	–		1,485
Cotton 75 cm apart rows (two hoeing)	90		1,970
Cotton 75 cm apart rows + single row of sorghum	89	721	1,211
Cotton 75 cm apart rows + two rows of sorghum	92	958	1,157
Cotton 75 cm apart rows + single row of soybean	83	274	1,367
Cotton 75 cm apart rows + two rows of soybean	92	348	1,202
Cotton 75 cm apart rows + single row of sesame	80	348	1,199
Cotton 75 cm apart rows + two rows of sesame	87	669	1,141

Data from Iqbal et al. (2007)

suppressed density and biomass of purple nutsedge, field bindweed and horse purslane compared with other treatments comprising of sunflower and mungbean (Khalil et al. 2010).

6.3 Allelopathy for Insect-Pest Control

Although fewer reports are available, allelopathy has also a potential in managing insect pests. Neem (*Azadirachta indica*) and its extracts are being used since decades for managing stored grain and other insect pests. Several other indigenous plants of Pakistan have also been evaluated in this regard (Jilani and Haq 1984; Jilani et al. 1989, 1991, 1993). For instance, Saljoqi et al. (2006) evaluated leaves and drupes of bakain (*Melia azdarach*), leaves of habulas (*Myrtus communis*) and mint (*Mentha longifolia*), shoots and seeds of harmal (*Pegnum harmala*) and lemon grass (*Cymbopogon citrates*) roots against rice weevil (*Sitophilus oryzae*) Maximum control was achieved from bakain drupes with 61.2 % mortality followed by habulas (48.40 %), mint (47.40 %) and bakain leaves (46.80 %). In a study, Zia et al. (2011) evaluated water extracts of olive (*Olea europea*), tea (*Thea chinensis*), *Canabis sativa*, elephanta (*Elephantia* sp.), neem, *Jacaranda mimosifolia*, garlic (*Allium sativum*), *Syzygium aromaticum* L., black pepper (*Piper nigrum*) and red chillies

(*Capsicum annum*) against stored chickpea beetle (*Callosobruchus chinensis*). Aqueous extract of black pepper was the most effective in this regard followed by cloves, neem and garlic.

Like stored grain pests, allelopathic plants may also be used for suppressing insect pests in field and horticultural crops. In this regard, Ahmad et al. (2011) reported that application of neem based insecticide, for example Neemosal, may effectively control the initial or low mealybug infestation. For controlling wheat aphids, extracts of orange peel *(Citrus sinensis*); bitter gourd (*Momordica dioica*); garlic (*Allium vineale*); hot pepper (*Capsicum frutescens*) and tobacco (*Nicotiana tabacum*) were evaluated in a field study. Application of orange peel extract was the most effective in this regard with 65.69 % aphid mortality followed by garlic (57.91 %), and tobacco (57.90 %) extracts (Iqbal et al. 2011).

Extractants are also very important in determining the efficacy of an allelopathic source, for example Iqbal et al. (2010) evaluated the petroleum ether, acetone and ethanol extracts of sweet flag (*Acorus calamus*), neem and turmeric (*Curcuma longa*) for growth inhibition of *Sitotroga cerealella*. Petroleum ether extract of sweet flag at application rates of 1,000, 500 and 250 μg g^{-1} and its acetone extract at 1,000 and 500 μg g^{-1} completely inhibited emergence of adults.

6.4 Allelopathy for Disease Management

Aqueous extract of many allelopathic plants are known to exhibit antifungal properties. Hassan et al. (1992) reported that leaf extracts of jimson weed (*Datura stramonium*) reduced the development of rust pustules on the leaves of wheat. Mughal et al. (1996) observed that aqueous leaf extracts of garlic, jimson weed and ashwagandha (*Withania somnifera*) inhibited the growth of *Alternaria alternate*, *A. brassicola* and *Myrothecium roridum*. According to Khan et al. (1998) aqueous extract of onion (*Allium cepa*) exhibited antifungal activity against *Helminthosporium turcicum* and *Ascochyta rabiei* and that of *Calotropis procera* against *A. redicina* Bajwa et al. (2004) evaluated the allelopathic potential of parthenium against three pathogenic fungal species viz. *Drechslera hawaiiensis*, *A. alternata* and *Fusarium monilifrome*. They concluded growth suppression of pathogenic species with lower concentrations (10–50 %) of the parthenium extracts. Nonetheless, higher concentrations (60 and 70 %) of parthenium extracts stimulated the biomass production of test fungal species.

Bajwa et al. (2006) investigated the allelopathic potential of aerial parts of chickpea (*Cicer arietinum*) against *D. tetramera* Subram. & Jain, and *D. hawaiiensis*. Chickpea was found to contain antimicrobial compound(s) for the control of plant pathogenic fungi. In another study, Shaukat et al. (2003) evaluated the impact of root leachates of spanish flag (*Lantana camara*), a tropical weed, against *Meloidogyne javanica* Treub., the root-knot nematode. Concentrated and diluted root leachate caused substantial mortality of *M. javanica* juveniles. Significant suppression of the nematode was achieved when soil was treated with a full-strength concentration of the leachate. While this high concentration retarded plant height and shoot fresh weight, more diluted concentrations actually enhanced plant growth. To establish whether this inhibition of plant growth from the leachate was the result of depleted nitrogen levels in the soil due to the leachate, soil treated with such leachates was given urea as an additional nitrogen source. Urea not only enhanced nematode suppressive activity of the root leachates but also increased seedling emergence and growth of mungbean. Application of *L. camara* root leachates in combination with *Pseudomonas aeruginosa*, a plant growth-promoting rhizobacterium, significantly reduced nematode population densities in roots and subsequent root-knot infection, and enhanced plant growth.

6.5 Allelopathy for Growth Enhancement

The promotion of plant growth by allelopathy is another aspect. Allelochemicals activate various enzymes, enhance cell division, increase ion uptake that ultimately increase plant growth and development. There are reports that lower concentrations of allelopathic extracts promote plant growth. In a field study on maize, two foliar sprays of 3 % moringa, 3 % sorghum, and 3 % Brassica water extract increased maize yield by 52, 42 and 42 % respectively over control (Jahangeer 2011). In another field study on canola, three foliar sprays of 2 % moringa + 2 % Brassica increased canola yield by 35 % over control (Iqbal 2011). In another field study on wheat, three foliar sprays of 2 % sorghum, sunflower, brassica, rice, and moringa water extracts improved the wheat grain yield by 22, 17, 18, 28 and 37 %, respectively (Cheema and Afzal unpublished work). The use of allelopathic water extracts in lower concentrations was highly economical and environmentally safe. This approach has a tremendous scope for use in organic agriculture for improving crop yield.

6.6 Allelopathy for Resistance Against Abiotic Stresses

More recently, the phenomenon of allelopathy has been evaluated for its potential in improving resistance against abiotic stresses in cereals. In this regard, Farooq et al. (2011b) soaked seeds of two rice cultivars Super Basmati and Shaheen Basmati in allelopathic extract of sunflower for 48 h. Seed soaking in sunflower water extracts significantly improved the germination and early seedling growth of both rice cultivars at 50 and 100 mM NaCl salinity levels. In another study, exogenous application of 0 % sorghum allelopathic aqueous extract substantially improved the stand establishment, morphology, allometry, leaf elongation, plant biomass, water relations, water use efficiency and total soluble phenolics under moderate and severe drought stress. Application of sorghum allelopathic extract also reduced the stomatal frequency and conductance in order to check water loss

(Munir 2011). In a similar study, exogenous application of sorghum extract (5 and 10 % aqueous extracts) at anthesis substantially improved the plant biomass, grain yield and yield related traits, water relations, membrane stability and total soluble phenolics in wheat plants subjected to heat stress (Munir 2011).

6.7 Conclusion

Allelopathy has great potential in improving the productivity of cropping systems, if used wisely. This phenomenon may be employed in organic agriculture for improving crop yields and for organic management of weeds, insect pests, and diseases to protect the environment from the hazards of agrochemicals. Development of crop cultivars with strong allelopathic potential may be strong enough to combat biotic (weeds, insect pests, and diseases) and abiotic (drought, salinity, heat, etc.) stresses. Inclusion of allelopathic crops in the rotations may also be helpful in minimizing the pest pressure. Utilization of allelopathic crop water extracts combined with reduced doses of herbicides could be the promising strategy for sustainable weed management. Focused interdisciplinary long-term research efforts should be initiated to boost the yield of crop plants by minimizing the vagaries of biotic and abiotic stresses.

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Chapter 7
Allelopathy in South China Agroecosystems

Shiming Luo

Abstract In humid subtropical and tropical South China, rich allelopathic phenomenon exists. Research in this area showed that exotic plant species like *Eucalyptus exserta*, *E. urophylla, Chromolaena odoratum*, *Mikania micrantha*, and *Ageratum conyzoides* used allelopathy as one of their weapons to expand their territory. Autotoxicity existed in *Camellia sinensis*, *Solanum lycopersicum*, *Casuarnia equisetifolia,* and *Wedelia trilobata.* However, research in *Wedelia trilobata* showed that the concentration for autotoxicity is much higher than toxicity to other species. The allelopathic effect of *Bidens pilosa, Eucalyptus citriodora,* and *Ageratum conyzoides* are strengthened by abiotic stress such as rainfall, soil fertility, or biotic stress like infection by powdery mildew disease. On the other hand, acceptor plants like radish and lettuce could be more seriously suppressed under the nonoptimum temperature than under optimum temperature. The allelochemical, like secalonic acid F from *Aspergillus japonicus* can reduce the superoxide dismutase and peroxidase activity in acceptor plant; hence increase the free radicals within the cell. The lipid in membrane is oxidized and cell structure be destroyed. The structure of cell organelles like chloroplast and mitochondrion be destroyed and it affects the photosynthesis and respiration eventually. The mixture of two allelochemicals from tomato often showed augmenting or diminishing effect(s) on acceptor plants. Volatile oil or ageratochromene from *Mikania micrantha* could inhibit not only other plants but also pathogens causing rice banded sclerotial blight, or phytothora foot rot of pepper, also pathogens like *Magnaporthe grisea, Fusarium oxysporum*, or *Phytophthora nicotianae.* The biochemical system, which can deal with varieties of biological stresses at the same time, certainly has its evolutionary advantage in terms of energy and material efficiency over those systems, which can only have one to one effect.

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7.1 Introduction

South China is located in tropical and subtropical monsoon area with average annual temperature around 20–26 °C and annual rainfall 1,500–2,000 mm. Except flat plains along the lower reaches of the rivers in this area, most of the landscape is covered by rolling hills and mountains. Major natural vegetation is evergreen broadleaf forest and tropical rain forest. Major cropping system is double rice with one winter crop. Because of the warm and humid environment, biodiversity is rich here. Allelopathic research in South China Agricultural University began in late 1980s. In order to recover vegetation in hilly area, we found that building complex multi-layer vegetation was a good practise. However, not all combinations among woods, shrubs, and grasses were feasible. Besides the limitation caused by factors like shading, nutrition and pathogens between plants, there were some other factors we did not account for. Allelopathic phenomenon was one of these factors. Since then, we have explored many interesting aspects in allelopathy. These research results not only provided us opportunities for sustainable agro-ecosystems, but also for better understanding of the natural ecosystems in the region.

7.2 Allelopathic Plants in South China

We found that allelopathic effect broadly existed between exotic plant species and local species, between two crops in cropping systems, between microorganisms and higher plants and between crops and weeds in South China agro-ecosystems.

7.2.1 Allelopathy in Exotic Plant Species

Many plants species were introduced to South China artificially like Eucalyptus since 1890 (Bo 1991), or naturally like bitter vine (*Mikania micrantha*) about 15 years ago. Allelopathy is one “weapon” used by exotic plants for their survival and expansion in new regions.

Eucalyptus is now one of the most important tree species for wood production in South China. It can be easily found that fewer plant species can exist under Eucalyptus canopy than under indigenous trees. Rensen and Pengwei (1997) found that volatile compounds from eucalyptus species *Eucalyptus exserta* and *E. urophylla* had allelopathic effects on the seedling growth of radish (*Raphanus sativa*), lettuce (*Lactuca sativa*), white leadtree (*Leucaena leucocephala*) and black wattl (*Acacia mangium*). Panrong and Shiming (1996) report that aqueous extract from bark, and leaf, and volatiles from leaf of *E. citriodora* showed allelopathic effect on the growth of nine species including weeds like Spanish needle (*Bidens pilosa)*, *Digitarie pertenuis*, candy grass (*Eragrostics cilianesis*), knotroot foxtail (*Setaria geniculata*), common stylo (*Stylosanthes guianensis*), and crops like maize (*Zea mays*), rice (*Oryza sativa*), cucumber (*Cucumis sativus*), and bean (*Phaseolus vulgaris*). Table 7.1 shows the allelopathic effects of four species of eucalyptus on radish seed germination and seedling growth. A study by Jie et al. (2003) showed that water, ethanol, or acetone extracts from *E. urophylla* also had allelopathic effect on *Pisolithus tinctorius*, a common fungus in South China.

An introduced weed christmas bush (*Chromolaena odoratum*) originated in South America is now a common weed in hilly plantation and upland field in South China. The research results from Yanbiao et al. (2002) indicated the 0.1 g mL^{-1} alcohol extracts from christmas bush had inhibitory effects on the germination, seedling growth and root growth of Chinese flowering cabbage (*Brassica parachinensis*), Chinese cabbage (*B. chinensis*) and celery cabbage (*B. perkinensi*), however, 0.01 and 0.002 g mL^{-1} alcohol extracts showed stimulatory effects on seedling growth.

South American Climber (*M. micrantha*) is a relatively new exotic plant species in South China, but it spread very quickly and destroyed many artificial and natural vegetations. The research results showed that the seedling growth of barnyard grass (*Echinochloa crus-galli*), cucumber, radish, rice, Chinese flowering cabbage, Chinese cabbage, Chinese kale (*Chinese alboglabra*), and annual ryegrass (*Lolium multiflorum*) decreased obviously when exposed to the increasing concentration (200, 400, 800, 1,600 mg l^{-1}) of the volatile oil from *M. micrantha*. The fresh weight of all test plants decreased and the germination of all test plants delayed for 1–2 days under volatile oil treatment (2,500 g hm^{-2}) (Maoxin et al. 2002).

A pure stand of only one weed species in a plant community is usually a clue for the existing of allelopathic effect. It is true for christmas bush (*C. odoratum*), South American Climber (*M. micrantha*), wedelia (*Wedelia trilobata*), and chick weed (*Ageratum conyzoides*), there are exceptions, however. Molasses grass (*Melinis minutiflora*) was introduced to South China in early 1980s. It can easily spread and suppress other grasses, then form a pure community. However, it did not show allelopathic effects on the germination and seedling growth of rice and cucumber by using 1:4 (fresh weight of upper plant part: water) extracts (Rensen 1991). Its competition advantage may rely heavily on strong seed spreading and root growth ability, and tolerance of low nutrition level rather than on allelopathy.

7.2.2 Autotoxicity and Continue Cropping

Autotoxicity is one of the factors affecting continued cropping of one plant species. We found that tea (*Camellia sinensis*), tomato (*Solanum lycopersicum*), *Casuarina equisetifolia,* and wedelia also have autotoxicity effects in South China.

Casuarina equisetifolia is adaptable to high salinity sandy soil along coastal beach in South China and has become a major tree species in windbreak system since 1960s. However, the wilting disease spread from early 1980s and the

Table 7.1 The influence of four species of eucalyptus on the growth of radish (RI)[a]

Treatment	Aqueous extracts from leaf (fresh weight:water = 1:8)				*Eucalyptus citriodora*		
	E. exerta	*E. camaldolensia*	*E. robusta*	*E. citriodora*	Stem extracts	Root excretion	Volatile oil
Germination rate	−0.21**	−0.18**	0	−0.38**	−0.26**	−0.29**	−0.51**
Root length	−0.19**	−0.20**	−0.11*	−0.71**	−0.51**	−0.34**	−0.93**
Bud length	−0.40**	−0.39**	−0.19**	−0.91**	−0.63**	−0.49**	−1.00**
Average	−0.27	−0.26	−0.098	−0.67	−0.20	−0.41	−0.81

[a] Respond Index (RI) of allelopathic effect RI = (treatment−CK)/CK

Source Shiming et al. (1995)

* the significance level of the difference between the treatment and the CK reached the standard of $p<0.05$

** the significance level of the difference between the treatment and the CK reached the standard of $p<0.01$

Table 7.2 Effect of aqueous extracts from *C. equisetifolia* branchlet on the root growth of its seedlings

Concentration (g FW mL^{-1})	Root	
	RI	t
0.01	−0.105	4.92^{*}
0.05	−0.269	7.05^{*}
0.10	−0.339	9.03^{*}
0.20	−0.485	10.12^{**}

Respond Index (RI) of allelopathic effect *RI* = (treatment-CK)/CK
t t test result, $t_{0.05} = 4.303$, $t_{0.01} = 9.925$
Source Langui et al. (1996)
* ,** ; refer Table 7.1

community degraded gradually. The research by Langui et al. (1996) showed that allelochemicals produced by *C. equisetifolia* could inhibit the growth of its own seedlings (Table 7.2). Allelochemicals from *C. equisetifolia* branchlet were isolated and identified by means of HPLC, IR, and NMR. It was found that kaempferol-3-α-rhamnoside, quercetin-3-α-araboside and luteolin-3′, 4′-dimenthoxy-7-*β*-rhamnoside could inhibit the growth of seedling, and especially the root elongation.

Tea was originated in China and is one of the most important crops in the hilly and mountainous area in South China. Research reported by Shiming et al. (1995) and Panrong (1992) showed that the aqueous extracts (3.5 dry weight: 100 water) from root, stem, fruit, and leaves of tea plant had inhibitory effect on the germination of tea seed. The respond index (RI) were −0.52**, −0.27**, −0.61**, and −0.38**, respectively. They also inhibited the growth of tea seedlings. For example, RI for the height of tea seedling was −0.55** by aqueous extracts from tea fruit, and was −0.61** by aqueous extracts from leaves. The polyphenol and caffeine in tea leaves could be partly accounted for the reason of this autotoxicity. RI of plant high inhibited by 7 % purified polyphenol from tea leaves was −0.26** and RI caused by 0.65 % purified caffeine from tea leaves was −0.11**.

Since more and more farmers for vegetation production in South China adapt hydroponic method, it is important to understand the allelopathic effect within the system. Zhihong et al. (1997) found that hydroponics medium and volatile components of tomato had allelopathic effects on cucumber, but had no significant effect on lettuce and cabbage. Tomato also showed autotoxicity. Both aqueous extracts of upper plant part and hydroponics medium from tomato culture had self-toxicity effect (Table 7.3). It suggests that the growth medium from tomato production should not be used for another crop of tomato or cucumber.

Wedelia is a common grass for landscaping in South China today. It can form a good coverage with yellow flower and can prevent the invasion of other weeds. Research by Chengrong et al. (2002a) indicated that it had inhibitory effect on weed species like candy grass, alligator weed (*Alternanthera philoxerides*), flatsedge (*Cypers difformis*), *Paspalum thunbergu* Kunth Exsteud, sessile joyweed

Table 7.3 Allelopathic effect (RI) of aqueous extract from tomato on its seedling growth

FW mL^{-1}	0.01	0.05	0.10
Seedling height	−0.065	−0.086	−0.161*
Root length	−0.121	−0.290**	−0.333**

RI = (treatment-CK)/CK
Source Zhihong et al. (1997)
*, ** ; refer Table 7.1

Table 7.4 Allelopathic effect (RI) of aqueous extracts from upper plant part of *W. trilobata* on the germination of stem cuttings of three species

g FW mL^{-1}	*Eragrostics cilianesis*	*Alternanthera philoxerides*	*Wedelia trilobata*
0.1	−0.336*	−0.539*	+0.252
0.4	−0.528*	−0.682*	−0.050
0.7	−0.514*	−0.820*	−0.482*
1.0	−0.603	−1.000*	−0.580*

RI = (treatment-CK)/CK
Source Shiming et al. (1995)
*, ** ; refer Table 7.1

(*A. sssilis*), and bermuda grass (*Cynodon dacylon*). It also showed autotoxicity effect on its own growth. However, the concentration needed for autotoxicity is much higher than those for other species (Table 7.4). When candy grass and alligator weed had already suffered in low concentration (0.1 g FW mL^{-1}), wedelia was still be stimulated (Shiming et al. 1995). This phenomenon is important for the competition of wedelia with other species grown at the same habitat.

7.3 Environment Effects on Allelopathy

The effect of environment on allelopathy includes the environmental factors affecting the allelopathic potential of donor plants, its effect on acceptor plants, and the change of allelochemicals in the environment.

7.3.1 Environmental Factors on Donor Plants

Allelopathic effect of Spanish needle (fresh weight: water = 1:4) to radish seed germination RI was negatively correlated (R = −0.674**) with rainfall 1 month before being harvested. Correlation of allelopathy effect of volatile compounds from leave of *E. citriodora* to radish seed germination was negative (R = −0.99**) with the rainfall of the month of harvest (Shiming et al. 1995). The amount of

Table 7.5 The contents of volatile oils from *A. conyzoides* in different growth stages under different nutrition conditions (mg g^{-1})

Soil fertility	Seedling	Vegetative stage	Blooming	Ripening stage
High	1.04 ± 0.30^{*}	1.41 ± 0.11^{*}	1.32 ± 0.13^{*}	1.13 ± $0.10^{*(}$
Low	1.55 ± 0.19^{*}	2.70 ± 0.19^{**}	2.45 ± 0.29^{**}	1.85 ± 0.28^{**}

Source Tao (2000)
*, ** ; refer Table 7.1

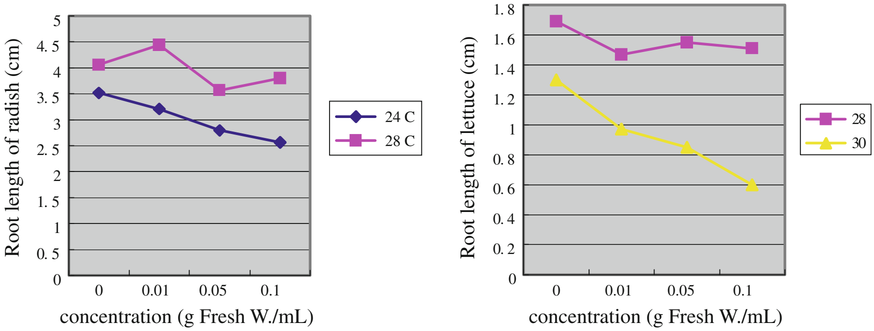

Fig. 7.1 Temperature effect on water extracts from leaflet of *Casuarnia equisetifolia* on root length of radish (*left*) and lettuce (*right*)

volatile oil in chick weed was affected by soil nutrition condition. The poorer the soil, the more volatile oil it produced (Table 7.5). It seems reasonable that plant can produce more allelochemical when competition for water and nutrition resources is more serious. Under optimum condition, plant saves energy by producing less allelochemicals. Tao (2000) also found that chick weed infected by powdery mildew disease could produce more volatile oil than healthy plants. It increased from 1.59 mg g^{-1} in healthy plants up to 2.80 mg g^{-1} in infected plants. The infection of disease stimulated the allelopathic production system of chick weed. It is a clue for the link of one defense mechanism to deal with multifold biocompetition.

Allelopathic effects on acceptor plant are also affected by environmental factors. The allelopathic effect of water extracts from leaflet of *C. equisetifolia* on root length of radish, lettuce, and barnyard grass were significantly affected by temperature. Two-way ANOVA results showed that temperature had significant additive effects.

Plant in suboptimum temperature suffered more when concentration increased (Shiming et al. 1995). Within a temperature range of plant stress, the effect of allelochemicals at same concentration was stronger than under an optimum temperature range. In Fig. 7.1, 28 °C was optimum for both radish and lettuce. However, 24 °C for radish or 30 °C for lettuce were not the optimum temperatures. With increase in concentration, the root growth under nonoptimum temperature suffered more than at optimum temperature (28 °C). It is interesting to note that stress environment affects allelopathy on both donor plant and acceptor plant. On one hand, it increases allelochemical production in donor plant while on the other hand it increases the concentration effect on acceptor plant.

7.3.2 Environmental Factors on the Fate of Released Allelochemicals

In general, allelochemicals in soil are absorbed by soil particles, decomposed by microorganisms and they move with water. The effect caused by volatile oils from *E. citriodora* was more difficult to be washed away by water than the effect caused by the aqueous extracts from the same plant (Shiming et al. 1995).

The decreasing inhibitory effect of soil added with eucalyptus leaf on the germination of radish seed (Y) over time (t) followed the negative exponential curve Y = 0.1−0.3731 × exp (−0.06) F = 12.2*). The same rule existed in the inhibitory effect of soil added with volatile oil of eucalyptus leaf on the germination of radish seed (Y) over time (t): Y = 0.1−0.4458 × exp (−0.0702 t) F = 63.8**).

7.4 Allelopathic Effect on Acceptor Plants

The mode of allelochemical effect on acceptor is quite complicated. Usually, the released chemicals are a mixture of many organic materials. We found that the result of combined materials was quite different from a single compound. The released chemical not only attacked other plants, but might also attack other competitors, like diseases, and insects as well.

7.4.1 Biochemical Mechanism of Allelochemicals on Acceptor Plants

Aspergillus japonicus is a common fungus, which can be found in soil and the surface of plant seeds. Rensen et al. (2001a, 2004) found that secalonic acid F (SAF) is responsible for the allelopathic effect of *A. japonicus* on higher plants. The biochemical mechanism of SAF on acceptor plant can be summarized as Fig. 7.2. The allelochemicals can decrease the activity of superoxide dismutase (SOD) and peroxidase (POD) of the acceptor plant, hence increasing free radicals in cell. The accumulation of free radicals will let more lipids become peroxides and the basic structure of the cell membrane system be destroyed. Cell electronic

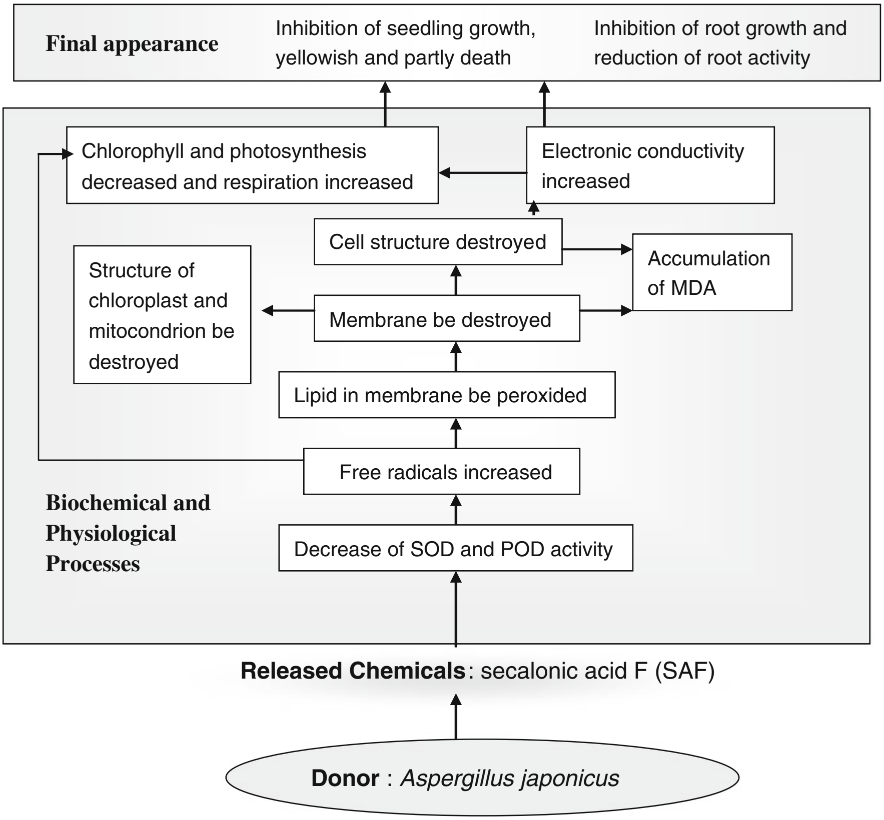

Fig. 7.2 The biochemical and physiological mechanism of Secalonic acid F on acceptor plant (Adapted from Rensen et al. 2001b)

conductivity increases because of the release of ions and organic compound through damaged cell membrane. The structure of organelles like chloroplast and mitochondrion was destroyed. The decrease in photosynthesis and increase in respiration lead to deficit in energy balance. Finally, it influences the growth and appearance like leaf color, and plant height.

Chengrong et al. (2002b) conducted an experiment of allelopathic effect of wedelia on peanut. After treatment with the aqueous extracts of 0.4 fresh weight mL^{-1} from wedelia for about 15 days, the same biochemical and physiological processes could be observed in peanut plant (Table 7.6).

Table 7.6 Effects of aqueous extracts *W. trilobata* on physiological activities and enzyme activities of the geminating seeds of peanut

	Lipase (U g^{-1} h^{-1})	Peroxidase (OD470. g^{-1} min^{-1})	Membrane permeability (%)	Respiration rate (mg CO_2 g^{-1} h^{-1})	Seed activity (μg g^{-1} h^{-1})
CK	23.6*	0.689*	100*	1.68*	68.2*
Treated	plant	18.2**	0.452**	127.7**	1.16**
48.3**					

*Different capitals at the same column indicates the significant difference at 1 % level
Source Chengrong et al. (2002b)
* ,** ; refer Table 7.1

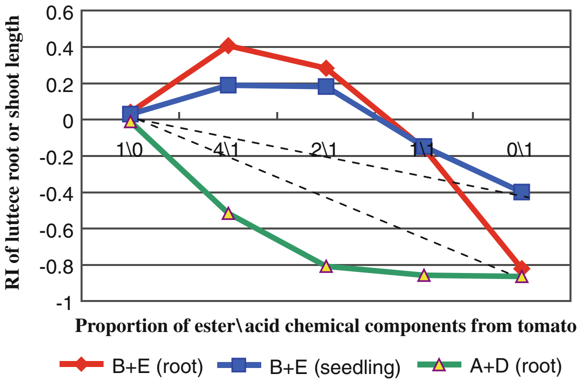

Fig. 7.3 Mixed allelochemicals from tomato had augment effect or diminishing effects on lettuce root or shoot length (Zhihong et al. 1998). A: di-iso-octyl-phthalate, B: di-iso-butyl-phthalate; E: tannic acid D: salicylic acid;
RI = (treatment-CK)/CK

7.4.2 *Effects of Mixing Allelochemicals*

In most cases, donor plants release a mixture of allelochemicals, rather than single chemicals. The effect of mixture is quite different from its components. Zhihong et al. (1998) used a series of allelochemicals from tomato to test the effect of different mixture on the acceptor plants including lettuce, cabbage, and radish. Fig. 7.3 shows few typical curves. If there is no augment effect in the mixture of ester and organic acid, there should be a straight line between the two end points under 1\0–0\1. Since the existing augmenting effect in B + E mixture (B: di-iso-butyl-phthalate, E: tannic acid), the lines of B + E are above the straight line. Because of the existing diminishing effect of A + D (A: di-iso-octyl-phthalate, D: salicylic acid), the line of A + D is below the straight line.

7.4.3 *Multifunctional Effects of Allelochemicals*

Ageratochromene of chick weed can act as anti-juvenile hormone on insect, at the same time had inhibition effects on the growth of radish, ryegrass, barnyard grass

Table 7.7 The effect of ageratochromene and its analogs on pathogens of rice and pepper

Treatment	Concentration (mg L^{-1})	Rice sclerotial blight		Foot rot of pepper	
		Diameter of conobium (cm)	Inhibition rate (%)	Diameter of conobium cm	Inhibition rate (%)
Water(CK)	0	9.0	0	9.0	0
Ageratochromene	400	2.2	75.6	3.6	60.0
Demethylate Ageratochromene	400	2.5	72.2	4.2	53.3

Source Yonghui (1999)

and on the pathogens like rice banded sclerotial blight, and phytothora foot rot of pepper (Table 7.7, Yonghui 1999).

Volatile oil from South American Climber also had inhibitory effect on both plants and fungi. Besides its allelopathic effect on the seedling growth of barnyard grass, cucumber, radish, rice, Chinese flowering cabbage, Chinese cabbage, Chinese kale, and annual ryegrass, it could also suppress the growth of rice blast fungus (*Magnaporthe grisea*) by 53.38 %, *Fusarium oxysporum* by 28.66 %, and *Phytophthora nicotianae* by 18.69 % under concentration of 400 mg L^{-1} (Maoxin et al. 2002).

The production of allelochemical consumes energy and materials. If the process of secondary metabolism can deal with multiple biological competitors and environmental stresses, it has obviously an evolutionary advantage. Further research on it will be very important, not only for the understanding of nature, but also for a revolutionary concept from pesticide to "plant protectant," which can have multiple protective functions.

7.5 Conclusion

Research conducted in South China revealed that allelopathy was very common in tropical and subtropical region. Besides many reports on allelopathy related with native crops, weeds and trees, many exotic plant species such as eucalyptus, bitter vine, and wedelia in South China also used allelopathy as their novel weapon to expand their territory, although allelopathy did not cover all introduced species such as molasses grass. Higher tolerance of wedelia to its own allelochemicals than the surrounding weed species such as candy grass and alligator weed can be able to explain the pure community structure of wedelia. Autotoxicity was found in crop, tree, bush and grass species such as tomato, *C. equisetifolia,* tea, and wedelia. It has significant effect on the production and plant community which could not be ignored in our agriculture and forestation practices.

Environmental factors are important for allelopathy not only because of the faith of allelochemicals in environment, but also the effects on donor plant and receptor plants. Research showed that stress environment such as low rainfall, low nutrition in soil, and present of disease and insect pest could stimulate the donor plant to produce more allelochemicals such as in cases of negative correlations between rainfall and allelopathic effect of Spanish needle, and between rainfall and volatile oils from chick weed. Stress environment such as high temperature for lettuce or low temperature for radish could increase the sensitivity of receptor plants on allelochemicals. Allelochemicals not only can help donor plants to compete other plants for scare resources such as nutrition and water, but also can help donor plants to fight against pathogens and insect pests such as ageratochromene from chick weed can act as anti-juvenile hormone on insect, pathogen inhibitor for rice banded sclerotial blight and phytothora foot rot of pepper, and weed suppressor to barnyard grass. So, allelopathy is more significant in both physical and biological stress environment. Plant using one set of biochemical process to deal with multiple stresses has its evolutionary advantage.

The toxicity to the receptor plant happened first from the decrease of SOD and POD, the increase of radicals, and the destroy of cell membrane systems, then appeared in the accumulation of MDA, the decrease of photosynthesis and the increase of respiration, finally caused the inhibition of germination and growth. The mixture of allelochemicals is much more complicated than a single allelochemical because of the possible augmenting effect or diminishing effect of interaction among those chemicals. The rules behind these interactions are needed further exploration in the future.

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Chapter 8
Allelopathy Research in Iran: Experiences, Challenges, and Prospects

Forough Abbassi, Reza Ghorbani and Surur Khorramdel

Abstract Allelopathy plays a major role in both natural and managed ecosystems regarding biodiversity and weed management in most countries. This chapter discusses the recent research on allelopathy carried out in Iran. Various research projects have been done in Iran in the last decades and reported in national and international journals. Iran has a long history in agriculture and so it is rich in indigenous knowledge on allelopathy. The review of recent publications showed that only in the last decade over 100 allelopathic species have been considered by Iranian researchers and as a matter of fact the most allelopathic investigations have been focused on economic crops and weed management.

8.1 Introduction

In Iran, agriculture plays an important role in the national economy. The multiplicity of climatic zones makes possible to cultivate a variety of crops. However, because of lack of adequate suitable water distribution in many areas, most of areas are not suited for agriculture. Weeds also are one of the important factors

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that reduce crops quantity and quality. For instance, wheat provides the core commodity of the Iranian food, its yield reduction due to weed infestation has been estimated up to 30 % in average (Labbafy et al. 2009). Although there are many different methods for weed management, using allelopathy has been known as one of the best environmentally friendly method.

Allelopathy has also been known as a major and prominent issue in agricultural and botanical sciences in Iran. This biological phenomenon is primarily based on the ability of certain plant species to produce secondary chemical compounds, which exert some sort of biological effects on other organisms (Waller 2004). Allelopathic compounds are released into the soil through root exudation, leaching by dews and rains, volatilization and decaying different plant tissues in soil (Rice 1984). In most cases, such compounds inhibit the germination or growth of neighboring plants (Ebana et al. 1981) and affect plant populations (Rice 1984; Waller 1989; Chase et al. 1991). Allelopathy is biochemical interaction between individuals and ecological communities systems. Production and release of allelochemicals are increasingly formed by the plants under the selection pressure of environmental stresses. This phenomenon is also considered as an adaptive mechanism in plants to environment over evolutionary time. Therefore, allelopathy could have a significant role in growth, development, and evolution of plants (Hedin 1990; Singh et al. 1992).

A wide range of allelopathic studies have been conducted in many crops, trees, shrubs, and weeds under laboratory, greenhouse, and field conditions in Iran, most of which are summarized in different sections including allelopathic effects of crops on weeds, weeds on crops, crops on crops, weeds on weeds, medicinal plants, and trees (Abbassi and Jahani 2007; Ghorbani et al. 2008; Labbafi et al. 2008a, b; Mohebi et al. 2008; Ghahary et al. 2009; Kolahi et al. 2009; Rashed-Mohassel et al. 2009; Dadkhah and Asaadi 2010; Pirzad et al. 2010; Safari et al. 2010).

The objective of this chapter is to have a report about the status of the recent allelopathic studies and the scientists who work on allelopathy in Iran in order to improve the scientific collaborations among biologists, agronomists, ecologists, and other related scientists around the globe.

8.2 Allelopathic Effects of Crops on Weeds

Allelopathic crops for weed suppression have been reviewed for years (Rice 1984). If a weed species can be suppressed by allelopathic crops during germination, emergence and seedling establishment stages, then the crops will gain a big advantage over weeds. Seedlings and different tissues of various plants possess allelopathic potential or weed-suppressing activity such as wheat (Kiarostami et al. 2007; Labbafi et al. 2008a, b), barley (Asghari and Tewari 2007; Ashrafi et al. 2009), rice (Ghahary et al. 2009), canola (Niakan et al. 2006, 2008; Zaji et al. 2009), sunflower (Ashrafi et al. 2008a, b; Ghorbani et al. 2008; Orooji et al. 2008), saffron (Abbassi and Jahani 2007; Rashed-Mohassel et al. 2009), almond (Astaraei and Sampietro-Diego 2008), *Eucalyptus* (Dadkhah and Asaadi 2010; Nasr-Esfahani and Shariati 2004, 2007; Niakan and Saberi 2009), *Pinus* (Alizadeh et al. 2009), walnut (Nasr-Isfahani and Shariati 2007; Abbassi et al. 2009) and some medicinal plants (including *Artemisia* sp. (Mohebi et al. 2008; Samedani and Baghestani 2005, 2006), John's wort (*Hypericum perforatum*) (Azizi and Fuji 2005), sage (*Salvia officinalis*) (Pirzad et al. 2010), thyme (Azizi et al. 2006; Safari et al. 2010), *Cenicus benidictus*, *Silybum marianum*, *Plantago lanceolata* (Azizi et al. 2006), *Peganum harmala* (Naghdi-badi et al. 2009), *Thymus vulgaris, Mentha piperita* (Arouiee and Azizi 2006; Azizi et al. 2006), and *Zhumeria majdae* (Soltani-poor et al. 2006; Soltanipor et al. 2007).

8.2.1 Cereals

Wheat (*Triticum aestivum*) is one of the main crops in the most provinces of Iran and its yield reduction due to weed infestation has been estimated up to 30 % in average (Labbafy et al. 2009). Although weed species in wheat fields of different areas vary, some of them are common in most areas. The most prevalent weed species in wheat fields are *Avena ludoviciana, Convolvulus arvensis, Galium tricornutum, Phalaris minor, Secale cereale, Sinapis arvensis,* and *Vicia villosa.* Application of allelopathic plants and suitable cover crops are recommended weed management methods (Inderjit and Streibig 2001; Rovira 1969). Labbafy et al. (2009) by application of equal compartment-agar method for studying allelopathic potential of wheat cultivars (Shiraz and Niknejad, as more competitive cultivars; Tabasi and Roshan, as less competitive cultivars) on the growth of field bindweed (*C. arvensis*) and rye (*S. cereale*). They revealed that higher seedling density of 24 seedlings in every flask had the greatest effect on decreasing rye growth (seedling, radicle and hypocotyl). All of the wheat cultivars showed a decrease in seedling, radicle, and hypocotyl length in comparison with the control. All studied wheat cultivars, especially at the highest density, decreased seedling and radicle length, but increased the hypocotyl length of field bindweed. In another study, Labbafi et al. (2010) evaluated activities of four allelopathic wheat cultivars on four weed species including *S.cereale*, oat (*A. ludoviciana*) (as monocotyledonous), *C. arvensis,* and vetch (*V. villosa*) (as dicotyledonous). They showed that the allelopathic activity of wheat was associated with wheat cultivar and number of wheat seedlings. In addition, whole plant and root length of weed species were significantly reduced in the presence of wheat cultivars. They further reported that the degree of weed growth inhibition was dependent on the number of wheat seedlings. Their results indicated that the length of whole plant (–30.22 %) and root (–57.74 %) of *C. arvensis* and shoot length (–13.24 %) of *S. cereale* had the highest sensitivity. Different concentrations (0, 5, 10, 25 and 40 %) of aqueous extracts of rye and wheat on lambsquarter (*Chenopodium album*) and black nightshade (*Solanum nigrum*) showed that lambsquarter was more sensitive than black nightshade. Also, organic extract reduced radicle growth compared with hypocotyl growth (Younesi et al. 2008). Kiarostami et al. (2007) studied the allelopathic potential of 10 wheat cultivars (Atrak, Dez, Pishtaz, Chamran, Darab2, Shiraz, Shirodi, Star, Marvdasht and Tagan) against wild barley (*Hordeum spontaneum*) and *Lolium rigidum*. They prepared the aerial parts aqueous extracts of these wheat cultivars at vegetative (27 days after sowing) and maturity stages then investigated the extracts effects on germination, shoot and root lengths, shoot and root fresh/dry weights of wild barley, and *L. rigidum* seedlings. Their study showed that the allelopathic effects of wheat extracts significantly differed between cultivars and two cultivars of Chamran and Pishtaz significantly reduced germination, shoot and root length, dry weights of wild barley, and *L. rigidum*. Out of 10, 2 wheat cultivars (Marvdasht and Star) showed least allelopathic effect against wild barley and *L. rigidum*. Cultivars of Chamran and Pishtaz had high allelopathic effects against wild barley and *L. rigidum*. Kiarostami et al. (2008) evaluated allelopathic effects of phenolic acid of wheat on few physiological parameters such as seed germination, seedling growth, photosynthetic pigments, chlorophyll content, polysaccharides, and proteins content of *A. fatua*. These authors found that increasing phenolic acid caused reduction in germination characteristics and chlorophyll, proteins, and carotenoid contents of oat. The highest reduction was observed for 5 mmol of vanillic acid (4-hydroxy-3-methoxybenzoicacid acid).

Seyed-Sharifi et al. (2007) in a field experiment at Agricultural Research Center of Jahad-Keshavarzi Ardabil in Iran, during 2003, compared the effect of various values of wheat, barley, safflower (*Carthamus tinctorius*), and sunflower residues on weeds control in chickpea (*Cicer arietinum*). The treatments were control plots, twist hand weeding, and use of 2 and 4 kg per plot of wheat, barley, safflower, and sunflower residues. They noted that the application of these crop residues decreased dry weight and number of weeds, while increased grains yield. The highest grain yield (0.767 t ha^{-1}) was obtained in treatment of twist hand weeding and in application of 2 kg per plot of barley residue (0.761 t ha^{-1}). The lowest grain yield (0.541 t ha^{-1}) was obtained in control plots. Allelopathic potential of different concentrations (0, 5, 10, 25, and 40 %) of aqueous extracts rye and wheat on lambsquarter (*C. album*) and black nightshade was studied and results showed that lambsquarter was more sensitive than black nightshade. Also, organic extract reduced radicle growth compared with hypocotyl growth. These findings suggested that the allelopathicity of rye and wheat could be a suitable method for control of those weeds (Younesi et al. 2008).

Rice, another main crop, that is mainly cultivated in north of Iran. There are many research programmes regarding allelopathy of rice in this country. Asghari et al. (2006) conducted several studies on rice allelopathy and found that seedling growth of barnyard grass (*Echinochloa crus-galli*) was very sensitive to rice tissues. Hull extracts of 46 rice cultivars at various concentrations had inhibitory effect on barnyard grass seedling growth; however, hull extracts of five rice cultivars were identified with highest effects. So, they concluded that the cultivars with more hull allelopathic effects can lead us to select cultivars with a natural source of herbicides. Since the genetic differences among rice cultivars exhibit variation in allelopathic effects on barnyard grass growth, therefore, breeding of rice cultivars with greater allelopathic potential may provide natural herbicides for controlling of weeds. Kolahi et al. (2009) from Iran tested the allelopathic effects of hull rice extracts to control weeds. They evaluated allelopathic potential of hull extracts of 13 rice cultivars, which had significant reduction on germination and seedling growth of wild oat (*A. ludoviciana*). They concluded that rice hull extracts might be a source of natural herbicides; however, genetic differences observed among rice cultivars for allelopathic potential may be possible. The most recent investigations by Mahmoodzadeh et al. (2011) determined the allelopathic potential of root exudates from early development stage of rice (*Oryza sativa*). They grew 6-day-old seedlings of two cultivars of rice with 3-day-old hedge mustard seedlings in petri dishes under control conditions. Rice leachate caused pronounced inhibitory effect on seed germination rate of receiver plants. Effectiveness of cv. Kalat was greater than cv. Shomal. These authors concluded that the rice root exudates and rice leachate contained water-soluble allelochemicals, which inhibited seed germination and reduced seedling growth of Hedgemustard. Berenji et al. (2011) evaluated the effects of hull water extracts on the seedling growth of arrowhead (*Sagittaria trifolia*) weed. The extracts of rice varieties, ‘Dinorado’ and ‘Neda’, were most suppressive to arrowhead seedling growth than other varieties. High performance liquid chromatography (HPLC) was used to analyze six phenolic acids in rice hull water extracts. Among the tested varieties, Dinorado variety hull extract had maximum phenolic acids content. None of the six phenolic acids were detected in extracts of Line-229, while, Dashti-sard had highest (*p*)-hydroxy benzoic acid content.

Barley (*H. vulgare*) is smoother crop and possesses the allelopathic potential to suppress many weeds (Liu and Lovett 1993; Overland 1966). Several phenols and terpenes related to its allelopathic effects were reported in various cultivars of barley (Gibson et al. 1990; Macias and Ridge 1999; Spring et al. 1992). Therefore, barley has been considered as an allelopathic plant by Iranian scientists as well. Asghari and Tewari (2007) investigated the allelopathic potential of the foliage tissues of eight barley cultivars using seedlings bioassays on Indian brown mustard (*Brassica juncea* L.) and green foxtail (*Setaria viridis*). The correlations of allelochemical compounds with germination of weed seeds were determined using the barley cultivars Jackson, Bronco, CDC Dolly, B1602, Harrington, UNA80, Standerand and TR251. Three diluted extracts of each barley cultivar (5, 10 and 20 g L^{-1}) plus deionized distilled water (as control) were assayed. The effects of barley cultivars and extract concentrations on seed germination and radicle and shoot lengths of the target weed were highly significant. With increased concentration of the allelopathic extracts, germination percentage, radicle and shoot lengths of both target plants decreased. Seed germination and seedling growth of *B. juncea* were more sensitive than those of *S. viridis*. Asghari and Tewari (2007) categorized the tested barley cultivars as being highly allelopathic, moderately allelopathic, and of low allelopathic potential. Among phenolic compounds detected, cumulative effect of four small-quantity compounds (vanillic, chlorogenic, *p*-coumaric, and ferulic acids) on average weed germination was very high ($R^2 = 0.83$), with *B. juncea* it was also high ($R^2 = 0.70$) but in *S. viridis* it was very low ($R^2 = 0.15$).

Ashrafi et al. (2008a, 2009) evaluated the effects of preceding crop, fresh barley residue in corporation; barley leaf, stem, flower, and root water extracts on green foxtail and quack grass (*Agropyrum repens*) germination and seedling growth. They found that plant height and weight of those weeds were significantly reduced when grown in a soil that was previously cropped by barley. Soil containing fresh barley roots and both roots and shoots reduced green foxtail germination, plant height, and weight when compared with a no-residue control. In bioassays, barley extracts reduced green foxtail hypocotyls length and dry mass, radicle dry mass, seed germination, and radicle length by 44,578, 61,686, and 79 %, respectively. Increase in the water extract concentrations from 4 to 20 g per 100 mL of water of all barley parts significantly increased the inhibitory effects on green foxtail germination, seedling length, and weight. They also realized that based on 7-day-old green foxtail radicle length, averaged across all extract concentrations, the degree of toxicity of different barley plant parts can be ranked in the order of inhibition as: leaves > flowers > mixture of all plant parts > stems >roots.

Interesting experiments were conducted (Oveisi et al. 2008) to determine the allelopathic potential of 17 Iranian barley cultivars in four development stages and their variations over the last 60 years of collection. Imbibed seeds and water leachates that were extracted from the barley plants at the seedling, tillering, stem elongation, and heading stages were used for the bioassays, including filter paper, neighboring barley seeds in soil, and soil mixed with dried barley residues. Wild mustard (*S. arvensis*) was used as the test plant. The germination rate index (GRI) and emergence of *S. arvensis* were inhibited on both the filter paper and soil. The highest inhibitory effect was seen with the tillering stage's water.

The allelopathic effects of different concentrations of water extracts of barley straw and root on germination and seedling characteristics of corn, sugar beet, and sunflower was studied by Naseri-Poor-Yazdi et al. (2008). In their field experiments, treatments included: 0, 200, 400, and 600 g m^{-2} of ground barley straw and also 0 and 50 g m^{-2} barley roots. Results showed that leaf area of corn was significantly affected by barley straw treatments. With reduction in weeds, shoot dry matter and seed weight per plant in corn, leaf and tuber weight in sugar beet and leaf, stem weights in corn, leaf and tuber weights in sugar beet and leaf, stem weights, plant height, head diameter, head weight, and seed weight in sunflower were significantly higher in treatment of 50 g m^{-2} barley roots.

The genus *Sorghum* has a number of species, one of which is raised for grain and many of them for use as fodder plants either cultivated or as part of pasture (Del-Giudice et al. 2007). There are many references about allelopathic ability of sorghum. Yarnia et al. (2009) studied allelopathic effects of sorghum extracts on redroot pigweed (*Amaranthus retroflexus*) seed germination and growth. They found that sorghum extract not only decreased germination but also decreased growth and dry matter accumulation in redroot pigweed seedlings. Pigweed seed germination was decreased by 20 % with sorghum extracts. In addition, the extract of sorghum stem at grain filling stage had the lowest effect because of assimilates transportation from lower leaves and stem to grains in low concentration of allelochemicals. Mohsenzadeh (2000) examined the effects of *Sorghum halepense* and Bermuda grass (*Cynodon dactylon*) on *T. vulgare* and found higher concentrations of allelopathic substance in their leaves. Also, the root extracts had lower effects on wet and dry weight of seedlings than aerial parts extracts.

8.2.2 Non-Cereal Crops

Soltanipour et al. (2005) investigated the effects of different concentrations of essential oils on seed germination and seedling growth, leaf chlorophyll content, fresh and dry weights of root and shoot, and peroxidase activity in roots of 21-day seedlings of *Lepidium sativum* and *E. crus-galli*. Essential oils prepared from leaves of *Z. majdae* inhibited seed germination and seedling growth drastically. In the presence of 50 and 100 % of stock solution, seed germination rate was reduced to zero. Moreover, they recorded that the activity of peroxidase enzyme, fresh and dry weights, and chlorophyll content reduced in all post-emergence treated plants.

Sunflower contains water-soluble allelochemicals that inhibit the germination and growth of other species (Sadeghi et al. 2010), which could be used in weed management programmes. Orooji et al. (2008) evaluated allelopathic potential of sunflower on redroot pigweed and common lambsquarter in two series of laboratory and greenhouse experiments. Ashrafi et al. (2008b) studied the allelopathic effects of sunflower on germination and growth of wild barley. Growth of wild barley considered in terms of plant height and weight was significantly reduced when they were grown in a soil that previously had sunflower compared with a soil that was cropped by wild barley. Soil incorporation of fresh sunflower roots and both roots and shoots reduced wild barley germination, plant height, and weight when compared with a no-residue control. In these bioassays, sunflower extracts reduced wild barley hypocotyl length, hypocotyl weight, radicle weight, seed germination, and radicle length. Increasing water extract concentrations from 4 to 20 g per 100 mL of water of all sunflower parts significantly increased the inhibition of wild barley germination, seedling length, and weight. Based on 8-day-old wild barley radicle length, averaged across all extract concentrations, the degree of toxicity of different sunflower plant parts were ranked in the order of inhibition as leaves > flowers > mixture of all plant parts > stems > roots.

Takayuki et al. (2007) investigated allelopathic effects of the essential oils of black zira (*Bunium persicum*) (200, 500, 700, 1,000 and 2,000 ppm) and *Cuminum cyminum* (100, 300, 500, 700 and 1,000 ppm) on germination characteristics of *Bromus tectorum, Centura ovina,* and *Descurainia sophia and* showed that germination percentage of all weed species was reduced in treated plants, although germination percentages were high in control plots (96.67, 73 and 96.67 percentage, respectively). Germination of *C. ovina* at 700 ppm and *B. tectorum* at 1,000 ppm were completely inhibited by black zira essential oils. *Descurainia* seeds were more sensitive to black zira essential oils and its germination was completely inhibited at 500 ppm. There was no significant difference between 200 and 500 ppm of black zira essential oils in germination percentage of *B. tectorum*. Black zira essential oils at 500 ppm decreased germination percentage of *C. ovina* by 25 %. However, concentration of 200 ppm of black zira essential oils decreased germination percent of *D. sophia* by 69 % (from 96.67 to 27.67 %). Increased concentration of *C. cyminum* essential oils from 100 to 1,000 ppm decreased germination percent of *B. tectorum* by 46.67, *C. ovina* by 51, and *D. sophia*, by 53 %.

Released toxic materials of Brassicaceae plants such as canola (*B. napus*) have decreased weed germination and establishment (Haddadchi and Gerivani 2009; Jahandideh and Latifi 2006; Mansouri et al. 2005; Niakan et al. 2006, 2008; Zaji et al. 2009). Zaji et al. (2009) investigated the allelopathic effects of canola varieties (Talaye, Okapi, and Opera) in different concentrations of aqueous extract (0, 50 and 100 %) on germination characteristics of *H. spontaneum*, *A. albus*, *Rumex crispus,* and *A. fatua* in Iran. Results showed that with increasing extract concentration of canola seed germination percentage and growth of those weeds were significantly reduced. The highest reduction was observed in *Amaranthus*. In another study conducted by Abbassi et al. (2007a), the allelopathic potential of three different plant parts (shoot, root, total plant) of canola (*B. napus* cv. PF) on some of physiological aspects of five weeds of green foxtail, *S. cereale*, *A. retroflexus*, *C. album,* and *A. fatua* was studied. Canola was harvested near the end of flowering phase and the materials were then dried and grounded (0.5 mm). The pots filled with 2,000 g sandy loam soil and then 5 g of different grounded materials separately added and mixed with pot soil. Control pots filled only with sandy loam soil. After two weeks, seeds were sown in pots and percentage and rate of emergence were recorded. Two and six weeks after sowing, shoot and root length, dry and fresh weights of root, shoot, and leaves and SPAD number of leaves were recorded. Although canola root showed a decreasing effect on the measured criteria, the total parts showed no effect on them.

Meighany et al. (2006) investigated allelopathic potential of shoot tissues of two clover species including Persian clover (*Trifolium resupinatum*) and berseem (*T. alexandrinum*) in different concentrations (0, 25, 50 and 100) of organic (with methanol) and aqueous (with distilled water) extracts on germination of *A. retroflexus, C. arvensis*, *S. cereale,* and *S. alba*. With increasing extract concentration seed germination percentage and growth of those weeds were decreased. Highest and lowest reductions were noted with *S. alba* and *C. arvensis*, respectively. Iranian clover inhibited weed germination higher than Berseem. Also, organic extract reduced weed germination compared to aqueous extract.

8.3 Allelopathic Effects of Weeds on Crops

Weeds can have allelopathic effects (positive or negative) on crops. It is always not easy to separate allelopathic and competition effects of weeds on crops.

8.3.1 Cereal Crops

The allelopathic activities of weed species such as *Centurea depressa*, *H. spontaneum*, *Hordeum* sp., *L. rigidum,* and *Senesio vulgaris* against 12 cultivars of wheat were investigated by Kiarostami (2003). His results showed that the allelopathic activities of aqueous extracts of those weeds were significantly different against wheat cultivars. Weeds had different effects on the percentage of seed germination coleoptile and root length and dry weight of 12 cultivars of wheat. Different parts (leaf, shoot and root) of field bindweed (*C. arvensis*) and extract concentrations (1:5, 1:10, 1:15 and 1:20 v/v) had different effects on germination and yield of wheat during 2007 and 2008. All extracts of bindweed decreased wheat germination characteristics and the highest reduction belonged to root extract. Decreasing in seed number per plant, 100 kernel weight and yield in concentration rate of 1:5 were 76.17, 94.66, and 99% compared to control, respectively. Field trial confirmed glasshouse results and in field conditions, applying bindweed extract and residue decreased wheat yield by 74.84 and 88 %, respectively (Yarnia et al. 2010).

The effects of winter wild oat (*A. ludoviciana*), annual canary grass (*P. minor*), and wild mustard (*S. arvensis*) at 0–61, 0–39 and 0–74 plants m^{-2} on yield of wheat (cv. Flat) was evaluated by Montazeri (2007). He reported that wild mustard at 12.5 or more plants m^{-2}, significantly reduced the height of wheat, whereas winter wild oat at 39 or more plants m^{-2} reduced 1,000 grain weight and number of grains per spike. This weed at 11.5–61 plant m^{-2} reduced the grain yield 18–44 %. Annual canary grass at 29–39 plants m^{-2} significantly reduced 1,000 grain weight and 18–19 % the grain yield, but had no effect on the number of grain per spike. Wild mustard at 12.5 and 22.5 plants m^{-2} reduced number of grain per spike and 1,000 grain yield, respectively. Wheat grain yield loss due to the presence of wild mustard at 12.5–74 plants m^{-2} was noted as 51–91 %, respectively.

Mojab and Mahmoodi (2008) carried out a growth chamber study to evaluate the allelopathic effects of 25, 50, 75, and 100 % of shoot and root water extract of hoary cress (*Cardaria draba)* on seed germination and seedling characteristic of sorghum (*S. bicolor*).

8.3.2 Non-Cereal Crops

Mansouri et al. (2005) studied the effects of aqueous extract concentrations of 0, 0.5, 1.5, 3.5, 5, and 7 % of root, shoot, seed, flower, stem, and leaf of wild mustard on germination percentage and seedling growth of canola. Results indicated that different aqueous extracts decreased germination percentage and radicle and coleoptile lengths. Maximum germination was observed in root extract treatments and minimum in leaf and flower extracts. Effects of flower extracts on length of radicle and coleoptile were higher than other organs. Rezaii et al. (2008) evaluated the allelopathic effects of shoot and root tissues of *A. retroflexus*, *C. album,* and *C. dactylon* on canola germination and growth. The highest and lowest range of reduction in dry weight and seedling length of canola were 4.16 and 98.28 %, respectively. A maximum reduction was obtained with *C. dactylon*. Charlock (*S. arvensis*), which is a serious weed in the crop fields in Iran, is other frequent weed that was found growing in canola crops. It was observed when canola fields infested with charlock allelochemicals released from this weed into the soil.

Govahi and Shajie (2005a) investigated the allelopathic effects of *C. album* water extracts on bean germination. Treatments used were: 0, 25, 50, 75, and 100 % of *Chenopodium* water extracts and results indicated that the effects of *Chenopodium* water extracts on germination percentage, radicle and plumule growth, and seedling dry weigh were significant. Increased water extracts of *Chenopodium* reduced characteristics of germination and seedling growth. Haddadchi and Massoodi-Khorasani (2006) studied the allelopathic effects of aqueous extracts of *S. arvensis* on growth and related physiological and biochemical responses of canola. They cultured etiolated seedling of canola in Hoagland's culture with or without shoot and root of charlock aqueous extraction at 0.5 and 1.5 % concentrations of stock solution (10 g dried material extracted in 100 mL DW) in 5–6 foliar leaf stage. Results revealed that shoot extract reduced shoot and root length, leaf area, and fresh weight of canola, but root extract were only significantly affected at 1.5 %. Shoot extract at 1.5 % reduced chlorophyll *a* and total chlorophyll compared to control plants, but root extract at the same concentrations reduced chlorophyll *b*. In addition, shoot extracts reduced Hill reaction. Shoot and root extracts of charlock increased soluble and decreased non-soluble carbohydrate content in canola. Charlock aqueous extraction reduced protein content and increased proline content in leaves. Shoot and root extracts of charlock at 1.5 % concentration increased peroxidase activity of canola leaf. *Datura stramonium* is a predominant weed in Iran and many other countries in the world that inhibits growth of chickpea, rice, barley, wheat, and a few vegetables. Shajie and Saffari (2009) studied the allelopathic effects of above ground parts of *D. stramonium* water extracts on canola (cv. Hayola 401). Results showed that the effects of *D. stramonium* water extract of above ground parts on germination percentage, radicle and plumule growth were prominent. Increasing water extract of *D. stramonium* concentration caused reduction in canola germination and growth significantly. In green house experiment, during three weeks the shoot extract of *D. stramonium* were applied to potted canola plants which were irrigated at 2-day intervals with the five concentrations of extract. They also in another greenhouse experiment mixed the residue of weed plants in soil before planting canola. The highest shoot dry weight, leaf area, and chlorophyll content of the canola were recorded at 60 days after sowing. Results indicated that shoot extract of *D. stramonium* and its residue reduced plant height, leaf area, and dry weight of canola.

Mohammadi et al. (2004) investigated the effects of shoots, rhizosphere soil, and extracted water from rhizosphere of *C. album*, *C. arvensis*, *Glyrrhiza glabra*, knotweed (*Polygonum aviculare*), and *S. halepense* on germination and seedling growth of chickpea. Shoots rhizosphere and extracted water from rhizosphere of *S. halepense*, *C. album,* and *C. arvensis* significantly decreased the germination and seedling growth of chickpea, while *G. glabra* and *P. aviculare* did not affect those traits. In most cases, *S. halepense* had more inhibitory effect on chickpea. Also, plumule growth was influenced more severely than radicle grown. In another study, the allelopathic effects of shoot and root powders and rhizosphere soil of several weed species were applied in vegetative, reproductive, and maturity growth stages on germination, lengths, and weights of seedling, radicle, and plumule of soybean cultivar Williams. Results showed that the allelopathic properties of all treatments in *A. retroflexus*, *S. viridis*, knapweed (*Acroptilon repens*), *C. album*, *Cirsium arvense*, Bermuda grass, and *C. arvensis* had significant effects on all traits. Growth stage had only significant effect on germination percentage. *A. retroflexus* and *C. arvense* had the largest inhibitory effects on seedling growth, while *C. arvensis* had largest inhibitory effects on germination percentage. Plumule growth was influenced more than radicle. Allelopathic factors at all growth stages of weeds had large amount of inhibitory effect on germination and seedling growth of soybean. The result of this study could be useful to recognize allelopathic effect of important weeds on decreasing germination and seedling growth of soybean (Shafagh-Kalvanag et al. 2008). Benyas et al. (2009) investigated the effects of aqueous extracts of different organs of lambsquarters (*C. album*) and common cocklebur (*Xantium strumarium*) including shoot, root, and whole plant (2 % w/v) on emergence percentage, growth and development, essential oil content, and yield of summer savory (*Satureja hortensis*). Results showed that the aqueous extracts of lambsquarters shoot and common cocklebur whole plant reduced emergence percentage of summer savory. Aqueous extract of different organs of both weeds had significant effect on morphological traits as well. The results indicated that the aqueous extract reduced summer savory bush height, number of leaves per plant, and dry weights of shoot and root. Despite increase in essential oil content of summer savory, essential oil yield of summer savory was reduced by different plant parts aqueous extracts of both weeds.

Common cocklebur is a predominant weed in Iran and many other countries in the world (Rashed-Mohasel and Mousavi 2007). Benyas et al. (2010) conducted an experiment in order to evaluate the allelopathic effects of the aqueous extract of common cocklebur on seed germination, seedling growth, and chlorophyll content in lentil (*Lens culinaris*). They concluded that that highest concentration of common cocklebur shoot aqueous extract negatively influenced seed germination rate, plumule length, and seedling dry weight of lentil. Shajie et al. (2005a, c) also investigated the allelopathic effects of various concentrations (0, 25, 50, 75, and 100 %) of common cocklebur above ground shoot water extracts on corn (S.C. 704), chickpea, sesame, and canola germination and radicle and plumule growth, and results indicated that increasing water extracts of common cocklebur concentration caused significant reduction in corn, chickpea, sesame, canola germination and growth.

Allelopathic effects of different concentrations (0, 25, 50, 75, and 100 %) of *Kochia scoparia* shoot water extracts on germination, radicle, plumule growth, seedling dry weight of bean an experiment performed by Govahi and Shajie (b) and they found that increasing water extracts of *K.* concentration caused reduction in bean germination and growth significantly. Sodaeizadeh and Hakimi-Maybodi (2009) conducted an experiment in Iran to investigate the allelopathic effects of three plant species of *Capparis spinosa, Herttia angustifolia,* and *P. harmala* and two extract concentrations (50 and 100 %) on germination and seedling growth of alfalfa and wheat. They found that *C. spinosa* extracts caused the greatest inhibitory effect on plants. Reductions in seed germination, shoot length, and weight were 86, 98 and 99 %, respectively.

Kazerooni-Monfared and Rashed-Mohasel (2006) investigated the allelopathic effects of knotweed (*P. avicular*) on emergence and seedling growth of tomato and corn. In this study, knotweed residues (0, 0.33, 0.67, 1 and 1.33 % w/w) were added to the pot soil. Corn and tomato seedlings showed different response to different rates of knotweed residues. Increasing residues increased the emergence percentage of tomato but decreased corn emergence. Higher rate of residues resulted in an increase of 33.9 and 39.3 % in leaf area of tomato and corn, respectively.

Allelopathic potential of hoary cress and *B. deflexa* on two ornamental plants of *Mathiola incana* and *A. caudatus* was studied (Rezaei-Nodehi et al. 2003). Results showed that water extracts of the plants had significant effect on germination percentage and radicle length of both ornamental plants. With increasing extract concentration, germination percentage, radical and hypocotyl lengths of both plants were significantly reduced and radicle growth compared to hypocotyl was more inhibited.

8.4 Allelopathic Effects of Crops on Crops

Crop rotation is practice of growing a series of dissimilar types of crop species in the same area in sequential seasons for various benefits such as to avoid the build up of pathogens and pests. Crop rotation also seeks to balance the fertility demands of various crops to avoid excessive depletion of soil nutrients. A traditional element of crop rotation is the replenishment of nitrogen through the use of green manure in sequence with cereals and other crops. So, crop rotation is one component of polyculture in time. Therefore, allelopathic effects of crops which are planted in a rotation should be carefully considered.

Saffari and Torabi-Sirchi (2011) conducted an experiment to estimate the effects of different concentrations of two native Iranian wheat (Alvand and Falat) straw extracts on germination, radicle growth, coleoptile length, plant height, leaf area (LA), wet weight (WW), and dry weight (DW) of two hybrid corn varieties (single cross 704 and single cross 647). Their results revealed that the straw extracts have negative and significant effects on both corn varieties growth and the significant allelopathic effects remained up to 90 days after wheat harvest, but decreased gradually up to 180 days after harvest. Therefore, it is concluded that before corn cultivation, wheat straw and residues should be eliminated from the field to avoid negative allelopathic effects of wheat straw on corn growth.

Ghahary et al. (2009) evaluated the effects of four concentrations (0, 5, 10 and 15 %) of hull extracts on growth of 10 Iranian rice (*Oryza sativa*) cultivars by doing two lab and greenhouse studies. Results of laboratory study showed that rice hull extracts and other plant tissues had stimulation and inhibitory effects on seedling growth of the same cultivar, respectively. Behnam Chalos cultivar had the highest stimulated effects on germination percentage, root length, and total dry weight of seedlings. The rice hull extract of Nemat and Tabesh cultivars had inhibitoriest effects on shoot length and germination rate of the same seedlings, respectively. Results of greenhouse study suggested that rice hull extract of Nemat cultivar had the greatest stimulated effects on shoot length and root dry weight of the same seedling. Root length in Tabesh cultivar, germination rate, and total dry weight in Gerdeh cultivar and shoot dry weight in Zarak cultivar were more stimulated than other cultivars. The results suggest that various allelopathic effects (inhibition and stimulation) exist in rice hull extract of different cultivars. Rice hull extract from breeded cultivar contrary to native cultivars had the greatest stimulatory effect on seedling growth. Enhancement of aqueous extract concentration increased stimulatory effects on seedling traits in breeded cultivars. Length and dry weight of seedling root decreased in rice native cultivars under rice hull extract.

Chickpea is a poor competitor against weeds and availability of post-emergence herbicides particularly against broad-leaf weeds is limited (Solh and Palk 1990). Jafarzadeh (2005) investigated the allelopathic potential of barley resides on weed control and growth of chickpea. Treatments included: no-weed control, hand weeding in two times, chemical control, and mixing barley residues in chickpea rows in 2.4 and 4.8 t h^{-1}. Dominant weeds were *Euphorbia* spp., *Centaurea depressa*, *Conringia orientalis,* and *Polygouum aviculare*. Barley residues affected germination and growth of weeds. Hand–weeding had significantly higher effects than other treatments. Hand-weeding increased yield by 186 % in comparison with control. Using barley residues at rate of 4.8 t h^{-1} reduced numbers and fresh weight of annual weeds, *C. orientalis* and *P. aviculare* by 42.4, 50.1, 53.6, and 47.8 %, respectively. In another experiment, allelopathic effects of chickpea stubble on germination and early growth of sorghum, soybean and sunflower was investigated in a greenhouse experiment conducted by Abbasdokht and Chaichi (2003). The experiment consisted of five chickpea accessions as main plots, four stubble concentrations (2.5, 5 and 7.5 g pot^{-1} and control) and three crop species (sorghum, soybean and sunflower). Germination percent, root dry weight and shoot/root ratio were significantly reduced by stubble concentration of chickpea.

Younesi et al. (2009) studied the allelopathic effect of extra-root of cold-season crops (including: wheat, barley, rye and chickpea and without- planting as control) on emergence and primary growth of sorghum, corn and soybean. They realized that experimental treatments had significant effects on seedling emergence percentage, seedling emergence rate, plant height, and shoot dry weight. Rye had the highest allelopathic effect on crops. Soybean was more sensitive than other crops. Delayed planting decreased the allelopathic effects of cold-season crops.

Canola contains allelochemical compounds as glucosinolate that under special conditions are released to environment and cause effects on seed germination and plant growth. Enzyme myrosinase catalyzes the hydrolysis of glucosinolate thereby resulting in the production of inhibitor compounds such as isothiocyanate and thiocyanate and nitrile (Jafariehyazdi and Javidfar 2011; Niakan et al. 2006). Planting soybean after canola reduced soybean germination and growth (Haddadchi and Gerivani 2009). Niakan et al. (2006) studied the inhibitory effects of water extracts of two cultivars of canola (PF and Hyola401) and decomposition extracts of two cultivars during different times on soybean germination and radicle growth. Results showed that inhibitory effect of shoot water extract in two cultivars was more than root and this effect on Hyola was more than PF cultivar. Jahandideh and Latifi (2006) evaluated the allelopathic effects of canola extract and stubble on germination growth of corn and soybean seedling with amount of canola stubble (0, 35 and 71 %) and stubble (w/w) based on percentage of soil dry weight at greenhouse conditions. The results showed that with increasing the amount of canola stubble and extract concentration, the rate, and the maximum emergence percentage of corn and soybean decreased. The stem height, root length, leaf area, root and shoot dry weights in 5 and 15 days after emergence were not affected compared to control. However, 10 days after emergence, the increase in canola extract and stubble decreased soybean root length and root dry weight. Also, increased application of canola extract significantly decreased corn rate and maximum germination percentage. Likewise, Jafariehyazdi and Javidfar (2011) investigated the allelopathic potential of *B. napus*, *B. rapa,* and *B. juncea* on seed germination and seedling growth of sunflower. Aqueous extracts of three species at two stages (full flowering and straw) of sampling were separately made with 0, 10, 20, 30, and 40 % concentrations. All aqueous extracts significantly affected sunflower germination rate, seedling root, and hypocotyl length, fresh and dry weight. The greatest concentration showed a stronger inhibitory effect. Root length was more sensitive to extracts than hypocotyl length. Response of cotton (*Gossypium hirsutum*) to different ages and rates of sunflower [esidues included 80 and 160 g of 6-, 8-, and 10-week-old residues and control (no residue)] was studied in a field experiment. Results showed that percent emergence, height, dry weight, and yield of cotton were significantly reduced. Reduction in percent emergence, height and dry weight were 62, 59, and 74 % two weeks after planting, respectively. Older plants had higher phytotoxic effects than younger plants (Zia-Hosseini et al. 2002). In another study, allelopathic potential of sunflower residues on growth and yield of cotton was studied by Aghajani et al. (2001). Sunflower fresh residuals rate (8 and 16 % soil weight) from root, shoot, leaf, leaf–shoot, leaf–root, shoot–root, leaf–shoot, and root that mixed with soil had inhibitory effects on cotton emergence, dry weight, height, and yield in which increasing of residues enhanced the inhibitory effect. The highest allelopathic effect was observed in root residue.

Effect of different rates (8 and 16 % soil weight) and ages (6, 8 and 10 weeks old) of sunflower residues on corn was studied in a field experiment. It was found that sunflower residues reduced seedling emergence, height, and dry weight of corn. Older residues did not significantly affect these traits for 6 and 8 weeks old residues, but 10 weeks old residue reduced all measured traits. Residues rate did not significantly affect these traits. Substantial reduction in final plant height and dry weight was observed in older residue (10 weeks old) mixed with soil treatment (22 and 52 %, respectively). Residues from older plants had more phytotoxic effects than younger plants (Zia-Hoseini and Barar-pour 2002).

Niakan et al. (2008) investigated the effect of salinity stress on allelopathic potential of canola by studying growth factors, chlorophyll *a* and *b* contents, antioxidant enzyme, and nitrate reductase activity of soybean seedlings in hydroponic culture. The seeds of canola (cv. Hyola 401) were grown in soils with salinity of 0, 6, and 10 dS m^{-1} in pots and in 3–5 leaves stage of total plant were extracted. This extraction was added to Hoagland culture containing soybean seedling in 70 % concentration. With increasing salinity, allelopathic potential of canola was also increased. The aqueous extract of canola grown in saline soils decreased chlorophyll *a* and *b* content in cotyledon, length of root and epicotyl, catalase and peroxidase activity in root and shoot, and nitrate reductase activity in cotyledons. They found that glucosinolates in canola had effect on soybean growth. Haddadchi and Gerivani (2009) studied the allelopathic effects of various parts of canola (*B. napuse*) on soybean (*Glycin max*) germination, seedling growth, and biochemical aspects. Phenolic extract of canola shoot (including leaf, stem, and flower) and root were made by methanol 70 %. Measured criteria of soybean were fresh and dry weights of hypocotyl and radicle of 8-day-old seedlings and activity of peroxidase (POD), catalase (CAT), superoxide dismutase (SOD), polyphenol oxidase (PPO), protein content of hypocotyl and radicle, and lipid peroxidation (MDA) of radicle. The results showed that there were no significant differences in CAT activity and protein content. Increased phenolic extract concentration of separated canola plant parts decreased soybean germination and seedling length and weight. Radicle growth was more sensitive to canola extract than hypocotyls growth. The POD and SOD activity of radicle and hypocotyl and lipid peroxidation of radicle increased by concentration of both phenolic extracts compared with control. The PPO activity of radicle and hypocotyl increased under root extracts, but shoot extracts had no significant effects. The degree of toxicity of canola root tissue was more than shoot tissue.

8.5 Allelopathic Effects of Weeds on Weeds

Weeds can compete with productive crops or pasture; weeds also differ in their competitive abilities. Although scientists have always been fascinated by the diversity and adaptability that typify weeds, their effects on each other have rarely been considered. Abbassi et al. (2007b) evaluated the potential allelopathic effects of *A. repens* on two weed species of wild mustard (*S. arvensis*) and wild barley (*H. spontaneum*) under greenhouse conditions. Treatments included different parts of *A. repens* (shoot and root) combined with four levels of concentration of dried powder of plant (0, 0.5, 0.75, 1, and 1.25 %) and three species (wild mustard, wild barley, and canola as a crop). Results showed that shoot and root of donor species affected different growth characters of canola and two weed species. In another study carried out by Abbassi et al. (2008), the allelopathic effects of different sections of Russian knapweed (*A. repens*) on canola seed germination were studied. Treatments were combinations of two different sections of Russian knapweed (shoot and root), ten different levels of water extracts (0, 15, 25, 30, 35, 40, 45, 50, 75 and 100 %) and three different kinds of seeds (canola, wild mustard and wild barley). Results indicated intense allelopathic effects but the magnitude was different in each species and different criteria of germination. Generally, germination criteria were significantly more affected than vegetative growth. The effects of Russian knapweed shoot was more intense than root section and wild mustard was the most sensitive plant, although wild barley was less sensitive plant to Russian knapweed.

Atriplex canescens is alien species in Iran, which is cultivated in many rangelands. *Salsola rigida* is a native species and has good nutrient quality in arid and semi-arid rangelands. Dehdari et al. (2008) studied allelopathic effect of *A. canescens* on germination of *S. rigida.* They reported that fruits and leaves of *A. canescens* had allelopathic effects on final germination, mean period of final germination, rate of germination and percentage inhibition, or stimulation of *S. rigida*.

8.6 Allelopathic Effects of Medicinal Plants

There are 7115 vascular plant species in Iran, which belong to 1206 genera, 173 families, and six phyla, many of them have potential medicinal properties (Yosofi 2007). Allelopathic medicinal plants usually produce and release many kinds of secondary metabolites with multiple functions that affect their neighbor plants. These secondary metabolites can be used for human well-being also. There are indications that secondary metabolites of medicinal plants decreased germination, growth, and establishment of different plant species (Azizi et al. 2009). Azizi and Fuji (2005) confirmed that medicinal plants have relatively strong allelopathic activities. Several allelochemicals have been shown to possess a broad activity spectrum. In vitro experiments with more than 70 alkaloids indicated that most alkaloids are toxic or inhibitory to more than one group of organisms including plant seedlings, bacteria, insects, and mammals. Alkaloids can be considered as “multipurpose” defense substances due to their wide range activities (Wink et al. 1998). Azizi et al. (2009) reported that 51 species out of 56 tested plants declined lettuce seedling growth. Ten species completely inhibited lettuce seed germination namely *Achillea wilhelms, Ailanthus altissima, Berberis vulgar*, *B. persicum*, *Carum copticum*, *Lavandula spica, Pulicaria gnaphalodes,* and *Ziziphora clinopodioides*.

Plantago is a genus of about 200 species of small, inconspicuous plants commonly called plantains. *P. psyllium* is an important herb that has been used as medicinal plant for centuries in South Asia and is now widely grown all over the world. *P. psyllium* is the common name used for several members of the plant genus *Plantago* whose seeds are used commercially for the production of mucilage (Munch et al. 2008; Zahoor et al. 2004). Rahimi et al. (2006) studied the allelopathic effects of *P. psyllium* on four major weeds species including wild barley, black mustard, pigweed, and lambsquarters. *P. psyllium* decreased the ability of weeds to germinate, grow, and survive especially in drought-prone environments. Moreover, the results indicated a different degree of sensitivity between target species and therefore suggested that if water resources be limited during plant growth, which is common in Mediterranean areas, poor germination percentage, root development, and dry matter accumulation of weeds may restrict the ability of weeds to cope with a water deficit and impair their ability to compete with *P. psyllium*. Inhibitory substances present in *P. psyllium* caused allelopathy, which could be used as a source of potential natural herbicide. However, they must first be identified and their modes of actions be studied.

Zhumeria majdae that belongs to Lamiaceae family is a medicinal and aromatic plant in Iran. The effects of different concentrations of essential oils prepared from leaves of *Z. majdae* on seed germination and seedling growth of tomato and wheat were studied. The results indicated that essential oils prepared from leaves of *Z. majdae* inhibited seed germination and seedling growth. In the presence of 50 and 100 % of stock solution, wheat seed germination was reduced to zero. Using different concentrations of essential oil as post-emergence treatment reduced both amounts of fresh and dry weights in tested plants. The most effective action was observed on dry weight of tomato as well. The chlorophyll content was reduced in all post-emergence treated plants. The activity of POD enzyme extracted from the mentioned plant roots in tomato was increased and in wheat was reduced (Soltanipoor et al. 2006). Soltanipor et al. (2007) studied the effects of aqueous extract from leaves of *Z. majdae* on seed germination of *Allium porrum, A. cepa, B. oleracea*, *Lactuca sativa*, *Lipidium sativum,* tomato, and *Raphanus sativus*. Aqueous extract from leaves of *Z. majdae* inhibited seed germination in all tested plants. Seed germination rates in *B. oleracea* and *L. sativum* were reduced to zero. Percentage of seed germination was more different between aqueous extract and control in *A. cepa, B. oleracea* and *L. sativum*.

Artemisia is a large and diverse genus belonging to the family Asteraceae and spreads throughout the world including Iran. It is considered as a medicinal plant in its use for therapeutic effects in folk medicine (Matsumoto et al. 2006). It comprises hardy herbs and shrubs known for their volatile oils. *Artemisia* is a plant with allelopathic activity, which could reduce seed germination rate and seedling growth of wild oat (Samedani and Baghestani 2005). Samedani and Baghestani (2005) showed that wild oat seed germination, root and shoot length were reduced by using *Artemisia* extracts. *A. auchary* had more effect on oat seed germination. *A. scoparia* had no effect on oat seed germination and while *A. auchary* and *A. sieberi* extracts applied at 80,000 ppm concentration reduced seed germination by 48 and 44.7 %, respectively. Estimated rates of *A. auchary* extract required for a 50 % reduction in oat root and shoot length were 6640 and 9970 ppm, respectively. Mohebi et al. (2008) evaluated allelopathic effects of *A. sieberi* on germination and initial growth properties of *Stipa barbata*. Extracts of root and aerial parts had positive and negative effects on seed germination properties of *S. barbata,* respectively. The difference in the effects of root and shoot extracts on germination might be due to different allelochemicals or their concentrations in mentioned tissues of *A. sieberi*.

Pirzad et al. (2010) investigated the effects of water extracts of sage and white wormwood (*Artemisia herba-alba*) on germination and seedling growth of purslane (*Portulaca oleracea*). They concluded that water extracts of those medicinal plants significantly influenced final germination percentage, germination rate and index, root and shoot length, root/shoot ratio, and fresh and dry weight of seedling of purslane. Similarly, Arouiee and Azizi (2006) showed that leaf extraction of *Datura* sp., *Carduus benidictus*, *Silybium marianum* and *Planta lanceolata* decreased and increased seed germination and mean germination time of weeds, respectively. Allelopathic effect of *Artemisia* on seed germination and seedling growth of *A. lodoviciana* and *A. retroflexus* was considered in a series of examinations by Ghorbanli et al. (2008). Thick aqueous extracts of each growing parts of *Artemisia* with 10 % density (100 g of the growing part per 1,000 mL distilled water) were prepared and then aqueous extracts of 0, 20, 60, and 100 % were made and the effect of each one on seeds germination and mentioned weed plants seedlings growth was taken into consideration. The effect of different *Artemisia* aqueous extracts on the germination, radicle, and coleoptiles lengths of *A. lodoviciana* and *A. retroflexus* showed different results. The results indicated that the effects of *Artemisia* leaf aqueous extract on germination and growth of *A. lodoviciana* and *A. retroflexus* was more than the other aqueous extracts of *Artemisia* vegetative parts. Safari et al. (2010) examined the allelopathic influence of aqueous extracts of *T. kotschyanus* on germination characteristics and seedling growth of *B. tomentellus* and *T. repens*. Aqueous extracts had a considerable inhibitory effect on target plant germination. Seedling length, in addition to fresh and dry weights were also reduced significantly over control. The inhibitory effect was increased as the extract concentration was increased. *B. tomentellus* showed a higher sensitivity against *T. kotschyanus* in allelopathic effects compared to *T. repens*.

Azizi and Fuji (2005) investigated the allelopathic effects of some medicinal plants on seed germination of *A. retroflexus* and *P. oleraceae*. They studied the effects of several concentrations of a hydro-alcoholic extract of St. John's wort (*H. perforatum)* and sage (undiluted, 1/5, 1/10 and 1/20 diluted) and different concentrations of Eucalyptus oil (*Eucalyptus globulus*) [0.1, 0.2, 0.5 and 1 % (v/v)] on seed germination percent and rate for two weeds, *A. retroflexus* and *P. oleraceae*. In the second experiment, they studied the effects of different concentrations of black zira on lettuce and radish seed germination and noted that concentrated extract of St. John's wort and sage had a significant inhibitory effect on seed germination percent and rate of *A. retroflexus,* but not of *P. oleraceae*. Eucalyptus essential oils had a strong inhibitory effect on the germination of both weed species at 0.7 % (v/v). Black zira essential oils also had an inhibitory effect on lettuce and radish seeds. Lettuce seeds were more sensitive than radish to these essential oils. Lettuce seed germination was completely stopped at 0.2 % (v/v), but radish required much higher concentration [1 % (v/v)]. Strong inhibitory effects of Eucalyptus and black zira essential oils may give promising results in the organic culture of plants. In another experiment, Azizi et al. (2009) investigated the genetic resources for allelopathic and medicinal plants from traditional Persian experiences. In this research, they studied the allelopathic activities of 56 aromatic and medicinal plants of 22 families, most of which are used in Persian traditional medicine. The assayed method was dish pack with lettuce seed. They showed that 51 out of 56 species decreased lettuce seedling growth. Ten species completely inhibited lettuce seed germination namely black zira, *C. copticum*, *A. wilhelms, P. gnaphalodes*, *B. vulgar*, *L. spica, Z. clinopodioide,s* and *Ailianthus altissima*.

Naghdi-Badi et al. (2009) evaluated the allelopathic effect of aqueous extract of different plant organs including root, shoot, leaf of *P. harmala* in five concentrations (0, 1, 5, 10, and 15 %) and capsule on seed germination and seedling growth of *C. album* and *P. oleracea*. *P. harmala* extracts decreased seed germination and seedling growth of these weeds. The highest inhibitory effect was observed in capsule extract. The lowest seed germination and seedling growth were obtained with 15 % concentration. *P. oleracea* was more sensitive than other species.

Germination inhibitory effects of *Zataria multiflora* on *S. arabica* and *Cymbopogon olivieri* (Ramzjuie et al. 2008) and *E. camaldulensis, Juglans regia*, *Onbrychis sativa* and *Lotus corniculatus* (Nasr-Esfahani and Shariati 2004) have been reported.

Saffron is an important crop in south Khorasan province of Iran, Abbassi and Jahani (2007) studied the allelopathic effects of saffron on seed germination of several important crops but using 0 (distilled water), 0.5, 1, and 3 % aquatic extracts of dried powder of corm (corms from 4 and 14 years stands). Ten days after application of extracts, percentage and rate of germination, plumule and radicle length, and weight of seedlings in barley, canola, corn, cotton, soybean, and wheat were measured. Results indicated that saffron had allelopathic effects on all species but the magnitude on each species and different germination criteria were different. Radicle length was more affected than other parameters. Eghbali et al. (2008) evaluated the effects of different rates (4.25, 15, 30, and 75 g of ground tissues in 1.5 kg soil) of saffron corm and foliage residues on wheat, rye, vetch, and bean. They showed that source of saffron tissues and the amount of added tissue to soil had a significant effect on some of the factors in four crops. With increasing amount of saffron leaf tissue added to the soil, chlorophyll content, plant height, leaf surface area, shoot and root biomass increased, but with increasing amount of saffron corm tissue all studied traits decreased. Summer crops (vetch and bean) were affected lowly by saffron corm and foliage tissues less than winter crops (wheat and rye). In another study, Hosseini and Rizvi (2006) conducted an experiment about the possible role of saffron allelopathy using soil collected from old farm, old farm from where saffron's were self-thinned, new farm, a farm where saffron had not been cultivated as control one and corms collected from old farm, new farm and distilled water as control two. Germination percentage and rate, radicle and plumule dry weights of wheat seeds were adversely affected only by extracts of old and new corms of saffron. Asghari-Pour et al. (2006) studied the allelopathic effects of different soil containing incorporated parts of saffron on emergence and seedling growth of tomato and wheat at greenhouse conditions. Leaves and corms incorporated in soil inhibited the emergence and growth of tomato and wheat. Significant reduction in emergence, shoot length, and dry weight of shoot were observed as the plant residues in the soil increased. The concentration-dependence response of the test plant to saffron suggested that it may contain allelochemicals. Apparently, saffron allelopathic effects on seed emergence and seedling growth of tomato and wheat were stronger. Soil under saffron cultivation also inhibited seed emergence and seedling growth of test plants. Age of saffron plantation did not explain the effectiveness of saffron on tested plants. In general, tomato was more sensitive than wheat to saffron residues.

Eskandari-Torbaghan et al. (2007) performed two experiments to investigate the effect of saffron petal water extracts with different concentrations of 0, 25, 50, 75, and 100 % made from 1 % water extract on germination and primary growth of cotton (var. Varamin) under laboratory conditions. Different concentrations had no significant effects on germination percentage and radicle dry weight but had significant effects on coleoptile dry weight. The highest coleoptile and radicle lengths were observed at 50 % concentrations of the extracts. A great amount of saffron petals are shed after harvesting every year while they could be used for weed control. Rashed-Mohassel et al. (2009) studied allelopathic effects of different concentrations (0.5, 1.5, and 4.5 per 1,000 mL of distilled water) saffron and corm leaves on redroot pigweed and lambsquarter seedling growth. Their results revealed that the leaf extracts of saffron reduced the plant height, leaf area, leaf weight, stem weight and dry weight of both weeds. Allelopathic effects of saffron leaves were more in redroot pigweed than another weed and the allelopathic effects of corms were more in lambsquarter compared to redroot pigweed. Alimoradi et al. (2008) indicated that with increasing concentration of saffron extract, germination rate, shoot length, root length, and seedling dry weight of *Rapistrum rogosum* and *Gypsophilla pillosa* decreased.

8.7 Allelopathic Effects of Trees

There are many references regarding research programmes conducted regarding allelopathic effects of trees in Iran. For example, almond (*P. dulcis*) flowers, leaves, and bark against seed germination and seedling growth of cress and

Table 1 Summary of the allelopathic studies conducted in Iran

Allelopathic plant	Susceptible species	References
(a) Weeds		
Acroptilon repens	*Sinapis arvensis* and *Hordeum spontaneum*	Abbassi et al. (2007b)
Acroptilon repens	*Brassica napus*, *Sinapis arvensis* and *Hordeum vulgare*	Abbassi et al. (2008)
Acroptilon repens	*Hordeum leporinum*	Roostanejad et al. (2008)
Amaranthus retroflexus, Convolvulus arvensis Secale cereale and *Sinapis alba*	*Trifolium resupinatum* and *Trifolium alexandrinum*	Meighany et al. (2006)
Amaranthus retroflexus, *Setaria viridis*, *Acroptilon repens*, *Chenopodium album*, *Cirsium arvense Cynodon dactylon* and *Convolvulus arvensis*	*Glycine max*	Shafagh-Kalvanag et al. (2008)
Amaranthus, *Chenopodium album* and *Cynodin dactylon*	*Brassica napus*	Rezaii et al. (2008)
Atriplex canescens	*Salsola rigida*	Dehdari et al. (2008)
Atriplex canescens	*Artemisia sieberi*	Henteh et al. (2005)
Avena ludoviciana, annual canary grass *Phalaris minor* and *Sinapis arvensis*	*Triticum aestivum*	Montazeri (2007)
Capparis spinosa, Herttia angustifolia and *Peganum harmala*	*Medicago sativa* and *Triticum aestivum*	Sodaeizadeh and Hakimi-Maybodi (2009)
Cardaria draba	*Sorghum bicolor*	Mojab and Mahmoodi (2008)
Cardaria draba and *Brassica deflexa*	*Mathiola incana* and *Amaranthus caudatus*	Kiarostami (2003)
Centurea depressa, *Hordeum spontaneum*, *Hordeum* sp., *Lolium rigidum* and *Senesio vulgaris*	*Triticum aestivum*	Kiarostami (2003)
Chenopodium album	*Phasaeolous vulgaris*	Govahi and Shajie (2005a)
Chenopodium album and *Xantium strumarium*	*Satureja hortensis*	Benyas et al. (2009)
Chenopodium album, *Convolvulua arvensis*, *Polygonum aviculare* and *Sorghum halepense*	*Cicer arietinum*	Mohammadi et al. (2004)
Convolvulus arvensis	*Triticum aestivum*	Yarnia et al. (2010)

(continued)

Table 1 (continued)

Allelopathic plant	Susceptible species	References
Datura sp., *Cenicus benidictus*,	*Silybum marianum* and *Plantago lanceolata*	Arouiee and Azizi (2006)
Datura stramonium	*Brassica napus*	Shajie and Saffari (2009)
Datura stramonium	*Lens culinaris*	Shajie et al. (2005b)
Haloxylon ammodenderon	Nematodicide effects	Hakimi-Meybodi et al. (2004)
Haloxylon aphyllum	*Agropyron elongatum* and *Agropyron desertorum*	Moameri et al. (2011)
Kochia scoparia	*Phasaeolous vulgaris*	Govahi and shajie (2005b)
Polygonum avicular	*Lycopersicon esculentum* and *Zea mays*	Kazerooni-Monfared and Rashed-Mohasel (2006)
Sinapis arvensis	*Brassica napus*	Mansouri et al. (2005)
Sinapis arvensis	*Brassica napus*	Haddadchi and Massoodi-Khorasani (2006)
Sorghum halepense and *Cynodon dactylon*	*Triticum vulgare*	Mohsenzadeh (2000)
Xanthium stramanium	*Cicer arietinum*	Shajie et al. (2005a)
Xanthium strumarium	*Lens culinaris*	Benyas et al. (2010)
Xanthium strumarium	*Zea mays*, *Cicer arietinum*, *Sesamum indicum* and *Brassica napus*	Shajie et al. (2005c)
(b) Crops		
Brassica napus	*Hordeum spontaneum*, *Amaranthus albus*, *Rumex crispus* and *Avena fatua*	Zaji et al. (2009)
Brassica napus	*Glycine max*	Niakan et al. (2006)
Brassica napus	*Zea mays* and *Glycine max*	Jahandideh and Latifi (2006)
Brassica napus	*Setaria virdis, Secale cereal, Amaranthus retroflexus, Chenopodium album* and *Avena fatua*	Jalili et al. (2007)
Brassica napus	*Setaria virdis*, *Secale cereale*, *Amaranthus retroflexus*, *Chenopodium album* and *Avena fatua*	Abbassi et al. (2007b)

(continued)

Table 1 (continued)

Allelopathic plant	Susceptible species	References
Brassica napus	*Glycin max*	Haddadchi and Gerivani (2009)
Brassica napus, *B. rapa* and *B. juncea*	*Helianthus annuus*	Jafariehyazdi and Javidfar (2011)
Cicer arietinum	sorghum, *Glycine max* and *Helianthus annuus*	Abbasdokht and Chaichi (2003)
Gossypium hirsutum	*Helianthus annus*	Zia-Hosseini et al. (2002)
Helianthus annuus	*Amaranthus retroflexus* and *Chenopodium album*	Orooji et al. (2008)
Helianthus annuus	*Amaranthus retroflexus* and *Chenopodium album*	Ghorbani et al. (2008)
Helianthus annuus	*Hordeum spontaneum*	Ashrafi et al. (2008b)
Helianthus annuus	*Gossypium hirsutum*	Aghajani et al. (2001)
Helianthus annuus	*Zea mays*	Zia-Hoseini and Barar-pour (2002)
Hordeum vulgare	*Brassica juncea* and *Setaria viridis*	Asghari and Tewari (2007)
Hordeum vulgare	*Sinapis viridis*	Ashrafi et al. (2008a)
Hordeum vulgare	*Agropyrum repens*	Ashrafi et al. (2009)
Hordeum vulgare	*Zea mays*, *Beta vulgaris* and *Helianthus annuus*	Naseri-Poor-Yazdi et al. (2008)
Hordeum vulgare	*Euphorbia* spp., *Centaurea depressa*, *Conringia orientalis* and *Polygouum aviculare*	Jafarzadeh (2005)
Hordeum vulgare (17 Iranian cultivars over 60 years of selection)	*Sinapis arvensis*	Oveisi et al. (2008)
Oryza sativa	*Echinochloa crus-galli*	Asghari et al. (2006)
Oryza sativa	*Avena ludoviciana* Durieu	Kolahi et al. (2009)
Oryza sativa	*Oryza sativa*	Ghahary et al. (2009)

(continued)

Table 1 (continued)

Allelopathic plant	Susceptible species	References
Oryza sativa	*Sisymbrium officinale*	Mahmoodzadeh et al. (2011)
Oryza sativa	*Sagittaria trifolia*	Berenji et al. (2011)
Secale cereal	*Triticum aestivum*	Baghestani-Meybodi et al. (2004)
Sorghum bicolor	*Amaranthus retroflexus*	Yarnia et al. (2009)
Triticum aestivum	*Convolvulus arvensis* and *Secale cereale*	Labbafy et al. (2009)
Triticum aestivum	*Secale cereale*, *Avena ludoviciana*, *Convolvulus arvensis* and *Vicia villosa*	Labbafi et al. (2010)
Triticum aestivum	*Hordeum spontaneum* and *Lolium rigidum*	Kiarostami et al. (2007)
Triticum aestivum	*Avena fatua*	Kiarostami et al. (2008)
Triticum aestivum	*Zea mays*	Saffari and Torabi-Sirchi (2011)
Triticum aestivum and *Secale cereale*	*Chenopodium album* and *Solanum nigrum*	Younesi et al. (2008)
Triticum aestivum and *Secale cereale*	*Chenopodium album* and *Solanum nigrum*	Younesi et al. (2008)
Triticum aestivum, *Hordeum vulgare*, *Secale cereale* and *Cicer arietinum*	sorghum, *Zea mays* and *Glycine max*	Younesi et al. (2009)
(c) Medicinal plants		
Artemisia	*Avena lodoviciana* and *Amaranthus retroflexus*	Ghorbanli et al. (2008)
Artemisia sieberi	*Stipa barbata*	Mohebi et al. (2008)
Artemisia siebery, *A. auchary* and *A. scoparia*	*Avena ludoviciana*	Samedani and Baghestani (2005)
Bunium persicum and *Cuminum cyminum*	*Bromus tectorum, Centura ovina* and *Descurainia sophia*	Takayuki et al. (2007)
Bunium persicum, *Carum copticum*, *Achillea wilhelms, Pulicaria gnaphalodes*, *Berberis vulgar var asperma*, *Lavandula spica, Ziziphora clinopodioides* and *Ailanthus altissima*	*Lactuca sativa*	Azizi et al. (2009)

(continued)

Table 1 (continued)

Allelopathic plant	Susceptible species	References
Glyrrhiza glabra	*Cicer arietinum*	Mohammadi et al. (2004)
Crocus sativus	*Amaranthus retroflexus* and *Chenopodium album*	Rashed-Mohassel et al. (2009)
Crocus sativus	*Rapistrum rogosum* and *Gypsophilla pillosa*	Alimoradi et al. (2008)
Crocus sativus	*Hordeum vulgare*, *Brassica napus*, *Zea mays*, *Gossypium hirsutum*, *Glycine max* and *Triticum aestivum*	Abbassi and Jahani (2007)
Crocus sativus	*Triticum aestivum*, rye, vetch and bean	Eghbali et al. (2008)
Crocus sativus	*Triticum aestivum*	Hosseini and Rizvi (2006)
Crocus sativus	*Lycopersicon esculentum* and *Triticum aestivum*	Asghari-Pour et al. (2006)
Crocus sativus	*Gossypium*	Eskandari-Torbaghan et al. (2007)
Crocus sativus	*Triticum aestivum*	Abbasi-Alikamar et al. (2007)
Hypericum perforatum and *Salvia officinalis*	*Amaranthus retroflexus* and *Portulaca oleraceae*	Azizi and Fuji (2005)
Mentha piperita and *Thymus vulgaris*	*Amaranthus retroflexus* and *Portulaca oleracea*	Azizi et al. (2006)
Peganum harmala	*Chenopodium album* and *Portulacea oleracea*	Naghdi-Badi et al. (2009)
Plantago psyllium	*Hordeum leporinum*, *Brassica nigra*, *Amaranthus retroflexus* and *Chenopodium album*	Rahimi et al. (2006)
Salvia officinalis and *Artemisia*	*Portulaca oleracea*	Pirzad et al. (2010)
Tagetes patula	Tomato early blight	Koocheki et al. (2008)
Thymus kotschyanus	*Bromus tomentellus* and *Trifolium repens*	Safari et al. (2010)
Zataria multiflora	*Stipa arabica* and *Cymbopogon olivieri*	Ramzjuie et al. (2008)
Zhumeria majdae	*Lepidium sativum* and *Echinochloa crus-galli*	Soltanipour et al. (2005)
Zhumeria majdae	*Lycopersicon esculentum* and *Triticum aestivum*	Soltani-poor et al. (2006)

(continued)

Table 1 (continued)

Allelopathic plant	Susceptible species	References
Zhumeria majdae	*Allium porrum*, *Allium cepa*, *Brassica oleracea*, *Lactuca sativa*, *Lipidium sativum*, *Lycopersicon esculentum* and *Raphanus sativus*	Soltanipor et al. (2007)
(d) Trees		
Amygdalus Persica	*Lepidium sativum* and *Trigonella gracum*	Astaraei and Sampietro-Diego (2008)
Eucalyptus	*Phalaris*	Niakan and Saberi (2009)
Eucalyptus camadulensis and *Juglans regia*	*Coronilla varia*	Nasr-Isfahan and Shariati (2007)
Eucalyptus camaldulensis	*Chenopodium album*	Najafi-Ashtiani et al. (2008a)
Eucalyptus camaldulensis	*Amaranthus blitoids*	Najafi-Ashtiani et al. (2008b)
Eucalyptus camaldulensis	*Acroptilon repens*, *Plantago lanceolata* and *Portulaca oleracea*	Dadkhah and Asaadi (2010)
Eucalyptus camaldulensis, *Juglans regia* and *Onbrychis sativa*	*Lotus corniculatus*	Nasr-Esfahani and Shariati (2004)
Eucalyptus globules	*Cynodon dactylon*	Daneshmandi and Azizi (2009)
Juglans regia	*Amaranthus hybridus* and *Acroptilon repens*	Abbassi et al. (2009), Nasr-Isfahani and Shariati (2007)
Pinus eldrica	*Lolium perenne*, *Festuca arundinacea* Schreb., *Poa pratensis* and *Agrostis capillaris*	Alizadeh et al. (2009)

fenugreek (Astaraei and Sampietro-Diego 2008), *E. camadulensis* and *J. regia* leaf on seed germination of *Coronilla varia* (Nasr-Isfahan and Shariati 2007), *E. camaldulensis* on growth and germination rates of *C. album* (Najafi-Ashtiani et al. 2008a), Eucalyptus on germination criteria and antioxidant enzyme activities in *Phalaris* (Niakan and Saberi 2009), *E. globulus* on Bermuda grass germination and rhizome growth (Daneshmandi and Azizi 2009), *Pinus eldrica* on *L. perenne*, *Festuca arundinacea*, *Poa pratensi,s* and *Agrostis capillaris* seed germination and seedling growth (Alizadeh et al. 2009), *Haloxylon aphyllum* lljin aerial parts and root extracts on germination characteristics and seedling growth of *Agropyron elongatum* and *A. desertorum* (Moameri et al. 2011), Walnut trees (*J. regia*) on germination criteria of two serious weeds of *A. hybridus* and *A. repens* (Abbassi et al. 2009) were studied by Abbassi et al. (2009). (Table 8.1).

8.8 Conclusions and Prospects

Having considered the recent botanical and agricultural research on allelopathy in Iran, it could be concluded that there is great scope related to allelopathic investigations. Moreover, very large amounts of these researches are on valuable plants including economic, aromatic and medicinal plants, field crops, trees, pasture, and forage plants. It is obvious that the results of the allelopathic studies have a very wide application in different cases such as ecological advantages, decreasing the economical costs for weed management and environmentally friendly subjects. Nowadays the biological activity of allelochemicals in plants has been considered mainly by agronomist, ecologists, physiologist, horticulturists, and biologists in Iran. However, a comprehensive organization and careful corporation among the scientists studying on allelopathy is expected with the special emphasis on holding national and international collaboration and having symposiums and conferences in this very diverse country.

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Chapter 9
Allelopathy of Bangladeshi Rice: Application in the Agricultural Systems

Hisashi Kato-Noguchi and Md Abdus Salam

Abstract Rice is the staple food of Bangladesh and about 80 % of agricultural land is used for its production. However, rice production rate is less than 50 % of the world average. Severe weed infestation is one of the major reasons for such low yield. Hand weeding is the most commonly used weed control method in Bangladesh. The allelopathic activity of 102 Bangladeshi rice cultivars (60 traditional and 42 high yielding) was evaluated as part of a strategy for the weed management. Among them, high yielding rice cultivar, BR17 and traditional rice cultivar, Kartikshail marked the greatest inhibitory activity. Main allelochemical in BR 17 was identified as 9-hydroxy-4-megastigmen-3-one. Two main allelochemicals in Kartikshail were 3-hydroxy-β-ionone and 9-hydroxy-4-megastigmen-3-one. Thus, Bangladeshi rice cultivars, BR17 and Kartikshail, may be potentially useful for weed management as weed suppressing agents when these rice cultivars are incorporated into the soil or included in rice-based cropping systems.

Keywords Allelopathy · Allelochemical · Bangladeshi rice · Biological activity · Echinochloa · Weed control

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9.1 Introduction

Bangladesh is an agro-based developing country in Southeast Asia and the economy of this country is primarily dependent on agriculture. About 84 % of the total population live in rural areas and are directly or indirectly engaged in a wide range of agricultural activities. Rice is the staple food of Bangladesh and about 80 % of agricultural land is used for rice production, with annual production of 27.3 million tons from 10.7 million ha of land. The average production is 2.6 t ha^{-1} (BBS 2007a, b; DAE 2007). This average rice yield is lesser than 50 % of the world average rice production. Severe weed infestation is one of the major reasons for such low yield.

Weeds reduce the grain yield of *aus* (summer) rice by 68–100 %, that of *aman* (autumn) rice by 16–48 % and that of *boro* (winter) rice by 22–36 % (Mamun 1988, 1990). The climatic and edaphic factors in the country are highly favorable for luxuriant growth of many weed species. Hand weeding is the most commonly used weed control method in Bangladesh, but it is often imperfect and/or delayed because of limited budgets for hiring labor and availability of labor during peak periods (Ahmed et al. 2005). Mechanical weed control is expensive for this country to buy equipments and hire labor. Chemical methods are also expensive and may lead to environmental pollution and some weed species acquire resistance against the particular herbicide.

Since the time Dilday et al. (1989) reported that some rice (*Oryza sativa*) varieties possess allelopathic activity in weed suppression, rice allelopathy has received great attention and may be an alternative to the chemical and mechanical control of weeds in paddy fields (Fujii 1992; Garrity et al. 1992, Olofsdotter et al. 1995; Chung et al. 1997, 2000; Olofsdotter 2001; Ahn and Chung 2000). A large number of rice varieties were found to inhibit the growth of several plant species when grown together under field and/or laboratory conditions (Dilday et al. 1998; Kim et al. 1999; Olofsdotter et al. 1999; Azmi et al. 2000). Lin et al. (1992) reported that rice flatsedge (*Cyperus iria*) was controlled by incorporated residues of allelopathic rice plants into the field soil. It was also reported that rice residues inhibited the growth of weeds by 70 % and increased rice crop yield by 20 % (Xuan et al. 2005). These findings suggest that rice plants could produce and release allelochemicals into the neighboring environment. Many compounds have been identified as potent allelochemicals from rice plants. Among these, phenolic compounds including *p*-hydroxybenzoic, vanillic, *p*-coumaric, and ferulic acids are the most widely studied with regard to rice allelopathy (Mattice et al. 1998; Chung et al. 2001; Kim and Kim 2002; Rimando and Duke 2003). An increasing number of studies have shown that some flavones, diterpenes, and other types of compounds are potent allelochemicals in rice (Lee et al. 1999; Kato-Noguchi et al. 2002, 2010; Kong et al. 2004). These findings suggest that rice allelopathy may be used to improve weed management in rice production. The use of rice cultivars that suppress the growth of weeds is likely to be a potent supplement to present weed management practices and may reduce production costs and environmental pollution.

There are hundreds of rice cultivars in Bangladesh. Therefore, determination of allelopathic activity and allelochemicals in Bangladeshi rice cultivars and their use as a possible means of weed control must be very beneficial for the resource-poor farmers of Bangladesh who mostly depend for weed control on human labor. In this chapter, we described the allelopathic activity of 102 Bangladeshi rice cultivars, and allelochemicals in the Bangladeshi rice.

9.2 Allelopathic Activity of Bangladeshi Rice

9.2.1 Bangladeshi Rice

Sixty traditional and 42 high yielding cultivars of Bangladeshi rice (*O. sativa*) were chosen for the determination of allelopathic activity (Table 9.1) based on the literature of BRRI (1995). High yielding rice cultivars are of short stature and leaves are dark green and vertical. All leaves receive sunlight and their productivities are high. Grain yield is almost equal with straw weight. Traditional rice cultivars are long stature and lodge easily. Their leaves are light green and horizontal and lower leaves are covered with upper leaves. Lower leaves do not receive enough sunlight and their productivities are low. Grain yield is half of straw weight (BRRI 1995).

9.2.2 Donor–Receiver Bioassay

It was assumed that most allelochemicals are released during the early developmental stage of plants when the plants are most stressed and competitive with neighboring plants for resources such as light, nutrients, and water (Dekker and Meggitt 1983). Therefore, allelopathic activity of 102 Bangladeshi rice cultivars was determined by "donor–receiver bioassay" as procedure described by Kato-Noguchi et al. (2002). Cress and lettuce were chosen as receiver plants because of their known germination and growth behaviors, and *Echinochloa crus-galli* and *E. colonum* L.) were also chosen as receiver plants because Echinochloa is the most significant biological constraint on rice production in Bangladesh (Begum et al. 1999).

In the "donor–receiver bioassay", cress and lettuce, *E. crus-galli* and *E. colonum* seedlings were grown with 6-day-old rice seedlings for 2 days. These receiver plants may grow with the rice seedlings without interspecies competition for nutrients, because no nutrients were added in the bioassay. Light is also unnecessary in the developmental stages of these seedlings, since early developing seedlings mostly withdraw nutrients from the reserve of their seeds (Fuerst and Putnam 1983). In addition during the bioassay, any significant pH changes in the medium in all dishes were not found. No effect of osmotic potential of the test solutions in all dishes was detected on the germination and growth of these plant species. Thus, the influence of

Table 9.1 Bangladeshi rice cultivars determined allelopathic activity

Traditional cultivar				High yielding cultivar		
Badshabhog	Deshibalam	Jhingashail	Manikjour	BR1	BR17	BRRI dhan35
Baron	Dhepa	Jogly	Marichbati	BR2	BR19	BRRI dhan36
Bashful	Dhepa2	Jotabalam	Matiagorol	BR3	BR20	BRRI dhan37
Bashiraj	Dudhkalam	Kachamota	Mohanbhog	BR4	BR21	BRRI dhan38
Bashmoti	Dudhlaki	Kalamanik	Motaman	BR5	BR22	BRRI dhan39
Binnaful	Dudshor	Kalizira	Nizershial	BR6	BR23	BRRI dhan40
Biroi	Dular	Kartikshail	Pajam	BR7	BR26	BRRI dhan42
Buta	Gabura	Kataribhog	Pashushail	BR8	BRRI dhan27	BRRI dhan43
Chandon	Gangasagor	Kazliboro	Patnai31-675	BR9	BRRI dhan28	BRRI dhan45
Chikon aman	Ganjia-3	Khoiyaboro	Pusur	BR10	BRRI dhan29	Binadhan-4
Chiniatop397	Goai	Kumari	Rajashail	BR11	BRRI dhan30	Binadhan-5
Chiniatop398	Gobolshail	Lakkhidigha	Sadajira19-287	BR12	BRRI dhan31	Iratom-24
Chinigura	Gobrijoshua	Lalaman	Shakkhorkona	BR14	BRRI dhan32	
Chinisagor	Hashikalmi	Madhabjota	Shorna	BR15	BRRI dhan33	
Choiyamura	Jamainaru	Maliabhangor	Tepiboro	BR16	BRRI dhan34	

rice seedlings on the receiver plants may not be due to the competitive interference for nutrients and the effects of pH and osmotic potential, but the allelopathic effect.

9.2.3 *Allelopathic Activity of Bangladeshi Rice Against Cress*

Twenty-six high yielding cultivars and 38 traditional cultivars significantly inhibited cress root growth at 5 % level of probability (Tables 9.2 and 9.3). Three high yielding rice cultivars, BR5 (53.2 % inhibition), BR20 (53.2 % inhibition), and BRRI dhan37 (53.3 % inhibition) showed more than 50 % growth inhibition on cress roots. Six traditional rice cultivars, Dudhlaki (51.2 % inhibition), Goai (55.8 % inhibition), Kachamota (53.4 % inhibition), Kazliboro (51.5 % inhibition), Lalaman (50.0 % inhibition), and Manikjour (50.6 % inhibition) showed more than 50 % growth inhibition on cress roots. Only Sadajiral9-287 significantly increased cress root growth.

Twenty high yielding cultivars and 13 traditional cultivars significantly inhibited cress shoot growth at 5 % level (Tables 9.2 and 9.3). Inhibition on the shoots by BRRI dhan37 was the greatest (34.4 %). The growth inhibition on cress roots by rice was relatively greater than that on cress shoots. High yielding rice cultivar, BRRI dhan37 had the greatest activity with an average of 43.8 % of the growth inhibition on cress roots and shoots.

9.2.4 Allelopathic Activity of Bangladeshi Rice Against Lettuce

Fifteen high yielding cultivars and 19 traditional cultivars significantly inhibited lettuce root growth at 5 % level of probability (Tables 9.2 and 9.3). Eight high yielding cultivars, BR2 (64.8 % inhibition), BR10 (61.9 % inhibition), BR17 (58.4 % inhibition), BR22 (90.3 % inhibition), BR23 (62.0 % inhibition), BRRI dhan28 (56.7 % inhibition), BRRI dhan28 (94.0 % inhibition), and Binadhan-4 (58.3 % inhibition), and 7 traditional rice cultivars, Badshabhog (51.1 % inhibition), Bashful (51.4 % inhibition), Biroi (62.0 % inhibition), Buta (60.1 % inhibition), Chikon aman (57.1 % inhibition), Jogly (71.4 % inhibition), and Shakkhorkona (52.9 % inhibition) showed more than 50 % growth inhibition on lettuce roots. BR1, BR4, BRRI dhan27, BRRI dhan29, BRRI dhan35, BRRI dhan39, BRRI dhan42, BRRI dhan45, Bashimoti, Chinatop398, Ganjia-3, Jotabalam, Kataribhog, and Matiagorol significantly increased cress root growth.

Eighteen high yielding cultivars and 14 traditional cultivars significantly inhibited lettuce shoot growth at 5 % level (Tables 9.2 and 9.3). Five high yielding cultivars, BR17 (56.5 % inhibition), BR12 (83.3 % inhibition), BRRI dhan30 (90.0 % inhibition), BRRI dhan32 (50.0 % inhibition), and Binadhan-4 (77.8 % inhibition), and 6 traditional rice cultivars, Baron (63.6 % inhibition), Buta (50.0 % inhibition), Dhepa (88.9 % inhibition), Chikon aman (57.1 % inhibition), Jogly (69.2 % inhibition), and Kalamanik (50.0 % inhibition) showed more than 50 % growth inhibition on lettuce shoots. BRRI dhan39, Chinatop397, and Jamainaru significantly increased cress root growth. High yielding rice cultivar, BRRI dhan30, had the greatest activity with an average of 92.0 % of growth inhibition on lettuce roots and shoots.

9.2.5 Allelopathic Activity of Bangladeshi Rice Against E. crus-galli

Twenty-three high yielding cultivars and 33 traditional cultivars significantly inhibited *E. crus-galli* root growth at 5 % level of probability (Tables 9.2 and 9.3). Inhibition on the roots by Kartikshail was the greatest (70.5 %). Eleven high yielding cultivars and seven traditional cultivars significantly inhibited *E. crus-galli* shoot growth at 5 % level. Inhibition on the shoots by Dular was the greatest

Table 9.2 Effects of high yielding Bangladeshi rice cultivars on the growth of shoots and roots of cress, lettuce, *E. crus-galli* and *E. colonum*

Cultivar	Cress		Lettuce		*E. crus-galli*		*E. colonum*		Total
	Shoot	Root	Shoot	Root	Shoot	Root	Shoot	Root	Average
BR1	5.8NS	23.5NS	−10.5NS	−81.4***	−10.3NS	10.5NS	14.3*	0.7NS	−5.9
BR2	20.6**	26.5NS	44.4NS	64.8***	8.3NS	35.6**	4.0NS	39.9***	30.5
BR3	13.4NS	24.2NS	46.7**	41.9***	19.4***	32.4***	8.8NS	13.6NS	25.1
BR4	−5.5NS	−23.7NS	6.7NS	−83.3**	9.9NS	30.6*	19.1*	−9.4NS	−7.0
BR5	29.8**	53.2***	16.7NS	5.7NS	10.7NS	18.4*	4.8NS	14.7NS	19.3
BR6	8.4NS	4.9NS	25.0*	3.3NS	7.0NS	26.1*	1.8NS	−17.7NS	7.4
BR7	9.9NS	−1.7NS	33.3*	28.3*	−9.9NS	21.6NS	14.4**	34.8NS	16.3
BR8	21.6*	29.8NS	18.2NS	−4.9NS	11.8NS	23.4NS	12.1NS	23.1NS	16.9
BR9	19.0**	35.2**	21.4*	48.7***	15.9**	43.1***	16.8**	30.9**	28.9
BR10	2.9NS	−23.8NS	30.8*	61.9***	1.6NS	18.3NS	6.7NS	−36.0NS	7.8
BR11	8.1NS	39.4**	−6.7NS	20.5*	7.3NS	15.0NS	8.4NS	28.6**	15.1
BR12	17.1NS	49.2**	−6.3NS	−9.9NS	5.3NS	19.7**	6.6NS	4.7NS	10.8
BR14	23.4**	−7.0NS	25.0*	−46.7NS	21.4**	40.7***	15.2*	0.0NS	9.0
BR15	7.9NS	33.1**	15.8*	22.3NS	12.7NS	33.2**	15.4NS	51.3**	24.0
BR16	25.6**	39.9**	44.8***	22.5NS	5.3NS	19.1NS	20.1*	39.8***	27.1
BR17	23.1**	47.4***	56.5***	58.4***	14.4NS	46.6***	26.5***	43.2***	39.5
BR19	−10.5NS	15.7NS	37.5**	28.1NS	7.6NS	25.8*	10.1*	29.1*	17.9
BR20	24.4*	53.2***	23.1NS	30.8NS	4.9NS	8.9NS	25.6***	34.8NS	25.7
BR21	13.3NS	33.7*	28.6NS	18.6NS	4.4NS	11.9NS	8.7NS	45.0***	20.5
BR22	11.4NS	38.9**	83.3*	90.3*	16.2NS	22.0NS	5.2NS	−2.6NS	33.1
BR23	28.5**	49.8**	39.1***	62.0***	19.5*	26.9***	1.9NS	19.1NS	30.9
BR26	21.2*	35.9*	37.5**	40.4**	20.0**	45.6***	11.0NS	43.9***	31.9
BRRI dhan27	15.4NS	14.4NS	5.9NS	−59.3**	15.0NS	13.3NS	14.2*	4.6NS	2.9
BRRI dhan28	26.4**	48.6***	41.2***	56.7***	19.2*	26.2*	18.6*	32.7*	33.7
BRRI dhan29	28.2*	46.2**	18.2NS	−38.3*	19.9**	39.7***	25.6***	40.9***	22.6

(continued)

Table 9.2 (continued)

Cultivar	Cress		Lettuce		*E. crus-galli*		*E. colonum*		Total
	Shoot	Root	Shoot	Root	Shoot	Root	Shoot	Root	Average
BRRI dhan30	−1.2NS	−2.9NS	90.0^{***}	94.0^{***}	14.1NS	19.4NS	22.8^{*}	15.3NS	31.4
BRRI dhan31	6.9NS	40.2^{*}	5.0NS	16.0NS	15.7NS	38.2^{***}	2.8NS	7.8NS	16.6
BRRI dhan32	1.0NS	21.6NS	50.0^{*}	47.7^{*}	−3.4NS	−8.9NS	2.3NS	4.7NS	14.4
BRRI dhan33	32.3^{*}	22.8NS	25.0^{*}	17.8NS	17.7^{*}	25.3^{*}	13.1NS	−13.6NS	17.6
BRRI dhan34	14.9^{**}	33.2^{***}	0.0NS	9.8NS	18.8^{**}	26.1^{***}	22.1^{**}	2.9NS	16.0
BRRI dhan35	14.2NS	20.0NS	6.3NS	-52.2^{**}	17.7NS	37.4^{***}	5.6NS	9.2NS	7.3
BRRI dhan36	−4.7NS	37.9^{**}	14.3NS	−16.0NS	1.9NS	24.0^{*}	9.5NS	9.5NS	9.6
BRRI dhan37	34.4^{***}	53.3^{***}	−7.14NS	−26.9NS	−2.9NS	1.2NS	7.9NS	12.0NS	9.0
BRRI dhan38	23.5NS	38.2^{*}	−40.0NS	12.7NS	−0.8NS	38.3^{**}	10.6NS	75.3^{***}	19.7
BRRI dhan39	10.7NS	44.4^{***}	-33.3^{*}	-142.0^{***}	−15.8NS	20.3NS	−7.6NS	19.7NS	−13.0
BRRI dhan40	26.2^{**}	36.6^{**}	−11.8NS	-65.4^{***}	8.3NS	10.7NS	15.8^{**}	20.9NS	5.2
BRRI dhan42	16.5^{*}	43.3^{***}	−25.0NS	-50.8^{*}	2.9NS	6.0NS	13.6^{*}	3.6NS	1.3
BRRI dhan43	23.6^{*}	37.4^{*}	7.1NS	41.8^{***}	18.4^{**}	37.7^{**}	21.7^{*}	37.2^{**}	28.1
BRRI dhan45	13.4^{*}	33.2^{**}	11.8NS	-29.1^{*}	13.4NS	1.4NS	6.0NS	2.2NS	6.5
Binadhan-4	20.2NS	17.7NS	77.8^{***}	58.3^{*}	5.4NS	0.0NS	10.8NS	−18.6NS	21.5
Binadhan-5	10.1NS	36.0^{**}	25.0NS	34.0NS	18.0^{*}	26.4^{*}	27.5NS	16.7NS	24.2
Iratom-24	26.3^{**}	49.8^{***}	5.6NS	9.1NS	1.4NS	1.8NS	2.9NS	13.0NS	13.7

Cress, lettuce, *E. crus-galli* and *E. colonum* seedlings were grown with 6-day-old rice seedlings at 25 °C and 12-h photoperiod for 48 h. Shoot and root length of their seedlings were then determined. Control bioassays did not contain rice seedlings. Percentage inhibition was then determined by the formula: [(control plant length—plant length incubated with rice)/control plant length] × 100

Asterisk indicates significant difference between control and treatment: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ NS, not significant

Source Salam and Kato-Noguchi (2009)

Table 9.3 Effects of traditional Bangladeshi rice cultivars on the growth of shoots and roots of cress, lettuce, *E. crus-galli* and *E. colonum*

Cultivar	Cress		Lettuce		*E. crus-galli*		*E. colonum*		Total
	Shoot	Root	Shoot	Root	Shoot	Root	Shoot	Root	Average
Badshabhog	15.9NS	36.5**	35.3***	51.1***	7.3NS	6.6NS	33.0***	41.0**	28.3
Baron	10.4NS	−24.0NS	63.6**	65.4NS	−9.2NS	−3.0NS	2.9NS	24.0NS	16.3
Bashful	6.7NS	45.7***	15.4NS	51.1**	−3.9NS	24.4**	24.4NS	12.3NS	22.0
Bashiraj	−8.6NS	28.1*	29.4**	40.5**	−4.7NS	10.6NS	14.6NS	7.9NS	14.7
Bashmoti	3.4NS	31.8NS	0.0NS	−129.4**	10.3NS	13.3NS	7.1NS	4.3NS	−7.4
Binnaful	−7.0NS	−19.7NS	16.7NS	31.0*	−6.5NS	14.5NS	6.9NS	6.4NS	5.3
Biroi	−2.1NS	39.7**	21.1*	62.0***	−2.0NS	13.5NS	−5.0NS	15.5NS	17.8
Buta	10.7NS	27.1NS	50.0**	60.1***	15.5*	15.8*	13.0NS	33.5**	28.2
Chandon	9.8NS	34.1***	27.9NS	48.9NS	4.8NS	33.9**	−11.4NS	32.8NS	22.6
Chikon aman	−24.0NS	−13.6NS	57.1**	57.1***	9.0NS	25.5*	8.1NS	13.2NS	16.6
Chiniatop397	4.2NS	32.9**	−57.9***	−20.0NS	11.7NS	27.2**	9.7NS	53.3NS	7.6
Chiniatop398	8.4NS	32.1**	−13.3NS	−38.1**	2.7NS	23.0**	−9.3NS	19.0*	3.1
Chinigura	15.8*	42.3**	5.6NS	9.7NS	8.6NS	21.9**	18.6**	−7.1NS	14.4
Chinisagor	−2.2NS	14.4NS	0.0NS	−18.4NS	9.6NS	24.2**	9.5NS	30.3*	8.4
Choiyamura	9.3NS	34.1*	11.8NS	−12.8NS	10.9NS	30.4**	12.6NS	20.8NS	14.6
Deshibalam	6.9NS	16.6NS	5.9NS	−16.7NS	4.7NS	12.4NS	16.4NS	24.2NS	8.8
Dhepa	−2.3NS	16.2NS	88.9***	47.6***	7.6NS	20.2**	3.1NS	−19.0NS	20.3
Dhepa2	5.9NS	41.5*	0.0NS	−1.9NS	−6.3NS	15.4NS	10.0NS	42.9NS	13.4
Dudhkalam	12.8NS	29.2*	11.1NS	14.1NS	4.1NS	25.5*	4.9NS	12.9NS	14.3
Dudhlaki	19.3*	51.2***	5.6NS	3.9NS	9.2NS	18.3NS	4.5NS	29.1*	17.6
Dudshor	−4.1NS	−19.3NS	0.0NS	−21.4NS	6.3NS	13.7NS	7.6NS	16.1NS	−0.1
Dular	19.2*	45.5***	6.7NS	27.9NS	25.2**	44.0***	9.2NS	29.9NS	26.0
Gabura	7.1NS	40.6***	0.0NS	11.0NS	6.7NS	39.3***	0.0NS	12.7NS	14.7
Gangasagor	−1.4NS	−20.2NS	−6.3NS	−8.8NS	5.8NS	8.2NS	−6.9NS	−17.1NS	−5.8
Ganjia-3	−2.3NS	−34.9NS	0.0NS	−85.1***	1.0NS	−13.7NS	6.1NS	15.0NS	−14.2

(continued)

Table 9.3 (continued)

Cultivar	Cress		Lettuce		*E. crus-galli*		*E. colonum*		Total
	Shoot	Root	Shoot	Root	Shoot	Root	Shoot	Root	Average
Goai	22.5^{*}	55.8^{***}	9.1NS	−17.7NS	9.0NS	27.8^{**}	−17.1NS	0.0NS	11.2
Gobolshail	10.9NS	40.0^{**}	11.1NS	−7.3NS	6.8NS	23.6NS	12.5NS	2.4NS	12.5
Gobrijoshua	6.8NS	42.7^{***}	0.0NS	36.9^{**}	7.7NS	26.7^{*}	8.5NS	2.9NS	16.5
Hashikalmi	9.8NS	39.8^{**}	26.3^{*}	31.1^{*}	7.8NS	30.6^{**}	−2.6NS	−11.5NS	16.4
Jamainaru	15.7NS	31.5^{*}	-43.8^{***}	−11.7NS	0.0NS	25.0^{**}	−22.5NS	38.4^{*}	4.1
Jhingashail	1.2NS	26.9^{*}	−9.1NS	16.7NS	−1.6NS	24.8^{*}	−23.3NS	4.4NS	5.0
Jogly	16.7^{*}	39.0^{**}	69.2^{***}	71.4^{***}	6.1NS	27.9^{**}	−2.0NS	−13.5NS	26.9
Jotabalam	1.0NS	22.5NS	−13.3NS	-71.2^{***}	10.1NS	22.3NS	−22.5NS	−27.2NS	−9.8
Kachamota	21.5^{*}	53.4^{***}	15.8NS	7.9NS	0.7NS	9.6NS	−8.9NS	−8.1NS	11.5
Kalamanik	16.0NS	14.0NS	50.0^{*}	45.0^{**}	−1.6NS	6.4NS	7.3NS	2.0NS	17.4
Kalizira	3.6NS	−15.9NS	23.1^{*}	5.7NS	6.2NS	19.0^{*}	11.9NS	30.4^{*}	10.5
Kartikshail	10.5NS	14.8NS	13.3NS	42.1^{*}	13.6NS	70.5^{***}	16.9NS	66.1^{***}	31.0
Kataribhog	21.8^{**}	40.3^{***}	−10.5NS	-30.9^{*}	1.9NS	24.8^{*}	13.3NS	25.0NS	10.7
Kazliboro	7.6NS	51.5^{***}	7.7NS	22.9NS	23.6^{***}	46.8^{*}	10.8NS	18.5NS	23.7
Khoiyaboro	13.3NS	40.1^{**}	14.3NS	−33.3NS	−1.4NS	30.7^{***}	20.0NS	24.1NS	13.5
Kumari	22.0^{**}	40.6^{**}	0.0NS	−29.6NS	−4.8NS	17.0NS	9.1NS	18.6NS	9.1
Lakkhidigha	−10.8NS	−23.1NS	0.0NS	23.2^{*}	9.1NS	27.8NS	12.1NS	40.0^{***}	9.8
Lalaman	12.1NS	50.0^{***}	0.0NS	−3.3NS	14.8^{*}	40.8^{***}	15.4NS	47.1NS	22.1
Madhabjota	5.2NS	37.9^{**}	18.5NS	36.6^{***}	10.1NS	19.4NS	−2.6NS	10.0NS	16.9
Maliabhangor	8.7NS	35.4^{***}	4.8NS	−17.5NS	11.1NS	20.9^{*}	15.2NS	−12.9NS	8.2
Manikjour	11.0NS	50.6^{***}	22.2^{*}	30.5^{*}	11.6NS	30.8^{**}	3.3NS	12.7NS	21.6
Marichbati	13.5^{*}	37.7^{**}	0.0NS	4.9NS	7.1NS	39.7^{***}	21.1NS	27.3NS	18.9
Matiagorol	−2.1NS	22.1^{*}	0.0NS	-29.6^{*}	7.9NS	28.6^{**}	8.6NS	11.5NS	5.9
Mohanbhog	12.1NS	5.8NS	9.1NS	0.0NS	4.5NS	4.8NS	7.3NS	−8.2NS	4.4
Motaman	−5.7NS	−16.9NS	13.3NS	−2.4NS	7.8NS	17.4NS	0.0NS	−15.1NS	−0.2

(continued)

Table 9.3 (continued)

Cultivar	Cress		Lettuce		*E. crus-galli*		*E. colonum*		Total
	Shoot	Root	Shoot	Root	Shoot	Root	Shoot	Root	Average
Nizershial	17.1NS	32.4NS	7.7NS	16.8NS	16.2^{**}	5.0NS	−3.9NS	12.9NS	13.0
Pajam	19.4^{*}	39.5^{**}	28.6NS	−9.0NS	−2.0NS	18.6NS	11.7^{*}	17.3NS	15.5
Pashushail	18.3^{*}	31.2^{**}	−12.5NS	−15.8NS	12.2^{*}	25.4^{**}	1.8NS	−13.9NS	5.8
Patnai31-675	3.6NS	7.9NS	13.0^{*}	−14.4NS	20.7^{**}	11.0NS	23.3^{*}	−26.1NS	4.9
Pusur	17.0NS	41.7^{*}	0.0NS	38.9^{***}	4.1NS	26.8^{**}	11.1NS	11.0NS	18.8
Rajashail	2.5NS	−7.2NS	27.8^{*}	20.0NS	4.3NS	9.0NS	−1.1NS	−6.4NS	6.1
Sadajira19-287	−7.5NS	-52.4^{**}	21.4NS	4.9NS	16.2NS	5.1NS	11.8^{*}	−26.2NS	−3.3
Shakkhorkona	−7.9NS	−10.1NS	30.0NS	52.9^{*}	14.8NS	38.6^{***}	3.7NS	6.9NS	16.1
Shorna	12.8^{*}	39.8^{**}	−7.1NS	3.8NS	4.5NS	32.8^{***}	7.4NS	27.4^{**}	15.2
Tepiboro	17.1^{*}	42.3^{**}	0.0NS	29.9^{*}	7.9NS	20.9NS	2.7NS	20.8NS	17.7

Asterisk indicates significant difference between control and treatment: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ NS, not significant

Source Salam and Kato-Noguchi (2009)

Table 9.4 Two-way analysis of variance (ANOVA) for relative shoot or root length of treated plants (%) to control plants of cress, lettuce, *E. crus-galli* and *E. colonum*

Factor	d.f.	Shoot				Root			
		SS	MS	*F*	*P*	SS	MS	*F*	*P*
Rice cultivar (C)	101	650300	6439	4.487	<0.0001	2111000	20900	7.69	<0.0001
Test plant species (T)	3	71310	23770	16.57	<0.0001	353000	117700	43.302	<0.0001
C × T	303	1301000	4295	2.993	<0.0001	4174000	13780	5.07	<0.0001
Error	7752	1112000	1435			21070000	2718		

d.f. degrees of freedom, *SS* sum of squares, *MS* mean square, *P* probability
Source Salam and Kato-Noguchi et al. (2009)

(25.2 %). Traditional rice cultivar, Kartikshail had the greatest activity with an average of 42.0 % of the growth inhibition on *E. crus-galli* roots and shoots.

9.2.6 Allelopathic Activity of Bangladeshi Rice Against *E. colonum*

Thirteen high yielding cultivars and 10 traditional cultivars significantly inhibited *E. colonum* root growth at 5 % level of probability (Tables 9.2 and 9.3). Two high yielding rice cultivars, BR15 (51.3 % inhibition) and BRRI dhan38 (75.3 % inhibition), and one traditional rice cultivars, Kartikshail (66.1 % inhibition) showed more than 50 % growth inhibition.

Seventeen high yielding cultivars and 5 traditional cultivars significantly inhibited *E. colonum* shoot growth at 5 % level. Inhibition on the shoots by Badshabhog was the greatest (33.0 % inhibition). High yielding rice cultivar, BRRI dhan38 had the greatest activity with an average of 42.9 % of the growth inhibition on *E. colonum* roots and shoots.

9.2.7 Allelopathic Activity of Bangladeshi Rice

Effects of 102 Bangladesh rice cultivar, four test plant species and their interactions were significant both for shoot and root growth ($P < 0.0001$ using two-way ANOVA; Table 9.4). Significant effects of cultivar and the interactions indicated that there was variation in allelopathic activity among 102 rice cultivars. This variation might result, in part, from the difference in sensitivity to allelochemicals of the test plant species. It was also found that rice cultivars which were allelopathic against one plant species, were not always allelopathic toward other plant species

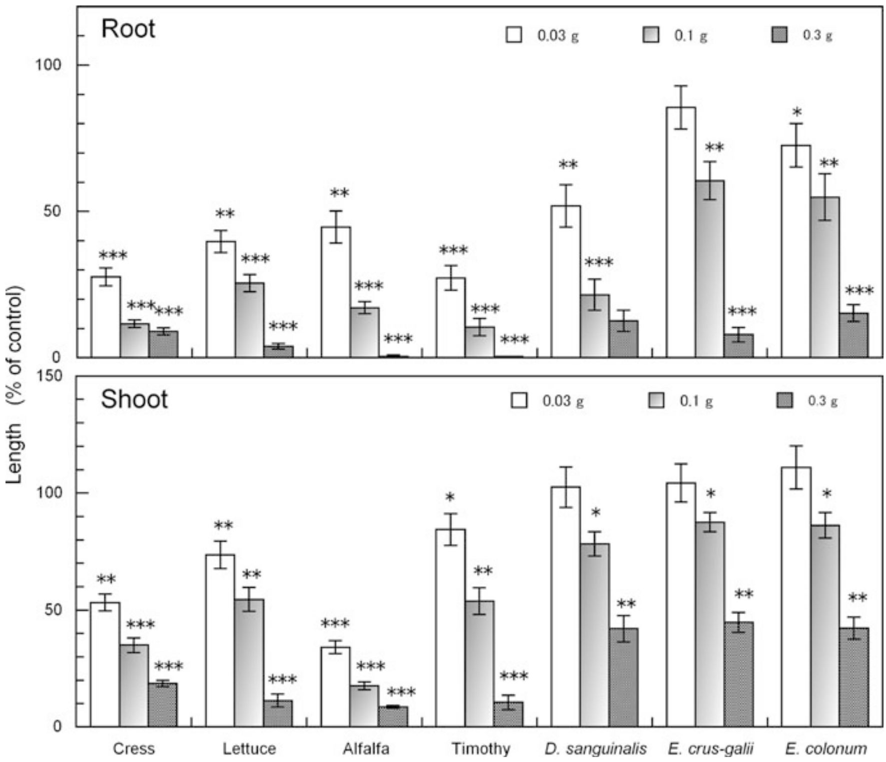
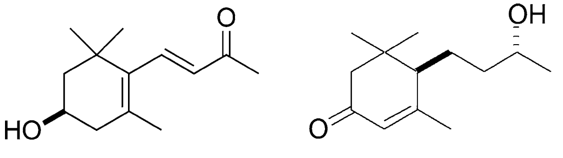


Fig. 9.1 Effects of aqueous methanol extract of BR17 on root and shoot growth of cress, lettuce, alfalfa, timothy, *D. sanguinalis*, *E. crus-galli*, and *E. colonum* (Salam et al. 2009). Concentrations of tested samples corresponded to the extract obtained from 0.03, 0.1, and 0.3 g fresh weight rice plants per mL. Shoot and root length of these test plants was measured after 48 h of incubation in the darkness at 25 °C. Percentage length was determined by the formula: [(plant length incubated with rice extract)/control plant length] × 100. Mean ± SE from 4 independent experiments with 10 plants for each determination are shown. Asterisk indicates significant difference between control and treatment: $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$

Fig. 9.2 Chemicals isolated from rice



3-Hydroxy-β-ionone **9-Hydroxy-4-megastigmen-3-one**

(Olofsdotter et al. 1995; Chung et al. 1997; Dilday et al. 1998; Hassan et al. 1998), which suggests that all allelochemicals released from rice plants may not be able to inhibit all plant species. However, high yielding rice cultivars BR17 marked the greatest inhibitory activity with an average of 39.5 % growth inhibition on shoots and roots of cress, lettuce, *E. crus-galli* and *E. colonum* (Table 9.2). Traditional rice

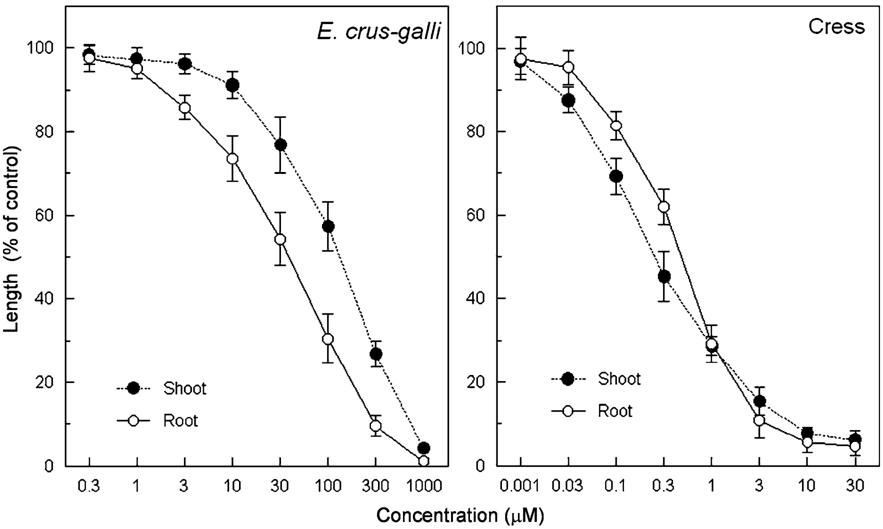


Fig. 9.3 Effects of 9-hydroxy-4-megastigmen-3-one on the root and shoot growth of cress and *E. crus-galli* seedlings (Salam et al. 2009). Shoot and root length of these test plants was measured after 48 h of incubation in the darkness at 25 °C. Percentage length was then determined by the formula: [(plant length incubated with compound)/control plant length] × 100. Mean ± SE from 4 independent experiments with 10 plants for each determination are shown

cultivars, Kartikshail marked the greatest inhibitory activity with an average of 41.8 % growth inhibition on shoots and roots of *E. crus-galli* and *E. colonum* (Table 9.3). Therefore, BR17 had the greatest inhibitory activity against all receiver plants, and Kartikshail had the greatest inhibitory activity against Echinochloa.

9.3 Allelochemical in BR17

9.3.1 Allelopathic Activity of BR17 Extract

Allelopathic activity of BR17 extract was determined because BR17 had the greatest inhibitory activity by donor–receiver bioassay as described above. Aqueous methanol extract of BR17 inhibited root and shoot growth of all plant species, and increasing the extract concentration increased this inhibition (Fig. 9.1). The extract obtained from 0.3 g fresh weight of BR17 inhibited the root growth of cress, lettuce, alfalfa (*Medicago sativa*), timothy (*Phleum pratense*), *Digitaria sanguinalis*, *E. crus-galli*, and *E. colonum* by 9.1, 3.9, 0.5, 0.4, 13, 7.9, and 15 % of control root growth, respectively, and inhibited the shoot growth of cress, lettuce, alfalfa, timothy, *D. sanguinalis*, *E. crus-galli*, and *E. colonum* by 19, 11, 8.6, 11, 4.2, 45, and 42 % of control shoot growth, respectively (Salam et al. 2009). The extract of BR17 therefore had an inhibitory effect on a wide range of plant species, both of

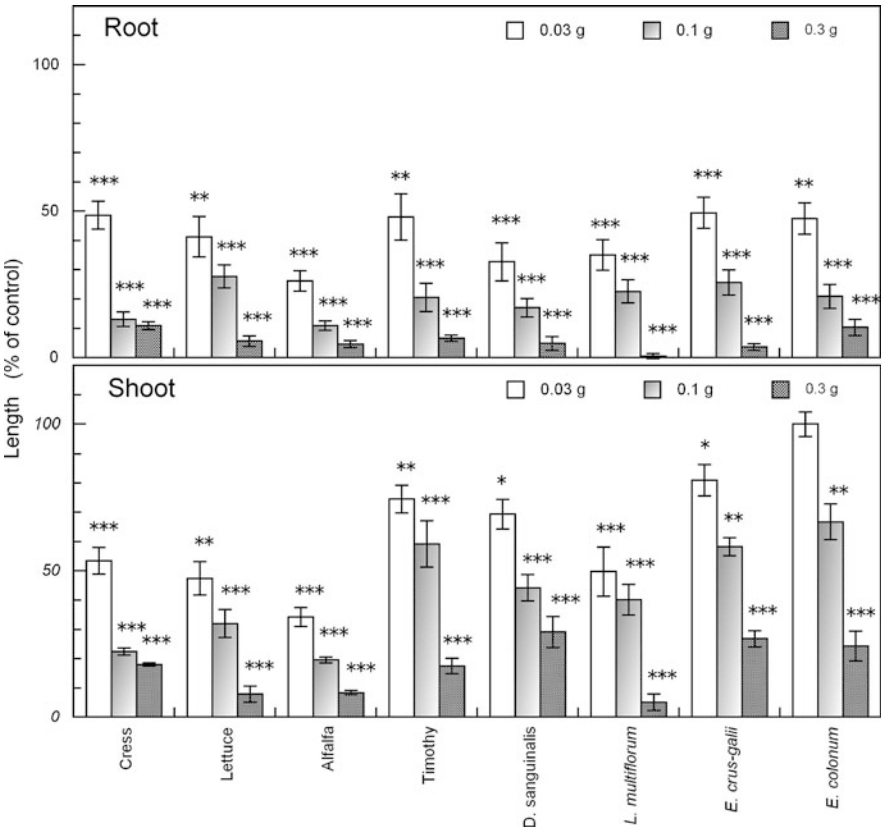


Fig. 9.4 Effects of aqueous methanol extract of rice on root and shoot growth of cress, lettuce, alfalfa, timothy, *D. sanguinalis*, *E. crus-galli*, and *E. colonum* (Kato-Noguchi et al. 2011). Concentrations of tested samples corresponded to the extract obtained from 0.03, 0.1, and 0.3 g dry weight of rice plant per mL. Shoot and root length of these test plants was measured after 48 h of incubation in the darkness at 25 °C. Percentage length was then determined by the formula: [(plant length incubated with rice extract)/control plant length] × 100. Mean ± SE from 4 independent experiments with 10 plants for each determination are shown. Asterisk indicates significant difference between control and treatment: $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$

dicotyledonous plants (cress, lettuce and alfalfa) and monocotyledonous plants (*D. sanguinalis*, *E. crus-galli*, and *E. colonum*). These results suggest that BR17 extract may contain allelopathic active substances.

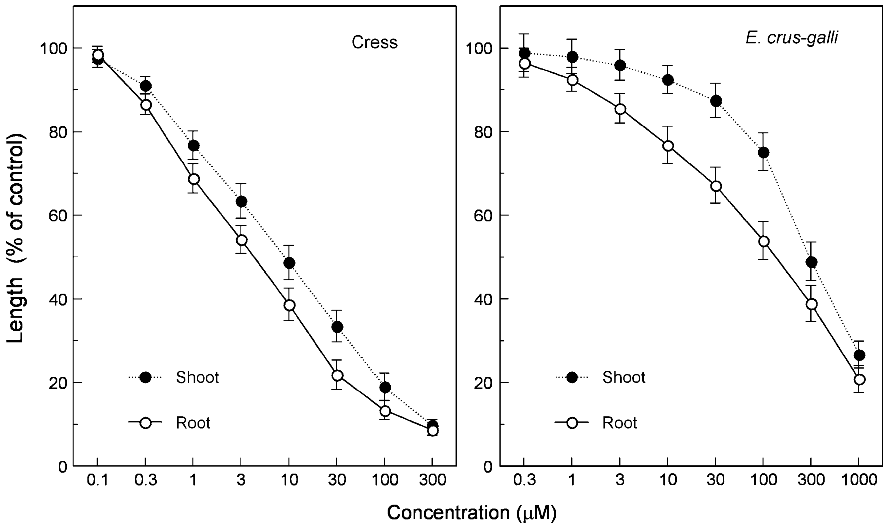


Fig. 9.5 Effects of 3-hydroxy-β-ionone on the root and shoot growth of cress and *E. crus-galli* (Kato-Noguchi et al. 2011). Shoot and root length of these test plants was measured after 48 h of incubation in the darkness at 25 °C. Percentage length was then determined by the formula: [(plant length incubated with compound)/control plant length] × 100. Mean ± SE from 4 independent experiments with 10 plants for each determination are shown

9.3.2 Allelochemical and its Biological Activity

The aqueous methanol extract of the BR17 was purified and main inhibitory substance was isolated and determined by spectral data as 9-hydroxy-4-megastigmen-3-one (Fig. 9.2). This substance was first isolated from *Cestrum parqui* as a new C_{13} *nor*-isoprenoid by D'Abrosca et al. (2004). However, it is the first report of the presence of 9-hydroxy-4-megastigmen-3-one in rice plants. This substance inhibited the root and shoot growth of cress at concentrations greater than 0.03 and 0.1 μM, respectively, and the root and shoot growth of *E. crus-galli* at concentrations greater than 3 and 10 μM, respectively (Fig. 9.3). The concentrations required for 50 % inhibition of the growth of cress and *E. crus-galli* in the assay (defined as I_{50}), as determined by a logistic regression analysis, were 0.22 and 0.47 μM, respectively, and on *E. crus-galli* roots and shoots were 36 and 133 μM, respectively (Salam et al. 2009).

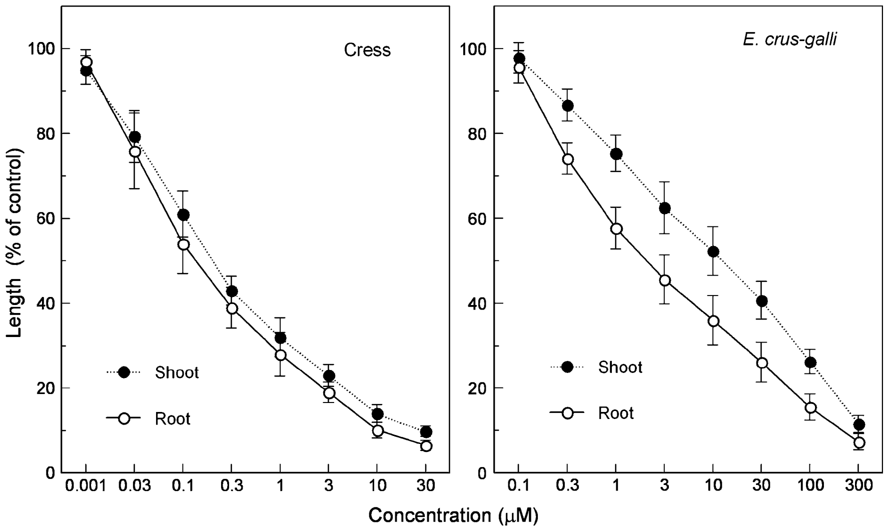


Fig. 9.6 Effects of a mixture of 3-hydroxy-*β*-ionone and 9-hydroxy-4-megastigmen-3-one on the root and shoot growth of cress and *E. crus-galli* (Kato-Noguchi et al. 2011). The concentration of 100 μM represents a mixture of 50 μM 9-hydroxy-*β*-ionone and 50 μM 9-hydroxy-4-megastigmen-3-one. Shoot and root length of these test plants was measured after 48 h of incubation in the darkness at 25 °C. Percentage length was then determined by the formula: [(plant length incubated with compounds)/control plant length] × 100. Mean ± SE from 4 independent experiments with 10 plants for each determination are shown

9.4 Allelochemicals in Kartikshail

9.4.1 Allelopathic Activity of Kartikshail Extract

Allelopathic activity of Kartikshail extract was determined because Kartikshail had the greatest inhibitory activity against *Echinochloa* (Table 9.3), which is the most significant biological constraint on rice production in Bangladesh (Begum et al. 1999). Aqueous methanol extract of Kartikshail inhibited the root and shoot growth of all test plant species, and increasing the extract concentration increased the inhibition (Fig. 9.4). The extract obtained from 0.3 g dry weight of Kartikshail inhibited the root growth of cress, lettuce, alfalfa, timothy, *D. sanguinalis*, *Lolium multiflorum*, *E. crus-galli*, and *E. colonum* by 10.9, 5.6, 4.6, 6.6, 4.8, 0.5, 3.6, and 10.3 % of control root growth, respectively, and inhibited the shoot growth of cress, lettuce, alfalfa, timothy, *D. sanguinalis*, *L. multiflorum*, *E. crus-galli*, and *E. colonum* by 18, 7.9, 8.4, 17.5, 29.1, 5.1, 26.8, and 24.3 % of control shoot growth, respectively (Kato-Noguchi et al. 2011). Therefore, the extract of cv. Kartikshail also had an inhibitory effect on both of dicotyledonous (cress, lettuce, and alfalfa) and monocotyledonous plants (timothy, *D. sanguinalis*, *L. multiflorum*, *E. crus-galli*, and *E. colonum*). These results suggest that Kartikshail may contain allelopathically active substances.

9.4.2 Allelochemicals and their Biological Activity

The aqueous methanolic extract of Kartikshail was purified and two main inhibitory substances were isolated and identified by spectral data as 3-hydroxy-*β*-ionone and 9-hydroxy-4-megastigmen-3-one (Fig. 9.2). 3-Hydroxy-*β*-ionone has previously been isolated from other higher plants species (Fujimori et al. 1974; Güldner and Winterhalter 1991; Kato-Noguchi et al. 1993; Dietz and Winterhalter 1996; Mathieu et al. 2005), but this is the first report of the presence of 9-hydroxy-*β*-ionone in rice.

The biological activity of 9-hydroxy-*β*-ionone isolated from cv. Kartikshail was determined with two test plant species, cress and *E. crus-galli* (Fig. 9.5). 9-Hydroxy-*β*-ionone inhibited the growth of cress roots and shoots at concentrations greater than 0.3 μM, and the growth of *E. crus-galli* roots and shoots at concentrations greater than 3 and 30 μM, receptivity. The concentrations required for 50 % inhibition of the growth of cress and *E. crus-galli* were 4.9 and 9.5 μM for cress roots and shoots, respectively, and 160 and 310 μM for *E. crus-galli* roots and shoots, receptivity. Growth inhibitory activity of 9-hydroxy-4-megastigmen-3-one was described in Fig. 9.3. Comparing I_{50} values, activity of 9-hydroxy-4-megastigmen-3-one was greater than that of 9-hydroxy-*β*-ionone (Figs. 9.3 and 9.5).

9.4.3 Synergistic Effect of 3-Hydroxy-β-ionone and 9-Hydroxy-4-megastigmen-3-one

Effect of a mixture of 3-hydroxy-*β*-ionone and 9-hydroxy-4-megastigmen-3-one on the growth of cress and *E. crus-galli* was determined (Fig. 9.6). I_{50} values of a mixture of two compounds were 0.15 and 0.21 μM for cress roots and shoots, respectively, and 2.7 and 15.3 μM for *E. crus-galli* roots and shoots, respectively. The effectiveness of a mixture of two compounds on cress roots and shoots was 33- and 45-fold greater than that of 3-hydroxy-*β*-ionone, respectively, and 1.5- and 2.2-fold greater than that of 9-hydroxy-4-megastigmen-3-one, respectively. The effectiveness of a mixture on *E. crus-galli* roots and shoots was 59- and 20-fold greater than that of 3-hydroxy-*β*-ionone, respectively, and 13- and 8.7-fold greater than that of 9-hydroxy-4-megastigmen-3-one, respectively. Therefore, the effectiveness of a mixture of two compounds was much greater than that of sum of two compounds, which suggests that the two compounds may act synergistically on the growth inhibition of cress and *E. crus-galli.*

9.5 Allelopathy of Bangladeshi Rice and Allelochemicals

Allelopathic activity of 102 Bangladeshi rice cultivars (60 traditional and 42 high yielding cultivars) has been determined by “donor–receiver bioassay” against cress and lettuce, *E. crus-galli* and *E. colonum.* Among them, high yielding rice cultivars BR17 marked the greatest inhibitory activity against all receiver plants, and Kartikshail had the greatest inhibitory activity against *Echinochloa*. Main allelochemicals in BR 17 was 9-hydroxy-4-megastigmen-3-one. This compound inhibited cress and *E. crus-galli* at concentrations greater than 0.03 and 3 μM, respectively (Fig. 9.3). Two main allelochemicals in Kartikshail were isolated and identified as 3-hydroxy-*β*-ionone and 9-hydroxy-4-megastigmen-3-one. 9-Hydroxy-*β*-ionone inhibited the growth of cress and *E. crus-galli* roots and shoots at concentrations greater than 0.3 and 3 μM, respectively. Thus, 9-hydroxy-4-megastigmen-3-one was the main allelochemical of two important rice cultivars.

Under certain conditions, allelopathic compounds are released into the plant rhizosphere, either as exudates from living tissues or by decomposition of plant residues in sufficient quantities to inhibit the growth of neighboring plants (Rice 1984; Putnam 1988; Seigler 1996; Einhellig 1999). The endogenous concentration of 9-hydroxy-4-megastigmen-3-one in BR17 was at least 3.7 μM kg^{-1} (Salam et al. 2009). The endogenous concentrations of 9-hydroxy-*β*-ionone and 9-hydroxy-4-megastigmen-3-one in Kartikshail were at least 10 and 17 μM kg^{-1} rice plants, respectively (Kato-Noguchi et al. 2011). If decomposition of 1 kg of BR17 rice plants occurs in 1 L soil water, the concentration of 9-hydroxy-4-megastigmen-3-one would be 3.7 μM. If decomposition of 1 kg Kartikshail rice plants occurs in 1 L soil water, 3-hydroxy-*β*-ionone and 9-hydroxy-4-megastigmen-3-one would be 10 and 17 μM, respectively. The threshold of 3-hydroxy-*β*-ionone and 9-hydroxy-4-megastigmen-3-one for growth inhibition was 0.03–30 μM (Figs. 9.3 and 9.4). The estimated concentrations of 3-hydroxy-*β*-ionone and 9-hydroxy-4-megastigmen-3-one in soil water were over the threshold of the growth inhibition except for 3-hydroxy-*β*-ionone on *E. crus-galli* shoots. In addition, the inhibitory activity of a mixture of two compounds was much greater that of sum of two compounds.

Many attempts have been made to exploit allelopathy of plants for weed control in a variety of agricultural settings (Inderjit 1996; Seigler 1996; Duke et al. 2000). Synthetic chemical herbicides may continue to be a key component in many integrated weed management systems, but controlling weeds through allelopathy is one strategy to reduce herbicide dependency (Einhellig 1996; Weston 1996; Narwal 1999; Duke et al. 2000). Thus, Bangladeshi rice BR 17 and Kartikshail may be potentially useful for weed management in a field setting.

9.6 Application in Agricultural Systems

Rice is grown two or three times in a year in Bangladesh. The main rice cropping systems are (1) a*man* (autumn) rice—*boro* (winter) rice and (2) a*us* (summer) rice—a*man* rice—*boro* rice (Mamun 1988, 1990). Selection of allelopathic rice cultivars Kartikshail and BR17 for *aman* and *boro* rice, respectively is beneficial because cultivation of the allelopathic rice is able to reduced weed infection (Dilday et al. 1998; Kim et al. 1999; Olofsdotter et al. 1999). Since BR17 is photo-insensitive and grows in three seasons, BR17 can be cultivated any for *aus*, *aman*, and *boro* rice as allelopathic rice.

The successive plantings of different crops on the same land (crop rotation) improve soil fertility and help control weeds, insects, and diseases. Cultivation of BR17 or Kartikshail is also beneficial for crop rotation because allelopathic rice cultivars suppressed weed infection during the rice growing season and the following season (Rice 1984; Narwal 1999).

In relay cropping, the seeds of the second crops are sown before the harvest of the first crops and the second crops develop fully before the harvest of the first crop. When Kartikshail is grown as the first crop and *rabi* (winter) such as lentil, khesari (grass pea) mustard are grown as the second crops, weed infection of the second crops may be reduced because of the allelopathy of Kartikshail.

Rice residues incorporated into the soil at the rate of 5 t ha^{-1} reduced the biomass of *E, colonum*, *Ammannia braccifera* and *Phyllanthus fraternus* (Khan and Vaishya 1992) and rice flatsedge (Lin et al. 1992). Bangladeshi rice cultivars BR17 and Kartikshail can be used as the residues incorporated into the soil, which may suppress weed infection in the field because of their allelopathic activity. In addition, rice straw of BR17 and Kartikshail can be used for mulching materials. Some allelochemicals may be released from straw into the soil by rain and irrigation, which may suppress weed infection. Rice straw of BR17 and Kartikshail is also valuable for soil compost to improve soil structure and provide nutrients and allelochemicals. Allelochemicals may be used as natural herbicides and lead compounds for developing eco-friendly weed control agents.

Since Bangladeshi rice cultivars BR17 and Kartikshail have allelopathic activity, the genes related to allelopathic properties can be incorporated into other rice cultivars through breeding programs. The breeding of new rice cultivars is an alternative for weed control to meet the demand of farmers. A multidisciplinary research work by a wide range of scientists including weed scientists, ecologists, natural-product chemists, plant breeders, and molecular biologists, could help achieve the goal of breeding the allelopathic rice cultivars.

9.7 Conclusions

Among 102 Bangladesh rice cultivars, BR17 and Kartikshail have strong allelopathic activity and main allelochemicals were determined as 9-hydroxy-4-megastigmen-3-

one and 9-hydroxy-β-ionone. The inhibitory activity of a mixture of two compounds was much greater than that of sum of two compounds, suggesting that the two compounds may act synergistically. Therefore, 3-hydroxy-β-ionone and 9-hydroxy-4-megastigmen-3-one can be very important allelochemicals of Bangladeshi rice. Bangladeshi rice cultivars BR17 and Kartikshail may be useful for weed management as weed suppressing agents when these rice cultivars are incorporated into the soil or included in rice-based cropping systems.

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Part III
Allelopathy in Pest Management and Crop Production

Chapter 10
Role of Allelopathy in Weed Management for Sustainable Agriculture

S. S. Narwal and Raabia Haouala

Abstract Use of smothering crops as allelopathic strategies could provide weed control, both in summer and winter crops. Although, these crops do not provide complete weed control they can manage weed population at economic threshold levels. This may either eliminate or minimize the use of present herbicides and thus overcome all the major problems associated with herbicides. These studies have shown the potential of weed control of summer and winter crops. Weed suppression in summer crops followed this order: pearl millet > maize > sorghum > cluster bean > cowpea and the order in winter crops was: Egyptian clover > oat > lentil > wheat. Studies with accessions of pearl millet and *Brassica* spp. (*B. juncea, B. napus, B. carinata*) exhibited greater variability in their weed smothering ability. Domesticated plants may offer a great scope for selection of weed smothering spp. In the promising crops, their varieties may be screened for smothering potential. The genes responsible for production of smothering allelochemicals may be identified and possibly transferred to develop new transgenic varieties of same or other crops using techniques of biotechnology so that plants could produce their own herbicides.

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10.1 Introduction

Allelopathy is a relatively newer and potential area of research. The term allelopathy was coined by Prof. Hans Molisch in 1937, which indicates stimulatory/ inhibitory biochemical interactions between the plants including microorganisms. Although allelopathy research started in the beginning of twentieth century (Scheriner and Reed 1907–1911) yet it became familiar among the scientific community with publication of a book on Allelopathy by E.L. Rice in 1974. Since then, allelopathy research had been conducted in diverse fields, hence, International Allelopathy Society in 1996 broadened its definition as "Allelopathy refers to any process involving secondary metabolites produced by plants, microorganisms, viruses and fungi that influence the growth and development of agricultural and biological systems (excluding animals)". It has been shown that allelopathy plays a major role in various disciplines of agricultural and biological sciences and could be used for pest (weeds, insects, nematodes, pathogens) management.

Sustainable agriculture aims at long-term maintenance of natural resources and agricultural productivity with minimal adverse impact on the environment. It emphasizes optimal crop production with minimal external inputs, reducing dependence on commercial inputs (fertilizer and pesticides) and substituting them with internal resources and relying on sustainable practices, which could maintain the productivity over long periods. Research has shown that allelopathic practices may meet all these requirements; hence in future, allelopathy may provide a basis to sustainable agriculture (organic, alternative, regenerative, biodynamic, low input, or resource conserving agriculture). To achieve the goals of sustainable agriculture, current research involves, plant breeding, soil fertility, tillage, crop protection, and cropping systems. Allelopathy, being an important phenomenon in agriculture, is also important in sustainable agriculture (Bruinsma 2003; Ramakudzibga 1991; Farooq et al. 2011). Thus for sustainability, future weed control practices must minimize the use of herbicides and use allelopathic strategies and other practices for weed management (Farooq et al. 2011).

Indiscriminate use of herbicides for weed control during the last 50 years has resulted in serious ecological and environmental problems as under: (A) Increasing incidence of resistance in weeds to important herbicides (Duke et al. 2001) such as S-triazines (Forney et al. 1985) and dinitroanilines (Mudge et al. 1984), and in contrast to pest-resistant crops, the introduction of herbicide-resistant crops will make farming increasingly dependent on herbicides and thus enhance herbicide use in agriculture, (B) Shifts in weed population (i) to species that are more closely related to the crops infested e.g., wild oat (*Avena fatua*) in oat (*A. sativa*) and sorghum (*Sorghum bicolor* M), wild okra (*Abelmoschus esculentus* Moench) in cotton (*Gossypium hirsutum*), and red rice (*Oryza fatua*) in rice (*O. sativa*) and (ii) minor weeds have become dominant. (C) Greater environmental pollution (Freitas et al. 2008; Debenest et al. 2008; FAO 1990) and health hazards (i) particularly from surface and groundwater contamination, which is used for human and livestock consumption, for example in USA, the groundwater contains sizeable quantity of alachlor and atrazine widely used herbicides (Ahrens 1989) and (ii) from their inhalation during handling and application. (D) Toxic residues of herbicides pollute the environment and may prove hazardous to even future generations. (E) Some agricultural commodities may contain minute quantities of herbicide residues, with long-term adverse effects on human and livestock health. Because of these reasons, serious ecological questions about the reliance on herbicides for weed control have been raised. FAO Expert Consultation Group on 'Weed Ecology and Management' has expressed great concern about the problems associated with the use of herbicides for weed control and has recommended minimizing or eliminating use of herbicides with alternative strategies viz., allelopathy (FAO 1997; Narwal 1997), reduced doses of herbicides to maintain weeds at economic threshold level and use of clean crop seed, etc.

Crops have been grown since ancient times without damaging the environment but the use of herbicides during the short span of last 64 years has raised serious doubts about their continued use. Prior to invention of herbicides, weeds were controlled through mechanical and cultural practices. Allelopathy may help in weed control through inhibition of weed seed germination and seedling growth. Present understanding of the plant biochemistry, physiology, morphology, inter- and intra-plant specific interactions and chemistry of natural products have shown that smothering crops, trap crops, and allelochemicals may be used in weed control, overcoming the problems associated with herbicides. Reinhardt et al. (1993) has suggested three allelopathic strategies for weed control (a) selection of weed smothering crops and breeding their varieties to control major weeds in a given area, (b) inclusion of allelopathic crops in rotation and/or use their residues as mulches (Liebman and Dyck 1993), and (c) selecting allelochemicals from plants or microbes with herbicidal activity (Elakovich 1989). This chapter discusses the application of allelopathy in weed management for sustainable crop production.

10.2 Smothering Crops

In crops, the smothering effect of one plant on another is mainly due to interference i.e. competitive and allelopathic interactions between the plant species (Sanjerehei et al. 2011). In agroecosystems, the competition for growth resources (sunlight, soil moisture, plant nutrients) and space starts few days after the emergence of seedlings and becomes intense with time. The competition may be interspecies and/or intraspecies. The later one, generally occurs in pure crops, while former occurs between different plant species e.g. between the component crops in mixtures/intercropping systems and/either between the crops and weeds or between the plants of the same crop sown in narrow rows or at higher plant density. The crop competition may not provide complete weed control but minimizes the weed growth and density through the smothering effect. On the other hand, allelopathy exerts considerable inhibitory effect on the germination and growth of weeds (Weston 1996). Hence, the combination of competitive and allelopathic effects (interference) may considerably reduce the weed density and growth. The interfering ability of crops may be harnessed for weed control through selecting weed smothering crops and breeding their weed smothering varieties.

Weed scientists have identified smothering crops that provide acceptable weed management in a crop production system and could possibly solve many problems associated with current practices of weed control. Tall growing crops having maximum growth rate exert greatest smothering effect on weeds, owing to their ability to out grow the weeds, intercept the incoming radiation, release inhibitory allelochemicals in the environment, etc. Therefore, fast growing crops with a thick canopy cause maximum weed suppression. Barley, rye, maize, sorghum, sudangrass, buckwheat, prosomillet, sunflower, rapeseed, soybean, hemp, sweet clover, alfalfa, and cowpea effectively smother various weeds (Robbins et al. 1982). Of these, barley, rye, sorghum, sudangrass, buckwheat, sunflower, and sweet clover are generally sown to suppress weeds. Maximum weed suppression potential exists in multicut fodder crops or pasture spp. viz., sorghum, sudangrass, alfalfa, and clovers, etc., because their frequent cuttings/grazing prevents or minimizes seed production and growth in weeds. The smothering effect of barley, rye, sorghum, wheat, alfalfa, clovers, vetches, *Brassica* spp., *Heracleum,* linseed, radish, sunflower, and sweet potato, however, has been attributed to allelopathic interactions, as discussed below.

10.2.1 Barley

In strawberry crop field, fall planted barley "Barstoy" provided weed suppression in early spring and not beyond. The strawberry yield was slightly reduced (Smeda and Putnam 1988). Creamer et al. (1996) in a field study screened barley, rye, crimson clover, and hairy vetch for weed suppression. Barley and rye inhibited the germination of yellow foxtail (*Setaria glauca*). Overland (Overland 1966) investigated the efficacy of this crop for weed suppression and reported that it affects weeds through interference. However, in the absence of competition, barley still inhibited the germination of *Amaranthus hybridus* and *C. album*, suggesting the involvement of phytotoxins (Overland 1966). Barley produces phenolic compounds (Quinde-Axtellz and Baikb 2006) and two alkaloids viz., gramine and hordenine have been identified (Hoult and Lovett 1993; Lovett et al. 1994). Overland (1966) showed that the gramine inhibited the growth of chickweed even in small concentrations. Liu and Lovett (Liu and Lovett 1993a, 1993b) confirmed the allelopathic potential of barley and reported that germination of white mustard (*Sinapis alba*) was delayed and radicle length was significantly inhibited at a density of 0.5 barley seeds cm^{-2}. In another study, when both the species were sown together, radicle elongation of white mustard was increasingly inhibited. Barley released allelochemicals for at least 70 days after its germination, which inhibited the growth of *S. alba.* The hordenine was released as root exudates up to

60 days after barley germination, its amount reached a maximum of 2 μg/plant/day for 36 days and then declined. Both hordenine and gramine decreased root length and vigor of root tips. Transmission electron microscopic examination *S. alba* radicle tips exposed to hordenine and gramine showed damage to cell walls, increase in both size and number of vacuoles, autophagy, and disorganization of organelles. In further studies, Hoult and Lovett (1993) reported significant differences in the ability of barley cultivars 'Proctor,' 'Skiff', and 'CH 140017' to produce hordenine and gramine.

Barley proved most potent because its root exudates inhibited the germination and growth of *S. media, C. bursapastoris,* and tobacco but had no effect on wheat. Live barley plants and their root exudates were more inhibitory than aqueous leachates of dead roots. This supported the concept of an active metabolic secretion of the allelopathic substances. In pot culture studies, the growth of *Sinapsis arvensis* and *Thlaspi arvense* weeds in pots was stronger in the beginning but were smothered at later stages. Many weeds remained suppressed during early growth but after its maturity their growth increased markedly e.g. *Viola arvensis.* A higher seed rate (7.5 kernels dm^{-2}) suppressed all weed species greater than a lower seed rate (3.0 kernels dm^{-2}). Weeds, such as *Chenopodium album, V. arvensis, S. arvensis, T. arvense,* and *Lamium amplexicaule* produced more dry matter in wheat pots than in barley pots (54). Barley generally suppresses the growth of weeds through competition for environmental resources and inhibits germination of *A. hybridus* and *C. album* through phytotoxins. The inhibitory activity was greater in broad-leaved weeds like *Stellaria media* than in *Capsella bursapastoris* (Overland 1966). The allelopathic potential of barley has been confirmed during germination and later stages of growth (Liu and Lovett 1993a, b).

10.2.2 Rye

Rye is the most studied cover crop for allelopathic weed suppression from its crop residues. Its high biomass production of shoots and roots, winter hardiness and phytotoxicity of the residue makes it a very effective crop in no-till soil conservation systems. Rye residues have been used to control weeds in fruit orchards (Olmstead 1981). Spring planted, cool season grasses may be used to control weeds in warm season vegetables and autumn-planted cover crops in perennial cropping systems viz., orchards, strawberry, and asparagus planting (Putnam et al. 1983). Rye proved best, because it produced more biomass and toxins prior to desiccation.

Smeda and Putnam (1988) compared the suppression effect of fall planted rye 'Wheeler', wheat 'Yorkstar', and barley 'Barstoy' on winter annual weeds in field trial in strawberry. The weed biomass of winter annual weeds was assessed in June and for other weeds in August. All cover crops significantly reduced weed biomass over the unseeded control; the weed suppression was directly increased with higher seed rates, which produced more crop residue. Rye suppressed weeds throughout the growing season, weed growth was reduced by 90 % in early spring and 55–85 % in mid-summer over the control, however, strawberry yield was slightly reduced. Przepiorkowski and Gorki (1994) studied the effect of rye residues on the germination and growth of barnyard grass (*Echinochloa crus-galli*), willoherb (*Epilobium ciliatum*), and horseweed (*Conyza canadensis*) weeds. Rye residues inhibited the germination of willoherb and horseweed up to 50 %. In soybean and sunflower crops, rye mulch reduced the height (61 %) and biomass (49.1 %) of sickle pod weed. Rye roots residues increased the grain yields of soybean and sunflower greater than its mulch (Brecke and Shilling 1996).

Smeda and Weller (1996) reported that rye residues mowed or desiccated with glyphosate herbicide controlled more than 89 % weeds and did not exert any harmful effect on tomato crop. Hoffman et al. (1996a) applied rye residues on soil surface in greenhouse experiments to determine effect on early growth of barnyard grass and velvet bean, using capillary mat irrigation to maintain a constant soil moisture and fertilizer supply. The presence of rye residues delayed emergence and decreased height of barnyard grass. In maize crop, rye residues were surface applied for weed control (Yenish et al. 1995). About 50 % residues were decomposed in 105 days and may fully decompose in 200 days (based on extrapolation of results), while 50 % DIBOA and DIBOA-glycoside in rye residues disappeared in 10–12 days after surface application of residues and may reach 0 % at 121–161 days after residue incorporation (based on extrapolation of results). The duration of weed suppression by rye cover crop closely follows the disappearance of allelochemicals from its residues than the disappearance of residue.

Chou and Patrick (1976) identified nine acids from ether extracts of decaying rye residues in soil. Phenylacetic, 4 phenylbutyric, vanillic, ferulic, p-coumaric, p-hydroxybenzoic, o-coumaric, and salicylic acids, all inhibited the growth in bioassay plants. The compounds isolated from water extracts of aboveground rye mulch inhibited weed growth in laboratory bioassays (Shilling et al. 1986). Barnes et al. (1986) isolated two hydroxamic acids viz., 2, 4-dihydroxy-l, 4-(2H)-benzoxazin-3-one (DIBOA) and 2(3H)-benzoxazolinon (BOA) with phytotoxicity to a large number of weed spp. tested. These two compounds were more phytotoxic than β-PLA or β-HBA to large crabgrass, barnyard grass, prosomillet, and redroot pigweed at concentrations of 67–250 ppm and DIBOA remained toxic in soil for extended period following soil application. Nair et al. (1990) and Chase et al. (1991) isolated a microbially produced 2, 2-oxo-l, 1-azobenzone (AZOB) from soil enriched with BOA and showed that DIBOA, BOA, and AZOB were inhibitory to barnyard grass and garden cress at concentrations of 67–250 ppm. In these tests, AZOB was more toxic to the test spp. than DIBOA and 10-fold toxic than BOA. In further studies, AZOB at 100 and 200 ppm produced 38–49 % more inhibition in test spp. (garden cress, barnyard grass, cucumber, and snapbean) than DIBOA (Chase et al. 1991). This indicates that a variety of natural products contribute to the herbicidal activity of rye residues.

The collective allelochemical action of rye mulch on weeds suppression in the field is outstanding. Barnes et al. (1986) reported that the weed biomass in a cover crop of rye was reduced by 90 % over unplanted controls. A mulch of 40-day-old spring-planted rye gave 69 % reduction. Shilling et al. (1985) found that rye mulch and root residues gave over 90 % decrease in early season biomass of lambsquarter, redroot pigweed, and common ragweed in no-till planted soybean, sunflower, and tobacco compared to tillage and no rye. Rye, sown in autumn and treated with glyphosate immediately before maize sowing, gave complete weed control in maize crop due to allelopathy. This system not only provided weed control but also reduced contamination of soil and groundwater with persistent herbicides (Zink and Hurle 1990). Killed mulch of rye and subterranean clover (*Trifolium subterranean*) controlled 80–90 % sicklepod, morning glory, prickly sida, and pigweed in soybean, tobacco, maize, sorghum, and sunflower (Worsham 1991). In field trials, 80–100 % *A. retroflexus, A. hybridus,* and *C. album* were controlled up to 4 weeks after sowing in killed cover crops of rye and subterranean clover without use of herbicides. Only rye mulch suppressed *Brachiara platyphylla.* Control of *Amaranthus* spp. increased with increase in soil pH and total phenolic acid content in various mulches. Shilling et al. (1985) studied the allelopathic effects of desiccated residues of rye and wheat on the germination and growth of maize, soybean, sunflower, and tobacco and their weeds. In maize crop, wheat mulch reduced *Ipomoea* spp. biomass by 79 %, while in tobacco crop, rye mulch decreased biomass of red root pigweed, lambsquarter, ragweed, and redroot pigweed by 51, 41, and 73 %, respectively. In soybean and sunflower, rye mulch reduced the biomass of lambsquarter, ragweed, and red root pigweed 99, 92, and 96 %, respectively. Further studies indicated the presence of β-phenyllactic acid (β-PLA) and β-hydroxybutyric acid (β-HBA) in the rye mulch and ferulic acid in wheat mulch. β-HBA and β-PLA at 8 mM inhibited the hypocotyl and root growth of these weeds, while ferulic acid inhibited seed germination and root length of pitted morning glory and prickly sida. In other field studies, rye ‘Forrajero-Baer’ exuding hydroxamic acids through its roots, resulted in 83 % less weed biomass than wheat and 76 % less than forage oats (*A. sativa* L.). Forage oats reduced broadleaf weed biomass by 40 % compared to wheat, but failed to suppress wild oats. In bioassays with 2-o-β-gluco pyranosyl-4-hydroxy-l, 4-dihydroxy-1, 4-benzoxazin-3-one (DIBOA-glc), the main hydroxamic acid found in rye, its aglycone (DIBOA), and its breakdown product BOA inhibited root and coleoptile growth of wild oat seedlings at concentrations above 0.25 mM. It shows that hydroxamic acids from rye ‘Forrajero-Bear’ suppressed the weeds (Leather 1983).

The live rye plants also smothered the weed spp. Creamer et al. (1996) reported that rye cover crop inhibited the emergence of yellow foxtail (*Setaria glauca*) seedlings. Hoffman et al. (1996b) studied the suppression effect of rye plants on barnyard grass. The increased density of rye, reduced the number of leaves, dry matter, and growth of barnyard grass seedlings due to allelopathy.

10.2.3 Wheat

Cold aqueous extract of wheat straw decreased the germination and growth of annual broad-leaved weed spp. (velvet leaf, ivy leaf, morning glory, prickly sida, hemp, sesbania) but the annual grass weed such as barnyard grass remained unaffected (Blum et al. 1991). Lovett (1983) reported that the residues of field pea, wheat, and oilseed rape reduced weed population by 71, 53, and 33 %, respectively. Liebl and Worsham (1983, 1987) reported significant reduction in morning glory and prickly side in field studies involving wheat mulch and isolated ferulic acid as the most phytotoxic compound from foliar wheat extracts. In strawberry crop, fall-planted wheat ‘Yorkstar’ reduced the growth of weeds by 90–95 % in early spring and up to 50–85 % in mid-summer over the unseeded control. The yield of strawberry was decreased slightly (Smeda and Putnam 1988). Rao and Pandya (1992) found that wheat up to 60 days age has significant inhibitory effects on *Asphodelus tenuifolius* weed. It was attributed to release of untriacontane compound present in root exudates of wheat plants. In bioassays, this compound strongly inhibited the seed germination and root and shoot elongation of *A. tenuifolius* at 240 μg/m^2. Young wheat plants (20 days old) were much more inhibitory to weed growth than older plants. In the wheat grown soil and straw extracts, 20 compounds were identified and the major ones were: p-hydroxybenzoic, vanillic, protocatechuic, azelaic, and syringic acids (Das Neves and Gaspar 1990). Kim et al. (1987) identified 12 simple free phenolic acids in wheat, barley, and rye straw. Ferulic acid content was maximum (>20 %) followed by p-coumaric, sinapic, protocatechuic, and caffeic acids, etc. Polyphenols (scopoletin and rutin) and fatty acids (linoleic and organic acids) were also present. These allelochemicals also exert their inhibitory effect on the growth of lettuce seedlings. The inhibitory order of aqueous and alcohol extracts of crop straw were: barley > wheat > rye. In incubation studies, wheat straw extract inhibited the weed germination (24 %) of *A. hybridus* and stimulated *Rottboelia cochinchinensis* and had slight inhibitory effect on *Nicandra physaloides, Acanthospermum hispidum, Urochloa panicoides, C. album, Tagetes minuta,* and *Portulaca oleracea* (Ramakudzibga 1991). In pot studies, decomposed wheat straw, hemp, and pea straw decreased the growth of *Elymus repens* (Muminovic 1991). In field studies mature crop residues of rice cv. ‘Sarjoo 52’, wheat cv. ‘HD 1553’, pea cv. ‘Rachna’, chickpea cv. ‘Type 3’, mustard cv. ‘Varuna’, linseed cv., ‘Neelam’ was incorporated into the soil at a depth of 5–6 cm at 5 t ha^{-1} followed by sowing of rice on the next day. The data on weed density and biomass recorded at 60 days after crop sowing showed that all crop residues inhibited the germination and growth of weeds. Wheat and pea residues inhibited germination of broad leaved weeds (*Ammania baccifera, A. multiflora* and *Phyllanthus niruri*). Rice residues reduced the population of *E. colonum* and broad leaved weeds by 40 and 56 % and biomass by 38 and 64 %, respectively (Khan and Vaishaya 1992).

Narwal and Sarmah (1996) evaluated the influence of wheat straw management and crops on weed density and dry matter. The weed population data at fodder crops’

Table 10.1 Effect of wheat straw management and crops on weed density and dry matter

Treatment	*Trianthema portulacastrum*	Weeds population			Weed dry matter
		Broad	Grasses	Total	
Straw management					
[% inhibition (−)/stimulation (+) over control (straw removal)]					
Burnt	+3.0	+23.3	+157.9	+40.3	+17.0
Soil incorporated	+39.8	+52.0	+195.6	+67.2	+27.9
Fodder crops					
[% inhibition (−)/stimulation (+) over control (fallow)]					
Sorghum	−55.3	−59.8	−87.3	−71.1	−78.1
Pearl millet	−82.9	−85.3	−91.8	−87.4	−92.9
Maize	−76.6	−46.9	−80.9	−79.4	−87.9
Clusterbeans	−78.3	−64.9	−65.5	−73.9	−63.6
Cowpea	−56.3	−63.2	−54.2	−64.0	−72.1

Source Narwal and Sarmah (1996)

harvest (70 DAS), showed that all crops suppressed the weeds over the fallow, but varied in their degree of suppression. Pearl millet proved to be the most smothering crop and suppressed the population of carpet weed up to 80.8 to 85.80 % and of broad leaved weeds up to 79.3 to 91.2 % over the fallow (Table 10.1). The broad leaved weeds suppression followed the order: pearl millet > maize > sorghum > cluster bean > cowpea. The burning or soil incorporation of wheat straw increased the population of grassy weeds (Table 10.1). The straw burning and soil incorporation of straw increased the weed population by 20.4 to 60.1 % and 49.5 and 84.8 %, respectively, over its removal (Table 10.1).

Schreiber (1992) studied the influence of continuous corn, corn-soybean, and soybean-wheat-corn rotations for 12 years (1980–1991) on the weed density of giant foxtail. Its stands were reduced following wheat in no-tillage due to allelopathic influence of wheat straw. The 2, 4-Dihydroxy- 7-methoxy-1, 4-benzoxazin-3-one (DIMBOA) has been identified as the main hydroxyamic acid or wheat, DIMBOA, and its decomposition product 6-methoxy-benzoxazolics-2-one (BOA) inhibited root growth of wild oat by 50 % at concentrations of 0.7 to 0.5 mM. BOA inhibited wild oat seed germination at all concentrations tested and stimulated root growth in wild oat at 1.5 mM but inhibited above this concentration (Perez 1990).

The wheat straw extract had variable effect on the germination and seedling growth of test weed spp. (Table 10.2). It stimulated the germination in carpet weed, barnyard grass, and crowfoot grass but inhibited that pigweed and sunberry. Except in carpetweed, the germination in all test weed spp. was inhibited at higher concentration (10 %) of extract. The degree of inhibition was greater in sunberry and pigweed (Das Neves and Gaspar 1990). The soil extracts, after the harvest of wheat, stimulated the germination of carpetweed and crowfoot grass over the control, while it inhibited the germination of pigweed, sunberry, and barnyard grass (Table 10.3). It proved less inhibitory to germination and seedling growth of

Table 10.2 Effect of aqueous extracts of wheat straw on germination and seedling growth of weeds

Extract concentration (%)	Germination	Shoot length	Root length	Seedling dry weight
[% inhibition (−)/stimulation (+) over control (Distilled water)]				
Trianthema portulacastrum				
5	+2.2	+13.4	+79.7	+100.0
10	+25.2	+148.0	+503.0	+20.0
Amaranthus spp.				
5	−12.0	+23.4	+12.1	+154.0
10	−19.6	+5.3	+4.2	+10.2
Physalis minima				
5	−13.5	−6.6	−3.1	−5.3
10	−23.2	−15.8	−12.4	−14.3
Echinochloa colonum				
5	−4.0	+2.0	+84.4	+9.5
10	−12.3	−34.2	−27.0	−2.7
Dactyloctenium spp.				
5	+9.7	+22.3	+14.3	+30.0
10	−11.0	−2.0	+9.0	−40.0

Source Das Neves and Gaspar (1990)

Table 10.3 Effect of aqueous extracts of wheat field soil on germination and seedling growth of weeds

Extract concentration (%)	Germination	Shoot length	Root length	Seedling dry weight
[% inhibition (−)/stimulation (+) over control (Distilled water)]				
Trianthema portulacastrum				
25	+6.7	+34.1	+0.6	+43.9
50	+15.3	+40.1	+11.4	+24.3
Amaranthus spp.				
25	−67.7	+13.0	+6.3	+104.9
50	−10.9	+8.0	+17.5	+109.8
Physalis minima				
25	−4.0	−5.5	−9.2	−12.5
50	−10.0	−22.0	−48.0	−26.1
Echinochloa colonum				
25	−5.5	+12.0	+41.6	+1.9
50	−6.4	+15.5	+50.2	+5.4
Dactyloctenium spp.				
25	+28.2	+30.5	+35.9	+70.0
50	−13.0	−31.8	+22.8	+70.0

Source Sarmah (1992)

weeds than the wheat straw extract, perhaps, owing to lower concentration of water extractable chemicals in soil than in wheat straw (Sarmah 1992).

Wheat and rye plants release hydroxamic acids through root exudates. In bioassay studies with the root exudates of wheat and rye seedlings, the root exudates of rye inhibited root growth of wild oat but had no effect on wheat (Perez and Juan 1991).

10.2.4 Sorghum

Sorghum has been reported allelopathic to several weed species (Cheema and Khaliq 2000; Einhellig and Souza 1992; Narwal 2000; Panasiuk et al. 1986). Sorghum and Sudan grass mulch applied to apple orchard in early spring decreased weed biomass by 85 and 90 %, respectively (Walker and Jankins 1986). Pritts et al. (1993) reported that Sudan grass (*S. sudangrass*) interplanted in between strawberry rows, suppressed growth of broad leaved weeds. Besides, its mowing for use as winter mulch provided good weed control. Sorghum proved highly toxic to annual grass weeds like *E. colonum* and barnyard grass compared with annual broad leaved spp. (Lovett 1983). Putnam (1986) suggested that cover crops for cool season vegetables viz., pea or cole crops may be sown in autumn and killed with contact herbicides in the spring i.e. at the sowing or transplanting of vegetables. Sorghum sown in summer and later allowed to freeze in winter controlled the weeds in these crops effectively. Putnam and DeFrank (1983) evaluated the weed suppressing ability of desiccated residues of wheat, barley, oat, rye, sorghum, and sudan grass. Sorghum residues reduced the population of common purslane and smooth crabgrass by 70 % and 80 %, respectively. Sorghum and sudan grass residues completely inhibited the germination of smooth crab grass for 60 days. Residues of wheat, barley, oats, and rye also decreased the total weed biomass and inhibited early season weed growth up to 75 %. Crop residues on the soil surface decreased the emergence of lambsquarter, common purslane, and red root pigweed compared with its soil incorporation. Sorghum, rye, and wheat residues release toxic compounds (Yongqing 2008; Shilling et al. 1985). In general, large seeded vegetables (maize, cucumber, pea, soybean) grow normally or were sometime stimulated by crop residues, whereas, several sp. of small seeded vegetables (carrot, lettuce, onion, etc.) were severely injured. Greenhouse experiments with two soils confirmed that sorghum residues have both weed suppressing and crop stimulating effects. Sorghum-sudan grass hybrid ‘sudex’ is generally grown as a summer cover crop because of its rapid growth and ability for excellent weed suppression (Forney et al. 1985).

Since sudex shows potential as a weed suppressive green manure crop, Weston et al. (1989) conducted studies to determine the stage of plant growth with maximum allelochemical production and to identify the allelochemicals. Greatest allelopathic potential of sudex tissue was at 7 days of age and it caused greater inhibition in broad leaf spp. (tomato and curly cress) than in grass spp. (*S. italica* and *E. crus-galli*). The phytoinhibitors were identified as p-hydroxybenzoic acid and p-hydroxybenzaldehyde (enzymatic breakdown products of cyanogenic glycoside dhurrin) and their 150 values against *Lepidium sativum* in seed, bioassays were 140 and 113 µg/mL, respectively. Seven days old sudex tissue had maximum content of these phyto-inhibitors on dry matter basis than older tissue. With increase in sudex age, the percentage of p-hydroxybenzaldehyde increased and that of p-hydroxybenzoic acid decreased and as the age of sudex increased from 7 to 28 days, allelopathic potential of tissue decreased.

Living plants and residues of sorghum and Sudan grass reduced the population of common purslane by almost 100 % and that of smooth crabgrass by 50 % (Dilday 1992). Forney et al. (1985) reported that growing a forage sorghum-sudan grass hybrid prior to late-summer planting of no-till alfalfa suppressed weeds and enhanced alfalfa growth. Einhellig and Leather (1988) monitored the weed biomass in strip cropping of grain sorghum, maize, and soybean (grown without herbicides) in the following year. Weed cover in early spring in former sorghum strips was <30 % of that in prior soybean strip. At mid-summer, plots where grain sorghum had been grown the year before had only about 60 % of the weed biomass. This decrease in biomass resulted from the suppression of broad leaved weeds, with no effect on grasses. It was found in laboratory studies, that grain sorghum inhibits early seedling growth and development more than germination. Farmers in South Dakota, strip plant grain sorghum, and sunflower without herbicides and find reasonable weed control. The summer sorghum delayed and reduced wild oat emergence in the following winter. The presence of a small quantity of sorghum stubble inhibited wild oat emergence and reduced root and shoot dry matter and leaf number over no stubble treatment (Jones 1992). In field studies, grain sorghum reduced weed density and growth in the following crop year compared with after maize and soybean. Sorghum inhibited the broad leaved weeds and had no effect on grassy weeds. The inhibitory effect of sorghum on weeds was attributed to allelopathy (Einhellig and Rasmussen 1989). Einhellig and Souza (Einhellig and Souza 1992) purified sorgholeone, a p-benzoquinone from the root exudates of 5-day-old Dekalb hybrid ‘KK 28’ sorghum seedlings. In laboratory studies, sorgholeone considerably reduced the root and shoot growth of *Eragrostis* spp., *Lemna minor,* and other test weed spp. through inhibition of photosynthesis (Einhellig and Rasmussen 1989). In undisturbed plots and sorghum crop, the residual effect of straw management treatments and preceding fodder crops persisted up to 45–75 days after harvest (DAH) of fodder ‘crops, respectively (Table 10.2; Sarmah 1992).

10.2.5 Pearl Millet

Sarmah (1992) studied the smothering effect of pearl millet, sorghum, maize, cowpea, and cluster bean grown for fodder on summer weeds under field conditions. At harvest (60 days after sowing) sorghum considerably smothered the weed growth over the fallow (non-crop control), while pearl millet provided complete (100 %) weed control. The residual suppression effect of pearl millet was also observed up to 45 days on the weed density and growth in the succeeding sorghum crop.

Table 10.4 Suppression effect of *pearl millet* accessions on the population of weeds (m^{-2})

Accession	[% suppression of weed population over control (fallow)]	
	Total weeds	*Chenopodium album* L.
HHB-68	72.3	73.0
8804A × 833-2	71.1	72.6
HHB-60	57.5	57.3
863A × HTP 88/33	57.2	42.4
88006A × 90/4-5	54.6	55.7
843A × HT 8 88/47	53.5	46.2
81A × HC-4	38.5	41.1
88006A × 833-2	36.7	26.9
861A × 77/273	34.2	38.5
HHB-67	32.6	74.8
843A × 8602	31.0	56.7
843A × 77/371	22.4	53.8
HHB-50	18.0	52.4

Source Narwal et al. (1992)

The maximum smothering effect of pearl millet on weeds as compared to other summer crops (Narwal and Sarmah 1996) encouraged the Author to screen pearl millet genotypes for weed suppression on the pattern of earlier studies with cucumber (Putnam et al. 1983), oat (Fay and Duke 1977) and sunflower (Leather 1987). A field trial was conducted to determine the smothering capability of 13 accessions of pearl millet (*Pennisetum typhoides*) on weeds. Since the field was highly infested with weeds, the studies were conducted with natural weed seed bank in the field. At pearl millet harvest, the weed population and dry weight were recorded. Two most dominant weed spp. (*T. portulacastrum* and *A. spinosa*) were recorded separately. While other species like *C. rotundus* and *Physalis minima* were present in some plots.

All the pearl millet genotypes reduced the weed population of *T. portulacastrum, Amaranthus* spp., and total weeds, compared with control (Narwal et al. 1992). Nine genotypes significantly smothered the total weed population over the control. Of these, HHB 67, ranked first in weed suppression (72.3 %) over the control, closely followed by 88004A × 833-2 (71.1 %), HHB 60 (57.5 %), and 863A × HTP 88/33 (57.2 %) (Table 10.4).

10.2.6 Maize

The aqueous extract of maize pollen strongly inhibited the growth of *Bidens pilosa, Rumex crispus,* and *Cassia jalapensis* (Jimenez-Osorino 1984). This indicates a great potential of maize pollen to control weeds (Anaya et al. 1987) as it is produced in abundance. Ethanol extract of pollens contained two chromatographic fractions 3A and 3B which inhibited the radicle growth of *A. leucocarpus* to 85 and 40 %, respectively, compared to the control. The phytotoxicity of decomposing maize residues in soil persisted for 22 weeks (Guenzi et al. 1967) and 18 compounds viz., salicylaldehyde, resorcinol, phloroglucinol p-hydroxybenzaldehyde and butyric, phenylacetic, 4-phenylbutyric, benzoic, p-hydroxybenzoic, vanillic, ferulic,*o*-coumaric, O-hydroxyphenylacetic, salycyclic, *p*-coumaric, trans-cinnamic, and caffeic acids were identified (Chou and Patrick 1976). These compounds were found phytotoxic to lettuce in bioassays but no information is available for weed species. Some of these compounds could be inhibitory to weed species as well.

10.2.7 Alfalfa

Abdul Rahman and Habib (1989) reported that *Imperata cylindrica* is a serious weed in Iraq. They found that alfalfa, reduced root and shoot growth of *I. cylindrica* by 80 %, decayed/undecayed mixture of alfalfa roots and soil (0.015:1 w/w) inhibited the germination (51–56 %), production of new plants (30–42 %) from *I. cylindrica* rhizomes. It may be due to the presence of caffeic, chlorogenic, isochlorogenic, p-coumaric, p-OH benzoic, and ferulic acids in root exudates and residues of alfalfa. Six months after decomposition of alfalfa roots in soil, 126 μg of phenolics per gram of soil were found. In nutrient culture, alfalfa root exudates significantly reduced the seedling growth of *I. cylindrica* when both plants were grown together. The extracts of dried alfalfa plants, inhibited the germination of *C. album* (44 %) and *Abutilon theophrasti* (25 %) and had no effect on giant foxtail (Chung and Miller 1995). Incorporation of alfalfa residues at 0.0–2.0 g kg^{-1} silica sand inhibited the growth of *C. album,* pigweed (*A. retrofiexus*) velvet leaf, and crabgrass (*Digitaria sanguinalis*). Saponins from alfalfa roots inhibited the germination of *E. crus-galli* and *Bromus secalinus* weeds at all concentrations (10–5,000 ppm), while that of pigweed, coffee weed (*Sesbania exaltata*), dandelion (*Taraxum vulgare*), and wheat crop at and above 1,000 ppm concentrations (Waller et al. 1995).

Alfalfa produces allelopathic saponins, which may be a major cause of yield reduction in subsequent crops (Wyman-Simpson et al. 1991). These are found as tri-terpenoid glycosides in roots, shoots, seeds, and flowers (Oleszek 1993). The detailed chemical structure of 30–40 alfalfa saponins with different properties of inhibition or stimulation is known. The alfalfa plant parts differ greatly in the types and amount(s) aglycones present, among which medicagenic acid glycosides are biologically most active and are dominant in alfalfa roots (Oleszek et al. 1992). Reduced yields are common in wheat, maize, soybean, and sorghum when sown after old alfalfa stands, even if the soil moisture and fertility is adequate and pests are fully controlled. In bioassay studies, six saponins from alfalfa 'cimmaron' were found to inhibit the root and shoot growth of barnyard grass and cheat (*B. secalinus*) at all tested concentrations (10–5,000 ppm), while in coffee weed, pigweed and dandelion (*Taraxacum vulgare*), root and shoot growth were stimulated at 10 and 100 ppm and inhibited at 1,000 and 5,000 ppm. It is suggested that more research is needed before alfalfa saponins could be used in weed control (Waller et al. 1993).

10.2.8 Sunhemp *(Crotolaria juncea)*

Leafy spurge (*Euphorbia esula*) has infested millions of acres of crop land, range land and conservation areas in central plains of USA and Canada.

10.2.9 Pigeonpea

Hepperly and Diaz (1983) reported that pigeonpea litter gave excellent weed control for 2 months in the succeeding crop. Its leaf litter significantly controlled the weed density/m^2 to 40 compared with 322 in controls and weed biomass g m^{-2} to 25 compared to 105 g in control. The leaf litter decreased the population of grassy weeds to one-seventh of that of control. Semiday and Almodovar (1987) reported that pigeonpea has the ability to suppress weeds 4–6 months after planting, irrespective of initial weed density. Semiday (1999) observed that preceding crop of pigeonpea, reduced the emergence, density (57 %), and biomass of weeds in the succeeding tomato crop in the plots where tomato followed other crops. However, the pigeonpea had no harmful effect on tomato crop.

10.2.10 Velvet Bean

Velvet bean (*Mucuna deeringianum* Borr. Merr) is reported to significantly decline the weed population. It suppressed broad leaved weeds and declined their population by 78 % at 120 days after sowing. However, grasses declined by 58 %, Cyperaceous weeds increased by 34 % (Anguilar-Erazo 1984).

In view of weed smothering abilities of velvet bean in Costa Rica, a velvet bean + maize intercropping system has been developed, which provides maximum suppression of weeds (Dela Cruz et al. 1994). Semiday (1999) reported that live velvet bean crop was incorporated into the field and after 4 weeks, tomato was transplanted. The velvet bean residues controlled the *C. rotundus* weed and had no harmful effect on tomato crop.

The velvet bean increased the yield of poaceae crops mixture and smothered notorious weeds like nutsedge and *I. cylindrica* (Myras and Olavi 1981). It is an allelopathic plant in seedling growth tests and effectively smothers the weeds in crop fields (Fujii et al. 1988). The weed emergence and population in fields after continuous cropping of velvet bean, upland rice, egg plant, and tomato was minimum (50 %) in the velvet bean plot, compared to other crop plots, where *Cerastium glomeratum* was the dominant weed. The emergence and hypocotyl length of lettuce seedlings were not affected but radicle growth was reduced significantly in plots with continuous cropping of velvet bean for 5 years; however, no such reduction occurred after one year of velvet bean cultivation. Crude methanol extracts of velvet bean leaves markedly reduced the growth of *C. glomeratum* and lettuce (Fujii et al. 1991a). The velvet bean leaves and roots were found to contain L-3, 4-dihydroxyphenylalanine (L-DOPA) in high concentrations (0.5–1.5 % of the fresh weight). The younger leaves contain more L-DOPA than mature leaves. L-DOPA strongly inhibited the growth of *C. glomeratum* and *Spergula arvensis;* moderately inhibited the growth of compositae but had little effect on graminae and leguminosae plants. Since fresh leaves of velvet bean contain 1 % of L-DOPA and it produces 20–30 tonnes of fresh leaves and stems per hectare, therefore about 200–300 kg L-DOPA is produced and added to soil per hectare per year. Therefore, the L-DOPA is apparently responsible for the weed control in velvet bean (Fujii et al. 1991a).

10.2.11 Stizolobium spp.

The legumes *Stizolobium deeriangianum* and *Canavallia ensiformis* interplanted in maize provide effective weed control (Burges and Talbert 1996; Dinardo et al. 1996). In the southeastern parts of Mexico, many peasants intercrop legumes such as *S. pruriens* (Gliessman and Garcia 1979) with maize. It incorporates nitrogen into the soil, increases corn yields, significantly reduces both the number and biomass of weeds, its forage is fed to livestock and seeds are used by humans. In laboratory bioassays, an aqueous leachate (1 %) of dried leaves of *S. pruriens* significantly inhibited the radicle growth of *A. hypochondriacus,* barnyard grass and tomato (Barragan et al. 1996).

10.2.12 Heracleum laciniatum hornem

H. laciniatum suppress the growth of plants under its canopy. In meadows, it inhibited the growth of various plant species without competition. Water percolating through its pots slightly inhibited the growth of *Poa pratensis* and *Phleum pratense.* The soil samples collected from meadow soil from mid-June to late October inhibited the germination of seeds of *P. pratense* than in plowed soil, thus, allelopathy was partly responsible for weed suppression (Myras and Olavi 1981). Its seeds contain inhibitors and the ethyl acetate fraction contained three main groups of inhibitors having Rf values: (a) 0.60–0.80 (b) 0.20–0.40 and (c) 0.0–0.10 (101). The group (a) inhibited seed germination and root growth of lettuce and hypocotyl growth of *Avena.* The group (b) contained the furanocoumarins, pimpinelin, bergapten, isobergapten and angelicin; synthetic pimpinelin, and sphondin inhibited seed germination of lettuce. Inhibitors present in group (a) and (c) were not identified.

10.2.13 Sweet Potato

Mere planting of sweet potato plants, between the cassava rows in field, effectively check the growth of weeds (Villamayor and Perez 1984) and even the soils, which have been planted to sweet potato show residual allelopathy (Pardales 1993). However, the degree of allelopathic effect varies with variety (Caracallas 1996).

Sweet potato (*Ipomoea batatas*) is a very efficient crop in controlling weeds through interference, where a very aggressive competition potential is supplemented with high allelopathic effect (Anaya et al. 1990; 1995). It is considered as an extremely successful competitor against some weeds under field conditions, including yellow nutsedge (Harrison and Peterson 1986) but not competitive with others. It interferes with crop growth and whole plant residues inhibited the growth of sweet potato vine and cowpea (Walker and Jankins 1986). Its tissues contain several allelochemicals viz., alcohols, fatty acids, caffeic, and chlorogenic acid (Rice 1984). Other compounds have also been identified but not tested as allelochemicals. Peterson and Harrison (1991a) found a high concentration of allelochemicals in its root periderm extracts and observed quantitative differences in the content of two cultivars. The hexane extracts were inhibitory to many weed spp., and I_{50} estimates were 0.5, 0.6, 2.8, 4.4, 5.1, 9.6, 15.7, 21.0, and 25.8 mg/mL for velvetleaf, prosomillet, black night shade (*Solanum nigrum*), goose grass, sweet potato, tall morning glory, *Eclipta alba, C. occidentalis,* and pigweed, respectively. In field studies, sweet potato ‘Regal’ at the end of growing season decreased the yellow nutsedge shoot dry weight/m^2 up to 90 % than nutsedge grown alone. In greenhouse experiments designed to minimize competitive effects of sweet potato, yellow nutsedge growth was reduced by more than 50 % by sweet potato at 8 and 12 weeks after planting. The polar fraction of sweet potato periderm tissue was highly inhibitory to yellow nutsedge root growth (Harrison and Peterson 1991). In further studies, sweet potato periderm tissue was found to contain 1.2 % active inhibitor, which was labile in methanol and various weed species exhibited extremely wide range of sensitivity. The I_{50} values were 0.16, 0.013, and 0.011 mg/mL for redroot pigweed, velvetleaf, and prosomillet, respectively (Peterson and Harrison 1991b). Reinhardt et al. (1993) reported glass house studies in the soils from control and plots of three sweet potato varieties ‘Bosbok’, ‘Brondal’, and ‘Koedoe’ indicator plants such as yellow nutsedge, purple nutsedge, common pigweed, carrot ‘Kaapse Mark’, tomato ‘Heinz 1370,’ cucumber ‘Special Rust Resistant’, radish ‘White Icicle’, onion ‘Pyramid’, lettuce ‘Great lakes’, and oats ‘SWK 001’ were grown. The soils from sweet potato cv. ‘Brondal’ plots significantly decreased the dry matter in yellow nutsedge plants than those grown in cvs. ‘Bosbok’, ‘Koedoe’, or fallow plots indicating the presence of substances inhibitory to yellow nutsedge growth in the soil after cv ‘Brondal’ sweet potato. Compared with fallow plots, the growth of carrots, cucumber, lettuce, oats, onion, and tomato plants was stimulated. The related species *I. aquatica* and *I. tricolor* have also been found allelopathic. *I. tricolor* is a major summer cover crop for adding organic matter and for weed control during the fallow periods in sugarcane fields of Mexico. Its aqueous and organic extracts exert allelopathic suppressive effect on seed germination and seedling growth of *A. leucocarpus* and barnyard grass owing to phytotoxic mixture of resin glucosides (Anaya et al. 1990).

10.2.14 Sunflower

Sunflower is allelopathic in nature and also exhibits autotoxicity. Its varieties are more inhibitory to weeds than native species. Growing plants inhibit the growth of weeds through the release of phytotoxic root exudates. The germination and growth of succeeding crops is reduced due to accumulation of phytotoxins from root exudates and release of allelochemicals from the decomposing crop residues. Allelopathic potential of sunflower weed control has been reported in wild as well in its cultivars viz., ‘Ramsum HS-52’, ‘Peredovik’, ‘Hybrids 201,’ ‘8941’ (Leather 1983). In greenhouse studies, sunflower ‘Russian Mammoth’ residues reduce both, seed germination and biomass of weeds (Hall et al. 1983). The aqueous extracts as well as growing plants inhibit seed germination and seedling growth of *A. theophrasti, Datura stramonium, Ipomoea* spp., and *Brassica kaber* (Dharamraj et al. 1994a, c). Its aqueous extracts reduced the germination (36–56 %) and seedling growth (22–57 %) of *Trianthema portulacastrum, A. virdis,* and parthenium (*Parthenium hysterophorus*). However, in field studies, drastic reduction occurred in germination (83–95 %), growth (79–94 %), and chlorophyll content of above weeds and also in *P. oleracea* and *Flaveria australasica* weeds (Dharamraj et al. 1994a; 1994c).

Although weed density increased in all plots over the five seasons, the rate of increase was less in sunflower plots. There was, however, little difference among the various sunflower cultivars. In further studies, weed biomass was equivalent in plots planted with sunflower, whether EPTC (S-thyldipropl carbamothioate) herbicide was applied or not, clearly showing the efficacy of sunflower mediated weed control (Leather 1987). In sunflower-wheat rotation field trials, sunflower decreased the density and dry weight of wild oat and *Cirsium arvense* in the following wheat crop (Cernusko and Boreky 1992). The potential of sunflower as source of allelochemicals is well-known (Varela 1982) and bioassays of leaf aqueous extracts show strong inhibition and stimulation in germination and root length of test plant species. The leaf aqueous extracts of sunflower ‘SH-222’ were found to contain five new guaianolides and the annuolides A-B have been tested as allelochemicals. All the guaianolides possess allelopathic activity over dicotyledon species and are likely to be involved in the allelopathic activity of sunflower cultivars (Macias et al. 1993). In pot experiments, sunflower straw depressed the plant height of wild oat, *Agropyron repens,* barnyard grass, *Ambrosia artemisifolia,* and lambsquarter and depressed the biomass of last three weed spp. (Muminovic 1991). Application of sunflower residues @ 2 t/ha or its preceding crop reduced population of *Cleome viscosa, Corchorus trilocularia,* and *C. iria.*

10.2.15 Brassica spp.

Brassica spp. (*B. hirta, B. juncea, B. nigra, B. napus*) suppress weeds through (a) vigorous early season growth, smothers the weeds before they are established, (b) release of allelochemicals into soil from the shoots of living plants, plant residues, or plants incorporated into the soil by tillage, and (c) leaching/secretion of glucosinolates into the growing media; their hydrolysis to isothiocyanates inhibits weed seed germination and growth (Al-Khatib and Boydston 1999). Benzyl isothiocyanate, breakdown product of white mustard (*B. hirta*) is phytotoxic to velvetleaf (*A. theophrasti*) and sicklepod (*C. obtusifolia*) (Dharamraj et al. 1994a). Allyl isothiocyanate isolated from black mustard (*B. nigra* L.) inhibits germination of *B. rigidus* (Bell and Muller 1973). Aqueous extracts from decayed residues of wild mustard (*B.kaber*) were toxic to Japanese millet (*E. crus-galli* var. *Frumentacea*) (Eliott and Stowe 1971). Rapeseed (*B. napus*) foliage incorporated into soil suppressed population of *C. album, A. retroflexus,* and *E. crus-galli* similar to standard herbicide treatment (Boydston 1993; Boydston and Hang 1996). Foliage of white mustard (*B. hirta*) and *B. napus* incorporated into the soil reduced *C. bursapastoris* and *Kochia scoparia* emergence and biomass (Boydston and AI-Khatib 1994). Rapeseed planted in fall and incorporated in spring before planting potato reduced weed density by 73–85 % and biomass by 50–96 % (Boydston and Hang 1996). In Russia, inclusion of rapeseed in rotation reduces the weed population up to 40 % (Grodzinsky 1992). Rapeseed foliage incorporated into the soil controls *S. media* through allyl isothiocyanate and the inhibition increases with the concentration of allyl isothiocyanates (Bell and Muller 1973). These results indicate the weed control potential of *Brassica* as green manure crops, the level of weed suppression depends upon the amount of foliage incorporated into the soil and *Brassica* spp. used. Wild types of *Brassica* spp. possess high allelopathic potential due to presence of higher concentration of potent glucosinolates (Choesin and Boerner 1991). Al-Khatib and Boydston (Al-Khatib and Boydston 1999) in their review have reported that methyl, phenyl, ethyl, and allyl isothiocyanate considerably inhibited the germination and growth of barnyard grass, redroot pigweed, cucumber, and pea than benzyl, butyl, propyl, and b-phenylethyl isothiocyanate. Besides, allelopathy may also result from additive or synergistic activity of many allelochemicals rather than from a single one. Green manuring of *Brassica* spp. suppresses the weeds but could also injure succeeding crops. Studies with potato, peppermint, cucumber, and peas following rapeseed and white mustard showed that rapeseed injured only pea and peppermint and white mustard was harmless to these crops.

Brassica spp. suppresses the weeds through their vigorous growth and release of allelochemicals. *B. nigra* and *B. juncea* were found the most potent (Nilsson and Halgren 1992) because they produced maximum volatiles particularly allyl isothiocyanate, a potent allelochemical (Joshi 1991). After mustard harvest, a large quantity of crop residues are incorporated into the soil and during decomposition, they release phytotoxic allelochemicals, which may be used for weed control. The mustard seed cake application @ 1.0 t/ha decreased density (56–100 %) of *C. album* and *Matricaria indora* and completely controlled *C. bursapastoris* (Ascard and Johanson 1991; Nilsson and Halgren 1992). *Brassica* residues are most suitable for weed control in transplanted vegetable crops, orchards, and woody cultivated plants. Oleszek et al. (1996) listed six glucosinolates viz., sinigrin, sinalbin, gluconapin, glucobrassicin, gluconastrutiin, and 4-hydroxyglucobrassicin found in cruciferae spp. to be useful in weed control strategies.

Among *Brassica* spp., *B. campestris* reduced the weed density in the same field in the following year, therefore, it is used as a weed controlling crop by the tarahumara Indians in North Mexico (Jimenez-Osorino and Gliessman 1987). There are reports on the use of winter and spring cruciferous crops as intermediate crops to reduce population of weeds. *B. campestris, B. juncea,* and *B. napus* significantly smothered the weeds over control (Salle et al. 1987). Bell (1970) and Bell and Muller (Bell and Muller 1973) reported that post-harvest cropping of cruciferous crops in maize fields reduced weed population by 90–96 %. Likewise, the intermediate crop of winter/spring rape reduced weed population by 40 to 47 % (Uteush 1979).

These are major oilseed crops of winter and are grown over large areas. Oleszek et al. (1996) in their review concluded that some *Crucifereae* spp. possess potential to inhibit germination and growth of weeds and thus these species could be successfully used in weed control. The degradation products of glucosinolates seem to be responsible for allelopathic potential of *Brassica* spp. The field studies were conducted to determine the smothering effect of three *Brassica* spp. viz., *B. juncea, B. napus,* and *B. carinata* accession on the weed spp. The crops were sown in completely randomized design with three replications in plots of 6 × 4 m. The crops were raised with the recommended cultural practices and uniform plant stand was maintained; however, no herbicide or cultural practices were applied for weed control. The weed population and dry weight were recorded at crop harvest. The genus *Brassica* is reported to have allelopathic properties that can affect germination, establishment, and growth of other species in agroecosystems (Jimenez-Osorino 1984). Broccoli also showed a potential for allelopathic interference on weeds depending upon the growth stage (Jimenez-Osorino and Gliessman 1987). Wild mustard has a complex reaction on the crop environment and controls weeds and pests. The complex of glucosinolates and their derivatives common to the genus *Brassica* are being explored as possible active agents for the control of both weeds and pests (Sarmah et al. 1992). Among the genotypes, RH 8689 showed maximum ability to smother the weed population (8.3 weeds m^{-2}), followed by RH 8605 (13.09 weeds $m^{-2)}$ and RH 8693 (18.1 weeds $m^{-2)}$ causing 91.6, 85.9,

Table 10.5 Suppression effect of *Brassica* accessions on weeds (m^{-2})

Accession	[% suppression of weed population over control (fallow)]	
	Total weeds	*Phalaris minor*
RH 8689	91.6 (78.0)	87.9
RH 8605	85.9 (78.7)	80.7
RH 8693	81.4 (76.8)	71.3
RH 8113	74.3 (82.0)	68.2
RH 8812	72.6 (77.7)	62.1
RH 8602	68.4 (77.2)	51.8

All the accessions reduced the *C. album* population by 80 %; % suppression of weed dry matter
Source Sarmah et al. (1992)

and 81.4 %, suppression, respectively, over the control (98.4 weeds m^{-2}); however, the genotype Varuna had the least smothering effect (Table 10.5).

10.2.16 Squash

The interplanting of squash (*Cucurbita pepo*) by peasants in maize/bean polyculture or in maize or bean monoculture provides weed control (Amador and Gliessman 1962). Squash is planted mainly owing to its ability to control weeds. It forms a continuous plant cover over the low growing weed species, eliminating them, and restoring soil productivity through the addition of large quantities of organic matter (8 to 10 t dry matter ha^{-1}). Laboratory bioassays partly implicate allelopathy in this inhibition. The extract proved most inhibitory to cabbage than to maize and cowpea.

10.2.17 Cassia spp.

Mahadeveppa and Kulkarni (1996), found that over sown *Cassia uniflora* (*C. sericea*) in parthenium plants completely eliminated this weed. In bioassays, aqueous leachates of various parts of C. *sericea* were very inhibitory to the seed germination of parthenium, with seed leachates being most inhibitory (14 %). It replaces parthenium through interference at three levels: (a) inhibits seed germination and seedling growth allelopathically, (b) over grows the summer parthenium and drastically decreased seed yield, and (c) prevents establishment of winter parthenium. Mahadeveppa and Kulkarni (1996) reviewed their work on suppression effect of *C. sericea* on parthenium and concluded that the weed is replaced by *C. sericea* mainly through allelopathic effects.

10.2.18 Miscellaneous Legumes

The residues of several annual legumes have also shown weed suppression. White et al. (1989) reported inhibition of several weeds from field residues and leachates of crimson clover and hairy vetch. Teasdale (Teasdale 1988) showed weed suppression from hairy vetch residues. In field studies at Beltsville and Ithaca, USA, the residues of hairy vetch and rye reduced weed emergence with an increase in biomass residue in no-tillage system. Decay models developed from these studies predicted emergence levels of 21 and 62 % of control level at a residue rate of 350 g/m^2 at Beltsville and Ithaca, respectively (Teasdale and Mohler 1992). Further studies showed that light interception and allelopathy are responsible for weed suppression by hairy vetch residues (Teasdale 1988; Teasdale and Daughtary 1993). Enache and llinicki (Enache and llinicki 1990) tested subterranean clover for weed control as a living mulch in corn crop. The mulch provided good control of *I. hederacea,* however, the control of fall panicum (*Panicum dichotomiflorum*) was little in the first year, but controlled it in later years. Enache and Illinicki (Enache and Illinicki 1988) concluded that subterranean clover has potential for controlling weeds in corn. Worsham (1991) reported that killed heavy mulches of subterranean clover among the legumes and rye among grasses, provided 80–90 % early control of sicklepod, morning glory, prickly sida, and pigweed in crops of soybean, tobacco, maize, sorghum, and sunflower. In field trials, *A. retroflexus, A. spinosus, A. hybridus,* and *C. album* were 80–100 % controlled, up to 4 weeks after sowing into killed cover crops of rye and subterranean clover (Worsham and Blum 1992). In pot studies, pea straw depressed the biomass of Johnsongrass and barnyard grass weeds (Muminovic 1991). Sahid et al. (1993) studied allelopathic potential of five species of legume cover crops viz., *Calopogonium caeruleum, C. mucunoides, C. pubescens, P. javanica,* and velvet bean (*M. cochinchinensis*) in bioassays, pot culture, and field studies on *Asystasia intrusa* and *Paspalum conjugatum* weeds. In bioassays, *C. caeruleum* and velvet bean exhibited greater phytotoxic effects on the germination and growth of these weeds. In pot culture, soil incorporation of *C. caeruleum* and velvet bean residues decreased the dry weight of both these weeds. Daroesman (1981) found that over planting of *Stylosanthes guyanensis* in heavily infested *I. cylindrica* fields, completely eliminated the weed through competition and allelopathy (Sajise and Lales 1975).

Gonzalez et al. (1992) studied the allelopathic potential of different plant parts of the four *Capsicum annuum* varieties (‘Padron’, Amoia’, ‘Tornado’, ‘ltaliano dulce’) in laboratory bioassays. The soil of decomposing aerial parts of all varieties strongly inhibited the germination and growth of lettuce seeds, while decomposing roots had no effect. The spraying of aqueous extracts of roots and roots exudates had no effect on lettuce seedlings.

Grechkanov and Rodionov (1971) reported benefits from mixing of 1–2 kg seeds ha^{-1} of wild heliotrope (*Heliotropeum europeum* L.) in several legumes. This plant not only reduced weeds from 30 to 70 % but also controlled other pests. The mulching of crop residues provides weed control for 30–75 days and depends upon soil and weather conditions. It persists longer, when rains occur early after the desiccation of crops followed by dry conditions. Experience with local conditions, crop tolerance, and integration with appropriate tillage practices are prerequisites for relying on crop residues for weed control. Crop injury from mulch related weed control may be overcome through adjustment of time between mulching and planting and use of tolerant crops.

Peters and Mohammed Zam (1981) observed that some tall fescue (*Festuca arundinacea*) genotypes in germplasm had no infestation of crab grass (*D. sanguinalis*), while other genotypes were heavily infested. The pot and bioassay studies showed that this inhibition was due to allelopathy. Hence, tall fescue could be used as cover crop, mulch, or in crop rotation for control of crabgrass weed in other crops. The aqueous straw extract (5 and 10 %) of buckwheat on *S. alba* and barnyard grass, reduced and delayed the germination of both weed spp. Spraying of extract, at 4 and 5 leaf stage of weeds also inhibited their growth (Gawronski and Ciarka 1994). Almeida and Rodrigues (1985) found that black oat (*A. strigosa*), rye, radish, and rape at their harvest leave the field with few weeds. These crops have longer allelopathic effect, specially black oat, which keep the field with low infestation of weeds for 85 days after the mulching. Because of its large biomass it retained allelochemicals for longer period in the field. Almeida et al. (1984) reported that rye grass mulch reduces weed infestation in fields for a longer period. Taro (*Colocasia esculenta* (L.) Schott) residues inhibited the establishment and growth of *C. rotundus*, *R. exaltata* L. F., and *I. tricolor* L. weed (Pardales 1994) and reduced the number and biomass of these weeds spp. (Pardales et al. 1991). The effects of aqueous extracts from various parts of sesame (*Sesamum indicum* L.) cv. 'Roied 1' were studied on the growth of 15 weed spp. Low concentrations (0.1 g of fresh plant) inhibited the growth of *A. spinosus*, *Celosia argentea*, *Gomphrena celosoides,* and *Dactyloctenium aegyptium*. The growth of other weed sp. was inhibited at higher concentrations (Premasthira and Zungostiporn 1996). Jackbean (*Canavalia ensiformis*) is an annual legume used for green manuring. Two weeks after incorporation of its biomass in soil, the weeds *Sida cordifolia, B. pilosa, R. exaltata, Cenchrus echinatus,* and *Eleusine indica* were sown. A 0.5 % concentration of *C. ensiformis* biomass (w/w) reduced the germination of *S. cordifola, C. echinatus,* while concentration of 1 and 2 % reduced germination of *B. pilosa* and *R. exaltata,* respectively. The aqueous extracts of roots of *Psacalium decompositum* was studied on germination and radicle growth of *A. hypochondriacus* and *E. crus-galli.* The extract significantly inhibited the germination and growth of both weed species (Anaya et al. 1996).

Bansal (1989) reported that intercropping of linseed with wheat controlled the obnoxious weed *Ranunculus arvensis*. Besides crops, there are many herbs and shrubs which suppress the growth of weeds. Broadcasting of *S. hamata* seeds after uprooting of parthenium significantly controlled the weed in the second year (Desai and Bhoj 1981). Aqueous extracts of *Hyptis suaveolens* completely inhibited the germination of parthenium seeds (Rao et al. 1987), while that of *Alstonia scholaris* inhibited both germination and seedling growth (Ghildiyal 1987). The aqueous extracts of *Lycoris radiata* control the growth of *Solidago* *altissima* and *R. crispus* weeds and may provide an effective control of these weeds (Takahashi 1989).

10.3 Breeding for Weed Smothering Varieties

Presently the ideal smothering crops does not exist; hence, new smothering plants must be bred for that specific purpose. Little research has been done in this regard. However, by combining weed science, biotechnology, and plant breeding, it may be possible to develop "smother plants" that effectively suppress weeds and reduce use of herbicide. For example, a new smother plant was developed by crossing a dwarf *B. campestris* with *B. campestris* spp. *perkinensis* (Haan et al. 1994). These dwarf *Brassica* lines when sown between the maize and soybean rows germinated well and smothered the weeds for 4–6 weeks and did not influence the crop development. Hence, newly bred smother crops are a realistic option for weed management in cropping systems. Crop interference with weeds is one of the primary non-chemical methods of weed control. Several major crop species have variability in traits that could be explored to develop varieties that interfere more with weeds (Callaway 1990; Shili-Touzi et al. 2010). This is the appropriate time for plant breeders and crop-weed ecologists to develop crop varieties with enhanced interference capabilities with weeds. Superior weed suppressing genotypes have been reported in oat (Fay and Duke 1977), rice (Dilday 1992; Xu et al. 2010), pearl millet (Narwal et al. 1992), and *Brassica* (Sarmah et al. 1992). Although insect and disease resistance has been incorporated into the crop varieties through crossing with wild types, only one such effort has been made to develop crops with higher allelopathic potential to smother the weeds, even though the character exists in the wild types. Rice is the only crop, in which breakthrough has been made to identify weeds smothering accessions and in the near future its transgenic lines with ability to control weeds may become available.

Studies show that rice could be a potential plant species for breeding as a smothering purpose. Dilday (1992) reported that 347 accessions for rice out of 16,134 from 99 countries showed allelopathic activity against five aquatic weeds viz., duck salad [(*Heteranthera limosa*) (sW) (Wild)], signal grass, redstem, flatsedge, and barnyard grass. Some of the accessions repelled weeds and maintained weed free area within a radius of 12–25 cm around their base. Since rice is planted in rows spacing of 15–20 cm, therefore, allelopathic activity would overlap the space between the rice plants or rows. Breeding for allelopathic traits has shown promise, the success has been achieved up to the third generation with continued research. Dilday et al. (1992) further reported that out of the tested accessions, 347, 161, and 6 accessions demonstrated allelopathic activity to duck salad, purple ammania, and broad leaf signal grass weeds, respectively. Some accessions from India and Bangladesh exhibited allelopathic activity against barnyard grass and *C. iria*. Fujii (1992) studied root exudates of 189 rice strains from the world over for the suppression effect on weeds in Plant Box method using lettuce as acceptor test spp.

Improved cultivars of *Japonica* rice showed little allelopathic activity, while native varieties of *Javanica* type and red rice strains showed strong inhibitory activity. Park (1996) evaluated 38 allelopathic rice germplasm against 8 weed spp. (barnyard grass, *Monchoria vaginalis, Persicaria hydropiper, Eleocharis kurguwai, B. tripartita, C. serotinus, Alopecurus equalis,* and *Leersia japonica*) for their control. Three accessions viz., 'Tona brea 439', 'CICA4', and 'Tong gan' provided 62–70 % weed control over the non-allelopathic variety 'Hwasungbyeo'. Wang and Olofsdotter (1996) studied the growth pattern of allelopathic and non-allelopathic varieties. The former had higher shoot: root ratio based on dry weight than in later ones. The allelopathic rice variety had higher root efficiency, either due to higher nutrient efficiency or allelochemicals released from their roots affect the nutrient availability. These studies indicated that there are no extraphysiological costs for allelopathic ability in the allelopathic cultivars.

10.4 Allelochemicals as Herbicides

Allelochemicals offer excellent potential as herbicides (Dayan et al. 2009; Bisio et al. 2011; Yan et al. 2011). First, they could be used directly as herbicides because these are free from all the problems associated with present herbicides. Second, their chemistry may be used to develop new herbicides. As traditional methods of discovering and developing new herbicides have become more difficult and expensive, the interest in natural products as sources of herbicide chemistry has increased. Besides, public awareness and demand for environmentally safer herbicides with less persistence, more specific targets and less potential for contaminating groundwater makes searches for new weed control strategies, using natural products more attractive. Plants and microorganisms produce hundreds of secondary compounds; many of these are phytotoxic and have potential as herbicides or as templates for new herbicide classes. It has been estimated that only about 3 % of possible 400,000 secondary metabolites from plant and microorganisms have been so far identified. Only a fraction of those identified have been evaluated for herbicidal or bioregulator activity (Einhellig and Leather 1988; Kaur et al. 2010).

10.5 Conclusions and Future Prospects

These studies have shown that allelopathic strategies including use of smothering crops could provide weed control, both in summer and winter crops. Although, these crops do not provide complete weed control but can manage weed population at economic threshold levels. This may either eliminate or minimize the use of present herbicides and thus overcome all the major problems associated with herbicides. These studies have shown the potential of weed control of summer and winter crops. The order of weed suppression in summer crops followed the order: pearl millet > maize > sorghum > cluster bean > cowpea and the order in winter crops was: berseem > oat > lentil > wheat. The studies with accessions of pearl millet and *Brassica* spp. (*B. juncea, B. napus, B. carinata*) exhibited greater variability in their weed smothering ability.

To provide satisfactory weed control in field crops using allelopathic strategies, we suggest research on the following aspects of crop interference:

(i) In the world about 500 domesticated plant spp. are grown as crops and these plants offer a great scope for selection of weed smothering spp.
(ii) In the promising crops, their varieties may be screened for smothering potential.
(iii) The genes responsible for production of smothering allelochemicals may be identified and possibly transferred to develop new transgenic varieties of same or other crops using techniques of biotechnology so that plants could produce their own herbicides.
(iv) Research may be directed to utilize microbial and fungal toxins to control weeds.
(v) New and cheaper synthetic analogues of natural products having greater selectivity, stability, and efficacy to control weeds may be developed.
(vi) The agronomical practices (sowing time, plant population, row spacing, crop geometry, crop mixture/intercropping) may be further improved to provide competitive edge to crops over weeds.
(vii) Crop rotations with allelopathic crops to control weeds may be developed.

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Chapter 11
Applied Allelopathy in Weed Management: An Update

J. R. Qasem

Abstract Allelopathic phenomenon perpetuating in nature is of considerable significance, which has gained even more importance these days. Field applications of allelopathy have attracted the attention of scientists as an alternate to weedicide use. In this chapter, allelopathy development and its application for weed management have been reviewed over the last two decades. Allelochemicals of potential herbicidal activity, developed bioherbicides from plants or microorganisms, plant species of allelopathic properties and the inflicted weeds, allelopathy forms, and methods of application have been documented. Some implications on allelopathic crops and their utilization in agricultural system, and positive and negative impact of allelopathy on cultivated crops and weeds have also been evaluated. Constraints associated with allelopathy application for weed management in the field, results obtained and conclusions drawn based on certain findings are discussed. Prospects of allelopathy as a possible strategy for weed management, for development of eco-friendly bioherbicides, and its importance for sustainable agriculture are also discussed. Some recent findings on molecular aspects of allelopathic species and the genetic basis of produced allelochemicals have been described.

Keywords Allelopathy • Field application • Weed management • Bioherbicides • Allelochemicals • Allelopathic crops • Weeds • Allelopathy formulations in the field

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11.1 Introduction

Allelopathy as a natural mechanism and new tool for pest management in the field has been more developed in the last 2–3 decades than its entire previous history (Willis 1996, 1997, 2004). A large number of publications is available; hundreds are yearly accumulating on different aspects of the subject, and published in a range of journals worldwide (Carral-Vilarifio 2002; Qasem 2007). A multidisciplinary allelopathy subject has been revealed in recent years and resulted in the discovery of a large number of allelochemicals that possess pesticidal properties and formulations of more are now being commercialized in world markets as alternatives to a number of synthetic pesticides. Many reference books were published, and several world congresses, national meetings, workshops, and symposia were held on the subject across the globe (Qasem 2010).

The last two decades have witnessed the birth of International Allelopathy Society (IAS) and the establishment of many new allelopathy societies/chapters worldwide. During the same period, many isolated and identified allelochemicals were biologically studied on plants and at the molecular level. These have been already tested against different agricultural pests and some proved potent, with no phytotoxicity (Rizvi 1994). These allelochemicals are known now to the industry and potentially considered as chemicals of the future pest control strategy with no adverse effects on environment.

Application of allelopathy under field conditions for pest management (including weeds) is another important development on the subject. New methods, techniques, and advance technologies are now employed for better pest control and for isolation of allelopathy from other mechanisms of plants interference in nature. However, significant achievement and the breakthrough in allelopathy research would be the development of genetically engineered allelopathic and self-defense crops that can avoid agricultural problems or pest hazards. This, however, remains the future task of researchers in this field of science by which allelopathy would be highly recognized.

The present chapter highlights recent developments on the role of allelopathy in weed management under field conditions, and its possible implementation or integration for more successful weed management programs. Crops or other plant species of allelopathic effects, inflicted weeds, and the treated crops have been reviewed. In addition, allelochemicals reported as potentially effective and important for herbicides industry have been tabulated. Updated research results, on applied allelopathy for weed management in different crops, would greatly help weed researchers as well as farmers in planning effective weed control programs for better crop production.

11.2 Bioherbicides of Plants/Microorganisms Origin and Allelopathic Chemicals of Potential use as Herbicides

Out of the 7,50,000 existing plant species only 5–15 % have been screened for biologically active compounds, and from the total 4,00,000 estimated secondary metabolites in plants, only 10,000 have been characterized. While almost all allelochemicals exist in plants in nontoxic, conjugated forms (Putnam 1988), chemicals of pesticide properties identified from 2,121 plant species belong to more than 30 plant families (Grainge and Ahmed 1988; Dhawan and Dhaliwal 1994). The main role of allelochemicals in plants is defensive, which is important and attractive for pesticide industry (Varma and Dubey 2006). However, allelochemicals are believed to affect plant germination, growth, densities and distribution, but only few were found active enough to be developed as commercial herbicides, including Callisto, Triketones, and Glufosinate (based on a natural product Bialaphos from phosphinothricin in plants), naphthalenediones (SeaKlean), and Neem (*Azadirachta indica*) that alone has more than 200 formulations in the world market. Natural products with herbicidal properties are believed to be less in number than for other pesticides (Pachlatko 1998), and generally less active than synthetic herbicides, although some are produced in relatively higher quantities (BIBOA and as much as 14 kg ha^{-1}). However, recent studies reported a large number of allelochemicals from microbes or plants of potential use as herbicides (Table 11.1), and have provided structural models for herbicides industry (Duke and Abbas 1995; Duke et al. 1996, 1997, 1998, 2000; Duke 2002; Belz 2007; Macias et al. 2007). Some work on the mode of action of these allelochemicals (Duke et al. 2005), and on their genetic basis has been reported.

11.3 Plants of Herbicidal Activities

Recommended allelopathic plant species for weed management in different crops and those for general weed control are shown in Table 11.2. A total of 111 species were reported to exert allelopathic effect under field conditions, used in 43 crops and in 11 uncultivated sites for general weed control. Target weeds were 78 species among which are many noxious species. The most frequently reported allelopathic species, inflicted weeds, and treated crops are summarized in Table 11.3.

Most literature is concentrated on certain allelopathic crops important for weed management including: cereals (*Avena* spp.*, Digitaria sanguinalis, Festuca* spp., *Hordeum vulgare*, *Imperata cylindrica, Lolium* spp., *Oryza sativa*, *Sorghum* spp., *Triticum aestivum*, and *Zea mays*), certain legumes (*Glycine max, Medicago* spp., *Vicia* spp. including *Vicia villosa*, and *Trifolium* spp.), and certain crucifer species (Oleszek et al. 1994). Genetic variations among cultivars of different crop species

Table 11.1 Natural herbicides and allelochemicals of potential use as herbicides and their origin

Natural chemical/bioherbicide name	Origin	Reference
1,8-Cineole	Plants	Duke and Abbas (1995)
2,5-anhydro-D-glucitol	Microorganisms (*Fusarium solani*)	Duke (2002)
AAL-toxin	Microorganisms (*Alternaria alternata*)	Abbas et al. (1995); Duke and Abbas (1995)
Agrostemin	Plants (*Agrostemma githago*)	Chou (2010)
Alaphos	Microorganisms	Putnam (1983)
Alectrol	Plants (*Vigna unguiculata*)	Qasem (2006)
Anisomycin	Microorganisms (*Streptomyces griseolus*)	Prakash and Pahwa (1994)
Acetic acid (organically produced)	Plants	Duke and Dayan (2009)
Australifungin	Microorganisms (*Sporormiella australis*)	Abbas et al. (1998)
Benzanin (based on Benzoxazinones)	Plants	Prakash and Pahwa (1994), Villagrasa et al. (2009)
Bialaphos (degraded to phosphinothericin in plants)	Microorganisms (*Streptomyces hygroscopicus*, *Streptomyces vividochromogenes*)	Putnam (1983); Prakash and Pahwa (1994); Duke and Abbas (1995); Duke et al. (2000)
Botcinol A	Microorganisms (*Botrytis cinerea*)	Chaudhari et al. (1994)
Botcinolide	Microorganisms (*Botrytis cinerea*)	Chaudhari et al. (1994)
Callisto	Plants (*Callistemon citrinus*)	An and Pratley (2005)
Catechin	Macrophyte (*Myriophyllum spicatum*)	Macias et al. (2007)
Cinmethylin (Cineole analog)	Plants	Prakash and Pahwa (1994); Duke et al. (2000); Varma and Dubey (2006)
Coaristeromycin	Microorganisms (Actinomycetes)	Cutler (1999)
Coformycin	Microorganisms	Cutler (1999)
Colletotrichin	Fungi (*Colletotrichum* spp.)	Duke et al. (1992)
Corn gluten meal (MGM)	Plants (*Zea mays*)	Christians (1995)
Coumarins	Plants (*Helianthus annuus*)	Macias et al. (1994)
Cyanamide	Plants (*Vicia villosa*, *Vicia cracca*, *Robinia pseudoacacia*)	Fujii et al. (2008)

(continued)

Table 11.1 (continued)

Natural chemical/bioherbicide name	Origin	Reference
Cyanobacterin	Microorganisms	Sobokta (1997)
Cytochalasins	Microorganisms and Plants	Prakash and Pahwa (1994)
DIBOA	Plants (*Triticum aestivum*)	Macias et al. (2005)
Dihydro prehelminthosporal	Microorganisms (*Bipolaris* sp.)	Varma and Dubey (2006)
DIMBOA	Plants (Cereals)	Kluge et al. (1995)
Dihydro-5,6-dehydrokawain (DDK)	Plants	Khanh et al. (2007)
Dimethyl phosphorothioate	Plants	Khanh et al. (2007)
Diterpene lactones (e.g. Artemisinin, Chaparrinon)	Plants	Dayan et al. (1999a, b)
Essential oils (carvacrol, linalool)	Plants (*Zataria multiflora*)	Saharkhiz et al. (2010)
Flavonoids	Plants (*Helianthus annuus*)	Macias et al. (1994)
Fumonisins	Microorganisms (*Fusarium moniliforme*)	Abbas et al. (1995)
Gallic acid	Plants	Prakash and Pahwa (1994)
Glucosinolates	Plants (*Rorippa sylvestris* and *Rorippa indica*)	Yamane et al. (1992a, b)
Glyphosinate (Phosphinothricin based)	Microorganisms (*Streptomyces* spp.)	Duke and Abbas (1995); Duke (2002)
Gostantin	Microorganisms	Sobokta (1997)
Heliannuol	Plants (*Helianthus annuus*)	Macias et al. (1994)
Herbicidins	Microorganisms (*Streptomyces saganonensis* No. 4075)	Prakash and Pahwa (1994), Cutler (1999)
Herboxidiene	Microorganisms	Sobokta (1997)
Homoalanosine	Microorganisms	Sobokta (1997)
Hydantocidin	Microorganisms (*Streptomyces hygroscopicus* SANK 63584)	Sobokta (1997); Hoagland and Cutler (1998)
Hypericin	Plants	Duke et al. (1996); Tellez et al. (1999)
Isoxazole-4-carboxylic acid	Microorganisms	Sobokta (1997)
Kerlinic acid	Plants (*Salvia beerlii*)	Gonzalez-Ibarra et al. (2002)
Koninginins A,B,C	Microorganisms (*Trichoderma koningli*)	Cutler and Parker (1994)

(continued)

Table 11.1 (continued)

Natural chemical/bioherbicide name	Origin	Reference
Leptospermone	Plants (*Callistemon citrinus*)	Mitchell et al. (2001)
Lignas	Plants (*Helianthus annuus*)	Macias et al. (1994)
Maize gluten	Plants (*Zea mays*)	Duke and Dayan (2009)
Malinoformin	–	Prakash and Pahwa (1994)
Margosan-O	Plants (*Azadirachta indica*)	Dhawan and Dhaliwal (1994)
Myrigalone A (3-(1-oxo-3-phenylpropyl)-1,1,5-trimethylcyclo-hexane-2,4,6-trione)	Plants (*Myrica gale*)	Popovici et al. (2011)
Mesotrione (modified structure of leptospermone)	Plants (*Callistemon citrinus*)	Mitchell et al. (2001)
Methoxyphenone (anisomycin based)	Plants	Prakash and Pahwa (1994)
Momilactone B	Plants (*Oryza sativa*)	Kato-Noguchi (2011)
Monesin	Microorganisms (*Streptomyces cinnamonensis*)	Hoagland and Cutler (1998)
Monoterpenes (citronellol, citronellal, linalool)	Plants	Singh (2004)
Naphthalendiones (SeaKlean, Vitamin K)	–	Cutler and Cutler (2002)
Neem (*Melia azedarach*) products	Plants (*Melia azedarach*)	Chou (2010)
Nigericin	Microorganisms (*Streptomyces hygroscopicus*)	Hoagland and Cutler (1998)
Orobanchol	Plants (*Trifolium pretense*)	Cited by Qasem (2006)
Parasorbic acid	Plants (Mountain ash, *Sorbus Americana*)	Putnam (1983)
Patulin	Microorganisms (Fungi including *Penicillium urticae*)	Putnam (1983)
Pelargonic acid-based products	Plants (*Pelargonium* sp.)	Duke and Dayan (2009)
Phenanthrenoids	*Juncus effuses*	DellaGreca et al. (2002)
Phosalacine	Microorganisms	Sobokta (1997)
Phosphinothricin (PPT) (Glufosinate)	Microorganisms (*Streptomyces viridochromogenes*)	Hoagland and Cutler (1998)

(continued)

Table 11.1 (continued)

Natural chemical/bioherbicide name	Origin	Reference
Phytobabine-2	–	Orel (1994)
phytobaphum	–	Orel (1994)
Phytopacine	–	Orel (1994)
Phytosphingosine	Microorganisms (fungi) and Plants	Abbas et al. (1995)
Prehelminthosporal	Microorganisms (*Bipolaris* sp.)	Varma and Dubey (2006)
Prohydrojasmon	Plants	Zuo et al. (2010)
Pseudoonic derivatives	Microorganisms (*Pseudomonas fluorescence*)	Sobokta (1997)
Pyridazocidin	Microorganisms (*Streptomyces species*)	Hoagland and Cutler (1998)
Quassinoids	Plants (Simaroubaceae)	Lin et al. (1995)
Rotenone	Plants	Putnam (1983)
Salannin	Plants (*Azadirachta indica*)	Dhaliwal and Arora (1994)
Sesquiterpenes	Plants (*Helianthus annuus*)	Macias et al. (1994); Dayan et al. (1999a, b)
Sorgeolon	*Sorghum* spp.	Nimbal and Weston. (1996); Hoagland and Cutler (1998); Rimando et al. (1998); Duke et al. (2002)
Sphingoid		Abbas and Boyette (1993)
Strigol	*Sorghum* spp.	Rimando et al. (1998)
Tentoxin	Microorganisms	Duke and Abbas (1995); Sobokta (1997)
Trialphos	Microorganisms	Sobokta (1997)
TRIBOA	Plants (Cereals)	Kluge et al. (1995)
Triketones herbicides	Plants (*Callistemon citrinus*, *Callistemon* spp.)	Lee et al. (1997); Duke et al. (2000); Mitchell et al. (2001); Duke (2002)
Triterpenes	Plants (*Helianthus annuus*)	Macias et al. (1994)
Usnic acid	Lichen (*Usnea* sp.)	Duke et al. (2002)
Zea maysexistin	Microorganisms (*Pacecilomyces variokii*)	Duke and Abbas (1995); Hoagland and Cutler (1998); Duke et al. (2000)
Ziniol	–	Prakash and Pahwa (1994)

Table 11.2 Plant species of herbicidal activity, target weed species, form used and rate of application under field conditions

Donor species	Crop/application place	Receiver weed species	Form used and rate of application	Effect/ % control	Reference
Acer rubrum	–	*Desmodium toruoston*	Woodchips mulch	–	Rathinasabapathi et al. (2005)
Acorus tatarinowii	–	Algae	Mixed growth Leachates	Chlorophyll destruction	Kong (2005)
Ageratum conyzoides	Citrus orchards	Weeds	Cover crop Intercropping	–	Kong et al. (2004); Kong (2005)
Ailanthus altissima	*Phaseolus vulgaris*	Weeds	Extract 99 kg/ha	40 %	Heisey and Heisey (2003)
Alchemilla mollis	Roadside	Roadside weeds	Groundcover	Nearly complete	Weston et al. (2005)
Amaranthus spinosus	*Oryza sativa*	Weeds	Residue in the soil at 0.5 kg/m^2	Lowered weed infestation	Gaffar et al. (1998)
Apium graveolens	*Allium porrum*	Weeds including *Senecio vulgaris*	Intercropping	58 % in biomass 98 % seedling emergence	Baumann et al. (2000)
Artemisia annua (source of Artemisinin)	*Triticum aestivum*	*Amaranthus retroflexus* *Chenopodium album*	Extract	66 % weed emergence and 80 % biomass	Delabays and Mermillod (1999)
Avena sativa		*Picris echioides*	Extract, flavonoid, residue	Reduced weed number by 94 %	Bertoldi et al. (2009)
Asparagus officinalis	–	Weeds	Cover crop or Living mulch	–	Weston (1996)
Azadirachta indica A. Juss	–	*Desmodium toruoston*	Woodchips mulch	Suppression	Rathinasabapathi et al. (2005)
Bidens pilosa	*Oryza sativa*	*Commelina diffusa* *Jussiaea decurrens* *Rotala indica*	Shoot residue at 2 t ha^{-1}	80 % reduction in weed density and weed dry weight and increased yield by 20 %	Rathinasabapathi et al. (2005)

(continued)

Table 11.2 (continued)

Donor species	Crop/application place	Receiver weed species	Form used and rate of application	Effect/ % control	Reference
Brassica (accessions) *B. Juncea* *B. nigra*	–	*Avena ludoviciana* *Cirsium arvense* *Chenopodium album* *Melilotus album* *Phalaris minor* *Rumex retroflexus*	–	75–98 % 80 %	(Narwal et al. 2002a); Ercoli et al. (2005)
Brassica crops	–	Small seeded weeds	Green manure	Suppression	Al-Khatib and Boydston (1999)
Brassica juncea cv. Jyti and *Carum carvi*	Stored potato tubers	sprouting	Essential oils mixture	31 %	Hannukkala et al. (1996)
Brassica nigra	–	Weeds	Cover crop or living mulch	Suppression	Weston (1996); Gavazzi and Paris (2000)
Brassica rapa (L.) var. *rapa* spp. *oleifera*	–	Weeds	mulch	Strong suppression	Peterson et al. (1999)
Brassica spp.	–	Weeds	Cover green crop	Strong suppression	Peterson et al. (1999)
Brassica spp. (*juncea, carinata, napus*)	Accessions	Weeds	Accessions volatiles	45-77 % population	Yadava et al. (1994)
Cajanus cajan	–	*Cyperus rotundus*	Residue	Effective	Hiremath and Hunshal (1998)
Cajanus cajan line I-58	*Lycopersicon esculentum*	Weeds	Residue	Effective	Semidey and Medina (1996)
Canavalia ensiformis	–	*Amaranthus hypochondriacus* *Echinochloa crusgalli*	Dried leaves	Effective	Torres-Barragan et al. (1996)
Canavalia ensiformis	*Zea mays*	Weeds	Living cover crop Dead mulch	68 %	Caamal-Maldonado et al. (2001)
Cannvalia ensiformis	–	Weeds	Cover crop	Smothering	Fujii (2001)
Carum carv	Stored potato tubers	sprouting	Essential oil	92 %	Hannukkala et al. (1996)

(continued)

Table 11.2 (continued)

Donor species	Crop/application place	Receiver weed species	Form used and rate of application	Effect/ % control	Reference
Carvone (*Carum carvi*)	Potato sprout inhibitor	Potato sprout inhibitor and against rotting	Talent formulation	Effective	Varma and Dubey (2006)
Cassia spp. (*siamea*)	Sustainable agriculture	Weeds	Mulch	Biomass and Density	Kamara et al. (1997); Narwal et al. (2001)
Chromolaena odorata	*Morus rubra*	Weeds, *Lathyrus sativus*	Mulching 1.5-3 kg/m^2	High leaf yield	Premasthira et al. (2002)
Croton laciferus	*Oryza sativa*	*Echinochloa crus-galli* *Leptochloa chinensis*	Green manure 14 t/ha	40 and 60 % reduction in germination 30 and 50 % in biomass	Abeysekera et al. (2002)
Cucurbita pepo	*Zea mays*	Weeds *Amaranthus retroflexus* *Convolvulus arvensis*	Dense stand Intercropping	Suppression	Fujiyoshi (1998) Fujiyoshi et al. (2007)
Cynodon dactylon	–	*Cuscuta* spp.	Extract	Effective	Hiremath and Hunshal (1998)
Cyperus alternifolius	–	*Microcystis aeruginosa*	Fragments Extracts	Growth inhibition	Kusumoto et al. (2002)
Cyperus rotundus	*Oryza sativa*	Weeds	Residue in the soil at 0.5 kg/m^2	Lowered weed infestation	Gaffar et al. (1998)
Deguelia rufescens var. urucu		*Mimosa pudica*	Natural chemical (3,5-dimethoxy-4'-O-prenyl-trans-stilbene)		Lobo et al. (2010)
Digitaria sanguinalis	*Vitis vinifera*	*Amaranthus retroflexus*	Cover crop	25 %	Dharmaraj and Sheriff (1994)
Dolicos lablab	–	Weeds	Cover crop	Smothering	Fujii (2001)

(continued)

Table 11.2 (continued)

Donor species	Crop/application place	Receiver weed species	Form used and rate of application	Effect/ % control	Reference
Echinochloa colonum	*Oryza sativa*	Weeds	Residue in the soil at 0.75 kg/m^2	Lowered weed infestation	Gaffar et al. (1998)
Eichhornia crassipes	*Microcystis aeruginosa*	*Microcystis aeruginosa*	Fragments Extracts	Growth inhibition	Kusumoto et al. (2002)
Eichhornis crassipes	–	*Chlamydomonas reinhardii*	Root exudates	Effective	Wu and Yu (1996)
Eriogonum cinereum	–	Dicotyledonous weeds	Mulches	Effective	Gavazzi and Paris (2000)
Eucalyptus sp.	*Cicer arietinum*	Weeds	Leaf powder 50 kg/ha	70 % in population	Mukhopadhyay and Monda (1998)
Euphorbia prostrate	–	*Cynodon dactylon*		–	Hiremath and Hunshal (1998)
Fagopyrum esculentum	–	*Agropyron repens* *Capsella bursa pastoris* *Thlaspi arvense*	Suppression	94 %	Golisz et al. (2002) Golisz et al. (2008)
Festuca arundinaceae	–	Dicotyledonous weeds	Mulches	Effective	Gavazzi and Paris (2000)
Festuca arundinasae	–	Weeds	Cover crop or Living mulch	Strong suppression	Weston (1996)
Festuca spp. (*rubra, arundinoca*)	–	Dicotyledonous weeds and *Digitaria sanguinalis*	Mulches, cultivars root exudates	Strong suppression	Gavazzi and Paris (2000) Bertin and Weston (2002);
Gliricidia sepium	–	Weeds	Mulch	Biomass and Density	Kamara et al. (1997)
Glycine max	Sustainable agriculture	Weeds	–	–	Narwal et al. (2001)
Gossypium hirsutum and *Arachis hypogea*	*Capsicum annuum*	–	Intercropping	Weed density by 92.3 %	
Helianthus annuus	*Gossypium hirsutum*	*Cyperus rotundus*	Extract + low rate of glyphosate	Density reduction by 59–99 %	Narwal et al. (2001)

(continued)

Table 11.2 (continued)

Donor species	Crop/application place	Receiver weed species	Form used and rate of application	Effect/ % control	Reference
Helianthus annuus	*Helianthus annuus* varieties	*Parthenium hysterophorus* *Trianthema portulacastrum*	Root leachates	75–96 % 56–84 %	Dharmaraj and Sheriff (1994)
Helianthus annuus	*Triticum aestivum*	Weeds	Cover crop, Mulch	Significant reduction in population	Gawronski et al. (2002); Gawtonski (2004)
Helianthus annuus	–	*Trianthema portulacastrum*	Cover crop	94 % population 96 % biomass	Dharmaraj et al. (1994)
Helianthus annuus/ Legumes (*Pisum arvense, Pisum sativum, Vicia sativa*) mixture	*Triticum aestivum* organic farming	Weeds (mustard)	Mulch	Management	Bernat et al. (2004); Gawtonski (2004)
Heracleum laciniatum	Sustainable agriculture	Weeds	–	–	Narwal et al. (2001)
Hordeum vulgare	Catfish bonds	Cyanobacteria	Decomposed straw		Wills et al. (1999)
Hordeum vulgare and accessions	–	*Avena ludoviciana, Cirsium arvense, Chenopodium album* *Melilotus album* *Phalaris minor* *Rumex retroflexus* *Setaria glauca* *Sinapis arvensis* *Solanum ptycanthum* *Stellaria media*	Cover crop Accessions, Foliage leachates Residues Rotation	Suppression 70–100 %	Creamer et al. (1996); (Narwal et al. 2002b); Kremer and Ben-Hammouda (2009)
Hyptis suaveolens	*Ulex europaeus*	Weeds	Mulching 1.5–3 kg/m2	High leaf yield	Premasthira et al. (2002)

(continued)

Table 11.2 (continued)

Donor species	Crop/application place	Receiver weed species	Form used and rate of application	Effect/ % control	Reference
Imperata cylindrica	*Oryza sativa*	Weeds *Parthenium hysterophorus*	Residue in the soil at 1 kg/m^2 Extract 10 %	Lowered weed infestation	Gaffar et al. (1998); Anjum et al. (2005)
Imperata cylindrica.	*Medicago sativa.*	*Cuscuta campestris*	Extract Extract + gas oil + 10 % engine oil	High killing	Al-Juboory and Al-Mohamadi (2006)
Ipomoea patatis	–	*Cyperus esculentus*		Reduced tuber viability	Miles (1994)
Ipomoea tricolor	*Saccharum officinarum*	Weeds	Cover crop residue	–	Anaya and Jimenez-Osornio (1999)
Juniperus silisicola	–	*Desmodium toruoston*	Woodchips mulch	–	Rathinasabapathi et al. (2005)
Kasarwala mundara	–	–	Residue	98 %	Jung et al. (2004)
Lavendula angustifolia	Stored potato tubers	sprouting	Essential oils mixture	73 %	Hannukkala et al. (1996)
Leucaena leucocephala	*Vitis vinifera* Sustainable agriculture *Zea mays*	Weeds	Residue, Living cover crop Dead mulch	68 %	Anaya and Jimenez-Osornio (1999); Caamal-Maldonado et al. (2001); Narwal et al. (2001)
Linum usitatisimum	*Lathyrus sativa* *Lens culinaris* *Oryza sativa*	*Melilotus* spp. *Vicia* sp.	Relay crop Rotation	87 %	Das and Das (1998)
Lolium spp. (*perenne*)	Pasture *Lactuca sativa*	*Calystegia sepium* Dicotyledonous weeds	Dead and Living mulches	Suppression	Wu et al. (1996); Gavazzi and Paris (2000)

(continued)

Table 11.2 (continued)

Donor species	Crop/application place	Receiver weed species	Form used and rate of application	Effect/ % control	Reference
Lysilema latisiliquum	*Zea mays* *Vitis vinifera*	Weeds	Living cover crop Residue or dead mulch	68 %	Anaya and Jimenez-Osornio (1999); Caamal-Maldonado et al. (2001)
Magnolia grandiflora	–	*Desmodium toruoston*	Woodchips mulch		Rathinasabapathi et al. (2005)
Mangifera indica	*Rosa* spp.	Different weeds	Leaf mulch 15 kg/ 25 m^2	80 %	Challa and Ravindra (1998)
Medicago sativa	–	Weeds *Cyperus rotundus*	Cover crop or Living mulch, Root exudation Root layer	71–78 %	Suzuki and Yoshida (1996); Weston (1996)
Medicago sativa (cv. WL605)	*Lactuca sativa*, *Brassica oleracea* var. *italica*, and *Lycopersicon esculentum*	Weeds	Residue as a soil cover	–	Stirzaker and Bunn (1996)
Menthe piperita	Stored potato tubers	sprouting	Essential oil	96 %	Hannukkala et al. (1996)
Mucuna spp.(*daeringiana*, *deeringiana*, *deeringianum*, *pruiens*, *pruriens* (var.*ana* and *utilis*)	*Glycine max* Orchards Smothring and food resource Sustainable agriculture *Vitis vinifera* *Zea mays*	Weeds *Imperata cylindrica* *Portulaca oleracea*	Living cover crop Dead mulch Extract	68 % Suppression	Anaya and Jimenez-Osornio (1999); Kim et al. (1999a); Udensi et al. (1999); Caamal-Maldonado et al. (2001); Fujii (2001); Narwal et al. (2001)

(continued)

Table 11.2 (continued)

Donor species	Crop/application place	Receiver weed species	Form used and rate of application	Effect/ % control	Reference
Myrathecium verrucaria (with surfactant SilWet-L-77)	–	*Pueraria lobata*	Bioherbicide (Fungus)	90–100 %	Hoagland et al. (2005)
Nepeta x Faassennii	–	Roadside weeds	Groundcover	Nearly complete	Weston et al. (2005)
Oryza sativa and rice germplasm (PI 312777, XL8, 4593, Damagung)	Different Crops Germplasm *Hordeum vulgare* *Ipomoea patatis* *Triticum aestivum* *Zingiber officinale*	*Alopecurus aequalis* *Ammannia coccinea* *Bidens tripartite* *Cyperus difformis* *Cyperus iria* *Cyperus serotinus* *Dinebra retroflexa* *Echinochloa crusgalli* *Eleocharis kuroguwai* *Heteranthera limosa* *Leersia japonica* *Leptochloa fascicularis* *Monochoria vaginalis* *Persicaria hydropiper* *Phalais minor* *Portulacastrum* sp. *Trianthema portulacastrum* Weeds	Living and Dead mulch Cultivars Extract exposure Accessions (TONO BERA 439, CICA4, TANG GAN, PI 312777)	Weed suppression Suppressing cultivars 37–97 %	YongQing and QingHua (1995); Park (1996); Kim et al. (1999b); Olfosditter et al. (1999); Okuno et al. (1999); Fujihara and Yoshida (1999); Lovelace et al. (2001); Hassan et al. (2002); Gealy et al. (2003); Ahn et al. (2005); Inderjit and Kaushik (2005); Kong (2005); Hu et al. (2008).
Oryza longistaminata	*Oryza* spp.	*Echinochloa crusgalli*	Accessions suppression	62 % weed growth suppression	Zhang et al. (2008)

(continued)

Table 11.2 (continued)

Donor species	Crop/application place	Receiver weed species	Form used and rate of application	Effect/ % control	Reference
Pachyrhizus erosus	–	Weeds	Cover crop	Smothering	Fujii (2001)
Passiflora incarnata	*Oryza sativa*	Different weed species	Shoot residues at 1.5 t ha^{-1} at 2 days after transplanting	Reduction in weed density and dry weight by 75 %	Khanh et al. (2008)
Passiflora edulis	*Oryza sativa*	Different weed species	Shoot residues at 1–2 t ha^{-1} at 2 days after transplanting	Reduction in weed dry weight by 40–73 %	Khanh et al. (2008)
Pennisetum glaucum	*Oryza sativa/ Triticum aestivum* and Varieties	Weeds *Parthenium hysterophorus* *Trianthema portulacastrum*	Rotation	Smothering 31–63 %	(Narwal et al. 2004a)
Phragmites communis	*Medicago sativa*	*Cuscuta campestris* *Microcystis aeruginosa*	Different parts extract Extract + gas oil + 10 % engine oil	Growth inhibition High killing	Kong (2005); Al-Juboory and Al-Mohamadi (2006)
Pinus resinosa	*Panax quinquefolius*	Weeds	Bark mulch	Suppression	Reeleder et al. (2004)
Pinus strobes	*Panax quinquefolius*	*Parthenium hysterophorus*	Bark mulch	Suppression	Reeleder et al. (2004)
Pisum sativum and cultivars	*Lycopersicon esculentum* *Capsicum* sp.	Weeds *Amaranthus dubius* *Cyperus rotundus* *Echinochloa colona* *Trianthema portulacastrum*	*Galinsoga*, killed cover crop Plant stubble Soil incorporation	Reduced density	Semidey and Bosques-Vega (1999); Akemo and Bennet (2000)
Polygonum aviculare	–	*Cynodon dactylon*	–	–	Hiremath and Hunshal (1998)
Pseudomonas isolates	*Triticum aestivum*	*Bromus tectorum*	Metabolites	50 %	Mallik and Williams (2005)

(continued)

Table 11.2 (continued)

Donor species	Crop/application place	Receiver weed species	Form used and rate of application	Effect/ % control	Reference
Pseudomonas isolates	*Hordeum vulgare*	*Phleum pratense* *Trifolium pratense*	Metabolites	Suppression	Mallik and Williams (2005)
Quercus mechausii	–	*Desmodium toruoston*	Woodchips mulch	–	Rathinasabapathi et al. (2005)
Ranunculus bulbosus	*Glycine max*	Weeds	Residue		Gander (1998)
Secale cereale	*Brassica oleracea var. Capitata* *Different crops* *Glycine max* *Helianthus annuus* *Lycopersicon esculentum* *Nicotiana tabacum* *Solanum tuberosum* *Sorghum bicolor* *Zea mays*	*Amaranthus retroflexus* *Amaranthus* spp. Boadleaf weeds *Capsella bursa-pastoris* *Cassia abtusifolia* *Chenopodium album* *Echinochloa crus-galli* *Galinsoga parviflora* *Galinsoga quadriradiata* *Ipomoea* spp. *Portulaca oleracea* *Setaria glauca* *Sida spinosa* *Solanum plycanthum* *Urtica urens* *Xanthium strumarium*	Cover crop 189 kg seeds/ha Intercropping Rotation Residue mulch	Suppression 49–100 %	Creamer et al. (1996); Smeda and Weller (1996); Weston (1996); Worsham et al. (1999); Akemo and Bennet (2000); Borowy and Jelonkiewicz (2000); Gavazzi and Paris (2000); Nagabhushana et al. (2001); Samedani et al. (2002); Ercoli et al. (2005); Uchino et al. (2005)
Sinapis alba	*Pisum sativum*	Annual weeds *Setaria viridis*	Seed meal Killed plants cover Soil residue incorporation	Reduced germination	Jaakkola (2002); Weidenhamer et al. (2005)

(continued)

Table 11.2 (continued)

Donor species	Crop/application place	Receiver weed species	Form used and rate of application	Effect/ % control	Reference
Solidago sphacelata	–	Roadside weeds	Groundcover	Nearly complete	Weston et al. (2005)
Sorghum bicolor genotypes (Giza 115, Giza 15, Enkath, JS.263)	Deciduous trees *Glycine max* *Gossypium hirsutum* *Hordeum vulgare* Orchards *Oryza sativa* *Oryza sativa*/*Triticum aestivum* rotation *Triticum aestivum* *Zea mays*	*Alternanthera tenella* *Avena fatua* *Chenopodium album* *Cyperus rotundus* *Echinochloa crus-galli* *Ipomoea grandifolia* *Lolium temulentum* *Parthenium hysterophorus* *Phalaris minor* *Rumex dentatus* *Sinapis arvensis* *Trianthema portulacastrum* Weeds	Cover crop Extract Rotation, Residue 0.5–8.5 t/ha Sorgaab Smothr crop Companion crop Mixing crop Varieties	Density 67 % Smothering 13–80 %	Weston (1996); Sene et al. (1999); Cheema and Khaliq (2000); Gavazzi and Paris (2000); Narwal (2000); Cheema and Khaliq (2002); Correia et al. (2002); (Narwal et al. 2004b); Irshad and Cheema (2004); Alsaadawi et al. (2005); Cheema et al. (2005); Urbano et al. (2006); Alsaadawi and Dayan (2009)
Sorghum bicolor x *Sorghum sudanense*	Nurseries	Weeds	Mulch	–	Gavazzi and Paris (2000)
Sorghum bicolor	*Gossypium hirsutum*	*Cyperus rotundus*	Extract + low rate of glyphosate	Density reduction by 59–99 %	Iqbal and Cheema (2007)
Sorghum bicolor + *Helianthus annuus* + *Brassica campestris* + *Oryza sativa*	*Brassica napus*	*Trianthema portulacastrum*, *Cyperus rotundus*, *Chenopodium album*, *Coronopus didymus*	water extracts at 15 L ha^{-1} tank mixed	Density and growth reduction	Jabran et al. (2010)

(continued)

Table 11.2 (continued)

Donor species	Crop/application place	Receiver weed species	Form used and rate of application	Effect/ % control	Reference
Sorghum halepense	*Medicago sativa*	*Cuscuta campestris* Yunk.	Extract Extract + gas oil + 10 % engine oil	High killing	Al-Juboory and Al-Mohamadi (2006)
Sorghum hybrids	–	Dicotyledonous weeds	Mulches	–	Gavazzi and Paris (2000)
Sorghum sudanense	*Hordeum vulgare*	*Sinapis arvensis*	Cover crop	–	Urbano et al. (2006)
Stizolobium pruriens	–	*Amaranthus hypochondriacus* *Echinochloa crus-galli*	Dried leaves	–	Torres-Barragan et al. (1996)
Trichoderma virens/ *Secale cereale*	Vegetables	Weeds	Cover crop	Suppression	Heraux et al. (2005)
Trifolium incarnatum	Sustainable agriculture	Weeds *Solanum plycanthum*	Cover crop	Suppression	Creamer et al. (1996); Narwal et al. (2001)
Trifolium pretense	*Brassica juncea* *Linum usitatisimum* *Pisum sativum* *Zea mays*	Dicotyledonous weeds *Brassica kaber*	Green manure Residue mulch	Reduced density and competitiveness 88–91 %	Gavazzi and Paris (2000); Blackshaw et al. (2001); Conklin et al. (2002)
Trifolium subterranean	Sustainable agriculture	Weeds	–	–	Narwal et al. (2001)

(continued)

Table 11.2 (continued)

Donor species	Crop/application place	Receiver weed species	Form used and rate of application	Effect/ % control	Reference
Triticum aesivum and accessions	Fields and orchards No-till system Orchards *Oryza sativa* *Triticum aestivum* *Zea mays*	*Amaranthus retroflexus* *Ammania coccinea* *Avena ludoviciana* *Chenopodium album* *Cirsium arvense* *Cyperus esculentus* *Digitaria ciliaris* *Echinochloa crus-galli* *Heteranthera limosa* *Imperata cylindrica* *Ipomoea hederace.* *Melilotus album* *Phalaris minor* *Rumex retroflexus* *Sida spinosa* *Stellaria media* Weeds	accessions Cover crop Extract Rotation Straw mulch 6 t ha^{-1}	Excellent control Reduced infestation 87–96 % density 78–100 % 100 % control	YongQing and QingHua (1995); Pereira et al. (1996); Weston (1996); Jordan et al. (1999); Li-Xiang et al. (2000); Blum et al. (2002); Narwal et al. (2002c); Ni and Zhang (2005); Kong (2005); Li et al. (2005)
Ulex europaeus	–	Dicotyledonous weeds	Mulches	–	Gavazzi and Paris (2000)

(continued)

Table 11.2 (continued)

Donor species	Crop/application place	Receiver weed species	Form used and rate of application	Effect/ % control	Reference
Vicia villosa	Crops in general, *Glycine max* *Ipomoea patatis* *Lycopersicon esculentum* Orchards *Oryza sativa* *Solanum tuberosum* Sustainable agriculture Vegetables landscape and abandoned fields *Zea mays* *Zingiber officinale*	*Amaranthus retroflexus* *Chenopodium album* Dicotyledonous weeds *Digitaria ciliaria* *Portulaca oleracea* *Solanum plycanthum* Weeds	Cover crop Dry shoot cover 500 g m^{-2} Intercropping	24–52 % density 60–93 % biomass	Creamer et al. (1996); Fujihara and Yoshida (1999); Gavazzi and Paris (2000); Narwal et al. (2001); Araki and Hatano (2002); Samedani et al. (2002); Ercoli et al. (2005); Fujii and Heradata (2005); Fujii et al. (2008)
Zea mays	*Oryza sativa/ Triticum aestivum* rotation *Poa pratensis*	Weeds *Digitaria* sp. *Trifolium* sp. *Taraxacum* sp.	Rotation *Zea mays* gluten meal	Smothering 58–91 %	Christians (1995); Narwal (2000)

Table 11.3 Most commonly reported allelopathic crops and other plant species, targeted weeds controlled and most commonly cultivated crops in which allelopathy was used

Allelopathic plants	Target weed species	Cultivated crops
Brassica (accessions)	*Amaranthus* spp.	*Brassica* spp.
Cajanus cajan	*Avena ludoviciana*	*Glycine max*
Echinochloa colonum	*Chenopodium album*	*Helianthus annuus*
Festuca arundinaceae	*Cyperus* spp.	*Hordeum vulgare*
Helianthus annuus	*Echinochloa colona*	*Lactuca sativa*
Hordeum vulgare	*Phalaris minor*	*Lycopersicon esculentum*
Lolium spp.	*Portulaca oleracea*	*Medicago sativa*
Oryza sativa and accessions	*Trianthema portulacastrum*	Orchards
Secale cereale		*Oryza sativa* (most frequent)
Sorghum bicolor	Unidentified weeds	Stored potato tubers
Sorghum halepense		*Triticum aestivum* (most frequent)
Sorghum hybrids		*Vitis vinifera*
Sorghum sudanense		*Zea mays* (most frequent)
Trifolium incarnatum		
Triticum aesivum and accessions		
Vicia villosa		
Zea mays		

and their competitiveness with weeds have been documented (Putnam and Duke 1974; Dilday et al. 1991). Different lines of *Beta vulgaris, Cucumis sativus, H. vulgare*, *Lupinus* spp., *O. sativa*, *Pisum sativum*, and *T. aestivum*, were reported to inhibit different weed species, and differences among these lines were detected biologically and at the molecular level (Kong 2005; Wu 2005). Other occasionally reported less important species including some annual and perennial herbs.

Treated crops showed variable response with the methods of allelopathy application. However, many of the crops used (*Avena* spp., *H. vulgare*, *Secale cereale, Sorghum* spp., and *T. aestivum*) have long been reported best for suppression of several noxious weeds and resulted in up to 95 % weeds density reduction (Putnam 1983). Accessions of certain crops have experimentally proved variations among germplasm in nature of allelopathic chemicals and/or their concentrations under field conditions. In addition, allelopathic features of these species were not linked to any of their competitive properties.

On the other hand, plant growth activators such as ComCat® (Carla GmbH) obtained from seed extract of *Lychnis viscaria* has been commercialized in Germany (Belz 2007). Several chemicals were isolated and identified as stimulants of seed germination in certain parasitic species (Zwanenburg and Reizelman 2001). Main parts of these are the sesquiterpenes lactones (Butler 1995) and some are alectrol from *Vigna sinensis*, orobanchol from *Trifolium pratense* (Sugimoto 2000) and strigolactones and orobanchol from *sorghum* (Yokota et al. 1998; Yoneyama et al. 2001; Bouwmeester et al. 2006). Strigol was first isolated and identified from the root exudates of *Gossypium hirsutum* and later from *Z. mays*, all are also produced by *Striga* host plants (Hsiao et al. 1981; Wegmann 1998). Some sesquiterpene lactones were found to induce seed germination of *O. cumana* (Perez-de-Luque et al. 2001) and better than the synthetic germination “GR24” stimulant. Sesquiterpenes were also detected from *H. annuus* plants (De-Luque et al. 2000),

Table 11.4 Trap crops for different *Orobanche* or *Striga* species

Scientific name	Common name	References
Orobanche ramosa		
Arabidopsis thaliana	Thale cress	Goldwasser et al. (2000)
Brassica rapa	Turnip	Al-Menoufi and Adam (1996)
Capsicum spp.	Capsicums	Sand (1983)
Coriandrum sativum	Coriander	Al-Menoufi and Adam (1996)
Cucumis sativus	Cucumber	Labrada and Perez (1988)
Linum usitatissimum	Linseed	Eplee (1984); Khalaf (1992)
Lupinus termis	Lupinus	Al-Menoufi and Adam (1996)
Phaseolus aureus	Mung bean	Kleifeld (1996)
Phaseolus vulgaris	French bean	Labrada and Perez (1988)
Sorghum bicolor	Sweet sorghum	Labrada and Perez (1988)
Trigonella foenum graecum	Fenugreek	Al-Menoufi and Adam (1996)
Orobanche aegyptiaca		
Arabidopsis thaliana	Thale cress	Goldwasser et al. (2000)
Capsicum annuum	Sweet pepper	Hershenhorn et al. (1996)
Linum usitatissimum	Linseed	Kleifeld et al. (1994)
Vigna radiata	Green gram	Kleifeld et al. (1994)
Orobanche cernua		
Crotalaria juncea	Sunhemp	Dhanapal and Struik (1996); Dhanapal et al. (2001)
Phaseolus aureus	Greengram	Dhanapal et al. (2001)
Sorghum bicolor	Sweet sorghum	Dhanpal and Struik1996; Hershenhorn et al. (1996)
Vicia dasycarpa spp. *villosa*	Vetch	Linke et al. (1991)
Vigna radiata	Green gram	Dhanapal and Struik(1996)
Orobanche crenata		
Allium sativum	Garlic	Hassan (1998)
Astragalus boeticus	Vetch	Schnell et al. (1994)

(continued)

Table 11.4 (continued)

Scientific name	Common name	References
Brassica rapa	Turnip	Al-Menoufi and Adam (1996)
Capsicum annuum	Pepper	Al-Menoufi and Adam (1996); Dhanpal and Struik1996; Hershenhorn et al. (1996)
Coriandrum sativum	Coriander	Al-Menoufi and Adam (1996); Zemrag and Bajja (2001)
Crotalaria juncea	*Orobanche cernua*	Dhanpal and Struik1996; Hershenhorn et al. (1996)
Glycine max	Soybean	Schnell et al. (1994)
Hedysarum coronarium	Sulla	Schnell et al. (1994)
Hordeum vulgare	Barley	Linke et al. (1991)
Lablab purpureus	Hyacinth bean	Schnell et al. (1994)
Lathyrus ochrus	Ochrus vetch	Schnell et al. (1994)
Linum usitatissimum	Linseed	Khalaf (1992); Abou-Salama (1995)
Lupinus termis	Lupinus	Al-Menoufi and Adam (1996)
Phaseolus vulgaris	French bean	Schnell et al. (1994)
Pisum sativum	Pea	Hassan (1998)
Saccharum officinarum	Sugarcane	Abou-Salama (1995)
Sesamum indicum	Sesame	Al-Menoufi (1991)
Trifolium alexandrinum	Berseem	Schnell et al. (1994); Al-Menoufi and Adam (1996)
Trigonella foenum graecum	Fenugreek	Al-Menoufi and Adam (1996); Zemrag and Bajja (2001)
Vicia dasycarpa spp. *villosa*	Vetch	Linke et al. (1991)
Vicia narbonensis	Narbonne vetch	Schnell et al. (1994)
Vigna radiata	Green gram	Schnell et al. (1994)
Vigna unguiculata	Cowpea	Schnell et al. (1994)
Orobanche minor		
Allium sativum	Garlic	Hassan (1998)
Arabidopsis thaliana	Thale cress	Goldwasser et al. (2000)
Pisum sativum	Pea	Hassan (1998)

(continued)

Table 11.4 (continued)

Scientific name	Common name	References
Orobanche spp.		
Allium cepa/*Arachis hypogaea*	Onion/Groundnut	Chttapur et al. (2001)
Bidens pilosa	Hairy beggarticks	Mitich (1993)
Crotolaria juncea	Sun hemp	Chttapur et al. (2001)
Linum usitattisimum	Flax	Qasem (2006)
Nicotiana tabacum/*Capsicum annuum*	Tobacco/Pepper	Chttapur et al. (2001)
Phaseolus aureus	Mung Bean	Chttapur et al. (2001)
Phaseolus mungo	Black gram	Chttapur et al. (2001)
Sesamum indicum	Sesame	Chttapur et al. (2001)
Sorghum bicolor/*Zea mays*/*Oryza sativa*	Sweet sorghum/Maize/Rice	Chttapur et al. (2001)
Tridax procumbens		Mitich (1993)
Striga asiatica		
Arachis hypogaea	Peanut	Prabhakarasetty (1980)
Cajanus cajan	Pigeon pea	Prabhakarasetty (1980)
Crotalaria juncea	Sunhemp	Prabhakarasetty (1980)
Gossypium hirsutum	Cotton	Prabhakarasetty (1980)
Helianthus annuus	Sunflower	Prabhakarasetty (1980)
Medicago sativa	Lucerne	Prabhakarasetty (1980)
Panicum miliaceum	Broomcorn millet	Chttapur et al. (2001)
Phaseolus aureus	Green gram	Prabhakarasetty (1980)
Sesamum indicum	Sesame	Prabhakarasetty (1980)
Sorghum bicolor	Sweet sorghum	Chttapur et al. (2001)
Sorghum sudanense	Sudan grass	Chttapur et al. (2001)
Zea mays	Maize	Chttapur et al. (2001)
Striga hermonthica		

(continued)

Table 11.4 (continued)

Scientific name	Common name	References
Abelmoschus esculentus	Okra	Hudu and Gworgwor (1998)
Aeschynomene histrix	Porcupine jointvetch	Merkel et al. (2000)
Arachis hypogaea	Groundnut	Parker and Riches (1993); Chttapur et al. (2001)
Cajanus cajan	Pigeon pea	Parker and Riches (1993)
Cicer arientinum	Chickpea	Parker and Riches (1993)
Corchorus olitrius	Jute	Parker and Riches (1993)
Cyamopsis tetragonoloba	Cluster bean	Bebawi and Mutwali (1991)
Glycine max	Soybean	Jost (1997), Kureh et al. (2000), Schulz et al. (2003)
Glycine max	Groundnut	Chttapur et al. (2001)
Gossypium hirsutum	Cotton	Bebawi and Mutwali (1991); Jost (1997)
Gossypium spp.	Cotton	Chttapur et al. (2001)
Helianthus annuus	Sunflower	Bebawi and Mutwali (1991); Hudu and Gworgwor (1998)
Hibiscus cannabinus	Kenaf	Parker and Riches (1993)
Lablab purpureus	Hyacinth bean, Egyptian kidney bean	Bebawi and Mutwali (1991)
Menispermum dauricum	Koumorikazura	Ma et al. (1998)
Sesamum indicum	Sesame	Bebawi and Mutwali (1991); Hudu and Gworgwor (1998)
Vigna subterranea	Bambara groundnut	Hudu and Gworgwor (1998)
Vigna unguiculata	Cowpea	Schulz et al. (2003)
Striga gesneriodes		
Lablab purpureus	Hyacinth bean, Egyptian kidney bean	Berner and Williams (1998)
Sphenostylis stenocarpa	African yam bean	Berner and Williams (1998)
Vigna catjang	Indian cowpea	Chttapur et al. (2001)

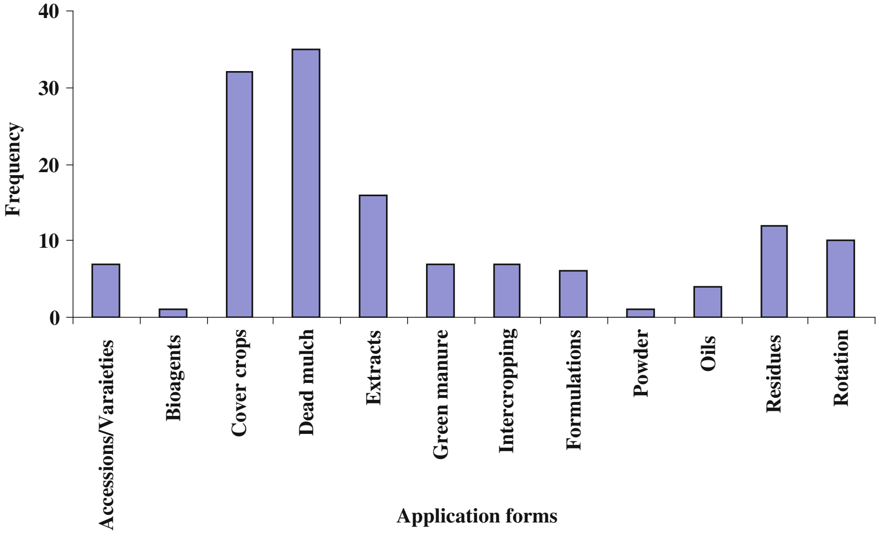

Fig. 11.1 Most common forms of allelopathic materials applied for weed control and their frequent uses (Qasem 2010)

Ambrosia artemisiifolia (Rugutt and Rugutt 1997), and *Pulicaria crispa* (Dendougui et al. 2000). Although amount, concentration, and environmental conditions are important factors determining the effectiveness of these chemicals under field condition, isolation, and identification of such allelochemicals would make possible large-scale production of these compounds or their synthetic analogs. However, an effective novel natural herbicide against parasitic weeds may be used in preplanting treatment in absence of host crop “suicidal germination”.

Allelochemicals are promising and effective natural tools for parasitic weed management either used as such or by incorporation of dead or living plants that releasing these into the surrounding environment as “catch” or “trap” species. Some of trap plant species reported for certain parasitic weeds are shown in Table 11.4. However, an early review study on plants possessing herbicidal activity was conducted by Rice (1983), while a more recent comprehensive review on allelopathy and parasitic weeds has been recently reported by Qasem (2006).

11.4 Methods of Allelopathy Application in the Field

Importance of allelopathy may be adjudged from its applicability to field conditions, and farmer’s responses toward this mechanism as a tool for pest management and sustainable agriculture. Since effectiveness of natural chemicals is mostly lower than of synthetic pesticides, farmers usually prefer a single active product rather than two (synthetic and/or natural). Natural products are necessary for organic farming. Hence to be attractive to farmers and for better commercialization for other systems, mixtures of synthetic, and natural products may be more suitable than any of them separately. This needs studies on chemicals compatibility and their weed or pest control spectrum. Pesticides of high activities, less persistence, reasonable rate of application, and wide spectrum of pest control are more acceptable. The marketing of natural products depends on farmer's trust and yield return. Successful natural product would benefit farmers worldwide, and help ecologist exploiting this biotechnology for higher yield and safe environment.

Methods for the application of allelopathy in weed control are many and variable. These include the use of crops accessions, varieties or cultivars, volatiles producing accessions, bark mulch, bioherbicides (fungus), cover crops or living mulch, dead mulch, dead woodchips mulch, decomposed straw, dense crop stand, dried leaves, dry shoot cover, extract, formulations, fragments, gluten meal, green manure, intercropping, killed plants cover, leachates, leaf powder, metabolites, oil or oils mixtures, plant stubble, relay crop, plant residue as a soil cover or soil incorporation, root layer, crop rotation, root exudates through rotation, and seed meal (Qasem 2010). However, most commonly used forms of allelopathy in weed management under field conditions and their frequency of use are shown in Fig. 11.1. Other less applied forms as dusting, foliage spray preparations (extracts or plant oils), or soil drenching are also reported.

11.5 Allelopathy Field Research, Problems and Prospects

Although a large number of publications is available on allelopathy application in the field, but most deal with a limited number of strong weed suppressant crops or those providing nutrients to the soil. However, reported data failed to separate the effect of allelopathy from that of competition (Qasem and Foy 2001). Intercropping and interpretation of results obtained on growth and yield, and the role of intercropped species in weed management, have neglected other positive effects of this system on intercropped species at which species complementing each other's needs for growth. Species interaction is additive in the absence of direct competition for growth factors, and thus better exploitation of resources and higher yields are possible than any of these grown separately. Intercropping system and yield obtained depend on species magnitude to share the same resource(s) or the differences in their requirements over growth factors. The possibility that one species facilitates other's growth in mixture through growth promoting substances in root exudates (Altieri and Liebman1988), or by symbiosis (Altieri and Liebman1988), are other factors to be considered. Higher weed smothering efficiency of *Capsicum annuum*, *G. hirsutum,* and *Phaseolus vulgaris* was found attributed to canopy coverage offered by *Arachis hypogea* and/or *P. vulgaris* as evident for higher light interception of intercrops (Shesshadri and Prabhakarasetty 2001).

Cover crops may affect weed growth through allelochemicals, competition or other mechanisms including stimulation of microbe's allelochemicals, physical barriers, shading effect of debris, and changes in soil physical properties (Lehman and Blum 1997). Cover crops are characterized by strong abilities to cover the soil surface and to effectively smother weeds (Qasem 2003). If these are legumes they could also elevate the soil nitrogen level. Legumes are less competitive than other crops (e.g. cereals and crucifers), their root systems with the associated bacterial nodules could modify the soil to be fluffier, enable better penetration of crop roots to deep soil layers, and thus effectively exploit water and nutrients (Qasem 2010). Soil mulching with living *V. villosa* has been reported to improve various soil physical properties including increase in water permeability and drainage, stabilization of soil temperature, and decrease of soil hardness (Fujihara and Yoshida 1999). In contrast, largest weed dry weight in mulched plots has been reported although mulch reduced number of weeds compared with the untreated control (Araki and Hatano 2002). Changes in physical environment reduce emergence of *Circium vulgare* seedlings in presence of leaf litter, although chemical effects were also possible (Dawson 1998). Kojima and Ohkubo (1999) reported good summer weed suppressions using *Cortalaria juncea*, *C. spectabilis*, *G. max*, *Mucuna prurience*, and *Panicum maximum* as green manure due to the quick growth and good ground cover of these species. Effect of allelopathy on crops and weeds is also implicated in the effect of cover crops or their residues. Bradow (1996) speculated that decomposed legume cover crop residue emit inhibitory chemicals to crop plants, while 2 % residue rate of *Sinapis alba* controlled weeds but decreased emergence of *P. sativum* by 90 %, and was highly phytotoxic to crop seedlings (Jaakkola 2002). The green manure of *S. alba* was more toxic to *Spinacia oleracea* and *P. sativum* than to weeds (Jaakkola 2005). Low density of *Cucurbita pepo* intercropped with *Z. mays* reduced weed biomass but high density was detrimental to both weeds and *Z. mays* (Fujiyoshi 1998). Stirzaker and Bunn (1996) showed that some or all benefits of soil mulch were eroded by phytotoxic leachates from residues of *S. cereale* and *Trifolium subterranean* as cover crops. However, allelochemicals are natural pesticides and may have their negative consequences on crop plants and environment.

In using allelopathy and cover crops for weed management, all of the above mentioned conditions should be considered. Most beneficial cover crops are legumes (Fujii and Heradata 2005), while the effect of these on crop plants needs to be compared with a weed-free crop of no cover crop. However, many of the allelopathic crops are used under field conditions as straw mulch, in which space between crop rows is mulch-covered or in some cases crop plants are grown in straw mulched soil. The most commonly used allelopathic straw mulches are those of *T. aestivum*, *H. vulgare* and *S. cereale*. *S. cereale* and *T. aestivum* have been reported to reduce emergence, height, and yield of *Z. mays* (Burgos and Ronald 1996). Water-soluble toxic substances of wheat straw mulch inhibited *Z. mays* growth, and the effect was more pronounced under wet conditions (YongQing 1994). Wheat residues were also reported to stimulate germination and growth of summer weeds and contrary to forage crops that smothered weeds up to 45 days in the next crop (Narwal 1996).

Beneficial impact of soil cover may be better observed in arid and semi-arid regions. Mulching prevents light from reaching small emerged seedlings and hence photosynthesis. The ability of emerged seedlings to establish depends on the thickness of straw mulch layer; therefore, it is difficult to separate the mechanical or physical effects of mulch from that of allelopathy. Residue of desiccated cover crops is influenced by different factors and generally at natural levels alone is not sufficient to provide full-season weed control, but requires integration with other management practices for optimum control (Teasdale 2002). Cover crops may antagonize the efficacy of some weed management practices such as preemergence herbicides and may increase the incidence of certain agricultural pests. Therefore, untreated weed-clean crop (control) is necessary to include for evaluation. Cover crops or residues may increase the incidence or population of certain agricultural pests, or their persistence; therefore, species of different families or their residues are always recommended in rotation. Increase in the incidence of *Pythium* spp. infection of wild mustard seedlings has been reported as a result of amended soil with *T. pratense* manure and compost (Conklin et al. 2002). Intercropping of *Cajanus cajan, G. max*, *G. hirsutum*, *Macrotyloma uniflorum*, or *V. radiata* with *sorghum* increased *Striga asiatica* infestation (Chttapur et al. 2001) and enabled establishment of stimulated parasite seeds on the true host sorghum (Prabhakarasetty 1980).

Inclusion of allelopathic cultivars or accessions for smothering or managing of weeds in the field should be carried out after full consideration of all competitive features of the used lines or cultivars. Low competitiveness and high smothering effect of a cultivar on weeds may indicate allelopathic character; otherwise, the effect may be due to competition, allelopathy, or both.

Direct application of aqueous crude extracts in the field has both positive and negative effects on weed control and crop plants. In most cases, extracts were found effective to certain limits against weeds or other agricultural pests, but negative effects such as partial weed control and serious crop injury have been also reported (Heisey and Heisey 2003). Extracts/herbicides mixtures may be more effective on weeds than the herbicide alone, and thus allow reduction in herbicide application rates. Since most plant extracts have low pH values with acidic nature they may act as surfactants, modify the leaf waxy layer of weed species (may be more in grasses), and enhance better herbicide penetration. The effect of herbicide/extract mixture may not be due to herbicidal activity of extracts rather than of a surfactant effect. However, some difficulties usually associated with allelopathy application for weed management, include (Qasem 2010):

- Techniques/methods used and difficulty in separating competition effects from those of allelopathy.
- Application at reasonable amounts of allelopathic materials (extensive rates applied in most cases)
- Absence of control treatments (untreated plots) in field studies in most cases.
- Problems associated with low stability and effectiveness of allelochemicals under field conditions.
- Time of allelopathy application, and interference or incompatibility with other agricultural or farm operations.

- Allelopathy impact (may be negative in certain cases) on the following crop plants.
- Effect of allelochemicals on treated crop plants.
- Yield economic wise of allelopathic crop accessions and how far they increase yield as a result of weed suppression through allelopathy mechanism.
- Integration of allelopathy with other methods of pest control or management.
- Imbalanced weed species and the need for integrated weed control program.
- Decision on whether the chemicals obtained are allelochemicals (naturally released) or phytotoxins (extracted)?
- Difficulty in explaining the promotory effects and whether these are due to nutrients or allelochemicals?
- Knowledge of whether the obtained effect is due to a single or mixture of allelochemicals that brought the ultimate effect on inflicted species.

11.6 Molecular Aspects and Genetic basis of Allelopathic Potential of Different Species

It is worth indicating that allelopathy research on *T. aestivum* has been rapidly progressed from the initial evaluation of allelopathic potential to the identification of allelochemicals and genetic markers associated with its allelopathy (Wu 2005). Correlation between allelopathic effect of *T. aestivum* genotype and their genes was detected and found increased as genome changed from 2n to 4n to 6n (Zuo et al. 2005). Further, novel selection methods of allelochemical fingerprinting were developed (Kong et al. 2002) and proved that concentrations of three types of glucosides produced by *Oryza sativa* plants were significantly different between allelopathic and non-alleloapthic accessions. Growth adaptation under water or nutrient stresses and allelopathic potential has been a subject of different studies (Fang et al. 2010; Zuo et al. 2010) and the link between these and the expression of genes associated with allelochemicals in different crop species have been thoroughly investigated (Wang et al. 2008, 2009; Fang et al. 2010). The responses of certain crops to exogenous treatment with inhibitory chemicals, the development of the defence mechanism in these crops, induction of allelochemicals against certain associated weed species and enhancement of certain enzyme production have been also implicated (Qiu et al. 2009; Fang et al. 2009). These results provide evidence for possible separation of allelopathy effect from that of competition under field conditions and on the role that allelopathy has in weed management.

11.7 Future Thrusts

Phytotoxic properties and ecotoxic features of allelochemicals from release to degradation, selectivity in relation to crop stages and concentrations, their joint actions with herbicides, and/or with their derivatives are important aspects to be considered. Studies on the biochemical signaling between interfering plants in nature and the resulting inducible allelopathic processes may merit future consideration. Future work should elucidate any biochemical communication among plants in nature and the importance of this phenomenon and its exploitation to imbalance crop/weed interaction in favor of crop production. New studies may be directed to screen for highly allelopathic germplasm of strong weed suppressive ability in collection crops, with the goal of transferring the allelopathic character into improved cultivars by either conventional breeding or other genetic transfer technique (Kim and Ho 1997). Choosing varieties with optimal production of allelochemicals and optimizing the time of sowing in relation to the formation of bioactive metabolites (Fomsgaard 2006) are another management practice that would greatly contribute to weed suppression.

The chemistry of allelochemicals (growth promoting or demoting) and development of more precise allelopathy techniques enable separation from other mechanisms of plant interference in nature, merit further search.

Research is needed on biological activity, mechanism and mode of action, gene expression, persistence, fate or dynamics of allelochemicals in soil, and on molecular biology of allelopathic plants (Macias et al. 2005; NI and Zhang 2005). Research efforts should be also directed to discovery of genes involved in the biosynthesis of potent allelochemicals and possible development of biopesticides (Baerson et al. 2005). Identification of genetic markers associated with crops allelopathy would enable researchers to locate allelopathic genes for transfer into modern varieties for weed suppression (Labrada 2002). Selection for allelopathic crops, using allelopathic companion plants or rotational crops, or by searching for natural product herbicides from both higher plants (cultivated or wild races) and microbes are another aspects of future allelopathy research line (Putnam 1988).

It seems appropriate for any researcher and/or farmer to consider the following measures or to address the below mentioned questions before setting an experiment or apply allelopathy tools for weed management.

- Determination of extract concentration, pH, volume, osmotic potential, mixtures compatibility, time of application in relation to weeds and crop plants, and their mechanism of action.
- Inclusion of control treatments at which crop plants treated only with extract and untreated weed-free crop, for comparison.
- Selectivity of allelochemical to crop plants grown from seeds or seedlings.
- Production and secretion of allelochemicals in response to stresses or certain agricultural practice(s).
- Role of microorganisms and availability on time and concentration to receiver plants.

- Effect of soil-residue compaction on seed germination and/or on seedlings emergence and growth.
- Type of allelochemicals uptake (passive or active) by different treated species.
- Selective uptake of allelochemicals in response to certain conditions.
- Effect of plant density on allelochemical/s accumulation in target weeds.
- How far the separation of allelopathy from other mechanisms of plant interference in the field is achieved?
- What are the other positive effects of intercropping on all interacting species?
- How far are the differences in species requirements for growth factors?
- What was the canopy coverage effect on crop plants and weeds?
- Consideration of other mechanisms, microbes' stimulation, physical barriers, shading, and changes in soil physical properties.
- Legume cover crops, physical smothering effects on weeds, and nitrogen supply to crop plants.
- The high demand of allelopathic cereal and crucifer species for water and nutrients and magnitude of soil depletion from these growth factors.
- Effect of soil mulch on moisture conservation, soil temperature, water permeability, drainage, and soil hardness.
- The correlation between weed suppressions effect and the rapid growth of ground cover crops.
- Physical effects of soil mulch versus phytotoxic leachates from residues of cover crops.
- Possible outcrossing of allelopathic traits to weedy relatives and possible production of chemotypes.

11.8 Conclusions

Allelopathy has been long considered as a branch of ecological sciences, and has rich history. Results of a huge number of publications on different aspects on the subject are promising and showed possible inclusion of this mechanism in weed management programs. However, exploitation of allelopathy under field conditions and the potential development of natural botanical- and/or mico-herbicides are still at their infancy. Literature indicated a high tendency toward recommending certain cover crops, crop residues, limited number of allelochemicals and herbicides based natural products, allelopathic crop cultivars, and intercropping system for weed management. In addition, crop rotation is regaining now as an agricultural practice for weed and soil weed seed-bank control.

The isolated allelochemicals from extracts, root exudates, or decomposed plant materials may be of great value for industry and for development and synthesis of safe and effective bio-herbicides or surfactants. Considering the difficulties and problems mentioned, allelopathy offers a great potential for weed management and a wide arry of research and may be regarded as a potentially future strategy for pest control in sustainable and organic farming agriculture. Some proofs and signs on allelopathy role for weed management may be drawn from,

- Gene studies and allelopathy characters of plant species.
- Differences between crops accessions in allelopathic activities and allelochemical contents.
- Effect of volatile materials of certain species inhibited weed growth in the field (e.g. cucumber)
- The poor competitive traits of certain weed species but their tendency to form colonies and ecological niche or to affect crop plants and *vice versa*.
- The poor receiver growth and performance in spite of the optimum condition available for its growth.

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Chapter 12
Allelopathy for the Management of Phytopathogens

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Abstract Plant pathogens including fungi, bacteria, viruses and nematodes are responsible for huge yield losses in many economically important crops. Use of synthetic agrochemicals as soil fumigation, foliar spray or seed dressing is the most popular strategy for the management of plant diseases in the recent days. However, due to adverse effects of these chemicals on health and environment, consumers are currently demanding produce, which is free of these chemicals. Natural compounds derived from plants are more environmentally safe than synthetic chemicals. Many recent studies have shown that allelochemicals can effectively be used for the management of plant pathogens. Members of plant families like Acanthaceae, Amranthaceae, Chenopodiacea, Brassicaceae and Magnoliaceae are famous for their antifungal properties while those of Asteraceae, Poaceae and Papillionaceae are known for their nematicidal properties. These plants secondary metabolites can be exploited for the management of plant pathogens following crop rotation, green manuring and cultivation of allelopathic plants as cover crops or using crude plant extracts. In addition, the structures of novel allelochemicals can be used as analogue for the synthesis of new natural product-based pesticides.

12.1 Introduction

Crop plants are attacked by a large number of pathogens namely fungi, bacteria, viruses, phytoplasmas and nematodes. These pathogens are responsible for substantial plant growth and yield losses (Saremi et al. 2011; Matarese et al. 2012).

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In the presence of a susceptible host and under favourable environmental conditions, total crop failure may occur after disease development (Bayraktar et al. 2007). There are many reports where these plant diseases spread in an epidemic form and caused very high yield losses in economically important crops such as chilli, wheat, rice, potato and tomato on large cultivated areas (Wang et al. 2009; Ristaino 2010; Zeng and Luo 2011; Senanayake et al. 2012). A number of methods are available for the management of plant diseases. These include cultural practises such as crop rotation, host eradication and sanitation; cultivation of resistant varieties (Agrios 2005), use of biological agents such as *Trichoderma* spp. (Hanada et al. 2009; McLean et al. 2012), and use of synthetic agrochemicals (Paulo and Gouveia 2009; Shukla et al. 2010). Growers are generally attracted by utilisation of synthetic agrochemicals to combat diseases, since this option is rapid and easy to practise, resulting in maximum profitable yield. Fungicides, bactericides and nematocides are being used to control fungal, bacterial and nematode diseases. These agrochemicals are generally used as seed dressing, soil fumigant or foliar spray (Agrios 2005). Although these synthetic agrochemicals are very effective in controlling crop diseases; however, their use is becoming more limiting due to environmental pollution, residual toxicity problems, carcinogenic effects and occurrence of microbial resistance (Rial-Otero et al. 2005). For more sustainable systems, there is an increasing trend towards search for natural and environmental friendly alternatives of these chemicals (Cuthbertson and Murchie 2005). Exploiting allelopathic potential of plants is one of the most popular alternative strategies to manage the phytopathogens (Farooq et al. 2011).

Several plant species are capable of producing and releasing biologically active compounds called allelochemicals (Uddin et al. 2011). Allelochemicals include phenolics, coumarins, alkaloids, terpenoids, steroids, tannins and quinines. These compounds are released into the environment by various mechanisms including root exudation, leaching from aerial parts especially leaves, volatile emissions and decomposition of plant material (Anaya et al. 1990; Xuan et al. 2005).

Allelopathy is beneficial or detrimental effect from a donor plant to the recipient by chemical pathway (Rice 1984). According to International Allelopathy Society, allelopathy concerns the study of any process involving secondary metabolites produced by plants, algae, bacteria and fungi that influence the growth and development of agricultural and biological systems (IAS 1996). The harmful impact of allelopathy can be exploited for the management of pests and diseases (Kohli et al. 1998). Ample research work has recognised the potential of allelopathic plants in suppressing the growth of plant pathogens (Riaz et al. 2007, 2010a, b; Deepak 2011; Javaid and Saddique 2011; Klein et al. 2011). Plant products are biodegradable, exhibit structural diversity and complexity and rarely contain halogenated atoms. These can act directly as pesticides or may provide structural lead for pesticide discovery (Duke et al. 2000). The phenomenon of allelopathy has recently received greater attention from researchers and farmers worldwide (De Albuquerque et al. 2011; Farooq et al. 2011). In this chapter, allelopathic potential of plants for the management of various phytopathogens viz. fungi, bacteria and viruses is discussed.

12.2 Management of Fungal Pathogens

Approximately 100,000 species of fungi have been described so far, of which a high percentage obtain nutrients by living in close association with other organisms, mainly plants (Gladieux et al. 2011). About 75 % of plant diseases are caused by fungi. On the basis of morphology and biology, plant pathogenic fungi are categorised into five major groups, Plasmodiophoromycetes, Zygomycetes, Oomycetes, Ascomycetes and Basidiomycetes (Koike et al. 2003). There are many notorious fungal pathogens such as *Macrophomina phaseolina, Sclerotium rolfsii, Fusarium solani, F. oxysporum* and many other that cause diseases on a large number of host plants. *M. phaseolina* is a soil-borne fungal plant pathogen that causes charcoal rot disease in more than 500 different monocotyledonous and dicotyledonous plant species including such important crops as sorghum, soybean, alfalfa, maize etc. (Wyllie, 1993; Ma et al. 2010). So far, there is no registered fungicide against the charcoal rot pathogen. Similarly, *S. rolfsii* is also a soil-borne plant pathogen responsible for significant economic losses on a wide range of agronomic host plants including 500 plant species, in over 100 plant families, in countries of Asia, Australia, Africa, America and Europe (Punja1985; Polizzi et al. 2010; Remesal et al. 2010). Plant diseases caused by fungi include leaf spots, root and crown rot, rust, smut, blight, wilt, dieback, powdery mildew, downy mildew etc. Triazole derivatives such as diniconazole, triadimefon, tebuconazole, and hexaconazole represent the most important category of fungicides to date, effective against a wide spectrum of crop diseases (Lu et al. 2011).

12.2.1 Antifungal Activity of Crude Extracts

Several plant families like Acanthaceae, Amranthaceae, Chenopodiacea, Brassicaceae and Magnoliaceae are known for their antifungal properties (Neerman, 2003; Javaid and Amin, 2009). Crude aqueous and organic solvent extracts of a large number of allelopathic plants have been investigated in vitro for their antifungal activity against a variety of fungal pathogens. Results of these studies clearly demonstrate that extracts of allelopathic plants have great potential for the management of fungal pathogens. Members of family Brassicaceae are especially known for their antifungal properties. Extracts of seed meal of *Brassica napus* were found inhibitory to the growth of *Aphanomyces euteiches* f. sp. *pisi* (Smolinska et al. 1970). Similarly, 0.2 % seed meal extracts of different varieties of radish (*Raphanus sativum*) completely inhibited conidial germination of *Acremonium lactucae*, the cause of lettuce brown spot. In further green house trials, foliar spray with 0.5 % (w/v) aqueous seed meal extract of radish cv. WS-T 2 days after inoculation or 3 days prior to inoculation of *A. lactucae* provided the consistent control of brown spot disease (Muto 2001). Recently, Iqbal and Javaid (2012) reported that methanolic extracts of different parts of a Brassicaceous weed

Coronopus didymus were highly effective for the management of *S. rolfsii*, the cause of southern bight disease of bell pepper. Aqueous extracts of *C. didymus* were also very effective in controlling *F. oxysporum* f. sp. *gladioli*, the causal agent of corm rot disease of gladiolus (Riaz et al. 2010a). They further reported that application of aqueous extracts of *Allium cepa*, *A. sativum* L. and *Zingiber officinale* Roscoe exhibited better antifungal activity than the fungicide carbendazim in reducing incidence and severity of corm rot disease of gladiolus. Jabeen and Javaid (2008) reported that 5 % aqueous leaf and root-bark extracts of *Eucalyptus citriodora* reduced the colony diameter of *Ascochyta rabiei* (Pass.) Lab. by 38 and 41 %, and ethanol extracts of fruit and root-bark reduced colony diameter of this fungal species by 25 and 42 %, respectively. Similarly, Aqueous extracts of leaves, fruit, stem bark and root bark of *Syzygium cumini* (L.) Skeels, showed significant antifungal activity resulting in 7–30 %, 22–59 %, 23–39 % and 21–64 % reduction in growth of *A. rabiei*, respectively (Jabeen and Javaid 2010). Javaid and Amin (2009) investigated antifungal activity of methanol and *n*-hexane leaf, stem, root and inflorescence extracts of three *Chenopodium album* L., *C. murale* and *C. ambrosioides*. (family Chenopodiaceae) against *M. phaseolina*. All the extracts of the three *Chenopodium* species significantly suppressed the test fungal growth. Aqueous root and rhizome extracts of an allelopathic invasive plant *Solidago canadensis* L. significantly suppressed the growth and pathogenic activity of soil-borne pathogens. *Pythium ultimum* and *Rhizoctonia solani* under Petri dish culture and sand culture (Zhang et al. 2009). Singha et al. (2011) found that crude chloroform extract of *Piper betle* L. was more efficient in reducing the population of tomato (*Lycopersicon esculentum*) wilt pathogen *F. oxysporum* f. sp. *lycopersici* than fungicide carbendazim. Yanar et al. (2011) demonstrated that aqueous extracts of *Laurus nobilis, Humulus lupulus, Cirsium arvense* and *Salvia officinalis* exhibited significant antifungal activity against *Alternaria solani,* the cause of early blight of potato (Table 12.1).

12.2.2 *Effect of Soil Amendments on Soil-Borne Diseases*

Many old and contemporary studies reveal that soil amendment with green manure or residues of allelopathic plants significantly reduce the fungal populations in the rhizospheric soil and reduce fungal infections of the cultivated host crop plants. During the decomposition process many allelochemicals are released into the rhizospheric, which reduced or weakened fungal inoculum in the soil, consequently reducing the infection and plant mortality (Choudhary et al. 1995; Rajesh and Sharma 2002). Many earlier studies showed that incorporation of plant materials of members of family Brassicaceae significantly reduced the incidence and severity of soil-borne plant pathogens namely *R. solani* (Manning and Crossan 1969), *Thielaviopsis basicola* (Adams 1971), *F. oxysporum* f. sp. *conglutinans* (Ramirez-Villapudua and Munnecke 1988), *A. cochlioides* (Lewis and Papavizas 1971),

Table 12.1 Role of crude extracts of allelopathic plants in the management of phytopathens

Plant species	Extract	Target pathogens	Effect	Reference
Fungal pathogens				
Eucalyptus citriodora	5 % aqueous root-bark extract	*Ascochyta rabiei*	41 % reduction in fungal growth	Jabeen and Javaid (2008)
Melia azedarach	1–5 % aqueous leaf extract	*A. rabiei*	24–54 % reduction in fungal growth	Jabeen et al. (2008)
Syzygium cumini	5 % aqueous stem-bark extract	*A. rabiei*	59 % reduction in fungal growth	Jabeen and Javaid (2010)
Oryza sativa	1–5 % aqueous shoot extract	*Macrophomina phaseolina*	21–52 % reduction in fungal growth	Bajwa et al. (2008)
Azadirachta indica	0.3–1.5 % ethyl acetate leaf extract	*M. phaseolina*	81–90 % reduction in fungal growth	Javaid and Rehman (2011)
Piper betle	chloroform extract	*Fusarium oxysporum*	Reduced pathogen population more than fungicide carbendazim	Singha et al. (2011)
Allium cepa	Aqueous extract	*F. oxysporum* f.sp. *gladioli*	Reduced corm rot incidence in gladiolus	Riaz et al. (2010a)
Solidago canadensis	Root and rhizome aqueous extracts	*Pythium ultimum, Rhizoctonia solani*	Suppressed the growth and pathogenic activity of both pathogens	Zhang et al. (2009)
Coronopus didymus	Methanolic leaf extract (5 mg mL^{-1})	*Sclerotium rolfsii*	Reduced fungal growth by 67 %	Iqbal and Javaid (2012)
Chenopodium album	Methanol inflorescence extract	*M. phaseolina*	4 % extract reduced fungal growth by 96 %	Javaid and Amin (2009)
Lauris nobilis	Aqueous leaf extract	*Alternaria solani*	Reduced fungal growth by 79 %	Yanar et al. (2011)
Bacterial pathogens				
Artemisia nilagirica	Hexane leaf extract	Xanthomonas campestris, Pseudomonas syringae, Clavibacter michiganense	A concentration of 32 µg mL^{-1} completely inhibited the bacterial growth	Ahameethunisa and Hopper (2010)
Camellia sinensis	Aqueous leaf extract	*Xanthomonas campestris* pv. *Campestris*	Significantly reduced bacterial growth	Bhardwaj and Laura (2009)

(continued)

Table 12.1 (continued)

Plant species	Extract	Target pathogens	Effect	Reference
Phyllanthus emblica, Acacia nilotica, Sapindus mukorossi, Terminalia chebula	Plant diffusate	*Xanthomonas campestris* pv. *Citri*	Reduced the number of lesions on detached leaves and fruits	Akhtar et al. (1997)
Dtura stramonium, Allium sativum, Nerium oleander	Aqueous leaf extracts	*Ralstonia solanacearum*	Reduced tomato wilt	Abo-Elyousr and Asran (2009)
Nematodes				
Tagetes erecta	20 % w/v aqueous extract	*Meloidogyne incognita*	Reduced galls on tomato roots	Natarajan et al. (2006)
Bidens pilosa var. *radiata*	Aqueous extract	*M. incognita*	immobilisation, lethality, repellence	Taba et al. (2008)
Chrysanthemum coronarium	Aqueous extract	*M. incognita, M. javanica*	inhibited hatching from eggs	Bar-Eyal et al. (2006)

A. euteiches (Muehlchen et al. 1990), *A. alternata* (Troncoso et al. 2005), and *Verticillium dahliae* (Subbarao et al. 1994). Riaz et al. (2010b) reported that incorporation of *C. didymus* aerial parts at 2–6 % in the soil can reduce incidence of corm rot disease of gladiolus (*Gladiolus grandiflorus* sect. Blandus cv. Aarti) caused by *F. oxysporum* f.sp. *gladioli* (Massey) Snyd. & Hans. by 71–88 %. Members of family Brassicaceae produce glucosinolates (Sun et al. 2011), which are responsible for control of fungal pathogens (Lewis and Papavizas 1971). Glucosinolates are important and unique class of secondary plant products composed of *β*-D-thioglucose and sulphonated oxime moieties (Vig et al. 2009). Enzymatic hydrolysis of glucosinolated by membrane-bound thioglucosidase produces many compounds viz. thiocyanates, isothiocyanates, nitriles, epinitiles, and glucose. Some of the hydrolytic breakdown products especially isothiocyanates possess fungicidal properties (Blažević et al. 2010). Allyl glucosinolate is one of the predominate glucosinolate in many Brassicaceous species and is generally converted into allyl isothiocyanate in the soil (Mayton et al. 1996), and is as toxic to fungi as methyl isothiocyanate, an active ingredient in soil fumigant (Vaughn et al. 1993). Recently, Klein et al. (2011) reported that soil amendment with residue of *S. officinalis, Artemisia dracunculus*, *Diplotaxis tenuifolia* and *B. oleracea* var. *italica* reduced incidence and severity of crown and root rot disease by 20–80 % in cucumber plants inoculated with macroconidia of *F. oxysporum* f. sp. *radicis-cucumerinum.* Núñez-Zofío et al. (2011) found that combination of amendments proved better than single amendment. They recorded up to 93 % reduction in incidence of pepper crown and root rot disease by *Phytophthora capsici* by the application of *B. carinata* pellets + *Sinapis alba* as fresh green manure. Javaid and Saddique (2011) recorded 80 % reduction in mortality of mungbean [*Vigna radiata* (L.) Wilzeak] by *M. phaseolina* by mixing leaf powder of *Datura metel* at 1.5 % w/w (Table 12.2).

12.2.3 Natural Antifungal Compounds

Several allelochemicals have been identified as potent antifungal agents. Zhang et al. (2011) observed that secondary metabolites flavones, total phenolics, and total saponins are released from *S. canadensis* and accumulate in the soil. The concentrations of these secondary metabolites were negatively with disease severity of tomato by *P. ultimum.* Momilactone A (3-oxo-9*β*-pimara-7,15-dien-19,6*β*-olode, $C_{20}H_{26}O_3$, M 314) and B (3,20-epoxy-3*α*-hydroxy-9*β*-pimara-7,15-dien-19,6*β*-olode, $C_{20}H_{26}O_4$, M 330) are two important allelochemicals produced by rice (Kato-Noguchi 2011). These two allelochemicals are known to exhibit antifungal activity against the rice blast pathogen *Magnaporthe oryzae,* the most serious fungal disease of rice (Kato et al. 1993). Momilactone A and B are known to inhibit 50 % growth of germ tube of *M. oryzae* at concentrations of 15 and 3 μM, respectively (Cartwright et al. 1977). Studies have shown that *M. oryzae*

Table 12.2 Role of soil amendments, intercropping and crop rotation in the management of phytopathens

Allelopathic plant species	Target pathogens	Effect	Reference
Fungal pathogens			
Eucalyptus citriodora	*Fusarium oxysporum* f.sp. *gladioli*	A 6 g 100 g^{-1} leaf amendment reduced disease incidence by 83 %	Riaz et al. (2010a, b)
Salvia officinalis, Diplotaxis tenuifolia Brassica oleracea var. *Italica*	*Fusarium oxysporum* f. sp. *radicis-cucumerinum*	Residue incorporation reduced root rot in cucumber by 20 to 80 % disease	Klein et al. (2011)
Brassica carinata pellets + *Sinapis alba*	*Phytophthora capsici*	Green manure reduced crown and root rot disease in pepper by 93 %.	Núñez-Zofío et al. (2011)
Datura metel	*Macrophomina phaseolina*	1.5 % leaf amendment reduced 80 % plant mortality in mungbean	Javaid and Saddique (2011)
Bacterial pathogens			
Allium tuberosum	*Pseudomonas solanacearum*	Intercropping with tomato inhibits multiplication of bacterial wilt pathogen	Yu (1999)
Cowpea	*Pseudomonas solanacearum*	Intercropping manage the bacterial wilt disease in tomato	Michell et al. (1997)
Nematodes			
Brassica juncea	*Meloidogyne hapla*	Gall numbers decreased on carrot roots	Douda et al. (2012)
Chrysanthemum coronarium	*Meloidogyne incognita, M. javanica.*	Green manure significantly reduced infection of tomato root	Bar-Eyal et al. (2006)
Chrysanthemum coronarium	*Tylenchorhynchus brassicae*	Soil amendment reduced populations of the nematode	Tiagi and Wani (1992)
Azadirachta indica, Calotropis procera	*M. incognita*	Leaf amendments significantly reduced infections in okra roots	Hussain et al. (2011)
Lolium multiflorum	*Heterodera glycines*	Reduced nematode population and infection in soybean	Riga et al. (2001)

may induce momilactone A production that enhance blast resistance in rice leaves (Hasegawa et al. 2010). These compounds are also known to possess antifungal activity against other fungal species namely *F. oxysporum, F. solani*, *Botrytis cinerae* and *Colletrotichum gloesporides* (Fukuta et al. 2007). Prats et al. (2007) identified three coumarins viz. scopoletin, scopolin and ayapin in *Sclerotinia sclerotiorum*-resistant sunflower. They also identified a new phenolic 3-acetyl-4-acetoxyacetophenone from sunflower that possessed antifungal activity against *S. sclerotiorum.* Kanwal et al. (2010) isolated five flavonoids namely (-)-epicatechin-3-*O*-*β*-glucopyranoside, 5-hydroxy-3-(4- hydroxylphenyl) pyrano[3,2-g]chromene-4(8H)- one, 6-*p*-hydroxybenzyltaxifolin-7-*O*-*β*-D glucoside (Tricuspid), Quercetin-3-*O*-α-glucopyranosyl-(1 → 2)-*β*-glucopyranoside and (-) epicatechin (2-(3,4-dihydroxyphenyl)-3,4-dihydro-2H chromene-3,5,7-triol) from mango leaves, which were very effective against charcoal rot fungus *M. phaseolina.* Recently, Jabeen et al. (2011) reported four *compounds* viz. *β*-amyrin, ursolic acid, benzoic acid and 3,5 dimethoxybenzoic acid from *Melia azedarach* leaves which exhibited antifungal activity against *Ascochyta rabiei*, the cause of destructive blight disease of chickpea (*Cicer arietinum*) (Table 12.3).

12.3 Management of Bacterial Pathogens

Bacteria are single-celled microscopic organisms, ranging in size from 1–2 μm. Plant pathogenic bacteria cause many serious diseases of plants throughout the world (Vidhyasekaran 2002). However, the bacterial diseases are fewer than fungi or viruses and they cause relatively less damage and economic loss (Kennedy and Alcorn 1980). There are about 200 bacterial species causing severe economically damaging diseases worldwide on 150 plant genera belonging to more than 50 families of higher plants. The majority of plant-associated bacteria are rods, however, by biochemical, genetic and molecular biological analyses, it has been shown that these bacteria are quite heterogeneous (Vidaver and Lambrecht 2004). Symptoms of bacterial diseases on plants ranging from spots, mosaic patterns or pustules on leaves and fruits, or smelly tuber rots to plant death (Kim et al. 2011a, b; Thiele et al. 2012). Some bacteria namely *Agrobacterium tumefaciens* and *A. vitis* cause hormone-based distortion of leaves and shoots called fasciation or crown gall (El-Beltagi et al. 2011). Amongst the pathogenic bacteria about one half of the species belong to genus *Pseudomonas* while rest belong to *Pectobacterium, Pantoea, Erwinia, Burkholderia, Acidovorax, Agrobacterium, Ralstonia, Streptomyces, Xanthomonas, Xylella, Spiroplasma, Clavibacter* and *Phytoplasma* (Vidaver and Lambrecht 2004).

There are many examples of exploiting allelopathic potential of the plants for the management of bacterial plant pathogens and diseases. Intercropping of Chinese chive (*A. tuberosum*) with tomato significantly delayed and suppressed the occurrence of bacterial wilt of tomato caused by *Pseudomonas solanacearum*

Table 12.3 Natural bioactive compounds isolated from plants for the management of phytopathogens

Natural compound	Source	Target pathogens	Reference
Fungal pathogens			
Allivin	*Allium sativum* var. round clove.	*Botrytis cinerea, Mycosphaerella arachidicola, Physalospora piricola.*	Wang and Ng (2001)
β-amyrin	*Melia azedarach* leaf	*Ascochyta rabiei*	Jabeen et al. (2011)
(−)-epicatechin-3-O-β-glucopyranoside	*Mangifera indica* leaf	*Macrophomina phaseolina*	Kanwal et al. (2010)
Genistein 7-O--glucoside	*Azadirachta indica*	*Macrophomina phaseolina*	Kanwal et al. (2011)
Momilactone A and B	*Oryza sativa*	*Magnaporthe oryzae*	Kato-Noguchi (2011)
3-acetyl-4-hydroxyacetophenone	*Helianthus annuus*	*Sclerotinia sclerotiorum*	Prats et al. (2007)
Bacterial pathogens			
2-isopropyl-5-methylphenol	*Thymus vulgaris*	*Ralstonia solanacearum*	Momol et al. (2005)
Nematodes			
5-(3-buten-1-yny1)-2,2′-bithienyl and α- terthienyl	*Tagetes* sp.	Nematodes	Uhlenbroek and Bijloo (1959)
sn-glycerol-1-eicosa-9, 12-dien-oate-2-palmitoleate-3-linoleate	*Argemone mexicana* seeds	*Meloidogyne incognita*	Saleh et al. (1987)
2-phenylethyl glucosinolate	*Brassica* spp.	*Pratylenchus* sp.	Potter et al. 1998
Cyclic hydroxamic acids	*Secale cereale*	*Meloidogyne incognita, Xiphinema americanum*	Zasada et al. (2005)
Essential oil	*Chrysanthemum coronarium* flower head	*Meloidogyne artiellia*	Perez et al. (2003)
α-terthienyl	*Tagetes* spp.	Plant-parasitic nematodes	Hooks et al. (2010)
methyl *trans*-cinnamate	*Gaultheria fragrantissima*	*Bursaphelenchus xylophilus*	Kim et al. (2011b)

Smith without having any negative effect on the tomato (Yu et al. 1999). Diffusates from various parts of *Sapindus mukorossi, Acacia nilotica, Phyllanthus emblica* and *Terminalia chebula* were highly inhibitory against *Xanthomonas campestris* pv. *citri* and reduced the number of lesions on detached leaves and fruits (Akhtar et al. 1997). Volatile plant essential oil thymol (2-isopropyl-5-methylphenol) application significantly reduced *Ralstonia solanacearum* wilt incidence and increased the yield of tomato under filed conditions (Momol et al. 2005). Aqueous extracts of fresh leaves of *Datura stramonium*, *A. Sativum* and *Nerium oleander* exhibited antibacterial activity against bacterial wilt pathogen *Ralstonia solanacearum* in vitro and in vivo (Abo-Elyousr and Asran 2009). The aqueous extracts of leaves of *Camellia sinensis* was found highly effective against *X. campestris* pv. *campestris*, the cause of black rot of cabbage and cauliflower (Bhardwaj and Laura 2009). The hexane leaf extract of *A. nilagirica* was found to be effective against *X. campestris, P. syringae* and *Clavibacter michiganense* with MIC of 32 μg mL^{-1} (Ahameethunisa and Hopper 2010). Momilactone A and B, the two potent allelochemicals of rice, are known to exhibit antibacterial activity *(*Fukuta et al. 2007*)*.

12.4 Management of Plant Nematodes

Nematodes are small wormlike multicellular organisms, and generally live freely in the soil. However, there are several nematode species that parasitize plant roots and are problematic in tropical and subtropical regions of the world. Plant-parasitic nematodes reduce productivity and general fitness of the plants by feeding plant nutrients. There are about 1,200 plant-parasitic nematode species responsible for drastic economic losses to a great range of hosts. Vegetable and agronomic crops, fruit, nut and forest trees, and turfgrass are attacked by nematodes. Typical root symptoms include knots or galls, root-lesions, excessive root branching, injured root tips and stunted root systems. Symptoms on the aboveground plant parts are wilting even with ample soil moisture, foliage yellowing and fewer and smaller leaves. Stem nematodes cause stem swellings and shortened internodes. Bud and leaf nematodes distort and kill bud and leaf tissue. The most damaging are root-knot nematodes (*Meloidogyne* spp.) that have quite a large host range (Douda et al. 2012). Global economic losses caused by *Meloidogyne* sp. nematodes were evaluated at 100 billion USD per year (Oka et al. 2000**).** Others are cyst (*Heterodera* spp. and *Globodera* spp.), root lesion (*Pratylenchus* spp.), bud and leaf (*Aphelenchoides* spp.), needle (*Longidorus* spp.), reniform (*Rotylenchulus reniformis*), burrowing (*Radopholus similis*), spiral (*Helicotylenchus* spp.), bulb and stem (*Ditylenchus dipsaci*), dagger (*Xiphinema* spp.), and stubby root nematodes (*Paratrichodorous* spp.), all are able to cause radical changes in root cells to facilitate their lifestyle (Koike et al. 2003). Soil fumigants namely methyl bromide, methyl iodide, propargyl bromide or 1, 3-dichloropropene are suggested for nematode management (Wang et al. 2006), however, many of these chemicals disturb soil ecosystems (Dungan et al. 2003). Various physical methods including steam disinfection, soil solarization and hot water injection have also been employed for the control of nematode with varying success as alternate to soil fumigation with synthetic chemicals. However, many factors including soil type, climatic conditions and water content of soil can affect the effectiveness of physical treatments (Nishi et al. 2000; Nico et al. 2003).

12.4.1 Nematocidal Activity of Crude Extracts

There are frequent reports of nematicidal chemicals in crude plant homogenates, leachates, and decomposing residues (Halbrendt 1996). Aqueous extract of *Chrysanthemum coronarium* showed nematostatic activity against *Meloidogyne incognita* and *M. javanica* second-stage juveniles and inhibited their hatching from eggs and egg masses. Aqueous extracts of this plant species also expressed nematostatic activity against other plant nematode species namely *Heterodera avenae* and *Pratylenchus mediterraneus*, but did not affect the beneficial entomopathogenic nematode *Steinernema feltiae* (Bar-Eyal et al. 2006). Taba et al. (2008) evaluated ethanolic and aqueous extracts of wild plant species growing on Okinawa Island on the viability and mobility of second-stage *M. incognita* juveniles (J2 s). Aqueous extracts of *Hydrocotyle dichondroides Bidens pilosa* var. *radiata* Scherff, *Oxalis corymbosa*, *Stenactis annus* and *Oxalis corniculata* gave 90 % or better immobilisation activity. Among these, *B. pilosa* var. *radiata* exhibited the best activity. Extracts of different parts of *B. pilosa* especially those of leaves showed significant immobilisation, repellence, lethality and egg hatching inhibition. They further reported that the effects of *B. pilosa* extracts were more pronounced on the mobility of *M. incognita* than on the free-living nematode *Panagrolaimus* sp.

12.4.2 Crop Rotation, Intercropping and Soil Amendments

There have been many attempts to use allelopathy for the management of nematodes either by intercropping, rotation or green manuring. Soybean cyst nematode *H. glycines* is the most important cause of soybean disease in Canada and USA (Riggs and Niblack 1993). In Ontario, in order to reduce nematode population, some farmers rotate soybeans with maize (*Zea mays*) and wheat (*Triticum aestivum*) because these are nonhost crops for *H. glycines* (Riga et al. 2001). Nematode antagonistic plants reduce nematode population density by producing substances that inhibit growth or are lethal to plant-parasitic nematodes in plant tissue and soil (Sano 2005). Generally, members of family Asteraceae and leguminous plants are known to exhibit antagonistic behaviour to nematodes (Sano 1992; Bar-Eyal et al. 2006). Examples of well known nematode antagonistic plants are *Azadirachta indica*, *Urochloa maxima Tagetes erecta*, *T. patula*, *Crotalaria juncea*, *C. spectabilis* and several species of grasses (Chitwood 2002; Ferraz and de Freitas 2004; Taba et al. 2008). With the recognition of nematode invasion and disruption of tissues, hypersensitive reactions can occur in the roots of nematode antagonistic plants, which lead to the release of nematicidal compounds such as phenols, terpenes, alkaloids and amino acids (Sano et al. 1983; Tanda et al. 1989). Various species of the genus *Tagetes* are especially planted as intercrops or in rotation with other crops to control nematodes (Natarajan et al. 2006). Alexander and Waldenmaier (2002) reported 98 % reduction in populations of *Pratylenchus penetrans*, the root-lesion nematodes, when *T. erecta* was grown in rotation with tomato (*L. esculentum*). Sipes and Arakaki (1997) obtained similar results when *T. erecta* was cultivated as a cover crop and incorporated residues into the soil before sowing of *Colocastia esculenta.* Similar results were obtained when *T. erecta* was intercropped with soybean (El-Hamawi et al. 2004).

Alternatives to rotation and intercropping with nonhosts are green manuring and plant residue amendments prior to the cultivation of nematode host crop. A range of different plant residues has been examined for their capability to control plant-parasitic nematodes. Significant suppression in *M. chitwoodi* and *M. hapla* populations was recorded by cropping *B. campestris* and *B. napus* var. *napus* for 2 months and then incorporating it into the soil as green manure (Mojtahedi et al. 1991). Soil amendment with plant residues from nonhosts *Medicago sativa*, *Melilotus officinalis*, *Lespedeza hirta*, *L. intermedia L. capitata*, *Trifolium pratense Lolium multiflorum*, *L. perenne*, *Lupinus perennis* L. and *Pisum sativum* reduced the number of cyst nematode *H. glycines* juveniles in soil prior to planting of nematode host soybeans and subsequently in the roots of soybeans. These soil amendments increased egg hatching of the nematode in the absence of host plant and depleted lipid reserves of the juveniles (Riga et al. 2001). The survival and infectivity of potato cyst nematode juveniles are influenced by the quantity of neutral lipid reserves (Holz et al. 1999). Different dosages of leaf amendments of *A. indica*, *T. erecta*, *D. stramonium*, and *Calotropis procera* significantly improved the plant growth in okra and reduced root-knot *M. incognita* infections over untreated control. *A. indica* and *C. procera* exhibited the highest reductions in number of galls, egg masses and reproduction factor of the nematode (Hussain et al. 2011). Application of *C. coronarium* green manure to the soil significantly reduced nematode infection of tomato roots and improved plant top fresh weight, both in the greenhouse and in microplots (Bar-Eyal et al. 2006). Soil organic matter amendments such as rice and wheat brans in combination with solarization or wet heat treatment, has given a much greater control (Niimura 2002; Taba and Moromizato 2003). Recently, Douda et al. (2012) reported that the number of galls on roots of carrot due to root-knot nematode (*M. hapla*) was decreased by ploughing Indian mustard (*B. juncea*) followed by covering the treated area with polyethylene sheets. Some compounds namely ammoniacal nitrogen and isothiocyanates (Rodriguez-Kabana 1986; Mojtahedi et al. 1993), produced from decaying plant material have nematode-suppressive properties (Riga et al. 2001). In addition to their adverse effects on nematode population, organic amendments with antagonistic plants increase water-holding capacity, improve soil texture, supply nutrients to deficient soil and stimulate population of beneficial microorganisms which might be antagonistic to nematodes (Godoy et al. 1983; Rodriguez-Kabana 1986). Several reports indicate neem (*A. indica*) products, such as dry leaf powder, seed powder and aqueous neem extracts exhibit good usefulness against root-knot nematodes (Akhtar and Malik 2000; Oka et al. 2007).

12.4.3 Natural Nematocidal Compounds

A large number of plant species, belonging to 57 families, has been shown to contain nematicidal compounds (Sukul 1992). Several secondary metabolites of plants namely polythienyls, glucosinolates, isothiocyanates, polyacetylenes, cyanogenic glycosides, lipids, alkaloids, sesquiterpenoids, terpenoids, diterpenoids, triterpenoids, quassinoids, steroids, phenolics and numerous other classes, have been tested for their nematocidal activity (Chitwood 2001). Some of these have been proved very effective for nematode control. Uhlenbroek and Bijloo (1959) reported 5-(3-buten-1- yny1)-2,2'-bithienyl and α- terthienyl as highly nematicidal compounds in *Tagetes* sp. Similarly, Saleh et al. (1987) isolated a triglyceride, sn-glycerol-1-eicosa-9, 12-dien-oate-2-palmitoleate-3-linoleate from petroleum ether extract of *Argemone mexicana* seeds that was effective against *M. incognita.* Debprasad et al. (2000) reported that *T. erecta* many compounds such as palmitic acid, dodecanoic acid, steric acid, octaeicosane-8-one, myristic acid, triacontane-1-o1, α- sesquiphellandrene, 2-methyl-6-(4- methyl cyclohexadienyl), *β*-sesquiphellendrene, hept-4-en-2-ol, myristoleic acid and tricosane which showed nematicidal activity against *M. incognita*. The suppressive effect of leaves and roots of *Brassica* spp. on the lesion nematode *Pratylenchus* sp. was related to enhanced levels of 2-phenylethyl glucosinolate in *Brassica* spp. (Potter et al. 1998). Cyclic hydroxamic acids are secondary metabolites found in the family Poaceae. Zasada et al. (2005) evaluated two such compounds namely 4-dihydroxy-(2H)-1, 4-benzoxazin-3(4H)-one (DIBOA), and 2, 4-hydroxy-7-methoxy-(2H)-1, 4-benzoxazin-3(4H)-one (DIMBOA) against *M. incognita* second-stage juveniles and mixed-stages of *Xiphinema americanum.* The later one was found more sensitive than the former to DIBOA and DIMBOA with a maximum apparent mortality of 96 and 92 % compared to 73 and 72 % at 90 μg mL^{-1}, respectively. Perez et al. (2003) evaluated the effects of essential oils, extracted from numerous Asteraceous species on *M. artiellia*; the highest nematicidal activity was demonstrated by the essential oil of flower heads of *C. coronarium*. Kim et al. (2008) identified various nematicidal compounds namely *trans*-cinnamyl alcohol, decanol, benzaldehyde, *cis*-asarone, decanal, *trans*-2-decenal, undecanal, octanal, nonanal, dodecanal and *trans*-2-decen-1-ol from essential oils of *Coriandrum sativum, Liquidambar orientalis* and *Valeriana wallichii.* Recently, Kim et al. (2011b) tested commercial essential oils from 29 plant species against the pine wood nematode, *Bursaphelenchus xylophilus*. Essential oils of *Gaultheria fragrantissima* and *Zanthoxylum alatum* exhibited good nematicidal activities. Two compounds from these essential oils namely methyl *trans*-cinnamate and ethyl *trans*-cinnamate gave 100 % nematode mortality at 0.0625–2.0 mg mL^{-1} and 0.25–2.0 mg mL^{-1} concentrations, respectively. Marigold (*Tagetes* spp.) is well known for its ability to produce compounds like α-terthienyl that are allelopathic to many species of plant-parasitic nematodes (Hooks et al. 2010).

12.5 Conclusion

Allelopathic potential of higher plants can be exploited for the management of a variety of phytopathogens especially fungi and nematodes. Allelopathic plants of many angiospermic families especially Brassicaeae and Chenopodiaceae contain antifungal constituents. Members of these families are nonmycorrhizal also because of presence of these naturally occurring antifungal compounds. Similarly, most of species of Asteraceae, Papilionaceae and Poaceae contain nematicidal constituents and are antagonistic to soil-borne nematodes. For the management of soil-borne plant pathogens especially fungi and nematodes, allelopathic plants should be planted in rotation with susceptible crops, or as cover crops before sowing of susceptible plant species. In addition, allelopathic crops can be incorporated into the soil as green manure to reduce the population of phytopathogens. Crude extracts of these crops may be used as foliar spray for the management of aerial pathogens. Finally, the structures of allelochemicals can be used as analogue for the synthesis of new pesticides. These natural product based pesticides will possibly be far less harmful for the environment as compared to synthetic agrochemicals.

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Chapter 13
Allelopathic Potential of Sorghum in Agroecosystems

Ibrahim S. Alsaadawi

Abstract The promising allelopathic potential of sorghum opened a fruitful area of research to exploit this phenomenon in weed control and regulation of nutrient cycle. The data suggests that sorghum allelopathy can be exploited in different cropping practices, such as cover crop, smother crop, companion crop, and mixing crop to control weeds and inhibition of nitrification. Also, application of water extracts of sorghum at field level appeared to be effective method to reduce weeds and enhance productivity of the test crops. The herbicidal and allelopathic properties of sorgoleone, a compound isolated from root exudates of sorghum, and other allelochemicals in sorghum deserve further work to identify the enzymes responsible for the biosynthesis of these compounds and the genes encoding them. The other necessary step is the use of genetic engineering to manipulate the identified genes in sorghum or in other crops to enhance their ability to suppress weeds. This chapter addresses the research activity on the role of allelopathic potential in different cropping systems and the approaches developed in weed management.

13.1 Allelopathy in Agroecosystems

Agroecosystems, man-made distinct unit in agricultural fields, is regulated by ecological principles where all biotic and a biotic factors play an important role (Singh et al. 2001). Several agricultural practices, such as domestication, monoculture of high yielding crop, utilization of new techniques, and high inputs of

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agrochemicals have been implicated in the agroecosystems with the aim of increasing food production to meet the human demand. These practices have led to modern agrosystems dominated by monocropping systems. The monocropping systems reduce overall plant diversity leaving crop susceptible to weeds, insects, and pathogens (Singh et al. 2001). The nutrient rich and environmentally disturbed field of monocropping systems is a suitable habitat for invasion of weeds and other pests. Elimination of these non-crop biological components relies heavily on the application of pesticides. However, the selection pressure imposed by these pesticides often leads to evolution of many pesticides resistant pests. Additionally, output of these synthetic compounds may impacts human health and quality of environment. The monoculture, application of synthetic agrochemicals, and less biological diversity render monocropping system unsustainable. Therefore, moving toward a holistic cropping system filled with crop rotation, companion planting, cover cropping, and polycropping has become essential to recover some sustainability (Allen and Van Dusen 1988). There is a large volume of evidence that allelopathy provides a wide array of chemical interactions between crop–crop, crop-weed, and tree-crop that may benefit agroecosystems (Rice 1984). Soil microbes, weeds, and crop influence each other through chemical signals. A better understanding of these interactions under field conditions may provide practical strategies to develop new sustainable cropping systems with improved crop productivity, genetic diversity, ecosystem stability, nutrient cycling and conservation, weed control and disease management (Einhellig 1996; Kholi et al. 1998, 1999; Anaya 1999).

13.2 Allelopathic Effect of Sorghum on Crops

The early work on the allelopathic effects of sorghum on crops was conducted by Guenzi and McCalla (1962). They collected residues of several crops including sorghum from fields in Nebraska. Sorghum stalks were extracted with cold and hot water and one half of each water extract was autoclaved for 1 h and used to assay its effectiveness. The bioactivity of sorghum extract was assayed against growth of wheat (*Triticum aestivum*) seedling. Seed germination of wheat was significantly reduced by cold and hot non-autoclaved extracts by 100 and 72 %, respectively. Hot and cold autoclaved water extracts had slight allelopathic effects on germination. Non-autoclaved extracts of sorghum inhibited root growth more than autoclaved water extracts. Cold water extracts were more inhibitory to root and shoot of wheat seedlings. Bhowmik and Doll (1982) found that sorghum and corn residues stimulated the growth (plant height) of soybean.

Kim et al. (1993) tested the allelopathic potential of sorghum residues on germination and growth of rice, wheat, and corn. They found that germination and lengths of roots and tops were significantly reduced by water extracts of sorghum residues while corn was less sensitive. Likewise, Chung and Miller (1995) studied the allelopathic potential of nine grasses including sorghum on seed germination and growth of alfalfa (*Medicago sativa*) under laboratory and greenhouse conditions. They found that seed germination was inhibited by 79.8 % of control by sorghum extracts. Similarly sorghum extracts caused the highest inhibition in total length and dry matter of alfalfa seedlings.

Ben-Hammouda et al. (1995) tested the allelopathic potential of different parts of several sorghum hybrids. All plant parts tested revealed significant differences in their phytotoxicity to wheat seedlings regardless of the hybrid. Sorghum root and stem residues appeared to be more inhibitory components of sorghum plants.

In Pakistan intensive research work has been conducted by a group of researchers at Weed Science Laboratory, University of Agriculture, Faisalabad to investigate the allelopathic potential of sorgaab (water extract of mature sorghum plant) and sorghum mulches on several crops namely wheat (Cheema and Ahmad 1992; Cheema and Khaliq 2000), maize (*Zea mays*; Ahmad et al. 2000), mungbean (*Vigna radiata*; Cheema et al. 2000a) soybean (*Glycine max;* Khaliq et al. 1999), cotton (*Gossypium arboreum*; Ahmad et al. 1995; Cheema et al. 2000b), and raya (*Brassica juncea*; Bahatti et al. 2000). These studies indicated that spray of sorgaab one time or more on the test crops at different times after sowing and application of sorghum mulch at different rates significantly increased the yield of the test crops over control. The increase of yield was very striking in some crops, for example, the yield of cotton and maize sprayed with sorgaab increased up to 69 and 44 % of control, respectively, (Cheema et al. 2000b, Ahmad et al. 2000). In all cases, the increase in yield of the test crops was attributed to the weed suppression by sorgaab and sorghum mulch and to increase in most of agronomic traits including some yield components (Farooq et al. 2011).

13.3 Allelopathic Effect of Sorghum on Weeds

The occurrence of allelopathic traits in crops has attracted the attention of scientists for their potential use in weed management. During the last four decades, extensive work has been done on this approach and the following methods have been developed for the control of weeds.

- Use of sorghum extracts to control weeds
- Use of sorghum residues as mulch
- Use of allelopathic crops in crop rotation
- Use of allelopathic crop in crop mixture and intercropping

13.3.1 Use of Sorghum Extracts to Control Weeds

In our previous work (Alsaadawi et al. 1986a) we tested the allelopathic activity of plant water extracts of four sorghum cultivars that varied in their allelopathic potential of root exudates against *Amaranthus retroflexus*. The plant extract of all genotypes was inhibitory to *A. retroflexus*. However, extracts of the genotypes 219 and 260 were more damaging than the plant extract of the genotypes 177 and 264 (Table 13.1). Similarly decaying residues of genotypes 219 and 260 showed maximum inhibition to germination and seedling growth of *A. retroflexus* (Table 13.2).

Cheema et al. (1997) tested the allelopathic potential of water extract of sorghum and sunflower against weeds in the field of wheat crop and found spray of 100 % water extracts of sorghum and sunflower applied 30 days after sowing significantly reduced total weed density up to 48 and 32 % and weed dry weight up to 51 %. The inhibition varied between weed species. In another work, Cheema et al. (2000b) showed that spray of sorgaab on cotton crop suppressed weed density by 13–54 % and weed dry weight by 87 %. Additional work indicated that spraying of sorgaab on wheat, maize, alfalfa, soybean *(G. max)*, and raya (*B. juncea*) at different time of sowing significantly reduced total density and dry biomass of weeds in these crops (Khaliq et al. 1999; Cheema and Khaliq 2000; Ahmad et al. 2000; Cheema et al. 2000b; Bahatti et al. 2000). However, in most of the work carried out in this respect, allelopathy cannot totally replace the herbicides in weed control. This leads scientists in Pakistan to attempt to integrate sorgaab with low doses of herbicides in order to increase efficacy of sorgaab and reduce herbicide inputs. A series of experiments has been conducted using sorgaab in combination with low doses of herbicides to control weeds of different field crops including wheat, cotton, maize, and canola. It has been reported that sorgaab mixed with reduced rate of herbicides decreased density and dry weight of weeds, and enhanced yield similar or better than using recommended dose alone (Cheema et al. 2003a, b; Khaliq et al. 2002; Razzaq et al. 2010).

13.3.2 Use of Sorghum Residues as Cover Crop and Mulch

Cover crops and smother crops are old practices used by farmers of different regions of the world to reduce soil erosion, conserve soil moisture, improve nutrient status, and manage weeds. However, during the last four decades, it has been noted that allelopathic cover crops may provide an alternative method of weed suppression. This method is first explored by Putnam and his colleagues who found that allelopathic crops used as cover crops provided a great weed suppressing capacity (Putnam and DeFrank 1979, 1983; Putnam et al. 1983).

Sorghum is one of the strongest allelopathic crops, which has been extensively used as a cover crop or through incorporation of its residue in soil to control weed. Putnam and DeFrank (1979) found that mulches of sorghum or Sudan grass *Sorghum sudanense* applied to apple orchards in early spring reduced weed biomass by 90 and 85 %, respectively.

Forney et al. (1985) indicated that sorghum is often selected as annual cover crop because of its rapid growth and ability to suppress weeds. They added that

Table 13.1 Comparison of allelopathic potential of aqueous extracts of selected genotypes of *S. bicolor* against *A. retroflexus*

Genotypes	Oven dry weight (mg)*			Seed germination % of control
	Root	Shoot	Whole plant	
Control	34.3^{a}	114.0^{a}	148.3^{a}	100
219	4.8^{c}	15.4^{c}	20.2^{c}	71
260	3.8^{c}	13.7^{c}	17.5^{c}	71
177	8.1^{c}	26.3^{b}	34.4^{b}	90
264	6.5^{b}	6.4^{b}	32.9^{b}	86

* Average of at least 20 seedlings, numbers within each column followed by the same letter are not significantly different at 0.05 level according to Duncan's multiple range test. *Source* Alsaadawi et al. (1986a)

Table 13.2 Comparison of allelopathic potential of decaying residues of selected genotypes of *S. bicolor* against *A. retroflexus*

Genotypes	Oven dry weight (mg)*			Seed germination % of control
	Root	Shoot	Whole plant	
Control	52.5^{a}	166.1^{a}	218.6^{a}	100
219	12.2^{c}	79.2^{d}	91.4^{d}	40
260	19.5^{b}	103.6^{c}	123.1^{c}	41
177	23.3^{b}	134.6^{b}	157.9^{b}	45
264	20.9^{b}	128.0^{b}	148.9^{b}	47

* Average of at least 20 seedlings, numbers within each column followed by the same letter are not significantly different at 0.05 level according to Duncan's multiple range test. *Source* Alsaadawi et al. (1986a)

sorghum incorporated as green manure strongly reduced annual weed population and growth in the succeeding alfalfa crop.

Sudex (*S. bicolor* × *S. sudanense*) is widely used in trees nurseries as a cover crop in USA. The growth of *Cerecis canadensis* was significantly reduced when fresh and dry leaves of sudex were incorporated into growing medium even with additional amount of NPK in the nutrient solution (Geneva and Weston 1988). The reduction was proportional to the amount of incorporated leaf materials. In personal communication with Smeda, Weston indicated that spring—planted sorghum residues provide up to 90 % reduction in weed biomass for 6–8 weeks in no-till summer planted soybean (Weston and Czarnota 2001).

In Pakistan, a multi-year investigation of the effects of sorghum mulching on density and growth of weeds grown in the fields of wheat, cotton, canola, and maize has been conducted (Cheema and Ahmad 1992; Ahmad et al. 1995, 2000; Cheema et al. 2000a, b). The results of these studies clearly indicated that sorghum mulches applied at different rates reduced the density and dry biomass of weeds. In some cases, the reduction depended on the stage of sorghum incorporation, the quality of sorghum biomass added into the soil, growth condition, and the weed species. The reduction in weed density and biomass led to a significant increase in the yield of the test crops.

Table 13.3 Effects of residues of sorghum genotypes incorporated in soil on above ground biomass (g plant^{-1}) of *L. temulentum*

Sorghum cultivars	Residues rate (g kg^{-1} soil)		
	3	6	Mean
Kafeer	0.856	0.734	0.799
Enkath	0.806	0.577	0.691
Giza 115	0.708	0.698	0.700
Dewardo	0.886	0.861	0.873
Rabeh	1.123	0.982	1.053
Giza 15	0.685	0.525	0.605
Arbel	0.916	1.100	1.008
Argence	0.835	0.803	0.819
Rabeh x F4	0.835	0.803	0.819
F10-R-2002	1.034	0.819	0.927
Control	2.217	2.617	2.410
Mean	0.887	0.825	

LSD = 0.05; Genotypes = 0.224; Residues rate = 0.141; Genotypes × Residues rate = 0.365.

Source Alsaadawi et al. (2007)

Recently, several hundreds of sorghum cultivars were introduced and cultivated in Iraq to select the most promising genotypes in terms of production, weeds competition, and fitness to local environment. Ten cultivars were selected. Field observations revealed that growth and population of companion weeds were variable among the stands of selected genotypes (Alsaadawi et al. 2007). Also, differential growth and population variation were observed on weeds grown in the field after sorghum harvest. This suggests that allelopathy could be the mechanism responsible for the reduction of weeds growth and population and the differences among stands could be due to differences in the allelopathic potential of the test cultivars. Several experiments were conducted to test this hypothesis. Results indicated that residues of all test cultivars significantly inhibited the growth of *Lolium temulentum* weed (Table 13.3). The phytotoxicity of residues differed among the test genotypes. Three out of 10 tested genotypes tested, three (Giza 15, Giza 115, and Enkath) reduced mean dry weight of weed by more than 71 %. Rabeh was the least allelopathic cultivar, with growth reduction of 56 %.

Additional experiment conducted in a field infested with *L. rigidum, L. temulentum, Malva pariflora, Carthumus oxycantha, Silybum marianum, Melilotus indica, Chenopodium album, Beta vulgaris, Polypogon monspeliensis, Trifolium repense, and Plantago ovata* revealed that the aboveground biomass and number of all weeds were reduced by the residues of test sorghum cultivars incorporated into field soil at rates of 3 and 6 g kg^{-1} soil. However, the response varied among the weed species (data not shown). Residues of cultivars Giza 15, Giza 115, and Enkath provided 67, 59, and 63 % reduction in average weed numbers and 58, 66, and 58 % reduction in average weed biomass, respectively (Table 13.4). Residues of Rabeh cultivars inhibited average weed numbers and average weed biomass by 41 and 52 %, respectively. Weeds numbers were

Table 13.4 Effects of residues of sorghum cultivars incorporated in soil on total number and total aboveground biomass of weeds

Rate of residues (g kg^{-1}soil)	Sorghum cultivars					
	Control	Giza 15	Giza 115	Enkath	Rabeh	Mean
Weed numbers (m^{-2})						
3	76.3	27.0	36.3	34.6	48.0	44.4
6	72.3	21.3	25.0	20.3	40.0	35.8
Mean	74.3	24.2	30.7	27.5	44.0	
LSD = 0.05; Genotypes: 15.3; Residues rate: 10.2; Genotypes x Residues rate: 11.2						
Weed biomass (g m^{-2})						
3	421.1	196.8	178.8	172.2	198.5	233.5
6	432.4	161.2	115.6	182.7	215.4	221.5
Mean	426.8	179.0	147.2	177.5	206.9	
LSD = 0.05; Genotypes: 00.8; Residues rate:159.3; Genotypes × Residues rate: 133.3						

Source Alsaadawi et al. (2007)

significantly decreased with increasing rate of residues of the stronger allelopathic cultivars in soil. The persistence of sorghum phytotoxic residues in soil was monitored using *C. album* in the bioassay (Table 13.5). The phytotoxicity started after 1 week of decomposition and persisted for 8 weeks at low rate of residues and for 10 weeks at the higher rate of residues. The reduction was proportional to the amount of residues in soil during the first 6 weeks of decomposition. Giza 15, Giza 115, and Enkath showed greater phytotoxicity than Rabeh cultivar at all decomposition periods.

Thus sorghum residues prove to have a significant approach in weed control. However, in most of the studies, the reduction by residues does not match with reduction of herbicides. Therefore, a program was initiated to test if the integration between allelopathic crop residues with sub recommended doses of herbicides. It could lead to improve the efficacy of allelopathic residues and may provide the opportunities of reducing the herbicidal doses. Results indicated that low herbicide application in plots amended with sunflower or sorghum residue recorded least total weed density and biomass in fababean and barley fields and resulted in similar crop yield or even better than was noticed with recommended herbicides dose (Alsaadawi et al. 2011; Alsaadawi and Al-Temimi 2011).

13.3.3 Use of Sorghum Residues for Weeds Smothering

Smother crops are grown in rotation or as catch crop and shade out the weeds due to their quick growth and thick stand (Singh et al. 2001). This practice has been used for several years to prevent soil erosion and control weeds. The farmers employed this practice assuming that smother crops have the ability to suppress weed through competition only. However during the past five decades it was found that these crops suppress weeds through competition and allelopathy. None crop

Table 13.5 Effects of residues of sorghum cultivars decomposed for different periods on seedling length (cm) of *C. album*

Sorghum cultivars	Residues mixed (g kg^{-1} soil)	Decomposition periods (weeks)*					
		1	2	4	6	8	10
Giza 15	0	4.72^{a}	5.41^{a}	4.93^{a}	3.75^{a}	4.19^{a}	4.33^{a}
	25	3.03^{b}	3.92^{b}	3.25^{b}	2.91^{b}	3.98^{a}	3.89^{a}
	50	2.85^{b}	2.59^{c}	2.75^{c}	2.33^{c}	2.93^{b}	4.03^{b}
Giza 115	0	4.77^{a}	5.45^{a}	5.28^{a}	4.34^{a}	4.21^{a}	4.22^{a}
	25	3.95^{b}	3.90^{b}	3.70^{b}	3.62^{b}	3.94^{a}	3.96^{ab}
	50	3.40^{c}	3.36^{c}	2.73^{c}	2.78^{c}	3.08^{b}	3.70^{b}
Enkath	0	4.83^{a}	5.29^{a}	5.13^{a}	4.33^{a}	4.19^{a}	4.63^{a}
	25	3.70^{b}	3.78^{b}	3.16^{b}	3.14^{b}	4.02^{a}	3.88^{b}
	50	2.96^{c}	2.84^{c}	2.61^{c}	2.46^{c}	3.08^{b}	3.25^{c}
Rabeh	0	4.64^{a}	4.58^{a}	4.42^{a}	4.49^{a}	4.45^{a}	4.43^{a}
	25	4.20^{ab}	3.88^{b}	3.93^{b}	3.91^{b}	4.15^{ab}	4.33^{ab}
	50	3.80^{b}	3.66^{b}	3.28^{c}	3.18^{c}	3.83^{b}	3.85^{b}

* Numbers with each column for each cultivar sharing with same letter are not significantly different according to Duncan's multiple range tests. *Source* Alsaadawi et al. (2007)

plant species could also offer a possibility to smother weeds when associated with crop or planted in rotational sequence with them by producing allelochemicals inhibitory to weeds but not harmful to the growing crop (Gliessman 1983).

Sorghum has been reported to have a greater ability to smother weeds. Putnam (1990) found that several smother crops including sorghum × Sudan grass hybrid were very effective in reduction of weed population. Wheat residues stimulated seed germination while forage crops smothered weeds (Narwal and Sarmah 1997). The smothering ability of the test crop was variable with test forage crop. Pear millet was most effective as it reduced weeds by 90 % followed by maize, sorghum, cluster bean, and cowpea (*V. unguiculata*). Narwal (2000) indicated that inclusion of fodder crops (sorghum, pearl millet, and maize) in the field before the rice crop in rice—wheat rotation significantly reduced weed biomass in the succeeding rice crop and may reduce the use of herbicides. In Southern USA, growers are customarily using sorghum × Sudan grass hybrid as a smother and cover crop to prevent soil erosion and reduced weed infestation during the succeeding year (Weston 1996). The hybrid is reported to have strong allelopathic inhibitory effects on weeds. The suppression effect of the residues was persistent even in the next crop.

13.3.4 Use of Sorghum in Crop Rotation

Crop rotation is defined as a cropping system in which two crops are in a fixed sequence on a piece of land without disturbing the soil fertility (Lockhart and Wiseman 1970). Several factors, such as soil fertility, soil structure, plant nutrient, choice of suitable crop have been considered in the developing of a crop rotation system. Allelopathy, however, was not included in these factors. Allelochemicals may be released into the soil in rotation system by root exudation and/or decomposition of the allelopathic crop and inhibited or stimulated the growth of the subsequent crop.

Sorghum has an allelopathic effect on the succeeding crops. The first indication of sorghum autotoxicity was observed by Burgos–Leon (1976). He observed that growth of sorghum is markedly reduced following sorghum in sandy soil but not in soil high in montmorillonite. Additional work Burgos-Leon et al. (1980) investigated the reasons of these observations and concluded that sorghum roots and tops incorporated in the sandy soil significantly inhibited growth of sorghum seedlings. No growth inhibition was observed when residues were added in such soil high in montmorillonite. However, sorghum residues incorporated in such soils significantly reduced growth of sorghum seedlings under sterile soil conditions. Water extracts of sorghum roots and tops significantly inhibited growth of sorghum seedlings. Three major phytotoxins *p*-coumaric, *m*-hydroxy-benzoic, and protocatecheuic acids were identified from root residues. Acid hydrolysis of root extracts released large quantity of *o*-hydroxybenzoic acid. When the sterile water extracts of sorghum root was inoculated with *Trichoderma viride* or *Aspergillus* sp, the toxicity disappeared in a short time (Burgos-Leon et al. 1980). Additional experiments with non-sterile and non-inoculated field soil revealed that several weeks were required to detoxify the soil after addition of root residues of sorghum.

Alsaadawi et al. (1986a) conducted screening experiment to examine the activity of root exudates of 100 cultivars of sorghum to inhibit seed germination and seedling growth of *A. retroflexus* in sand culture. The response of weed varied among the test cultivars. They found 82 % of the control reduction in seed germination in 25 cultivars. Ten cultivars inhibited growth of *A. retroflexus* by more than 79 % of control. Collection and identification of root exudates revealed that neutral fraction was inhibitorier than acidic and basic fractions.

Netzly et al. (1988) demonstrated that hydrophobic root exudates of sorghum significantly stimulated witch weed (*Striga asiatica*) parasite and this can furnish a potential method to reduce the seed bank of this weed in soil. Einhellig and Leather (1988) determined weed biomass in strip cropping of sorghum, soybean, and maize in the following year. They found that weed biomass was significantly reduced in plot where sorghum had been grown a year before compared to soybean and maize plots. Further work by Einhellig and Rasmussen (1989) revealed that grain sorghum crop reduced weeds in crop of the following year. They attributed the reduction of weed biomass in the sorghum plot to allelopathic effects of sorghum. Others found that incorporation of plant residues of various crops including sorghum reduced weed biomass and density in the order pearl millet > maize > sorghum > cluster bean > cowpea (Narwal and Sarmah 1997).

Sene et al. (2000) found that peanut seedling establishment was better between rows than on rows of previous sorghum crop. They proposed a geometrical sowing pattern for peanuts between the rows of previous sorghum crop to escape the latter "allelopathic heritage". They also examined the phenolic content of the row and inter row soils but did not find consistent data from year-to-year suggesting possibly that phenolics are not the principle compounds responsible for sorghum allelopathy.

Prompt tillage of mature sorghum delayed the growth of the following wheat crop but did not affect yield probably due to allelochemicals degradation; however, no-tillage stovers reduced grain yield of wheat crop possibly because the allelopathic compounds leached slowly (Roth et al. 2000).

Alsaadawi et al. (2007) screened the allelopathic activity of root exudates of sorghum cultivars varying in their allelopathic potential to the companion weed *Echinochloa colonum*. All cultivars significantly reduced biomass of the test weed. However, cultivars with high allelopathic potential (Giza 15 and Enkath) were found to be more effective than those with low allelopathic potential ones (Table 13.6).

13.3.5 Use of Sorghum in Crop Mixture and Intercropping

Intercropping is an ancestral practice used by the farmers of the developing world to maximize crop production, reduce risk failure, soil erosion, and suppress weeds (Altieri et al. 1983; Moody 1980). Narwal (1994) stated that productivity of crop mixture may be increased or decreased depending on stimulatory and inhibitory effects of component crops on each other provided growth resources, such as light, water, nutrients, and space are not limiting factors. Root exudates play a major role in increasing growth and yield of crop mixtures by improving ions uptake and reducing weed population. Sorghum is one of the allelopathic crops used in intercropping systems to increase yield of crop components and reduce weed infestation (Kondap et al. 1990; Sistachs et al. 1991). Intercropping practice may be enhanced using crops with highly allelopathic root exudates that can suppress weeds without harming the crop. This approach could help in controlling weed infestation and reduce herbicide application. It has been reported that the allelopathic potential of root exudates was variable among the sorghum genotypes. More recent work by Weston and Czarnota (2001) on the allelopathic potential of root exudates of 25 genotypes of sorghum to *A. retroflexus* using hydroponic culture system revealed that root and top growth of the weed varied among the test genotypes.

13.4 Allelopathic Effect of Sorghum on Nitrogen Cycle

Allelopathy affects several biological processes in nitrogen cycle, such as nitrogen fixation and nitrification (Jobidon and Thibault 1982; Weston and Putnam 1985; Rice 1984; Alsaadawi et al. 1986a, b; Alsaadawi 1988; Zwain et al. 1998). However, much needs to be done to integrate this allelopathic mechanism in cropping systems in order to regulate the utilization of nitrogen added to the soil by plants through nitrification inhibition and avoid the inhibition of biological

Table 13.6 Effects of root exudates of sorghum cultivars on growth of *E. colonum* weed

Sorghum cultivars	*Echinochloa colonum*[*]	
	Dry weight (mg)	Inhibition %
Control	177.0[a]	–
Giza 15	142.5[b]	19.5
Giza 115	127.3[c]	28.1
Enkath	122.5[c]	30.8
Rabeh	151.0[b]	14.7

[*] Numbers within each column followed by the same letter are not significantly different at 0.05 level according to Duncan's multiple range test. *Source* Alsaadawi et al. (2007)

nitrogen fixation. Huber et al. (1977) concluded that inhibition of nitrification may markedly increase the efficiency of food production, reduce energy requirements for growing crops, decrease the incidence of plant disease, and reduce the pollution potential of nitrogen fertilizers. Some crops appeared to have potential inhibitory effects on nitrogen fixation and nitrification processes (Alsaadawi 1988; Rice et al. 1980, 1981; Rice 1992).

With respect to sorghum, Alsaadawi et al. (1986a) reported that growth demotion effects of four sorghum genotypes varied in their allelopathic potential on soil nitrification using soil incubation method. Residues of all test genotypes were found to reduce nitrification rate with maximum inhibition achieved by the higher allelopathic cultivars. Further work by Alsaadawi et al. (1986b) revealed that sorghum plants from seeds exposed to doses of gamma irradiation (0.5, 1, 1.5 kRad) had more inhibitory level in their extract and decaying residues on nitrification.

The allelopathic effects of the hybrid (*S. bicolor* × *S. sudanese*) on growth and nitrogen fixation were investigated under greenhouse conditions by Alsaadawi and Sakeri (unpublished data). It was found that residues of the hybrid incorporated at rates of 4.4 and 8.8 g/kg soil significantly inhibited growth of kidney bean, nodulation, and hemoglobin content of nodules. The reduction of hemoglobin was increased with increased concentration of the hybrid residues in soil.

13.5 Allelochemicals in Sorghum

The inhibitory compounds occurring in sorghum plants are mostly phenolic acids. Guenzi and McCalla (1966) isolated several phenolic acids, such as vanillic, syringic, ferulic, *p*-hydroxybenzoic, and *p*-coumaric acids from some cereal crops including sorghum.

Alsaadawi et al. (2007) quantified the level of phenolic acids in the extracts of highly allelopathic cultivars of sorghum (Giza 115, Giza 15 and Enkath) and low allelopathic cultivar (Rabeh) by HPLC. The analyses revealed the presence of vanillic, syringic, ferulic, *p*-hydroxybenzoic, *p*-coumaric, and gallic acids in the residues of Giza 15 and Enkath cultivars (Table 13.7). All these phytotoxins except gallic acid were found in the residues of Giza 115, while, residues of Rabeh cultivar contained all phytotoxins except *p*-coumaric acid. Residues of Giza 115 and Giza 15 contained up to 5 times more *p*-hydroxybenzoic acid than Rabeh cultivar, whereas, Enkath accumulated up to three times more than Rabeh cultivar. Total isolated phytotoxins were higher in Giza 115 and Giza 15 than in the other cultivars.

During the last three decades considerable work has been done on the phytotoxicity of root exudates of sorghum. It has been shown that the major component of root exudates is an oxidized hydrophobic *p*-benzoquinone called sorgoleone. The presence of this compound in root exudes was first reported by Netzly and Butler (1986). Sorgoleone shows considerable phytotoxicity in different growth assays and is inhibitors of plant growth through inhibition of photosynthesis (Einhellig and Souza 1992; Einhellig et al. 1993). Additional work documented that sorgoleone is a potent inhibitor of photosynthesis and its site of inhibition is within the PSII complex (Nimbal et al. 1996; Gonzalez et al. 1997). Weston and Czarnota (2001) evaluated the competitive binding of sorgoleone versus atrazine and found that sorgoleone has the ability to bind to the D1 protein of PSII complex. Dayan et al. (2003) demonstrated that the herbicidal and allelopathic properties of sorgoleone make the isolation of the genes responsible for the biosynthesis desirable. They further indicted that the manipulation of those genes in sorghum or their introduction into other plant species through genetic engineering could provide a better understanding of the role of sorgoleone in plant interaction and enhance the natural weed control provided by sorghum and its residues.

13.6 Conclusion and Future Needs

The present review addresses the allelopathic potential of grain sorghum and other related species for their ability to control weeds and improve yield of crops in different cropping systems. In order to achieve these goals under field conditions the following approaches need to be adopted:

1. The traditional cropping pattern in which sorghum is used needs to be revived with the new approaches, such as cover crop, smother crop, intercropping, and crop rotation.
2. The allelopathic potential of sorghum in crop rotation could be used to enhance production of crop simply by exploiting favorable interactions such as weed control and avoiding inhibitory effects of sorghum by selecting crop resistant to sorghum phytotoxins**.** Thus sorghum to crop relationship need to be investigated thoroughly to determine which crop can follow sorghum with least inhibitory or having stimulatory effect.
3. Screening of sorghum genotypes needs to be continued in order to select genotypes with greater weed suppression ability to exploit them in the new developed approaches of cropping systems.

Table 13.7 Phytotoxins isolated from the residues of different sorghum cultivars

Sorghum cultivars	Phytotoxins (μg g^{-1} residues)*, **						
	Vanillic acid	Syringic acid	Ferulic acid	*p*-hydroxybenzoic acid	*p*-coumaric acid	Gallic acid	Total
Control	–	–	–	–	–	–	–
Giza 15	1.42^b	1.50^a	5.10^a	8.00^a	1.24^a	1.60^a	18.84^a
Giza 115	1.10^b	0.94^b	3.20^b	8.14^a	0.80^b	–	14.80^b
Enkath	1.00^b	0.41^c	2.53^c	4.40^b	0.90^b	1.05^b	10.29^c
Rabeh	4.30^a	1.04^b	2.33^c	1.66^c	–	1.15^b	10.48^c

** Numbers within each column followed by the same letter are not significantly different at 0.05 level according to Duncan's multiple range test. * Each value is an average of 3 replicates. *Source* Alsaadawi et al. (2007)

4. The promising herbicidal and allelopathic properties of sorgoleone and other allelochemicals in sorghum deserve further work to identify the enzymes responsible for the biosynthesis of these compounds and the genes encoding them. The other necessary step is to use genetic engineering to manipulate the identified genes in sorghum or in other crops to enhance their ability to suppress weeds.
5. Application of water extract and residues of sorghum plants is a promising method to control weeds and enhance crop production. However, more work is imperative to test the water extracts of highly allelopathic accessions of sorghum and species of the related genus *Sorghum* such as *S. halepense*. Also, it would be fruitful to test the combined effect of different concentrations of sorghum extract and residues with low doses of herbicides in order to obtain a more effective control of weeds and reduce the input of synthetic herbicides in agroecosystems.

In conclusion, the future looks bright for using allelopathic properties of sorghum in the developed approaches of cropping systems to control weeds and develop sorghum cultivar(s) with superior ability to inhibit weeds by using biotechnology techniques.

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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 ‘allelos’ 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

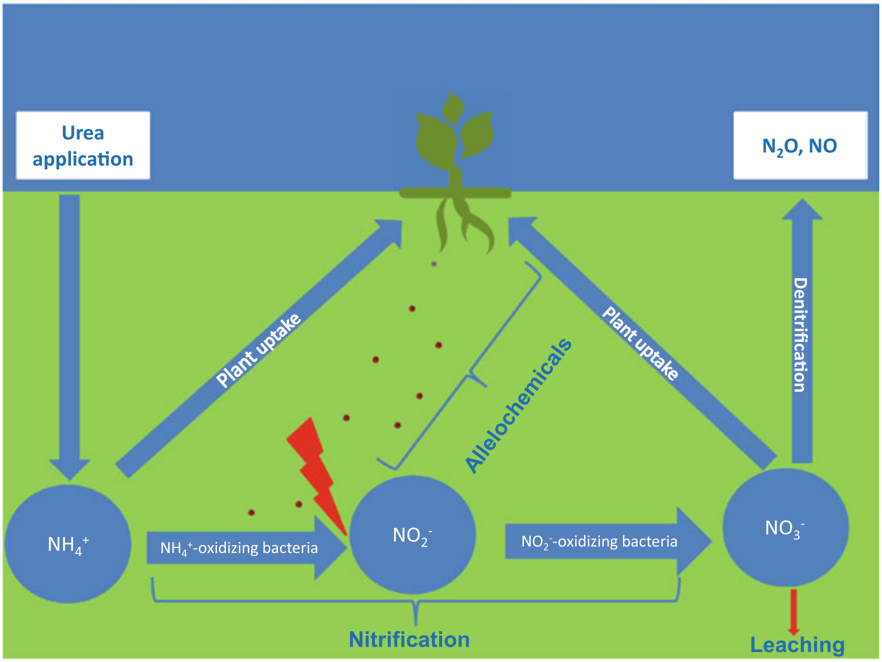

Fig. 14.1 Influence of allelopathy on biological nitrification inhibition and nitrogen dynamics

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 europea*, 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 *Leymus racemosus*	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 *Leymus racemosus*	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 *Brachiaria humidicola* in barren soil	30	28	Gopalakrishnan et al. (2009)
Root exudates of *Brachiaria humidicola* in Rhizosphere soil	30	08	Gopalakrishnan et al. (2009)
Root exudates of *Brachiaria humidicola* in barren soil	60	56	Gopalakrishnan et al. (2009)
Root exudates of *Brachiaria humidicola* 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 N_2. 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 benzofuran] 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 efficieny 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
Gallic acid Protocatechuic acid *p*-Hydroxy benzoic acid Caffeic acid	*Phalaris minor*	Decreased P and Zn uptake in wheat	Chakraverty et al. (2005)
Gallic acid Protocatechuic acid *p*-Hydroxybenzoic acid Vanillic acid	*Chenopodium album*	Decreased P and Zn uptake in wheat	
Gallic acid Protocatechuic acid *p*-Hydroxybenzoic acid	*Polygonum hydropiper*	Decreased P and Zn uptake in wheat	
Protocatechuic Ferulic acid *p*-Coumaric acid Syringic acid	*Chenopodium murale*	Suppressed nodulation in chickpea	Batish et al. (2007)
Protocatechuic Ferulic acid *p*-Coumaric acid Syringic acid		Suppressed nodulation in pea	
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)
Syringic acid Caffeic acid Protocatechuic acid	–	Decreased Fe, Mo, N, P and K in cowpea	Alsaadawi et al. (1986a)
Caffeic acid *p*-Coumaric acid	–	No effect on autotrophic nitrifying microorganisms	McCarty et al. (1991)
–	*Ipomoea batatas*	Reduced uptake of P, K, Ca, Mg, S, Zn, B and Cu by sweet potato	Walker et al. (1989)
Citric acid	*Cucurbita pepo*	Improved uptake of K, Mg, Fe, Zn by summer squash	Gent et al. (2005)
Citric acid Oxalic acid	*Vigna mungo*	Improved P uptake by blackgram	Jakkeral and Kajjidoni (2011)

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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Chapter 15
Implications of Potential Allelopathic Crops in Agricultural Systems

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Abstract Allelopathic phenomenon is being successfully employed in field crop production for agricultural pest management. Allelopathic crops exude diverse and numerous types of allelochemicals with potential to suppress weeds and other crops pests. Crops including rice, sunflower, sorghum, wheat, rye, maize, barley, alfalfa, *Brassica* spp., and cucurbits exhibit strong allelopathic potential. The allelopathic potential of crops possesses pertinent implications in the agricultural systems. Allelopathy helps plants in strengthening their defense system against biotic and abiotic stresses, and also aids in regulating the nutrients transformations. Allelopathic potential of the crops can be wisely manipulated by adjusting these crops in the crop sequences as rotational crops, cover crops, or intercrops to reduce the pest pressure and judicious nutrient management. This chapter provides an overview of potential allelopathic crops and their potential applications in agricultural systems.

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15.1 Introduction

Pest pressure, their control expenditures, as well as the food demands are rising continuously. Rapid increase in world population has necessitated producing foods in higher quantities to diminish the hunger. Cropping intensity, cost of production, and the area under food crops has increased world over. There is a subsequent higher pest pressure on crops and an ultimate desire to control these pests with minimum reliance on pesticides in the wake of food quality and environmental degradation. Addition of herbicide residues in the food web and the ground water are the concerns of intense gravity. Resistance in weeds against the herbicides is the other most important issue desired to be addressed. Effective manipulation of allelopathic phenomenon in the agroecosystems holds the scope to address many of these gravities, or at least dilute their deleterious impacts.

Allelopathy is the phenomenon of chemical interactions among the plants and/or among plants and other organisms (Farooq et al. 2011a). Plant species produce secondary metabolites or allelochemicals, which are involved in these chemical interactions. There are a number of allelopathic crop plants, weeds, and trees with diverse significance in the natural ecosystems as well as the human managed agroecosystems. The allelochemicals perform diverse activities in the plant ecosystems. For example, allelochemicals are involved in the rhizosphere interactions among plants and among plants and microflora and microfauna. Organisms other than plants for interactions in the rhizosphere can be soil insects, soil bacteria, fungi, etc. Autoinhibition (a form of autotoxicity) is the important phenomenon mediated by the allelochemicals whereby germination is inhibited or delayed to avoid interspecific competition or unsuitable environmental conditions. Allelopathic potential of crops can be effectively manipulated to tackle the serious threats to the sustainability of agroecosystems, such as the resistance in weeds against herbicides (Farooq et al. 2011a; de Albuquerque et al. 2011). For example, fitting an allelopathic crop in a cropping sequence lowers the weed pressure for routine crops and enhances their output. It is highly advisable to formulate a crop rotation, which utilizes the allelopathic influence of sequence crops for weed suppression (Farooq et al. 2011a). Cover crops and crop residues mulches are the other attractive options for the utilization of allelopathic properties of field crops for the suppression of weeds and other pests (Tabaglio et al. 2008). In addition, some researchers have focused on the use of plant water extracts of allelopathic properties for the pest control (Jabran et al. 2008a, 2010a, b, c; Saffari et al. 2010). All these strategies are concerned with improving the food and environment quality through chemical-free pest management with the manipulation of the natural allelopathic phenomenon. Efforts are underway to produce crop cultivars with stronger allelopathic potential through conventional breeding and genetic engineering. Newly evolved cultivars with stronger allelopathic potential would be better able to withstand biotic and abiotic stress.

In this chapter, an overview of potential allelopathic crops, the allelochemicals present in these, and their utilization in crop production systems is discussed.

15.2 Potential Allelopathic Crops

Several plant species including crop plant as well as weeds have been found to possess strong allelopathic potential. However, only the crop plants received the prominent focus for evaluation of allelopathic potential in greenhouse bioassays as well as under field conditions. Allelopathic potential of many of field crops was evaluated for the possibility of chemical-free weeds and other pest suppression.

Also, several allelochemicals were identified, isolated, and quantified from these crop plants. These allelochemicals were found inhibitory to the growth and development of plants in the bioassays. Most diverse allelochemicals include phenolics, hydroxamic acids, glucosinolates, momilactone, etc. The allelopathic potential of the crops can be further exploited through selection of cultivars with better pests suppression capability. Similarly, the allelopathic potential of crops can be further strengthened through conventional breeding and use of modern tools of biotechnology and genomics. Improving the allelopathic potential of crops against weeds, insect pests, and disease pathogens through conventional breeding, molecular genetics, and the biotechnology holds a great promise for effective pest suppression.

15.2.1 Rice

Many studies report the allelopathic potential of rice (*Oryza sativa* L.), one of the most important cereal crops worldwide (Mattice et al. 2001; Chon and Kim 2004; He et al. 2004; Farooq et al. 2008; Jabran et al. 2010a). Several allelochemicals and quantitative trait loci (QTLs) have been correlated with rice allelopathic potential (Jensen et al. 2001; Okuno and Ebana 2003; Khanh et al. 2007). Chromosomes 1, 3, 5, 6, 7, 9, 10, 11, and 12 contained the QTLs for the allelopathic activity of rice (Jensen et al. 2001; Zeng et al. 2003). Japonica rice varieties are reported to possess higher allelopathic potential than the indica varieties (Jensen et al. 2001).

Okuno and Ebana (2003) examined QTLs of rice allelopathy by crossing cultivars PI312777 and Rexmont (having more suppressive and less suppressive effects on associated weeds, respectively). The differential proteomic analysis confirmed that increased allelopathic potential in rice exposed to stress was due to increased expression of enzyme genes involved in the biosynthesis of phenolic compounds and decreased expression of enzyme genes associated with terpenoid biosynthesis. Hence, isoprenoid and phenylpropanoid metabolic pathways may be important for the production of allelochemicals in rice (Shen et al. 2008). He et al. (2010) reported that cultivating allelopathic (PI312777) and non-allelopathic (Lemont) rice cultivars in the vicinity of barnyard grass (*Echinochloa crus-galli*) enhanced the allelopathic activity and growth of cultivar PI312777. This was due to improvement in carbon assimilation resulting from the regulation of photosynthesis genes and the activation of the enzyme system.

Phenolic compounds extracted from decomposing rice residues and straw in soil had synergistic effects on suppressing three *Rhizobium* strains, reducing nitrogen fixation, and decreasing nodulation and hemoglobin content of common bean (*Phaseolus vulgaris*), which most likely reduced soybean (*Glycine max*) yield following rice (Rice et al. 1981). Olofsdotter et al. (1999) studied the allelopathic potential of more than 100 rice cultivars for variation in suppression of a major rice weed, barnyard grass. Of 10,000 rice accessions tested for their allelopathic activity against ducksalad (*Heterenthera limosa*), purple ammannia (*Ammannia coccinea*) or both weed species, 557 had allelopathic potential (Dilday et al. 1994, 1996). In Egypt, of 1,000 rice cultivars tested for their allelopathic potential, 45 suppressed barnyard grass and flatsedge (*Cyperus difformis*) (Hassan et al. 1998). In another study, seven rice cultivars (four from the USA, three from Asia) were evaluated for allelopathic potential, wherein cultivars from Asia strongly suppressed the barnyard grass (Gealy et al. 2003). Likewise, Salam and Kato-Noguchi (2009) evaluated 102 rice genotypes (high yielding = 42; low output = 60) from Bangladesh for their allelopathic potential against several plant species such as cress (*Lepidium sativum*), barnyard grass, jungle rice (*E. colonum*), and lettuce (*Lactuca sativa*). Many of the cultivars suppressed weeds growth; however, the cultivars BR17 and Kartikshail had the highest allelopathic activity. Nevertheless, these cultivars were species specific for their allelopathic activity (Kato-Noguchi et al. 2009). Kartikshail rice cultivar was further explored to contain two allelochemicals, 3-hydroxy-β-ionone and 9-hydroxy-4-megastigmen-3-one; and the extracts from this cultivar inhibited the root and shoot growth of many weed and crop species (Kato-Noguchi et al. 2011a).

Khanh et al. (2009) evaluated 73 rice accessions from Vietnam for their allelopathic activity against barnyard grass in controlled environment as well as field conditions. The accessions showing highest allelopathic potential were four in bioassay, three in green house, and one in field conditions. Hybrids had the highest allelopathic activity compared with other accessions. The greenhouse results for inhibition of weed growth and allelopathic activity of rice accessions were correlated with their performance under field conditions. Seal and Pratley (2010) screened 27 rice cultivars against five problematic and herbicide resistant weeds. The rice cultivars possessed a variation in their allelopathic ability; seven cultivars were highly allelopathic with a weed inhibition of over 90 %.

Several allelochemicals such as phenolic acids, phenolic aldehydes, aliphatic acids, flavone, cyclohexane, and momilactones have been found in rice straw (Table 15.1; Pramanik et al. 2001; Kong et al. 2004). Momilactone A and B are growth inhibitors exuded from rice roots, which act as potent allelochemicals (Kato-Noguchi et al. 2003, 2008; Kato-Noguchi and Ino 2005). Barnyard grass growth was suppressed by eight rice cultivars, which exhibited their allelopathic activity against weed by exudation of momilactone A and B with a concentration of 0.21–1.5 and 0.66–3.8 μmol L^{-1}, respectively for various cultivars under study. The results were confirmed by exogenous application of these allelochemicals to suppress barnyard grass growth. Momilactone B was the major inhibitor of weed growth in comparison with momilactone A (Kato-Noguchi et al. 2010a). Likewise,

Table 15.1 Allelochemicals reported in rice

Allelochemicals	Reference
Salicylic acid, *p*-coumaric acid, *o*-hydroxyphenylacetic acid, syringic acid, ferulic acid, benzoic acid, *p*-hydroxybenzoic acid, *m*-coumaric acid, *o*-coumaric acid	Chung et al. (2002)
p-hydroxybenzoic, *p*-coumaric acid, vanillic acid, ferulic acid, *o*-hydroxyphenylacetic acid	Chou and Lin (1976)
5-hydroxy-2-indolecarboxylic acid, 5-hydroxyindole-3-acetic acid, Mercaptoacetic acid, 4-hydroxyphenylacetic acid, 4-vinylphenol, *trans*-ferulic acid, *p*-hydroxybenzoic acid, caffeic acid, abietic acid	Seal et al. (2004)
Ergosterol peroxide, 7-oxo-stigmasterol	Macías et al. (2005)
Momilactone B, momilactone A	Kato-Noguchi et al. (2003); Kato-Noguchi and Ino (2005) Kato-Noguchi et al. (2008)
1-Tetratriacontanol, *β*-sitosterol-3-*O*-*β*-D-glucoside	Chung et al. (2005)
Momilactone B, 3-isopropyl-5-acetoxycyclohexene-2-one-1, 5,7,4′-trihydroxy-3′,5′-dimethoxyflavone, *p*-hydroxybenzoic acid, *p*-coumaric acid, ferulic acid, syringic acid, vanillic acid	Kong et al. (2006)
Azelaic acid, stearic acid, tetradecanoic acid, 1,2-benzenedicarboxylic acid bis(2-ethylhexyl)ester, 1H-indole-3-carboxyaldehyde, 1H-indole-3-carboxylic acid, 1H-indole-5-carboxylic acid, 3,4-dihydroxyhydrocinnamic acid, 3-hydroxy-4-methoxybenzoic acid, 3-hydroxybenzoic acid, 4-hydroxybenzaldehyde, 4-hydroxybenzoic acid, 4-hydroxycinnamic acid, 4-hydroxyhydrocinnamic acid	Mattice et al. (1998), Rimando et al. (2001)
β-sitosterol-*β*-d-glucoside, dicyclohexanyl orizane	Park et al. (2009)
3-hydroxy-*β*-ionone, 9-hydroxy-4-megastigmen-3-one	Kato-Noguchi et al. (2011a)

seven rice cultivars exuded variable quantities of momilactone B, which inhibited the hypocotyls and roots of lettuce (Kato-Noguchi et al. 2010b). Momilactone B was exuded in greater concentration (nearly seven folds) from rice roots if the rice was grown in vicinity of barnyard grass; and this increased momilactone B production may be due to sensing of barnyard grass root exuded chemicals by rice roots (Kato-Noguchi 2011a, b). Khan et al. (2007) evaluated rice bran compost for weed control in organically grown spinach at 10, 20, and 30 % of soil in the greenhouse and 2 kg m^{-2} in the field. Rice bran compost significantly reduced weeds density and dry weight in both greenhouse and field experiments. Ahn and Chung (2000) explored allelopathic potential of rice hull extracts against barnyard grass with 91 rice cultivars. Root length and root dry weight were more sensitive to hull extracts in most cultivars. In another study, investigating allelopathic potential of roots, stems, and leaves of rice cultivars on lettuce and ducksalad, Ebana et al. (2001) found that rice root extracts were less effective than the others.

Seal et al. (2004) identified 25 compounds from rice including phenolics, phenylalkanoic acids, and indoles. Two new indoles—5-hydroxy-2-indolecarboxylic acid and 5-hydroxyindole-3-acetic acid—were detected in root exudates

(Table 15.1). Other newly identified compounds were mercaptoacetic acid, 4-hydroxyphenylacetic acid, and 4-vinylphenol. Greater amounts of *trans*-ferulic acid, *p*-hydroxybenzoic acid, and caffeic acid were detected in exudates of allelopathic cultivars. The seventh compound, abietic acid, was significantly higher in non-allelopathic cultivars. Macías et al. (2005) isolated 15 bioactive compounds from rice; eight of which were novel. The most active compounds were ergosterol peroxide and 7-oxo-stigmasterol, which displayed higher activity than the commercial herbicide Logran. Allelochemicals momilactone A and B, 1-tetratriacontanol and *β*-sitosterol-3-O-*β*-D-glucoside from rice hull inhibited chlorophyll contents of duckweed (*Lemna paucicostata* Hegelm.). Germination of the red sprangletop (*Leptochloa chinenesis* L.) red-root amaranth (*Amaranthus retroflexus*), and flatsedge was inhibited by momilactone A and B (Chung et al. 2005).

Allelochemicals released by allelopathic rice roots and residues in soil interfere with growth of neighboring or successive plants, which can respond to certain allelochemicals released into soil by barnyard grass. Synthesis of these allelochemicals, which inhibit growth of barnyard grass, can increase up to three folds, although this was not evident in non-allelopathic rice cultivars (Kong et al. 2006). Rice parts such as leaves, straws, and hulls are phytotoxic against barnyard grass, and can be exploited as natural herbicides (Chung et al. 2003). Rice byproducts including medium-grain fatty rice bran, long-grain fatty rice bran, defatted rice bran, long-grain and medium-grain hull were incorporated at pre-planting time at 0, 125, 250, 500, and 750 g m^{-2}. Medium- and long-grain fatty rice bran were the most effective in controlling emergence and shoot weight of weeds while 250 g m^{-2} was the minimum effective rate (Kuk et al. 2001). Water extracts of roots and shoots from three rice cultivars grown in hydroponics inhibited growth of jungle rice, barnyard grass, horse purslane (*Trianthema portulacastrum*) and lettuce (Kim et al. 2005).

The extracts of rice hulls as well as the purified allelochemicals (*β*-sitosterol-*β*-d-glucoside and dicyclohexanyl orizane) were inhibitory to the aquatic algae *Microcystis aeruginosa* (both uni- and multicellular). Hull extracts were more suppressive to the growth of unicellular *M. aeruginosa* while purified allelochemicals inhibited the algae in colonies more effectively and both allelochemicals were highly and equally effective in controlling these algae (Park et al. 2009).

Presence of phenolics and other allelochemicals in rice makes it a stronger competitor of weeds, insect pests, and disease pathogens. Presence of allelochemicals especially the phenolic compounds in rice enables it to better withstand against abiotic stresses like drought while momilactones are important for rice competitiveness against weeds. Only few studies explored the allelopathic rice cultivars, which can deter or tolerate the insect pests pressure and disease pathogens' attack. More emphasis have been put on the identification of weed suppression ability of the rice cultivars. Screening of allelopathic cultivars showing resistance against insect pests and pathogens is highly desirable.

Some allelopathic rice cultivars are also involved in the biological nitrification inhibition, a phenomenon to lower the pace of nitrogen loss from soil. Allelopathic root exudates from rice cultivars were involved in inhibiting the nitrogen loss from the soil (Tanaka et al. 2010). The exploitation of the nitrification inhibition ability of the rice cultivars can be an important breakthrough to improve the nitrogen use efficiency (NUE) and alleviate nitrogen deficiency in the cropping systems.

In summary, a large number of allelochemicals have been isolated in rice. Of those, momilactones and phenolics are the most important. Allelopathic potential of rice can be exploited to suppress associated weeds under field conditions as well as improve NUE.

15.2.2 Sorghum

Sorghum (*Sorghum bicolor*) is an important cereal crop, with well-established allelopathic effects (Lehle and Putnam 1984; Einhellig and Rasmussen 1989; Einhellig and Souza 1992; Einhellig et al. 1993; Cheema et al. 2005, 2008; Alsaadawi and Dayan 2009). Most of the 100 screened sorghum cultivars were allelopathic against red-root amaranth, while two of the most phytotoxic cultivars suppressed the germination and nitrification compared with two non-phytotoxic cultivars (Alsaadawi et al. 1986). Weed density in field crops sown after sorghum was also decreased (Einhellig and Rasmussen 1989). Phenols in sorghum ranged from 1.1 to 1.5 % and from 1.1 to 2.2 % in roots and aboveground parts, respectively. The most effective among phenolics were *p*-hydroxybenzoic, *p*-coumaric, and ferulic acids (Table 15.2 Séne et al. 2001). Interestingly, inhibition of wheat (*Triticum aestivum*) radical growth was correlated with phenolic concentration in different sorghum hybrids (Ben-Hammouda et al. 1995).

Root exudation of allelochemicals varies between sorghum cultivars; sorgoleone (2-hydroxy-5-methoxy-3-[(8′Z, 11′Z)-8′, 11″, 14′-pentadecatriene]-*p*-benzoquinone) excreted by sorghum roots is the major weed inhibitor through the inhibition of photosystem-II (Netzly and Butler 1986; Nimbal et al. 1996) along with other closely related compounds such as 5-ethoxysorgoleone, 2, 5-dimethoxysorgoleone (Czarnota et al. 2003; Yang et al. 2004a). Sorgoleone reduced water uptake and nutrient use of soybean seedlings and decreased H^+-ATPase activity in maize (*Zea mays* L.) root microsomal fractions. It is likely that essential plant processes—such as solute and water uptake driven by proton pumping across root cell plasmalemma (Hejl and Koster 2004) and photosynthesis possibly due to blockage of oxygen evolution (Einhellig et al. 1993) were impaired. Sorgoleone suppressed growth of weeds—velvetleaf (*Abutilon theophrasti*), jimson weed (*Datura stramonium*), red-root amaranth, bush mantis (*Sphodromantis viridis*), crabgrass (*Digitaria sanguinalis*) and barnyard grass by inhibition of chlorophyll synthesis (Einhellig and Souza 1992). Rasmussen et al. (1992) reported disturbance of mitochondrial functions by sorgoleone in soybean and maize. Sorgoleone caused mitotic inhibition in common bean due to depolymerization of microtubular proteins and formation of colchicine metaphases causing polyploid nuclei (Hallak et al. 1999). Sorghum root hair contains the genes and enzymes responsible for sorgoleone production (Dayan et al. 2010).

Table 15.2 Allelochemicals reported in sorghum

Allelochemicals	Reference
Dhurrin, *p*-hydroxybenzaldehyde	Haskins and Gorz (1984)
Sorgoleone	Netzly and Butler (1986), Czarnota et al. (2003)
5-ethoxysorgoleone, 2,5-dimethoxysorgoleone	Czarnota et al. (2003)
Vanillic acid, *p*-hydroxybenzoic acid, *p*-hydroxybenzaldehyde, *p*-coumaric acid, Ferulic acid	Séne et al. (2001)
Sorgoleone (2-hydroxy-5-methoxy-3-[(8′*Z*, 11′*Z*)-8′, 11′, 14′-pentadecatriene]-*p*-benzoquinone)	Netzly and Butler (1986), Nimbal et al. (1996)

Alsaadawi and Dayan (2009) suggested that identification of enzymes involved in the synthesis of sorgoleone in the sorghum root hair and the genes, which encode these can be incorporated in non-allelopathic crops to make them withstand against stresses. Baerson et al. (2008) identified *O*-methyltransferase (SbOMT3) as the enzyme involved in the biosynthesis of sorgoleone in the sorghum root hair.

Cheema and Khaliq (2000) performed a series of experiments in a semi-arid region of Punjab, Pakistan to explore allelopathic properties of sorghum for weed control in irrigated wheat. Spraying mature plants with sorgaab reduced weed density and increased wheat biomass by 35–49 %, leading to a yield advantage of 10–21 % compared to the control. They also found that mature sorghum herbage, added to soil at 2–6 Mg ha^{-1}, reduced weed density by 40–50 % and increased wheat yield by 15 %. This substantiated the usefulness of sorgaab as a natural weed inhibitor for irrigated wheat. Allelopathic extracts of sorghum mixed with *S. metolachlor* (reduced to half and one-third) effectively suppressed the weed density and dry weight of purple nutsedge (*C. rotundus*) in the cotton (*Gossypium hirsutum* L.) crop and decrease in weed intensity and increase in cotton yield were comparable with the full dose of the herbicide (Iqbal and Cheema 2008). Recently, Razzaq et al. (2010) reported that allelopathic sorghum extracts in combination with reduced doses of various herbicides were as effective in controlling wheat weeds as were the full doses of these herbicides. The spray of the sorghum water extract was helpful in reducing the weeds dry weight by nearly 65 % and also resulted in a significant increase in the grain yield of lentil (*Lens culinaris*). The sorghum residues were also effective in suppressing the weeds and increasing grain yield of lentil (Hozayn et al. 2011). Very few studies have reported the ineffectiveness of sorghum extracts or residues for suppressing the weeds (Jabran et al. 2010b).

The allelopathic effects of sorghum on crops in sequence or component crops also exist. For example, sorghum crop grown prior to peanut (*Arachis hypogea*) had negative allelopathic effects on the succeeding peanut crop through exudation of phenolic compounds (Séne et al. 2000). Such impacts can be avoided through choosing the suitable planting geometry (Séne et al. 2000). Sorghum cropping in a grazing land was effective in reducing the weed species (Milchunas et al. 2011).

Alsaadawi et al. (2007) tested ten sorghum cultivars for their suppressive effects against weeds and concluded that all the sorghum cultivars had an inhibitory effect against cockle (*Lolium temulentum* L.) and barnyard grass. Kumar et al. (2010) reported that the formulations prepared from the exuded materials of sorghum root hairs were suppressive against fungi such as *Sclerotinia sclerotiorum*, *Rhizoctonia bataticola, Alternaria alternate, Choenephora cucurbitarum, Fusarium udum, and F. oxysporum* in terms of reducing their number and size.

Allelopathic potential of sorghum can help reduce the nitrogen (N) losses in the form of nitrate and thus improving the NUE. Enormous quantities of N are lost from the soil every year as nitrate and contribute to environmental pollution and global warming as well as reduce the soil fertility. The loss of N is due to swift biological change of ammonium to nitrate, which can be slowed down through addition of allelopathic plant residues in the soil. Nitrification inhibition is of ecological significance for sorghum. According to Alsaadawi et al. (1986), nitrification inhibition was higher by the allelopathic sorghum cultivars compared with non-allelopathic cultivars. Phenolic compounds have been found as the major players of reduced nitrification of ammonium through diminution of ammonium oxidation to nitrate. However, the cultivars vary for the nitrification inhibition ability. The selection of cultivars with higher nitrification inhibition activity as well as the nitrification inhibition through incorporation of allelopathic plant residues holds a good scope to economize the N use in agroecosystems.

In crux, sorghum is highly allelopathic with numerous allelochemicals beneficial for weeds control and plant diseases management as well as other ecological benefits like reduction of N losses. Sorgoleone from sorghum roots is the most potent allelochemical, effective at lower concentrations and able to be synthesized into a natural herbicide.

15.2.3 Wheat

Wheat cultivars with allelopathic potential are strong competitors of insect pests, disease pathogens, and weeds (Bertholdsson 2005a; Yongqing 2005; Bertholdsson 2010; Li et al. 2011). Allelopathic wheat cultivars were resistant against the insect pest wheat midge (*Sitodiplosis mosellana*), the allelochemicals including ferulic acid and *p*-coumaric acid were synthesized, which possibly caused this resistance. These allelochemicals were inhibitory to the larvae of this insect in the bioassay (Ding et al. 2000). Wheat plants with allelopathic potential can detoxify the aluminum through exudation of higher quantities of malic acid (Delhaize et al. 1993). Wheat residues have suppressed other plant species (Alsaadawi et al. 1998; Alsaadawi 2001; Bruce et al. 2006; Flood and Entz 2009; Faisal et al. 2010). Wheat rhizospheres contain several phytotoxic substances (Young et al. 1989). Wu et al. (2000c) collected 453 wheat accessions from 50 countries to evaluate wheat seedling allelopathy against annual ryegrass (*L. rigidum*) and found that they inhibited root growth of ryegrass by 10–91 %. Water extracts from wheat or decomposing residues inhibited germination and growth of plant species such as rice (Kimber 1966, 1973), maize (Zhang and Ma 1994), cotton (Hicks et al. 1989), annual rye grass (Wu et al. 2000a; Huang et al. 2003; Li et al. 2011), perennial rye grass (*L. perenne*) (Inderjit et al. 2001), common bean (Flood and Entz 2009), lettuce and pumpkin (*Cucurbita pepo* L.) (Leyuan et al. 2010), cucumber (*Cucumis sativus* L.) (Wang et al. 2009), and wheat itself (Faisal et al. 2010; Leyuan et al. 2010). Miri (2011) evaluated the allelopathic impact of 68 Iranian wheat genotypes on the germination and seedling growth of 3 weed species; red-root amaranth, wild barley (*Hordeum spontaneum*), and wild oat (*Avena fatua*). Most of the cultivars were found allelopathic in nature and inhibited weed growth; nevertheless, the water extracts from shoot were more inhibitory to weed growth than root extracts. Similarly, Saffari et al. (2010) reported that winter wheat in Kerman province of Iran exhibited an allelopathic effect and depressed the growth and yield of the following corn crop. Further studies will help devising a cropping system for the wheat based systems where the residual allelopathic effects of the wheat may not affect the subsequent crop in the sequence.

The main classes of allelochemicals produced and excreted by wheat include phenolic acids, hydroxamic acids, 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one, and short-chain fatty acids (scopoletin, etc.) (Baghestani et al. 1999; Wu et al. 2001a; Huang et al. 2003). The allelochemical 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one from wheat is further degraded into 6-methoxybenzoxazolin-2-one, which inhibits germination and α-amylase production in different weed and crop species (Kato-Noguchi and Macías 2008). Acetic acid, butyric acid, iso-pentanoic acid, propionic acid, isobutyric acid, and pentanoic acid are short-chain fatty acids from wheat straw (Wu et al. 2001a). Wheat mulch residues and the associated soil contain allelochemicals such as ferulic, *p*-coumaric, *p*-OH benzoic, syringic, and vanillic acid (Lodhi et al. 1987).

Wu et al. (2001a) evaluated 58 wheat accessions from around the world to compare their ability to produce phenolic acids including *p*-hydroxybenzoic, vanillic, syringic, *trans*-*p*-coumaric, *cis*-*p*-coumaric, *trans*- and *cis*-ferulic acid. Total phenolic acids varied from 93.2 to 453.8 mg kg^{-1}. Chon and Kim (2004) reported that wheat extracts reduced root growth of barnyard grass, alfalfa (*Medicago sativa*), and eclipta (*Eclipta prostrate*) with more allelopathic effects compared to rice, oat (*A. sativa*), and barley (*H. vulgare*), while phenolics were the main growth retarding compounds. Wu et al. (2000b) used roots, shoots, and agar medium of 17-day-old wheat seedlings to identify allelochemicals including *cis*-ferulic acid and 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one, which retarded growth of rye grass (Table 15.3).

Wheat stubbles retained in the field suppressed growth of the following crop by disturbing leaf area development and dry mass accumulation (Bruce et al. 2006). Wu et al. (2001a) assessed roots and shoots of 58 wheat accessions (using 15-day-old seedlings) for their potential to produce 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one and excrete it into agar medium; only 11 cultivars exuded it, while most retained it in their roots. They suggested that this information would help in breeding wheat cultivars with strong allelopathic potential (Table 15.3).

Table 15.3 Allelochemicals reported in wheat

Allelochemicals	Reference
Ferulic acid, *p*-coumaric acid, *p*-OH benzoic acid, syringic acid, vanillic acid	Lodhi et al. (1987)
p-hydroxybenzoic, vanillic acid, syringic acid, *trans*-*p*-coumaric acid, *cis*-*p*-coumaric acid, *trans*-ferulic acid, *cis*-ferulic acid	Wu et al. (2001a, b)
cis-ferulic acid, 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one	Wu et al. (2000b)
Benzoxazolin-2(3*H*)-one, 6-methoxy-benzoxazolin-2(3*H*)-one	Friebe et al. (1998)

Allelopathic wheat cultivars at higher density suppressed the growth of annual ryegrass by decreasing the surface area and length of roots (Li et al. 2011). Likewise, four wheat cultivars from Iran decreased the growth and density of companion weeds; this effect was robust at higher wheat seedling density (Labbafi et al. 2010). Decomposing wheat residues in the soil and the soil samples from the previously wheat cropped soil had enormous quantities of phenolics as well as the antioxidant enzymes compared with control; moreover, the decomposing wheat residues and soil samples from field previously put under wheat obstructed the germination and growth of horse purslane as well as reduced its chlorophyll contents (Khaliq et al. 2011). In another study, Javaid et al. (2011) found that four wheat cultivars from Pakistan were inhibitory to the invasive weed parthenium (*Parthenium hysteroforus*), both in the forms of water extracts and residues.

Wang et al. (2009) collected wheat root's allelopathic exudates by some device and applied them on cucumber seeds. The allelopathic exudates inhibited the germination of cucumber seedling when applied at lower concentration; however, the results were otherwise when wheat exudates were applied at higher concentration. Likewise, the allelochemicals from wheat leachates (50 and 100 % concentration) were found to improve the germination, plant height and root length of cucumber compared with the control (Wang et al. 2010). Nevertheless, the higher concentrations of wheat leachates were helpful in suppressing the growth of fungus *F. oxysporum*, while low concentration leachates improved growth of this fungus (Wang et al. 2010). Flood and Entz (2009) evaluated the influence of wheat allelopathic extracts on germination of common bean and two weeds including green foxtail (*Setaria viridis*) and red-root amaranth; they found that weeds and common bean germination was inhibited by application of wheat allelopathic extracts. Similarly, the water extract from the wheat cultivar Abu-Ghraib-3 was found to inhibit the germination of two other cultivars of wheat while leachates from the same wheat variety decomposing residues upon incorporation in the soil not only reduced the yield of test variety but also disturbed the physiological functions including relative water content and proline root diameter (Faisal et al. 2010). Leyuan et al. (2010) made a soil like substrate from wheat and rice residues and tested its allelopathic potential against lettuce, wheat, and pumpkin. They found that this substrate inhibited the germination, growth, root fresh weight, and root length of test species.

Wu et al. (2001b) reviewed the negative impacts of allelopathy on cultivated crops including its autotoxic effects especially in a wheat–wheat system. Wheat varieties differ in their autotoxic effects. Wheat had toxic effects on crops such as soybean, maize, sorghum, rice, barley, rye, rice, oat, clovers, etc., while the response of crops and their varieties was variable to wheat allelopathy. Wise selection of varieties, thoughtful composition of crop rotation, minimized straw input in the soil, management to decompose wheat straw before sowing the next crop, and addition of fertilizer nitrogen were suggested as remedial strategies to neutralize allelopathic effects of wheat in soil.

In summary, wheat allelopathy can be used for insect pests, disease pathogens, and weed management under field conditions. The negative influences of wheat allelopathy may be reduced by management practices. Furthermore, competitiveness of wheat against biotic stresses may be enhanced by producing cultivars with stronger allelopathic potential.

15.2.4 Maize

Maize plants produce large quantities of cyclic hydroxamic acids such as 2, 4-dihydroxy-7-methoxy-2H-1, 4-benzoxazin-3-one (DIMBOA) and 2, 4-dihydroxy-3H-1, 4-benzoxazin-3-one under stress conditions, which restrict plant growth and make them resistant against chewing insects and pathogens (Table 15.4; Richardson and Bacon 1993; Sicker et al. 2000). Benzoxazinoids, chemicals involved in grass defense systems, are stored as glucoside in vacuoles (Rad et al. 2001). Maize seedlings and root exudates had 43 and 0.38 mol kg^{-1} fresh weight, respectively of 2, 4-dihydroxy-3H-1, 4-benzoxazin-3-one; visible light increased these levels and hence allelopathic activity (Table 15.4; Kato-Noguchi 1999). Some maize plants may be resistant to certain insects due to the presence of allelopathic defense mechanisms; some maize hybrids disturbed the oviposition of *Sesamia nonagrioides,* a noxious insect pest of maize in some countries (Konstantopoulou et al. 2004). Kato-Noguchi (2000) investigated the effects of maize allelochemicals benzoxazolinone, 5-chloro-6-methoxy-2-benzoxazolinone and 6-methoxy-2-benzoxazolinone on seed germination and growth of various weeds. These allelochemicals inhibited weed growth of cockscomb (*A. caudatus*), cress (*L. sativum*), lettuce, crabgrass, timothy (*Phleum pratense* L.), and ryegrass. The water extracts from the tissue parts (stems, leaves, roots) of maize were found to obstruct the germination and growth of wild barley (Al-Tawaha and Odat 2010) while the maize residues applied in the winter wheat were effective in controlling wheat soil born diseases (Zhen et al. 2009). In another study, the allelopathic extracts from two maize cultivars were found to reduce the coleoptile length and the number of roots in wheat (Panahyan-e-Kivi and Tobeh 2010). Methyl jasmonate application induced the production and the assemblage of allelochemicals including phenolic acids, DIMBOA, and its derivatives in roots as well as the leaves of maize and resulted in an expression of the genes including

Table 15.4 Allelochemicals reported in maize

Allelochemicals	Reference
2,4-dihydroxy-7-methoxy-2H-1,4-benzoxazin-3-one, 2,4-dihydroxy-3H-1,4-benzoxazin-3-one	Richardson and Bacon (1993) Kato-Noguchi (1999)
3,7,11,15-tetramethyl-2-hexadecen-1-ol (phytol), (*Z*)-3-hexenol, nonanal, pentadecanal, neophytadiene, (*Z*)-3-hexenyl acetate	Konstantopoulou et al. (2004)
Benzoxazolinone, 5-chloro-6-methoxy-2-benzoxazolinone, 6-methoxy-2-benzoxazolinone, 2,4-dihydroxy-3H-1,4-benzoxazin-3-one	Kato-Noguchi (2000) Kato-Noguchi et al. (2000)

AOC, *PAL,* and *BX9* in leaves in the first 48 h of methyl jasmonate; while the water extracts from these maize leaves were inhibitory to the weed barnyard grass (Wang et al. 2005). This indicates that the allelopathic activity can be enhanced by methyl jasmonate application for a strenghened plant defense against weeds and other biotic stressed (Xu et al. 2003). Frey et al. (1997, 2003) reported that nine genes *BX1* to *BX9* were involved in the biosynthesis pathway of DIMBOA in the maize. Soybean and maize intercropping reduced the density of *Striga hermonthica* and increased the maize grain yield (Odhiambo et al. 2011). Application of maize residues as surface mulch in transplanted and direct seeded rice in Pakistan not only decreased the weed density and dry weight but also enhanced the grain yield and quality of the produce (Rehman et al. 2007a; Jabran et al. 2010c).

In summary, allelochemicals from maize suppress pests. Moreover, maize plants with stronger allelopathic potential are better able to withstand biotic stresses including diseases, insect pests, and weed interference.

15.2.5 Barley

Barley grains and straw are used for a number of purposes, and have allelopathic potential (Bertholdsson 2004), despite being autotoxic (Ben-Hammouda et al. 2002). The level of allelochemicals in barley varies with age and plant part; wheat plants were depressed by barley allelopathy with radicle growth more suppressed than coleoptile length (Ben-Hammouda et al. 2001; Oueslati et al. 2009). Autotoxicity in the barley cultivars was strongly correlated with the concentration of the phenolics in these cultivars while five phenolic compounds including vanillic acid, syringic acid, *p*-hydroxybenzoic acid, ferulic acid, and *p*-coumaric were identified in various plant parts of barley (Oueslati et al. 2009). Hordenine (N,N-dimethylthramine) and gramine (N,N-dimethylindolemethylamine) are important allelochemicals from barley (Chaniago et al. 2011).

Some barley cultivars are more competitive against weeds than others, allowing for reduced herbicide use (Didon 2002; Bertholdsson 2005a; Watson et al. 2006).

Table 15.5 Allelochemicals reported in barley

Allelochemicals	Reference
Hordenine and gramine	Liu and Lovett (1993a, b) Hoult and Lovett (1993)
Caffeic acid, hydrocinnamic acid, ferulic acid, *m*-coumaric acid, *p*-coumaric acid, coumarin	Chon and Kim (2004)

Barley hampered germination and radicle length of mustard in Petri dish bioassay (Hoult and Lovett 1993; Liu and Lovett 1993a, b). Moyer and Huang (1997) reported that extracts from barley were toxic to various weed species like flixweed (*Descurainia sophia*), stinkweed (*Thlaspi arvense*) and downy brome (*Bromus tectorum*). Water extracts from barley reduced root length in certain crops (alfalfa) and weeds (barnyard grass and eclipta), and contained phenolic compounds such as caffeic acid, hydrocinnamic acid, ferulic acid, *m*-coumaric acid, *p*-coumaric acid, and coumarin (Table 15.5; Chon and Kim 2004). Likewise, Panahyan-e-Kivi and Tobeh (2010) reported that barley allelopathic extracts reduced the number of root and the coleoptiles length as well in the wheat crop while the water extracts of barley decreased germination, root, and shoot growth of wheat (Sadeghi et al. 2010). Bertholdsson (2004, 2005b) evaluated 127 barley cultivars from different European countries for their allelopathic activity against ryegrass. Most cultivars reduced ryegrass root growth by 42–70 %. He opined that breeding for over 100 years appears to have diluted the allelopathic potential of barley. Out of 50 barley cultivars, most were found allelopathic in nature and inhibited the germination and growth of weeds like barnyard grass, sterile oat (*A. sterilis* spp. *Sterilis* L.), blackgrass (*Alopecurus myosuroides*), wild mustard (*Sinapis arvensis*), and hood canarygrass (*Phalaris paradoxa*) plants (Vasilakoglou et al. 2009).

Dhima et al. (2008) evaluated ten barley cultivars for their allelopathic potential against barnyard grass, common poppy (*Papaver rhoeas*) and ivy-leaved speedwell (*Veronica hederifolia*) under field as well as laboratory conditions. Most of the barley cultivars suppressed the weeds in terms of their dry weight. Barely extracts reduced the growth of barnyard grass under laboratory conditions. According to Ashrafi et al. (2008), the barley water extracts from roots, shoots, leaves, and flowers were inhibitory to the germination as well as the growth of the weed green foxtail.

Treating barley with carboline, an allelochemical from couch grass (*Elytrigia repens*) makes strong the defense of barley plants against aphids. Aphids are less likely to attack the carboline treated barley plants (Bais et al. 2006). Although very few allelochemicals have been identified from barley, it is a potent weed inhibitor and can be grown as cover crop as well as intercropped to suppress weeds in the companion crops (Bertholdsson 2005a; Kremer and Ben-Hammouda 2009).

In summary, barley cultivars with higher allelopathic potential may be screened to avoid herbicide use for weed control in barley.

Table 15.6 Allelochemicals reported in *Brassica* spp.

Brassica spp.	Allelochemicals	Reference
Black mustard (*Brassica nigra*)	Allyl isothiocyanate (ITC)	Vaughn and Boydston (1997)
Broccoli (*Brassica oleracea*)	Glucosinolates	Chuanphongpanich et al. (2006)
White mustard (*Brassica hirta* L.)	Benzyl-ITC Isoprenoid Benzenoid	Tollsten and Bergstrom (1988)
Turnip-rape (*Brassica rapa*)	2-phenylethyl-ITC, *n*-butyl, 3-butenyl-ITC, benzyl, allyl-ITC and 4-pentenyl-ITC	Petersen et al. (2001)
Abyssinian mustard (*Brassica carinata*)	Allyl isothiocyanate Methyl isothiocyanate Benzyl isothiocyanate	Papadopoulos and Alderson (2007)
Radish (*Raphanus sativus*)	4-methylsulfinyl-3-butenylglucosinolate	Brown and Morra (1997)
Mustard (*Brassica juncea*)	Allylglucosinolate	Brown and Morra (1997)
Cabbage (*Brassica oleracea*)	2-hydroxy-3-butenylglucosinolate Allylglucosinolate	Brown and Morra (1997)

15.2.6 Crucifers

Cruciferous (family Brassicaceae) plants are known for synthesizing secondary metabolites in considerably high quantities (Warwick 2011). Crucifers such as brown mustard (*Brassica juncea*), black mustard (*B. nigra*), white mustard (*B. hirta*), leafy turnip (*B. campestris*), canola (*B. napus*), Abyssinian mustard (*B. carinata*), broccoli (*B. oleracea*), and garden cress (*L. sativum*) possess strong allelopathic potential and contain glucosinolates which strengthen plant defense system (Grodzinsky 1992; Jabran et al. 2008b; Assayed and El-Aty 2009; Warwick 2011). The glucosinolates are distributed throughout the plant and are in higher concentration in younger (100 μmol g^{-1} fresh weight) than older (1 μmol g^{-1} fresh weight) plants (Haig 2008). According to Velasco et al. (2007), however, the glucosinolates concentration increased with the plant age until the flowering started. Antonious et al. (2009) inferred that the contents of glucosinolates, phenols, and ascorbic acid in the crucifer plants were dependent on the plant species and the environment with a negative relation to the total biomass. Glucosinolates are converted to various products mainly isothiocynates, which inhibit many weeds and diseases (Smolinska et al. 2003; Norsworthy et al. 2006). Black mustard contains allyl isothiocyanate, a potential inhibitor of germination and growth in many plant species (Vaughn and Boydston 1997). Isothiocyanates from mustards suppress wheat germination and seedling growth (Table 15.6; Bialy et al. 1990). Crushed leaves of cruciferous plants especially as brown mustard and black mustard exuded volatiles (glucosinolates), which delayed the germination and obstructed the growth of plant and weed species including lettuce, barnyard grass, and wheat (Oleszek 1987).

Incorporating black mustard into soil or when used as water extract obstructed germination, plant height, and plant weight of wild barley (Tawaha and Turk 2003). White mustard decomposition released benzyl allyl isothiocyanate, which is harmful to certain weeds and crops while volatile compounds such as isoprenoid and benzenoid from *Brassica* spp. are harmful to weeds (Tollsten and Bergstrom 1988). Leafy turnip mulch also contains isothiocyanates including 2-phenylethyl- and allyl-isothiocyanate; n-butyl-, 3-butenyl- and allyl-isothiocyanate; benzyl- and allyl-isothiocyanate; and 4-pentenyl- and allyl-isothiocyanate; which, after release into soil, suppressed germination of spiny sowthistle (*Sonchus asper* (L.) Hill), scentless mayweed (*Matricaria inodora*), smooth pigweed (*A. hybridus*), barnyard grass, and blackgrass (Petersen et al. 2001). Small-seeded species are more affected by allyl-isothiocyanate than large-seeded species (Petersen et al. 2001). Brown mustard and white mustard, grown as green manure, suppressed weeds in cowpea (*Vigna unguiculata* L.) and improved yields by about 415 kg ha^{-1} compared with controls (Norsworthy et al. 2005).

Five broccoli cultivars had glucosinolate contents between 20.3 and 65.5 μmol g^{-1} dry weight (Chuanphongpanich et al. 2006). Abyssinian mustard released allyl isothiocyanate, methyl isothiocyanate, and benzyl isothiocyanate by hydrolysis of plant tissues (Papadopoulos and Alderson 2007). Five liquid isothiocyanates (benzoyl, *o*-tolyl, *m*-tolyl, *tert*-octyl, and 3-fluorophenyl) inhibited growth of purple and yellow nutsedge (*C. esculentus*), albeit to a greater extent in purple nutsedge, and benzoyl and 3-fluorophenyl were the most effective (Norsworthy et al. 2006). Total glucosinolates levels in the kale (*B. oleracea* Acephala group) were increased with the increasing age and were maximum before flowering. After the onset of flowering, aliphatic glucosinolate concentration decreased in leaves but increased in flower buds at the same time. Indolyl glucosinolate and aromatic glucosinolate attained the highest concentration in leaves if harvested at consumption stage with highest concentration of aliphatic glucosinolates in flower buds at the same stage. The plants with higher levels of total glucosinolates had lower levels of insect pest attack compared with the ones with lower total glucosinolates (Velasco et al. 2007). Similarly, in another study, glucosinolates including progoitrin and gluconapin (seeds), glucobrassicanapin, glucobrassicin, and gluconasturtiin (roots) were detected in the rape cultivars; these compounds were the possible cause of allelopathic inhibition in the following crops (Yasumoto et al. 2010).

Field amended with white mustard as a green manure crop had a lower population of cyanogenic *Pseudomonas* strains compared with those amended with farmyard manure or NPK fertilizer (Paszkowski and Dwornikiewicz 2003). Fodder radish (*Raphanus sativus* L.) in mixture with other crops proved to be the best cover crop for weed suppression in vegetable fields of Brazil under the organic conservation agriculture as a result of high biomass and allelochemicals production (Altieri et al. 2011). Black mustard roots and aerial parts, when incorporated into soil, reduced dry weight, height, and emergence of canary grass (*P. minor*). Moreover, increasing concentrations of water extracts of stem, leaf, root, and flower of black mustard reduced germination, and radical and hypocotyl length of canary grass (Turk and Tawaha 2003). Shoot powder extracts of *Brassica* spp. including garden radish, white radish, black radish, little radish, turnip, and rapeseed inhibited growth of the weed cutleaf ground-cherry (*Physalis agulata*) under laboratory conditions with the effects more pronounced on germination than seedling growth (Uremis et al. 2005). Mustard water extracts in combination with 67 % reduced rates of pendimethalin were highly effective in suppressing the weeds [purple nutsedge, lambsquarters (*Chenopodium album*), horse purslane (*T. portulacastrum*), swine cress (*Cronopus didymus*)] and increasing the grain yield of canola compared with the control (unweeded) treatment and full dose of herbicide (Jabran et al. 2008a, 2010a). Increase in wheat grain yield and yield related parameters compared with untreated plants were recorded as a result of the spray of canola extracts at grain development stage (Jabran et al. 2011). This was possibly due to the growth promoting activity of brassinosteroids in the canola extracts (Krishna 2003).

Application of black mustard aqueous extracts affected germination, seedling growth, and dry weights of 5-day-old alfalfa seedlings across a range of extract concentrations (Turk et al. 2003) Likewise, aqueous extracts from different plant parts of black mustard also inhibited germination, seedling length, and hypocotyl dry weight of 5-day-old wheat seedlings in the order leaf > flower > mixture of plant parts > root > stem (Turk and Tawaha 2002). Black mustard leaf, stem, flower, and root aqueous extracts are phytotoxic against radish significantly decreasing germination, seedling growth, and hypocotyl dry weight of radish (Turk et al. 2005).

In summary, cruciferous plants may be included in cropping systems to suppress pest pressure but the allelopathic effect of these crops can also pose deleterious effects on crops. Allelopathic potential of *Brassica* spp. can be improved through breeding.

15.2.7 Sunflower

Sunflower (*Helianthus annuus*) is one of the important oilseed crops and has strong allelopathic activity against other plant and weed species (Irons and Burnside 1982; Leather 1983a, b; Yamada et al. 1997; Jabran et al. 2008a; Anjum and Bajwa 2010). Chou and Patrick (1976) identified a number of allelochemicals in the decomposing residues of the sunflower crop such as syringic acid, salicylaldehyde, *p*-hydroxybenzaldehyde, butyric acid, phenylacetic acid, 4-phenylbutyric acid, benzoic acid, *p*-hydroxybenzoic acid, caffeic acid, vanillic acid, ferulic acid, *trans*-cinnamic acid, *o*-coumaric acid, *o*-hydroxyphenylacetic acid, salicylic acid, *p*-coumaric acid, resorcinol, phloroglucinol. These allelochemicals showed suppressive effects against weeds in the laboratory conditions. Ghafar et al. (2001) identified five allelochemicals (chlorogenic, caffeic, syringic, vanillic, and ferulic acid) in sunflower leaves, three (chlorogenic, ferulic, and vanillic acids) in stems and one (ferulic acid) in roots (Table 15.7). Anjum and Bajwa (2005) isolated

Table 15.7 Allelochemicals reported in sunflower

Allelochemicals	Reference
Chlorogenic acid, caffeic acid, syringic acid, vanillic acid, ferulic acid	Ghafar et al. (2001)
Annuionone	Anjum and Bajwa (2005)
7-hydroxylated coumarins	Serghinin et al. (2001)
Tambulin, chalcones kukulcanin B, heliannone A, heliannones B, heliannones C	Macías et al. (1997)
Sundiversifolide,4,15-dinor-3-hydroxy-1(5)-xanthene-12,8-olide	Ohno et al. (2001)

annuionone from aqueous extract of sunflower cv. Suncross-42 leaves and found that growth and dry mass of weed species including lambsquarters, swine cress, toothed bur clover (*M. polymorpha*), toothed dock (*Rumex dentatus*), and canarygrass were inhibited; broad-leaved weeds were more sensitive. Anjum et al. (2005) identified sesquiterpene lactones in three cultivars of sunflower, which were effective against five most problematic weeds of wheat viz., canarygrass, lambsquarters, swine cress, toothed dock, and toothed bur clover. In another study, Serghinin et al. (2001) described that resistant sunflower cultivars produced 7-hydroxylated coumarins to combat parasitism by broomrape (*Orobanche cernua*).

In contrast, sunflower allelopathy may have some damaging impacts. For instance, soil from sunflower fields was rich in phenolics, which were phytotoxic in laboratory analysis. The density, seed weight, and total yield of the crop following sunflower were also reduced due to phenolics added to soil from the previous sunflower crop (Batish et al. 2002). Aqueous extracts of sunflower leaves inhibited seed germination in mustard, which was attributed to reverse hydrolysis during germination (Kupidłowska et al. 2006). Kaya et al. (2005) reported that 100 % concentrations of biodegradation products from sunflower decreased germination and seedling growth of common bean, chickpea (*Cicer arietinum*), and wheat while Anjum and Bajwa (2010) reported that aqueous extracts of three sunflower varieties were responsible for the inhibition of growth and yield of four wheat varieties. Nitrification in soil is also inhibited by sunflower due to effects on microbial activities (Alsaadawi 1998). Allelochemicals (flavonoids) from sunflower (10^{-4}–10^{-9} M) affected shoot growth of tomato and barley (Macías et al. 1997).

Sunflower water extracts applied mixed in the reduced doses of herbicides for weed control wheat were not only effective in reducing the weed density and dry weight over untreated control but also increased the grain yield; nevertheless, the results from these experimental units were comparable with those applied with sole herbicides in full dose (Razzaq et al. 2010). Sunflower crop residues and the allelopathic water extracts were effective in controlling lentil weeds and increasing grain yield (Hozayn et al. 2011). Sunflower allelopathic potential has a tremendous scope for practical utilization for the sake of weed management in field crops without reliance on herbicides and in some instances less use of herbicides (Jabran et al. 2008a, 2010a; Farooq et al. 2011a). For example, sunflower allelopathic water extracts synergistically worked with lower herbicide rates to offer weed control and increase in maize grain yield statistically comparable with the full dose of herbicide (Khan et al. 2011). Similarly, the application of sunflower residues for weed management in the rice crop not only offered attractive weed control potential but also delivered a significant increase in rice grain yield over the unweeded control (Rehman et al. 2007a). In another study, Jabran et al. (2010c) reported the utilization of sunflower residues for weed control as well the improvement in grain yield and quality of direct seeded fine grain rice. Here, application of sunflower residues at 6 t ha^{-1} effectively reduced the weed pressure and enhanced the grain yield and quality as well in the direct seeded rice compared with the weedy check. Sunflower allelopathic water extracts were effective in controlling weeds and improving the lint yield in cotton and grain yield in wheat and transplanted fine grain rice (Khaliq et al. 2007; Cheema et al. 2007; Rehman et al. 2007b). Some reports suggest that the allelochemicals from sunflower also inhibit the insect pests of field crops (Jabran et al. 2007).

The allelochemicals from sunflower were found to cause oxidative stress in white mustard due to production of reactive oxygen species and a decrease in antioxidant activity, which lead to the cellular damage in the test species and hence the reduced vigor and germinability (Oracz et al. 2007).

Moreover, sunflower residues from roots and shoots as well as the sunflower water extracts have been found to inhibit the process of nitrification with the variable capability of cultivars for nitrification inhibition (Alsaadawi 1998). This characteristic of the sunflower cultivars can be employed to improve the nitrogen availability as well as reduce the nitrogen losses from soil. Improved nitrogen utilization as a result of maize allelopathic potential may be harnessed for the other crops through intercropping.

In summary, sunflower has strong allelopathic potential against crops as well as weed species, which needs to be exploited in existing cropping systems.

15.2.8 Alfalfa

Alfalfa is a forage legume also used in hay making and as pasture. A number of studies have found allelopathic potential of alfalfa (Miller 1983; Chung and Miller 1990; Hedge and Miller 1990; Xuan and Tsuzuki 2002; Chon et al. 2003; Ferreira and Reinhardt 2010). Miller (1983) reported that certain phytotoxic compounds were exuded from roots under field conditions, which were responsible for autotoxicity in alfalfa. However, no phytotoxicity was observed in alfalfa when the preceding crop was maize or soybean. Duke (1981) identified toxins such as choline, citric acid, hydrocyanic acid, limonene, malic acid, malonic acid, oxalic acid, pantothenic acid, pectin, quinic acid, saponin, shikimic acid, tannin, trigonelline, and tryptophane (Table 15.8). These organic acids possess pertinent

Table 15.8 Allelochemicals reported in alfalfa

Allelochemicals	Reference
Choline, citric acid, hydrocyanic acid, limonene, malic acid, malonic acid, oxalic acid, pantothenic acid, pectin, quinic acid, saponin, shikimic acid, tannin, trigonelline, trytophane	Duke (1981)
Medecarpin, 4-methoxymedicarpin, sativan, 5-methozysativan	Dornbos et al. (1990)
Saponins	Okumura et al. (1999) Guenzi et al. (1964)
Ferulic acid, salicylic acid	Nakahisa et al. (1994)
Caffeic acid, *trans*-cinnamic acid, hydrocinnamic acid, coumarin, ferulic acid, *m*-coumaric acid, *o*-coumaric acid, *p*-coumaric acid, salicylic acid	Chon and Kim (2002)
Catechin, gallic acid, ferulic acid, protocatechuic acid, *p*-coumaric acid, *p*-hydroxybenzoic acid, syringic acid, sinapic acid, vanillin, vanillic acid	Xuan et al. (2003b)

implications in nutrient availability in the soil. They improve the nutrient availability through chelation especially for iron and phosphorus. Many plants have been found to exude higher concentrations of organic acids in the soils where the micronutrients are deficient. Quantification of the organic acids concentrations for affecting the phosphorus solubility and other nutrient availability is desirable. Similarly, another allelochemical {isoflavonoid phytoalexin [2-(3,5-dihydroxyphenyl)-5,6-dihydroxybenzofuran]} is exuded from alfalfa plant roots under Fe deficiency, which helps in solubilizing ferric phosphate and improves the availability of P and Fe for plant uptake (Masaoka et al. 1993). Hedge and Miller (1990) reported that alfalfa possessed both allelopathic and autotoxic effects; however, the allelopathic effect of alfalfa on other plant species (sorghum) was more pronounced than its toxic effects. Chon and Kim (2002) identified 9 phenolics including caffeic acid, *trans*-cinnamic acid, hydrocinnamic acid, coumarin, ferulic acid, *m*-coumaric acid, *o*-coumaric acid, *p*-coumaric acid, and salicylic acid from alfalfa leaves and found leaves in bioassay to be phytotoxic, which was correlated with the concentration of allelochemicals. Allelopathic extracts from alfalfa residues disturbed the root morphology of barnyard grass and alfalfa itself (Chon et al. 2002). Barnyard grass germination (>50 %), seedling growth (>85 %), and rhizomes reproduction (>40 %) were inhibited by alfalfa plant extracts. Barnyard grass seedling growth, grown together with alfalfa in a hydroponic culture was also reduced by alfalfa root exudates and the allelochemicals including *p*-OH-benzoic, chlorogenic acid, isochlorogenic acid, caffeic acid, *p*-coumaric, and ferulic acids were identified in the root exudates as well as the residues of alfalfa (Abdul-Rahman and Habib 1989).

Aerial parts of alfalfa are capable of suppressing weeds. Alfalfa cultivars vary in their allelopathic potential to inhibit growth; aqueous extracts from fresh or dried alfalfa plant tissues inhibited germination, and growth of other plant species (Xuan and Tsuzuki 2002). Alfalfa plants incorporated into soil inhibited emergence (65 %), shoot elongation (73 %), and dry weight (81 %) in radish seedlings compared with the control (Nakahisa et al. 1994). Alfalfa plant parts, when incorporated at 1 t ha^{-1} for weed control in rice fields, exhibited more than 90 % weed control and increased paddy yield by about 80 % (Xuan et al. 2003a). Alfalfa pellets (1–2 t ha^{-1}) were successful for weed control in paddy fields while 1–3 t ha^{-1} of alfalfa powder fully restricted weed germination thus offering effective control of weeds like abunome (*Doparium junceum*), false pimpernel (*Lindernia pyxidaria*) and long stemmed water wort (*Elatine triandra*) (Xuan et al. 2001). Alfalfa plant residues as well as the water extracts inhibited the weeds barnyard grass and annual bluegrass (*Poa annua*) in terms of their emergence and radical growth.

Alfalfa allelopathic extracts were found to decrease the coleoptile length and the number of roots of wheat (Panahyan-e-Kivi and Tobeh 2010). Goławska et al. (2008) identified two saponins (zanhic acid tridesmoside and 3-GlcA,28-AraRh-aXyl medicagenic acid glycoside) and three flavones (7-*O*-*β*-D-glucuronopyranosyl-4′-*O*-[2′-*O*-E-feruloyl-*O*-*β*-D-glucuronopyranosyl(1 → 2)-*O*-*β*-D-glucuronopyranoside] apigenin, 7-*O*-{2-*O*-E-feruloyl-[*β*-D-glucuronopyranosyl(1 → 3)]-*O*-*β*-D-glucuronopyranosyl(1 → 2)-*O*-*β*-D-glucuronopyranoside} apigenin, and 4′-*O*-[2′-*O*-E-feruloyl-*O*-*β*-D-glucuronopyranosyl(1 → 2)-*O*-*β*-D-glucuronopyranoside] apigenin) from alfalfa cultivars; these cultivars were inhibitory to the survival and reproduction of pea aphid; the cultivar with higher sanonins concentration was more suppressive against the aphid.

15.2.9 Cucumber

Cucumber possesses allelopathic activity that causes autotoxicity and soil sickness (Yu et al. 2000) and exudes certain allelochemicals (Yu and Matsui 1993, 1994). Putnam and Duke (1974) tested cucumber accessions for their allelopathic potential; growth of test species was inhibited by more than 50 %, while leachates from pots where cucumber was grown were also phytotoxic. Lockerman and Putnam (1979) used the allelopathic cucumber cultivar as a tool to suppress weeds; population as well as the growth of weed proso millet (*Panicum miliaceum*) was suppressed by the cucumber plants grown mixed with the weed. Yu et al. (1997) determined the effects of cucumber root exudates on ion uptake by intact cucumber seedlings and found that uptake of NO_3, K^+, Ca^{2+}, Mg^{2+}, Fe^{2+}, and BO_3 was inhibited but not of H_2PO_4. Pramanik et al. (2000) identified benzoic acid, cinnamic acid, and their derivative compounds as being exuded from hydroponically grown cucumber (Table 15.9); root growth and dry matter production of cucumber was severely affected due to these phytotoxic substances compared to the culture where they were absorbed by activated charcoal. However, some identified compounds were inhibitory to cucumber and radish. Yu et al. (2003) determined the allelopathic effect of cucumber on itself in terms of stomatal conductance, root antioxidant enzymes, transpiration, and leaf photosynthesis by

Table 15.9 Allelochemicals reported in *Cucurbit* spp

Cucurbit spp.	Allelochemicals	Reference
Cucumber (*Cucumis sativus*)	Benzoic, *p* hydroxybenzoic, 2,5-dihydroxy-benzoic, 3-phenylpropionic, cinnamic acid, *p*-hydroxy cinnamic acid, myristic acid, palmitic acid, stearic acid, *p*-thiocyanatophenol	Yu and Matsui (1994)
	Benzoic acid, cinnamic acid	Pramanik et al. (2000)
Watermelon (*Citrullus lanatus*)	Cinnamic acid, *p*-coumaric acid, ferulic acid, vanillic acid	Yang et al. (2004b)
	α-hydroxybenzoic acid	Yang et al. (2005)

incubating cucumber seedlings with its root exudates at variable rates. Stomata conductance, transpiration, net assimilation rate were decreased while leaf temperature, root peroxidase, membrane peroxidation, and superoxide dismutase activities were increased as a result of cucumber allelopathic influence. Kato-Noguchi et al. (2011b) identified two allelochemicals from the cucumber plants including 9-hydroxy-4,7-megastigmadien-9-one (HMO) and (6*S*,7*E*,9*S*)-6,9,10-trihydroxy-4,7-megastigmadien-3-one (THMO). These allelochemicals were inhibitory to the weeds including cress (*L. sativum*) and barnyard grass in the bioassay. The authors suggested the use of cucumber leaves for weed management in agricultural settings.

15.2.10 Rye

Rye is well known for its allelopathic potential (Shilling et al. 1986; Barnes et al. 1987; Masiunas et al. 1995; Understrup et al. 2005) and for natural weed management (Barnes and Putnam 1983; Altieri et al. 2011). Rye is effective in suppressing the weeds in either of the forms including living mulch, rye residues, or the root leachates (Barnes and Putnam 1983). Rye residues inhibited the emergence, radicle elongation of cress, barnyard grass, proso millet, and lettuce (Barnes and Putnam 1986).

Certain allelochemicals have been discovered from rye residues (Barnes et al. 1987) such as 2,4-dihydroxy-1,4-benzoxazin-3-one, 2,4-dihydroxy-1,4-benzoxazin-3-one-glucoside, and 2(3H)-benzoxazolinone (Table 15.10; Yenish et al. 1995). Decomposing rye residues were found to possess a number of phenolic compounds which were inhibitory to the lettuce. These allelochemicals included 4-phenylbutyric acid, ferulic acid, *o*-coumaric acid, phenylacetic acid, *p*-coumaric acid, *p*-hydroxybenzoic acid, salicylic acid, vanillic acid, and salicylaldehyde (Chou and Patrick 1976). However, another study indicated that the young rye tissues had much higher concentrations of allelochemicals than the decomposing

Table 15.10 Allelochemicals reported in rye

Allelochemicals	Reference
2,4-dihydroxy-1,4-benzoxazin-3-one 2,4-dihydroxy-1,4-benzoxazin-3-one-glucoside, 2(3*H*)-benzoxazolinone	Yenish et al. (1995) Burgos et al. (2004)

residues. The identified allelochemicals included *p*-hydroxybenzoic, protocatechuic, gallic, vanillic, syringic, *p*-coumaric, ferulic as well as benzoic acid while several other allelochemicals were suspected to be present in his plant (Wójcik-Wojtkowiak et al. 1990). Shilling et al. (1985) identified two allelochemicals from the extracts of killed rye residues, β-phenyllactic acid (βPLA), and β-hydroxybutyric acid (βHBA); both the allelochemicals (βPLA, βHBA) were found potent suppressive against the weeds (red-root amaranth, annual ragweed (*Ambrosia artemisiifolia*), lambsquarters). Further, the application of rye mulch suppressed these weeds by 51, 41, and 73 %, respectively in a no-till field of tobacco crop and by 99, 92, and 96 %, respectively in soybean and sunflower crops. Phytotoxic potential of rye varies with cultivar and plant age and is correlated with 2,4-dihydroxy-1,4-benzoxazin-3-one concentration in residues (Burgos et al. 1999; Reberg-Horton et al. 2005). The exudates from rye plants roots inhibited the wild oat and these exudates were found to possess the allelochemicals (hydroxamic acids) (Pérez and Ormenoñuñez 1991). Rye residues have the potential to obstruct growth of triazine resistant and sensitive biotypes of barnyard grass, willowherb (*Epilobium angustifolium*), and horseweed (*Conyza canadensis* L.) (Przepiorkowski and Gorski 1994). Burgos et al. (2004) extracted rye allelochemicals 2(3H)-benzoxazolinone and 2,4-dihydroxy-1,4(2H)-benzoxazin-3-one to test their allelopathic potential against cucumber. The allelochemical 2(3H)-benzoxazolinone reduced root elongation and lateral root number at 0.1 and 0.43 mg mL^{-1} deionised water while the allelochemical 2,4-dihydroxy-1,4-benzoxazin-3-one inhibited root growth by disrupting lipid metabolism and reducing protein synthesis. The degradation of 2-benzoxazolinone into 2-amino-(3H)-phenoxazin-3-one and 2-acetylamino-(3H)-phenoxazin-3-one from rye was studied by Understrup et al. (2005). The methods for the identification of rye allelochemicals have also been documented and evaluated. The steps included the ethanol extracting the rye residues and then partitioning, evaporation, and derivatization of the allelochemicals; and then the identification of allelochemicals through the flame ionization detection method in gas chromatography. A confirmation of the identified rye allelochemicals (such as 2,4-dihydroxy-1,4-benzoxazin-3-one, 2-benzoxazolinone, β-hydroxybutyric acid, β-phenyllactic acid and others) was sought (Finney et al. 2005).

Soils amended with rye green manures had less chance of being contaminated with cyanogenic *Pseudomonas* strains (Paszkowski and Dwornikiewicz 2003). Rye cover crop, especially, when grown in mix with fodder radish and vetch in the organic conservation agriculture, produced higher biomass of allelopathic material and effectively suppressed the weeds for vegetable production in the Brazil (Altieri et al. 2011). Similarly, Leavitt et al. (2011) also reported the effectiveness of utilizing the rye cover crop as intercrop and mulch for weed control in the organic agriculture, however, the yield of test was declined as well. In contrast, Smith et al. (2011) reported that rye mulch application not only decreased the weeds biomass but also improved the yield of soybean. Rye mulch when incorporated in the soil as green decreased the intensity of weed palmer amaranth (*A. palmeri*) in terms of density and biomass and inhibited (*Meloidogyne* spp.; Timper et al. 2011).

15.3 Breeding for Allelopathic Potential

Over the times, the major objective of the crop breeding programs world over has been the improvement in yield potential and resistance against biotic and abiotic stresses. Development of cultivars with strong allelopathic potential holds an attractive scope for weeds, insect pests, and disease pathogens management (Kong et al. 2011; van Bueren et al. 2011) but this has often been ignored. Improvement in allelopathic potential is expected to enhance the plant competitiveness against biotic and abiotic stresses (Kliebenstein 2009; Farooq et al. 2011b). Several researchers have screened the crop accessions for their allelopathic ability against plant species including weeds and crop plants (Seal and Pratley 2010). Quick crop emergence and dry matter gain, high root volume, and fast tillering are the ways by which the plants exhibit their competitive/allelopathic ability (Kim and Shin 2008). Some work has been conducted to improve the allelopathic potential of rice and wheat (Kim and Shin 2008; Bertholdsson 2010). Traditional breeding, genetic engineering and the allelopathic hybrids synthesis are the possible ways of producing crop cultivars with improved allelopathic potential. A cross between an allelopathic cultivar and a non-allelopathic cultivar resulted in a cultivar with much improved allelopathic potential (Kim and Shin 2008). Nevertheless, the breeding programs worldwide, in general, do not consider the allelopathic potential of crops, instead they focus on crop growth and yield, this lead to the dilution of allelopathic potential of crop varieties over the centuries of crop breeding (Bertholdsson 2004).

Targetted breeding of crop plants with stronger allelopathic potential would make plant highly resistant to agricultural pests and abiotic stresses (Kliebenstein 2009). However, some research workers have suggested that the newly evolved cultivars, even though having a strong allelopathic influence, would not completely suppress the pests (Duke 2005). Jensen et al. (2001) mapped QTL in 142 inbred lines obtained after the cross of an allelopathic japonica upland cultivar (IA 165) and an upland indica cultivar of poor allelopathic potential (CO 39). Chromosomes 2 and 3 had the three main loci for allelochemicals production. Kim and Shin (2008) suggested that the identified allelochemicals and genes responsible for allelopathic activity can further be incorporated into the cultivars through breeding or genetic engineering. For example, momilactones and phenolics are the major allelochemicals responsible for allelopathic potential of rice; and they can be produced in a conventional rice cultivar by inserting the genes CA4H and OsDTS2 for *p*-coumaric acid and momilactone, respectively through genetic engineering or even conventional breeding (Kim and Shin 2008; Kong et al. 2011). Ma et al. (2006) reported that the newly bred rice cultivar K21 was highly allelopathic and agronomically fit; this cultivar inherited its good agronomic performance from the female parent (Dongjinbyeo) and attained its potent allelopathic potential from male parent (Kouketsumochi).

Bertholdsson (2010) crossed Swedish and Tunisian cultivars (poor and strong allelopathic potential respectively); there were two lines with 20 % improved allelopathic activity than the parent and one line with unaffected allelopathic activity in the F6 and F7 generation; the allelopathic lines reduced weed biomass by 19 %, at cost of 9 % decrease in grain yield. The factors which need an attention before commercially growing the allelopathic crops in the agricultural fields include the investigation of the chances for resistance development among weeds against the allelopathic cultivars, the risks of autotoxicity, as well as the impact of residual allelochemicals on the following crops in the sequence. Improvement of the allelopathic potential of the crop plants would help to manage weeds with minimum or no reliance on herbicides. Crossing among the high yielding, low allelopathic potential with the high allelopathic potential, low yielding cultivar would strengthen the allelopathic competitiveness of plants against stresses. Genetic potential of allelopathic crops with strong allelopathy can be manipulated by isolating the genes of allelopathic potential and inserting these genes in the crops of the poor allelopathic potential.

15.4 Conclusion

The crops and the crop cultivars with higher allelopathic ability are better competitors of weeds and effectively repel the insect pests as well as the disease pathogens. Occasionally, some deleterious effects of allelopathic crop species are also expected on the other crops. This limitation can be dealt with the careful selection of cropping sequences and the companion crops. Many crop plants, in particular rice, sunflower, sorghum, wheat, rye, maize, barley, alfalfa, crucifers, and cucurbits, have strong allelopathic potential, which may be used for managing weeds, insect pests, and diseases. Another important significance of the allelopathic potential is the improved NUE and enhanced nutrient availability in the agroecosystems. Nonetheless, a special care is required in this regard to avoid any detrimental impact of the allelopathic phenomenon on agricultural systems.

Interactions among allelopathic plants, host crops, and other non-target organisms also needed to be considered. Furthermore, allelochemistry may provide basic structures or templates for developing new synthetic pesticides. An allelopathic crop has the potential to control weeds by planting either as smother crops, in rotational sequence, or left as a residue or mulch, especially in low-till systems, to control subsequent weed growth. Alternatively, application of allelopathic compounds before, with, or after synthetic herbicides may increase the overall effect of both, thereby reducing application rates of synthetic herbicides.

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Part IV
Allelopathy: Some Emerging Concepts

Chapter 16
Multifaceted Attributes of Allelochemicals and Mechanism of Allelopathy

S. R. Ambika

Abstract These allelochemicals are phytochemicals belonging to the class of phenolics, terpenoids, flavonoids, glucosinolates, cyanogenic glycosides, saponins, and alkaloids that are capable of causing "allelochemical stress" on the receiver plants and influence the pattern of vegetation in a forest, agriculture fields, uncultivated open areas, and also affect crop productivity. Allelochemicals are involved in plant invasion and plant–plant communication in the rhizosphere, replant problems in orchards of peach, citrus, jackfruit, mango, etc., and exhibit selective toxicity. Allelochemicals and their analogs are used commercially as herbicide, growth promoter, and as a sweetener. Allelochemicals can affect a number of physiological actions such as alter the membrane functions, plant metabolism, photosynthesis, respiration, flowering, fruiting, seeding, and ultimately even cause death of the organisms.

16.1 Introduction

Allelopathy is chemical interference in which a plant releases chemicals that exert an effect on associated plants. These are phytochemicals synthesized in plants as secondary metabolites that appear to have no direct functions in their growth and development but serve for defensive adaptation. The significance of their synthesis seems to be an interaction between the plant and its environment and is called allelochemicals. Plant allelochemicals are generally localized and sequestered in

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glandular or subepidermal layers. Both crops and weeds contain allelochemicals. Species with allelopathic potential have been given greater attention during the last two decades (Shilling et al. 1985; Weston 1996; Chou 1999; 1999).

The distribution of particular secondary metabolite is restricted within a group of taxonomically related species. For example, salicacin, a phenol glucoside, is characteristic of the members of the family Salicaceae while sesquiterpene lactones are found in the members of the family Asteraceae. They not only dispel harmful insects, pests, and pathogens but also increase reproductive fitness of the plants (Taiz and Zeiger 1998). There is a general feeling that selection pressure has favored plants with allelopathic phenomenon. Allelochemicals are now also being considered even for their role in biological life support system for long duration space missions (Stutte 1999).

Allelochemicals are also known to have detrimental effects on the receiver plants causing “allelochemical stress”. This environmental stress factor can act as a mechanism of interference and can influence the pattern of vegetation, weed growth, and productivity. Allelochemicals are involved in plant–plant interactions. Their release is facilitated by a variety of processes such as leaching from the above ground plant parts, volatilization, root exudation, stem flow, microbial activity, plowing of plant residues in soil and dry residue decomposition. Secondary metabolites such as terpenoids, phenolics, flavonoids, lignin-related phenolic acids, fatty acids, alkaloids, steroids, and polyacetylenes may act as allelochemicals (Waller 1987).

Crops with allelopathic properties may suppress subsequent crop growth. Utilization of the allelopathic potential of plants for weed control instead of herbicide application is given great emphasis, because it would reduce the risk of environmental toxicity (Grodzinsky 2006).

16.2 Attributes of Allelopathy

16.2.1 Allelopathy and Allelochemicals as Regulators in Biodiversity

The allelopathic effects of many crop species have been observed on other crop and weed species. It is well known that crops cultivated in rotation produce higher yields than when grown in monoculture. Similarly, many weeds are also considered troublesome in cropping systems and allelopathy has been suggested as a likely mechanism of interference in many weed species, also (Rice 1984; Putnam and Weston 1986; Rice 1995; Inderjit and Einhellig 1995; Wu et al. 1999a). Secondary metabolites of plants include a variety of compounds which, when released from plants into the environment often attract or repel, nourish or poison other plants/organisms. De Candolle (1832), a Swiss Botanist, suggested that the soil sickness problem in agriculture might be due to exudates of crop plants. Later, Stickney and Hoy (1881) reported a deleterious effect by black walnut on the growth of plants nearby. Yang and Tang made an extensive review of plants used for pest control and found 267 plants containing pesticide activity; many of them also exhibited allelopathic potential. Chou (1989) indicated that the plant constituents might play a role in plant–plant interaction and that the nature of the active compounds might be affected by habitat.

Schreiner and Reed (1907, 1908) isolated soil organic acids released by plant roots that suppressed the growth of some crops. About a century after De Candolle's work, allelochemicals came into use as natural growth regulators, such as herbicides, fungicides, and pesticides and their popularity is increasing (Chou and Waller 1989).

Root exudation of small molecules play a major role in plant ecosystems and is often associated with the development of competitive advantage through allelopathy (Wu et al. 1999; Bais et al. 2003; Bertin et al. 2007). Juglone, a highly phytotoxic naphthoquinone produced by black walnut (*Juglans nigra*), interferes with growth of other plants and its inhibition is selective. *Eucalyptus* leaf litter and root exudates are allelopathic to certain microbes and plant species. *Ailanthus altissima* (tree of heaven) produces allelochemicals from roots affecting the growth of many plants. Garlic mustard is an invasive plant in North American temperate forests. Its success is partly due to its excretion of allelochemicals, which interferes with mutualisms between native tree roots and their mycorrhizal fungi (Nardi et al. 2000). Sorgoleone, substituted quinine, is a potent allelochemical produced in the root hair cells of *Sorghum bicolor*, which inhibits the growth of the neighboring species. Catechin a phytotoxin exuded from the roots of *Centaurea maculosa* (spotted knapweed), an invasive species in the Western United States, displaces native plant species and meta-tyrosine, a herbicidal non-protein amino acid from *Festuca* sp. (grasses), interferes with the root development of many neighboring competing plants. These are few classic examples of potentially active allelochemicals deposited via the plant's living root system (Bais et al. 2003).

Fagopyrum esculentum (buckwheat) can be used as a cover crop because the allelochemicals released from the living or decaying plant material reduce the growth of various co-occurring weeds effectively (Isojima et al. 2000). Many troublesome weeds such as mug weed, *Chromolaena,* and *Lantana* influence biodiversity besides their adverse effects on growth and yield of many crop species. More studies on the ecological, physiological, and molecular aspects of weed allelopathy should be conducted in order to better understand the community structure and declining biodiversity (Gentle and Duggin, 1997).

16.2.2 Dominance of Exotic Plants

Many exotic plant species undergo astounding increases in dominance when introduced to new communities by humans. Callaway et al. (2005) have used ecological, physiological, biochemical signal transduction, and genomic approaches to develop evidence for showing how allelopathy may enhance the invasive ability of *C. maculosa.* They have reported the presence of racemic catechin in the biologically active fraction of *C. maculosa* root exudates, which showed much stronger allelopathic effects in invaded than in native ranges of *C. maculosa and C. diffusa*, suggesting the "novel weapons" hypothesis for invasive success or these may probably possess novel biochemical weapons that function as unusually powerful allelopathic agents against species without evolved tolerance. Other recent work suggests that some native species may resist the allelopathic effects of *C. maculosa* via exudation of high concentration of oxalic acid, and that field applications of (positive/negative) (+/−) catechin has demonstrated strong inhibition of a number of native North American species (Thelan et al. 2000).

16.2.3 Allelopathy and Orchard Replant Problems

Allelopathy is one of the main and poorly understood causes of replant problems in peach, citrus, and other nectarine orchards (Hassan et al. 1989; Dullhide et al. 1994). It generally originates from the successive planting of fruit trees in the same land, especially if trees of the same species follow each other. It is hypothesized that the compounds exuded into the soil by vegetative structures, seeds, and root exudates have specific effects on the developments of new plantings. It has been recognized that several compounds that are present in the soil in replant situations actively or passively alter the prevailing soil conditions, reducing the plant population, microorganisms, and insect reduction that may inhabit the soil environment. Therefore, due to their allelopathic characteristics, these substances could somehow act as a pesticide.

The compounds released by *Prunus* species roots are the cyanogenic glycosides; amygdalin and prunaxine (Selmar and Lieberei 1988). These compounds are enzymatically degraded in injured tissues or by microbial activity in the soil, generating D- glucose, benzaldehyde, and hydrocyanic acid. The latter is highly phytotoxic and allelopathic, inhibiting the respiratory functions on plant and animal cells and in other processes closely related to growth (Meehan 2000). Rice (1974) indicated that there are concentrations of cyanide in the soil, preferably close to 2000 mg L^{-1} that would create certain toxicity in the environment for those microorganisms that are present in the soil, while other much smaller concentrations would undergo degradation by microbial activity or by physical and chemical factors of the environment. Similar situations of replant problem were reported with the failure of Chinese-fir seedlings to grow normally in Chinese-fir woodland.

In orchards microbes play an important role in replant problem besides the autotoxicity. Presence of *Pencillium expansum* in apple orchards facilitates the release of allelochemicals. Arbuscular mycorrhizae also helps in changing microflora and help in increasing biomass of apple seedling. In case of peach orchards, nematodes are known to play an important role in releasing and hydrolyzing amygdalin—cyanogenic compound causing autotoxicity and replant problem. In case of *Asparagus* it has been shown that allelochemicals synergize with fungal pathogens thereby markedly increasing incidence.

16.3 Nature and Mode of Release of Allelochemicals

Allelochemicals are released from plants/plant parts by a variety of processes such as leaching from above ground plant parts, volatilization, root exudation, stem flow, microbial activity, plowing of plant residues in the soil, and dry residue decomposition. Secondary metabolites such as phenolics, fatty acids, steroids, flavonoids, isoflavonones, glucosinolates, non-protein amino acids, cyanogenic glycosides, acids, aldehydes, saponins, mono- and di-sesquiterpenes function as allelochemicals.

Phenolics active in allelopathy are most commonly accepted to be cinnamic acids, simple phenols, benzoic acids, and closely related derivatives such as chlorogenic acid, an ester of caffeic acid, several coumarins, the highly polyphenolic hydrolyzable and condensed tannins, flavonoids, and a diverse group of closely related structures. Although flavonoids constitute a very large grouping of phenolic substances, only a relatively small number of them have been established as agents in the phenomena of allelopathy.

The cinnamic and benzoic acid families of compounds have been identified in releases from plant residue and are the most widely distributed compounds in the soil of both natural plant communities and agronomic fields. There are hundreds of studies establishing that these are inhibitors of plant and microbial growth. The evidences are reported from diverse field situations such as: (a) the role of allelopathy in the succession sequence in “old fields” in Oklahoma part of the explanation for the patterning of vegetation in the California Chaparral, (b) humus phenolics in the failure of natural regeneration of conifers in the Boreal forests of North America and Northern Europe, (c) in the agricultural sector, the yield reduction problems in sequential cropping with rice in Taiwan (Chou 1989), and (d) phenolics and other allelochemicals being responsible for *Sorghum* allelopathy.

It has been recognized that dramatic differences occur in concentrations of phenolics at various locations and points in time in a plant community and hence can be accepted to be active contributors of allelopathy. At the same time the receiver plants differ in their tolerance and capacity to detoxify phenolic and other allelochemicals. Certain phenolic acids implicated in allelopathy also have functional importance to internal physiology. Notable among these is salicylic acid acting as a mediator for the development of systemic acquired resistance in a plant’s defense against disease.

These phytochemicals can also have detrimental effects on the receiver plants and hence can be considered as “allelochemical Stress”. This environmental stress factor can act as a mechanism of interference and can influence the pattern of vegetation in a forest, patterns of forest regeneration, agricultural fields, uncultivated open areas, and also affect weed growth and crop productivity (Barnes and Putnam 1986; Barnes et al. 1986, 1987).

16.3.1 Allelopathy of the Transformation Products

Microbes have a profound effect on the allelopathic activity by altering and/or transforming the amount of allelochemicals, particularly the phenolic acids in the soil depending upon the available carbon source and other environmental factors (Blum et al. 1999; Pellissier and Sonto 1999). The microbes may metabolize the released phenolic acids by addition or deletion of side groups, polymerization, and production of other organic molecules and/or incorporation of carbon from other phenolic acids into microbial biomass (Martin and Haider 1976; Blum 1998; Blum et al. 1999). The transformed or newly synthesized phenolics may differ in their phytotoxicity from the original ones that entered the soil (Blum 1998). Further, in the soil the preferential utilization of carbon sources may also affect the plant–plant, microbe-soil system, and the allelopathic phenomenon.

Transformation products have been shown to be important allelochemicals and may even intensify the activity of those already present. For example, maize, wheat, and rye release biologically active aglycones, DIMBOA (2,4-Dihydroxy—7-methoxy-1,4—benzoxazin-3-one) and DIBOA, which are degraded spontaneously to the corresponding benzoxazolinones—MBOA (6-methoxy–benzoxazolin-2-one) and the desmethoxy derivate BOA. These compounds are also allelopathic. Additional phytotoxic compounds may be formed in the presence of microorganisms (Barnes and Putnam 1986; Barnes et al. 1986; Nair et al. 1990; Niemeyer 1998). Consequently, attempts to identify allelochemicals responsible for an observed effect must consider biotic and abiotic transformation of released compounds.

Some of the bacteria such as *Streptomyces sagononensis*, *S. hygroscopicum*, *Pseudomonas fluorescences,* and many others are allelopathic and inhibit the growth of the nearby plants. The allelochemicals from microorganisms are generally nonspecific and inhibit the growth of several annual and perennial species (Hoagland 1990). They may be effective at very low concentration and have variable effects on the different cultivars.

On the other hand, allelochemicals may influence the growth of microbes positively or negatively and, thereby indirectly interfere with the availability of nutrients, particularly N and P, in the soil (Wardle and Nilson 1997; Anaya 1999). Residues of several crops such as corn, barley, and potato in the continuous single crop cultivation support several non-pathogenic microbial populations, which may considerably harm the growth of plants (Bakker and Schippers 1987). Phenolic compounds released in soil from decomposing residues may cause microbial imbalance (Chou 1995). However, flooding may eliminate phytotoxins leading to improved microbial balance and restoring the yield (Wang et al. 1984).

16.3.2 Allelochemicals and Rhizosphere Effect

Allelochemistry is also a biologically and ecologically sound explanation for plant invasion and plant–plant communication in the rhizosphere. The rhizosphere is the zone surrounding the roots of the plants in which complex relations exist among the plants, the soil microorganisms, and the soil itself. The plant roots and the biofilm associated with them can profoundly influence the chemistry of the soil including the pH and Nitrogen transformations. The chemicals secreted into the soil by roots are broadly referred to as root exudates. Through the exudation of a wide variety of compounds roots may regulate the soil microbial community in their immediate vicinity, cope with herbivores, encourage beneficial symbiosis, change the chemical and physical properties of the soil, and inhibit the growth of competing plant species (Macias et al. 1998; Nardi et al. 2000). Various compounds such as amino acids, vitamins, sugars, tannins, phenolics, alkaloids, etc., are exuded by roots.

Further, fungi and bacteria may produce and release inhibitors or promoters. Some bacteria enhance plant growth through fixing nitrogen, others through providing phosphorus. The activity of nitrogen-fixing bacteria may be affected by allelochemicals, and this effect in turn may influence ecological patterns. The rhizosphere must be considered the main site for allelopathic interactions.

16.3.3 Allergenic and Antimicrobial Activity

A number of secondary metabolites such as coumarins, furane coumarins, hypericin, and helenalin influence the immune system of the animals. Common to these compounds is a strong allergenic effect on those parts of the skin or mucosa that have come to contact with the compounds. Activation or repression of the immune response is certainly a target that was selected during evolution as an anti-herbivore strategy. These secondary metabolites that influence the immune system of animals are coumarins, furanocoumarin, hypericin, and helenalin. Secondary compounds are also known for their antimicrobial activity and these include phenolics, glucosinolates, non-proteinogenic amino acids, cyanogenic glycosides, acids, aldehydes, saponins, triterpenes, mono- and di-sesquiterpenes and alkaloids.

16.4 Commercial Use of Allelochemicals

In recent times unprecedented interest has been generated globally toward use of 'Green Technology' and organic cultivation in view of residual toxic effects of food, feed, pharmaceutical, and cosmaceutical products. In these areas, biologically active natural molecules play pivotal role in agricultural production and management.

The use of such biomolecules is also increasing day-by-day for higher yield per unit area. The purified allelochemicals and/or their derivatives and even the compounds synthesized on their chemistry are used as novel agrochemicals for sustainable agricultural management in an eco-friendly manner (Macias 1995).

Leptospermone is a purported allelochemical in lemon bottle brush *(Callistemon citrinus).* It was investigated as a possible herbicide but was found to be too weak. However, a chemical analog of leptospermone, i.e., mesotrione, trade name Callisto (Chou 1999), was found to be an effective herbicide. It is sold to control broad leaf weeds in corn and also seems to be an effective control for crabgrass in lawns.

A phyllocladane diterpenoid isolated from the plant *Callicarpa macrophylla* Vahl. (Family-Verbenaceae) has been found to promote the plant growth and alleviate the effects of growth-retardant allelochemicals. Among the phyllocladane diterpenoids, calliterpenone from *C. macrophylla* was found to be most promising. Experimentally, it has been proven that calliterpenone not only enhances the seed germination and production of biomass of roots, shoots, and flowers in angiosperms, but it is also effective in enhancing the population of beneficial microorganisms such as *Rhizobium* and *Bacillus* and behaves synergistically with bioinoculants while retarding the detrimental effects produced by allelochemicals. Thus, this unique natural molecule has enormous potential for commercial utilization (Singh 2008).

The extract and Stevioside from *Stevia rebaudiana* have been used since long as a sweetener in South America, Asia, and in different countries of Europe. In Brazil, Japan, and Korea, *Stevia* leaves and its highly refined extracts are officially used as low calorie sweetener. Residues and extracts of *S. rebaudiana* exhibited plant growth-promoting activity on lettuce, cucumber, and other crop plants.

Allelopathy allows scientists today to make new herbicides that are better than before. “The development and commercial success of mesotrione illustrates the potential for the use of allelochemicals as leads for the development of new herbicides. It is unlikely that many allelochemicals will have the potential to be developed as commercial herbicides *per se*, but in the increasingly difficult search for new chemistry and new modes of action, allelochemicals can provide the base structures for further chemical modification and the development of commercially viable herbicides”.

Allelochemicals produced by plants are something humans cannot duplicate on their own. And by using the technology of today to chemically enhance these “natural herbicides”, better and more sustainable agriculture can be reached. We all need agriculture to live, so the better study of allelopathy, the better living for everyone.

16.4.1 Action of Allelochemicals

Allelopathy is a chemical interference achieved through allelochemicals produced and released by plant species. These plants usually produce and release many kinds of secondary metabolites with multiple functions that affect their neighbors.

Chemical interactions occur through chemical recognition and information transfer among inter- and intraplant species.

Allelochemicals depending on the concentration, type, and the amount released would alter the membrane functions, plant metabolism, physiological processes such as cell elongation, photosynthesis, respiration, synthesis of certain compounds, flow of carbon, water relations, mineral uptake, stomatal function, and activity of number of enzymes besides ultimately causing even death of the organisms when in contact. However, they do not seem to alter cell division or directly affect gene translation (Einhellig et al. 1970; Rice 1984; Ortega et al. 1988; Li et al. 1993; Einhellig et al. 1993; Stiles et al. 1994; Blum 1996, 1997; Macias et al. 1998).

Besides the harmful effects, allelochemicals are reported to have a vast array of beneficial effects. Allelopathy is a chemically mediated phenomenon, and growth responses are concentration dependent. A compound may be inhibitory at high concentration, stimulatory at low concentration, or have no effect at other concentrations. Allelochemicals also influence the availability of nutrients to the plants. For instance, some phenolic acids are known to bind with the minerals such as iron, manganese, and aluminum and increase the availability of phosphate, which otherwise forms complex with these metal ions. There are several other allelochemicals that are used as growth regulators and natural pesticides to promote sustainable agriculture (Neill and Rice 1971; Rice 1986). Nowadays allelopathic interactions in general and the allelochemicals in particular are viewed as an important tool for sustainable weed and pest management and disease control.

In this direction, a number of strategies such as use of cover or smother or companion crops for weed management, direct use of allelochemicals as natural pesticides, and even the transfer of allelopathic traits/principles to modern day cultivars are being adopted. The purified allelochemicals and/or their derivatives and even the compounds synthesized on their chemistry are used as novel agrochemicals for sustainable management in an eco-friendly manner.

16.4.2 Effects of Allelochemicals on Water Relations and Membranes

Cinnamic and Benzoic acids have been reported to have bewildering array of deleterious effects on the plasma membrane. They reduce the transmembrane electrochemical potential (Einhellig 1995; Blum 1996, 1997) and depolarize membranes causing a non-specific efflux of both anions and cations accompanying the increased cell membrane permeability. These membrane effects correlate with inhibition of ion uptake. Phenolic acids suppress absorption of phosphate, potassium, nitrate, and magnesium ions thereby affecting the content of mineral ions in the tissue.

It was reported that benzoic acid and cinnamic acid damaged cell membrane integrity by a decrease in sulfhydryl (-HS) groups. These induced lipid peroxidation resulted from free radical formation in membranes and inhibition of catalase and peroxidase activities. Oxidation or cross-linking of plasma membrane HS groups was suggested as their first mode of action. Hence, it is likely that the cinnamic and benzoic acid derivatives cause structural changes in membranes that include alterations in a variety of membrane proteins. These authors suggested that they suspect that further work will reveal action on specific channel proteins, proton pumps, or some of the membrane transporters. It is also reasonable to project that these phenolics influence yet-to-be identified membrane hormone-binding sites and other signal receptors. It is also known that any effect on membrane proteins coupled with the known permeability effects will interfere with cell regulation mediated through signal pathways and transduction events (Einhellig 1995; Blum 1996, 1997).

Phenolic acids reduce the hydraulic conductivity of roots as evidenced in changes in plant-water parameters. All phenolic acids [ferulic, *p*-coumaric, caffeic, hydrocinnamic, salicylic, *p*-hydroxybenzoic, gallic and chlorogenic acids as well as hydroquinone, vanillin, and umbelliferone (coumarin)] and closely related compounds altered normal water balance in soybean seedlings. This was established by reductions in leaf water potential, turgor pressure, conductance, or a change in tissue carbon isotope ratio. The carbon isotope ratio in C_3 plants is an indicator of the extent of stomatal resistance or water stress during the growth period.

16.5 Mode of Action of Allelochemicals

Little is known concerning the mode of action of allelochemicals or plant defense responses mounted against them. Theoretically, changes in the expression of genes encoding the primary target or other proteins in the same pathway should occur soon after phytotoxin exposure. Defense responses, such as the induction of genes involved in chemical detoxification, may occur later, depending on the nature of the chemosensors which presumably exist in plant cells. A battery of xenobiotic defense-associated genes were found to be dramatically induced in *Arabidopsis* following exposure to an array of structurally unrelated xenobiotics, including a herbicide, an allelochemical, and herbicide safeners. These genes are unlikely to be strongly linked to the mode of action of a specific phytotoxin, rather constitute a coordinately controlled xenobiotic defense gene network (Duke et al. 2005). These authors suggested that allelochemicals induce a wide range of genes involved in detoxification of potential phytotoxins.

Buckwheat is an important annual plant cultivated for grain or as a cover crop in many countries, and it is also used for weed suppression in agroeconomic systems through its release of allelochemicals. Little is known, however, concerning the mode of action of allelochemicals or plant defense response against them. Microarrays revealed 94, 85, and 28 genes with significantly higher expression after 6 h of exposure to the allelochemicals—fagomine, gallic acid, and rutin, respectively, compared with controls. These induced genes fell into different functional categories, mainly: interaction with the environment, subcellular localization, protein with binding function or cofactor requirement, cell rescue, defense and virulence, and metabolism. Consistent with these results, plant response to allelochemicals was similar to that for pathogens (biotic stress) or herbicides (abiotic stress), which increase the concentration of reactive oxygen species (ROS) in plant cells (Fujii et al. 2005; Iqbal et al. 2005; Golisz et al. 2007a, b).

Microarray results have indicated that plant response to allelochemicals may be caused by reactions that are similar to those occurring during biotic and/or abiotic stress. There are several reports stating that the cross-talk between abiotic and biotic stress response pathways as well as cross-talk among various signaling pathways under each type of stress regulate the expression of different but overlapping sets of genes (Knight and Knight 2001; Chinnusamy et al. 2004; Narusaka et al. 2004; Taylor et al. 2004; Kaur and Gupta 2005). The generation of ROS has been proposed as a key process shared between biotic and abiotic stress response (Apel and Hirt 2004; Narusaka et al. 2004; Golisz et al. 2008).

These reactive molecules are generated at a number of cellular sites, including mitochondria, chloroplasts, peroxisomes, and at the extracellular site of the plasma membrane. ROS include not only free radicals (superoxide radicals and hydroxyl radical), but also molecules such as hydrogen peroxide, singlet and triplet oxygen, superoxide, nitric oxide, and ozone (Blokhina et al. 2003). ROS control and regulate many different processes in plants, such as growth, cell cycle, programmed cell death, pathogen defense, hormone signaling, stomatal behavior, and development (Apel and Hirt 2004; Mittler et al. 2004; Laloi et al. 2007). ROS induce the production of plant stress hormones such as ethylene, jasmonic acids, salicylic acid, abscisic acid, and nitric oxide. However, it is also thought that during stress ROS are actively produced by cells (e.g., by NADPH oxidase), and these act as signals for the induction of defense pathways. Thus, ROS may be viewed as cellular by-products of stress metabolism, as well as secondary messengers involved in the stress response signal transduction pathway. Because ROS are toxic and also participate in key signaling events, plants also require different mechanisms to regulate their intracellular ROS concentrations (Fig. 16.1).

The influence of these molecules on cellular processes is mediated by the perpetuation of their production and their amelioration by scavenging enzymes such as superoxide dismutase, ascorbate, peroxidase, and catalase. These also trigger signal transduction events such as mitogen-activated protein kinase cascades, eliciting specific cellular responses. The location, amplitude, and duration of production of these molecules determine the specificity of the rapid responses they direct. Though these antioxidant systems keep the levels of ROS low but can never completely eliminate them, and repair systems are necessary to repair the damage that occur. The perception and propagation of ROS signals and how these signals then induce specific cellular responses are not well known. The study by Gadjev et al. (2006) sought to address these questions by the use of transcriptome data generated from ROS-related microassay experiments.

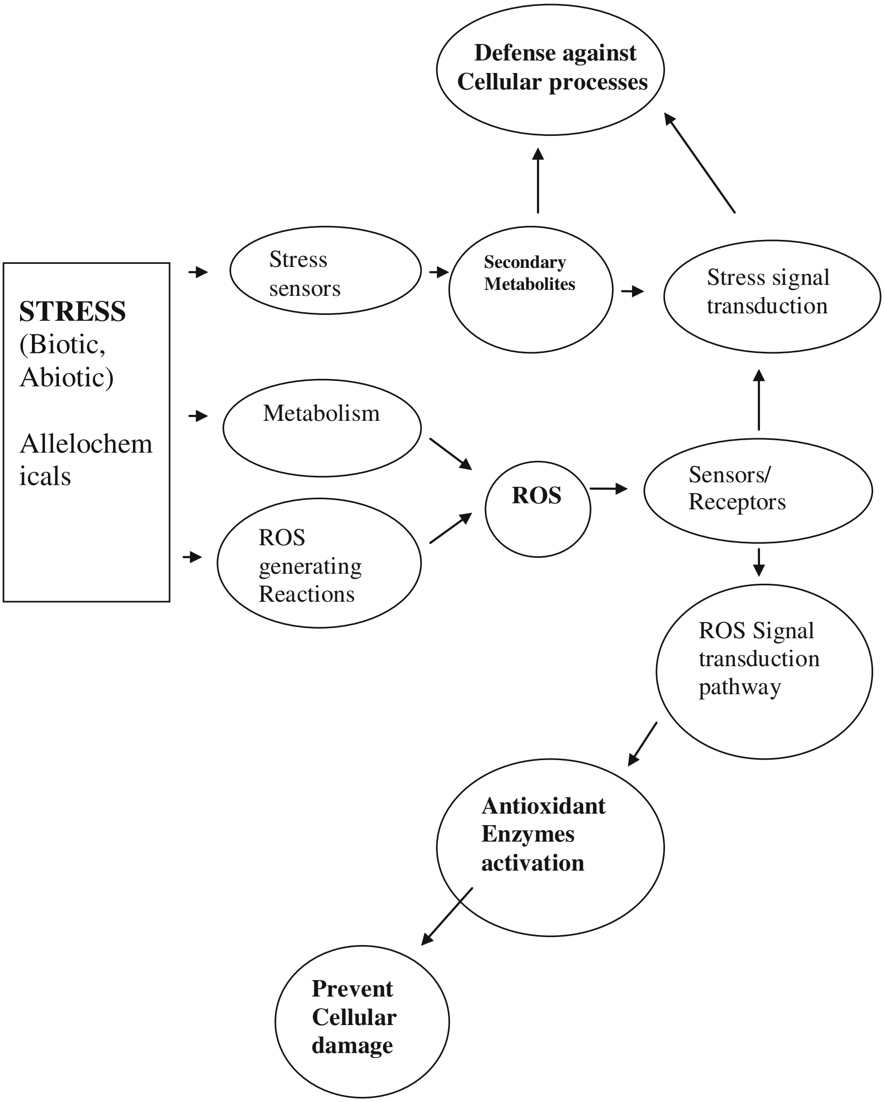

Fig. 16.1 Mechanism of allelopathic interaction

Antioxidants such as ascorbic acid and glutathione, found at higher concentrations in chloroplasts and other cellular compartments, are also important for the defense of plants against oxidative stress. Consequently, mutants with suppressed ascorbic acid levels, and transgenic plants with suppressed ROS-scavenging enzymes are hypersensitive to pathogen attack and abiotic stress conditions. In addition, overexpression of ROS-scavenging enzymes increases the tolerance of plants to abiotic stresses.

Allelochemicals such as gallic acid, fagomine, and rutin have also been reported to upregulate stress-related genes producing heat shock proteins. These proteins are expressed in plants not only when they experience high temperature stress but also in response to a wide range of other environmental insults, such as water stress, salinity, osmotic stress, and cold and oxidative stress (Grover et al. 2001; Wang et al. 2004). Heat shock proteins/chaperones play a crucial role in protecting plants against stress and in the reestablishment of cellular homeostasis by binding to and sequestering misfolded or unfolded proteins. Moreover, they also act synergistically with other cellular stress response pathways to limit cellular damage (Wang et al. 2004). Cucumber and fig leaf gourd seedlings were experimented for their interspecific interactions mediated by allelochemicals by exposing them to cinnamic acid, an autotoxin from root exudates of cucumber. ROS metabolism and plasma membrane H^+-ATPase activity were examined in roots upon exposure to cinnamic acid. This exposure resulted in significant increases in activities of NADPH Oxidase, superoxide dismutase, guaiacol peroxidase, and catalase as well as in O_2^- production and H_2O_2 content, in cucumber roots but not in fig leaf gourd roots. Notably the cucumber roots produced significant amount of ROS immediately after cinnamic acid treatment, consequently increasing membrane peroxidation, decreasing membrane H^+-ATPase activity, and losing root viability. In contrast, no such changes were observed in fig leaf gourd roots. This suggested interspecific difference in the recognition of allelochemicals (Ellis and Say 1991; Ding et al. 2007).

Methyl jasmonate and methyl salicylate are important signaling molecules that induce plant defense against insect herbivores and microbial pathogens. Hong Bi et al. (2007) tested the hypothesis that allelopathy is an inducible defense mechanism, and that the jasmonic acid (JA) and salicylic acid (SA) signaling pathways may activate allelochemicals release. Exogenous application of methyl JA and Me SA to rice enhanced rice allelopathic potential and led to accumulation of phenolics, an increase in enzymatic activities, and gene transcription of phenylalanine ammonia lyase (PAL) and cinnamate-4-hydroxylase (C_4H), two key enzymes in the phenylpropanoid pathway.

16.6 Conclusions

Allelochemicals are synthesized in plants as a result of interaction between the plants and its environment. These are secondary metabolites with no direct functions in plant growth and development but serve for defensive adaptation. Looking at their properties there is a general feeling that selection pressure has favored plants with allelopathic phenomenon. Several attributes are assigned allelopathy, which are to regulate biodiversity, establish and give dominance to exotic plants, cause replant problems in orchards, cause rhizosphere effect, and exhibit antimicrobial activity based on their concentration. These phytochemicals affect a number of physiological actions in plants such as membrane functions, plant metabolism, photosynthesis, respiration, flowering, fruiting, and seeding. The mode of action of these are envisaged partly to be through the production of ROS which act as secondary messengers and trigger specific responses resulting in activation of antioxidant enzymes that synergistically act with other cellular stress response pathways to limit cellular damage.

The possible mode of action of allelopathy partly through the production of ROS is envisaged. ROS production is sensed by plant cells as a “warning” message and genetic programs leading to stress acclimation or cell death are switched on. These natural compounds are commercially exploited in Green technology for synthesizing novel agrochemicals for sustainable agricultural management with an eco-friendly approach.

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Chapter 17
Microscopy for Modeling of Cell–Cell Allelopathic Interactions

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Abstract The application of various microscopy methods—from stereomicroscopy to luminescence microscopy, microspectrofluorimetry and laser-scanning confocal microscopy—has been considered as an approach to model the cell–cell contacts and interactions in allelopathy. It bases on the direct observations of both secretions released from allelopathic species and the interaction(s) with the cell acceptors as biosensors (unicellular plant generative and vegetative microspores). Special attention was paid to the interactions with pigmented and fluorescing components of the secretions released by the cell donors from allelopathically active plant species. Colored allelochemicals are considered as histochemical dyes for the analysis of cellular mechanisms at the allelopathic contacts.

17.1 Introduction

The study of cell–cell interactions in allelopathy has been achieved using various types of microscopic methods as has been shown for analysis of pollen–pollen interactions analyzed by microspectrofluorimetry (Roshchina and Melnikova 1996, 1999) or laser-scanning confocal microscopy (Roshchina et al. 2007, 2008, 2009a, b; Roshchina 2008). The technique may be suitable for the investigation of allelopathic mechanisms when one cell (a donor cell) releases a molecule that is received by another cell (an acceptor cell) belonging to different species. For this aim it should consider the microscopy for the observation of plant cell, viz.

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(a) modeling of direct cellular contacts through the addition of the allelochemicals to acceptor cell, (b) observation of the behavior of acceptor cell as a respond to the addition of allelochemicals, and (c) analysis of the interactions of allelochemicals with cellular organelles.

The success of such investigations requires models, mainly pigmented and/or fluorescent cells suitable for visual manipulation under microscope and, in some cases, measurable for absorbance or fluorescence parameters. Multicellular or unicellular objects may be chosen as models in a dependence on the purpose. Use of the cellular models is possible to observe by microscopic methods: (a) the transport of the compounds analyzed into an acceptor cell selected as a model (biosensor); (b) changes in the autofluorescence or color of cells; (c) the subcellular location where the allelochemical acted within the acceptor cell (model) and interaction with certain compartments. The purpose of this chapter is to show possibilities of various microscopic methods for the modeling of cell–cell contacts and interactions using some examples.

17.2 Microscopic Observation of Model Cells

17.2.1 Images of Contacting Surfaces with Secretions

Contacting surfaces of models for the studies of allelopathic interactions may be analyzed in vital conditions by stereomicroscopy (better for multicellular objects) or modifications of luminescence microscopy such as usual luminescence microscopy, laser-scanning confocal microscopy, and microspectrofluorimetry. Stereomicroscopy is used mainly for multicellular objects to see them in bright light whereas luminescent microscopy—both for microscopic multicellular and unicellular models having fluorescent secretory products such as allelochemicals. A researcher could see different components of secretion from plant, donor of allelochemicals, or the changes in the images of plant-acceptors undergoing the treatment with an allelochemical (Roshchina 2008). In some cases (pollen–pollen contacts at pollen allelopathic interactions) it is possible to observe direct interaction between contacting cells (Roshchina et al. 2008, 2009a).

17.2.2 Stereomicroscopy

Modern stereomicroscopes are equipped with a zoom lens system or a rotating drum (containing Galilean telescopes) that are utilized to increase and decrease overall magnification (achieved by objective and eyepiece magnifications, plus that contributed by any intermediate or external auxiliary magnifying lens systems). Stereomicroscopes are used for the observation of secretory structures and the natural secretions on the surface of allelopathic plants, in particular essential oil-containing structures on leaves and flowers (Gerbach 2002; Pacek and Stpiczynska 2007) or roots (Hazak et al. 2010) as well as for the collection of secretory structures necessary for chemical analysis of the secretions (Huang et al. 2009).

As models, pollen and pistils sensitive to allelochemicals were found (Roshchina and Melnikova 1996, 1999; Roshchina et al. 2008, 2009a). Pollen allelopathy (a competition between pollen grains of different species on the pistil stigma) is now actual problem due to the importance for normal fertilization. By stereomicroscopy we may see the secreting hairs of the pistil of *Tulipa* spp. or *Hippeastrum hybridum* as well as pollen in anthers of *Aloe vera* (Fig. 17.1, images 1–3). Pistils of similar objects are found suitable for analysis of mechanisms of allelopathic interactions, in particular with such excretion as acetylcholine and histamine (Roshchina and Melnikova 1998). There is a difference in the components of secretions on the cell surface (Fig. 17.1, images 1c, 3b). The secretions look as colorless and oil yellow. The excreted products may be colorless due to the presence of nicotinic acid or yellow color—due to riboflavin (Golovkin et al. 2001). Pollens in anthers (image 2) or individual pollen of *Lilium spp*. (image 4a) and on the pistil (images 3a, b) in various flowers have orange or slightly yellow products. This is due to the reason that pollen cover bodies including pigments from phenols to carotenoids (Stanley and Linskens 1974).

By stereomicroscopy flower capitate glandular trichomes of *Rubus odoratus* are seen as multicellular structure with transparent head filled of oleoresin and red-colored stalk (Fig. 17.3, image a). Oil secretion is accumulated on the bottom of the head.

17.2.3 Luminescence Technique

The light emission of living plant cells is the subject of attention in plant physiology (Gilroy 1997). Fluorescence from intact secreting plant cells was observed and photographed under usual luminescence microscope (Roshchina and Melnikova 1995, 1999; Roshchina et al. 1998) or its derivatives: confocal microscope (Roshchina et al. 2004, 2007, 2008, 2009a, b; Roshchina 2008), and microspectrofluorimeter (Roshchina and Melnikova 1995, 1999; Roshchina et al. 1998, 2002; Roshchina 2003, 2007b, 2008). In luminescent microscope, light from the ultraviolet source (UV source) excites the fluorescence of the object; the luminescent image might be catched directly with an eye of observer. Microspectrofluorimetry as modification of luminescent microscopy permits to receive fluorescence spectra from the individual cells or to measure the fluorescence intensity at one or double wavelengths. Unlike usual luminescent microscopy, confocal microscope has a special confocal aperture (pinhole), from which a fluorescence of the object excited with laser beam with a certain wavelength passes and multiples by photomultiplier before the eye visualization. Construction of aperture permits to focus the light beam on the different depth of

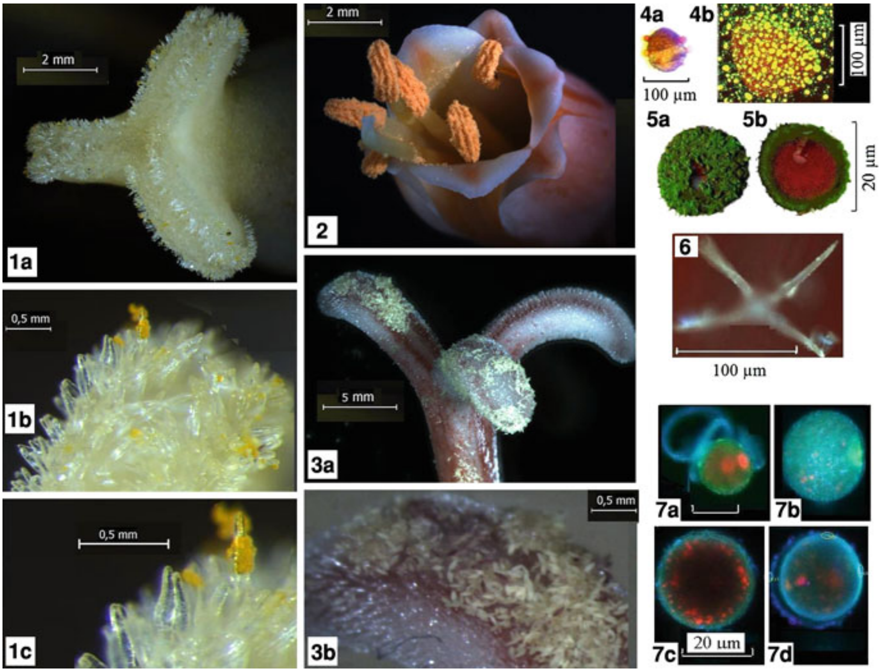

Fig. 17.1 The images of contacting surfaces in model systems. Samples were analyzed by under stereomicroscope Leica MZ 16A (**1**, **2**, **3**, **4a**), luminescence microscope Leica DM 6,000 (**6**, **7a**—excitation 360–380 nm), and laser-scanning microscopes Leica TSC SP 5 (**7b**, **c**, **d**—laser excitation 405 nm) and LSM 510 NLO "Carl Zeiss" (**4b**, **5a, b**, **6**—laser excitation 480 nm). 1—the secreting pistil of *Tulipa sp.*, (**1a**) common images; (**1b**) and (**1c**)—part of secreting surface hairs with various types of secretions—*yellow* and colorless; **2**—anthers with pollens in flower of *A. vera*; **3**—the secreting pistil of *H. hybridum* (**3a**) common image; (**3b**) part of secreting surface with secretions; **4**(**a**, **b**)—pollen grain from *Lilium spp.* with secreting drops—*red* under stereomicroscope and *greenish-yellow*-fluorescing—under laser-scanning confocal microscope; **5**—pollen grain of *Tagetes patula* under confocal microscope, front view (**5a**) and optical slice (**5b**); **6**—fluorescing leaf secretory hairs of *H. rosa-sinensis*; **7**—vegetative microspore of *E. arvense*, where (**7a**) common view of the cell with *red*-fluorescing chloroplasts and *blue*-fluorescing elaters, (**7b**–**d**)—various optical slices of the microspore through 1 µm

the object. Well-seen image of a cellular structure and its optical slices permit showing changes induced by many experimental factors, including allelochemical testing.

17.2.3.1 Luminescence Microscopy

Fluorescence from intact secreting plant cells, that induced by ultraviolet light 360–380 nm or violet light 400–430 nm, was observed and photographed under luminescence microscope. Fluorescing secretory cells are well seen among non-secretory or secretory cells with other non-fluorescing products. Figure 17.1 (images 6 and 7a) demonstrates the examples of the light emission that is seen under luminescent microscope for the rosette containing from leaf secretory glandular hairs of *Hibiscus rosa-sinensis* (blue-greenish emission, especially bright for crystals of released secretion, mainly due to terpenes and phenols) and unicellular vegetative microspore of *Equisetum arvense* having red-fluorescing chloroplasts and blue-green-emitted elaters—branches of cell wall served for the anchoring to a soil. Microscopy of donor cells (secretory cells) enriched in fluorescent allelochemicals was specially considered earlier in some special publications (Roshchina 2008; Roshchina et al. 2011a).

17.2.3.2 Microspectrofluorimetry

The recording microspectrofluorimetry is also applied for cellular biology as one of the non-invasive methods used for a cellular diagnostics. Luminescence of microobjects excited by short wave radiation of an arc lamp and after spectral decomposition is registered by detectors-photomultiplier(s). They can detect fluorescence from individual cells and even from a cell wall, large organelles and secretions in periplasmic space (space between plasmalemma and cell wall), as well as from the drops secreted by secretory cells and remaining on the cellular surface. This method permits the investigation of physiological activity of a secretory process in vivo (Roshchina et al. 2007, 2011a; Roshchina 2008).

Microspectrofluorimeters, having a detector with optical probes of various diameters up to 2 μm (the changed areas or probe holes composed with the system of mirrors), have been constructed in the Institute of Cell Biophysics of Russian Academy of Sciences (Karnaukhov et al. 1982, 1983, 1987, 2010), and may record the fluorescent spectra or measure the emission intensities or the fluorescence intensity at two separate wavelengths (Karnaukhov et al. 1982, 1987, 2010). Micro-spectrofluorimeters can receive a magnitude fluorescence image of a certain area of the specimen that appears on a spherical mirror. The emission data may be written in a form of the fluorescence spectra by the help of XY-recorder (could be coupled with a computer). The fluorescence spectra of secretory cells were registered recently with microspectrofluorimetric technique (Roshchina et al. 1995, 1996, 1997, 1998, 2002; Roshchina and Melnikova 1995, 1996, 1999). The examples of the fluorescence spectra of some secretory cells from allelopathic species are on Fig. 17.2. Optical probe shows the emission from part of cell from leaf secretory hair (emission maximum 530–540 nm) and gland (emission maximum 470 nm and shoulder 530–540 nm) to root hairs and idioblasts (maxima 440, 530 and 590–585 nm, relatively). At excitement by UV (360–380 nm)-or violet (420–430 nm) light secretory cells with allelochemicals fluoresce in wider spectral region—from blue (460–480 nm), green (520–530 nm), orange (560–590 nm) to red (chlorophyll 675–680 nm). Among studied allelochemicals bright fluorescence peculiar to flavonoids and alkaloids has been reported (Table 17.1). The fluorescence spectra were also measured by other microspectrofluorimetric technique

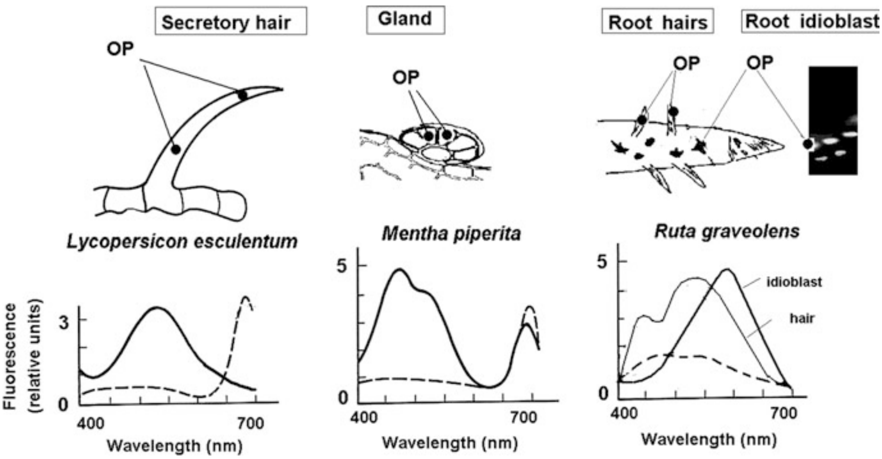

Fig. 17.2 The fluorescence spectra of secretory cells measured by microspectrofluorimetry. Unbroken line—secretory cells; broken line—non-secretory cells. The position of optical probe (OP) is shown for leaf secretory leaf hairs of *Lycopersicon*, leaf gland of *Mentha*, and on the surface of root with idioblasts from *Ruta graveolens*. Excitation 360–380 nm. *Source* Roshchina (2008)

(Leitz MPV-SP microspectrophotometer), in particular for the analysis of the flavonoid accumulation in Fabaceae at the nodule formation (Mathesius et al. 1998).

17.2.3.3 Confocal Microscopy

Unlike usual luminescent microscope, in confocal microscopy before catching by photomultiplier, the fluorescence beam from the sample studied passes through confocal aperture named pinhole (Pawley and Pawley 2006). Changing the diameter of the aperture, pinhole limits a scattered light from the object points which are out a focal plane and contrasts the volume image. Construction of a laser-scanning confocal microscope permits to observe cellular structures by the mode of a regulation of the depth of an object slide (LSCM images). The advantages of the technique are (1) to receive common complicated interference image of the object; (2) a possibility to have the increased depth penetration for the receiving of 20 visual slices (optical sections) or the complete volume (the information must also be quantitatively extracted); (3) Pattern analysis of the structure. (4) Registration and analysis of the fluorescence spectra of some part of a cell. Confocal microscopy offers several advantages over conventional optical microscopy, including controllable depth of field, the elimination of image degrading out-of-focus information, and the ability to collect serial optical sections from thick specimens. The key to the confocal approach is the use of spatial filtering to eliminate out-of-focus light or flare in specimens that are thicker than

Table 17.1 Fluorescence of secretory cells located in some allelopathically active species

Species	Secretory cells	Color of fluorescence	Fluorescence maxima, (nm)	Fluorescent components
Betula verrucosa, birch	secretory cells of woody bud scales	Bright blue (exudate), blue-green (secretory hair), blue-green (secretory cell)	460–470 500, 520 80–495, 520, 680	Flavonoids quercetin, kaempferol and others
Solanum tuberosum, potato	Leaf secretory hairs	Blue-green	465. 550 or 475–540	Alkaloids noscapine, β-solamarine
Campanula persicifolia, bellflower	glandular surface of pistil stigma	Blue-green	475, 560	Phenolcarbonic acids, vanillic acid, flavonoid diosmetin, caffeic acid, ferulic acid, chlorogenic acid,
Ruta graveolens, rue	Root tip surface, idioblasts	Orange (root tip), idioblast, yellow-orange (root secretory hair). Leaf secretory cell	500, 590 585–590 480, 575 565	Flavonoids rutin and quercetin, alkaloid rutacridone

Source Roshchina and Roshchina (1993), Roshchina (1999, 2001b, 2008)

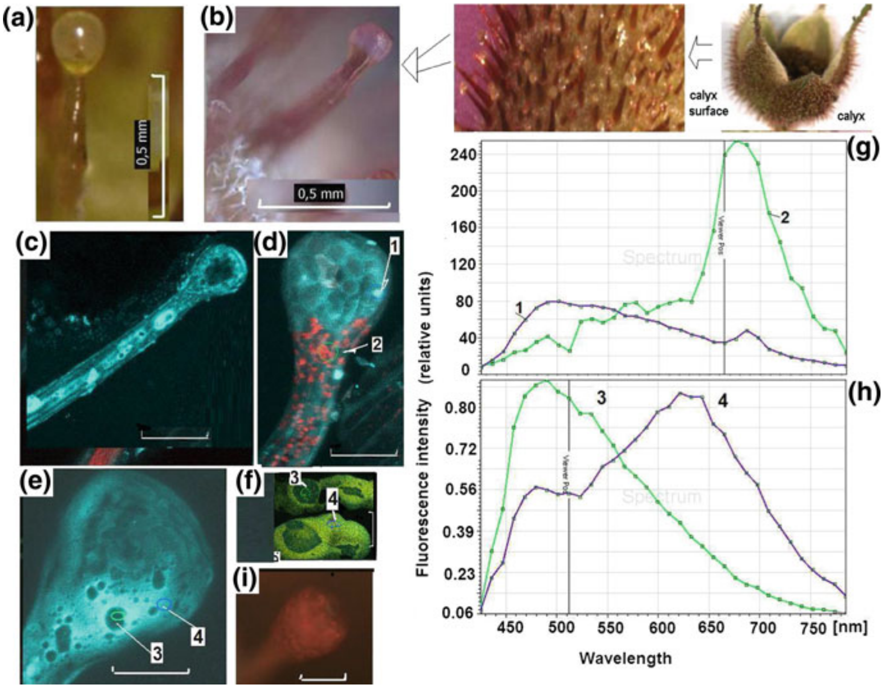

Fig. 17.3 The images (*left*) and the fluorescence spectra (*right*) of calycinal glandular resin-containing hairs from flower of *R. odoratus* with resinous secretion. Leaf secretory hairs of *R. odoratus*: **a**—the under stereomicroscope; **b**—under luminescence microscope (excitation 360–380 nm); **c**–**i**—seen under laser-scanning confocal microscope Leica TSC SP 5. Laser excitation 405 nm. **c**—Optical slice of the hair. Bar = 250 µm. Oil drops of blue fluorescent secretion were seen. *Blue* and *blue-green* fluorescence seen appears to be due to various flavonoids and terpenes. **d**—Stack of the image of the hair head and stalk. *Red*-fluorescing chloroplasts are seen. Bar = 100 µm. **e**—Head of the trichome covered by evolved secretion (Bar = 50 µm). **f**—Oil resin drops (Bar = 20 µm). Numerols of rings mean the parts of the structures from which the fluorescence spectra (**g**) and (**h**), were measured. **i**—Hair after the extraction of the oleoresin. Chloroplasts are seen. Bar = 50 µm

the plane of focus. Cells of algae and non-secretory cells of some higher plants were studied by the method, mainly labeled with immunofluorescent probes or fluorescent dyes (Wymer et al. 1999). Confocal imaging (LSCM) of secreting plant cells was studied for pollen and vegetative microspores analysis (Salih et al. 1997; Roshchina et al. 2004; Roshchina 2008). Scanning of the object studied along the Z-coordinate (see image of slice (c) in Fig. 17.3) with an interval of 1.0 µm was seen for the slices and stack of the slices of the leaf secretory hairs on *Solidago virgaurea* or on *S. canadensis* species rich in allelochemicals of the terpenoid nature (Roshchina et al. 2007; Roshchina 2008). The slices can be collected with the help of special computer program. Figure 17.1 shows some examples of the pollen images registered by this technique—release of greenish-

Table 17.2 Acceptor cells biosensors for testing of various allelochemicals

Plant species	Plant part or isolated organelles	Reference
Hippeastrum hybridum, knight's star (Amaryllidaceae)	Pollen	Roshchina (2004, 2007a, 2008); Roshchina and Karnaukhov (2010)
Plantago maior, plantain (Plantaginaceae)	Pollen	Roshchina et al. (2008, 2009a, b)
Vallota speciosa L., scarborough lily * (Amaryllidaceae)	Pollen	Roshchina and Karnaukhov (2010)
Equisetum arvense, common horsetail (Equisetaceae)	Vegetative microspores	Roshchina (2004, 2007a, 2008) Roshchina and Karnaukhov (2010)
Matricaria reticuta, matricary (Asteraceae)	Nuclei	Roshchina et al. (2011b)
Philadelphus grandiflorus, mock-orange (Hydrangeaceae)	Pollen, nuclei	Roshchina (2005, 2006b, 2008)
Raphanus sativus, radish (Brassicaceae)	Seeds and seedlings	Roshchina et al. (2009b)
Lemna minor, common duckweed (Lemnaceae)	Leaves and roots	Roshchina et al. (2009b)
Chara carolina, stonewort (Characeae)	Branches	Roshchina et al. (2009b)
Trifolium pretense, red clover (Fabaceae)	Chloroplasts	Roshchina et al. (2011b)

yellow-fluorescent (due to carotenoids abd anthocyanins) secretions from pollen of *Lilium spp*. (image 4b), front and back optical slices of green-fluorescent pollen (with red-fluorescing interior with rose-fluorescing secretion) from *Tagetes patula* (images 5a and b). The green fluorescence may be connected with flavonoids luteolin and patuletin contained while red-fluorescence with anthocyanins. We also see optical slices of vegetative microspore of horsetail *E. arvense* (images 7 b–d) demonstrating blue-green emission from surface and red-fluorescing chloroplasts within the cell. Laser beam of sufficiently high power, at the short time of observation does not prevent normal development of some plant cells for LSCM 510. Figure 17.3 analyzes the oleoresin-evolving calycinal secretory hair from flower of fragrant thimbleberry (purple-flowering raspberry; *R. odoratus*). A common view of the trichome on the calyx surface is observed under stereomicroscope Leica MZ 16 A (Fig. 17.3a) and luminescence microscope Leica DM 6,000 (Fig. 17.3b) and compared with the images (Fig. 17.3c–i) under confocal microscope Leica TSC SP 5. The fluorescence spectra were measured from parts of the secretory structures in rings (Fig. 17.3d, e 1–4). Oil in the trichome head (Fig. 17.3a–c) and evolved along the capitate hair (Fig. 17.3d) has one and the same emission maximum 520 nm peculiar to terpenes and phenols. The stalk fluoresces red due to chlorophyll in chloroplasts. After the 10 min extraction from calyx by water (1:10 w/v) and then the same volume of ethanol, the head was liberated from oleoresinous secretion, and chloroplasts became visible here.

17.2.4 Biosensors Served as Acceptor Cells

The success of such investigation requires suitable sensitive model-biosensors (acceptor cells) and pigmented (fluorescent) allelochemicals from donor cells. Table 17.2 demonstrates the acceptor cell biosensors studied. As biosensors may be unicellular microspores—generative (pollens of various seed-bearing species) and vegetative microspores of spore-bearing species such as horsetail *E. arvense* Roshchina 2004, 2006a, 2007a, b, 2008, or multicellular objects such as leaves of *Lemna minor* and radish *Raphanus sativus* seed and seedlings (Roshchina et al. 2009b). Approach to the analysis of plant unicellular microspores interactions basing on cellular spectral characteristics was considered for pollen allelopathy (Roshchina 2004, 2005; Murphy 2007; Roshchina et al. 2007, 2008, 2009a, b). For in-depth study of cellular mechanisms, isolated organelles are also used for modeling. In particular, nuclei from non-pigmented tissues from petals of mock-orange *Philadelphus grandiflorus* Willd. (Fam Hydrangeaceae) or *Matricaria reticuta* (Fam. Asteraceae) were isolated and tested for effects of some allelochemicals (Roshchina 2006b; Roshchina et al. 2011b). For the same aim chloroplasts were also isolated from leaves of *Trifolium pratense* (Roshchina et al. 2011b).

Application of allelochemical may change the color and/or fluorescent model system seen as alterations in, (1) a color of the biosensor, (2) a color of fluorescence and a position of maxima in the fluorescence spectrum, (3) the fluorescence intensity. The approach permits to see fast and direct changes in the state of cell analysed before changes in the rate of germination and growth become visible.

17.3 Modeling of Cell–Cell Contacts Based on Microscopic Observation

Modeling of cell–cell contacts is possible by several modes. Direct contact observed on the fluorescence alterations was studied on pollen mixtures (Roshchina and Melnikova 1996, 1999; Roshchina et al. 2008, 2009a). Other mode of modeling includes the interaction of acceptor cell—biosensor with allelochemical from excretion of donor cell. For this purpose multicellular and unicellular biosensors are suitable (Table 17.2). The changes in color or fluorescence in the model system could be registered (Roshchina 2004, 2005; Roshchina et al. 2011a, b). Some approach and examples of the studies will be considered below.

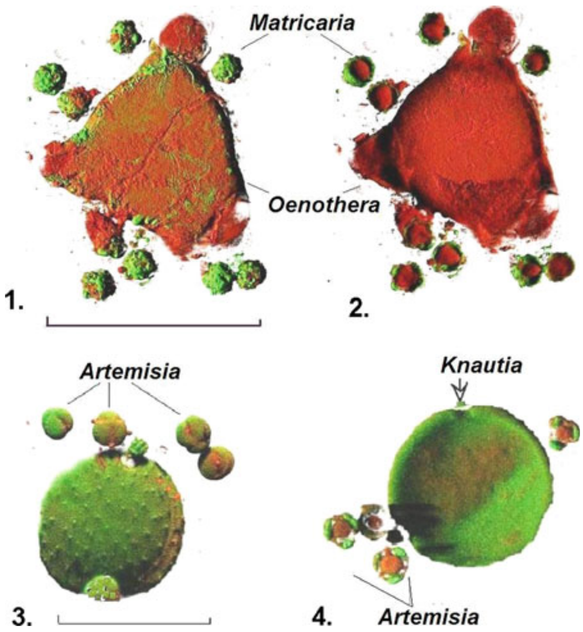

Fig. 17.4 Visualization of mixture containing fluorescent pollen grains on white background under laser-scanning microscope LSM 510 NLO "Carl Zeiss" (laser 488 nm). *Sources* Roshchina et al. 2008; 2009a. *1* and *2*. Frontal view and optical slice of pollen from *Oenothera biennis* (single large microspore) interacting with pollen grains from *Matricaria chamomilla* (small microspores). *3* and *4*. Frontal view and optical slice of pollen from *Knautia arvensis* (single large microspore) interacting with pollen from *Artemisia absinthium* (small microspores). *Orange/red*—fluorescing emission from *A. absinthium* pollen is seen on the *blue-green* fluorescing surface of pollen *K. arvensis*. Bars = 100 μm

17.3.1 Direct Cell–Cell Contacts at Pollen–Pollen Interaction

Modeling of cell–cell contacts occurred on the pistil stigma between own and foreign pollen grains was on the in vitro mixture of pollens studied (Roshchina et al. 2008, 2009a). Foreign pollen which can be carried by wind or insect on the surface of pistil stigma, interacts with pollen of own spp. that may lead to the antagonistic or favorable effects on the pollen germination. Pollen allelopathy plays major role in normal plant fertilization in biocenosis (Murphy 1992, 1999; Gaur et al. 2007). Studies reported the stimulatory or inhibitory effect of pollens mixture from different species, e.g., *Lilium*, *Tulipa*, *Narcissus*, *Corylus avellana*, *Linaria vulgaris*, *Papaver somniferum*, etc. Figure 17.4 shows the observation of similar pollen mixtures under laser-scanning confocal microscope (LSCM images). Contacting pollens have different colors of their fluorescence as well as their excretions. LSCM images of fluorescent pollens in their mixtures demonstrated how secretions are released and contacted, e.g., in *Oenothera biennis* (considered

Table 17.3 The effect of biogenic amines (10^{-5} M) on the fluorescence intensity (% of control) at 640–680 nm on the thallus meristem of *Chara carolina* and leaf of *Lemna minor* measured with microspectrofluorimeter MSF–2

Plant biosensor (acceptor cells)	Serotonin	Histamine
Chara carolina	192 ± 20	95 ± 4
Lemna minor	90 ± 10	236 ± 25

Source Roshchina et al. (2009b)

as pollen-acceptor) and *Matricaria chamomilla* (considered as pollen-donor). Red fluorescing secretion is characteristic for large pollen of *Oenothera,* while, small pollens of *Matricaria* emitted green (frontal view) and liberated green-fluorescing secretions (Fig. 17.4 image 1). Optical slices showed the interior of contacted pollen grains, green fluorescence was seen only on the surface of *M. chamolilla* spore, while red emission was also seen inside the pollen grain of *O. biennis* (Fig. 17.4 image 2). This picture explains why the red fluorescence intensity of *Matricaria* pollens increased after mixing with pollens of *Oenothera*. Besides, secretions from the pollen-acceptor enhanced the germination of *M. chamomilla* pollens. Similar findings about the contacts of pollen grains from *Knautia arvensis* and *S. virgaurea* have been reported (Roshchina et al. 2008). The interaction of blue-green fluorescent pollen of *K. arvensis* and orange/red fluorescing secretion of pollen from *Artemisia absinthium* decreased the germination in both contacting types of microspores. Orange/red-fluorescing secretion from *A. absinthium* was located on the green fluorescent surface of pollen of *K. arvensis*, and part of the secretion was also seen within acceptor pollen grain (Fig. 17.4 images 3 and 4). LSCM images of fluorescent pollen made it possible to directly observe, viz (i) the contact of intact cell, (ii) changes in their emission, and (iii) location of contacting secretions.

Changes in the fluorescence intensity of both cell-acceptor and cell-donor in green (maximum 520 nm) and/or red (maximum 680 nm) spectral regions accompanied by following alteration in the pollen germination were observed for 42 plant species (Roshchina et al. 2009a).

17.3.2 Modeling with Biosensors (Acceptor Cells) Treated with Allelochemicals

17.3.2.1 Multicellular Biosensors

Multicellular biosensors (Table 17.2) such as leaves of *L. minor* or branches of *Chara carolina* as well as root tips of seedlings of *R. sativus* were analyzed with the addition of the allelochemicals (Roshchina et al. 2009b). The changes in the fluorescence treated with allelochemicals found in plant secretions could be used as a response to the allelochemical tested, in particular biogenic amines serotonin

Table 17.4 The effect of biogenic amine dopamine (10^{-5} M) on the fluorescence intensity (relative units) at 530 nm on the *Raphanus sativus* seedlings measured with microspectrofluorimeter MSF–2

Part of seedling	Primary root meristem	Root hairs
Control	0.11 ± 0.01	0.02 ± 0.03
+Dopamine	0.29 ± 0.02	0.23 ± 0.03

Source Roshchina et al. (2009b, 2011a)

and histamine (Table 17.3) or dopamine (Table 17.4). Microspectrofluorimetry permits to measure the changes in the fluorescence intensity of the chlorophyll in leaves of *L. minor* and branches of *C. carolina* in red spectral region or of dopamine oxidative product in green spectral region for roots of *R. sativus*. Serotonin and histamine stimulated the chlorophyll fluorescence in the objects whereas dopamine enhanced the green emission related to the dopamine oxidation. The effects of physiologically active compounds released from water-lived plant species show possible interactions between allelochemicals excreted and acceptor cells. Dopamine is known to be excreted from green algae *Ulvaria obscura* (van Alstyne et al. 2006) and contained in *Lemna* spp. (Roshchina 2001a). The above-mentioned water-lived species could be suitable for modeling of allelopathic relations like algae and other representatives of phytoplankton (Solé et al. 2005; Roy et al. 2007).

17.3.2.2 Unicellular Biosensors

Modeling with unicellular biosensors includes the treatments with colorless or colored allelochemicals that induced various changes in the color or fluorescence of the acceptor cells. Some of the allelochemicals may fluoresce, and in this case we can see how they penetrate or do not penetrate into a cell-acceptor and where they are linked.

i. Allelochemicals as dyes and markers for the modeling

Colored allelochemicals are considered as possible histochemical dyes and markers in modeling (Roshchina et al. 2011b). Candidates for similar studies were red pigments (anthocyanins), blue pigments (azulenes), and yellow alkaloids. Some of the examples of modeling of the cell–cell interactions with anthocyanin pelargonidin, azulene, alkaloid rutacridone, and anthraquinone hypericin are given in Fig. 17.5. When the pollen of *H. hybridum* was used as acceptor cells treated with anthocyanin pelargonidin, the cell wall was stained and fluoresced in green (Fig. 17.5 image a). The fluorescence spectrum (excitation by laser 405 nm) of the pollen surface stained with the anthocyanin had maximum 450 nm and a shoulder at 520 nm (Roshchina et al. 2011b). *Pelargonidin glucoside* purified from water extracts of red petals of *H. hybridum* colored in red at pH 6.0–6.5 with 520–530 nm maxima and in blue at pH > 7.0 with 590–600 nm maxima in the absorbance spectra (Roshchina et al. 2011b). Acidic samples had 470 nm maximum in the fluorescence

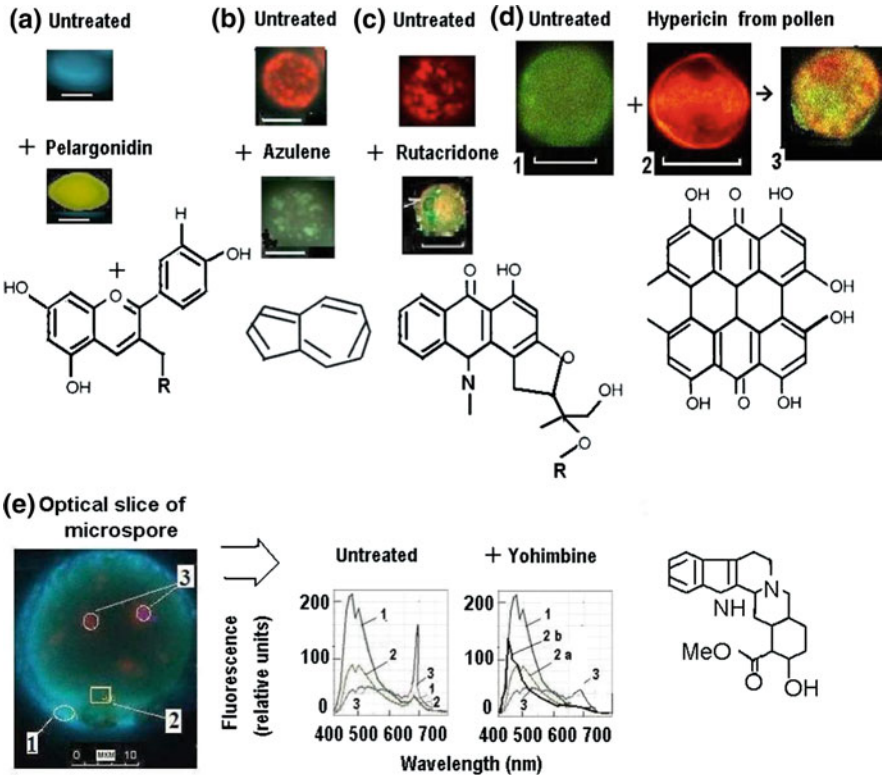

Fig. 17.5 The interaction of acceptor cells—biosensors with colored and fluorescent allelochemicals (10^{-5} M). *Source* Roshchina et al. (2008, 2011b, c) Images are seen under luminescence microscopes Leica DM 6,000 (**a**, **b**—excitation 360–380 nm), laser-scanning microscopes LSM 510 NLO "Carl Zeiss" (**c**, **d** laser 480 nm), and Leica TSC SP 5 (**e**, laser 405 nm). **a** Pollen of *H. hybridum* (Bar = 50 µm); **b** and **c**—vegetative microspores from *E. arvense* (Bars = 20 µm); **d** Pollen of *Plantago major* before (1) and after (3) the interaction with *red* pigment hypericin released from added pollen from *H. perforatum* (2). Bar = 20 µm. *Green*-fluorescing pollen of *P. major* after the staining has *red*-fluorescing parts. **e** Optical slice (*left*) and the fluorescence spectra (*right*) from different parts of vegetative microspore from *E. arvense* before and after the treatment with yohimbine (10^{-5} M). (1)—exine, i.e., outer layer of cell wall, (2)—together intine, i.e., inner layer of cell wall and plasmalemma, (2a)—only intine, (2b)—plasmic membrane that is seen only after addition of yohimbine, (3)—chloroplast

spectra, while basic ones demonstrated absence of any picks. The staining was compared with the stimulating effects of the anthocyanin on the pollen germination. If vegetative microspores of horsetail *E. arvense* were used as biosensors one has seen their interaction with azulene and rutacridone (Fig. 17.5b and c). In microspores of *E. arvense* (chloroplast-containing models) azulene induced blue (excitation 360–380 nm) or blue-green (excitation 420–430 nm) fluorescence of nucleus and chloroplasts (i.e. DNA-containing structures) instead of the fluorescence seen in the

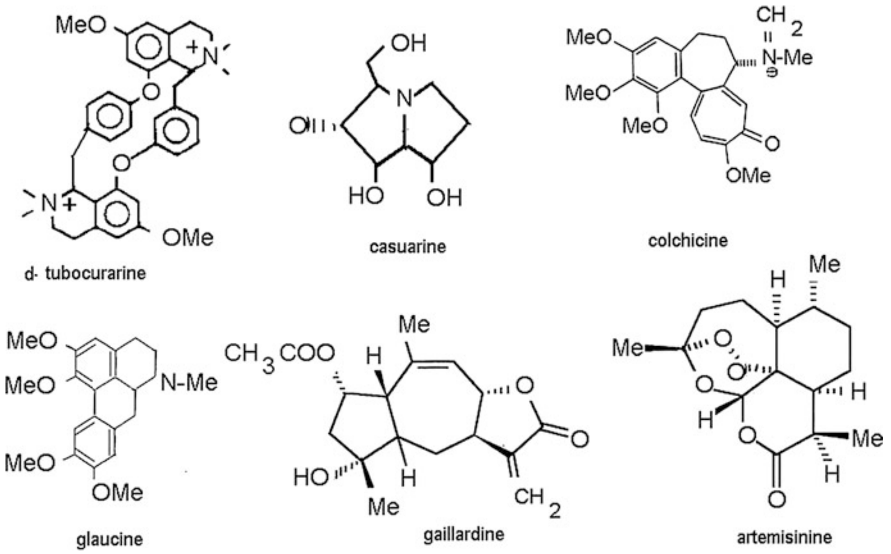

Fig. 17.6 The fluorescent allelochemicals binding with different cellular compartments

control. Rutacridone also penetrated into cell and bounded with DNA-containing organelles to made them green-emitted. Azulene is known to modulate the germination of plant microspores, in particular bind to cell wall and nucleus of pollen grains (Roshchina 2008). The chloroform extracts from chamazulene-containing species *A. absinthium* and *Achillea millefolium* that after drying mixed with water-inhibit the germination of pollen from *H. hybridum* and *V. speciosa* (Roshchina and Karnaukhov 2010; Roshchina et al. 2011a). The blue fluorescence intensity was also seen on the fluorescence spectra of the pollen nuclei. Besides, isolated chloroplasts treated with azulene had an increase in blue fluorescence intensity and a decrease in red emission of the organelles (Roshchina et al. 2011b). The intensity of the rutacridone fluorescence in orange spectral region (590–595 nm) is far more significant, as those of flavonoids and the flavonoids which have maxima in blue region of the spectra, but the flavonoid concentration was ten times smaller, than fluoresced alkaloid. The fluorescence also depends on the medium (solvent). In oil and non-polar chloroform red–orange (580–600 nm) fluorescence is observed, but polar solvents and water shift the maxima to short wavelength (Roshchina 2008).

In mixture of the green fluorescing pollen from *Plantago major* (biosensor) with red-lightening pollen from *Hypericum perforatum* released anthraquinone hypericin there is interaction of the red-fluorescing pigment with acceptor cell (Fig. 17.5d). Confocal microscopy of the acceptor cell showed only surface binding of hypericin (Roshchina et al. 2008).

Fluorescent non-pigmented secondary products released by allelopathic plants are also suitable biomarkers for such microscopic observations (Roshchina 2003, 2005, 2007a, b, 2008). Formulae of some from the fluorescent allelochemicals are

Table 17.5 The fluorescence intensity of chloroplasts isolated from leaves of red clover *Trifolium pratense* treated with 10^{-5} M azulene (excitation 360–380 nm)

Variant	Blue emission at 430–460 nm (relative units)	Red emission at 640–680 nm (relative units)
Control	0.01 ± 0.001	0.21 ± 0.010
±azulene	0.02 ± 0.002	0.07 ± 0.014

Each value is the mean of 400 counted cells analyzed per variant (four slides in every variant as independent measurements) followed by SD
Source Roshchina et al. (2011b)

given on Fig. 17.6. All compounds binding with plasmatic membrane, in particular with membrane receptors, fluoresce in blue or blue-green spectral region. Alkaloids d-tubocurarine and yohimbine are bounded in plasmalemma with the receptors of acetylcholine and noradrenaline, relatively (Roshchina 2004, 2005). Acetylcholine antagonist d-tubocurarine and catecholamine antagonist yohimbine, as well as an antihistamine agent azulene significantly (by 60–70 %) reduce the intensity of fluorescence and the germination of horsetail vegetative microspores that indicate the presence of cholino- and adrenoreceptors in the cells analyzed (Roshchina 2001a, b; Roshchina and Karnaukhov 2010; Roshchina et al. 2011c). Figure 17.5e demonstrates the example of the vegetative microspore fluorescence in the presence of yohimbine that will be considered in following section.

Other alkaloids such as glaucine and casuarine as well as sesquiterpene lactones artemisinine and gaillardine penetrate into the acceptor cell and fluoresce here, binding with nucleus and chloroplasts (Roshchina 2008). Alkaloid colchicine and microbial lactone cytochalasin B mark the sites of the tubulin (near nucleus) and actin (along the cell wall cytoplasm) location, relatively (Roshchina et al. 2007; Roshchina 2008).

ii. Targets for allelochemicals at cell–cell interactions

For the understanding of mechanisms of allelochemical interactions with the acceptor cell targets of the compounds in the cell tested may be analyzed visually and by the registration of the fluorescence spectra measured either with microspectrofluorimeter or confocal microscope as seen in Fig. 17.5e. According to information received at different depths optical slice with the help of confocal microscopy, as shown for yohimbine in Fig. 17.5 (similar phenomenon was observed and for d-tubocurarine), the main antagonist binding occurred on the surface of the biosensor (Roshchina et al. 2011c). One can see from the fluorescence spectra of single sections of exine (1) and intine (2a) with adjacent plasmatic membrane (2b) and chloroplasts (3). In untreated acceptor cell, protoplasmic membrane has no fluorescence and became visible only after the addition of fluorescent yohimbine that binds with adrenoreceptors in the plasmalemma.

Chloroplasts are also considered as targets for fluorescent allelochemicals. Isolated plastids, in particular stained with azulene (Table 17.5), show the same changes in the fluorescence intensity that were seen in the acceptor cell, the increase in blue and decrease in red emissions.

Microspores of horsetail *E. arvense* (chloroplast-containing models) treated with azulene fluoresce in blue (excitation 360–380 nm) or blue-green (excitation 420–430 nm), were chloroplasts located, instead of the red fluorescence seen in the control. Direct measurements of the interaction of azulene with chlorophyll were unsuccessful. Possible target of azulene is DNA-containing structures because the compound also interacts with nuclei. The blue fluorescence of the cell nucleus in the presence of azulene has been demonstrated earlier (Roshchina 2004, 2005) as well nuclei isolated from white petals of *P. grandiflorus* and *M. recutita* (Roshchina et al. 2011b). The extracts from *A. absinthium* or *A. millefolium* riched in chamazulene also induced nuclei blue fluorescence in pollen grains of *H. hybridum* and *Vallota speciosa* as biosensors (Roshchina and Karnaukhov 2010; Roshchina et al. 2011a).

Yellow alkaloid rutacridone, active allelochemical of rue roots participated in root–root interspecies interactions (Aliotta and Cafiero 1999), binds with nucleus of acceptor cells—*H. hybridum* pollen (Roshchina 2002) as well as with chloroplasts and nuclei of vegetative microspores of *E. arvense* (Roshchina et al. 2011b). The analysis of the isolated organelles' emission showed the shift in the orange fluorescence of rutacridone with maximum 580–590 nm to green emission.

Interactions of allelochemicals, in particular azulene and rutacridone, with DNA or RNA on subject glasses by microspectrofluorimetry show direct changes in the fluorescence of nucleic acids, mainly in DNA, correlated with the pictures observed for whole acceptor cells models (Roshchina 2002, 2004). DNA is proposed to be a target for the allelochemicals in the cell. The interaction of the allelochemicals with the components of nucleic acids—nucleosides, i.e., pyrimidine and purine bases bound to ribose or deoxyribose: thymidine, cytosine, adenosine, and guanosine as well as ribose (deoxyribose) itself—was studied using the films of the compounds on the subject glass (Roshchina et al. 2011b). Modeling with the films (their solid systems fluoresce in region 380–410 nm) was due to several circumstances, viz., (a) in nature nucleic acids are in solid form and (b) in the solutions of the nucleosides and sugars their fluorescence was very small if any. If the films of the above-mentioned components of nucleic acids were stained with pelargonidin only in variant with ribose (deoxyribose) the anthocyanin blue fluorescence was quenched. Fluorescent pelargonidin may be transformed to non-fluorescent cyanidin. The site of the binding of cyanidin is proposed phosphorus lied between two deoxyribose residues of the DNA near the contact of ribose (deoxyribose) with nucleotides (Jaldappagari et al. 2008). Anthocyanin-DNA copigmentation complex forming becomes the protection against oxidative damage (Sharma and Sharma 1999). Unlike pelargonidin, among the films staining by azulene only guanosine increased the fluorescence at 420–430 nm, while other nucleosides—not (Roshchina et al. 2011b). DNA-azulene complex emits in blue-green with 440 and 520 nm maxima (Roshchina 2004). Guanosine may be considered as a potential target for the allelochemical. Another picture was after the films staining by rutacridone because blue-green emission was observed mainly for cytosine (maxima 415 and 445 nm in the fluorescence spectra) and in small degree for ribose (smooth pick 445 nm was seen), while solution of rutacridone had no maxima in the spectral region. Cytosine appears to be one of targets for rutacridone on the nucleic acid. Tested allelochemicals may be considered as histochemical dyes and also used for indication of DNA-containing cellular structures.

17.4 Conclusions

Unlike motile animals, plants attached to a substrate adopt to a life within biocenosis mainly through chemical (allelopathic) interactions, via the biosynthesis of numerous secondary metabolites and their excretion. Some of the exometabolites having color or/and being fluorescent may be suitable for the study of allellelopathic mechanisms on cellular level. The fast changes in cell-acceptor received chemosignal as allelochemical from cell-donor in their contacts precede more distant integral processes such as plant-acceptor growth and development. Stereomicroscopy and various types of fluorescence microscopy from luminescence microscopy to microspectrofluorimetry and confocal microscopy is useful tool for the study secretory cells containing allelochemicals and the cell–cell interactions. The technique permits analysis of the images of contacting secreting surfaces in both donor cell and acceptor cell and possible location of excreted allelochemicals in the acceptor cell biosensor. Modeling of the cell–cell interactions using colored allelochemicals and unicellular models (biosensors) showed possible way for analysis of allelopathic mechanisms on cellular level. Color and fluorescence of acceptor cells were demonstrated as indicators of cellular reactions on the addition of the allelochemicals from excretions of donor cells. The compounds bounded to the surface or/and penetrate and act on cellular organelles. Some parts of plasmalemma (receptors to acetylcholine or dopamine) and DNA were shown to be potential targets for allelochemicals excreted by donor cell. The colored allelochemicals could be recommended as histochemical dyes for the analysis of cellular mechanisms at the allelopathic interactions.

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Chapter 18
Host Allelopathy and Arbuscular Mycorrhizal Fungi

Ghazala Nasim

Abstract Allelopathy is a phenomenon, which affects the growth regulating process in all living organisms through the production of special compounds. Innumerable cases of allelopathic phenomenon have been reported in the literature where most of the species have been suggested to have chemical effects against other species. In view of increasing cost and environmental impact of synthetic chemicals, scientists are looking forward to using allelochemicals as bio-management tools. Studies are underway to integrate it with mycorrhizal technology to make it more useful. Preliminary investigations have shown that certain allelochemicals released into the rhizosphere by the host plants are able to trigger growth, colonization potential, and sporulation in certain arbuscular mycorrhizal fungi. It is also being suggested to raise cultivars with enhanced ability to produce allelochemicals which promote the mycorrhizal responsiveness of host plants and colonization potential of mycorrhizal fungi.

18.1 Introduction

Allelopathy is a biological phenomenon that is characteristic of some plants, algae, bacteria, coral, and fungi by which they produce certain biochemicals that influence the growth and development of other organisms (Narwal 2010). In this phenomenon an organism produces one or more biochemicals that influence the growth, survival, and reproduction of other organisms. These biochemicals are

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known as allelochemicals and can have beneficial (positive allelopathy) or detrimental (negative allelopathy) effects on the target organisms. Allelochemicals are a subset of secondary metabolites, which do not directly participate in the metabolism (i.e. growth, development, and reproduction) of allelopathic organisms. Allelochemicals with negative allelopathic effects are an important part of plant defense against herbivory. Allelopathy is characteristic of certain plants, algae, bacteria, coral, and fungi. Allelopathic interactions are an important factor in determining species distribution and abundance within plant communities, and are also thought to be important in the success of many invasive plants like Spotted Knapweed (*Centaurea maculosa*), Garlic Mustard (*Alliaria petiolata*), and Nutsedge (Pedrol et al. 2006; Barrett and Richardson 1986).

The term allelopathy, from the Greek words *allele* and *pathy* (meaning mutual harm or suffering), was first used in (1937) by the Austrian professor Hans Molisch in the book *Der Einfluss einer Pflanze auf die andere—Allelopathie* (The Effect of Plants on Each Other) published in German (Willis 2007). He used the term to describe biochemical interactions that inhibit the growth of neighboring plants, by another plant. Whittaker and Feeny (1971) defined allelochemicals as all chemical interactions among organisms (Reigosa et al. 2006). In 1984, Elroy Leon Rice in his monograph on allelopathy enlarged the definition to include all direct positive or negative effects of a plant on another plant or on microorganisms by the liberation of biochemicals into the natural environment (Rice 1984). Over the next 10 years the term was used by other researchers to describe broader chemical interactions between organisms, and by 1996, the International Allelopathy Society defined allelopathy as “Any process involving secondary metabolites produced by plants, algae, bacteria and fungi that influences the growth and development of agriculture and biological systems” (Reigosa et al. 2006). In more recent times, plant researchers have begun to switch back to the original definition of substances that are produced by one plant that inhibit another plant (Willis 2007). Confusing the issue more, zoologists have borrowed the term to describe chemical interactions between invertebrates like corals and sponges (Willis 2007).

Long before the term allelopathy was used, people observed the negative effects that one plant could have on another. Theophrastus, who lived around 300 BC, noticed the inhibitory effects of pigweed on alfalfa. In China, around the first century A.D., Yang and Tang described 267 plants that had pesticidal abilities, including those with allelopathic effects. The Swiss botanist De Candolle, in 1832 suggested that crop plant exudates were responsible for an agriculture problem called soil sickness.

Allelopathy has not been universally accepted among ecologists, and up to the early part of this century many ecologists argued that the effects of competition could not be distinguished from so-called allelopathy. Competition is a negative effect that happens when two or more organisms attempt to directly use the same resource; allelopathy, on the other hand differs by indirectly affecting other organisms after the input of substances into the environment. In the 1970s great effort went into distinguishing competitive and allelopathic effects by some researchers, while in the 1990s others argued that the effects were often interdependent and could not readily be distinguished.

One of the most studied aspects of allelopathy is its role in agriculture (Kong et al. 2006). Current research is focused on the effects of weeds on crops, crops on weeds, and crops on crops (Kong et al. 2008). This research advances the possibility of using allelochemicals as growth regulators and natural herbicides, to promote sustainable agriculture (Chen et al. 2008). A number of such allelochemicals are commercially available or are in the process of large-scale manufacture. For example, Leptospermone is a purported thermochemical in lemon bottlebrush (*Callistemon citrinus*). Although it was found to be too weak as a commercial herbicide, a chemical analog of it, mesotrione (Callisto), was found to be effective (Cornes 2005). It is sold to control broadleaf weeds in corn but it also seems to be an effective control for crabgrass in lawns. Sheeja (1993) reported the allelopathic interaction of the weeds *Eupatorium odoratum* and *Lantana camara* on selected major crops.

A famous case of purported allelopathy is in desert shrubs. One of the most widely known early examples was *Salvia leucophylla*, (Muller et al. 1964). Bare zones around the shrubs were hypothesized to be caused by volatile terpenes emitted by the shrubs. However, like many allelopathy studies, it was based on artificial lab experiments and unwarranted extrapolations to natural ecosystems. In 1970, *Science* published a study where caging the shrubs to exclude rodents and birds allowed grass to grow in the bare zones (Bartholomew 1970). A detailed history of this interesting story can be found in (2004).

Allelopathy has been shown to play a crucial role in forests, influencing the composition of the vegetation growth, and also provides an explanation for the patterns of forest regeneration. The black walnut *(Juglans nigra)* produces the allelochemical juglone, which affects some species greatly while others are not at all affected. *Eucalyptus* leaf litter and root exudates are allelopathic for certain soil microbes and plant species. The tree of heaven *(Ailanthus altissima)* produces allelochemicals in its roots that inhibit the growth of many plants. The pace of evaluating allelochemicals released by higher plants in nature has greatly accelerated, with promising results in field screening (Khanh et al. 2005).

Many crop cultivars show strong allelopathic properties, of which rice (*Oryza sativa*) has been most studied (Pheng et al. 2009). Rice allelopathy depends on variety and origin: Japonica rice is more allelopathic than Indica and Japonica-Indica hybrid. More recently, critical review on rice allelopathy and the possibility for weed management reported that allelopathic characteristics in rice are quantitatively inherited and several allelopathy-involved traits have been identified (Khanh et al. 2005).

Garlic mustard is an invasive plant species in North American temperate forests. Its success may be partly due to its excretion of an unidentified allelochemical that interferes with mutualisms between native tree roots and their mycorrhizal fungi (Stinson et al. 2006).

A study of *Kochia scoparia* in northern Montana by two high school students showed that when *Kochia* precedes spring wheat (*Triticum aestivum*), it reduces the spring wheat's growth. Effects included delayed emergence, decreased rate of growth, decreased final height, and decreased average vegetative dry weight of spring wheat plants (Overcast and Brimhall 2000). A larger study later showed that *Kochia* seems to exhibit allelopathy on various crops in northern Montana (Overcast and Cox 2001).

Many different secondary metabolites—e.g., phenolics, terpenoids, alkaloids, polyacetylenes, fatty acids, and steroids—can act as allelochemicals (Rice 1984; Waller 1987; Inderjit et al. 2008). These chemicals are present in various plant parts; however, their mere presence does not establish allelopathy (Putnam and Tang 1986; Heisey 1990). To demonstrate their involvement in allelopathy, it is important to establish (1) their direct release or indirect origin from plant-derived materials in the environment and (2) that the chemicals are present in sufficient quantities and persist for a sufficient time in the soil to affect plant species or microbes (Putnam and Tang 1986).

The overwhelming evidence indicates that phenolics do play a significant role in allelopathy. Several researchers have reviewed the biochemistry and ecology of phenolics (Levin 1971; Harborne 1989a; Kuiters 1990; Siqueira et al. 1991a, b; Appel 1993; Waterman and Mole 1994). Phenolics have been implicated as having a role in allelopathic interactions among different groups of plants such as algae, fungi, lichens, bryophytes, pteridophytes, gymnosperms, and angiosperms (Rice 1984; Fisher 1987; Inderjit et al. 1994d; Lawrey 1995). The present review throws light on allelopathy as a plant growth affecting phenomenon with particular reference to soil microbes. Moreover, how the relationship of mycorrhizal fungi and higher plant root system are regulated by this phenomenon.

18.2 Plant Allelopathy and Soil Biota

Allelopathic effects of higher plants may affect soil microbial communities in a highly different way. This has been variously shown by a number of investigators. Rai and Tripathi (1984) have submitted that the extracts of *E. riparium* stimulate the growth of *Trichoderma viride* while inhibiting *Aspergillus flavus*. Dhaliwal et al. (1990) highlighting varietal differences in rice have shown that certain varieties of rice inhibited the growth of plant pathogens like *Xanthomonas campestris* and *Rhizoctonia solani* while others did not produce marked inhibition in growth. Even during the decomposition of leaf litter the microbial community composition and species richness keeps on changing (Chander et al. 1995). Soil microorganisms are an important determinant of allelopathic activity. The phenomenon of allelopathy can be better understood in terms of soil microbial ecology, and appropriate methodologies are needed in order to evaluate the roles of soil microorganisms in chemically mediated interactions between plants (Inderjit and Duke 2005).

Under field conditions, multiple stresses develop progressively and gradually, and elicit morphological, physiological, physiological, and biochemical responses (Hussain et al. 2010). Allelopathic interactions are mediated by secondary metabolites released from the donor plants in the environment and influence growth and development on natural and agroecosystems (Inderjit and Duke 2003).

Allelochemicals phytotoxic effects are called ‘allelochemical stress’ (Pedrol et al. 2006). Allelochemicals directly affect many physiological and biochemical reactions and thereby, influence the growth and development of plants (Lara-Nuflez et al. 2006; Weir et al. 2004). The allelochemicals reduce the cell division (Sanchez-Moreiras et al. 2008) and have several phytotoxic effects (Einhellig 2002). Allelochemicals may be released in the form of volatile materials, foliage leachates, and root exudates or during the decay of the host are left in the soil. However, chemicals released into the soil are also affected by soil factors among which microorganisms play a major role (Sadaqa et al. 2010).

With extensive agriculture for longer periods of time, the problem of “soil sickness” has arisen (Asao et al. 2003; Young 1984). Soil sickness, a common problem in agriculture production, is due to the accumulation of pathogens and pests in soil, and deterioration of the physical and chemical properties of soil (Huang et al. 2006; Ye et al. 2004). Recent investigations have shown that this autotoxicity is a type of allelopathy closely related to the soil sickness (Chung et al. 2000; He et al. 2009; Hedge and Miller 1990; Yu et al. 2000). Although root exudates are one of the main sources of autotoxins or allelopathic compounds in soil, these compounds are produced in plants and stored in root cells and released into the rhizosphere (Harttung et al. 1989; Rice 1984). Researchers have shown that the main inhibition mechanism of autotoxicity of allelopathic compounds is through the enhanced ion leakage and inhibition of mineral uptake (Baziramakenga et al. 1994; Yu and Matsui 1994). In plants under environmental stress, the imbalances in active oxygen metabolism and lipid peroxidation are the main causes of membrane damage (Shalata and Tal 1998).

Microorganisms including bacteria and fungi have also been reported to produce exudates of allelopathic potential. Ma et al. (1997) have reported the production of allelochemicals by microbes in the rhizosphere of wheat. The biochemicals included phenolic acids, organic acids, aldehydes, alcohols, ketones, nitrogen containing chemicals, and many more. Production of secalonic acid by *A. japonicas* has been reported by Zeng et al. (2001a). The effect of this metabolite on higher plants, particularly on crops, has also been documented (Zeng et al. 2001a, b). A potential bioactive agent by the name of Brevione B has been isolated from *Penicillium brevicompactum* by Takikawa et al. (2003). Sidorova and Velikanov (2000) have indicated the production of bioactive substances by members of agaricales, which were tested on the growth of some soil bacteria and fungi. They have also discussed the possible role of these allelopathic substances in regulation of the structure of microbial communities in forest soils and litter.

18.3 Allelopathy in Natural Settings

Allelopathy evolved in nature through millions of years, enabling plants to combat with potential competitors. On the basis of this ability plants could win ecological success even during scarcity of nutrients and other resources. There is a rich

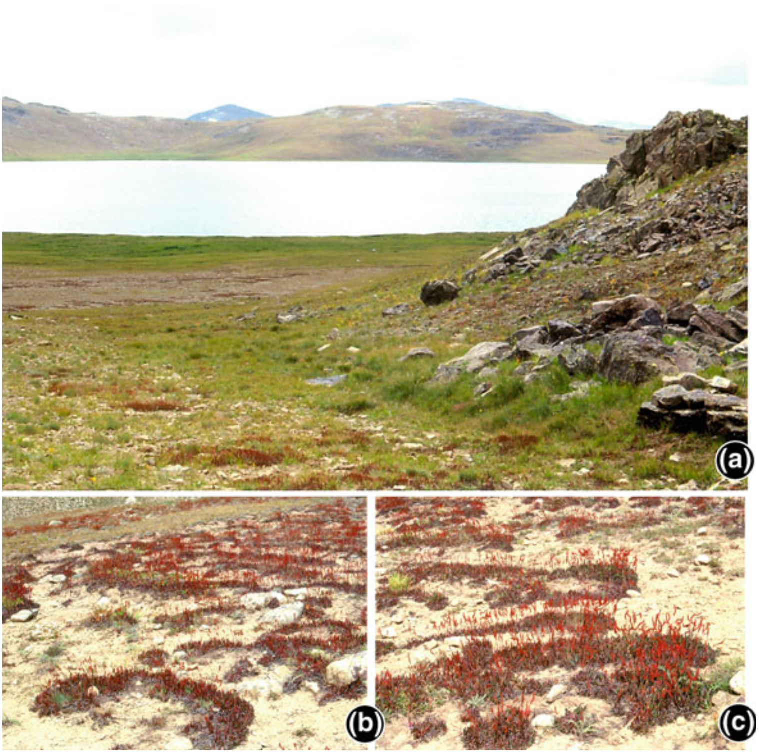


Fig. 18.1 **a** Deosai lake; **b** and **c** polygonum allelopathy in the wild (Nasim, unpublished work)

literature available regarding the prevalence of strong allelopathic potential in wild plant communities. This sometimes results into highly unique spatial distribution patterns (Fig. 18.1).

The study conducted by Nasim (Unpublished data) presents an observation of strong allelopathic potential in a species of *Polygonum*, which grows in high alpine meadows in the Karakoram mountain range of Pakistan. This is extremely rugged mountain terrain with a problem of unavailability of nutrients and water. Therefore, the plants must be equipped with abilities such as allelopathy to remain ecologically dominant in the ecosystem. The plant inhibits seed germination and subsequent growth of other wild plants and does not allow establishing in its vicinity. Laboratory studies and pot experiments were carried out to confirm the findings. The results have shown that the aqueous extracts of the plant significantly inhibit the seed germination and growth of selected wild plants found in the area. A potential allelochemcial namely Emodin also occurs in the soil of this plant community with effective concentration in the fall. The results indicate that these anthraquinones are responsible for the observed interference and are potent allelopathic substances. Scientists have also reported that in plants allelochemicals such as phenolics and carotenoids increase with increasing altitude (Mooney and

Billings 1961; Pekka et al. 2000; Todaria 1990). *Polygonum* seems to use the natural defense strategy of allelopathy for ecological success in the Northern Alpine meadows of the Karakoram Mountain Range, Pakistan. A similar survey conducted by Mutlu and Atici (2009) for wild vegetation found in Turkey has revealed that a plant *Nepeta meyeri* does not permit the germination of other wild plant species into its natural environment. Such inhibition zones around dominant plant species can provide an important ecological context for allelopathic studies (Kocacaliskan and Terzi 2001).

18.4 Allelopathy in Managed Agro-Ecological Systems

Allelopathy plays a highly significant role in agroecosystems and affects the growth, quality and productivity of crops (Kohli et al. 1998; Singh et al. 2001). The literature is now teaming with evidence stating the effects of allelopathy on natural vegetation (Bajwa 2007). Most plants exhibit the allelopathic effects on seed germination, growth, and development of other plants by releasing allelochemicals into the soil, either as exudates from living organs or by decomposition of plant residues (Narwal 1999; Noguchi and Ino 2005; Singh et al. 2003). Allelopathic plant interactions can have either harmful or beneficial effects and are generally evaluated by testing some physiological mechanisms that inhibited/stimulated the seed germination, plant growth, and development due to the presence of another plant (Suman et al. 2002; Weston and Duke 2003). Allelochemicals are present in all plant tissues including leaves, flowers, fruits, stems, roots, rhizomes, seeds, and pollen, and can affect the growth, productivity, and yield of other crops or the same crop (Batish et al. 2001).

The allelopathic potential of plants can be exploited to control obnoxious weeds (Jung et al. 2010). Cheema and Khaliq (2000) conducted a comprehensive study on the use of Sorghum allelopathic properties to control weeds in irrigated wheat in semiarid regions of Pakistan. According to results, two foliar sprays of the extract after sowing was the most economical method for controlling weeds in wheat with minimum net benefit and 535 % marginal rate of return. In a further study Cheema et al. (2002) have enumerated the effect of Sorghum allelopathy on wheat varieties and some winter weeds. Working on the same lines Cheema et al. (2000) have used sorghum allelopathic potential for weed control in cotton.

18.5 Mycorrhiza

The structure and function of terrestrial plant communities are strongly influenced by interactions of microorganisms with roots. About 90 % of land plants exist in a symbiotic association with soil fungi forming mycorrhizal associations (Smith and Read 2008). Mycorrhizas comprise several distinctive groups on the basis of structures that are formed on root systems (Graham and Miller 2005). However, the most common types are arbuscular mycorrhiza and ectomycorrhizas. The functions that these mycorrhizas perform are based upon the transfer of carbon from plant to fungus and mineral nutrients from fungus to host plant. The list of benefits conferred by the associations includes many more such as improved soil structure, plant water relations, and resistance to pathogens under certain conditions (Smith and Read 2008).

Arbuscular mycorrhizal associations are initiated when a spore of these fungi comes in contact with the host roots and starts to germinate. The hypha on penetration forms appressoria at the entry points from where the intraradical hyphae grow into the cortical region of the root. These intraradical hyphae penetrate the cortical cells and form profusely branched tree-like structures called arbuscules between the host cell wall and plasmalemma. Now, the fungus further establishes itself by developing an extensive network of extraradical hyphae in the soil. These hyphae perform a highly crucial role in uptake of Pi and other mineral nutrients from the soil and their subsequent translocation to the plant. These hyphae colonize roots of other plants and form spores extramatrical. Inside the roots cortex fungus form balloon-like structures called vesicles to perform as storage organs for the fungus. Sometimes these vesicles may transform into spores for propagation (Nasim 2010a, b).

AM associations are the most widespread symbiosis occurring in the roots of most angiosperms and pteridophytes, along with certain gymnosperms and gametophytes of some lower plants (Nasim et al. 1987; Iqbal et al. 1988, 1990; Nasim 1990a, b; Nasim 1995; Nasir et al. 1991; Graham and Miller 2005). The fungi have also been reported in association with underground portions like rhizomes, corms, bulbs, and runners of some plants (Nasim 2010a, b).

18.5.1 Arbuscular Mycorrhiza

Arbuscular mycorrhizal (AM) fungi are distributed worldwide, forming symbiosis with most plant families. Their importance in natural and semi-natural ecosystems is commonly accepted and materialized by improved plant productivity and diversity as well as increased plant resistance against biotic and abiotic stresses (Smith and Read 2008). The studies conducted during the past 2–3 decades have indicated that these fungi are present in underground portions other than roots. These portions include the epidermis and scale leaves of rhizomes, corms, and other perinating plant organs and decaying leaf litter of certain plants. The decaying crop stumps and sheathing leaf basis are the sporulating niches for certain unique species of AM fungi (Nasim 2010a, b). In view of the potential benefits of AM associations to the host plants, they are increasingly considered in agriculture, horticulture, and forestry programs, as well as for environmental reclamation, to increase crop yield and health and to limit the application of agrochemicals (Gianinazzi et al. 2002; Johansson et al. 2004). IJdo et al. (2011) have very nicely highlighted the methods for large-scale production of AM fungi.

Spore germination to initiate colonization in the host root is the prerequisite for successful AM establishment. The phenomenon of spore dormancy has been exhibited by many species of AM fungi. Different germination factors have been identified, which play important roles in growth activation of quiescent spores. Although the effect of host on spore germination is still highly controversial, studies have shown that in case of some rhizomatous medicinal plants like ginger, turmeric, Colocasia, cardamom, Agave, and others there is the indication of host specificity (Iqbal and Nasim 1986a, b, 1991; Iqbal et al. 1990; Nasim et al. 1991a, b, 1993a, b; Nasim and Zahoor 1995a, b). In these studies it was observed that only certain species of AM fungi could proliferate in the rhizosphere of these plants and were also able to colonize their roots and other underground portions. Pardales and Dingal (1988) have already reported negative effects of allelopathy of Taro residues (*Colocasia esculaenta*) on germination of mungbean. Limited spore germination and hyphal growth has been observed in some AM species in various investigations (Hepper 1979), however, in the absence of host the growth ceases (Beilby and Kidby 1980).

18.5.2 AM and Host Allelopathy

Allelochemicals produced by plants affect the establishment of both ectomycorrhizal and arbuscular mycorrhizal associations in plants. In the case of AM associations the allelopathy has not only been reported to induce host specificity but it also affects the extent of colonization by these fungi in plant roots. In some cases, high levels of root allelochemcials render a plant non-host for AM fungi. In angiospermic plant families like Brassicaceae, Chenopodiaceae, Amaranthaceae, and Commelinaceae the AM fungi do not colonize due to the same reason (Nasim et al. 1993a, b). In natural ecosystems non-mycorrhizal plants are outcompeted by mycorrhizal species (Brundrett 1991; Francis and Read 1995; Brundrett and Abbott 2002). This may be due to the reason that mycorrhizal species are more efficient at acquiring limiting soil nutrients especially phosphorus (Newman 1988; Brundrett 1991). In some plants, especially those with underground rhizomes, there is an indication of host specificity among these fungi. This has been observed in a wide range of plants with rhizomes, corms, bulbs, and other forms of rhizome or root stocks. In plants like *Zingiber officinale, Curcuma longa, C. antiquorum, Agave spp. Cana indica, Ellettaria cardemomum, Chlorophytum commosum*, only certain species of AM fungi are associated with the roots and underground storage organ (Nasim 2010a, b). The fungi have been frequently observed forming spores, thick hyphal mats, and vesicles in the scales of these underground plant organs. While in other cases some species select very unusual habitat niches for sporulation. The example in this case is of *Glomus monosporum* which sporulate in decaying sheathing leaf bases of wheat stumps. These wheat stumps which are lying half buried in the field soil are in a process of rapid decomposition and release a variety of allelochemicals in the soil. These stumps have been studied periodically to investigate the complete dynamics of *G. monosporum* in the sheathing leaf basis of wheat. It has been observed that only

G. monosporum colonizes and sporulate this unusual habitat niche. Zeng (2006) has documented in a review that AM fungi induce disease resistance in host plants through the production of allelochemicals.

Through a series of survey tasks and a number of experiments conducted at the University of Punjab by Javaid et al. (1995, 1996); Bajwa et al. (1995); Afzal et al. (2000); Nasim et al. (1999) it has been shown that the allelochemicals produced by the host plants adversely affect the status of this relationship. Afzal et al. (2000) have reported that the application of aqueous extracts of *Imperata cylindrica*, an allelopathic grass, markedly reduced AM colonization in *Vigna radiata*. In a review article by Javaid (2007), the two allelopathic grasses namely, *I. cylindrica* and *Dichanthium annulatum,* have been shown to adversely affect the AM colonization extent in the associated weed species. This reduction in AM colonization under the allelopathic effects is mediated by an array of biochemicals released into the soil by plants. These may include phenolic substances, flavonoids, and many more (Siqueira et al. 1991a, b; Lynn and Chang 1990). These phenolic compounds are produced as plant exudates or as a result of decomposition of plant debris. These biochemicals are signal transduction molecules and are liable to produce both stimulatory and inhibitory effects depending upon the concentration (Becard et al. 1992). Young and Wu (1997) have reported that species of *Rhizobium* and *Bacillus* are capable of decomposing phenolic acids produced by plants in the soil. The phenolic compounds are inhibitory to the growth of a number of plants like lettuce. The bacterial treatment improved lettuce growth in this experiment.

18.6 Case Studies

18.6.1 Tobacco Allelopathy and Sporulation by Glomus intraradices

Host-fungus contact is a crucial event for the fungal partner. AM fungi recognize their host plants and respond to their proximity (Balestrini and Lanfranco 2006). Mosse and Hepper (1975), Giovannetti et al. (1993), Buée et al. (2000) and Nagahashi and Douds (2000) have shown that only molecules released from the host plant stimulate hyphal branching in AM fungi, indicating that discrimination between host and non-host already occurs at this stage. The active molecules (branching factors) released by Lotus japonicas were recently characterized as sesquiterpenes by Akiyama et al. (2005). These findings clearly indicated that the fungus possesses the mechanism to perceive active root molecules and to switch on specific transcriptional pathways. This signaling cascade is necessary to induce morphological changes in the fungus and to activate growth (Balestrini and Lanfranco 2006). The work of Grunwald et al. (2004) has shown that gene-mediated biochemical induction also occurs at later stages of *Pisum sativum* and *G. mosseae* interactions.

Experiment carried out by Zhang et al. (2005) on allelopathic effects of grafted eggplant root exudates has indicated that the root exudates of grafted plants have promoted the seed germination and seedling growth of eggplant. They have emphasized that the grafting was one of the effective methods for relieving the continuous cropping obstacle caused by autotoxicity. In a study conducted by Anjum et al. (1983) the allelopathic inhibition of three algal species by tobacco litter has been indicated. They used the aqueous extracts from fresh and dried shoots and roots of tobacco (*Nicotiana rustica*). Extracts caused loss of sheath, isolation and deshaping of cells, disintegration, and ultimate death of the algae.

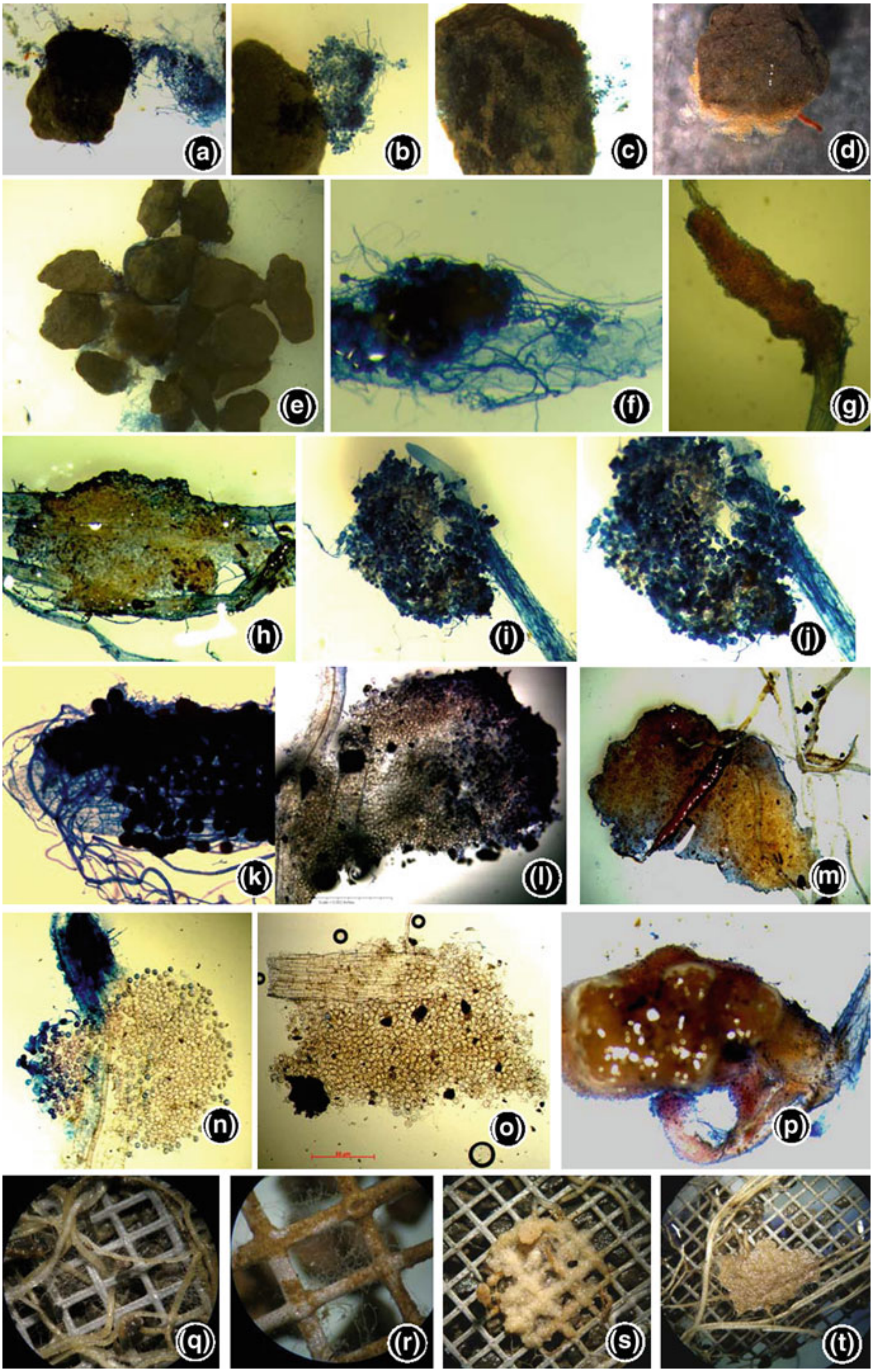
The AM fungus, *G. intraradices* was selected to be used in the present study due to many reasons. This morphotype is cosmopolitan being found in many ecosystems including the tropics. As a symbiont this species has been studied extensively and is highly effective in uptake and transfer of mineral nutrients. The fungus readily colonizes many agriculturally important crops (Martin et al. 2007). It can also be grown in vitro in dual culture with transformed carrot roots (St-Arnaud et al. 1996).

The active compounds (most probably phenolics) exuded from the roots of some transgenic lines have resulted in the enhancement of branching of intra and extrametrical hyphae, and production of arbuscules, vesicles, extraradical hyphal mats, extraradical vesicles and spores, and extrametrical sporocarp-like very large size spore clusters. It also resulted in the colonization of grass blades and decaying tobacco leaves (Nasim, Unpublished work). In some other transgenic lines the stimulation has resulted into severe deformation of roots (Figs. 18.2, 18.3).

18.6.2 Rice Allelopathy and Sporocarp Formation by Glomus monosporum

Rice–wheat cropping system is the lifeline of this mushrooming population. The system occupies 24 million hectares of cultivated land in Asia and this system covers 2.2 million hectare of land comprising 32 % of the total rice area and 42 % of the total wheat area in Pakistan. This system has been practices by farmers in Asia for more than 1,000 years. Continuous cropping of the rice–wheat system for several decades has shown that the yield have stagnated below potential level due to a number of pressures including nutrient scarcity. The crop straw is therefore either burnt resulting in air pollution or is mixed in the soil to enhance soil health. Rice has a diversity of phytochemicals, which show inhibitory action on germination of rice itself and also the germination and suppression of weeds (Chung and Ahmad 2010). Substances like momilactone B are released into the surrounding environment throughout the life of rice and affect seed germination and other growth attributes.

Nasim (2008) studied the effect of rice allelopathy on the sporulation of *G. monosporum* in wheat-rice cropping system. For this purpose wheat stumps left after crop harvest and the rhizosphere soil were sampled 10 days after crop harvest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◀**Fig. 18.2** **a**–**e** Colonization and sporualtion of *G. intraradices* on surface particles in pots of transgenic tobacco lines; **f**–**o** Steps for the development of extremely large-sized sporocarp by *G. intraradices* in some transgenic lines; **p** Root deformation induced in some transgenic tobacco lines; **q**–**t** Colonization of synthetic mesh and formation of giant sporocarp at the bottom of the pots by *G. intraradices* in some transgenic lines

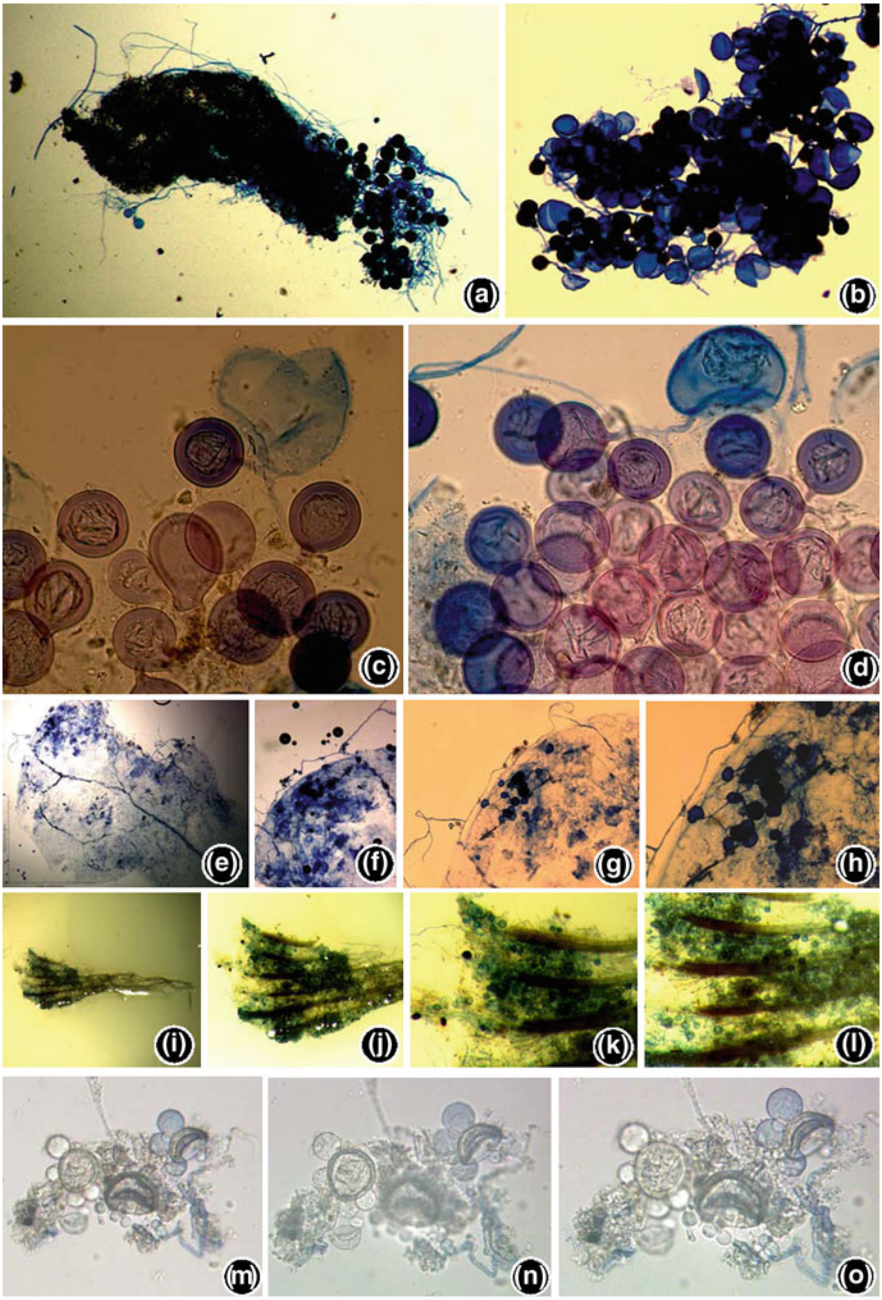
from five sites. It was found that when wheat is cultivated after rice and in soils having rice straw mulch the ability of *G. monosporum* to form spores/sporocarp was decreased as compared to monoculture in field and pot culture. The spore counts recorded in the soil samples after crop harvest also supported the leaf sheaths data.

Arbuscular mycorrhizal fungi are most ubiquitous soil fungi and play a major role in establishment of plant communities in natural or managed ecosystems (Barea et al. 2002). Mycorrhizal fungi are well adapted for nutrient acquisition, their small size allowing them to act as microscopic pipelines that can transport carbon and minerals to and away from the plant (Barrow 2004). These are 60 fungi belonging to Glomeromycota and forms association with 90 % of land plants (Krishna 2005). These fungi reproduce asexually through formation of spores and sporocarp in the soil. However, *G. monosporum* and some others form the propagules in a rather unusual niche (Nasim 2010a, b).

The sporulation sites may be the scale leaves and epidermis of underground portions (corms and rhizomes) or decaying sheathing leaf bases of grasses (Iqbal and Nasim 1991; Nasim and Iqbal 1991b). *G. monosporum* forms spores in the decaying leaf sheath bases of wheat (Gerdemann and Trappe 1974; Nasim and Iqbal 1991a, b; Nasim et al. 1998; Nasim 2010a, b) and has mycorrhiza forming potential and enhances the growth of wheat (Nasim et al. 1998). The sporocarp contains 13 spores and is formed at the end of the crop growing season, when peridium dissolves to liberate light brown spores into the soil (Nasim and Zahoor 1997).

Rice allelopathy is now well known and the (Takeuchi et al. 2001) rice straw mulch influences the mycorrhizal status of many crop plants (Shah 2008). However, there were no reports of allelopathic effects on the sporulation of AM fungal species on individual basis. In brief, the experiment consisted of five treatments: (i) wheat monoculture, (ii) wheat–rice rotation, (iii) pot culture without any treatment, (iv) pot culture with rice mulch, and (v) pot culture with aqueous extracts of rice. Likewise, previous studies indicated the significance of left over wheat straw as AM inoculum for the succeeding crop (Nasim et al. 1998) and the crop straw burning threatens the associated AM fungal communities in field soil in which crop straw is set on fire (Nasim 2011).

This study elucidated that the spore bank in the soil is maintained due to the yearly addition of spores in the soil and the spore and sporocarp development is affected significantly by rice cultivation system than wheat monoculture. Fageria and Baligar (2003) reported that when upland rice is grown in monoculture for more than 2–3 years on the same land, allelopathy or autotoxicity occurred. Rice allelopathy involves complex plant–plant chemical interactions and the phytotoxicity of allelochemicals depends on abiotic and biotic soil factors. Adopting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◀**Fig. 18.3** **a** Colonization of decaying plant debris by *G. intraradices* in pots of some transgenic tobacco lines; **b–d** Extramatrical vesicles transforming into spores in the vicinity of roots of specific transgenic lines; **e–h** Decaying tobacco leaf colonized by the fungus; sheathing leaf bases of *S. bicolor* used as inoculum for transgenic tobacco lines; older spores of *G. intraradices* showing a rare phenomenon of budding in pots of some transgenic lines

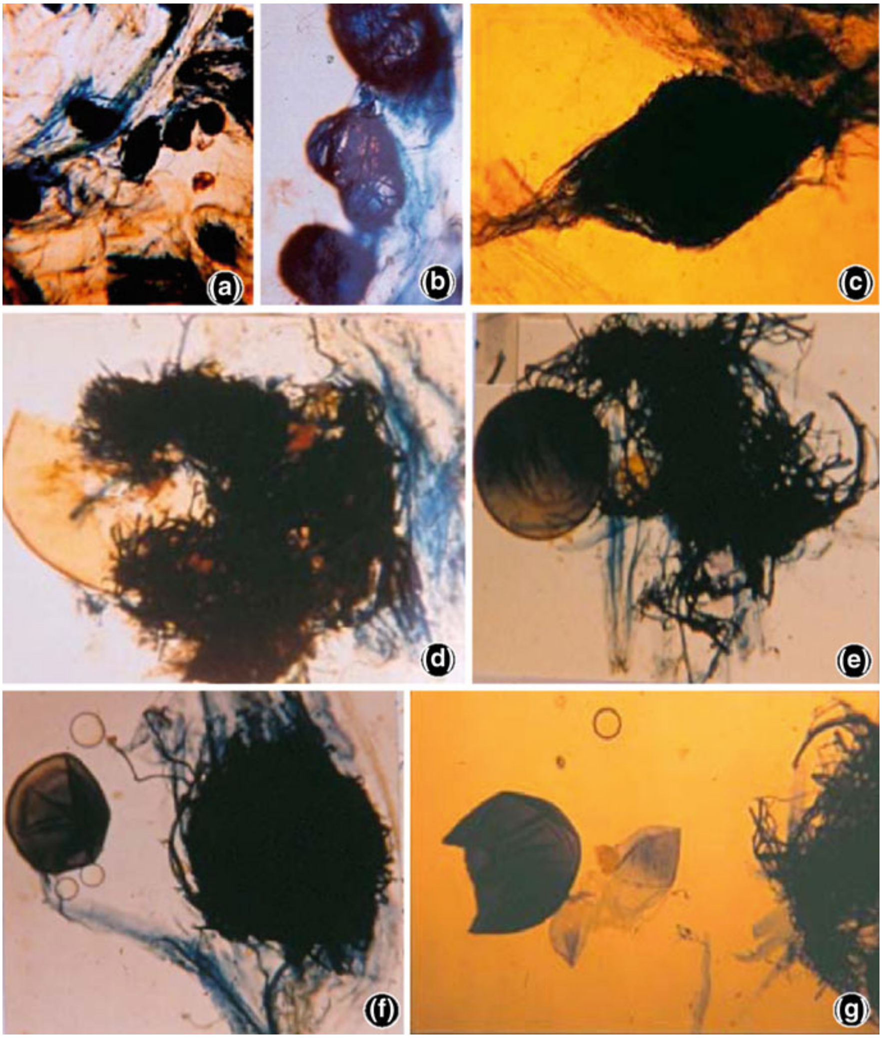

Fig. 18.4 Stages of sporocarp formation and release of spore by *G. monosporum* (Bar = 50 μm)

suitable management strategies in crop rotation can reduce or eliminate the allelochemicals' phytotoxicity. They also emphasized that rice yields can be improved by growing rice in rotation with other crops.

Sporocarp of *G. monosporum* was always observed forming in the senescing leaves of decaying wheat stumps (Fig. 18.4). Further research is underway to identify rice allelochemicals and their screening for the most significant inhibitory effects on AM species.

18.7 Conclusion and Future Perspectives

An enormous amount of literature has been published in the last 3–4 decades on allelopathy, most of which has shown that allelopathy in plants is a powerful phenomenon. Plants are able to outcompete in the natural ecosystems if they are able to produce active metabolites which are effective in impacting the growth and distribution of other species. In the managed ecosystems, plants are able to make benefit if they exhibit allelopathy. This may either be the case with a crop plant or an unwanted weedy fellow. The literature has also documented that plants achieve this ecological success mediated through the associative microorganisms especially arbuscular mycorrhiza. The active metabolites secreted by the roots of these plants are able to stimulate AM fungi for rapid colonization and proliferation. Such plants achieve better nutrition and are more competitive than the others without this ability. Modern techniques may be followed to develop crop plants, which are more responsive toward AM fungi through active allelochemicals.

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Chapter 19
Allelopathy and Abiotic Stress Interaction in Crop Plants

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Abstract Global climate models predict the increase in daily mean temperature, changed patterns of precipitation, increase in episodes of drought, and floods in future, the abiotic stresses; all posing threats to crop production and food security. Plants have evolved several mechanisms to cope with abiotic stresses. Ecological interaction of production and release of secondary metabolites among organisms in ecosystems, the allelopathy, has been associated with the tolerance mechanism against abiotic stresses. Endogenous levels of secondary metabolites, defined as allelochemicals, have been taken as indices of abiotic stress resistance. Exogenous application of allelochemicals has been found to increase their endogenous level with simultaneous increase in growth and resistance against abiotic stresses. Identification of genes responsible for allelochemicals production, and development of transgenic crops with these genes is becoming an attractive option for improving resistance against abiotic stresses. In this chapter, the production of allelochemicals under abiotic stresses in plants, strategies to enhance their production, and role in improving resistance against abiotic stresses is discussed.

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19.1 Introduction

Climate change may seriously influence the production levels required to feed future generations in the whole world. Climate change has many facets including changes in long-term trends in temperature and rainfall regimes as well as increasing variability in extreme events (Semenov 2009). Moreover, deficiency and/or toxicity of minerals, high irradiance, salinity, etc. are also important abiotic stresses, which threaten global food security (Tamaoki et al. 2004).

The lack of motility and immune system in plants resulted in the evolution of alternative defense strategies including the production of secondary metabolites as a tool to overcome stress constraints and adapt to the changing environment. These secondary metabolites are of major interest because of their multiple functions and impressive biological activities ranging from antimicrobial, antibiotic, insecticidal, hormonal properties to highly important pharmacological and pharmaceutical activities (Stockigt et al. 1995; Taiz and Zeiger 2010).

Allelopathy is direct or indirect, has stimulatory or inhibitory influence on plants by the release of certain secondary metabolites into the environment by other plants (Rice 1984; Molish 2001; Farooq et al. 2011a). These secondary metabolites (allelochemicals), including phenolics, brassinosteroids, jasmonates, salicylate, polyamines, etc. are involved in resistance against several biotic and abiotic stresses (Inderjit and Duke 2003; Singh and Usha 2003; Popa et al. 2008; Farooq et al. 2009a, b). For example, antioxidant potential of phenolics in plant cells under heat, drought and salinity stresses have been elucidated by several researchers (Dixon and Paiva 1995; Sgherri et al. 2004; Wahid and Ghazanfar 2006; Wahid 2007; Farooq et al. 2010, 2011b).

Exogenous application of allelochemicals, at higher concentrations, suppresses the growth of invasive plants and weeds by disrupting the plant water relations especially in root cell membrane and other biochemical changes that subdue CO_2 assimilation (Kpoviessi et al. 2006; Singh et al. 2009; Farooq et al. 2011a). However, potential of these allelochemicals in improving resistance against abiotic stresses is ignored, although a few reports indicated the improved resistance against abiotic stresses by these allelochemicals (Pedrol et al. 2006; Farooq et al. 2011b). In this chapter, production of allelochemicals under abiotic stresses is discussed. Moreover, potential of allelopathy in improving resistance against abiotic stresses is also an important part of this chapter.

19.2 Allelochemicals Production Under Abiotic Stresses

While living in the same biota, plants compete within their species and with species of other plant communities for nutrients and space. Allelochemicals are produced as tools for survival under these conditions. Allelochemicals are excreted

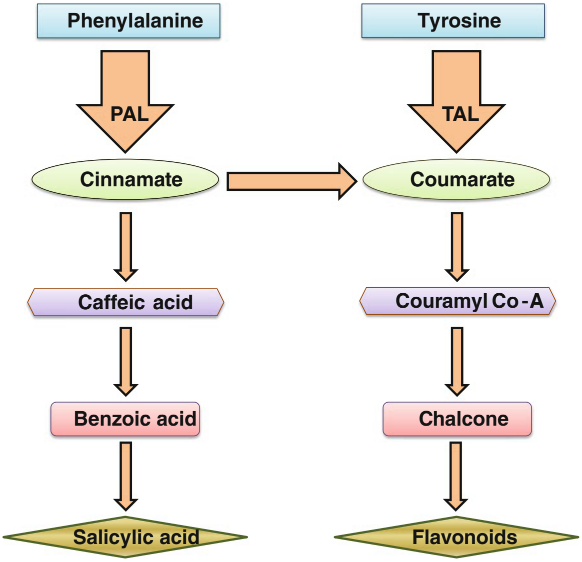

Fig. 19.1 Proposed scheme of simple and complex secondary metabolites synthesis in plants. The flux of these metabolites increases manifold under stressful conditions. PAL and TAL are phenylalanine ammonia lyase and tyrosine ammonia lyase, respectively (redrawn from Buchanan et al. 2002)

as root exudates and by volatilization from other plant parts for competition for nutrients (by inhibiting the adsorption of ions on the roots of neighboring plants), sunlight etc. (Rice 1984). General pathways for the synthesis of most secondary metabolites (the allelochemicals) involve shikimic acid pathway, melonic acid, mevalonic acid, and methylerythritol phosphate pathways, which mainly use acetate as an intermediate from primary metabolism, while phenylpropanoid and terpenoids are produced by isoprenoid pathway (Taiz and Zeiger 2010). Cinnamic acid formed from phenylalanine is the precursor of many phenolic acids, such as coumaric acid, caffeic acid, vanillic acid, ferulic acid, benzoic, and salicylic acids (Pedrol et al. 2006; Fig. 19.1).

Production of allelopathic compounds depends upon the growth stage and sensitivity of plant to abiotic stresses and/or prevalent environmental conditions (Argandona et al. 1980). These allelochemicals produced in different parts of plants (Table 19.1), act as first line of defense against abiotic stresses (Jimanez et al. 2003; Asao et al. 2004).

The exploration of the group of allelochemicals that induce tolerance against abiotic stresses is the subject of active research these days. Greater yield of allelochemicals stimulate the resistance of plants against stresses (Einhellig and Erickson 1984). Allelochemicals produced by plants under stress comprise mainly high amount of phenolic acids and terpenoids (Li et al. 2001). Tang et al. (1995) noticed increase in concentration of free phenolic acids in Marigold (*Tagetes erecta* L.) under stress. Nonetheless, various stress conditions substantially modulate the levels and types of allelochemicals biosynthesis.

Increase in allelochemical production has been reported under drought as well (Einhellig 1995; Chaves and Escudero 1997; Inderjit and Moral 1997). In several

Table 19.1 Allelochemicals from some commonly cultivated plant species

Crops	Allelochemicals	Plant parts	Reference
Wheat	*p*-hydroxbenzoic, vanillic, *p*-coumaric, syringic, ferulic acids.	Shoot	Wu et al. (2000, 2001)
Rice	*p*-coumaric, azelaic, vinillic acids, 1H-indole-3-carboxylic acid, 1H-indole-5-carboxylic acid, sterols, benzaldehydes, benzene derivatives, long chain fatty acid esters, aldehydes, ketones, amines, momilactone B	Root	Blum (1998); Rice (1987); Kim et al. (2000); Rimando et al. (2001) Noguchi (2004, 2008) Mahmoodzadah et al. (2011)
Maize	Fumaric acid, succinic acid, and coumaric acids	Stem > root > leaves	Nardi et al. (2000); Warnock et al. (2001) Al-Tawaha and Odat (2010)
Sorghum	Sorgoleone, dhurrin, kinetin	Root > stem > Leaves	Nimbal et al. (1996); Al-Tawaha and Odat (2010)
Mung bean	Vitexin, isovitexin, C-glucosyl flavonoid	Stem	Waller et al. (1994)
Mustard	Allyl isothiocyanate	leaves > flowers > mixture of all plant parts > stems > root	Vaughn and Boydston (1997); Tawaha and Turk (2003)
Rye	Benzoxazolinone, 2, 4-dihydrox-1, 4-(2H) benzoxazine	Roots	Barnes et al. (1987)
Oat	L-Tryptophan, Scopoletin	Roots	Kato Noguchi et al. (1994); Weston (1996)
Barley	Gramine, Hordenine, ferullic acid, vanillic acid, *p*-hydroxybenzoic acid	Roots	Lovett and Hoult (1994); Borner (1960)
Sunflower	Collorogenic, caffeic, Syringic, vanillic, ferulic acid	Leaves > stem > roots	Ghafar et al. (2001); Kamal (2011)
Soybean	Daidzein, Coumestrol, Vanillic acid, *p*-hydroxbenzoic acid	Shoot > roots	Granato et al. (1983); Du and Jin (1999) Han et al. (2000); Imam et al. (2006)
Canola	Sinapic, gentisic, coumaric, syringic, ferulic, salicylic caffeic, p-hydroxbenzoic acid	Roots > shoot	Haddadchi and Gerivani (2009) Olkowski et al. (2003)

plant species including cassava (*Manihot esculenta* Crantz), grain sorghum [*Sorghum biclor* (L.) Moench.], sudangrass [*S. sudanense* (Piper) Stapf] (Nelson 1953; Gershenzon 1984; Majek et al. 1980), Mexican sunflower [*Tithonia diversifolia*] (Tongma et al. 2001), and purple nutsedge (*Cyperus rotundus*) (Tang et al. 1995), cyanogenic glycoside level was significantly increased under drought. Increased amount of chlorogenic, isochlorogenic acids, and flavanoid in cucumber cotyledons has been reported (Tevini et al. 1983; Pedrol et al. 2006). Hura et al. (2007) reported the increased amounts of ferulic acid under drought in wheat (*Triticum aestivum*). Freeman and Mossadeghi (1971) reported enhanced production of isothiocyanates and sulfur containing secondary metabolites in water cresses (*Rorippa nasturtium-aquaticum*) under drought.

Changes in temperature modulate the allelochemicals production and their effectiveness. Both high and low temperatures influence the allelochemicals production in plants. High temperature ($\geq$30/25 °C) enhanced the production of hordenine and gramine contents in barley (*Hordeum vulgare* L.) (Hanson et al. 1983). Photoperiod (8–16 h) and temperature (15–25 °C) affected the concentration of hydroxamic acid in wheat (Gianoli and Niemeyer 1997), whereas chilling increased the total chlorogenic acids in older tobacco (*Nicotiana tabacum*) leaves (Koeppe et al. 1970).

Reduced availability of nutrients in the soil is also responsible for increase in production of allelochemicals (Gianoli and Niemeyer 1997). The release of phenolics may influence the nutrients availability, dynamics of organic matter, humus formation, and nitrogen mineralization, etc. (Makoi and Ndakidemi 2007). Tall fescue (*Festuca arundinacea* Schreb.) plant grown under phosphorus (P) deficiency showed specific changes in the root architecture, such as reduced root diameter and longer root hairs together with lignifications (Malinowski and Belesky 2000). The release of specific phenolic compounds benefitted the plant in the establishment of endomycorrhizal infection with the root under P deficiency regulates glycoflavanoids in arbuscular mycorrhizal fungal colonization in melon (*Cucumis melo*) roots (Akiyama et al. 2002). Higher scopolin levels favor the survival of tobacco plants in boron deficient soils (Watanabe et al. 1961). Similarly, scopolin helped to improve the magnesium, calcium, and P availability in tobacco (Loche and Chouteau 1963). In another study, 10-fold increase in the ratio of caffeic and chlorogenic acid improving boron deficiency in sunflower (*Helianthus annuus*) has been documented (Dear and Aronoff 1965). Nearly 2-fold increase in scopolin concentration and 5-fold increase in chlorogenic acid in leaves, roots, and stems acclimatized tobacco plants and sunflower plants to potassium, sulfur, and nitrogen deficiency was found (Armstrong et al. 1970, 1971; Lehman and Rice 1972).

Cinnamic and benzoic acid excreted from cucumber (*C. sativus*) root seedlings stimulated Mg^{2+}, Ca^{2+}, K^+, and SO_4^{2-} uptake in alkaline soils (Yu and Matsui 1997). Cucumber root seedlings grown in 0.5 mM Ca_2SO_4 for 24 h and then shifted to KH_2PO_4 solution containing ferulic acid showed an increase in K^+ uptake over short duration in linear concave manner; while, either no contact or increased duration of contact with ferulic acid solution decreased K^+ uptake in the same manner (Lyu and Blum 1990).

Heavy metals also increased the allelochemicals production (Pedrol et al. 2006). Zobel and Clarke (1999) reported the enhanced synthesis of allelochemicals in two *Acer* spp. under high heavy metal contents of soil. In another experiment, Kato Noguchi (2009) reported that both heavy metal stress and pathogen infection increased the concentrations of momilactone B in rice shoot extracts and root exudates.

19.3 Stress Signaling by Allelochemicals

Plants receive environmental cues as stimuli that follow different signal perception or transduction pathways, resulting in metabolic responses, and activation of gene expression. The processes usually cued in response to the external stimuli include synthesis of enzyme, stress proteins, stress hormones, and stress metabolites synthesis, which is under feedback control (Pedrol et al. 2006). Experiments have shown that allelochemicals present in the vicinity of plant roots or induced by neighboring plants acts as secondary oxidative stress for plants (Ortega et al. 2007). This is manifested as increase in generation of reactive oxygen species (ROS) accompanied by activation of cellular antioxidant system (Bogatek and Gniazdowska 2007) and hormonal imbalance (Weir et al. 2004). ROS are the second messengers for the hormonal signal transduction as in case of ABA signaling for stomatal closure, GA_3 signaling in alurone layer, and cell death in plants (Kwak et al. 2006). Allelochemicals also modify the mitogen-activated protein kinases (MAPKs); a key enzyme group involved in ethylene production (Pitzschke and Hirt 2006). A schematic view of allelochemicals signaling mechanisms is given as (Fig. 19.2).

Allelochemicals synthesis occurs by intervention of strong antioxidants, suggesting the catechin facilitated ROS production in death of root cells (Taiz and Zeiger 2010). Allelochemical induced genome-wide changes in gene expression pattern of root meristematic zone, eventually decease ramification of root system (Callaway and Vivianco 2005). Gene expression studies in Arabidopsis (*Arabidopsis thaliana*) roots evoked up-regulation of ten genes within ten minutes of catechin treatment and returned to normal after 1 hour; out of which functions of four genes are unknown and six genes were found to be involved in cell death (Bais et al. 2003). Work done on rice roots has shown that allelochemical juglone also up-regulated the gene expression of two calcium-dependent protein kinases (CDKs) and six MAPKs. Juglone treated roots modulated the Ca^{2+} and ROS, which signaled abscisic acid and jasmonic acid biosynthesis while inactivated gibberellic acid (Chi et al. 2011).

Hormones are among other secondary messenger triggered by the allelochemicals, which altered the gene expression, enzymes activities, and their functions and protein biosynthesis, thus affecting the physiology of plant (Li et al. 2010). Three concentrations (0.5, 1.0 and 1.5 mM) of allelochemical 4,7-dimethyl-1-(propan-2-ylidene)-1,4,4a, 8a-tetrahydronaphthalene-2, 6(1H, 7H)-dione (DDT), and

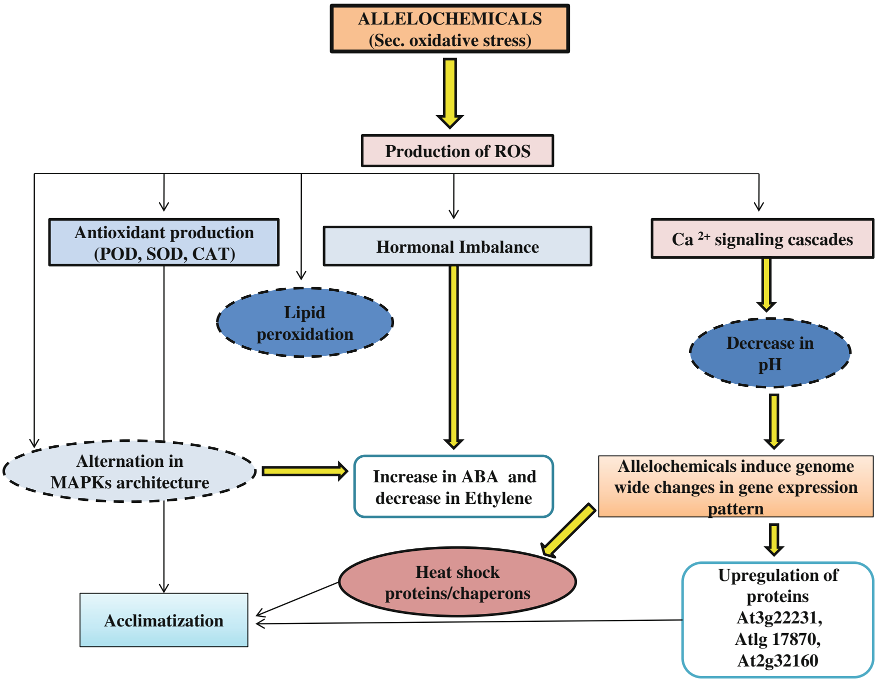

Fig. 19.2 Possible mechanism of signaling by allelochemicals to trigger stress response in plants

6-hydroxyl-5-isopropyl-3, 8-dimethyl-4a, 5, 6, 7, 8, 8a-hexahydronaphthalen-2(1H)-one (HHO) isolated from Mexican Devil [*Ageratina adenophora* (Spreng.) King and H.Rob.] weed decreased the indole-3-acetic acid (IAA), and zeatin riboside (ZR) and increased ABA in the roots of rice seedlings; however, higher concentration of these allelochemicals reduced all three hormones (Yang et al. 2008).

A decrease in ethylene biosynthesis in mustard seeds was observed in response to decreased ACC synthase (1-aminocyclopropane-1-carboxylate synthase) and ACC oxidase (1-aminocyclopropane-1-carboxylate oxidase) by sunflower extract (Gniazdowska et al. 2007). Increase in ABA simultaneously reduced the amount of ethylene thus induced seed dormancy and reduced seed germination (Kucera et al. 2005) by restricting mobilization of reserves (Kupidłowska et al. 2006).

19.4 Allelochemical Biosynthesis and Abiotic Stress Resistance

The allelochemicals can be used to induce resistance against abiotic stresses in plant species and to maintain their metabolic processes for better growth (Einhellig 1996). The production of these stress resistance provoking compounds can be enhanced using various strategies. More important of these strategies may be the induction of the synthesis of these compounds in non-allelopathic plants so that they may become capable of defending themselves against any type of stress. Rice (1984) opined that subjecting plant to one stress type may acclimatize the plants to other types of stresses. Various ways and means have been used to enhance the production of allelochemicals as described below.

19.4.1 Screening Protocols

To evaluate crops for their allelopathic potential, some protocols and tools have been used. Important of these are stair-step method (Bonner 1950; Liu and Lovett 1993), hydroponic culture test (Einhellig et al. 1985), relay-seeding technique (Navarez and Olofsdotter 1996), agar medium test (Fujii 1992; Wu et al. 1999), cluster analysis using HPLC (Mattice et al. 2001), water extract method (Kim et al. 1999, 2000; Ebana et al. 2001), and well plate bioassay (Rimando et al. 1998). However, all these produced contrasting results with relatively lesser efficiency in large-scale screening of germplasm. Thus development of universal bioassay method would be required to obtain reliable results.

In traditional breeding, crossing between the wild and relatives, production of near isogenic lines (NILs) and derivation of recombinant inbred lines (RILs) are useful strategies (Lin et al. 2000). Numerous studies performed on rice revealed greater genetic variability in the tested germplasm. Out of 12,000 rice accessions, 412 showed allelopathic potential against duck salad [*Heteranthera limosa* (Sw.) Willd] weed (Dilday et al. 1998). In another study, more than 400 accession of wheat contained allelopathy-related traits (Bertin et al. 2003).

In screening experiments, it is noted that wild accessions have greater allelopathic potential as compared to modern cultivars as the former are subjected to multiple stresses in nature; therefore have stronger defense system (Lovett 1985). Wild rice varieties showed greater allelopathic potential against weeds as compared to domesticated ones (Jensen et al. 2001). In this respect, selection pressure for greater economic yield appears to have eroded several genes encoding allelochemicals synthesis. Traditional management practices inclusive of crop rotation and co-cultivation of crops have paid fair dividends in controlling weeds (Farooq et al. 2011a).

19.4.2 QTL Analysis

Finding quantitative trait loci (QTL) is an important tool to understand the genetics of allelopathy in crops. Our knowledge on the QTLs of allelopathy is poor. However, the work of Jensen et al. (2001) followed by Okuno and Ebana (2003) and Dong et al. (2005) set the trend in this field by mapping QTLs for recombinant inbred lines derived from a cross between Japonica upland variety having strong allelopathic potential and Indica irrigated variety with weak allelopathic potential. The QTLs for allelopathy were found to be localized on 2 and 3 chromosome of rice, which were responsible for about 10 % of the allelochemical production. Likewise, two similar QTLs were mapped at chromosome 2B of wheat (Wu et al. 2003; Macías et al. 2007; Bertholdsson 2010). Information on the QTLs mapping in major allelopathic crops, such as rye (*Secale cereal*), maize (*Zea mays*), oat (*Avena sativa*), and barley is available (Belz 2007).

The F_2 generation of two rice varieties, one allelopathic (P1312777) and other non-allelopathic (Rexmont) expressed seven QTLs on chromosomes 1, 3, 5, 6, 7, 11, and 12. Positive allelopathic effect was shown by QTL located on chromosome 7 that inhibited root growth and necrosis on lettuce root tips. Seven phenolic compounds (camphor, pyrogallic acid, protocatechuic acid, *p*-hydroxybenzoic acid, syringic acid,) out of 20 that were identified in rice showed allelopathic effect (Okuno et al. 2008).

19.4.3 Gene Expression

Nine possible differentially expressed genes (DEGs) associated with allelopathic potential of Indica type rice variety, Sathoi, capable of producing nicotianamine, effective against barnyard grass (*Echinocloa crus-galli*) were identified by gel electrophoresis. Out of these, six genes (DEG 1, 4, 5, 7, 8 and 9) showed higher while three (DEG 2, 3 and 6) showed low expression. These respective genes were found to be homologous to other genes. BLAST-n and BLAST-x studies suggested that DEG-1, 2, 8, 5, 6, 3, 7, and 4 are homologous to a gene for S-adenosylmethionine synthetase, chloroplast gene for ribulose 1, 5-bisphosphate carboxylase large subunit, oxysterol-binding protein, histone 2B protein, nicotine amine aminotransferase, nucleotides sequence of oxygen evolving complex protein in photosystem II, serin/threonine protein kinase, and putative transposable element and an unknown protein (Junaedi et al. 2008). The enhanced expression of six genes against barnyard grass showed allelopathic behavior of rice but which allelochemical was active and how it affects, is still unknown.

19.4.4 Proteome Analysis

Proteomics assist in identification of positional, functional, and expressional genes that cannot be denoted by QTLs. QTL mapping contain positional candidate genes that hinder the detection of functional genes. Expressional candidate genes that encode stress responsive proteins will assist in tracing the stress tolerant traits expression in non-allelopathic plants would be possible (Valliyodan and Nguyen 2006). Differential expression of proteins in allelopathic rice (PI 31277) treated with barnyard grass induced proteins that were closely related to isoprenoid and phenylpropanoid biosynthesis pathway, implying that terpenoid and phenolic acids are strong allelochemicals against weeds (Lin et al. 2004).

19.5 Management of Abiotic Stress Tolerance using Allelochemicals

Various management strategies are being employed to produce abiotic stress tolerance in plants. As these allelochemicals are secondary metabolites and have no direct roles in primary metabolism, they are also involved in defense against abiotic stresses (Wahid and Ghazanfar 2006), although exact mechanisms of their beneficial roles are still elusive. Seed treatments with aqueous extract of allelochemicals, their foliar, and root applications have been investigated to determine their exact concentration that could be beneficial for crops.

19.5.1 Seed Pretreatments

Germination is one of the critical and sensitive stages. Initial stages, such as radical and plumule emergence, germination rate, germination energy, and fresh and dry weight of the seedling is greatly inhibited by higher concentration of allelochemicals but low concentration stimulates the growth (Maqbool 2010). Use of furanocumarins at 100 ppm concentration inhibited mitosis but at 10 ppm, mitochondrial activity was stimulated. At higher concentration seed germination was inhibited but when spring rains leached away the coumarins, they switched over to stimulate germination (Orcutt and Nilsen 2000).

The increased concentration of coumarin (0, 25 μM and 0.1, 1, 2.5, and 5 mM) grown under nitrate deficient conditions accelerated the nitrate translocation from roots to shoots (Abenavoli et al. 2001). Likewise, Han et al. (2008) assayed aqueous extract of rhizome, leaf, and stem of ginger (*Zingiber officinale*) at 10–80 g L^{-1}, which enhances the drought resistance in soybean (*Glycine max*) seeds by stimulating the water uptake with a course of time that decrease with increased concentration of extract. In a laboratory experiment, maize seeds were soaked in diluted concentrations of sorghum extract for 12 h and sown in washed sand for 7 days and submitted to drought. The emergence of seedlings decreased with increased dilutions, and the minimum germination was observed at 2 mL L^{-1} sorghum extract; the most effective dilution under control was 0.25 mL L^{-1}, while 0.75 mL L^{-1} under drought (Maqbool 2010). Similarly, the salinity tolerance of Shaheen Basmati and Super Basmati was alleviated when seeds were primed with 5 % sunflower water extract (Table 19.2) (Farooq et al. 2011b).

Table 19.2 Influence of exogenous application of allelochemicals on the growth of different plants under abiotic stresses

Allelochemical	Mode of application	Plant species	Stress type	Improvement over control (%)	Reference
BOA (1 mM)	Soil	*Lectuca sativa*	Salt (60 mM NaCl)	5 % RWC[a] 4 % Fv/Fm[b]	Sanchez-Mareiras et al. (2009)
Ferulic acid (0.25 mM)	Hydroponic	*Cucumis sativa*	Drought (0.25 % PEG)	11.96 % P uptake per g dry wt.	Lehman and Blum (1999)
			Nutrient deficiency (1/4 Hoagland Solution)	2.09 % P uptake per g dry wt.	
Cinnamic acid (50 µmol L^{-1})	Vermiculite	*Cucumis sativa*	Salt (200 mmol/L NaCl)	3.62 % RWC;[a] 18.42 % Chlorophyll content	Wang et al. (2007)
Putrescine (0.01 mM)	Seed treatment	*Atropa bellandoma*	Salt (50 mM)	95 % germination; 90.92 % RWC[a]	Ali (2000)
Putrescine (100 µM)	Foliar spray	*Oryza sativa*	Salt (20, 30, 40, 50 mM)	90 % in fresh weight	Lutts et al. (1996) Gill and Tuteja (2010)
Coumarin (0.1 mM, 1 mM)	Hydroponic	*Triticum durum*	No NO_3^- supplied in nutrient solution	48 % nitrate uptake	Abenavoli et al. (2001)
Coumarin (25 µM)				54 % root length	
Sunflower extract (20 %)	Seed treatment	*Oryza sativa*	Salt (50 mM NaCl)	60 % fresh wt and dry wt	Farooq et al. (2011b)
Nicotiana plumbagmifolia leachate (25 %)	Soil	*Zea mays*	Drought (withholding water supply for 6 days)	11.89 % RWC,[a] 4.15 % root length,18 % shoot length	Singh et al. (2009)
Ipomoea cairica aqueous leachate (0.025 g mL^{-1})	Soil	*Raphanus sativus*	Elevated temperature (26 °C)	5.2 % in germination	Wang et al. (2011)
		Brassica compastris		3.7 % in shoot and root length	
Cinnamic acid, benzoic acid (0.1 mmol L^{-1})	Filter paper	*Cucumis sativa*	Alkaline pH (7.5)	33 % H_2PO^{4-}, 52 % Mg^{2+} uptake	Yu and Matsui (1997)

[a] RWC: Relative water contents

[b] Fv/Fm: Photochemical yield of PSII

19.5.2 Foliar Spray

Like seed treatments, foliar spray of allelopathic extracts was also helpful in improving growth under stressful conditions (Table 19.2). The foliar application of water extract of various plants in high doses has been used on high scale for the suppression of weeds utilizing the inhibitory character of allelochemicals (Mehmood 2010). For instance, exposure of 7-day-old maize seedlings to 0, 100 and 300 μM concentrations each of ferulic acid, trans-cinnamic acid, and *p*-coumaric acid for 48 h in hydroponic culture devoid of nitrogen strongly curbed nitrate uptake in a concentration dependent manner, primarily decreasing the H^+-ATPase activity. Conversely, low concentration of caffeic acid stimulated the nitrate uptake (Abenavoli et al. 2010). In another experiment on maize, foliar application of sorghum extract dilutions on maize under drought stress at vegetative stage manifested that low concentrations enhanced the morphological as well biochemical attributes. Photosynthetic pigments increased free amino acids and anthocyanins, which acclimatized the maize plants to drought at 0.25–0.75 mL L^{-1} of sorghum extract (Maqbool 2010).

Foliar spray of more diluted concentrations of *N. plumbaginifolia* leachate improved relative water contents, chlorophyll concentrations, accumulation of free proline, enhanced nitrate reductase activity of leaves, and antioxidative defense as compared to more concentrated leachates in water stressed maize (Singh et al. 2009). Although studies are lacking, it is likely that more diluted concentration of the allelopathic extracts may have stimulatory effects on the crop growth under stressed or stress-free conditions.

19.5.3 Root Application

As shown in Table 19.2, soil application of allelochemicals can also produce changes in the roots characteristics. In a study, treatment of (*Vicia faba* L.) roots with low concentration of aqueous extracts of guasca (*Galinsoga parviflora*) at low temperature (5 °C for 24 h) induced changes in the cytological characters, such as increased mitotic index, micronuclei, and aberrations, which acclimatized the roots to chilling stress (Ma et al. 2008). Coumarin concentrations induced swelling of the sub-apical part of root tip of wheat that increased root surface area for nitrate absorption, thus enhanced the root affinity to overcome nitrate deficiency (Abenavoli et al. 2001).

19.6 Conclusion

The allelochemicals may be effectively used to improve the resistance against abiotic stresses if used at pre-optimized concentrations. Various factors, such as temperature extremes, deficiency of nutrients, and heavy metals enhance the allelochemicals production in many plant species. Mapping of QTLs and gene expression studies have revealed that allelochemicals synthesis is a genetically-related phenomenon. The allelochemicals can act as signaling agents for the production of abiotic stress tolerance in plants. Few preliminary studies are available for exogenous use of allelochemicals with seed pretreatments and with foliar applications. Although some evidence is available, there is certainly more room for in-depth research on the growth stimulatory role of allelochemicals under stress from diverse sources.

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Chapter 20
Application of Moringa Allelopathy in Crop Sciences

M. Hussain, M. Farooq, Shahzad M. A. Basra and Dong-Jin Lee

Abstract Allelopathy, the natural phenomenon of production and release of secondary metabolites and interactions amongst organisms, is a subject of diverse significance and applications in biological sciences. Moringa (*Moringa oleifera*) is known as a miracle plant due to its multiple uses. Being rich in amino acids, ascorbate, zeatin, minerals, and many other compounds, moringa has several applications in agriculture and medical sciences. Secondary metabolites isolated from this plant promote the plant growth and defense mechanisms against abiotic stresses. In crop sciences, water extracts from moringa leaves may be used as seed treatment and foliar application to augment the growth and productivity. Moringa extracts accelerate the growth of plants, strengthen plants, and improve resistance against pests and diseases. Other than their role in plant defense against biotic and abiotic stresses, moringa leaves being rich in essential macro- and microelements

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play a significant role in crop nutrition. In this chapter, the application of moringa allelopathy in crop sciences has been discussed.

20.1 Introduction

Allelopathy is combination of two Latin words ‘allelos’ meaning ‘each other’ and ‘pathos’ meaning ‘to harm’. Allelopathy is a natural phenomenon of interference among organisms having stimulatory or inhibitory effect among them (Farooq et al. 2011). Organisms manipulate the growth of other organisms through release of some secondary metabolites into external environments (Rice 1984). Phenomenon of allelopathy is reported in various fungi, microorganisms, and plants as well (Torres et al. 1996). These chemical compounds or secondary metabolites synthesized and released by plants are known as allelochemicals. Allelochemicals are synthesized in all plant organs such as roots, shoots, leaves, seeds, and flowers (Weston 1996) and are released into the external environment through volatilization, leaching, root exudation, and decomposition of plant residues (Rice 1984). In crop science, mechanism of allelopathy is exploited successfully by exogenous application of plant extracts, used as intercrops and mulches and fitting into the crop rotation for weeds suppression, insects and disease management, and growth enhancement (Farooq et al. 2011).

Moringa (*Moringa oleifera*) is an important plant of Moringaceae family having tremendous allelopathic potential. There are about 13 species of genus Moringa reported in total and among them *M. oleifera* is the most known and widely cultivated species throughout the world (Fuglie 1999). *M. oleifera* is believed to have originated from sub-Himalayan tracts of India, Pakistan, Bangladesh, and Afghanistan but is currently found in all tropical and subtropical regions of the world (Fahey 2005; Anwar et al. 2007; Ayerza 2011; Muhl et al. 2011). Moringa is recognized by so many names in the world such as ‘drumstick tree’, ‘horseradish tree’, ‘kelor tree’, ‘benzolive’, ‘marango’, ‘sajna’, ‘Shagara al Rauwaq’ ‘Sohanjna’ ‘Shojne’, etc. (Anwar and Bhanger 2003; Fahey 2005; Anwar et al. 2005; Anonymous 2012).

Moringa is a high esteem plant as every part of the plant has been consumed by humans to overcome malnutrition especially for infants and nursing mothers, and also used for various domestic, industrial, and agricultural purposes such as alley cropping, fodder for livestock, biogas generation, domestic cleaning agent, cosmetics, blue dye, fertilizer, foliar nutrient, green manure, sugar cane juice-clarifier, biopesticides, water purifier, machine lubricant oil, remedy for numerous ailments, and biofuel production, etc. (Fuglie 1999; Fahey 2005; Kawo 2007; Anwar et al. 2007; Rashid et al. 2008; Ayerza 2011; Khalafalla et al. 2010; Moyo et al. 2011). Moringa leaves and seeds are rich source of essential macro- and micronutrients, β-carotene, proteins, vitamins A, B, C, D, and K, along with more than 40 natural antioxidants (Fuglie 1999; Anwar et al. 2005, 2007; Aslam et al. 2005; Mahmood et al. 2010; Basra et al. 2011; Table 20.1). Likewise, leaves, roots, seeds, bark,

Table 20.1 Mineral composition (mg 100 g^{-1}) of pods, leaves, and seed powder of *M. olifera*

Minerals	Pods	Leaves	Seed powder	References
N	–	–	2980.00	Kawo et al. (2009)
	400.00	1070.00		Fuglie (1999)
Ca	–	–	60.20 ± 12.20	Kawo et al. (2009)
	–	364.50	122.30	Anjorin et al. (2010)[a]
	156.40 ± 0.29	2274.30 ± 0.83	–	Aslam et al. (2005)[b]
	30.00	440.00	–	Fuglie (1999)
K	–	–	73.20 ± 6.40	Kawo et al. (2009)
	259.00	259.00	–	Fuglie (1999)
	1969.20 ± 0.73	2170.40 ± 0.78	–	Aslam et al. (2005)[b]
	–	1500.00	–	Moyo et al. (2011)
P	–	–	0.06	Kawo et al. (2009)
	110.00	70.00	–	Fuglie (1999)
	197.60 ± 0.64	128.90 ± 0.38	–	Aslam et al. (2005)[b]
	–	300.00		Moyo et al. (2011)
Mn	–	–	17.50 ± 0.40	Kawo et al. (2009)
	5.77 ± 0.08	9.58 ± 0.14	–	Aslam et al. (2005)[b]
	–	8.68	–	Moyo et al. (2011)
Mg	–	76.60	79.70	Anjorin et al. (2010)[b]
	24.00	24.00	–	Fuglie (1999)
	9.78 ± 0.15	10.24 ± 0.10	–	Aslam et al. (2005)[b]
Fe	–	6.00	9.70	Anjorin et al. (2010)[a]
	5.30	7.00	–	Fuglie (1999)
	29.06 ± 0.22	39.17 ± 0.34	–	Aslam et al. (2005)[b]
Cu	–	4.40	2.45	Anjorin et al. (2010)[a]
	2.66 ± 0.04	0.93 ± 0.01		Aslam et al. (2005)[b]
	3.10	1.10	–	Fuglie (1999)
Zn	–	1.80	0.96	Anjorin et al. (2010)[a]
	2.19 ± 0.05	2.70 ± 0.03	–	Aslam et al. (2005)[b]
	–	1.30	–	Moyo et al. (2011)
S	137.00	137.00	–	Fuglie (1999)
	–	630	–	Moyo et al. (2011)

[a] Average value from two sites of Nigeria

[b] Average value at three sites of Pakistan

fruit, and flowers of moringa act as cardiac and circulatory stimulants, and exhibit antitumor, anti-inflammatory, antiulcer, antispasmodic, diuretic, antioxidant, antibacterial, and antifungal activities and used as herbal medicines (Anwar et al. 2007).

Several allelochemicals have also been found in different parts of moringa. For instance, moringa seeds contained 4-(R-L-rhamnopyranosyloxy)-benzylglucosinolate whereas 4-(R-L-rhamnopyranosyloxy)-benzylglucosinolate and benzyl glucosinolate were isolated in moringa roots. Moringa leaves contained 4-(R-L-rhamnopyranosyloxy)-benzylglucosinolate, 3-caffeoylquinic acid, 5-caffeoylquinic acid, and three monoacetyl isomers of this glucosinolate, whereas 4-(R-L-rhamnopyranosyloxy)-benzylglucosinolate was detected in moringa bark (Bennett et al. 2003). Faizi et al. (1995, 1997) reported several allelochemicals including isothiocyanates and nitriles in moringa; whereas Eilert et al. (1981) identified 4-(R-L-rhamnopyranosyloxy)-benzyl in moringa seeds.

With its versatile utility in domestic, industrial, medical, water purification, and agriculture enterprises; moringa is truly considered as a "Miracle Tree". Being a rich source of amino acids, essential macro- and microplant minerals, vitamins, natural antioxidants, and plant growth regulators such as zeatin (cytokinins) and gibberellins; moringa leaf extract (MLE) can be effectively exploited as plant growth enhancer (Makkar and Becker 1996; Mahmood et al. 2010; Basra et al. 2011). Foliar spray of leaf extracts of moringa accelerates the growth of plants, improves resistance to pests and diseases, and enhances the yield by 20–35 % in different crops (Fuglie 2000). In this chapter, we have briefly described the role of moringa allelopathy in crop science.

20.2 Moringa for Growth Promotion

Plants growth and development is regulated by certain growth substances such as auxins, gibberellins, and cytokinins, etc., produced internally called phytohormones and if applied externally called growth regulators, and are always required in minute quantities to modulate plants growth (Farooq et al. 2009; Taiz and Zeiger 2010). Being a rich source of growth regulators such as zeatin (a cytokinin), ascorbate, phenolics, and many essential plant minerals such as Ca, K, Mg, Mn, P, B, Zn, and Fe (Makkar and Becker 1996; Fuglie 1999; Anwar et al. 2007; Basra et al. 2011; Table 20.1), MLE application has proven its worth as an excellent source of plant growth-promoting substances. MLE is either used as foliar spray or seed priming agent for growth promotion (Table 20.2 Mehboob et al. 2011; Nouman et al. 2012).

20.2.1 MLE as Priming Agent

Seed priming refers to controlled hydration of seeds in water or solutions of low water potential allowing pre-germination metabolic activities to proceed without actual germination, and seeds are then removed from the solution, rinsed, and re-dried near to original weight to permit routine handling (Bradford 1986). Establishment of an early and optimum crop stand is vital for harvesting maximum productivity and seed priming ensures quick and uniform emergence to maintain early stand establishment. Seed priming with diluted MLE enhanced the final germination percentage in several species ranging from 4 to 143 % (Table 20.3). Seeds primed with MLE also exhibited earlier and synchronized emergence as

Table 20.2 Effect of foliar application of *M. olifera* leaf extract on productivity of arable crops

Crops	Crop yield with foliar application of MLE (t ha^{-1})	Crop yield without MLE application (t ha^{-1})	Increase in productivity (%)
Peanut (*Arachis hypogaea*)	5.32	4.19	26.97
Soybean (*Glycine max*)	3.10	2.26	37.17
Corn (*Zea mays*)	8.57	6.32	35.60
Sorghum (*Sorghum bicolor*)	4.59	3.95	16.20
Onion (*Allium cepa*)	4.19	3.68	13.86
Sugarcane (*Saccharum officinarum*)	116.88	109.67	6.57
Black bean (*Phaseolus vulgaris*) cv. Dor-363	1.60	1.34	19.40
Black bean (*Phaseolus vulgaris*) cv. Esteli 150	1.19	1.26	−5.56
Coffee (*Coffea arabica*)	2.39	2.00	19.50
Bell pepper (*Capsicum annuum*)	24.65	16.67	47.87

Data taken from Foidl et al. (2001)

evident from notable reduction in mean emergence time (MET) and energy of emergence (EE) (Table 20.3). Likewise, MLE-primed seeds exhibited higher vigor with considerable increase in plumule and radicle length in several crop species. Results shown in Table 20.3 indicate that improvement in emergence and early stand establishment with MLE priming is truly concentration dependent; as diluted MLE (1:30) paves beneficial effects while seed priming with concentrated MLE (1:10 or 1:20) may have less effectiveness or even detrimental effects on final germination and early stand establishment in some species such as groundnut (*Arachis hypogaea* L.), rice (*Oryza sativa* L.), barnyard grass (*Echinochloa crus-galli*. B), blue panic grass (*Panicum antidotale*), and buffle grass (*Cenchrus ciliaris* L.) (Table 20.3). Optimization of MLE concentration for seed priming in different crops is thus vital prior to use on commercial scale.

Seed priming with diluted MLE not only ensures quick and uniform crop stand but also has the potential to perk up the growth and grain yield of crops. Seed priming with MLE diluted 20 times with water improved root length in sunflower (Basra et al. 2009b). Seed priming with diluted MLE (1:30) lessened the days to tasseling, silking, and maturity along with higher number of grains rows per cob, higher number of grains per cob, biological and economical yield, and harvest index under both optimum and delayed planted hybrid maize (*Zea mays*) (Mehboob et al. 2011). Increase in yield by MLE priming was attributed to improvement in seedling emergence and chlorophyll contents (Mehboob et al. 2011). Likewise, seed priming with 30 times diluted MLE not only ensured quick and uniform crop stand but also improved the grain yield in direct seeded rice irrigated either at field capacity or with alternate wetting and drying (Kamran et al. 2011), and in spring maize under chilling and high temperature stresses (Basra et al. 2011). Similarly, seed priming with MLE was effective in improving the

Table 20.3 Effect of seed priming with MLE on emergence and early seedling establishment of different genotypes

Genotypes	Levels of MLE	Improvement in FEP (%)	Decrease in MET (%)	Decrease in E_{50} (%)	Increase in plumule/shoot length (%)	Increase in radicle/root length (%)	References
Maize (*Zea mays*)	MLE (1:10)	92.76	24.88	33.86			Basra et al. (2011)
	MLE (1:30)	143.07	47.10	56.69	59.92	26.52	Basra et al. (2011)
	MLE (1:10)					77.80	Phiri (2010)
Groundnut (*Arachis hypogaea*)	MLE (1:10)	−4.00				−21.00	Phiri and Mbewe (2010)
Cowpeas (*Vigna sinensis*)	MLE (1:10)	4.00				−24.00	Phiri and Mbewe (2010)
Rice (*Oryza sativa*)	MLE (1:10)	−7.00	−25.00			28.60	Phiri (2010)
Sorghum (*Sorghum bicolor*)	MLE (1:10)	29.00					Phiri (2010)
Beans (*Phaseolus vulgaris*)	MLE (1:10)					4.00	Phiri and Mbewe (2010)
Buffle grass (*Cenchrus ciliaris*)	MLE (1:10)	0.00	12.10	27.59	103.81	164.13	Nouman et al. (2012)
	MLE (1:20)	−12.06	13.44	41.55	116.10	121.74	Nouman et al. (2012)
	MLE (1:30)	131.54	19.34	51.83	169.49	271.74	Nouman et al. (2012)
Blue panicgrass (*Panicum antidotale*)	MLE (1:10)	−33.33	2.68	9.12	161.40	58.82	Nouman et al. (2012)
	MLE (1:20)	−12.5	2.33	20.96	166.05	120.59	Nouman et al. (2012)
	MLE (1:30)	91.68	32.38	44.95	252.56	247.06	Nouman et al. (2012)
Barnyard grass (*Echinochloa crus-galli*)	MLE (1:10)	−3.83	10.32	11.02	29.30	170.54	Nouman et al. (2012)
	MLE (1:20)	26.93	12.45	17.80	47.80	150.89	Nouman et al. (2012)
	MLE (1:30)	92.31	44.90	57.75	118.50	227.68	Nouman et al. (2012)

performance of pea (*P. sativum*), tomato (Basra et al. 2011), and rangeland grasses (Nouman et al. 2012). In a recent study Nouman et al. (2012) reported that seed priming with MLE (1:30) substantially increased the number of leaves, roots and tillers, shoot vigor, and root length and weight in three rangeland grasses including barnyard grass, blue panic grass, and buffle grass.

There are some controversial reports as well, which highlight the negative effects of seed priming with MLE on germination and seedling survival in some crop species. Seed priming with MLE reduced seedling growth of hybrid maize (Basra et al. 2009a). Phiri (2010) also reported decrease in radical length and germination percentage of rice, hypocotyls length, and seedling survival of sorghum (*Sorghum bicolor*) by seed priming with MLE. Likewise, moringa extract lowered the seedling survival by 3.7 % each in beans (*Phaseolus vulgaris* L.) and cowpea (*Vigna sinensis* L.) and 10 % in groundnut (*A. hypogaea* L.) due to considerable reduction in radicle and root length of legume crops (Phiri and Mbewe 2010). As described earlier, seed priming with diluted MLE has beneficial effects; however, priming with MLE may have some detrimental effects. Therefore, use of concentrated MLE (1:10 w/v) in aforementioned cases might be the possible reason of adverse effects of seed priming with MLE.

20.2.2 Foliar Application of MLE

Foliar application of growth regulators, nutrients, and antioxidants often promotes the plant growth and development but these are costly techniques for farmers on commercial scale. MLE being rich in zeatin, ascorbates, carotenoids, phenols, antioxidants, and essential plant nutrients has the potential to modulate plant growth and often applied as exogenous plant growth enhancer (Fuglie 1999; Foidl et al. 2001; Table 20.1). Three foliar sprays of 2 % moringa + 2 % brassica water extract increased canola (*Brassica napus*) yield by 35 % over control (Iqbal 2011). Exogenous application of MLE at heading stage in late sown wheat (*Triticum aestivum*) improved 1000-grain weight, biological yield, grain yield, and harvest index by 6.84, 3.17, 6.80, and 3.51 %, respectively, compared with control (Basra 2011). Yasmeen et al. (2012) also reported significant improvement in grain weight, biological yield, grain yield, and harvest index by foliar application of MLE in late sown wheat. In another study, Yasmeen (2011) reported substantial improvement in growth and yield of tomato by MLE application. MLE accelerates growth of young plants, produces firm stems, enhances resistance against biotic and abiotic stresses, prolongs lifespan, elevates number of roots, stems, and leaves along with additional and bigger fruits and usually enhances yield by around 20–35 % (Fuglie 2001; Foidl et al. 2001). Similarly, Price (1985) reported an increase in growth and yield of crops by use of moringa due to presence of zeatin, a plant growth hormone from the cytokinin group.

Foliar application of MLE enhanced the productivity of several arable crops such as soybean (*Glcine max*), sugarcane (*Saccharum officinarum*), corn, sorghum, black bean (*P. vulgaris*), coffee (*Coffee arabica* L.), bell pepper (*Capsicum annuum* L.), and onion (*Allium cepa* L.) ranging from 6.57 to 47.88 % (Table 20.2) in general but different cultivars behave differently. One cultivar of black bean (Dor-163) exhibited 16.04 % elevation while other cultivar (Steli 150) exhibited 5.34 % decrease in grain yield (Table 20.2). Price (1985) also reported improvement in growth and yield of crops by moringa.

In conclusion, being rich in growth regulators, essential plant elements and antioxidants, MLE has the potential to enhance growth and productivity of several arable crops when used in priming media or sprayed exogenously on crops foliage.

20.3 Role in Defense Against Biotic Stresses

Insects, weeds, and diseases are among the major biotic stresses causing considerable reduction in crop productivity. Although synthetic pesticides such as fungicides, insecticides, and herbicides are often very effective to control biotic stresses with significant increment in productivity, many concerns such as potential harms to human health and livestock, elevated environmental pollution, and occasional toxicity and resistance among genotypes compelled the researchers to explore natural environment friendly approaches (Demoz and Korsten 2006; Macedo et al. 2007; Farooq et al. 2011).

Allelopathic potential of moringa offers an attractive alternative in this regard. Various parts of moringa such as leaves, roots, and seeds possess strong antibacterial and antifungal activities, and therefore can be used as a potential biopesticide to control many diseases (Anwar et al. 2007). Ethanol extracts of moringa showed strong antifungal activities in vitro against many pathogenic fungal strains such as *Trichophyton rubrum*, *T. mentagrophytes*, *Epidermophyton xoccosum*, *Aspergillus tamarii*, *Rhizopus solani*, *Mucor mucedo*, *A. niger,* and *Microsporum canis* (Chuang et al. 2007; Jamil et al. 2007). Stem rot and damping-off are important diseases occurring in more than 500 plant species in tropics and subtropics caused by soil-borne pathogenic fungus *Sclerotium rolfsii* (Punja 1985; Adandonon et al. 2003). Yisehak et al. (2011) reported that incorporation of moringa leaves into the soil before sowing is effective to control damping-off disease (*Pythium debaryanum*). Seed treatment with MLE was effective against some soil-borne fungi in cereals such as *Rhizoctonia*, *Pythium,* and *Fusarium* (Stoll 1988). MLE has systemic action to protect the seedlings from pathogen attack. MLE inhibited the growth of some fungal pathogens in vitro and lessened the *Pythium* damping-off occurrence in legumes, vegetables, and cereals (Stoll 1988; SIBAT 1993). Presence of some crystalline alkaloids, fatty acids, proteins, peptides, glycosides, and niazirins in moringa leaves are responsible for these antimicrobial activities (SIBAT 1993; Jamil et al. 2007).

Seed treatment with concentrated MLE (15 or 20 g leaves 10 mL^{-1} of water in laboratory and 15 kg leaves 10 L^{-1} water) inhibited the mycelium growth of *S. rolfsii* in cowpea (*Vigna unguiculata*) (Adandonon et al. 2006). Seed treatment with Moringa seed crude extract for 24 h caused rupturing of cytoplasmic membrane of fungal cell and damaging the intracellular components (Adandonon et al. 2006). Nonetheless, combination of moringa extracts with other biocontrol agents had synergistic effects against pathogens. Seed treatment with moringa extract together with *Trichoderm*a soil drenching exhibited 94 and 70 % control for *Sclerotium* damping-off and stems rot of cowpea in the greenhouse and targeted field conditions, respectively, with significant increase in yield (Adandonon et al. 2006).

In another study, primed seeds of pearl millet (cv. 7042S) with gum biopolymers of moringa (1:3 w/v) with 3 g kg^{-1} metalaxyl 35 SD showed more germination with significant decrease in pearl millet downy mildew caused by *Sclerospora graminicola* under both laboratory and greenhouse conditions. In addition, seed priming with gum biopolymers of moringa (1:3 w/v) with 3 g kg^{-1} metalaxyl 35 SD resulted in more plant height, fresh and dry weight of seedlings under both laboratory and greenhouse conditions, while superior grain yield was recorded only in greenhouse (Sudisha et al. 2009).

Some reports highlight the insecticidal role of lectins isolated from seed powder of moringa especially against stored grain pests. Coagulant lectins of moringa (cMoL) isolated from moringa seeds at 1 % enhanced the pupal mortality rate of moth flour (*Anagasta kuehniella*) by 27.6 %. The moth flour midgut proteases were unable to digest cMoL after 12 h of incubation. Tight binding of lectin with chitin column suggests that the insecticidal activity of cMoL involves carbohydrate–lectin interactions on the surface of the digestive tract in midgut and resistance to enzymatic digestion (de Oliveira et al. 2011). WSMoL (water-soluble *M. oleifera* lectin) has larvicidal activity against *Aedes aegypti*, the vector of dengue virus (Coelho et al. 2009). Likewise, seed powder of moringa incorporated into 20 g of wheat grains at 12.5 and 25.5 % (w/w) perk up the mortality of maize weevil (*Sitophilus zeamais*) adults after 24, 48, 72, and 96 h of incubation compared with untreated seeds (Ileke and Oni 2011). Similarly, incorporation of moringa powder into wheat grains prevented the emergence of maize weevil adults; and did not show any sign of grain weight loss and seed viability even after 3 months of seed treatment, which suggest that seeds treated with moringa is suitable for consumption and as planting stock (Ileke and Oni 2011). Therefore, seed powder of moringa can be used as a good alternative to pesticides against maize weevil.

Diluted MLE extract either as priming agent or applied on foliage acts as growth enhancer, whereas concentrated MLE (1:10 or 1:20 w/v) impaired germination and early seedling growth in some crop genotypes and weeds as well (Table 20.3). Seed priming with MLE (1:10 w/v) reduced the germination percentage of blue panic grass, barnyard grass, buffle grass, cowpea, and rice (Table 20.3). Nonetheless, concentrated MLE seed treatment hampered radicle and hypocotyl length and condensed the seedling survival rate in sorghum and legumes (Phiri 2010; Phiri and Mbewe 2010). Therefore, it is necessary to optimize MLE concentrations lethal to a variety of weeds in laboratory conditions to explore the allelopathic potential of moringa for weeds suppression under field conditions.

20.4 Role in Defense Against Abiotic Stresses

Abiotic stresses such as drought, temperature extremes, salinity, and nutrient imbalances adversely affect the plant growth and development with notable reduction in crop productivity (Farooq et al. 2009; Hamdia and Shaddad 2010). Plants experiencing abiotic stresses lead to elevated oxidative stress with overproduction of reactive oxygen species (ROS), which are highly toxic and cause damage to proteins, lipids, carbohydrates, and DNA (Apel and Hirt 2004). Plant growth substances modify growth and development processes from seed germination to senescence either through enhancement or stimulating the natural plant regulatory system. Being a rich source of plant growth regulators like zeatin and gibberellins, proteins, vitamins such as B, C, D, and K, minerals such as Ca and K, and more than 40 natural antioxidants such as ascorbic acid, flavonoids, phenolics, and carotenoids (Makkar and Becker 1996; Anwar et al. 2005; Mahmood et al. 2010; Luqman et al. 2012), moringa extract has the potential to modulate the crops growth and productivity under abiotic stresses. Moringa leaves possess a high total antioxidant capacity (TAC) (260 mg 100 g^{-1}) being rich in total polyphenols (TPP) (260 mg 100 g^{-1}), quercetin (100 mg 100 g^{-1}), kaempferol (34 mg 100 g^{-1}), and b-carotene (34 mg 100 g^{-1}) (Lako et al. 2007).

The aqueous and ethanolic extracts of moringa leaf perk up the reduced glutathione (GSH) synthesis and reduce malondialdehyde (MDA) level along with strong free radical scavenging ability in a concentration-dependent manner in living systems (Luqman et al. 2012). Application of MLE ameliorated the detrimental effects of salinity in wheat with quick and uniform emergence, elevated antioxidant activities and soluble proteins, and consequently improved grain yield of wheat (Basra et al. 2011). Improvement in wheat grain yield with MLE application was positively associated with delayed crop maturity, extended seasonal leaf area duration, and grain filling period under delayed planting and salinity stress (Basra 2011). Yasmeen (2011) also reported significant improvement in salinity resistance in wheat by exogenous application of MLE. Increase in enzymatic and non-enzymatic antioxidants coupled with decrease in Na and increase in K uptake contributed for improvement in salinity resistance (Yasmeen 2011).

Chilling stress leads to generation of ROS in maize, which may react with important macromolecules and impair the normal cellular functions (Farooq et al. 2008). Seed priming with MLE 1:30 improved the emergence and early seedling stand establishment of maize under low and high temperature stress. Nonetheless, elevated seedling growth with MLE seed priming is due to higher chlorophyll and phenolic contents of seedlings compared to overnight soaking, hydropriming, and control (Basra 2011). The improved performance of maize with MLE seed priming under temperature stress was due to higher phenolic contents in moringa leaves; as plant phenolics have a beneficial role during oxidative burst, soluble phenolics also contribute to high antioxidant activity (Randhir et al. 2004). Nonetheless, higher contents of antioxidants such as ascorbic acid and glutathione in moringa chloroplasts are vital for plant resistance against oxidative stress (Noctor and Foyer 1998).

20.5 Moringa as Natural Fertilizer

Modern high yielding crop genotypes are highly responsive to adequate supply of essential plant elements, which is generally met by the application of synthetic fertilizers. Continual increase in the price of synthetic fertilizers, short supply at the time of sowing in many developing countries along with elevation in land and water pollution due to continuous and over use of inorganic fertilizers forced the researchers to explore some cheaper and environment friendly alternatives (Phiri 2010). Nonetheless, advances in mechanization aggravate the problem with considerable reduction in farm yard manure due to limited number of farm animals.

Being rich in all macro and micro elements essential for plant growth such as N, P, K, Ca, Mg, S, Mn, Fe, B, and Zn, etc., moringa has the potential to fulfill the nutrient demands of crops and can be utilized as natural fertilizer (Table 20.1). Therefore, *M. oleifera* is being investigated for its effects on crops growth and productivity and should be promoted as a potential supplement or alternate to inorganic fertilizer among the farmers (Phiri 2010). Moringa can be used as green manure or its leaves, stems, and seeds can be incorporated in soil, or its leaves extracts can be used as foliar spray to fulfill the nutrient demands of crops (Fuglie 1999; Davis 2000; Foidl et al. 2001).

Yisehak et al. (2011) reported that seed cake of moringa after oil extraction can be effectively used as nitrogen-rich source of fertilizer. When 25 days old seedlings of moringa are plowed into the soil to a depth of 15 cm, soil fertility significantly improved the nutrient demand of next crop (Davis 2000; Fuglie 2001). Likewise, application of 0.08 % aqueous solution of moringa leaves enhanced the nodulation of black gram (*V. munga*) by about 230 % (Bose 1980), resulting in improved fixation of atmospheric nitrogen. Being deciduous in nature, fallen leaves of moringa can be incorporated in soil to improve the nutrient status of soil (Table 20.1). Foliar sprays of MLEs enhance 14–48 % yield of many crops such as peanut (*A. hypogaea*), maize, sorghum, bell pepper, coffee, black bean, onion, soybean, and sugarcane (Table 20.2).

20.6 Conclusion

Moringa oleifera, the miracle tree, has multifarious application in crops sciences starting from improvement in stand establishment and growth promotion to resistance against biotic and abiotic stresses. Extracts from moringa leaves and seeds may be thus used for seed treatment and foliar application. Moringa cultivation should therefore be propagated and its new uses and applications should be exploited.

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Chapter 21
Cyanobacterial and Algal Allelopathy

A. S. Ahluwalia

Abstract Allelopathy has been known in both aquatic as well as terrestrial ecosystems. Most of the detailed studies have employed terrestrial areas, whereas aquatic ones took the back seat in terms of studies conducted, primarily due to dilution of allelochemicals in such habitats. However, phytoplankton dominance in a water body depends upon many complex factors, including release of allelochemicals by these organisms. These tiny organisms release a spectrum of metabolites in water, which differentially regulate the growth of various algae and cyanobacteria. Allelochemicals produced from these organisms cause habitat shift, control water bloom formation, biofertility, and other growth functions.

21.1 Introduction

Allelopathy is a widespread phenomenon not only in terrestrial but also in aquatic ecosystems. The research on allelopathy of aquatic macrophytes and microphytes (including macroalgae and microalgae) in marine and freshwater habitats could be traced back to the twentieth century. In water medium, production of allelochemicals will be shared by nonproducers as well and further diluted through dispersion in water column.

The word allelopathy is derived from two Greek words. They are *allelon* which means “of each other”, and *pathos* which means “to suffer”. Allelopathy refers to the chemical inhibition or stimulation of one species by another. The “inhibitory” chemical is released into the environment where it affects the development and

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growth of neighboring plants, animals, or microbes. Allelopathy is defined as the beneficial or harmful effects of chemicals contributed directly or indirectly by a plant (including microbes) on other plants (Rice 1984). Allelopathic plants prevent other plants from using the available resources and hence influence the evolution and distribution of other species. In other words, such plants control the environment in which they live. Allelopathy is a phenomenon in which plant leachates cause chemical effects on other plants and microorganisms. One of the widest definitions proposed for allelopathy is an activity in which a plant or a microorganism produces secondary metabolites that inhibit or stimulate the growth and development of another by both direct and indirect interactions (Inderjit and Callaway 2003; Mallik and Williams 2005). However, another view is that only negative and direct biochemical effects should be included in allelopathic interactions (Inderjit 2001). The growth of phytoplankton assemblages is influenced not only by physical and chemical environmental factors, but also by allelopathic interactions between the members of same assemblage and with the members of other assemblages.

Algae and cyanobacteria constitute an important group of organisms from which all the subsequent groups of plants evolved including the flowering ones. These form a diverse assemblage of chlorophyll-containing organisms occurring in a wide variety of aquatic and terrestrial ecosystem. These organisms represent a wide range in their size, shape, reserve food materials, life cycles, etc., which is unparallel in any other group of plant kingdom (Ahluwalia 1993). Cyanobacteria produce few hundred diverse bioactive secondary metabolites originating mainly through non-ribosomal peptide synthetase. These show toxicity toward animals, plants, and microbes and disturb issues of public health concern. Allelopathic activity of *Oscillatoria* species has been found to be maximum during early growth stages through cyclic peptides with unusually modified amino acids found in cells and spent medium (Leao et al. 2010).

Allelopathy is an area of science, which indicates inhibitory or stimulatory biochemical interactions between the two plant species. It is a form of chemical competition and the allelopathic plant is competing through ‘interference’. Competition, by definition, takes one of the two forms—exploitation or interference. Competition is used by microbes, plants, and animals to assure a place in nature. Plants and algae (including cyanobacteria) compete for sunlight, water, and nutrients like animals for territory. Competition like parasitism, disease, and predation influences distribution and population of organisms in an ecosystem. The interactions of ecosystems define an environment. Allelopathy is the impact of secondary metabolites from algae and cyanobacteria, on growth and functions of other microbes and plants (Ionora et al. 2006).

As the organisms compete with one another, they create the potential for resource limitations and possible extinctions. Allelopathic plants prevent other plants from using the available resources and thus influence the evolution and distribution of other species. One might say that allelopathic plants control the environment in which they live. Aquatic autotrophs often face severe competition for resources like light, space, or nutrients. Allelopathic compounds can influence the competition between different photoautotrophs for resources and change the succession of species.

Allelopathy is a form of interference competition and together with resource exploitation, used to explain patterns in plant competition dynamics (Rice 1984). Thus, factors that enhance the allelopathic effect may change the competitive balance in favor of allelopathic organisms. Since all plants including algae experience some kind of stress during growth, it is probable that the stress may enhance the effect of allelopathy. Allelopathy has been very much in limelight of plant ecology in the past few decades. It has remained a controversial topic but surprisingly a lot of literature on various aspects of terrestrial allelopathy is available. Thereafter worldwide, a lot of allelopathic research had been initiated in the aquatic ecosystems.

Allelopathic compounds comprise metabolites released from algal or cyanobacterial cells whether beneficial or detrimental. The metabolites are released into the environment broadly by means of volatilization, leaching, decomposition of algal residues in soils, and their exudation in soil and water. Allelopathic chemicals can be present in any part of the organism. The toxic chemicals may even inhibit shoot or root growth, nutrient uptake, physiological, and metabolic processes of other microorganisms and plants.

Field evidence and laboratory studies indicate that allelopathy occurs in all aquatic and marine habitats as well as in freshwater ecosystems. In recent years, aquatic allelopathy has attracted more and more attention among scientists, which is reflected by the increasing number of articles that review or at least mention allelopathy in different types of micro- and macrophytes present in aquatic systems (Rice 1984; Gopal and Goel 1993; Inderjit and Dakshini 1994; Gross 2003).

Algae constitute an important group of organisms from which all the subsequent groups of plants evolved including the flowering ones. These form a diverse assemblage of chlorophyll containing organisms occurring in a wide variety of aquatic and terrestrial ecosystem. These organisms represent a wide range in their size, shape, reserve food materials, life cycles, etc., which is unparallel in any other group of plant kingdom (Ahluwalia 1993). A number of algal and cyanobacterial species often result in the formation of harmful blooms in both freshwater as well as in marine water ecosystem (Dhingra and Ahluwalia 2007). Still a large number of algal species, mostly belonging to cyanobacteria, are important in freshwater and terrestrial ecosystems for a number of reasons including nitrogen fixation and allelopathic interactions.

Allelopathic research has received great attention in last 20 years. There is an increasing awareness of the importance of biological diversity and the role of allelopathy under different habitat conditions. More reports are available in higher plants concerning allelopathy. However, aquatic photoautotrophs often face severe competition for resources, space, light, or nutrients through allelopathy. Allelopathy in aquatic environment may provide a competitive advantage to angiosperms, algae, or cyanobacteria in their interaction with other primary producers (Gross 2003).

Algal allelopathy has received much less attention than that of higher plants, in spite of reports on the presence of such phenomenon in cyanobacteria and other classes of algae (Keating 1977; Peterson et al. 1979; Rice 1984). Algae include a large heterogeneous assemblage of relatively simpler plants that have little in common except for their characteristic autotrophic mode of nutrition. In spite of the large number of reviews on allelopathy, only a limited number of reviews appears concerning algal and cyanobacterial allelopathy. In comparison to terrestrial plants, the progress of algal allelopathy research is slower and our understanding of presence of algal toxins is relatively poor (Carmichael et al. 1990; Carmichael and Falconer 1993).

In aquatic allelopathy, the allelochemicals are released by donor organisms into the water, which have to be sufficiently hydrophilic and reach their target organisms. One major difference in aquatic habitats compared with terrestrial system is that the sediments is water logged, creating anaerobic environments. Aquatic angiosperms create microzones around roots, which have an impact on the transfer of allelopathically active compounds. Both algae and higher plants release organic compounds, usually referred to as DOC (dissolved organic carbon/compounds) or EOC (extracellular organic carbon/compounds) (Sieburth 1968; Gross 2003). Leachates from allelopathic plants contain mainly carbon based organic compounds, which are considered to be surplus photosynthates (Wetzel 1969).

21.2 Allelopathic Interactions among Macrophytes and Algae

Macrophytes and algae are known to have an antagonistic relationship in both natural and experimental aquatic ecosystems. Fitzgerald (1969) indicated that macrophytes inhibit algal growth by competing for the available nutrient supply; while release of allelochemicals by macrophytes to inhibit algal growth has been suggested (Hogetsu et al. 1960). The production of such allelopathic effects could be used as a tool to control algal growth. Yu et al. (1991) showed that a green alga (*Chlorella pyrenoidosa*) and three other species were inhibited by the ethyl ether fraction of an extract from a culture solution of water hyacinth (*Eichhornia crassipes*). *Potamogeton perfoliatus* and *Anacharis canadensis* (*Elodea canadensis*) have been reported to suppress cyanobacterial growth (Hasler and Jones 1949). They noticed that ponds containing *Elodea* plants had lower phytoplankton densities than ponds without the plants. Proctor (1957) investigated the dominating factor for distribution of *Haematococcus pluvialis* and considered that *Eleocharis microcarpa* might be releasing some chemical compounds (long-chain fatty acids) to inhibit algal growth. Later, Van-Aller et al. (1985) reported that *E. microcarpa* could inhibit the growth of *Anabaena flos-aquae* and *Oscillatoria tenuis*, while stimulating the growth of *Euglena gracilis*. The leachates of *Hydrilla erticillata, Nymphoides indicum*, and *Vallisneria asiatica* inhibited the growth of *C. vulgaris* (Hogetsu et al. 1960). However, the inhibitory effect decreased when the leachates were heated, thus indicating that the growth inhibition might be derived from potential heat-unstable compounds.

The extract of *Ceratophyllum demersum* stimulated the growth of *Chorella* and *Scenedesmus* (Kogan and Chinnova 1972), whereas it inhibited *Anabaena* (Van-Vierssen and Prins 1985). The liquor of floating dicotyledonae, such as *Brasenia schreberi*, suppressed the growth of *C. pyrenoidosa* and *A. flos-aquae* (Elakovich and Wooten 1987). Weaks (1988) indicated that several kinds of aquatic submerged and emergent macrophytes including *Myriophyllum spicatum* showed inhibition on a green unicellular alga *Selenastrum capricornutum*. Sun et al. (1988) conducted precise experiments to preclude the interference of light, nutrition, and microorganisms; and confirmed that *E. crassipes* had the inhibitory effect on several species of microalgae.

Yu et al. (1992) reported that the green unicellular alga *Chlamydomonas reinhardtii* was inhibited by the leachates of *Alternanthera philoxcroides*, *Pistia stratiotes*, *Azolla imbricata*, *Spirodela polyrhiza*, and *Lemna minor* with different sensitivities, and stimulated by *Nasturtium officinale*; however, their inhibition was less than that of *E. crassipes*.

Sun et al. (1988) studied the damage on the photosynthesis of algal cells by recording the disintegration of chloroplasts of *Scenedesmus* sp. by root exudates of *E. crassipes*. The content of chlorophyll *a* decreased significantly and the content of its degradation products increased. They observed that photosynthetic rate dropped sharply, resulting in serious damage to thylakoid reaction (light reaction). Korner (2006) observed suppression of growth of several species of algae by inhibiting their photosystem II with exudates of *C. demersum* and *M. spicatum*. The respiration rate was increased early at low concentration but decreased at high concentration, and with the extension of time the respiration rate decreases gradually.

Gross et al. (1996) and Nakai et al. (2000) found that eugeniin from *M. spicatum* as well as several other phenolic acids like allelochemicals inhibited the alkaline phosphatase activity in algal cells. The allelochemicals of *Phragmites communis* reduced the activities of superoxide dismutase (SOD) and peroxidase (POD), as also declined the scavenging ability of reactive oxygen species to disorganize the cell redox state causing cell death (Li and Hu 2005). The exudates of *E. crassipes* stressed the SOD activity of *Scenedesmus* from initial increase to gradual decrease, whereas (POD) activity increased throughout the experimental period (Tang et al. 2000).

Hu and Hong (2008) reported that allelochemicals from *P. communis* could destroy the membrane structure of *C. pyrenoidosa* and *Microcystis aeruginosa*. Li and Hu (2005) found that unsaturated fatty acid contents increased in both of these algal species. This increase of unsaturated fatty acids in the algal cell membrane directly caused the increase of fluidity of cell membrane, decrease of cell stability, and the leakage of intracellular contents (K^+, Mg^{2+}, Ca^{2+}). It is also found that the thylakoid lamellar structure disappeared, the nucleolus area became irregular, starch grains increased, and the volume of vacuoles increased. Men et al. (2006) found that nucleus disappeared and cell organelles like mitochondria disintegrated by allelochemicals released from *P.communis* on *Scenedesmus obliquus*.

Inhibitory effects of macrophytes on the blue-green algae (*M. aeruginosa*, *A. flos-aquae*, and *Phormidium tenue*) in a coexistence culture system were observed in which concentrations of different macrophytic species (*Egeria densa*, *Cabomba caroliniana*, *M. spicatum*, *C. demersum*, *E. acicularis*, *P. oxyphyllus*, *P. crispus*, *Limnophila sessiliflora*, or *Vallisneria denseserrulata*) were varied (Nakai et al. 1999). Coexistence assay showed that only the macrophyte *C. caroliniana* or *M. spicatum* inhibited the growth of all blue-green algae, with the inhibitory effects of *M. spicatum* being stronger than those of *C. caroliniana* and being produced by the release of allelopathic compounds. In subsequent initial addition assays using *M. spicatum* with the alga *M. aeruginosa*, no significant growth inhibition was observed; whereas, in contrast, quasi-continuous addition assays showed strong inhibition by *M. spicatum*. The study provided the first evidence that unstable, growth-inhibiting allelopathic compounds are continuously secreted by *M. spicatum* (Nakai et al. 1999).

Most of the allelopathic studies were based on the lab-scale experiments with the co-culture system, leachate collection system, and plant extract preparation system. Some investigators developed field-scale tests to support or dispute the lab-scale allelopathic results. Jasser (1995) showed that some submerged plants had obvious allelopathic inhibitory effects on cyanobacteria, no growth effect on many kinds of algae, and even facilitated the growth of some green algae.

A negative effect of *Stratiotes aloides* was shown upon the growth of phytoplanktons, mainly *A. planctonica* and *Oscillatoria* species. The effect was probably mediated through nutrient competition to change water carbon and metal ion composition, which was less likely to be allelopathy (Brammer 1979). Forsberg et al. (1990) demonstrated that the green macroalgae *Chara* (Stone Wort) showed almost no allelopathic effect on phytoplankton under field conditions. *Posidonia oceanica* may be effectively competing with *Caulerpa taxifolia* in areas with limited urban pollution.

Reviews against the allelopathy of aquatic macrophytes on phytoplankton also pointed out the variations that existed between the results based on lab-scale and field-scale experiments. In-depth investigations should be done for elucidating the relationships between allelopathy and other environmental factors (Gopal and Goel 1993; Van-Donk and Van de Bund 2002). However, another view was that it was not appropriate to strip the allelopathy from complicated and combined environmental factors, such as nutrient and light competition in studies (Inderjit and Dakshini 1997). As the potential factors are undefined in the complicated allelopathic system, to date, the field-scale allelopathic researches still lag behind with considerable difficulty. Earlier studies mainly focused on the elucidation of allelopathic phenomena between aquatic macrophytes and freshwater algae; and less reported the extraction, separation, and identification of the highly effective allelochemicals. As the techniques to separate compounds and determine their structures have been developed rapidly, the study on the allelopathy of aquatic macrophytes on algae penetrated into the allelochemical level researches.

Allelochemicals are the effective secondary metabolites excreted by the donor plants (including microorganisms) to act on the recipients (Whittaker 1970). Various allelochemicals with different structures have been identified. However, the allelochemicals which have been identified from aquatic macrophytes are limited mostly to organic polyphenols. Dedonder and Van-Sumere (1971) observed stimulated respiration in *C. vulgaris* at higher concentrations of the phenolics of *Parthenium hysterophorus,* which ultimately caused growth inhibition of the alga. While studying the toxicity of *P. hysterophorus* extracts on the *C. vulgaris* and *Synechococcus elongates,* Megharaj et al. (1986) found that the algicidal effect of aqueous leaf extract of *P. hysterophorus* inhibit the growth of these two algae. Epicuticular rinses from leaves of *Dittrichia viscosa* also showed strong allelopathic effect against N_2-fixing soil cyanobacteria (*Nostoc* and *Anabaena* species) as these algal species fix nitrogen with the help of nitrogenase complex contained actively in specialized cells called heterocysts (Ahluwalia 2004). Korner (2006) noted that *M. spicatum* showed allelopathic activity on green algae *Stigeoclonium tenue*, diatom *Gomphonema parvulum,*, and the cyanobacterium *O. limosa* and the growth of these algae were significantly decreased. Allelopathic effect of substances released from the macrophytes *E. canadensis*, and *M. spicatum* on the common green alga *S. obliquus* showed severe growth inhibition (Lurling et al. 2006).

Kong et al. (2006) showed that extracts of *Lantana camara* leaves reduced the biomass of *E. crassipes*, and the alga *M. aeruginosa*. Two fractions with highly inhibitory activity from the extract were identified as the pentacyclic triterpenoids, lantadene A, and lantadene B. At all concentrations, their inhibitory activities were much higher than that of salicylic acid, a putative allelochemical from *L. camara*. They showed that the predominant allelochemicals involved in *L. camara* against either *E. crassipes* or *M. aeruginosa* are not phenolic acids, but lantadene A and B. *V. spiralis* a common submerged macrophyte, which is widely distributed in quiet waters of lakes, ponds, marshes, and streams in Southeast Asia plays a significant role not only in decreasing eutrophication of water body for its productivity, but also in inhibiting the growth of some bloom-forming blue-green algal species as *M. aeruginosa* (Xian et al. 2006).

Mulderij et al. (2006) showed that the density of phytoplankton (except cyanobacteria) was always higher outside than between the rosettes of *S. aloides*. Analyses of water samples revealed that nutrition was unlikely to have caused the lower phytoplankton biomass in the vicinity of *S. aloides,* the antialgal substances secreted by aquatic macrophyte *S. aloides* produced significant reduction in the biomass of phytoplanktons by decreasing their growth rate (Mulderij et al. 2008). Allelopathic interactions among angiospermic or macrophytic plants and algal species may play a significant role in algal succession. Allelopathic effects of three angiospermic plants *P. hysterophorus* Linnaeus, *Eucalyptus citriodora* Hook, and *Cuscuta reflexa* Roxb. were investigated on a beneficial microalgal unicellular eukaryotic green alga *C. vulgaris* Beijerinck. A reduction in algal growth has been observed with the increasing concentrations of the leachate. Leachates of fresh leaves of these plants also showed an identical trend of growth, cell number/mL, and chlorophyll *a* content in *C. vulgaris* under these concentrations.

Dedonder and Van-Sumere (1971) observed stimulated respiration in *C. vulgaris* at higher concentrations of the phenolics of *P. hysterophorus,* which probably caused growth inhibition of the alga. The toxicity of *P. hysterophorus* extracts on

C. vulgaris, and *S. elongatus* showed algicidal effect which inhibits the growth of these two algae (Megharaj et al. 1986). Growth of *C. vulgaris* cannot take place in the highest concentration of such leachates because the cells which have been in high concentrations for a long time practically start losing their chlorophyll and turn pale leading ultimately to lysis.

Juncus effuses, a cosmopolitan angiosperm produces algicides as dihydrophenantherene and tetrahydropyrene (Della Greca et al. 2002). *E. crassipes* seedlings inhibited the growth of *Chlaymydomonas reinhardtii*. *Typha latifolia* produces antialgal secondary metabolites (Aliotta et al. 1990). The aquatic macrophyte *S. aloides* also show allelopathic interactions with *Cladophora* and *Spirogyra* species (Mulderij et al. 2008).

21.3 Interspecific Allelopathic Interactions among Algae and Cyanobacteria

Keating (1977) provided examples that the allelopathic substances significantly exhibit succession of phytoplanktons. Furthermore, Keating (1978) depicted inhibition of diatom growth upon addition of filtrates of lake water dominated by cyanobacteria and unialgal or axenic cultures of cyanobacteria, respectively. Similar results were reported by low biomass of *Fragilaria crotonensis* (Lafforgue et al. 1995). Allelopathic interactions among *A. oscillarioides, M. aeruginosa*, and *Chlorella* species were studied by Lam and Silvester (1979). *A. oscillarioides* and *M. aeruginosa* inhibited *Chlorella* species whereas *M. aeruginosa* also affected growth of *A. oscillarioides.* Juttner (1984) points out those volatile odorous excretions of algae may act as natural inhibitors to algae and other microorganisms in aquatic ecosystem. The antialgal compounds produced by the freshwater *M. aeruginosa* and *A. spiroides* were later identified as peptides (Ishida and Murakami 2000). A list of common algae and cyanobacteria has been given in Table 21.1.

Many algal species mostly belonging to cyanobacteria (blue-green) influence the aquatic ecosystems. Toxic effects produced by blue-green algae (BGA), which may be included under allelopathy, result in the formation of harmful algal blooms (HAB). Competition among phytoplankton is often chemically mediated, but no studies have considered the modification of allelopathic compounds by biotic interactions. Chemicals produced by algae can influence (i) their own growth potential (autotoxicity), (ii) other algae in their close vicinity, (iii) associated microorganisms (e.g. epiphytes), and (iv) nearby higher plants and animals (Inderjit and Dakshini 1994). Mohamed (2002) noted allelopathic activity of green alga *Spirogyra* stimulating the growth and toxin production in bloom-forming alga *O. agardhii*.

Two nitrogen-fixing, brackish-water cyanobacteria, *Aphanizomenon flos-aquae* and *Nodularia spumigena*, are the most common species that form cyanobacterial blooms in

Table 21.1 Algae and cyanobacteria showing allelopathic behavior

Algae	Cyanobacteria
Chlorella vulgaris	*Microcystis aeruginosa*
Kirchneriella species	*Anabaena flos-aquae*
Pandorina morum	*Scytonema hofmanni*
Skeletonema costatum	*Nodularia spumigena*
Caulerpa taxifolia	*Fischerella muscicola*
Asterionella Formosa	*Oscillatoria virense*
Hormidium nitiens	*Anacystis nidulans*
Nitzschia palea	*Nostoc* species
Codium fragile	
Sargassum miticum	
Ulva pertusa	
Gracelaria lemaneiformis	
Alexandrium affine	
Chattonella marina	
Prorocentrum micans	
Scenedesmus bijugatus	

the Baltic Sea, and result in reduced population of the cryptophytes *Rhodomonas* species and the diatom *Thalassiosira weissflogii* grown in monocultures (Suikkanen et al. 2004). In a comparison between the allelopathic effects of exponential and stationary *N. spumigena* cultures on cell numbers of a diatom and a cryptophyte species, it was revealed that allelopathic activity was only expressed by the exponential culture, with a lower nodularin concentration (Suikkanen et al. 2004). Allelopathic effect of substances released from the alga *Chara globularis* on the common colonial green alga *S. obliquus* showed strong growth inhibition of *S. obliquus* (Lurling et al. 2006). Bloom-forming cyanobacterium *M. aeruginosa* produced hazardous effect in eutrophic freshwater ecosystem. *Cylindrospermopsis raciborskii*, a planktonic filamentous alga became dominant in Lagoa Santa, a small natural lake in Southern Brazil, by producing allelopathic chemicals (Figueredo et al. 2007).

Haslea ostreata, a marine diatom, distributed worldwide, shows the growth inhibition of several species of marine diatoms induced by the shading effect and allelopathic activity (Pouvreau et al. 2007). Allelopathic effects of green macroalga *Ulva lactuca* on the growth of three species of red tide macroalgae (*Heterosigma akashiwo, Alexandrium tamarense*, and *Skeletonema costatum)* showed inhibition of growth (Nan et al. 2008). Zhang et al. (2009) reported that the allelochemicals extracted from *C. vulgaris* have potential to inhibit growth of the cyanobacterium *M. aeruginosa.*

Prince et al. (2008) observed the allelopathic effect of one red tide dinoflagellate, *Karenia brevis* on competing phytoplankton species (diatoms *Asterionellopsis glacialis*, *S. costatum*, and the dinoflagellate *Prorocentrum minimum*). They further found that the most allelopathic compounds produced by *K. brevis* are unstable, polar, organic molecules produced at lower concentrations, which are either neutral or positively charged (Prince et al. 2010).

21.4 Chemical Nature of Allelochemicals from Aquatic Plants and Algae

The allelopathy of aquatic macrophytes on algae needs great development on the allelochemical level studies in comparison with the allelopathic researches in other fields, especially on allelochemical isolation and identification. Allelopathic inhibition is complex and can involve the interaction of different classes of chemicals like phenolic compounds, flavonoids, terpenoids, alkaloids, steroids, carbohydrates, amino acids, etc., with mixture of different compounds. Among marine microalgae, diatoms and other phytoplanktons have been shown to produce toxins capable of impairing the feeding, growth, and reproduction of various organisms and among themselves, by direct or indirect interactions (Rice 1984).

Algal allelochemicals usually inhibit phytoplankton growth through nutrient dynamics, resource competition and role of microbial ecology. Doan et al. (2000) found impairment of DNA replication in the presence of two allelochemicals i.e. 12-epi-hapalindole E isonitrile from *Fischerella* species and indolephenanthridine calothrixin A from *Calothrix* species. A limited number of allelochemicals have been identified from cyanobacteria (Smith and Doan 1999; Leao et al. 2009; Table 21.2). *A. laxa*- a freshwater cyanobacterium produced cyclic peptides having antifungal activity (Frankmolle et al. 1992).

Phenolic compounds represent major soil pollutants by virtue of their importance as pesticides and also as key intermediates in the breakdown of several aromatics by soil microorganisms (Megharaj et al. 1986). Most of the allelopathic substances released by the allelopathic plants are water soluble as *p*-hydroxy benzoic acid, vanilic acid, *p*-caumaric acid, ferulic acid, and alkaloids. Various algae belonging to Cyanophyceae, Chlorophyceae, Bacillariophyceae, Phaeophyceae, Rhodophyceae, and Chrysophyceae yield more than 50 phenolic compounds; majority of these have allelochemical properties (Rogan and Craigie 1978).

It was suggested that the allelochemical separation and identification is a bottleneck to block the study on action modes of allelochemicals (Einhellig 1986). The field for allelopathy of aquatic macrophytes on algae also validates this point. The reports on the action modes of allelochemicals from aquatic macrophytes (e.g., *M. spicatum*, *P. communis*, *Acorus tatarinowii*, *E. crassipes*, and *C. demersum*) on algae are still limited with no systematic and coherent outcome (Leu et al. 2002; Li and Hu 2005). The allelochemicals showed strong allelopathic potential and inhibited the growth of *C. pyrenoidosa* and *M. aeuruginosa* but had no inhibition on growth of *C. vulgaris.* These allelochemicals are species-dependent and caused metal ion leakage from algal cells.

E. interstincta is believed to release catechol acid and salicylates to affect the growth of the plants around (Sutton and Portier 1989, 1991). Stevens and Merril (1980) isolated dihydroactinidiolide from *E. coloradoensis* with highly effective inhibition on several kinds of aquatic weeds and algae, especially on *M. aeruginosa* (Xian et al. 2006). Yang and Sun (1992) identified *N*-phenyl-1-naphthylamine, *N*-phenyl-2-naphthylamine, linoleic acid, and linolein from *E. crassipes*

Table 21.2 Allelochemicals from algae and cyanobacteria

Allelochemical	Producer alga/Cyanobacterium
Nostocyclamide	*Nostoc* species
Fischerellin A and B	*Fischerella muscicola*
Cyanobacterin	*Scytonema hofmanni*
Hapalindole	*Hapalosiphon fontinalis*
Protoamide A and B	*Oscillatoria species*
Cyclic peptides	*Anabaena laxa*
Microcystin	*Microcystis aeruginosa*
Nodularin	*Nodularia spumigena*
Sesquiterpenes, Isololiolides	*Galaxaura filamentosa*
Acetylated diterpenes	*Chlorodesmis fastigata*
Culerpenyne or caulerpicin Sesquiterpenes, monoterpenes	*Caulerpa taxifolia*

which significantly inhibited the growth of *C. reinhardtii*. Sutfeld (1998) isolated resorcinol from *Nuphar lutea* which remarkably suppress the growth of *Cryptomonas* sp. The extract of *M. spicatum* inhibited several kinds of cyanobacteria and green algae, in which tannins, phenols, fatty acids, such as eugeniin, and non-anoic acid were verified with highly effective inhibition (Nakai et al. 2000, 2005). A number of plants as well as algae possess inhibitory effects on populations of microalgae by releasing phytotoxic chemical substances into the aquatic ecosystem (Gross 2003). The allelochemicals extracted from *C. demersum*, *Elodea* sp., *Myriophyllum* sp., *Najas marina*, and *S. aloides* produced harmful effect on the growth of cyanobacterial species (Erhard and Gross 2006; Mulderij et al. 2007). In aquatic systems, plants can release allelochemicals into the water and complex interactions between phytoplankton and submerged macrophytes has been shown (Gross et al. 2007; Mulderij et al. 2008). Effective synergistic activity of portoamide A and B has been recorded in a specific ratio in *Oscillatoria* species (Leao et al. 2010). *Galaxaura filamentosa* affected coral population through production of loliolide derivatives and *Chlorodesmis fastigata* through 2-acetylated diterpenes.

Zhang et al. (2009, 2010) investigated the allelopathic effects of *C. vulgaris* on growth and development of toxic, major algal bloom-forming cyanobacteria in eutrophic freshwater alga *M. aeruginosa*. The allelochemicals of *C. vulgaris* were purified and identified and their allelopathic effects were studied in cyanobacterial assays. They found that reciprocal allelopathic effect exists between the *M. aeruginosa* and *C. vulgaris*. Allelochemicals from *C. vulgaris* included 3 fatty acids [(Z, Z)-9, 12 -octadecadienoic (ODEA, 18:2), tetradecanoic (TDA, 14:0) and hexadecanoic acids (HAD, 16:0)], which inhibited the growth of toxic *M. aeruginosa*, and the ODEA proved the most potent. The combined activity of these three fatty acids exerted synergistic inhibitory effects on the growth of toxic *M. aeruginosa*. They found that *C. vulgaris* and its allelochemicals may control the *M. aeruginosa* bloom and it may be useful to recover the eutrophic waters. Only few aquatic angiosperms live in marine littoral areas and produce water soluble extracts from both green and dead leaves (Orth et al. 2000). Several phenolic compounds, i.e., allelochemicals with algicidal activity against cultured algae and natural phytoplankton communities were isolated from such plants. Allelochemicals are the secondary metabolites that can act either as positive or negative regulators of the growth of algal species. As such, allelopathy can be considered as an adaptation to achieve a competitive advantage over other members within the same community.

Water soluble allelochemicals of green and dead leaves of *Zostera marina* inhibited growth of algae and bacteria (Harrison and Chan 1980). *Rupia maritime* (Potamogetonaceae) growing in brackish or salt water produces antialgal diterpenes (Della Greca et al. 2000).

21.5 Importance of Allelopathic Interactions

Eutrophication in water bodies has become much more serious problem worldwide in recent years. It causes explosive growth of phytoplankton, i.e., algal bloom, associated with various negative impacts, decreases water quality and releases algal toxins to poison ecosystems thereby affecting animals and even humans (Lam et al. 1995). Verschuren et al. (2002) observed that algal mats are responsible for blockage of light and exhausting dissolved oxygen in water, which results in suffocation of aquatic animals and plants and reduction of biodiversity. Therefore, algal bloom control is an important issue for aquatic environment protection. To control algal blooms, macrophytes can be exploited as an alternative strategy in addition to physical methods, chemical treatments and biological manipulation (Hu and Hong 2008). Ferrier et al. (2005) found Barley straw as the most successful macrophyte in algal bloom control. Ridge et al. (1999) observed that leaf litter had inhibitory effects on algae but was reported to be less effective than barley straw. Wang and Zhang (2000) found similar inhibitory effects of decomposed rice straw with barley straw on various types of cyanobacteria, e.g., *M. aeruginosa* (major algal bloom-forming alga).

Allelopathy plays an important role in regulating biodiversity of plant species. Olabarria et al. (2008) predicted that in plots where plants of invasive brown algal species *Sargassum muticum* were removed, the structure of native algal assemblages would differ from that where these plants were untouched. In addition, they observed that the effect of *Sargassum* removal would be more important than other causes of variability at the small scale investigated. Results indicated limited impact of *S. muticum* on native assemblages. The impact was only evident on the total number of native taxa and two understory morpho-functional groups, filamentous and foliose algae, rather than on the entire macroalgal assemblages. Allelopathic potential of cyanobacteria got highlighted through field derived studies of Keating (1977, 1978). These organisms are expected to have algicidal, cyanobactericidal, and herbicidal properties (Smith and Doan 1999).

The invasive algal dominance in the Hawaiian Island reefs include loss of productivity and biodiversity, a decrease in the intrinsic value of the reef, changes in community structure of the reef fishes dependent upon corals and algae, and ultimate erosion of physical structure of the reef. Caulerpenyne, a secondary metabolite which was produced by *C. taxifolia* is lethal in tropical water to the sea urchin *Lytechinus pictus* (fertilized eggs, sperm, and larvae). Marine microalgae including diatoms produce toxins, which are capable of impairing the growth feeding and reproduction of various organisms like copepods, polychaetes, and mammals (Ionora et al. 2006). *Kappaphycus alvarezil*, a fast growing alga, known to absorb high amount of nutrients from sea water and having deleterious effect on endemic corals of Hawaii. *Alexandrum minute,* forming red tides in the Eastern Harbor of Alexandria, usually resulted in the death of a large number of fishes.

Fergola et al. (2007) reported the allelopathic competition between the two algal species *C. vulgaris* and *P. subcapitata*. They showed that the growth rates of the two species are different and can be modeled by the Andrews function (*Pseudokirchneriella subcapitata*) and Michaelis–Menton one (*C. vulgaris*). They also proved that the two species have different yields and that allelochemicals produced by *C. vulgaris* (called chlorellin) produce inhibitory effects on *P. subcapitata*. These results have been used to validate a mathematical modeling approach widely applied in ecotoxicology. The validation test being based on the comparison between the experimental outcome of the competition and the possible dynamical behaviors exhibited by the mathematical model.

Chlorella is an important sequester of carbon dioxide and can play important role in regulating the level of atmospheric CO_2 (Morais and Costa 2007). Besides this, such allelopathic interactions play a significant role in algal succession, which may show feasibility that the growth of harmful bloom-forming algae can be controlled by such interactions, which may be used as a tool for abatement of nuisance algal blooms in aquatic ecosystems.

Control of algal blooms is an important issue for water environment protection as it induces several negative impacts on the lives of aquatic organisms, aquaculture, landscaping, and human health. The development of an environment-friendly, cost-effective, and convenient alternative for controlling algal bloom has gained much concern. Using the allelopathy of aquatic macrophytes as a novel and safe method for algal bloom control is a promising alternative. Development and potential application about allelopathy of aquatic plants on algae, including the allelopathic research history, the potential research problems, the research methodology, and the reported aquatic macrophytes and their inhibitory allelochemicals have been reviewed by Hu and Hong (2008). Potential modes of inhibition action of allelochemicals on algae, possible ways for application, and future directions of research on algal-bloom control by aquatic macrophytes need to be investigated thoroughly.

Hong and Hu (2007) reported inhibitory allelopathic effect of *Arundo donax* on the growth of a bloom-forming cyanobacterium *M. aeruginosa* and three green algal species *S. capricornutum, S. obliquus*, and *C. pyrenoidosa*. Allelopathy may prove harmful as plants containing allelochemicals release these chemicals to the soil, water bodies, plant environment and thus can cause various problems. Apart from its competitive ability, the invasiveness of the noxious weed *P. hysterophorus L.*, is thought to be due to an ability to displace other species by means of allelopathy. The sesquiterpene lactone parthenin that is biosynthesized by this species is thought to play an important role in its allelopathic interference with surrounding plants (Regina et al. 2007). *Parthenium* root extracts significantly reduced the germination and growth of maize and barley (Rashid et al. 2008).

21.6 Marine Algae and Cyanobacteria

Allelopathic interaction in marine ecosystem occurs between randomly floating phytoplankton species or in benthic areas where macroalgae, corals, and few species of plants may be present. Such interactions may be broad among animals and plants or plants and algae and so on. Mainly bloom-forming microalgae are seriously competing with each other for dominating a particular niche through allelopathic interactions among planktonic algae (Smayda 1997). Allelopathic interactions in marine ecosystem occur among a variety of organisms comprising plants, corals, macroalgae, microalgae and cyanobacteria. etc. With allelopathic capabilities of marine algae, increased introduction of many non-indigenous species in the sea is a matter of concern.

Macroalgae generally belong to Phaeophyceae, Chlorophyceae, and Rhodophyceae, although allelochemical interference of macroalgae with microalgae has long been known (Sieburth 1968), yet much is not known about these interactions. Extracts of various macroalgae inhibited the settlement and growth of the chlorophyte *Enteromorpha prolifera* (Chlorophyceae) (Cho et al. 2001), a common epiphytic alga on other macroalgae. *Laurencia pinnatifolia* (Rhodophyceae) produces strong antifouling activity against microalgae, which can be compared with heavy metals and biocides currently used in antifouling paints (Hellio et al. 2002). Crustose algae are mostly affected by canopy formation. Toxic effect of macroalgae on microalgae may be increased due to allelochemicals and shading. Macroalga *Lithophyllum* species (Rhodophyceae) produces allelochemicals like monoterpenes which severely damaged the zoospores of phaeophyte *Laminaria religiosa* (Suzuki et al. 1998). In the Mediterranean, the macroalga *C. taxifolia* out competes the seagrass *Posidonia oceanica* (NIMPIS 2002). Few of marine macroalgae like *U. pertusa, Corallina pilulifera* etc. produce allelochemicals into the culture medium that inhibited toxic bloom-forming microalgae like *Cochlodinium polykrikoides* (Jeong et al. 2000). Bloom-forming macroalgae are harmful to marine intertidal ecosystem by their rapid nutrient uptake, high growth, and broad environmental tolerance (Nelson and Lee 2001). Caulerpenyne provided an advantage to the green alga *C. taxifolia* in reduced feeding by sea urchins with increased production of this secondary metabolite (Amade and Lemee 2008).

Introduction of this marine tropical alga influenced the biodiversity of marine biota in Mediterranean (Bellen-Santini et al. 1996).

Lytic strain of the dinoflagellate *A. tamarense* has been reported to suppress phytoplankton growth whereas non-lytic strain exhibited positive effect on diatoms (Weissbach et al. 2010). Various phyla of algae include variety of microalgae. Blooms of dinoflagellates in marine phytoplankton communities are considered to be mediated by the production of poisoning toxins, okadoic acid (OA) and dinophysistoxin-1 (DTX-1) (Windust et al. 1996; Plumly 1997). These bloom-forming microalgae may dominate phytoplankton not only because they have feeding deterrents, but also responsible for allelopathic competition between diatoms and organisms like bacteria, dinoflagellates, and unicellular green algae (Pouvreau et al. 2006). The abundance of *H. ostrearia* decreases the number of other microalgae, including several diatom species whereas *Alexandrium* species exuded allelopathically active compounds inhibiting other microalgae (*Chaetoceros gracile, Gymnodium mikimotoi*, and *Scrippsiella trochoides*), both at exponential and stationary growth phase (Arzul et al. 1999). Dominance of *M. aeruginosa* blooms is associated with Zebra mussels. The blooms of this colonial cyanobacterium are well known for disrupting food chains, phytoplankton removal, clogging water treatment, and affecting the feeding of larvae and fish (Keating 1977). Effect of macroalgae and algal extracts on corals has been reported through transfer of hydrophobic allelochemicals present on algal surface. These decreased photosynthesis, caused bleaching and even death of corals in 79 % of the cases (Rasher et al. 2011).

21.7 Allelopathy in Freshwater Ecosystem

Members of all groups of primary producers in freshwater have been shown to be involved in different types of allelopathic interactions (Gopal and Goel 1993). Allelopathic interactions in freshwater ecosystem occur among cyanobacteria, microalgae, macroalgae, and plants.

Secondary metabolites are produced by cyanobacteria like *Lyngbya majuscule* are allelopathic in nature. Nitrogen-fixing cyanobacterium *N. harveyana* produces strong allelopathic activity against other cyanobacteria, antibiotic activity against Gram-positive pathogenic bacteria and antifungal activity against two plant pathogens. Allelopathic activity of filtrates from the cyanobacterium *Oscillatoria* species grown at different cell densities has been studied on *C. vulgaris* (Leao et al. 2010). Maximum inhibition in growth was recorded during 10–15 days of culture. Portoamide mixture A and B exhibited inhibitory activity on *Ankistrodesmus falcatus*, *C. reinhardii* and *C. raciborskii* while the mixture had no effect on *Cyclotella meneghiniana*, *Anabaena* species, *Aphanizomenon* species and *M. aeruginosa* (Leao et al. 2010). Cyanobacterial allelochemicals from *Scytonema hofmanni* have been found to inhibit the growth of terrestrial flowering plants.

Spray of cyanobacterin of this cyanobacterium on various plants resulted in reduction of dry weight and frequency of plants actually affected. *Zea mays* and *Pisum sativum* showed maximum mortality.

Mostly charophytic macroalgae are prominent in fresh water ecosystem, such as Characeae and Nitellaceae. *Chara* species dominated lakes are generally clear and exhibit low phytoplankton densities (Crawford 1997), bioactive cyclic sulfur compounds are produced by *C. globularis* (Anthoni et al. 1980) which causes inhibition of photosynthesis in planktonic algae. However, it has been found that exudates of *C. tomentosa, C. delicontula*, or *C. hispida* had no stimulatory effects on other algae. Allelochemicals released by filaments of *Cladophora glomerata* lowered the photosynthetic rates of the epiphytic alga *Nitzschia* species. Allelopathic effect of the *U. lactuca* on the growth of three species (*Heterosigma akashiwo*, *A. tamarense*, and *Sketonema costatum*) of red tide microalgae were tested in laboratory co-culture precluding the light limitation and the effect of high pH (Nan et al. 2008).

A variety of algal toxins has been reported during last few years from Carmichael's laboratory (Carmichael and Falconer 1993). In mixed culture of *Nitzchia frustulum* and *C. vulgaris*, the former grows well, while *C. vulgaris* suffers 40 % reduction in population size to that when grown alone (Rice 1984). *Pediastrum borynatum, P. clathratum, Cosmarium lundellii*, and *P. uncinatum* inhibited the growth of *Microsterias pappilafera. O. planctonica* killed *C. pyrenoidosa, C. lundellii*, and *S. quadricauda* (Rice 1984). *O. late-virens* affected growth, photosynthesis and toxicity of *M. aeruginosa* (Bagchi et al. 1993; Bagchi 1995). *Peridinium gatunense*—a bloom-forming dinoflagellate has been found to influence *Microcystis species* (Vardi et al. 2002).

Bloom-forming pelagic cyanobacteria are well known for their neuro-or hepatotoxic metabolites (Skulberg 2000; Kaebernick and Neilan 2001). Allelochemical cyanobacterin secreted by *S. hofmanni* was found to inhibit growth of other cyanobacteria (Gleason and Paulson 1984), and eukaryotic algae (Gleason and Baxa 1986). *Fischerella* species exhibit allelopathic activity toward many cyanobacteria and eukaryotic algae (Flores and Wolk 1986). *Calothrix* species inhibited RNA synthesis of various organisms (Doan et al. 2000). *Trichormus doliolum* inhibited the growth of other cyanobacteria and some chlorophytes. *Oscillatoria* species released allelochemicals inhibiting other cyanobacteria and chlorophytes. *Nostoc* species releases allelochemicals named cyanobacterin LU-1, that inhibited the growth of many cyanobacteria and eukaryotic algae (Gromov et al. 1991). *M. aeruginosa* inhibits growth of *C. pyrenoides* (Ikawa et al. 1996). Extracellular products of *A. flos-aquae* inhibited the growth of a green unicellular motile alga *C. reinhardtii* (Kearns and Hunger 2001). *Microcystis* species inhibited photosynthesis of the dinoflagellate *Peridium gatunese* by interference with its internal carbonic anhydrase activity (Sukenik et al. 2002).

21.8 Algal Allelopathy and Agroecosystem

The blue-green algae are of much ecological importance in paddy fields, maintaining their soil fertility and reclaiming alkaline soil (Singh 1961). Due to modern agricultural practices in Northern part of India, specially Punjab and Haryana, the paddy crop is harvested by harvester combines, thereby leaving most of the rice straw in the fields. Rice straw residue has been known to release some allelochemicals on their decomposition that affect the growth and nitrogen-fixing potential of blue-green algae (Chou and Lin 1976; Rice 1984). Many compounds known as allelochemicals have been reported in decomposing rice straw and in the rice fields (Stevenson 1967; ChandraMohan et al. 1973; Tang and Waiss 1978).

It was suggested that decline in the productivity of rice subsequent to the first crop was due chiefly to allelopathic effect of decaying rice residue in the paddy soil. Rice et al. (1981) investigated the effect of five phenolic inhibitors that are produced by decomposing rice straw on growth and nitrogen fixation of *Aegilops cylindrica*. Among these, four were found to be inhibitory and also showed synergistic effect when used in combination. The phytotoxin released by decomposing rice straw were also observed to inhibit the nitrogen fixation by *Rhizobium*. Since the blue-green and green algae are the dominating forms that grow in the field during the rice crop, therefore, it is worthwhile to study the effect of rice straw on algal characteristics as a whole and interactions among blue-green algae.

The basal portion of rice plant, left in the field, due to use of harvester combines is plowed back or burnt which on decomposition release water soluble allelochemicals (Phenolic compounds) that may be affecting the algal dynamics and the next crop (Ahluwalia 1998; Ahluwalia and Ghawana 1998). Because, blue-green and green algae are the dominant organisms available in the fields, the allelochemicals first become available to algae and then to the next crop. Interactions of these algae might be affecting the growth and nitrogen fixation of blue-green algae, as observed in *Nostoc puntiformae* by Harder (1917).

The addition of blue-green algae to the field for nitrogen fixation is normally recommended but these affect the growth of green algae. Murphy et al. (1976) reported that excretion of hydroxamate chelators by certain blue-green algae bind iron and make its unavailability to other algae, thus inhibiting their growth, resulting from addition of the organic compounds released from *A. flos-aquae* and *M. aeruginosa*. Green algae were also known to produce allelochemicals to affect their own growth or of other algae (Wolfe and Rice 1979). Since algae grow in water so water-soluble chemicals are of more ecological relevance rather than volatile chemicals. Otherwise also, the phenols are water soluble and are well established as potent allelochemicals (Rice 1984).

A significant number of cyanobacterial strains show negative effect on rice germination. Such information is of immense value in making recommendations regarding inocula of cyanobacterial consortium in the paddy fields as biofertilizer. The allelochemics, at their low concentrations cause promontory effect, while at moderate concentrations become inhibitory. These compounds also influence the nutrient status and hence their uptake, thereby creating a condition of nutrient stress. It is known that nitrogen stress conditions increase the concentration of phenolic compounds, which then influence the growth and nitrogen-fixing potential of blue greenalgae (Fitzgerald 1969).

Some algae acquired resistance to such hazardous allelochemicals present in the environment and get acclimatized accordingly (Gapoctika and Karaush 1985; Karaush 1985). However, the blue-green algae are most sensitive to phenolic environment and cannot survive in such conditions. All allelochemicals added to aquatic or agroecosystem, are either of blue-green algal or plant origin or various residues left in the field, on their decomposition get added to the system. Decomposing rice-straw and algal material present in the field can contribute towards the pool of allelochemical compounds. These can influence the seed germination and growth of next crop in those fields.

21.9 Implication of Algal Allelopathy

The algal allelochemicals at their low concentrations can be implied in various ways in solving certain problems in algal research, such as bloom control (Keating 1977). Algal allelopathy also determines why the alga *H. pluvialis* is common ephemeral in rain-water pockets and is never found in permanent water bodies (Proctor 1957). Allelopathy has been in use to check algal blooms through phenolic acids which generate superoxide anion radicals, causing lipid peroxidation and change in cell permeability leading to cell death. A higher level of total phenolics in soil, amended with different levels of algal inoculum, has been shown as a potential cause of inhibition of rice seedlings in such soils (Inderjit and Dakshini 1997).

Among green algae *Chlorella* species has got maximum attention for secretion of some growth inhibitory substances. This influences the growth of other algae, aquatic macrophytes and even seed germination of vegetable crops (Jorgenson 1950; Makisimnova and Pinninova 1969). Some other green algae like *Pandorina morum* and *Scenedesmus* species can also influence the growth of aquatic macrophytes and blue-green algae (Sharma 1985; Gopal et al. 1984). Algal allelochemicals have also been known for causing habitat shift for a xanthophycean alga *Botrydium becherianum*.

Allelopathy may explain the dominance of a particular species or formation of its bloom. However, Jonsson et al. (2009) has doubted the involvement of allelopathy in formation of algal blooms. Dinoflagellates usually have an ability of bioluminescence and production of toxins. These qualities prevent or reduce their grazing appreciably by acting as grazer deterrents and allelopathic agents. It has been shown that the red tide dinoflagellate *K. brevis* is allelopathic to several co-occurring phytoplankton species but its natural products are responsible for suppressing most of these species (Kubanek et al. 2005). However, *S. costatum* reduced its allelopathic effect and degraded its brevetoxins.

The allelochemic cyanobactericin, obtained from *S. hofmanni* (UTEX, 2349), has been reported to inhibit the PS II (Mason et al. 1982; Pignatello et al. 1983; Gleason and Bax 1986; Gleason 1990). Recently antibiotics obtained from the *Oscillatoria* species and *O. virense*, have been shown to influence the algal populations and photosynthesis in higher plants (Bagchi et al. 1993). Another allelochemic called Fischerellin has been isolated from the blue-green alga, *Fischerella muscicola* (Elisabeth et al. 1991).

Allelopathy has been implicated in bloom formation and its control. Phytoplankton blooms in ponds are known to be controlled by introduction of *Chara* (Crawford 1979). If it is possible to identify these allelopathic chemicals, it would be easy to control blooms of species of algae like *Pediastrum, Chlorella, Phormidium, Scenedesmus* etc. Algal allelopathy in chemical signaling needs to be probed for diverse applications. Although work of Keating (Keating 1977, 1978) suggests that natural control of eutrophication but little progress has been taken place in use of algal allelochemicals for lake management and ecotechnological control of eutrophication. More research is required on chemical warfare between and among algae and cyanobacteria for better understanding of wetland and aquatic ecology, bloom formation, lake succession, algal invasion, and dominance of certain algae in a given ecosystem.

21.10 Conclusions

Allelochemicals have been significant in agricultural practices, health of aquatic bodies, and soil chemistry. These compounds are produced by decomposing rice/wheat straw and directly affect the soil fertility, photosynthesis, and the growth performance of the plants. Phenolics usually increase under stress conditions, and show their effect. There are interactions among algae, cyanobacteria and algae, algae/cyanobacteria, and higher plants. Care needs to be taken in selecting algal inoculum for biofertility program through heterocyst frequency and implications of algae bloom control through other algae.

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