Allelopathy: The Interaction Between Plants

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History and Introduction
Knowingly or unknowingly the phenomenon of interaction between plants were studied since last 10,000 years as the cultivation of crop plants started. Theophrastus in his book 'Enquiry into Plant' pointed out that chickpea destroyed weed and it did not reinvigorate soil as other legumes did but rather exhausted it. Democritus earlier than Theophrastus reported the existence of natural plant products which can be used for weed control. Plinins in first century wrote about the existence of interaction between plants in his book 'Natural History'. The first scientific report on allelopathy comes from Japanese workers about 300 years ago. They found that water falling from the leaves of red pine (Pinus densiflora) was harmful to crops growing under the pine tree. DeCandolle (1832) also pointed out the existence of such interaction. He suggested that the soil sickness problem (the decline in yield of a crop if cultivated every year in the same field) is due to the deposition of chemicals exuded by the crops plant and rotation of crop alleviate the problem.

Stickney and Hoy in 1881 observed that vegetation under black walnut tree (Juglans nigra) was very sparse as compared to other tree species and crops also did not grow under or very near to it. They supposed that the main cause of this is due to the release of poisonous chemicals by root and leaves of this plant.

The term allelopathy was first coined by Molisch in 1937 to refer both the detrimental and the beneficial biochemical interactions between all types of plants including micro-organisms. The word allelopathy is derived from two Greek words allen and pathos. Allen means 'of each other' and pathos means 'suffer'. Considering the meaning of the word allelopathy, Rice (1974) included only direct and indirect harmful effects in allelopathy. Most organic chemicals show both inhibitory and stimulatory effects depending upon the concentration. So, Rice in 1984 changed his definition of 1974 in the second edition of his book and included beneficial effects also in allelopathy. The allelopathy is now defined as 'any direct or indirect harmful or beneficial effect by one plant including micro-organisms on another through production of chemical compounds that escape into the environment. This definition is still considered as correct definition. However, the term is generally referred to detrimental effects. Chemicals released by plant with allelopathic effects are known as allelochemicals. The allelochemicals released from the plant affect the plants of same species or other species. This paper mostly deals with the effects of chemicals released by one plant affecting other plants growing near it.

The term allelopathy is generally considered under the competition process of different organism found in same environment. In reality, the process of allelopathy is different from the process called as competition in ecology which also involves two organisms. The competition process involves the use of same environmental factors like water, minerals, food, light by different plants or organisms. In allelopathy such competition does not occur. The process known as interference between two organism covers the both processes competition and allelopathy.

Chemical Nature of Allelopathy
Chemicals of allelopathic nature are found in all plants tissue. If such chemical is released from the plant in the environment in sufficient amount to affect other plant or micro-organisms then it shows the allelopathic effect. Most of these chemicals are called as secondary metabolites, because of their sporadic nature and as they do not play role in basic metabolism of the organism. The secondary products are classified by Whittaker and Feeny in 1971 in five major categories: phenylpropane, acetogenins, terpenoids, steroids and alkaloids.

The allelochemicals may be released from plant tissue in a variety of ways: as root exudation, leaching, volatilisation and also by decomposition of plant residue (Putnam 1985). Plant roots release many compounds as root exudate. Some of the root exudates showing allelopathic effect are benzoic acid, cinnamic acid and phenolic acids. Many plants in and region release volatile substances. The plants...
of different genera like Artemisia, Salvia, Ocimum, Eucalyptus release volatile substances. The volatile compounds are mainly mono- and sesqui-terpenes. Vapour of these substances or these substances dissolved in water may be absorbed by neighbouring plants and they affect the growth and development of these plants.

The chemical compounds are also leached from the aerial parts of the plant by rain water. Such compounds include organic acids, sugars, aminoacids, pectic substances, gibberlic acids, terpenoides, alkaloides and phenolic compounds. Chemicals are also released directly from the plant residue after the death of the plant. Both the chemicals after direct release from plant tissue and the chemicals produced by enzymatic degradation of conjugates or polymers in plant tissue may have the allelopathic effects.

Fig. 1. Probable major biosynthetic pathways leading to production of the various categories of allelopathic agents. Numbers refers to the categories as described in the text (Rice 1984).

Rice (1984) classified allelochemicals into fourteen major categories:
1. Simple water soluble organic acids, straight chain alcohols, aliphatic aldehydes and ketons
2. Simple unsaturated lactones
3. Long chain fatty acid and polyacetylenes
4. Naphthoquinones, anthraquinones, and complex quinones
5. Simple phenols, benzoic acid and derivatives
6. Cinnamic acid derivatives
7. Coumarins
8. Flavonoids
9. Tannins
10. Terpenoides and steroids
11. Aminoacids and polypeptides
12. Alkaloides and cyanohydrins
13. Sulphides and glycosides
14. Purines and nucleotides
The probable metabolic pathways of these allelochemicals as suggested by KCE (1984) are shown in Fig. 1.

The main groups of compounds considered as allelopathic agent by Mandava (1985) are as follows.

1. **Aliphatic compounds**

   These are water soluble organic compounds like organic acids, alcohols, aldehydes, ketons etc. These compounds inhibit seed germination and plant growth. As these compounds are readily metabolised in soil so they are not the major source of allelopathic agent.

2. **Unsaturated lactones**

   Patulin, a lacton, is the most potent allelochemical. It inhibits germination of seeds completely in very low concentration at 10 µg.ml⁻¹ also (Rice 1984). Parascorbic acid extracted from the fruit of Sorbus aucuparia is inhibitory to seed germination and seedling growth. The compound protoanemone produced by several members of Ranunculacea is also inhibitory to seed germination and bacterial growth (Fig. 2).

3. **Fatty acids and lipids**

   Several fatty acids are known to be toxic and affect the growth of some plant species. It is found that unsaturated fatty acids are more toxic and generally the toxicity increase with an increase in double bonds.

4. **Cynogenic glycosides**

   Amygdalin (found in the seed of Sorghum bicolor) and dhurrin (in Johnsongrass, Sorghum haleperose) are known to be allelopathic. The enzymes found in seedlings of these plants hydrolyse the glycoside to glucose, HCN and p-hydroxybenzylaldehyde. HCN and benzylaldehyde are inhibitory to the growth of seedlings (Abdul-Wahab & Rice 1967). Many species of Rosaceae contain large amounts of cynogenic glycosides. The HCN released from these glycosides is exuded out and it inhibit the germination. (Fig. 3).

5. **Terpenoids**

   Terpenoids are the chemicals made of five carbon units of isoprene or isopentane units linked together in various ways. The basic types of terpenoids found in plants are monoterpenoids (C₁₀), sesquiterpenoids (C₁₅), diterpenoids (C₂₀), triterpenoids (C₃₀) and tetraterpenoids (C₄₀). The terpenoids are toxic to seed germination and seedling and plant growth. Camphor and cineole (produced in Salvia spp and Eucalyptus spp) are found toxic to root growth. (Fig. 4)

6. **Aromatic compounds**

   The compounds known as phenolics are the most commonly identified allelopathic compounds produce in higher plants. These compounds include following different compounds.

   (a) **Simple phenols and their derivatives**

   Arbutin, cinnamic acid, coumaric acid, etc. are some examples of simple phenols and their derivatives commonly found as allelopathic agents (Fig. 5). These compounds are found in leaf leachates and soil (added to soil as root exudates) and they show the allelopathic effects.
Fig. 5. Phenol derivatives

(b) Cinnamic acid derivatives

These compounds are widely distributed in higher plants. Many cinnamic acid derivatives like chlorogenic acid are identified as germination and growth inhibitors. Chlorogenic acid and isochlorogenic acid are chief inhibitors found in Helianthus annus (Fig. 5).

(c) Coumarins

The coumarins are the lactons of O-hydroxy cinnamic acid. They occur in all parts of plant and are widely distributed in plant kingdom. They occur mostly as glycosides and are readily leached into the environment. The common coumarins with allelopathic nature are esculetin, scopuletin, umbelliferon, etc. (Fig. 6).

(d) Flavonoids

Flavonoids are compounds with C6–C3–C6 skeleton. A huge variety of flavonoids are found in higher plants some with allelopathic effects. Phloretin found in the apple root residues inhibit the growth of apple seedling. This compound is the 6-glucoside of phloretin (Börner 1959). Glycosides of kaempferol, quercetin, catechin, etc. are known as allelopathic agents (Fig. 7).

(e) Quinones

A toxin from walnut trees known as juglone (Fig. 8) is a 5-hydroxy naphthoquinons. It occurs only in genus Juglans and is reported as a potent allelochemical. Massey (1925) found that the tomato plants wilted and died whenever their roots came in contact with walnut roots. The effect of root exudation was so strong that he was able to trace the distribution of walnut roots in under soil just by observing the wilt in test plant. Quinones are also produced by pathogenic fungi, which affect the physiology of host plant. Novarubin is produced by fungus Fusarium solani. This chemical causes the host plant to wilt.
(f) Tannins

Both hydrolysable tannins and condensed tannins are reported to have allelopathic activity. Gallic acid (Fig. 9) is produced by the hydrolysis of digallic acid (a hydrolysable tannin). Such tannins are widespread in dicotyledon plants. These chemicals act as growth and germination inhibitors, and growth retarder of nitrogen fixing and nitrifying bacteria.

![Gallic acid](image)

Fig. 9 Tannins

7. Alkaloids

Alkaloids are known as seed germination inhibitors. The high alkaloid contents of seeds and fruits inhibit seed germination. Cocain, caffein, quinone are the strong inhibitor of seed germination. Atropin (Fig. 10) is another alkaloid known as week inhibitor of germination. Overland in 1966 found that the barley root exudate with alkaloid gramine is inhibitory to the growth of *Stellaria media*.

![Atropine](image)

Fig. 10. Alkaloids

**Mode of Actions of Allelochemicals**

Physiological effects of allelochemicals is the less studied field in allelopathy. However, this is the most important topic in allelopathy research. The great difficulty in such research is to separate the secondary effects from primary effects. The effects of allelochemicals seen in germination and growth of plant is the secondary effects caused by the effects of these chemicals in molecular level. The action of allelochemicals is broadly divided into direct (effects on various aspects of plant growth and development) and indirect (the effects on plant caused by the change in physical properties of soil and altered biological component and their activity). The seedlings of plants are destroyed easily than the mature plants. So, the majority of allelochemicals affect the germination of seeds and growth of seedlings.

New chemicals are constantly extracted from plant. It is expected that there might be approximately 400,000 chemical compounds in plants. Some of these chemicals could provide important agriculture chemicals to fight with weeds and diseases.
oxidised by soil microbes to juglon. The reduced growth and wilting of herbs growing under walnut tree is due to the presence of juglon in soil. In such allelopathic effects six different processes involve. The processes are: synthesis of a chemical by a plant, release of the chemical to environment, spread of the chemical, change of chemical to active compound by microbes, absorption of the active substance by another plant and the production of allelopathic effect.

The important processes affected by allelochemicals in plant are described here.

1. Effects on structure and development of cell

Saturated solution of coumarin blocked the mitotic process in onion root (Cornmann 1946). Destruction of spindle fibre, interruption of anaphase are the effects observed. The extract of Juglans nigra slowed the mitosis (Jensen & Welboume 1962) and decreased the number of root cells in Pisum sativum. Volatile terpene (cineole, camphor) of Salvia sp. completely prevented mitosis and the cell elongation in root and hypocotyle (Muller 1965). The terpene also inhibited growth of several bacteria. Umbelliferon decreased the rate of cell elongation in cucumber (Jankay & Muller 1976). Volatile terpene reduced the number of cell organelles, disrupted the biological membrane and lastly death of seedling occurred in cucumber (Lorber & Muller 1976).

2. Effect on phytohormone activity

Allelochemicals may enhance or inhibit hormone activity. Phenol and phenol derivatives (scopoletin, clorogenic acid etc.) inhibited oxidation of indolacetic acid by IAA-oxidase (Sondheimer & Griffin 1960). However some allelochemicals (like coumaric acid) act as activator of IAA-oxidase and decrease the IAA activity. Flavonoid, glycosides show the inhibitory effect on IAA because they are the strong stimulator of IAA-oxidase. Phenolic compounds also inhibit gibberelin induced growth in Pea (Corcoran 1970) and in cucumber (Green & Corcoran 1975).

3. Membrane structure and its permeability

Terpene and cineole from leaves of Salvia leucophylla decreased the permeability of cell membrane (Muller et al. 1969). Several allelopathic chemicals like cinnamate, salicylate, benzoate and their derivatives increased the permeability of membrane to potassium and decreased permeability to chloride (Levitan & Barker 1972). Aquas leaf leachates of some wood plants increased the permeability to membrane to anthocyanine. The change in permeability of membrane is an important mechanism of action for allelopathic substances.

4. Mineral uptake

Some allelopathic chemicals affect the mineral uptake of plant. The corn and bean are seen severely zinc deficient when they follow beets in cropping sequence. The sugar beets add some toxin to the soil that interferes with the zinc uptake of other crops. The uptake of phosphorus decreased in bean plant when it is cultivated with other crops in association (Chambers & Holm 1965). This shows the allelopathic interrelationship between same species. Phenolic acids inhibit phosphorus and potassium uptake. It is caused by the increase in membrane permeability to these ions. The effect on mineral absorption may be due to the effects of allelochemicals on respiration and ATPase activity.

5. Stomatal opening and photosynthesis

Scopoletin and chlorogenic acid inhibited the photosynthetic rate in various plants. The reduction increased with the increase in concentration of scopoletin (Einbellig et al. 1970). Scopoletin reduces turgor presser and affect the opening stomata. Several allelochemicals show their effect on stomatal opening.

Some quinones reduce photosynthesis as they are strong inhibitor of both photosystem I and II. Kaempferol, a allelopathic flavenol, inhibit electron transport in both cyclic and noncyclic
photophosphorylation (Arntzen et al. 1974).

6. Respiration and protein synthesis

The respiratory activity is adversely affected by many allelopathic agents. The effect on respiration may be the important mechanism of action for some allelochemicals. Chemicals like quinones, ferulic acid, cinamic acid are found as inhibitors of protein synthesis.

7. Enzyme activity

The allelopathic agents also affect the activity of various enzymes. The activity of enzymes like pectolytic enzyme, cellulase, catalase, phosphorylase, phenylalanin amonia lyase, invertase, etc. is affected by allelochemicals.

8. Conduction

Most allelochemicals are found to affect the conduction of water and minerals. Scientist working in allelochemicals have observed in several experiments the wilting effect on plants. The results on the effects of allelochemicals on plant are mostly the result of experiments treating a particular chemicals singly to the plant. Under natural condition such compounds may act together on one or more than one processes resulting different effects than the effects observed when treated singly.

Role of Allelopathy

The allelopathic interaction between plants play a crucial role in both manipulated and natural ecosystems. The studies in this field will help to understand interaction between plant-plant and plant-microbes. Such knowledge will be helpful to increase the production of agriculture. The production can be increased by avoiding deleterious interactions between crops and supporting the beneficial interactions in crop rotation and mixed cropping, and allelopathic control of weeds.

1. Impact on Agriculture

The most studied effects of allelochemicals is in the manipulated ecosystems. Generally the effects of weed on crops, crops on weed, weed on weed, and crops on crops are studied. The development of beneficial cropping systems such as crop rotation, mixed cropping is possible only after the study of the allelopathic interaction between the crops. The proper understanding of allelopathic interaction will help to avoid deleterious interaction between crops and help to establish the beneficial interaction between crops in mixed cropping and crop rotation. Allelochemicals can be a good source of environment friendly chemicals to control weeds.

Many agricultural weeds markedly inhibit germination of seeds, coleoptile and stem growth, and root growth. The ultimate effect is the reduction of crop yield. Allelopathy play an important role in such interaction. The chemicals produced by one plant may be toxic to other plant. The toxicity of these allelochemicals may be autotoxic (toxic to same crop species) or allotoxic (toxic to other species).

Soil sickness, a serious problem in agriculture and horticulture, is due to allelochemicals. Trifolium partense (red clover) show autotoxic effect the plant releases isoflavan in soil which is changed to different allelopathic phenols by the action of soil microbes. These phenols allelopathic to red clover itself. The rice straw on decay add phenolic acids in soil which show both autotoxic and allotoxic effects. These phenolics also inhibit the growth of Bradyrhizobium japonicum, the root nodule bacteria of soybean, and the development of root nodule. The decrease in soybean yield is due to the inhibition of biological nitrogen fixation. Burning of the rice straw remained in the field increases the production of soybean.

Allelopathic effects are some time beneficial to other plants. The roots of rapeseed and tobacco release strigol from their root the strigol is a potent seed germination stimulant for witchweed like Orobranche spp., a harmful parasitic plant acting upon these plants as root parasite. The parasite reduces the yield of plant drastically. These root parasites are also common in Nepal and are responsible to reduce the yield of mustard and tobacco remarkably. Structure analogue of such natural strigol are used commonly to control such parasite. The seeds of the parasitic plants germinate in presence of such analogue but they die as they will not get appropriate host plant.

One of the important use of allelopathy in agriculture is their possible use in biological control of weeds. As some crop plants are resistant to some weeds, it should be possible to breed crop plants resistance to selected weeds. Mixed cropping with legumes is beneficial as the atmospheric nitrogen is brought to soil by increasing biological nitrogen fixation. However, many legumes are known to be allelopathic to some crop plants. Selection of compatible legumes and crop plant for mixed cropping is desirable. Biological control of weeds is found successful in many ecosystems by introducing new plant in the system.
2. Impact on Forestry

Allelopathic interactions are also seen in both natural and antifical forests. Such interaction is one of the factor to determine the type of vegetation of a particular area. In Canada the interaction of pine and walnut was seen soil dependent (Fisher 1978). On excessively drained sites pine often suppressed the walnut, whereas on imperfectionly drained site walnut suppressed or even killed the pines. The leachates from many trees are deleterious for many herbs. In the agroforestry practice, which combines the production of crop and forest plant simultaneously or sequentially, trees are grown in association with crop plants. There is a good chance that the allelochemicals produced by one plant will affect the growth of other plant. Therefore, it is essential to study the allelopathic compatibility of crops with trees before being introduced to an agroforestry system.

3. Impact on Horticulture

The soil sickness problem leading to replant problem in apple, peach and citrus is also due to the allelochemicals. The yield of citrus begin to diminish after citrus tree have been grown for several years. The growth of citrus slows in spite of fertilisation, pest control and good management. Young citrus trees replanted in such soil grow very slow in comparison to the citrus planted in noncitrus soil. This decline problem is due to the accumulation of allelochemicals in soil and enrichment of some soil fungi due to the previous citrus plantation.

4. Impact on Vegetation patterning and succession

The process of succession and patterning of vegetation of particular area is mostly attributed to the competition between species. Evidences are also accumulating in support on the role of allelopathy in the distribution of plant. All plants allelopathically affect the vegetation in their vicinity and create the special patterning of the vegetation.

Succession is mostly tried to explain on the basis of the changes in physical factors, availability of minerals and competition between species. The process of allelopathy may have also played an important role in plant succession. The effects of allelopathy on succession in ecosystem is an interesting subject to study.

References


