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Allelopathy for sustainable weed management

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Abstract
Allelopathy is biochemical interaction among plants, stimulatory as well as inhibitory. Allelochemicals released by crop plants are the subset of secondary metabolites not required for metabolism (growth and development) of the allelopathic organism. These enter the environment from plants in a number of ways, such as plant degradation, volatilization, leaching from plant leaves, and from root exudation. Allelopathy in the crop lands bears a great significance. The allelopathic effects of the crops can be summarized as follows: (a) It affects the growth, productivity and yield of other crops, (b) It may affect the same crop growing in monocultures or grown in succession, (c) Crop allelopathy can be exploited selectively to suppress the weeds through various manipulations.

Keywords: Allelopathy, Allelochemicals, Crop, Sustainability, Weed management

Introduction

The term allelopathy is from the Greek-derived compounds allelon 'of each other' and pathos 'to suffer' and means the injurious effect of one organism upon the other. The term 'allelopathy' was first used in 1937 by Austrian scientist Hans Molisch (Willis, 2010) [36]. Allelopathy is any direct or indirect effect by one plant, including micro-organisms, on another through production of chemical compounds that escapes into the environment to influence the growth and development of neighbouring plants (Bahadur *et al*., 2015) [1]. Allelopathy is described as the beneficial and deleterious biochemical interaction between plants and microorganisms. The bio-chemicals that are released by plant parts, which have inhibitory (negative allelopathy) or stimulatory (positive allelopathy), effect on each other. The allelochemicals are mostly secondary metabolites, which are produced as byproducts during different physiological processes in plants (Bhadoria, 2011) [3]. Important secondary metabolites identified as allelochemicals are phenolics, alkaloids, flavonoids, terpenoids, momilactone, hydroxamic acids, brassinosteroids, jasmonates, salicylates, glucosinolates, carbohydrates and amino acids (Jabran and Farooq, 2012) [13]. Allelopathy is existent in the natural ecosystem and it occurs widely in the natural plant communities.

Allelopathy is possibly a significant factor in maintaining the present balance among various plant communities. Allelochemicals inhibited the growth of some species at certain concentrations may stimulate growth of some or different species at lower concentration. Allelochemicals with negative allelopathic effects are an important part of plant defence against herbivory (i.e., animals eating plants as their primary food) (Stamp, 2003) [31]. Some allelochemicals are accumulated at various stages of growth while accumulation of some compounds depends upon time of day and season. Allelopathic inhibition is complex and can involve the interaction of different classes of chemicals, such as phenolic compounds, flavonoids, terpenoids, alkaloids, steroids, carbohydrates, and amino acids with mixtures of different compounds sometimes having a greater allelopathic effect than individual compounds alone. Allelopathy is characteristics of certain plants, algae, bacteria and fungi. Allelopathic interactions are an important factor in determining species distribution and abundance within plant communities.

Types of Allelopathy

***Alloallelopathy*:** It is inter- specific chemical co-action. Allelochemicals are toxic to other species, other than which release it. E.g. maize (*Zea mays*) is allelopathic for *Chenopodium* and *Amaranthus*

***Autoallelopathy*:** It is intra-specific chemical co-action. Allelochemicals are toxic to same species from which they are released. E.g. wheat (*Triticum aestivum*), alfalfa (*Medicago sativa*), cowpea (*Vigna unguiculata*), rice (*Oryza sativa*), and apple (*Malus domestica*)

***True allelopathy*:** It refers to the release into the environment of chemical compound that are toxic the form they are produced by the plant.

***Functional allelopathy*:** It refers to the release into the environment of chemical compound that are toxic after chemical modification by microorganisms.

***Concurrent/ direct allelopathy*:** It refers to the instantaneous direct effect of released toxin from the living plant to another growing in vicinity. It is also called 'living plant effect'. E.g. sorghum (*Sorghum bicolor*) suppresses many weeds growing in the vicinity.

***Residual allelopathy*:** It is the effect obtained on the plants growing in succession from the decaying residues, leaf litters, stem, and roots of the previous plants. E.g. sorghum is allelopathic to wheat and *Phalaris minor* and sweet potato (*Ipomoea batatas*) to cowpea.

Allelopathic interaction

Allelopathic interactions between crops and weeds in agro ecosystems can be of four types as describes below:

Weed on crops

Weeds	Effect on	Cause/source	Effect
Quack grass (*Agropyron repens*)	Maize, potato (*Solanum tuberosum*)	Ethylene produced by the activity of microorganism on rhizomes	Decrease uptake of manures (N, K) followed by yield reduction
Wild oat (*Avena fatua*)	Wheat, barley (*Hordeum vulgare*), oat (*Avena sativa*)	Root exudates	Growth of leaves and roots of wheat
Bermuda grass (*Cynodon dactylon*)	Barley	Decayed grass residues	Seed germination, root and op growth
Yellow Nut sedge (*Cyperus esculentus*)	Grain crops, soybean (*Glycine max*), orchard	Vanillic acid, Hydrobenzoic acid in sedge extract	Root and shoot growth of maize and soybean
Johnson grass (*Sorghum halepense*)	Sugarcane (*Saccharum officinarum*), maize, soybean	Root exudates and decaying residues	Root and shoot growth
Gaint foxtail (*Setaria viridis*)	Maize	Roots and leachates of dead roots	Yield reduction
Cogon grass (*Impereta cylindrical*)	Tomato (*Solanum lycopersicum*) and cucumber (*Cucumis sativus*)	Root exudates	Inhibit growth
Field bind weed (*Convolvulus arvensis*), Canada Thistle (*Cirsium arvense*)	Cabbage (*Brassica oleracea* var. *capitata*), carrot (*Daucus carota* subsp. *sativus*), tomato	Root exudates	Seedling growth

Weed on another weed

Weeds	Effect on	Cause/source	Effect
Cogon grass	Button weed (*Borreria hispada*)	Exudates of inhibitory substances through rhizomes	Inhibits the emergence and growth
Johnson grass	Giant foxtail (*Setaria faberi*), Large crabgrass (*D. sanguinlis*)	Living and decaying rhizomes and leaves	Inhibit growth

Crop on weed

Recently some rice genotypes have already been identified which have allelopathic effects on weeds. Allelopathic effect of crops and weeds on other weeds may be applied to develop natural herbicide.

Crops	Effect on	Cause/source	Effect
Coffee (*Coffea Arabica*)	Spiny amaranth (*Amaranthus spinosus*)	1,3,7-trimethylxanthin	Inhibit germination
Maize	Associated weeds	Increased Catalase and Peroxidase activity by root extract	Inhibit growth
Oat, wheat, pea (*Setaria faberi*)	Lams quarter (*Chenopodium album*)	Root exudates	Suppress growth

Crop on another crop

Volatile compounds from the top of soybean, chickpea and beans reduced the uptake of P by corn plants. Allelopathic effects of pearl millet on the germination and seedling growth of wheat, barley, lentil etc. and aqueous root extract of soybean on rape and mustard.

Need of allelopathy in weed control

In agro-ecosystems, weeds compete with crop plants for resources, interfere in crop handling, reduce crop yield, deteriorate their quality, and thus result in huge financial losses. In light of these characteristics of weeds and their hazards, it becomes imperative to control them. Several techniques (e.g. mechanical and chemicals) are used for weed control. These techniques attempt to achieve a balance between cost of control and crop yield loss. Mechanical methods, such as hand weeding require enormous labour and time input. Now days, chemical method provides an effective strategy for weed control. Since their discovery in the 1950s, synthetic herbicides have developed as a major tool for weed management (Sodaeizadeh and Hosseini, 2012) [30]. Herbicides have helped farmers to increase yields while reducing labour. Indeed, without herbicides, labour would be a major cost of crop production in developed countries. However, the indiscriminate use of herbicides to control weeds has resulted in very serious ecological and environmental problems like herbicide resistance, shift in weed flora, environmental pollution and health hazards due to toxic residues of herbicide in soil, water and food chain. The negative impact of commercial herbicides makes it desirable to search for other alternative weed management options (Nirmal Kumar *et al*, 2010**)** [20], and allelopathy seems to be one of the options (Tesio and Ferrero, 2010) [32]. Momilactone B inhibits the growth of typical rice weeds like *Echinochloa crusgalli* and *E. colonum* at concentrations greater than 1 µmol/L (Kato-Noguchi *et al*, 2008) [14].

Allelopathic compounds

The secondary products could be classified in the following categories but it is impossible to enumerate each and every chemical identified as an allelochemicals. Rice (1984) [26]; Putnam and Tang (1986) [23] divided allelochemicals into various major chemical groups:

1. Simple water-soluble organic acids
2. Simple unsaturated lactones
3. Long-chain fatty acids and polyacetylenes
4. Simple phenols
5. Naphthoquinone, anthroquinones and complex quinones
6. Flavonoids
7. Benzoic acid and derivates
8. Steroids
9. Cinnamic acid and derivates
10. Tannins
11. Amino acids and polypetides
12. Coumarins
13. Sulphides and glucosides
14. Purines and nucleotides
15. Alkaloids and cyanohydrins
16. Thiocyanates
17. Lactones
18. Actogenins

Phenolic acid

Species which have been noted to produce phenolic acids include: rice, wheat, mango (*Mangifera indica*) and spotted knapweed (*Centaurea stoebe*) (El-Rokiek *et al*., 2010) [8]. Many species, such as rice, contain multiple phenolic compounds along with other allelopathic compounds.

Phenolic acids could function through increasing cell membrane permeability thus affecting ion transport, disruption of cell division and malformed cellular structures in plants reduced respiration and reduced photosynthetic rates, due to decreased photosynthetic products such as chlorophyll. Altered plant enzymatic functions, inhibited protein synthesis and inactivated plant hormones as inhibitory mechanisms from these allelochemicals (Li *et al*. 2010) [17].

Each mechanism of plant inhibition can lead to the reduced growth and/or death of an exposed plant; however, it is likely multiple functions within a plant are being affected simultaneously due to the mixture of allelochemicals released from a plant species.

Coumarins

Coumarin compounds are found in a range of plant species, particularly from the Apiaceae, Asteraceae and Fabaceae families (Razavi, 2011) [24]. Coumarins and their derivatives have been identified in plants such as lettuce (*Lactuca sativa*), wild oat, sweet vernalgrass (*Anthoxanthum odoratum*) and a number of other species (Razavi, 2011) [24].

Like many other allelochemicals, coumarins have been found to inhibit plant growth by reduced seedling germination and reduced root and shoot growth, likely with interference in photosynthesis, respiration, nutrient uptake and metabolism (Razavi *et al*., 2010) [25]. Block mitosis in onion by forming multinucleate cells.

Terpenoids

Terpenoids as herbicides and reported that these are potent growth inhibitors than as germination inhibitors. The sesquiterpenoids are less phytotoxic than sesquiterpenoid lactones. Strigol application results in inhibit germination and death of a large number of striga seeds. The disappearance of phytotoxic sesquiterpenoid lactone, isolactolactone in the soil was complete within 90 days indicating no residue problem in the soil.

Scopulatens

It inhibits the process of photosynthesis with significant effect on respiration.

Mode of allelochemicals release

Mode of transfer may play a great role in its toxicity and persistence. The donor plant which release these chemicals, generally store in plant cells in a bound form, such as water soluble glucosids, polymers including tannins, lignin and salts. It has been suggested that upon cleavage by plant enzyme or environmental stress, the toxic chemicals are released into the environment from special glands on the stems or leaves.

First the terpenoids such as α-pinene, β-pinene, cineole and camphor are released through volatilization in the environment, which is noticeable under drought conditions. Water borne phenolics and alkaloidsz are then moved out by rainfall through leaching. Scopoletin and hydroquinones may be released to the surrounding soil through root exudates.

The pool of allelochemicals in soil is replenished by volatilization, leachates, root exudates and decomposition of crop residues and at the same time, it is exhausted through absorption by plants, decomposition by micro-organisms and carried away by wind and water.

In higher plants allelochemicals are released from through:-

- Vapour- from roots and leaf (from stomata)
- Stem or leaf leachate
- Root exudates
- Decomposition of plant residues
- Seed extract

Volatilization

Allelopathic tree release a chemical in gas form through small openings in the leaves. Other plants absorb the toxic chemical and die. Several terpenoids transfer, higher plants produce a variety of terpenoids and monoterpenoids as major components of essential oils of plants. From the plants rich in such compounds, these may be released continuously to the atmosphere, this process enhanced in hot weather, observed in arid region. The genera, which release volatiles, are parthenium and eucalyptus.

Leaching

Leaching is the removal of water-soluble substances from plants by the action of aqueous solvents such rain, dew, mist and fog. All plants lose leaves. Some plants store protective chemicals in the leaves they drop. When the leaves fall to the ground, they decompose and give off chemicals that protect the plant. Fall foliage tends to release more potent allelochemicals than fresh, spring foliage. Water-soluble phytotoxins may be leached from roots or above ground plant parts or they may be actively exuded from rhizomes or cut leaves.

All plant seems to be leachable, although the degree depends on type of tissue, stage of maturity and type, amount and duration of precipitation. Toxins bearing leachats are important in crop-weed association. Rainfall leachates from the leaves of *Camelina* weed adversely affected the growth of linseed plants. *Camelina* leaf washing contained toxic chemicals including benzylamine, which retarded the seedling growth of linseed.

Root exudates

Root exudates are those substances released from intact plants roots into atmosphere. Although, their volume is small accounting about 2-12% of the total gross photosynthates. In some cases, (a) they provide plants with immunity against phytopathogens (b) Sustain the life activity of microflora in the rhizoshere (c) Sustain the life of mycorrhiza to improve mineral nutrition in the plants. The root exudates of wheat, barley, oat, carrot and radish contain inhibitors. Exudates vary according to the plant species and age, temperature, light, plant nutrition, microorganism activity around the roots and nature of the medium supporting the roots. Exudates are usually various phenolic compounds (e.g. coumarins) that tend to inhibit development.

Decomposition of residues

Decomposition provides the largest quantity of allelochemicals that may be add to the rhizosphere. The important variable in this process are (a) nature of plant residues (b) soil type (c) condition of decomposition. In general, more sever and persistent toxicity has been reported from cold and wet soils. The soil is a dynamic system, where activity of substances released can be quite transitory, as they are subjected to destruction, soil absorption, inactivation, and transformation by soil micro flora. It is estimated that up to 30% of the plants dry matter entering the decay cycle was lignin which is formed from alcohols and acids with the skeleton of phenylpropane, which are known inhibitors.

Mode of action of allelopathy

Affect many aspects of plant ecology, including

- Occurrence
- Growth
- Plant succession
- The structure of plant communities
- Dominance
- Diversity and plant productivity

The mode of action of a chemical can broadly be divided into a direct and an indirect action (Rizvi *et al*., 1992) [28]. Effects through the alternation of soil properties, nutritional status and an altered population or activity of microorganisms and nematodes represent the indirect action. The direct action involves the biochemical/physiological effects of allelochemicals on various important processes of plant growth and metabolism. Processes influenced by allelochemicals involve:

- ***Mineral uptake*****:** Allelochemicals can alter the rate at which ions are absorbed by plants. A reduction in both macro- and micronutrients are encountered in the presence of phenolic acids (Rice, 1984) [26]
- ***Cytology and ultrastructure*****:** A variety of allelochemicals have been shown to inhibit mitosis in plant roots (Rice, 1984) [26]
- ***Phytohormones and balance*****:** The plant growth hormones indoleacetic acid (IAA) and gibberellins (GA) regulate cell enlargement in plants. IAA is present in both active and inactive forms, and is inactivated by IAA-oxidase. IAA- oxidase is inhibited by various allelochemicals (Rice, 1984) [26], other inhibitors block GA-induced extension growth.
- ***Membranes and membrane permeability*****:** Many biological compounds exert their action through changes in permeability of membranes. Exudation of compounds from roots on root slices have been used as an index of permeability because plant membranes are difficult to study (Harper and Balke, 1981) [11].
- ***Photosynthesis*****:** Photosynthetic inhibitors may be electron inhibitors or uncouplers, energy-transfer inhibitors electron acceptors or a combination of the above (Patterson, 1981) [21].
- ***Respiration*****:** Allelochemicals can stimulate or inhibit respiration, both of which can be harmful to the energy-producing process (Rice, 1984) [26].
- ***Protein synthesis*****:** Studies utilizing radio-labelled C^{14} sugars or amino acids, and traced incorporation of the label into protein, found that allelochemicals inhibit protein synthesis (Rice, 1984) [26].
- ***Specific enzyme activity*****:** Rice (1984) [26] reported on a number of allelochemicals that inhibit the function of enzymes in the plant.
- Water relations (Rice, 1984) [26].
- Genetic material (Rice, 1984) [26].
- Under natural conditions the action of allelochemicals seems to revolve round a fine-tuned regulatory process in which many such compounds may act together on one or more of the above processes (Rizvi *et al*., 1992) [28].
- Inhibition of porphyrin synthesis.
- Corking and clogging of xylem elements and stem conductance of water and internal water relations.

Indication of allelopathy

- ***Autotoxicity*****:** Allelopathy occurring among individuals of the same species is termed autotoxicity. Autotoxicity is known for example in alfalfa, clovers (*Trifolium* spp.) and asparagus (*Asparagus officinalis*).
- ***Residue effect*****:** Inhibitory effects on germination and establishments of crops caused by residues of either crops or weeds have led to investigation of the release of toxic compounds from such residues. For example, the allelopathic interference of both living plant and of plant residues of the highly aggressive weed *Elytrigia repens*, quack grass, has been strongly indicated (Weston and Putnam, 1985) [34].
- ***Hazardous weeds*****:** In cases where the success of a plant, typically a weed, cannot be explained by the competitive ability, allelopathy has been suspected to play a role. Investigations of such observations have established or

strongly indicated an allelopathic activity of weeds, e.g. wild oat, quack grass, Canada thistle and common chickweed (*Stellaria media*) (Putnam and Weston 1986; Seigler, 1996; Inderjit and Dakshini, 1998) [22, 29, 12]. Reduced weed problems within a crop may indicate that the seed germination or development of weedy species is inhibited by the release of allelochemicals from the crop. This has for example been reported in cultivated fields of some Brassica species, where no herbicides were applied (Weston, 1996) [33]. Also in fields of cultivated sunflower, the weed biomass was equally reduced in plots with or without herbicide treatments (Leather, 1983) [16].

- ***Halo zone and fairy rings*****:** The observation of a weed-free zone around some up-land rice cultivars in a germplasm collection growing in a weed infested field has initiated an extensive research programme with the aim of finding allelopathic rice cultivars for weed control. Weed free zones (80-90% weed control) with a radius of up to 20 cm has been observed (Dilday *et al*., 1994) [7]. Fairy rings" has also been observed both in fields with wild and cultivated sunflower (*Helianthus rigidus* and *H. annuus*, respectively). These rings are characterised by a decrease in the number of plants, and inflorescences as well as smaller size of individual plants in the middle of the ring (Rice, 1984) [26]. Distinct zones with sparse or without vegetation has been observed around some shrubs in chaparrals (Rice 1984; Williamson, 1990) [26, 35] and under a number of trees (reviewed by Kohli, 1998) [15]. This includes the observation of the inhibition of adjoining plants by black walnut (*Juglans nigra*) back in 1881 by Stickney Hoy (Rice, 1984) [26].

- ***Replanting and agroforestry problems*****:** Allelopathy has been investigated as an explanation of the difficulties of replanting fruit trees in orchards – for example apple, citrus (*Citrus* spp.) and peach (*Prunus persica*) (Rice 1984; Putnam and Weston, 1986) [26, 22]. The role of allelopathy in the interaction between forest trees and their understory species is also of current interests. For example, inadequate natural regeneration and reduced growth of planted seedlings has been attributed to the release of allelochemicals by herbaceous vegetation. Especially ericaceous shrubs have been investigated for their effect on seed germination, rooting ability and seedling growth of conifers (Mallik 1998; Pellisier and Souto, 1999) [18]

- ***Pure stand*****:** An example frequently referred to, is the formation of pure stands of black mustard (*Brassica nigra*), after invading annual grasslands of coastal California. In these pure stands of *B. nigra*, other plant species could not successfully invade (Bell and Muller, 1973) [2].

- ***Minor changes*****:** In other cases, the effect of allelopathic activity may not be observed immediately if the development of visual symptoms is slow (Putnam and Tang, 1986) [23]. Interactions may be caused by marginal but persistent presence of allelochemicals. This can result in changes in floristic diversity and in changes in the distribution patterns of some plant species within a community (Chaves and Escudero 1997; Gentle and Duggin, 1997) [6, 10]. A reduction in the number of the plant species sensitive to allelochemicals might not be noticed at short term.

Toxicity determining factors

Several factors determine their toxicity such as concentration, flux rate, age and metabolic state of plant and prevailing climatic and environmental conditions. Their amount and production varies in quality and quantity with age, cultivar, plant organ, and time of the year. Allelopathic interactions in soil environments depend greatly on the turnover rate of allelochemicals in the soil rhizosphere and their interaction with clay, organic matter and other factors which change the physico-chemical and biotic characteristics of the soil (Blum and Shafer, 1988) [5]. Blum (2002) [4] suggested that enhanced evapotranspiration and lower soil moisture resulted in decreased plant phytotoxicity of allelochemicals in the soil solution.

The soil is important in allelopathic interactions. The level of toxins in the soil is affected by soil types, drainage, aeration, temperature, and microbial activity. For example, clay soils drain poorly, and toxins do not leach readily. By contrast, coarse, well-drained, sandy soils tend to maximize leaching. In one study (Fisher, 1978) [9], juglone from black walnut damaged and sometimes killed red and white pine on wet sites, but on dry sites juglone had little effect. Toxin-sensitive plants may be at higher risk when planted in heavy soils.

Role of allelopathy in sustainable weed management

Allelopathy could be used to increase crop production, to reduce crop production expenses and to diminish the current reliance on synthetic agrochemicals that degrade the environmental quality. Allelopathic substances, if present in crop varieties, may reduce the need for weed management, particularly herbicide use. Allelochemicals act through direct interference with physiological functions of 'receiver' such as seed germination, root growth, shoot growth, stem growth, symbiotic effectiveness or act indirectly through additive or synergistic impact along with pathological infections, insect injury and/or environmental stress.

The use of allelopathy for controlling weeds could be either through directly utilizing natural allelopathic interactions, particularly of crop plants, or by using allelochemicals as natural herbicides. In the former case, a number of crop plants with allelopathic potential can be used as cover, smother, and green manure crops for managing weeds by making desired manipulations in the cultural practices and cropping patterns. These can be suitably rotated or intercropped with main crops to manage the target weeds (including parasitic ones) selectively. Even the crop mulch/ residues can also give desirable benefits. Caffeine derived from coffee showed considerable selectivity in inhibiting germination of *Amaranthus spinosus* at a concentration that has no effect on black gram.

Allelopathic potentiality of crop plants

Different crops such as beet (*Beta vulgaris* L.), lupin (*Lupinus lutens* L.), maize, wheat, oats and barley are known to have allelopathic effect on other crops (Rice, 1984) [26]. Different allelopathic compounds of some crops, important in weed management are presented in following table –

Crops	Allelochemicals	References
Rice	Phenolic acids	Rimando *et al*., 2001
Wheat	Hydroxamic acids	Niemeyer, 1988
Cucumber	Benzoic and Cinnamic acids	Yu and Matsui, 1994
Black mustard	Allyl isothiocyanate	Weston, 1996 [33]
Buck wheat (*Fagopyrium esculentum*)	Fatty acids	Weston, 1996 [33]
Clovers	Isoflavonoids	Weston, 1996 [33]
Oat	Phenolic acids and Scopoletin	Weston, 1996 [33]
Sorghum	Sorgoleone	Netzley and Butler, 1986

Conclusion

The growing demand for sustainable agricultural systems requires that researchers reevaluate current production methods and inputs. To ensure continued productivity and potentially reduce synthetic herbicide requirements, allelopathy has become a focal point for research in the agricultural community. Although, many questions have yet to be resolved, the utilization of allelochemicals for weed suppression remains a promising avenue for reducing herbicide usage. Whether through the development of natural herbicides from isolated allelochemicals or through the application of cover crops with allelopathic properties, allelopathy will most likely be a factor in providing sustainable systems in the future.

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