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ALLELOPATHY

Allelopathy as a Possible Cause for Crop Yield Reductions

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Sometimes an individual plant can have a depressive effect on its neighbours. It is therefore more common that a neighbouring plant will interact in a negative manner, where the emergence or growth of one or both is inhibited. Muller (1969) described the adverse effect of a neighbouring plant in association with others and defined it as interference. According to Szczepanski (1977) the potential causes of interference include:

- Allelospoly (competition) L the depletion of one or more resources required for growth;
- Allelopathy L the addition of chemical toxins by one or more species in association, and
- Allelomediation L selective harbouring of a herbivore that might selectively feed on one species, thus lending to the advantage of another.

Interference refers, therefore, to the overall effect of one plant upon another and encompasses both allelopathy and competition. Competition involves the removal or diminution of a shared resource, while allelopathy involves the addition of a chemical compound to the environment through different processes (Rice, 1984; Putnam, 1985). Confusion has occurred because some consider allelopathy to be part of competition. In addition, competition has been misused by many to describe interference. It is a specific mechanism for interference, but not the end result.

Allelopathy

The allelopathic effect of one plant upon another is so striking that competition for a common resource does not seem adequate to explain the observation. In organism communities, many species appear to regulate one another through the production and release of chemical attractants, stimulators or inhibitors (Putnam & Tang, 1986).

1.1 **Definition**

Allelopathy is derived from the Greek words allelon "of each other" and pathos "to suffer" (Rizvi, Haque, Singh & Rizvi, 1992). It therefore translates literally as mutual suffering. Allelopathy is described as the beneficial and deleterious biochemical interaction between plants and micro-organisms. Rice (1974) defines allelopathy as any direct or indirect effect by one plant, including micro-organisms, on another through the production of chemical compounds that escape into the environment and subsequently influence the growth and development of neighbouring plants. It includes both inhibitory and stimulative reciprocal biochemical interactions. The use of the term "allelopathy" may therefore be somewhat controversial. Chemicals found to inhibit the growth of a species at a certain concentration may stimulate the growth of the same species or another at a lower concentration (Rice, 1984; Putnam & Tang, 1986). Aldrich (1984) describes two types of allelopathy:

- True type L the release into the environment of compounds that are toxic in the form in which they are produced, and
- Functional type L the release into the environment of a substance that is toxic as the result of transformation by micro-organisms.
- Many extremely important ecological roles of allelopathy may have been overlooked because of the focus on the detrimental effects of the added chemicals, only.

1.2 **History**

In a historical overview, Wills (1985) pointed out that allelopathy is not a new concept. Theophrastus (300 BC) first noticed the deleterious effect of cabbage on vine and suggested that it is due to odours. A common problem in both Greek and Roman times was the so-called soil sickness, the declining yields of fields. They did not understood that the condition could be caused by various factors such as mineral deficiencies, toxin accumulation, pathogens and the imbalance of micro-organisms. In the seventeenth and eighteenth centuries, botanists relied strongly on a comparative approach. They compared both plant form and function, particularly in relation to nutrition. The Dutchman Boerhoove suggested that root exudation may play a role in plants. Stephen Hales believed that root exudates facilitated excretion of used compounds. The theory of root excretions was a bais for the concept of allelopathy. Swiss botanist Auguste Pyrame de Candolle developed the plant interaction theory via root excretions. He was influenced by the increasing information on phytochemistry and the effects of diverse compounds on plant growth. Interest in the concept of allelopathy was rekindled at the close of the nineteenth century, principally for two reasons. The first was that careful agricultural experiments yielded results that could not adequately be explained by the exhaustion of soil nutrients. Secondly, improved techniques in chemistry allowed organic toxins to be identified from unproductive soils.

1.3 **Proof of allelopathy**

Many field studies implicate allelopathy, but isolation and identification of the chemical agents require a rigorous laboratory effort (Putnam & Tang, 1986). It is extremely difficult to prove that any deleterious effect is due to allelopathy rather than to competition for essential products. Numerous studies have provided evidence, but seldom has a specific protocol been followed to achieve convincing proof (Putnam & Tang, 1986). These authors pointed out that the shortcomings of the discipline make it hard to differentiate between allelopathy and competition. These shortcomings include:

- A general lack of nomenclature to adequately describe the plant responses that occur in this manner;
- A dearth of techniques to separate allelopathic interactions from competition and
- A failure to prove the existence of direct vcompared with indirect influences via other organisms/micro-environmental modification.
- A considerable body of information has accumulated implicating allelopathy as an important form of plant interference. According to Willis (1985), Putnam & Tang (1986) and Cheng (1992) the methodology dictates certain points for allelopathic research to be established to suggest that it is operative:
- A pattern of inhibition of one species by another must be shown using suitable controls, describing the symptoms and quantitative growth reduction;
- The putative aggressor plant must produce a toxin;
- There must be a mode of toxin release from the plant to the environment and thus the target plant;
- Mode of toxin transport or accumulation in the environment must be evident;

- The afflicted plant must have some means of toxin uptake, be exposed to the chemical in sufficient quantities and time to cause damage, and to notice similar symptoms;
- The observed pattern of inhibition should not be explained solely by physical factors or other biotic factors, especially competition.
- It is important to stress that the above points do not prove that allelopathy is operative, only that it offers the most reasonable explanation for the observed pattern. According to Cheng (1992), once the chemical enters the environment, a number of interacting processes will take place. These processes have been identified as:
- Retention L the retarded movement of the chemical from one location to another, through soil, water and air;
- Transformation L the change in form or structure of the chemical, leading to partial change or total decomposition of the molecule;
- Transport L defines how the chemicals move in the environment.
- Cheng (1992) pointed out that these processes are influenced by the nature of the chemical, the organisms present, the properties of the soil, and environmental conditions. The fate of the chemicals depend on the kinetics and interactions of individual processes with time, at a particular site under a particular set of conditions.

1.4 **Allelochemicals**

According to Putnam & Tang (1986) all alleged cases of allelopathy that have been studied appear to involve a complex of chemicals. No single phytotoxin was solely responsible for or produced as a result of interference by a neighbouring plant. ore, Rizvi et al., (1992) pointed out that the subject not only deals with the gross biochemical interactions and their effects on the physiological processes but also with the mechanism of action of allelochemicals at specific sites of action at the molecular level.

Few studies on allelopathy concentrate on the mechanisms and processes involved in the production of allelochemicals. Einhellig (1987) and Putnam & Tang (1986), raised the question whether alleged biochemical agents were in sufficient concentrations and with enough persistence in the environment to affect a neighbouring or succeeding plant. These chemicals could be transformed during the course of extraction. According to Cheng (1992), allelopathic symptoms may not be manifested at the time or site where plant damage has actually occurred.

1.4.1 **Sources of allelochemicals**

Radosevich & Holt (1984) stated that the primary effect of allelopathy seems to result from an association with plant litter in or on the soil. Rice (1984) and Putnam (1985) reported that allelochemicals are present in virtually all plant tissue, i.e. leaves, fruit, stems, and roots. These allelochemicals are released by such processes as volatilization, root exudation, leaching and decomposition of plant residues. Leaves may be the most consistent source, while roots are considered to contain fewer and less potent toxins. According to Aldrich (1984), allelochemicals must be concentrated in the leaves, stem or roots rather than in the fruit or flowers. If it is concentrated in these organs it is unlikely that it could be available in time to interfere with neighbouring plants.

- According to Rice (1984) and Putnam (1985), there are four ways in which the chemicals are released:
- Volatilization L release into the atmosphere. It is only significant under arid or semi-arid conditions. The compounds may be absorbed in vapour by surrounding plants, be absorbed from condensate in dew or may reach the soil and be taken up by the roots.

- Leaching L rainfall, dew or irrigation may leach the chemicals from the aerial parts of plants that are subsequently deposited on other plants or on the soil. Leaching may also occur through plant residues. Their solubility will affect their mobility in soil water.
- Root exudation L from plant roots into the soil environment. Whether these compounds are actively exuded, leaked or arise from dead cells sloughing off the roots is not clearly understood at this time.
- Decomposition of plant residues L it is difficult to determine whether toxic substances are contained in residues and simply released upon decomposition, or produced instead by micro-organisms utilizing the residues.

1.4.2 **Natural products identified as allelopathic agents**

Alleged allelochemicals represent a myriad of chemical compounds from simple hydrocarbons and aliphatic acids to complex poly-cyclic structures. The secondary products could be classified in the following categories but it is impossible to enumerate each and every chemical identified as an allelochemical. Whittekar & Feeney (1971), Rice (1984) and Putnam & Tang (1986) divided allelochemicals into various major chemical groups:

- Simple water-soluble organic acids
- Simple unsaturated lactones
- Long-chain fatty acids and polyacetylenes
- Naphthoquinone, anthroquinones and complex quinones
- Simple phenols
- Benzoic acid and derivates
- Cinnamic acid and derivates
- Flavonoids
- Tannins
- Terpenoids and steroids
- Amino acids and polypetides
- Alkaloids and cyanohydrins
- Sulphides and glucosides
- Purines and nucleotides
- Coumarins
- Thiocyanates
- Lactones
- Actogenins

1.4.3 **Mode of action of allelochemicals**

Most of the allelochemicals are secondary metabolites and are produced as byproducts of primary metabolic pathways (Rice, 1984; Putnam & Tang, 1986 and Rizvi et al., 1992). Secondary compounds have no physiological function essential for the maintenance of life (Aldrich, 1984). Reports most frequently identified effects which are readily observed in the field or under controlled conditions. Delayed or inhibited germination and the stimulation or inhibition of root and shoot growth are often reported (Rizvi et al., 1992). The major difficulty is to separate secondary effects from primary causes. An important question that always remains is whether the inhibitor reaches the site in the plant in sufficient concentration to specifically influence that reaction and whether other processes may be affected more quickly.

The mode of action of a chemical can broadly be divided into a direct and an indirect action (Rizvi et al., 1992). Effects through the alternation of soil properties, nutritional status and an altered population or activity of micro-organisms 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 L 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, 1974)
- Cytology and ultrastructure L a variety of allelochemicals have been shown to inhibit mitosis in plant roots (Rice, 1974)
- Phytohormones and balance L 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, 1974) Other inhibitors block GA-induced extension growth.
- Membranes and membrane permeability L 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 & Balke, 1981).
- Photosynthesis L photosynthetic inhibitors may be electron inhibitors or uncouplers, energy-transfer inhibitors electron acceptors or a combination of the above (Einhellig & Rasmussen, 1979; Patterson, 1981)
- Respiration L allelochemicals can stimulate or inhibit respiration, both of which can be harmful to the energy-producing process (Rice, 1974)
- Protein synthesis L 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, 1974)
- Specific enzyme activity L Rice (1984) reported on a number of allelochemicals that inhibit the function of enzymes in the plant
- Conducting tissue (Rice, 1974)
- Water relations (Rice, 1974)
- Genetic material (Rice, 1984, Aldrich, 1984).
- 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).

1.5 **Methods for isolation, bioassay and identification**

The concept of allelopathy is still a matter of controversy (Aldrich, 1984) and is plagued with methodological problems, particularly those of the distinguishing effects of allelopathy from those of competition (Willis, 1985). Only a few investigations have separated the components of interference because of the complexity of the ecological phenomenon (Fuerst & Putnam, 1983). The authors reported that evidence must be put forward before any attempt is made to determine the cause(s) of interference. The symptoms will vary from the most obvious germination and mortality responses to the more subtle plastic responses such as a reduction in size, mass or number of organs. Therefore observations and results are largely descriptive rather than analytical and provide only circumstantial evidence for allelopathy, leaving room for explanations other than allelopathy. Care must be taken to exclude competition as a factor. Competition can be selectively eliminated by adding limiting resources.

The effects of allelopathy are manifested in the soil environment which provides a myriad of physical, chemical and biological processes that may interact with allelochemicals that could influence the study. It is impossible to prove that chemicals released by plants do not affect neighbouring plants. Harper (1977) proposed a rigorous protocol to search for the cause and effect. The cause-and-effect relationship cannot be established merely by observing the appearance of phytotoxic symptoms, on the one hand, and showing the presence of chemicals of demonstrated toxicity in the vicinity of an affected plant, on the other.

According to Putnam & Tang (1986), most research activities on allelopathy were concentrated on apparent cases that were conspicuous under field conditions. Under controlled conditions, factors in competition may be segregated. It is possible to prove that chemical interactions are either totally or partially responsible for the interference observed. Since allelochemicals differ in terms of source and type, different methods have been devised for greenhouse and laboratory verification of their presence.

1.5.1 **Extraction or leaching from plant tissue**

Plant leachates have been collected to support the presence of extracellular bio-active compounds. Isolation of a compound involves collection in an appropriate solvent or adsorbent. According to Putnam (1985), a commonly used extract solvent is water or aqueous methanol in which dried or living plant material is soaked. After extracting the material for varying lengths of time, the exuded material is usually filtered or centrifuged before bioassay. In other cases the material is macerated together with distilled water.

Putnam (1985) also pointed out that under field conditions leaching may be caused by dew, rain or irrigation. Leachates do not include intracellular metabolites released because of physical damage inflicted during sample collection. In many cases, it is impossible to judge whether or not damage of the living tissue has occurred and the sample in a strict sense would be of doubtful origin.

1.5.2 **Root exudates**

According to Putnam & Tang (1986), several techniques have been employed. Sand can be used in which both donor and recipient plants are present. The effects on early plant development before competition for growth factors occurs can then be evaluated. Also, donor plants can be grown in sand. The sand can then be leached and the leachate evaluated in terms of influence on recipient plants. Bell & Koeppe, (1972) devised a system where donor and recipient plants can be grown together in a system where the pots are altered so that the nutrient solution flows from the donor to the recipient and back to a reservoir, flowing back and forth for varying periods of time.

1.5.3 **Release from plant litter**

Rice (1984) reported that soils collected in the field were used as sources of allelochemicals. Live or dead material can be placed on or in the soil for a selected period of time before receptor plants are planted directly in the soil for bioassay or the soil can be extracted for allelochemicals.

1.5.4 **Volatile compounds**

Muller, Muller & Haines (1964) germinated seed on filter paper sheets on a cellulose sponge placed in a large container adjacent to beakers containing the donor plants. The only contact between plant material and seed was aerial. Significant inhibition of germination occurred.

1.5.5 **Bioassays**

Bioassays are an integral part in all studies of allelopathy. They are necessary for evaluating the allelopathic potential of species and following the activity during extraction, purification and identification of bio-active compounds. In their simplest form, bioassays, and the isolation and identification of allelochemical, are regarded by some as techniques for providing initial information only. Both these aspects of allelopathy research are important and should be used together. Failure to do so would make results inconclusive (Reinhardt, Khalil, Labuschagne, Claassens & Bezuidenhout, 1996). Bioassay techniques vary greatly and no researcher follows the same procedure. This is clearly demonstrated in the treatise by Rice (1984). The greatest problem with bioassays is the lack of standardized bioassays. Incomplete information on the allelochemical source, method of extraction, fraction concentrations and the absence of known compounds with demonstrated activity in bioassays are also hampering useful bioassays. Stowe (1979) challenged the validity of bioassays. He concluded that, frequently little agreement between bioassay results and distinctive patterns of vegetation in the field is obtained.

According to Rice (1984) and Putnam & Tang (1985), the most widely used bioassay test is the influence on seed germination. Different types of techniques are used. All, however, include seed placed on substrate saturated with the test solution. Germination is often defined as the emergence of the radicle 2 mm beyond the seed coat and is scored over a period of time. Factors to consider are oxygen availability, osmotic potential of the test solution, pH and temperature. Properly conducted bioassays of this nature have great value. They are simple to conduct and require a small quantity of test solution.

The elongation of the hypocotyl or coleoptile can be used in conjunction with germination percentage. The elongation is, however, tedious to measure and instead dry mass can be used as a measure of growth (Bhowmik & Doll, 1984). Growth bioassays are often more sensitive than germination bioassays. When the quantity of test solution poses a problem, agar cultures can be used. Pre-germinated seed can be placed on the surface of the agar containing the allelochemicals.

1.5.6 **Separation and characterization of chemicals**

Rice (1984) pointed out that chemical separation can be accomplished by partitioning the chemicals on the basis of polarity into a series of solvents. Compounds can also be separated by molecular size, charge or adsorptive characteristics. Various chromatography methods are utilized.

There is little doubt that plants do release significant amounts of substances into the environment. However, their fate remains poorly understood. Limited studies using C14-labelled compounds suggest that most simple organic compounds such as phenolic acids are rapidly assimilated by soil micro-organisms or incorporated into humic acids (Willis, 1985). It may well be that addition of organic compounds to the soil environment is more important in determining the composition of the soil micro- flora and thus the effects of most allelopathic substances are probably indirect.

1.6 **Factors affecting production of allelochemicals**

Plants vary in their production of allelochemicals according to the environmental conditions to which they are exposed. Stress has a marked effect on the production of allelochemicals. According to Aldrich (1984) and Rice (1984), a variety of environmental conditions influence the quantity of chemicals produced:

Light L some allelochemicals are influenced by the amount, intensity and duration of light. The greatest quantities are produced during exposure to ultraviolet and long-day photoperiods. Thus under-storey plants will produce fewer allelochemicals because over-storey plants filter out the ultraviolet rays. At the peak plant growing period, it could be expected that more allelochemicals are produced than earlier or later in the growing season.

- Mineral deficiency L more allelochemicals are produced under conditions of mineral deficiency.
- Drought stress L under these conditions, more allelochemicals are produced.
- Temperature L in cooler temperatures, greater quantities are produce. The location within the plant and effects in specific allelochemicals seem to be variable.
- There are also numerous other factors influencing the production of allelochemicals. The type and age of plant tissue during extraction is important since compounds are not uniformly distributed in plants. Production differs between species as well as within species.
- Aldrich (1984) stated that environmental conditions that restrict growth tend to increase the production of allelochemicals. One could postulate that allelopathy may frequently be an accentuation of competition although not part of competition. If stress from competition increases the quantities of allelochemicals produced, it is conceivable that allelochemicals will inhibit the growth of some species and not others, thereby reducing the ability of the affected species to compete. The allelopathic plant and those affected by them are part of the ecosystem. If one factor changes, changes will occur in one or more factors. For example, light can be expected to interact with temperature and indirectly with soil moisture and other factors.

Much of the evidence indicates that several chemicals are released together and may exert toxicities in an additive or synergistic manner. Sometimes the allelopathic effect will be obvious and startling, but in the majority of cases the effects are subtle and thus more difficult to assess.

1.7 **Roles of allelopathy in natural and manipulated systems**

There is convincing evidence that allelopathic interactions between plants play a crucial role in natural as well as manipulated ecosystems. According to Rizvi et al., (1992), studies of these interactions provided the basic data for the science of allelopathy. The data were applied to understand the problems of plant-plant, plant-microbe and plant-insect interactions and to exploit these in improving the production of manipulated ecosystems.

1.7.1. **Patterning of vegetation and succession**

Natural successions of plants occur in nature (Aldrich, 1984). Plants modify the environment, thus leading to a predictable succession, with the early colonizers being those species that rely upon large numbers of seed, and late entrants those species that rely on their competitive ability. Perennial species concentrate offshoots around a parent and allelopathy could thus be beneficial to the spread of such species. The fact that dense colonies of some perennials frequently occur essentially as pure stands in itself implicates allelopathy (Aldrich, 1984). The explanation for a specific vegetational pattern has mostly been given to competition. In recent times, evidence is accumulating that points to the fact that, apart from competition, allelopathy does play an important role. According to Rizvi et al. (1992), allelopathic plants affect the patterning of vegetation in their immediate vicinity.

1.7.2 **Allelopathy and agriculture**

The effect of weeds on crops, crops on weeds and crops on crops have invariably been emphasized. Results obtained so far clearly demonstrate that some of the findings on allelopathic control of weeds, elimination of deleterious allelopathic effects of crops on crops, or exploitation of beneficial interactions in a rotation or mixed cropping system have a direct bearing on crop production (Rizvi et al., 1992). According to Aldrich (1984), weeds interfere with crops in two ways:

- Inhibiting germination and seedling establishment and
- Inhibiting the growth of the crop.

Cyperus esculentus (yellow nutsedge) is a herbaceous perennial that is considered as one of the world's worst weeds. It is a problem in cropping systems in tropical and temperate climates, where it causes large losses in crop yields. The weed is characterized by prolific vegetative activity which produces a complex underground system of basal bulbs, rhizomes and tubers. Stoller, Wax & Slife (1979) investigated the competition effect of C. esculentus on maize (Zea mays). They identified a relationship between nutsedge density (shoot/m2) and percentage reduction in crop yield. An 8% yield reduction was achieved for every 100 shoots/m2. Yield reduction of 41% occurred when no weed control was carried out in a field initially infested with 1200 shoots/m2.

Cyperus esculentus and Cyperus rotundus (purple nutsedge) are known for their allelopathic abilities. Drost & Doll (1984) concluded that extracts and residues of C. esculentus have an inhibitory effect on the growth of soyabeans (Glycine max) and maize. Tames, Getso & Vieitez (1973) found compounds in C. esculentus tubers that were inhibitory to oat coleoptiles and seed germination of other crops. Horowitz and Friedman (1971) dried C. esculentus tubers and mixed with soil. The root and top growth of barley planted in the soil were significantly reduced. Meissner, Nel & Smith (1979) grew C. rotundus in sterilised, well-fertilized soil. Growth of barley, cucumber and tomato in the soil were considerably reduced.

1.7.3 **Allelopathy and forestry**

Allelopathic interactions have been demonstrated to play a crucial role in natural and man-made forests. Such interactions are pivotal in determining the composition of the vegetation growing as under-storey vegetation in understanding forest regeneration (Rizvi et al., 1992). It can, however, not be used as an universal explanation for regeneration failures or poor stand growth. Rice (1995) described various trials conducted to gain information on the allelopathic effects, not only of woody species, but herbaceous species as well.

1.7.3.1 **Allelopathy of woody species**

Thobiessen & Werner (1980) reported that hardwood seedlings do not grow under P. resinosa but do grow under P. sylvestris in spite of the fact that P. resinosa has a higher light intensity and the soil a higher nitrate level.

Kil & Yim (1983) expanded research on the allelopathic potential of P. densiflora (red pine). They found that toxic substances inhibited seed germination and growth of the species in the forest. These substances were released in fresh and fallen leaves, roots, pine forest soil and pine pollen rain. Kim (1989) studied the allelopathic potential of five species of the Pinaceaes, viz. P. densiflora, P. thunbergii, P. rigida, Larix leptolepis and Cedrus deodora. All five species inhibited germination of test species, but the most severe inhibition in all cases was on dry-mass growth of the test species.

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