ALLELOPATHY: FROM CONCEPT TO REALITY

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Abstract

The phenomenon of allelopathy has existed for thousands of years. Intensive scientific research into the recognition and understanding of allelopathy has only occurred over the past few decades. These activities have shown significant prospects for allelopathy being utilised for increasing crop productivity and the quality of food for humans, decreasing our reliance on synthetic pesticides and improving the ecological environment. Recent research has demonstrated possibilities of such prospects in reality, especially in weed control. This paper briefly reviews the history of allelopathy research and discusses the reality of allelopathy prospects by presenting recent achievements of its use in practice.

Key words: Allelopathy, allelochemical(s), allelochemic(s), weed management, herbicide(s).

Allelopathy occurs through the release by one plant species of chemicals which affect other species in its vicinity, usually to their detriment. This phenomenon has been observed for over 2000 years. Reports as early as 300 BC document that many crop plants (eg. chick pea, barley, bitter vetch) destroyed weeds and inhibited the growth of other crop plants. The soil sickness problem in agriculture was specifically related to exudates of crop plants (19). However, intensive scientific research on this phenomenon only started this century. The term allelopathy was first introduced by a German scientist Molisch in 1937 to include both harmful and beneficial biochemical interactions between all types of plants including microorganisms. Rice (19) reinforced this definition in the first monograph on allelopathy. Research on the recognition and understanding of allelopathy has been well documented over the past few decades (19, 20). These include the symptoms and severity of adverse effects of living plants or their residues upon growth of higher plants and crop yields, interactions among organisms, ecological significance of allelopathy in plant communities, replanting problems, autotoxicity, problems with crop rotations, and the production, isolation and identification of allelochemicals in both natural and agroecosystems.

Contemporary researchers have tended to broaden the context of allelopathy to include interactions between plants and higher animals (20), and have suggested that allelopathy may be part of a whole network of chemical communication between plants, and between plants and other organisms, and that such communication may contribute to plant defence (12).

Chemicals that impose allelopathic influences are called allelochemicals or allelochemics. They may be largely classified as secondary plant metabolites, which are generally considered to be those compounds (such as alkaloids, phenolics, flavonoids, terpenoids, and glucosinolates) which do not play a role in primary metabolic processes essential for a plant's survival, and are produced as offshoots of primary metabolic pathways. In contrast to primary metabolism, which comprises several hundreds of low molecular weight compounds, tens of thousands of secondary substances are known today, but only a limited number has been implicated as allelochemicals (19).

Allelochemics are present in virtually all plant tissues, including leaves, flowers, fruits, stems, roots, rhizomes, seeds and pollen. They may be released from plants into the environment by means of four ecological processes: volatilisation, leaching, root exudation, and decomposition of plant residues. Several chemicals can be released together and may exert toxicities in an additive or synergistic manner. The concentration of a single substance in field situations is generally below its inhibitory threshold. Allelopathic interferences often result from the joint action of several different compounds.

Biological activities of receiver plants to allelochemicals are known to be concentration dependent with a response threshold. Responses are, characteristically, stimulation or attraction at low concentrations of allelochemicals, and inhibition or repellence as the concentration increases (10). These phenomena have been widely observed in allelochemicals from living plants, in allelopathic effects from decaying plant residues, and from the gross morphological level to the biochemical level, including other growth-regulating chemicals and herbicides.

When plants are exposed to allelochemicals, their growth and development are affected. The readily visible effects include inhibited or retarded germination rate; seeds darkened and swollen; reduced root or radicle and shoot or coleoptile extension; swelling or necrosis of root tips; curling of the root axis; discolouration, lack of root hairs; increased number of seminal roots; reduced dry weight accumulation; and lowered reproductive capacity. These gross morphological effects may be secondary manifestations of primary events, caused by a variety of more specific effects acting at the cellular or molecular level in the receiver plants (18).

As a scientific discipline, allelopathy is still relatively new. But it has already contributed to the solution of practical problems in agriculture and provided explanations for observed plant-plant interactions. Some recent achievements in allelopathy research are discussed in this paper.

Prospects for the application of allelopathy

As demand increases for sustainable agriculture and concern grows regarding the extensive use of synthetic chemicals (eg. contamination of environment, herbicide resistance, increasing cost), attention is focused on reducing reliance upon synthetic herbicides and finding alternative strategies for weed management. Allelo-pathy holds great prospect for meeting some of those demands. Allelopathic potential can be used in several ways in agroecosystems.

Enhance crop allelopathic traits for weed suppression.

Putnam and Tang (17) suggested that allelopathic characteristics are more likely to occur in crop predecessors or "wild types" that have evolved in the presence of allelopathic and competitive influence from other species, while the currently used cultivars would be expected to have diminished or reduced allelopathic capacity. Therefore, it is possible to enhance weed suppressive potential of crop cultivars or to transfer allelopathic characteristics from wild types or unrelated plants into commercial crop cultivars through conventional plant breeding methods or other genetic recombination strategies. Research on cucumber and rice germplasm has found large differences in allelopathic potential among accessions. Certain accessions strongly inhibited weed germination and growth (13, 15). In some cases, up to 70% population of rice weeds, such as duck-salad [Heteranthera limosa (Sw.) Willd.], purple ammania (Ammania coccinea Rottb.), and broadleaf signalgrass [Brachiaria platyphylla (Griseb.) Nash], were controlled by those accessions with strong allelopathic potential (4). More recently at Charles Sturt University, some wheat cultivars were found to significantly inhibit both germination and radicle growth of annual ryegrass. The allelopathic potential of wheat cultivars was positively correlated with their allelochemical (total phenolics) contents (23).

Use of allelochemicals as natural herbicides or pesticides.

eg. pyrethrins extracted from a species of Chrysanthemum) as well as models for developing new pesticides (eg. Cinmethylin derived from the natural product cineol of certain desert plants). By modifying these allelochemicals, the end product could be more active, selective, or persistent. In a review of the potential use of allelochemicals as herbicides, Putnam (14) listed 6 classes of allelochemicals isolated from over 30 families of terrestrial and aquatic plants. These classes are alkaloids, benzoxazinones, cinnamic acid derivatives, cyanogenic compounds, ethylene and other seed germination stimulants, and flavonoids. All these chemicals possess actual or potential phytotoxicity.

Our own work with vulpia has identified and quantified more than twenty allelochemicals in its residues. All of them demonstrated various herbicidal effects when tested by a specially developed bioassay. Those present in large quantities possessed low biological activities, while those present in small quantities possessed strong inhibitory activities. Individual contributions from different allelochemicals to the overall phytotoxicity of vulpia residues were variable according to chemical structure, and influenced further by their relative proportions in the residue. Artificial combinations of these allelochemicals prepared in aqueous solution exerted similar phytotoxicity to individual com- pounds and to the aqueous vulpia extracts. Tests on biological strength indicated the existence of strong synergistic effects among the identified allelochemics.

Our work suggests that exploration of the composition of a cluster of allelochemicals, which are simple in structure, possess various biological activities and few barriers to synthesis and production, may be another alternative for developing new herbicides from individual plant allelochemicals.

Use of allelopathic plants in companion cropping.

It is possible to utilise a companion plant that is selectively allelopathic against certain weeds and does not interfere appreciably with crop growth (16). Rice (19) lists a number of crop species whose presence or leachates have been shown to have inhibitory effects on a number of weeds. The list includes beets (Beta vulgaris), lupin (Lupinus sp.), corn, wheat, oats, peas, buckwheat (Fagopyrum esculentum), hairy vetch (Vicia villosa Roth.), millet (Panicum sp.), barley (Hordeum vulgare L.), rye, and cucumber.

Weeds in cropping systems are most often considered to be detrimental. However, the interaction of weeds with crops may be positive. In a study where controlled densities of wild mustard (Brassica campestris L.) were interplanted with broccoli (Brassica oleracea var. Premium crop), crop yield increased by as much as 50% compared with broccoli planted alone (8).

Use of allelochemicals to stimulate weed seed germination.

Striga asiatica (L.) Ktze, #STRLU), which is parasitic to cereal grains in the southeastern United States, normally germinates in response to compounds released from its host plants (14). Chang et al. (3) identified a germination stimulant, a p-benzoquinone compound from a natural host (sorghum) for Striga. Ethylene was found to be a very effective germination stimulant. Egley and Dale (6) demonstrated that ethylene would stimulate Striga to germinate in the absence of a host. This gas at about 1.5kg/ha has been used effectively via a soil injection to trigger "suicidal" germination of Striga and to deplete the numbers of dormant seeds in soil (7). Under growth chamber conditions, ethylene induced germination of common cocklebur (Xanthium pensylvanicum Wakkr.) and redroot pigweed in soils (5).

Plant residue management.

Utilising residue allelopathy as a management tool may be one of the more readily applicable uses of allelopathy in agroecosystems. Of all the possible strategies involving allelopathy for weed control, management of selectively toxic plant residues is the most successful, effective and readily available (11, 14). Management methods might include incorporating allelopathic crops in crop rotation, applying phytotoxic mulches, and cover cropping with allelopathic plants or smother crops.

Plant residue management may also overcome the negative effects of plant residues, and meet the increased demand for conservation and no-tillage farming systems. An et al. (1) simulated allelopathic phenomena caused by decaying plant residues. Their theoretical analyses revealed that decomposing plant residues may either inhibit or stimulate plant growth, and that inhibition may be confined to a limited period, ie., the most severe inhibition by plant residues occurs at the early stages of residue decomposition, whereas at later stages the inhibition declines while stimulation gradually emerges. The inhibition and stimulation periods can be manipulated through a wide variety of management means. This approach has significant potential. For example, by analysing risk situations with respect to residue retention, a crop manager may avoid the inhibitory period of decaying residues, thus minimising their negative effects and await the stimulatory effect to crop plants, thereby enhancing the benefits of residue retention on the soil. By extending the inhibitory period of decaying residues and enhancing its effects, weeds may be controlled.

Application of allelopathy in field: two case studies

An et al. (2) described difficulties associated with pasture establishment into vulpia residues which possess strong allelopathic potential. The use of cultivation, and then delaying sowing for about three weeks enabled the allelochemicals to dissipate, avoided the peak inhibitory period from vulpia residues, and allowed successful pasture establishment.

The decline of legume content in older perennial pastures is considered to be a major constraint to animal production in both the cereal zones and the permanent grazing areas (9). Leigh et al. (9) found the problem of subterranean clover decline in phalaris swards to be associated with the deleterious effects of retained phalaris residues on the soil surface. Removal of pasture residues before the opening autumn rains ensured good germination and early seedling vigour of the clover, and enabled maintenance of a legume based sward.

Conclusion

The development of weed management strategies that make use of allelopathic crop plants is receiving increased national and international attention (21). Key areas of allelopathy research are: selectively to enhance allelopathic traits of crop cultivars in breeding programs; to transfer allelopathic genes into commercial cultivars through modern biotechnology; to enhance their weed-killing capability; and to identify and characterise those substances involved in strong allelopathic activity and to use them either directly as natural herbicides, or as models for developing new and environmentally friendly herbicides. With the rapid development of analytical techniques and biotechnology, research on these areas will be enhanced. Allelopathy will become an important component in the development of future integrated weed management strategies.

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