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ALLELOPATHY: ITS ROLE, RECENT DEVELOPMENTS AND FUTURE PROSPECTS

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ABSTRACT

Allelopathy is an important mechanism of plant interference mediated by the release of plant produced secondary metabolites called allelochemicals to the soil rhizosphere. Allelochemicals are present in all types of plants and tissues and are released into the soil rhizosphere by a variety of mechanisms including decomposition of residues, volatilization and root exudation. The chemical nature of allelochemicals may be of diverse types such as, phenols, glycosides, amino acids, terpenes, flavoinoids, steroids and sugars. Primary effects of allelopathy include reduced seed germination and seedling growth. However, certain allelochemicals severely affect cell division, pollen germination, nutrient uptake, photosynthesis, and specific enzyme function. Allelopathy offers natural control of weeds, insect-pests and diseases thus increases the crop production. Allelochemicals promote growth at low concentration. However, allelochemicals suppress the growth if applied at high concentration. In addition, allelopathy helps plant species to combat against a number of abiotic stresses. Furthermore, several allelochemical structures are also of potential uses for their roles in the development of future herbicides to mitigate the environmental hazards posed by the wild application of synthetic chemicals in agricultural fields.

INTRODUCTION

The term allelopathy was coined in the mid 19^{th} century by Austrian plant pathologist Hans Molisch who investigated the effects caused by volatile emissions of various fruits, such as apple, pear etc, on the development of pea seedlings. The volatile compounds were later identified as ethylene. He originally defined allelopathy as chemical plant-plant interaction. Today, allelopathy is more understood to comprise a broad range of interaction in the rhizosphere including those that involve microorganisms as well. Allelopathy plays an important role in biodiversity as the dominant species may limit the population of another species therefore regulating the density of the plant community.

The word allelopathy has been derived from two Latin words 'allelos' and 'pathos' meaning 'each other' and 'harm', respectively. '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' [1]. Allelopathy refers to the beneficial or harmful effects of one plant on another plant, both crop and weed species, from the release of biochemicals, known as allelochemicals, from plant parts by leaching, root exudation, volatilization, residue decomposition, and other processes in both natural and agricultural systems. Action of these compounds is concentration dependent as these inhibit the plant growth at high concentrations and promote that at low concentrations [2]. These allelochemicals may thus be used as natural pesticides at high concentration. Allelopathy is an important ecological process in vegetational composition and agricultural sciences [3]. Allochemicals such as, phenols, glycosides, amino acids, terpenes, flavoinoids, steroids and sugars are released from different parts of the plants like leaves, stems, trichome, rhizomes, roots, flower, seeds and fruits [4] . As many allelochemicals are toxic to plants, research has been conducted to investigate the use of allelopathic plants as natural, environmentally friendly herbicides.

MECHANISM OF ALLELOPATHY AND NATURE OF ALLELOCHEMICALS

A key concept in allelopathy is the chemical transfer through the environment from one organism to another. Compounds released from higher plants may be altered by the microorganisms before the altered substances is contacted by the another plants. Allelochemicals with negative allelopathic effects are an important part of plant defense against herbivory. Commonly cited effects of allelopathy include reduced seed germination and seedling growth. However, known sites of action for some allelochemicals include cell division, pollen germination, nutrient uptake, photosynthesis, and specific enzyme function.

Allelopathic inhibition typically results from a combination of allelochemicals which interfere with various physiological processes in the receiving plant or microorganisms. Allochemicals were classified into five categories viz., phenylprpopane, acetogenins, terpenoids, steroids and alkaloids. Many coumarins, cinnamic and benzoic acids, flavonoids, monoterpenes, sesquiterpene lactones affect the growth of whole plant seedlings at higher inhibition threshold. But sorgoleone, p-benzoquinone is more toxic than the phenols and terpenes at low concentrations. Polyacetylenes are also highly toxic reducing root elongation in *Echinochloa crusgalli.* Interesrtingly often inhibitory compounds stimulate growth when its concentration is low. Certain allelopathic compounds such as cinnamic, ferulic and coumaric acid also play structural and physiologically important role in plant body and some of them are intermediate in liginification. For example, one study that examined the effect of an allelochemical known in velvetbean, 3-(3',4'-dihydroxyphenyl)-l-alanine (l-DOPA), indicated that the inhibition by this compound is due to adverse effects on amino acid metabolism and iron concentration equilibrium. There is evidence that volatile seed germination inhibitors that include C_2-C_{20} hydrocarbons, alcohols, aldehydes, ketones, esters and monoterpenes arise from a variety of weeds and crop plants. Allelopathic effects of *Amranthus palmeri* and *Cyperus rotundus* by way of volatile seed germination inhibitors hexenal are well documented. The Clifornia chapperal shrub, *Salvia leucophylla* produces volatile turpenes which appears to suppress competitor cucumber seedlings by way of inhibiting stem growth substantially. Many volatile phytotoxic monoterpenes such as cineole, piene and camphor were also reported as allelopathic chemicals. But on the contrary, methanol, which appears to be a routinely released volatile compound from plants leaves relatively, serves as a carbon source for methylobacteria that inhabit phyllosphere. In the field, the black walnut (*Juglans nigra*) of north America which suppresses plant growth upto 25 m from trunk, killing many plants outright. The root extract contains quinine which kills alfafa and tomato plants. In the reedmace, *Typha latifolia*, intraspecific allelopathy occurs, so that the centre of stand dies back.

Studies have elucidated specific allelochemicals involved in weed suppression, including benzoxanoids in rye; diterpenoid momilactones in rice; tabanone in cogongrass; alkaloids and flavonoids in fescue; anthratectone and naphthotectone in teak *(Tectona grandis);* abscisic acid beta-d-glucopyranosyl ester in red pine; cyanamide in hairy vetch; and a cyclopropene fatty acid in hazel sterculia (*Sterculia foetida*). Application of allelopathic compounds before, along with, or after synthetic herbicides could increase the overall effect of both materials, thereby reducing application rates of synthetic herbicides. In one study, an extract of brassica (*Brassica napus*), sorghum, and sunflower was used on rain-fed wheat to successfully reduce weed pressure. When an allelopathic plant water extract was tank-mixed with atrazine, a significant degree of weed control was achieved in wheat with a reduced dose of herbicide. In forest ecosystems, allelochemicals produced by invasive plants can inhibit the growth of competing vegetation through direct or indirect means, thereby providing the invader with a competitive advantage. In addition to effects on other plants, the allelochemicals produced by invasive plants can also contribute to pest and disease resistance, and subsequently confer a competitive advantage to the invader in the host range.

Selective activity of tree allelochemicals on crops and other plants has also been reported. For example, *Leucaena leucocephala*, the miracle tree promoted for revegetation, soil and water conservation, and livestock nutrition in India, contains a toxic, non-protein amino acid in its leaves that inhibits the growth of other trees but not its own seedlings. *Leucaena* species have also been shown to reduce the yield of wheat but increase the yield of rice. Time, environmental conditions, and plant tissue all factor into variations in allelochemical concentrations in the producer plant. Gamma irradiation of wheat increases the allelopathic potentialities of future roots. The allelopathic potential of mile-a- minute vine (*Ipomoea cairica)* is significantly greater at higher environmental temperatures. One study indicated that soil biota reduced the allelopathic potential of sticky snakeroot (*Ageratina adenophora*). Allelopathic chemicals or allelochemicals can also persist in soil, affecting both neighboring plants as well as those planted in succession. Although derived from plants, allelochemicals may be more biodegradable than traditional herbicides, but allelochemicals may also have undesirable effects on non-target species, necessitating ecological studies before widespread use.

ROLE OF ALLELOPATHY:

A. ALLELOPATHY IN RELATION TO PLANT PHYSIOLOGY

1. ***Impact of Allelopathy on plant physiological processes*:** Allelopathic compounds are known to modify growth, development of plants, including germination and early seedling growth. There are increasing evidences that allelochemicals have significant effects on cell division, cell differentiation, ion and water uptake, water status, phytohormone metabolism, respiration, photosynthesis, enzyme function, signal transduction as well as gene expression [5-6].

Coumarins were seen consistent regarding their germination inhibition feature while caffeic acid and ferulic acid suppressed germination and growth at high concentration (10^{-5} M or more) but improved at low concentration (10^{-3} M or less). A diterpenoid phyllocladane produced by *Callicarpa macrophylla* plant, stimulate growth by reducing the effectiveness of growth inhibiting allelochemicals. Similar activity was observed by another allelochemical calliterpenone produced by *C. macrophylla*. Promising results by calliterpenone regarding improvement of seed germination, root growth, shoot growth and floral development have been observed [7]. Several natural chemicals have been also isolated and identified as seed germination stimulants of parasitic species. The main parts of these are the sesquiterpenes lactones and some are alectrol from *Vigna siensis*, orobanchol from *Trifolium pratense* and strigolactones and orobanchol from sorghum. Strigol was first isolated and identified from the root exudates of *Gossypium hirsutum* plants and later from *Zea mays*, all are also produced by *Striga* host plants.

Extracts of *Stevia rebaudiana* containing a secondary metabolite stevioside, promoted the growth of cucumber and lettuce [7]. A little knowledge on the positive effects of allelochemicals on plant conducting tissues i.e. xylem and phloem is also present. Impact on these tissues surely affect water, nutrients and assimilates translocation which ultimately contribute towards plant growth. Enzyme activity is another key phenomenon affected by allelochemicals. They suppress or facilitate the enzymatic action depending upon their concentration and substrate conditions [8]. The sensitivity of *Rhizobium* sp. to allochemicals leads to poor nodulation and subsequent reduction of nitrogen available to the legumes growing in association with the allelopathic plants or residues. Allochemicals from higher plants have been reported to alter microbial respiration. Furthermore, growth promotion by these allelochemicals was associated with test species, environmental conditions and growth stages at which they are applied.

2. ***Effect on Chlorophyll Content***: Treatment of soybean plants with phenolic acids such as ferulic, p-coumaric, and vanillic acids greatly decreased the biomass associated with reduced chlorophyll content in leaves [9] . Allelochemicals may reduce Chl accumulation in three ways: the inhibition of Chl synthesis, the stimulation of Chl. degradation, and both. Some allelochmicals interferes with the synthesis of porphyrin, precursors of Chl biosynthesis. Chlorophyll content is decreased by phenolic acids in rice [10]; secalonic acid in sorghum [11] and monoterpenes in *Cassia occidentalis* [12].

3. ***Effect on Stomatal Physiology**:* Allelochemical treatment frequently resulted in a decrease in stomatal conductance together with loss of leaf turgor. In cucumber, allelopathic agents would result in a reduction in stomatal conductance in several hours after the treatment [13]. In tobacco and sunflower, the effects lasted as long as several days [14]. Stomata function is influenced by a lot of factors such as water status, K concentration and ABA signals. Since root is the first organ that comes into contact with allelochemicals in most cases, impaired water and ion uptake and increased ABA accumulation are the most possible mechanism involved. It was found that inclusion of volatile essential oils from *Prinsepia utilis L*. or its leaves greatly inhibited the stomatal opening and reduced the stomatal conductance [15]. Stomatal conductance is decreased by phenolic acids in cucumber and hydroxybenzoic acid in soybean [16].
4. ***Photoinhibition and Electron Transport Photosystem:*** At high concentrations allelochemicals may act as photosynthetic inhibitors. They can block electron acceptors, act as energy uncouplers and reduce the activity of photosynthetic pigments and enzymes. However, a positive role can be predicted at their lower concentrations. Growth has been promoted through optimum CO_2 fixation under normal conditions at relatively low concentrations of secondary metabolites. A few studies have showed that allelochemicals or phytochemicals from higher plants, cyanobacteria and algae exhibited inhibition to the ATP synthesis, uncoupled electron transport and phosphorylating electron flow. Xanthorrhizol and trachyoban-19-oic acid from *Iostephane heterophylla*, sorgoleone [17] and resorcinolic lipids from *Sorghum bicolor*, polyphenolic allelochemicals from aquatic angiosperm *Myriophyllum spicatum*, all significantly inhibited PSII.
5. ***Interference of Allelochemicals with Mitochondrial Respiration**:* Allelochemicals may exert positive or negative impact on the process of respiration. Allelochemicals from phenolic acids, quinones, coumarins, terpenoids and flavonoids have been shown to affect the respiratory activity of intact plant tissues and isolated mitochondria. In general terms, however, it can be concluded that the quinines, sorgoleone and juglone are the most active compounds, being effective in isolated mitochondria at concentrations near to 1.0 µM [18]. Flavonoids are active at the concentration range of 20 to 1000 µM (Takahashi et al. 1998) and the phenolic acids affect mitochondrial metabolism at relatively high concentrations The potency of the monoterpenes, on the other hand, has been shown to vary within two orders of magnitude (50-5000 µM) [19]. The adverse effects on mitochondria depend on the access of the allelochemical to the mitochondria, which, in

turn, depends on the permeability of the plant cell membrane to the compound as well as on its possible chemical transformations within the cells. They are important, however, because it is evidently possible that the compound never attains those concentrations within the cell at which the compound is active on isolated mitochondria. This occurs possibly with those allelochemicals which cause adverse effects on isolated mitochondria only at relatively high concentrations, such as ferulic, vanilic and coumaric acids, caffeine, rutin and the monoterpenes camphor, eucalyptol and limonene. It should be considered, however, that the tissue concentrations may be higher than those ones in the medium as it was recently demonstrated for salicylic acid [20].

6. ***Impact on Carbohydrate Metabolism**:* Stunted growth with increased carbohydrate content was frequently observed in plants receiving allelochemical treatment. An increase in carbohydrate metabolite such as sugars would lead to a reduction in CO_2 assimilation as reported in other stressed plants. It is not clear whether the reduced carboxylation efficiency arose from the reduction in Rubisco content or in activity or both.
7. ***Allelochemicals as Growth Regulators**:* Allelochemicals regulate the production of plant hormones. Growth hormones gibberellins and auxins are affected by secondary metabolites, which significantly affect cell enlargement in plants. Phytohormones such as auxins, gibberellins and cytokinins are growth promoters, which are added by different microorganisms in agricultural systems. IAA-oxidase inactivates the IAA and hinders cell enlargement and plant growth. Some allelochemicals inhibit IAA-oxidase which activates IAA. In this way, allelochemicals affect the role of a major plant hormone and resultantly improves plant growth. Gibberellins-induced growth extensions are also affected by allelochemicals. Microorganisms also produce allelochemicals or compounds and enzymes similar in nature to allelochemicals. They act in same way and assist the functioning of other secondary metabolites synergistically. Some Plant Growth Promoting Rhizobacteria (PGPR) use to release enzyme, 1-aminocyclopropane-1-carboxylate (ACC) deaminase causing hydrolysis of ACC (precursor of ethylene) resulting in decrease of ethylene concentration and thus its inhibitory effects to improve root and plant growth [21].

B. *ALLELOPATHY IN RELATION TO STRESS PHYSIOLOGY*

1. ***Allelopathy as Stress Factor**:* Production of allelochemicals at higher rates induces resistance in plants against stresses [22] and helps them grow vigorously under such conditions. The production of allelochemicals is influenced by age of plant, type of stress, intensity of stress and ambient surroundings. For instance, cyanogenic glucoside synthesis

is enhanced in several drought resistance plants when exposed to drought Likewise; cucumber produced more phenolics and flavanoids when exposed to dry conditions. Similarly, biosynthesis of ferulic acid in wheat and isothiocyanates in watercress were also increased under drought. Temperature fluctuations also cause change in the production rate of allelochemicals. In general, biosynthesis of allelochemicals is increased under high temperature. Production of chlorogenic acid is enhanced with temperature just above freezing point in case of tobacco. Production of these allelochemicals serves as tool for plant survival. They help to avoid, tolerate and mitigate the catastrophes in an efficient way. In this way allelochemicals significantly impart resistance against environmental stresses and consequently make plants able to grow better. Many of transporters have been shown to be induced by cadmium, cold, or salt stress treatments, pathogen infection, salicylic acid, ethylene, and methyl jasmonates, whereas others have been reported to play specific roles in the elimination of phytotoxins unrelated to pathogen defence [23].

2. ***Allelopathic Stress Signalling****:* From the emanation of a wide variety of allelocompounds (exudation of soluble chemicals or releasing volatile organic compounds) plants can regulate the soil microbial community in their immediate vicinity (terrestrial plants), endure herbivores, encourage beneficial symbiosis, change the chemical and physical properties of the surrounded environment, and directly inhibit the growth of competing plant species. Some elucidated factors involved in signal transduction pathways of allelochemical defence response in *Arabidopsis* had been previously reported to play roles in mediating transcriptional responses to both abiotic and biotic stresses [24], as well as physiological processes such as leaf senescence [25]. Under heat, drought or salinity stress allelochemicals play a vital role in reactive oxygen species (ROS) production initially and then activation of antioxidant defense system. Allelochemicals actively work for signaling mechanism. Simply induce secondary oxidative stress in plant functioning system. It produces ROS which trigger antioxidants production as tool to scavenge them. Moreover, hormonal imbalance is created which cause over production of some useful plant hormones essential for smooth running of physiological processes [26].
3. ***Allelopathy and Abiotic Stress****:* Some of the pioneer investigations of the effects of abiotic stress on allelochemicals demonstrated that coumarins such as scopoletin and scopolin in tobacco and sunflower increased in response to herbicide, nutrient, temperature and radiation stresses. Similarly, barley alkaloids were found to increase when plants were grown under high temperature. Moisture stress caused an increase in

monoterpenes in *Pinus taeda* and hydroxamic acid in *Zea mays*. Nutrient and water stress generally favor the increase in secondary metabolite production. It was also found nutrient deficiency increased the allelopathic activity of *Helianthus annuus* and this was attributed to the modification of total phenoloic compounds.

4. ***Allelopathy and Biotic Stresses:*** In plants, defensive mechanisms are triggered that lead to a increased production, degradation of conjugates, and /or to synthesis de novo of the secondary metabolites of defensive mode of action that often also show allelopathic activity. Ultimately, such plants, their litter, mulch, and residues having a higher content of allelochemicals would be of a higher allelopathic activity when allelochemicals will be released to environment. Contrary to the above and common opinion that stresses would increase allelopathic activity of the affected plant.

C. ALLELOPATHY IN RELATION TO ECOLOGY

1. ***Allelopathy and Environment Interactions:*** When allelochemicals enter the soil, microbial transformation often occurs or their biological activity may be altered as they are adsorbed on the soil particle. Recent reports claim that the amount of nitrate and other organic carbon sources in the soil modified the allelopathic action of p-coumaric acid. High levels of nitrate increased the amount of p-coumaric acid required to reduce the growth of Ipomoea sp. but elevated glucose of methionine in the soil reduced the concentration for growth inhibition.
2. ***Autotoxicity:*** Autoallelopathy (autotixicity, autointoxication, intraspecies allelopathic interferences), a biotic stress of allelochemical deleterious interference between plants of the same species, occurring both in natural and agroecosystems, creates a serious problem in replanting fruit trees in orchards (peach, apple, apricot, cherries, citrus), shrubs and perennial plantations (grape, asparagus, coffee, tea, alfalfa) and in some annual crops when grown successively year-by-year [27].
3. ***Competition:*** Competition is another biotic stress, which triggers or changes plant allelopathic properties. Allelopathic potential of plants competing for limited resources such as nutrients, water, oxygen or growing under unfavourable light conditions will, most likely, be enhanced due to increased biosynthesis of allelochemicals and the deleterious effects of allelocompounds on target plants may be greater. It was shown experimentally that increased allelopathic activity of *Ageratum conyzoides* when exposed to competition with *Bidens pilosa* [28]. competition as a result of an increased plant density

diminishes allelopathic properties of the leachates, volatiles and exudates of donor plant, as well as its litter, mulch and residues due to the dilution effect in density dependent phytoxicity.

4. ***Exotic Species and weed Invasion**: Centaurea* species are among the most destructive exotic invasive plant species to North America and there is evidence that allelopathy is one of the mechanisms through which rapid displacement of native species takes place [29-30]. Experimental studies pinpointed the importance of allelopathy as a mechanism of the success of invaders because native species are more likely to be "naive" than those in origin communities to released by invaders allelochemicals as they did not co-evolve [30]. *Parthenium hysterophorus*, a tropical weed endemic to America had done great damage since arriving as exotic to the Indian landscape and other place. Several sesquiterpene lactones, phenolic acid and other organic acids have been identified as responsible gents.

5. ***Parasitism**:* Host-parasitic plant interactions are mediated by secondary metabolites some of which are known for their allelopathic activity [31]. Thus parasitic stress would change the allelopathic properties of the host and an increased allocation of carbon skeletons into the secondary metabolites by host plants was reported for several species. when sunflower was infected by *Orobanche cernua* Loefl. a higher accumulation of coumarins and greater root exudation in resistant genotypes was recorded as compared to susceptible ones [32]. Plants when invaded by herbivores activate defense responses that consist of several mechanisms including increase in the concentration of secondary metabolites, many of which are phenolic compounds [33]. Phenolic compounds, on the other hand, are among those very often implicated as allelochemicals [34]. Higher resistance of tomato (*Lycopersicon esculentum* Mill.) cv. Slonka to carmine spider mite (*Tetranyhus cinnabarinus*) among others is also attributed to increased concentration of free phenolics.

D. ALLELOPATHY IN RELATION TO AGRICULTURAL ECOSYSTEM

1. ***Nutrient Uptake:*** Upon release, the allelochemicals affect the availability and uptake status of nutrients for plants in vicinity of source plant. Plants may release allelochemicals under stress conditions to facilitate their nutrition by altering nutrient forms, microbial populations and activities, availability modes and uptake channels. 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. Under nutrient deficiency, plants use to release allelochemicals in interaction with soil microbes [35]. They facilitate nutrient

solublization and release from complex forms. Under low phosphorus (P) levels plant release phosphatases, which improve P availability through hydrolysis [36]. Phenolics improve release and uptake of P, Iron (Fe) and other nutrients under their less availability. Citric acid and oxalic acid have been reported for nutrients uptake promotion under deficient conditions. They improved the uptake of P, K, Mg and Fe and resultantly root and shoot growth of plants in stress conditions [37]. Allelochemicals act to bind certain nutrient radicals in organic complexes forming chelates. They hold the nutrients and improve their stay in rhizosphere to minimize losses. They make nutrients more mobile and thus improve their uptake in plant body. It also helps to avoid toxicity of metal ions. The role of cucumber-exuded allelochemicals on the uptake of several nutrients (N,P, S, K, Ca, Mg) by intact seedlings of cucumber was evaluated , while cinnamic acid inhibited the uptake of nearly all nutrients [38] . It was 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 [37] . Improvement in exudation of allelochemicals, coupled with increased proliferation of the root system, enhances the ability of plants to acquire more Pi under conditions of Pi deficiency [39].

2. ***Improving Nitrogen Use Efficiency:*** Biological nitrification inhibition (BNI), nutrient acquisition through solublization, nutrient uptake and nutrient retention are strongly influenced by allelochemicals to play key role in crop nutrient management. Allelochemicals are involved in BNI, which reduces the nitrogen losses and improves nitrogen use efficiency (NUE). Crop water extracts have shown good BNI potential. Sorghum is on the top regarding this activity. Sorgoleon helps BNI by reducing *Nitrosomonas* and *Nitrobacter* (nitrifying bacteria) populations. Methyl-p-coumarate and methyl ferulate are two potential phenolics involved in BNI. Some varieties of sunflower and rice have also shown potential for this phenomenon. Hence, it is a key process for nitrogen regulation, availability and uptake driven by allelochemicals. Allelochemicals such as methyl 3-(4-hydroxyphenyl) propionate, linoleic acid, a-linolenic acid, methyl-p-coumarate, and methyl ferulate are also responsible for BNI.
3. ***Weed Management:*** Seedlings and different tissues of various plants possess allelopathic potential or weed- suppressing activity such as wheat, barley, rice, and canola. It was suggested that genetically improving crops with allelopathic potential and the allelopathy can play an important role in future management [40]. When applied at high concentrations, these allelochemicals interfere with the cell division, hormone

biosynthesis, and mineral uptake and transport, membrane permeability, stomatal oscillations, photosynthesis, respiration, protein metabolism and plant water relations which may cause substantial growth reduction. This phytotoxic activity of allelochemicals is responsible for growth suppression of weeds. Allelopathic water extracts have reduced herbicide doses by half of standard giving effective control over noxious weeds of major crops. Sorghum, sunflower, eucalyptus, sesame, brassica and rice water extracts have effective results in controlling weeds by reducing herbicide dose up to half of recommended one. In this way allelochemicals can control weeds to reduce weed-crop competition and to enhance crop growth and yield.

4. ***Cover Crops and Residue Mulches****:* For weed management in ecological sustainable agriculture, the use of phytotoxic mulches and cover crops is very effective. Reports of 98 % reduction in populations of *Pratylenchus penetrans*, the root-lesion nematodes, when *T. erecta* was grown in rotation with tomato *(L. esculentum)* [41] . Siimilar results were obtained when *T. erecta* was cultivated as a cover crop and incorporated residues into the soil before sowing of *Colocastia esculenta* [42]. Similar results were obtained when *T. erecta* was intercropped with soybean [43]. 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 [44].
5. ***Intercropping***: The mixing or intercropping of plant species with different growth habits and morphology e.g. melons + plantains provides effective weed control [45]. Generally, members of family Asteraceae and leguminous plants are known to exhibit antagonistic behaviour to nematodes. Ranunculus species, which cause severe infestation and suppression of wheat in mid-hill conditions of Himachal Pradesh, India, could be effectively controlled by planting linseed with wheat. Various species of the genus *Tagetes* are especially planted as intercrops or in rotation with other crops to control nematodes [46].
6. ***Crop Rotation****:* In order to reduce nematode population, some farmers rotate soybeans with maize (*Zea mays*) and wheat (*Triticum aestivum*). 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 [47]. Generally, members of family Asteraceae and leguminous plants are known to exhibit antagonistic behaviour to nematodes.

E. ALLELOPATHY IN RELATION TO PEST MANAGEMENT

1. ***Nematode Management:*** Plants with allelochemical properties were found also effective against different nematode species and their fresh or dried parts and their natural products to control these pests under field conditions. These may be considered as a source of natural nematicides. 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 [48]. Neem (*Azadirachta indica*) seed kernel is more toxic followed by its seed and seed coat. Addition of decomposed *A. indica* seed, seed kernel and seed coat drastically reduced the root-knot nematode population in soil and increased the yield of mungbean. *A. indica* and *C. procera* exhibited the highest reductions in number of galls, egg masses and reproduction factor of the nematode [49].
2. ***Insect Pest Management***: Allelopathic plants may also be used for suppressing insect pests in field and horticultural crops. Natural compounds have been identified as potent weapons against certain insect pests. These compounds also have the advantages of biodegradation, economic affordability, environmental safety and easy handling. Many plants have natural defense mechanism against insect pests. They utilize the arsenal of secondary metabolites for this purpose. Neem (*Azadirachta indica*) produces allelochemicals, azadrachtin, salannin and nimbin. They inhibit or reduce the growth of different insect-pests. They inhibit green cicadellid (*Jacobiasca lybica*) and whitefly (*Bemisia tabaci*). Similarly neem oil shows antifeedant action against strawberry aphids (*Chaetosiphon fragaefolii*). Some phenolics restrict wheat midge (*Sitodiplosis mosellana*). Some indigenous plants like bakain (*Melia azdarach*), habulas (*Myrtus communis*), mint (*Mentha longifolia*), harmal (*Pegnum harmala*) and lemon grass (*Cymbopogon citrates)* produce certain allelochemicals, which act as insecticide against rice weevil (*Sitophilus oryzae*). Secondary metabolites from olive (*Olea europea*), tea (*Thea chinensis*), bhang (*Canabis sativa*), elephanta (*Elephantia sp*.), garlic (*Allium sativum)*, black pepper (*Piper nigrum*) and red chillies (*Capsicum annum*) were effective against chickpea beetle (*Callosobruchus chinensis*) [50]. Volatile oils from eucalyptus (*Eucalyptus globulus*) were effective against rice moth (*Corcyra cephalonica*). Allelopathic water extracts of sorghum, mustard, mulberry and sunflower were very effective in controlling aphids and sucking insects of *Brassica spp*. Water extracts of Tomato (*Lycopersicon esculentum*) controlled flower thrip (*Taeniothrips sjostedti*) and pod borer (*Heliothis armigera*) efficiently [51]. Insect pest control through allelochemicals

is a naturally driven phenomenon. It could be a beneficial tool to control harmful insects organically. Insect pest resistance against synthetic insecticides can be reduced in this manner. 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 [52].

3. ***Management of Fungal Pathogen***: Several plant families like Acanthaceae, Amranthaceae, Chenopodiacea, Brassicaceae and Magnoliaceae are known for their antifungal properties [53]. Recently, it was 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 blight disease of bell pepper [54]. Several allelochemicals have been identified as potent antifungal agents. It was also 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.* Some of the flavones and cyclohexenones from rice have suppressing potential against spore formation of *Rhizoctonia solani* and *Pyricularia oryzae*. These allelochemicals are suggested as the part of plant defense mechanism against biotic stresses [55]. Leaf water extracts of jimson weed (*Datura stramonium*) are effective for rust control in wheat. Aqueous extracts of onion, garlic, parthenium and *Calotropis procera* have inhibitory effects on different fungal strains [56]. Leaf water extracts of neem, eucalyptus and Tulsi (*Ocimum sanctum* L.) can cause up to 50% reduction in growth of a fungus *Fusarium solani* [57]. Antifungal activity of allelochemicals is well reported but they also are effective against other pathogens causing severe diseases in plant.
4. ***Management of Bacterial Pathogen****:* 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 [58]. Momilactone A and B, the two potent allelochemicals of rice, are known to exhibit antibacterial activity [59].

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RECENT RESEARCH TRENDS AND ADVANCEMENTS

- The allelopathic effect of *Artemisia princeps* L. and *Launae sonchoids* L. from Taif Governorate, Saudi Arabia was measured in terms of germination rate and radicle length of a bread wheat variety ‘Ariana’ (*Triticum aestivum* L.). The allelopathy of *A. princeps* and *L. sonchoids* varied with the concentration and type of species [60].

- Allelopathic effects of five biocontrol agents viz., *Trichoderma longibrachiatum, Trichoderma asperellum, Bacillus subtilis, Bacillus cereus* and *Pseudomonas flourescens* in the control of six fungal pathogens associated with the tuber rot of *Dioscorea caryensis* were evaluated. The establishment of distinct zone of inhibition, especially by bacterial antagonists attests to the fact that they produced allochemical substances [61].
- The comparative allelopathic effects of leaf extracts of three species viz., garlic mustard (*Alliaria petiolata*), amur honeysuckle (*Lonicera maackii*) and lesser celandine (*Ranunculus ficaria*) on germination and reproduction of *Arabidopsis thaliana* were investigated in a growth room. The results showed differential allelopathic effects of these invasive species, which varied with test species and experimental conditions [62].
- *Cytisus scoparius*, a nitrogen-fixing, putatively allelopathic shrub invading the western US on which allelopathy plays a critical role in the depressive effect of *Cytisus* on the key native Douglasfir, both directly on tree growth and indirectly via effects on its ectomycorrhizal fungi [63].
- The comparative allelopathic potential of *Fumaria indica* L. and *Polygonum plebejum* L. leaf, stem, root, fruit and whole plant aqueous extracts was evaluated on germination and seedling growth of *Triticum aestivum L., Cicer arietinum L., Lens culinaris* Medic. and *Brasica napus* L. in laboratory condition. Chromatographic analysis revealed presence of six phytotoxins, viz., ferulic acid, m-coumaric, syringic acid, caffeic acid, gallic acid and 4- Hydroxy-3-Methoxybenzoic acid in aqueous leaf (1:10) fraction of *F. indica*. Ferulic acid, syringic acid, caffeic acid and vanillic acid were recorded in aqueous leaf extract of *P. plebejum* [64].
- Allelopathic potential of invasive species giant goldenrod *(Solidago gigantea* Ait.) on germination and initial growth crops (carrot, barley, coriander) and weed species velvetleaf (*Abutilon theophrasti* Med.) and redroot pigweed (*Amaranthus retroflexus* L.) was determined [65].
- Inhibitory effect of aqueous extracts of *Lantana camara* L. (a globally recognized invasive alien weed) on garden pea (*Pisum sativum* L.) was recognized. The inhibitory effect was much pronounced in radical and plumule development [66].
- Milk thistle (*Silybum marianum*) is common weed species in Australian cropping rotation. Allelopathic potentiality of milk thistle on different crops has also been documented [67].

- Allelopathic effects of *Eclipta alba* weed on seed germination and seedling growth of weed plants (*Cassia tora* L., *Cassia sophera* L.) and crop plants (*Phaseolus aureus* L., *Oryza sativa* L.) were investigated [68].
- Production of allelopathic chemicals by the toxic dinoflagellate *Alexandrium fundyense* is one suggested mechanism by which this relatively slow grower outcompetes other phytoplankton, particularly diatoms [69].
- The existence of inhibitory effect of leaf extracts and leaf leachates noxious weed *Eupatorium odoratum* using fully viable seeds of mung bean (*Vigna radiata*) as the bioassay material was evaluated [70].
- Allelopathic effect of Purple nutsedge (*Cyperus rotundus* L.) on seed germination, germination rate and seedling growth characters of tomato (*Lycopersicum esculentum*) was investigated [71].
- The allelopathic effects of extract of stem, root, leaf and inflorescence of *Chrozophora tinctoria* A. Juss was reported and a very strong allelopathic properties was studied on *Cicer arietinum* L. (Chana) during seed germination [72].
- The effect of leaf leachates of *Parthenium*, *Hyptis* and *Tridax* on the germination of black gram (*Vigna mungo* L,) [73].
- Inoculation with VAM significantly reduced the negative impact of allelopathy stress caused by *Melia azedarach* leaf extract on maize and by *Syzygium cumini* on cheackpea (*Cicer arietinum* L.). Amelioration of the negative impact of allelopathy and benefit to the host by rhizosphere microbes were also attributed to ectomycorrhizal fungi [74].

FUTURISTIC CONSIDERATION

Allelopathy is a novel approach offering multiple solutions to conundrum of decreasing food availability under rising global population. With vast application in weed management, it can replace hazardous chemical and mechanical approaches being used in crop production. Development of crop cultivars with more allelopathic potential may help in better resistance to biotic and abiotic stresses. Allelopathic water extracts offer better alternative for this purpose due to being cost-effective, eco-friendly, easy to use, efficient and safe. Research efforts should be focused on screening more allelopathic plants, to search potential cultivars producing more allelochemicals and to identify promotory allelochemicals in plant water extracts. It would be a luminous direction to proceed in order to achieve agricultural sustainability, environmental safety, food security, resource conservation and economic stability.

Allelopathic interactions in soil and environments depend greatly on the turnover rate of the allelochemicals in the soil rhizosphere and their interaction with clay, organic matters and other factors that change the physicochemical and biotic characteristics of the soil. Recent research by Blum and his laboratory associates has shown that soil texture, soil pH, organic carbon and other available nitrogen sources are important in influencing uptake of allelochemicals and their ability to persist in the presence of soil microbes. Soil moisture dynamics can also influence the phytotoxicity of the allelochemicals. In recent studies, the data suggested that enhanced evapotranspiration and lower soil moisture will also result in decreased plant phytotoxicity of the allelochemicals in the soil solution [75].

Unfortunately, traditional breeding methods have not been generally employed to produce highly allelopathic crops with good yield potential [76]. Recent discussions of the use of genetic engineering to enhance allelopathic traists indicate that this is not a simple task due to multigenic nature of allelochemicals biosynthesis. Genes involved in production of allelochemicals are not being elucidated using a variety of molecular techniques. A reexamination of the older germplasm may actually assist todays breeders in developing crops that are inherently more weed suppressive, as the tendency towards reduced herbicide usage continues.

New frontiers will focus on its ways to capitalize on allelopathy to enhance crop production and develop a more sustainable agriculture, including weed and pest control through crop rotation, residue management and a variety of approaches in biocontrol. The others goals are to adapt allelochemicals as herbicides, pesticides, growth stimulants, modify crop genomes to manipulate allelochemical production and better chemical communication that generate association between plants and microbes.

CONCLUSION

Increasing global population is a threat to food security and agricultural sustainability. Allelopathy has emerged as a pragmatic approach to solve multiple issues in modern agriculture. Multiple approaches including crop rotations, cover crops, intercropping, mulching, crop residue incorporation and water extracts application are being used to explore allelopathy for pest management, stress mitigation, and growth enhancement in crop production. Allelopathy offers natural control of weeds, insect-pests and diseases. Biosynthesis of secondary metabolites at higher rates and their role in stress signaling provides excellent defense against abiotic stresses.

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. 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.

Much time and efforts have been spent on identifying novel secondary products isolated from higher plants, as phytochemicals with biological activity have had great utility as pharmaceuticals and pest management products. Furthermore, as rhizosphere and plant root ecology remain as areas relatively understudied in terms of allelopathic interaction, more attention to the novel allelochemicals contained in the root exudates and their interactions with the soil microorganisms, weed propagules and microbiota would be helpful in advancing our understanding of plant interactions. A new challenge that exists for the plant scientists is to generate additional informations on the allelochemical mechanism of release, selectivity and persistence in the rhizosphere, mode of action and genetic regulation. In this manner, we can further protect plant biodiversity and enhance weed management strategies in a variety of ecosystems.

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