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ALLELOPATHY: A COMMON WARFARE AMONG THE PLANTS

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ABSTRACT: Allelopathy is a common biological phenomenon by which one organism produces biochemicals that influence the growth, survival, development, and reproduction of other organisms. These biochemicals are known as allelochemicals and have beneficial or detrimental effects on target organisms. Plant allelopathy is one of the modes of interaction between receptor and donor plants and may exert either positive effects (e.g., for agricultural management, such as weed control, crop protection, or crop re-establishment) or negative effects (e.g., autotoxicity, soil sickness, or biological invasion). To ensure sustainable agricultural development, it is important to exploit cultivation systems that take advantage of the stimulatory/inhibitory influence of allelopathic plants to regulate plant growth and development and to avoid allelopathic autotoxicity. Allelochemicals can potentially be used as growth regulators, herbicides, insecticides, and antimicrobial crop protection products. Here, we reviewed the plant allelopathy management practices applied in agriculture and the underlying allelopathic mechanisms described in the literature. The major points addressed are as follows: (1) Description of management practices related to allelopathy and allelochemicals in agriculture. (2) Discussion of the progress regarding the mode of action of allelochemicals and the physiological mechanisms of allelopathy, consisting of the influence on cell micro- and ultra-structure, cell division and elongation, membrane permeability, oxidative and antioxidant systems, growth regulation systems, respiration, enzyme synthesis and metabolism, photosynthesis, mineral ion uptake, protein and nucleic acid synthesis. (3) Evaluation of the effect of ecological mechanisms exerted by allelopathy on microorganisms and the ecological environment. (4) Discussion of existing problems and proposal for future research directions in this field to provide a useful reference for future studies on plant allelopathy.

KEYWORDS: allelopathy, plants, protection, autotoxicity, biochemicals, environment, invasion, detrimental

I.INTRODUCTION

Allelopathy is a biological phenomenon by which an organism produces one or more biochemicals that influence the germination, growth, survival, and reproduction of other organisms. These biochemicals are known as **allelochemicals** and can have beneficial (positive allelopathy) or detrimental (negative allelopathy) effects on the target organisms and the community. Allelopathy is often used narrowly to describe chemically-mediated competition between plants; however, it is sometimes defined more broadly as chemically-mediated competition between any type of organisms. Allelochemicals are a subset of secondary metabolites, which are not directly required for metabolism (i.e. growth, development and reproduction) of the allelopathic organism.

Allelopathic interactions are an important factor in determining species distribution and abundance within plant communities, and are also thought to be important in the success of many invasive plants. For specific examples, see black walnut (*Juglans nigra*), tree of heaven (*Ailanthus altissima*), black crowberry (*Empetrum nigrum*), spotted knapweed (*Centaurea stoebe*), garlic mustard (*Alliaria petiolata*), *Casuarina/Allocasuarina* spp., and nutsedge.

It can often be difficult in practice to distinguish allelopathy from resource competition. While the former is caused by the addition of a harmful chemical agent to the environment, the latter is caused by the removal of essential nutrients (or water). Often, both mechanisms can act simultaneously. Moreover, some allelochemicals may function by reducing nutrient

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availability. Further confounding the issue, the production of allelochemicals can itself be affected by environmental factors such as nutrient availability, temperature and pH. Today, most ecologists recognize the existence of allelopathy, however many particular cases remain controversial.

Allelochemicals are a useful tool in sustainable farming due to their ability to control weeds. The possible application of allelopathy in agriculture is the subject of much research. Using allelochemical producing plants in agriculture results in significant suppression of weeds and various pests. Some plants will even reduce the germination rate of other plants by 50%. Current research is focused on the effects of weeds on crops, crops on weeds, and crops on crops. This research furthers the possibility of using allelochemicals as growth regulators and natural herbicides, to promote sustainable agriculture. Agricultural practices may be enhanced through the utilization of allelochemical producing plants. When used correctly, these plants can provide pesticide, herbicide, and antimicrobial qualities to crops. number of such allelochemicals are commercially available or in the process of large-scale manufacture. For example, leptospermone is an allelochemical in lemon bottlebrush (*Callistemon citrinus*). Although it was found to be too weak as a commercial herbicide, a chemical analog of it, mesotrione (trade name Callisto), was found to be effective. It is sold to control broadleaf weeds in corn but also seems to be an effective control for crabgrass in lawns. Sheeja (1993) reported the allelopathic interaction of the weeds *Chromolaena odorata* (*Eupatorium odoratum*) and *Lantana camara* on selected major crops.

Many crop cultivars show strong allelopathic properties, of which rice (*Oryza sativa*) has been most studied. Rice allelopathy depends on variety and origin: Japonica rice is more allelopathic than Indica and Japonica-Indica hybrid. More recently, critical review on rice allelopathy and the possibility for weed management reported that allelopathic characteristics in rice are quantitatively inherited and several allelopathy-involved traits have been identified. The use of allelochemicals in agriculture provide for a more environmentally friendly approach to weed control, as they do not leave behind residues. Currently used pesticides and herbicides leak into waterways and result in unsafe water qualities. This problem could be eliminated or significantly reduced by using allelochemicals instead of harsh herbicides. The use of cover crops also results in less soil erosion and lessens the need for nitrogen heavy fertilizers.

Various parts of plants can have these allelopathic properties, from the foliage and flowers to the roots, bark, soil, and mulch. Most all allelopathic plants store their protective chemicals within their leaves, especially during fall. As leaves drop to the ground and decompose, these toxins can affect nearby plants. Some plants also release toxins through their roots, which are then absorbed by other plants and trees.

Trees are great examples of allelopathy in plants. For instance, many trees use allelopathy to protect their space by using their roots to pull more water from the soil so other plants cannot thrive. Some use their allelochemicals to inhibit germination or impede the development of nearby plant life. Most allelopathic trees release these chemicals through their leaves, which are toxic once absorbed by other plants. Black walnut is a prime example of this. In addition to its leaves, black walnut trees store allelopathic properties within their buds, nut hulls, and roots. The chemical responsible for its toxicity, called Juglone, remains in the soil around the tree and is most potent at the drip line, though the roots can spread out well beyond this. Plants most susceptible to the black walnut's toxicity include nightshade plants (tomatoes, peppers, eggplants, potatoes), azaleas, pines, and birch trees.

Plant allelopathy is the 'chemical warfare' among the plants imposed by one plant on another to suppress the latter and take advantage from that suppression. The word allelopathy comes from two Greek words *allelon* and *pathos*; where *allelon* means 'each other' and *pathos* means 'to suffer'. Thus in the phenomenon of plant allelopathy, allelopathic plants create adverse conditions to other neighboring plants by reducing their seed germination and seedling growth. The allelopathic plants are very effective in weed killing and known as Nature's Weed Killers. Using synthetic chemical compounds in agriculture has brought various types of ecological and environmental disasters to the present world. These toxic chemicals

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are damaging the ecological balance to a severe extent and introducing many fatal diseases. That's why the demand of sustainable agriculture and eco-friendly alternatives to chemical compounds has been increased. Plant allelopathy is a great alternative of using toxic chemical herbicides in weed management. Competition is a very common phenomenon in the Earth's Biosphere. Like other living organisms, plants also compete for sunlight, nutrients, water, space etc. and this competition is the basis for allelopathy. Some plants, known as allelopathic plants, use their chemical tools to win the competition and use the available resources more efficiently. Allelopathy can be carried out by allelopathic plants by the following processes-

- Allelopathic plants release chemical compounds from their roots into the soil, and these chemicals suppress or even kill the neighboring plants when they are absorbed by the plants. The harmful chemicals released by allelopathic plants are known as allelochemicals. Some allelochemicals change the amount of chlorophyll production in a plant and thus, they slow down or stop the photosynthesis process of that plant which ultimately leads to the suppression or death of that plant.
- Many allelopathic plants release allelochemicals in gaseous forms. These gaseous allelochemicals are released from the small pores of their leaves. When the neighboring plants absorb these gasses, they are suppressed or killed.
- When leaves drop from the allelopathic plants to the ground, they are subjected to decomposition; when the leaves decompose they release their noxious chemicals as a way to inhibit the growth of other neighboring plants.

II.DISCUSSION

Advantages of Allelopathy

Allelopathic plants can be introduced in agroecosystems to get some advantages from that-

- Allelopathy can be used for beneficial purpose through using allelochemicals as natural herbicides or pesticides. Various allelochemicals classes including alkaloids, flavonoids, cyanogenic compounds, cinnamic acid derivatives, benzoxazines, and ethylene and some other seed germination stimulants can be isolated from various families of terrestrial and aquatic plants. These allelochemicals are readily or potentially phytotoxic to many unnecessary plants.
- Using allelopathic plants in companion cropping may bring a great advantage to an agroecosystem. A selectively allelopathic plant can be used as a companion plant with a certain crop plant. The selectively allelopathic plant will suppress certain weeds and will not disturb the growth of the main crop. The introduction of a number of crop species such as- corn, lupin, oats, beets, wheat, peas, millet, barley, rye etc. in companion cropping has been proved effective in suppressing a number of weeds.
- Some parasitic weeds produce seeds which germinate in response to chemical compounds released from their hosts. For instance, Striga, a parasitic plant to cereals, germinates in response to p-benzoquinone compound released from its natural host sorghum. Ethylene is also effective to stimulate Striga to germinate. Thus, ethylene can be applied to make Striga germinate in the absence of a host. Using allelochemicals to stimulate the suicidal germination of weed seeds reduces the number of dormant seeds in soil.

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- The allelopathic characteristics of wild types plants can be transferred into the commercial crops to boost up their allelopathic traits for weed suppression.
- Selectively toxic plant residues can be managed in a proper manner to control weeds efficiently. Using allelopathic crops in crop rotation, cover cropping with smother crops, using phytotoxic mulches etc. can be the examples of some good allelopathic residue management practices.

The production and composition of allelochemicals

Allelopathy can be considered to be a form of communication among plants. Plants synthesize a multitude of compounds via secondary metabolism. The production of these compounds depends on the existence of precursor molecules and the activation of specialized genes. The activation of genes required for biosynthesis of allelochemicals is often dependent on environmental stimuli.

Genetic factors

The production of compounds via secondary metabolism in plants (including allelochemicals) is dependent on the appropriate genetic components. For example, a rice (*Oryza sativa* L.) breeding program that pursued the development of cultivars with increased allelochemical production has benefited from the elucidation of the enzymes and genes involved in momilactone B synthesis. Momilactone B is a rice allelochemical that has one of the highest activity levels against weeds. It is a diterpene compound biosynthesized from geranylgeranyl pyrophosphate by diterpene synthase enzymes using the methylerythritol phosphate (MEP) pathway. Using reverse genetic tools, it was possible to elucidate the two genes encoding diterpene synthases responsible for its production: 4-copalyl-diphosphate synthetase and kaurene synthase-like 4.

Another study with rice used an RNA interference technique (RNAi) to establish a cause-effect relationship between the expression of the phenylalanine ammonia-lyase (PAL) gene and the biosynthesis of phenols. Gene-silenced plants showed reduced amounts of PAL enzyme, a low phenol concentration in the tissues and a limited amount of root exudates compared to wild plants. Thus, the results of these experiments provide strong evidence for the allelochemical potential of wild plants associated with the synthesis of phenols. Phenols have at least six distinct mechanisms of action within plants. Nevertheless, the occurrence of other substances together with phenols, or a combination of different phenolic compounds, might also result in synergistic effects, increasing their phytotoxicity even at low concentrations. Advances in technological and research methods have allowed the identification of several factors that control the gene expression of the enzymes involved in the synthesis of plant allelopathic compounds. For example, the importance of many jasmonates (methyl jasmonate and jasmonic acid) in the regulation of expression of the gene encoding the enzyme o-methyltransferase has been understood following the elucidation of the biosynthetic pathway of sorgoleone in epidermal cells of the sorghum root system. The progress in this area is likely to increase the identification of other biosynthetic pathways, enzymes and genes responsible for producing several other allelochemicals.

Environmental factors

Environmental conditions can directly or indirectly affect the allelopathic performance of a plant. The most important environmental factors that influence allelopathy include UV radiation, temperature, water and nutrient availability and competition stress. The environment can affect allelopathy in at least three ways: the production of compounds (through

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gene interaction), their bioavailability and their effect on target species. There is strong evidence to support the hypothesis that environmental stress can increase the production of allelochemicals. For example, stresses from UV radiation, nutrient shortage, plant pathogen infection and wounding are reported to stimulate the activity of PAL, which is the first committed step in the biosynthesis of phenolic compounds. The phenol cinnamic acid is produced by some plant species, such as cucumber (*Cucumis sativus* L.), and is a precursor of several phenylpropanoids that cause peroxidation and a reduction of the cell membrane H^+ -ATPase activity, consequently decreasing the root viability of target plants. Jasmonate synthesis is also stimulated by environmental stress. As a consequence, these hormones can trigger the expression of genes related to secondary metabolism in several plant species. The presence of other plants surrounding sorghum can exacerbate the impact of the environmental stress on the production of sorgoleone. Similarly, the environmental stresses arising from the interaction among plants are also important for the production of other allelochemicals. For example, rice seedlings cultivated with *Echinochloa crus-galli* L. Beauv. (barnyardgrass) showed a concentration of momilactone B almost seven times higher than that in rice seedlings grown alone. The momilactone B concentration in some rice cultivars can reduce the number of *E. crus-galli* shoots by 81%.

The bioavailability of allelochemicals in the soil is dependent on processes of transference (mainly adsorption and leaching) and degradation (abiotic and biotic). Several factors can affect the bioavailability of allelochemicals in the soil, including the clay and organic matter content, water availability, soil pH, and biological activity. Thus, the allelopathic potential of many compounds is not expressed in some soils because of the chemical adsorption to soil colloids. For instance, sorgoleone binds strongly to soil colloids because it is a highly lipophilic allelochemical, with a log P (log octanol-water partition coefficient) of 6.1. The allelopathic compounds 1-3,4-dihydroxyphenylalanine and catechin are also strongly adsorbed by soil colloids, possibly due to the catechol group present in these molecules. The benzoxazinoid compounds 2-aminophenoxazin-3-one and DIBOA (2,4-dihydroxy-(2H)-1,4-benzoxazin-3(4H)-one) are other examples of compounds that have a reduced allelopathic potential due to their adsorption by soil colloids.

The chemical compounds that are not adsorbed onto colloids or minerals are usually in the soil solution. Thus, they can be absorbed by plants or leached. A study with rice plants has shown that flavonoids with a high mobility in the soil profile were less phytotoxic than those with a reduced soil mobility. Similarly, an analysis of ten potential allelochemicals revealed an inverse relationship between soil mobility and their toxic effect on target plants.

Environmental factors can affect the degradation of allelochemicals in the soil, reducing their efficacy. In non-sterilized soil, for instance, DIBOA showed a half-life of 43 h. However, 2-aminophenoxazin-3-one (APO), the final degradation product of DIBOA, has a low mineralization rate and therefore, a half-life greater than 90 days. In addition, some flavonoid glycoside molecules exuded by rice plants can suffer high mineralization by soil microorganisms, resulting in aglycosylated compounds. Flavonoid glycosides and aglycosides have a half-life of 2 h and 30 h, respectively, suggesting a higher allelopathic activity for the second group. The biodegradation of the sorgoleone quinone ring is relatively slow, with only 21% being mineralized 77 d after incubation in soil. However, the sorgoleone methoxy group was biodegraded within a few days, particularly in soils with a low colloid content (Gimsing et al. 2009).

The environmental fate of allelochemicals is a complex issue that is affected by the donor and target plant species, as well as environmental variables and other processes that affect the fate of the chemicals in the environment. Knowledge concerning the variation in these factors is essential to use the allelopathic relationship among plants in agroecosystems to promote weed control.

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III.RESULTS

Theophrastus (ca. 300 B.C.E.), a student and successor to Aristotle, wrote about allelopathic reactions in his botanical works. He has been called the "father of Botany", and wrote of how chickpea "exhausts" the soil and destroys weeds.

In 1 C.E., Gaius Plinius Secundus, also known as Pliny the Elder, a roman scholar and naturalist, wrote about how chick pea and barley "scorch up" cornland. He also mentioned that Walnut trees are toxic to other plants.

Augustin Pyramus De Candolle, a botanist and naturalist, in 1832, suggested that soil sickness was caused by chemicals released by the crop.

And, in 1907-1909, two researchers, Schreiner and Reed investigated the isolation of a number of phytotoxic chemicals from plants and soils.

Chemical Warfare in the Plant Kingdom

Black Walnut

One of the most famous allelopathic plants is Black Walnut (*Juglans nigra*). The chemical responsible for the toxicity in Black Walnut is Juglone (5 hydroxy-1,4 naphthoquinone) and is a respiration inhibitor. Solanaceous plants, such as tomato, pepper, and eggplant, are especially susceptible to Juglone. These plants, when exposed to the allelotoxin, exhibit symptoms such as wilting, chlorosis (foliar yellowing), and eventually death. Other plants may also exhibit varying degrees of susceptibility and some have no noticeable effects at all. Some plants that have been observed to be tolerant of Juglone include lima bean, beets, carrot, corn, cherry, black raspberry, catalpa, Virginia creeper, violets, and many others.

Juglone is present in all parts of the Black Walnut, but especially concentrated in the buds, nut hulls, and roots. It is not very soluble in water and thus, does not move very rapidly in the soil. Toxicity has been observed in all soil with Black Walnut roots growing in it (roots can grow 3 times the spread of the canopy), but is especially concentrated closest to the tree, under the drip line. This is mainly due to greater root density and the accumulation of decaying leaves and hulls.

Tree-Of-Heaven

The Tree-Of-Heaven, or *Ailanthus* (*Ailanthus altissima*) is a recent addition to the list of allelopathic trees. Ailanthone, an allelotoxin extracted from the root bark of *Ailanthus*, is known for its "potent post-emergence herbicidal activity". *Ailanthus* poses a serious weed problem in urban areas.

Sorghum

The major constituent of sorghum that causes allelopathic activity is sorgolene (2-hydroxy-5-methoxy-3-((8z,11z)-8',11',14'-pentadecatriene)-p-benzoquinone). Sorgolene is found in the root exudates of most sorghum species and has been shown to be a very potent allelotoxin that disrupts mitochondrial functions and inhibits photosynthesis. It is being researched extensively as a weed suppressant.

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Others

There are many other known allelopathic species, and many that are highly suspected of being allelopathic including various wetland species, grasses, and other woody plants such as Fragrant Sumac (*Rhus aromaticus*). Tobacco (*Nicotiana rustica*), Rice (*Oryza sativa*), Pea (*Pisum sativum*), and many others, are known to have root allelotoxins.

Procedures and Protocol

Protocol 1. Learning To Identify Signs of Allelopathy

The best way to study allelopathy is to find signs of it occurring in nature. It is impossible to "see" the toxins at work, but it is possible to see the signs and symptoms caused by the chemicals on surrounding plants. For example, very few plants grow under a Black Walnut and those that do often times look sickly and chlorotic. This is a sign of the allelotoxin, Juglone, at work.

Along with recognizing the signs of allelopathy, one must also be able to identify the plants. Some allelopathic plants, such as Black Walnut, grow in our backyards and on our streets and are easy to identify. Others, like sorghum or chick pea, may be easier to find in rural areas where they are grown as crops or alongside farm land. Some allelopathic plants, especially many of the wetland species, may require special field trips and extra time to find them first and then identify them.

Protocol 2. Harvesting Plants and Plant Parts

Many of the known allelotoxins are very expensive and not easy to come by. Some companies such as Sigma Chemical and Caroline Biological may carry the chemicals, but in solid form that will require extra time and effort to bring to a soluble form that can be used in the lab. However, not every class will have the funds or the access to these chemicals. Thus, it may be that the only way to run the experiments is to have the class harvest their own allelotoxins.

Some research will be required to investigate what plant parts have the highest concentrations of allelopathic species. For instance, the Juglone found in Black Walnut can be found throughout the plant but particularly within the nut hulls, leaves, and roots. Therefore, a class project may be to break into groups and harvest each part and test them accordingly.

It is important when harvesting plants or plant parts to be sure that the plant is not endangered and to be sure that the procedure is carried out in such a way as to bring no harm to the plant or the surrounding area. Of course, in the case of harvesting the entire plant, accommodations must be made.

Protocol 3. Testing for Allelopathy in the Lab

The effects of allelopathic toxins on sensitive plants can easily be tested in the lab or greenhouse setting. Seeds are the easiest and least expensive to test. Seeds that do not germinate in the presence of allelotoxins are probably displaying toxicity effects. Plants that become chlorotic and eventually die in the presence of allelotoxins are also showing signs of toxicity to the chemical.

Solanaceous crops, such as tomatoes and peppers, are most susceptible to juglone (the allelotoxin found in Black Walnut trees). The laboratory setting is the perfect place to test the susceptibility of certain plants to various allelotoxins.

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Other scientific or research based concepts, such as graphing, dilutions, and general lab protocol will also be covered when certain allelopathy activities are conducted in the lab or classroom setting.

Procedures

1. Familiarize yourself with the allelopathic species in your area. In particular, focus on mature species that are established. These tend to have higher concentrations of the allelotoxin and thus will display better signs and symptoms on any susceptible surrounding plants.
2. If possible, contact a local conservation organization or extension agency, that might have some insight about allelopathy. Your research may be of interest to them and they may offer professional advice or important information.
3. Decide which species and areas should be the focus of your survey.
4. Decide on a survey method. For instance, you may want to conduct the identification field trip one day and then follow up with the harvest field trip another, or you may want to conduct both on the same day.
5. Learn how to identify the species that you will be studying. There are many good Field Guides available, as well as many excellent web sites.
6. Decide how to divide up the area you will be working in.
7. Record what allelopathic signs and symptoms were found, and the species they were found by.
8. Discuss ways to study allelopathy in the laboratory.
9. Gather needed materials. See the materials list at the end.

IV.CONCLUSIONS

Allelopathy is the detrimental effects of chemicals or exudates produced by one (living) plant species on the germination, growth or development of another plant species (or even microorganisms) sharing the same habitat.

Allelopathy does not form any aspect of crop-weed competition, rather, it causes crop-weed interference, it includes competition as well as possible allelopathy.

Allelo chemicals are produced by plants as end products, by-products and metabolites liberalised from the plants; they belong to phenolic acids, flavanoides, and other aromatic compounds viz., terpenoids, steroids, alkaloids and organic cyanides.

Allelopathic Effects of Weeds on Crops

(1) Maize:

- Leaves & inflorescence of Parthenium sp. affect the germination and seedling growth
- Tubers of Cyperus esculentus affect the dry matter production

(2) Sorghum:

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- Stem of *Solanum* affects germination and seedling growth
- Leaves and inflorescence of *Parthenium* affect germination and seedling growth

(3) Wheat:

- Seeds of wild oat affect germination and early seedling growth
- Leaves of *Parthenium* affects general growth
- Tubers of *C. rotundus* affect dry matter production
- Green and dried leaves of *Argemone mexicana* affect germination & seedling growth

(4) Sunflower:

- Seeds of *Datura* affect germination & growth

Allelopathic Effects of crop plants on weeds

- Root exudation of maize inhibits the growth of *Chenopodium album*
- The cold water extracts of wheat straw when applied to weeds reduce germination and growth of *Abutilon* sp.

Allelopathic effects of weeds on weeds

- Extract of leaf leachate of decaying leaves of *Polygonum* contains flavonoides which are toxic to germination, root and hypocotyls growth of weeds like *Amaranthus spinosus*
- Inhibitor secreted by decaying rhizomes of *Sorghum halepense* affect the growth of *Digitaria sanguinalis* and *Amaranthus* sp.

Factors influencing allelopathy

a. Plant factors

- Plant density: Higher the crop density the lesser will be the allelo chemicals it encounters
- Life cycle: If weed emerges later there will be less problem of allelochemicals
- Plant age: The release of allelochemicals occurs only at critical stage e.g. in case of *Parthenium*, allelopathy occurs during its rosette & flowering stage.
- Plant habit: The allelopathic interference is higher in perennial weeds.
- Plant habitat: Cultivated soil has higher values of allelopathy than uncultivated soil.

b. Climatic factors: The soil & air temperature as well as soil moisture influence the allelo chemicals potential

c. Soil factors: Physico-chemical and biological properties influence the presence of allelochemicals.

d. Stress factors: Abiotic and Biotic stresses may also influence the activity of allelochemicals

Mechanism of action of allelochemicals

- Interfere with cell elongation
- Interfere with photosynthesis
- Interfere with respiration
- Interfere with mineral ion uptake
- Interfere with protein and nucleic acid metabolism

Use of Allelopathy in biological control of weeds:

- Use of cover crop for biological control
- Use of allelopathic chemicals as bio-herbicides

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