Allelopathy and Its Potential Applications in Right-of-Way Management

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ABSTRACT

The use of herbicides for control of undesirable vegetation along highway, railroad, and utility rights-of-way has been a valuable tool for many years. As energy and labor have become more expensive so have mowing and hand clearing of brush, and a greater dependence on herbicide use has been created. Today, however, environmental concerns about herbicides are threatening their usefulness for the future. Herbicide programs as they exist today will undoubtedly be cut substantially or eliminated completely in many states. It is becoming increasingly urgent that alternatives to longstanding vegetation maintenance practices be developed. A greater understanding of chemical ecology, and more specifically allelopathy, may well lead to the development of more economical and environmentally sound right-of-way maintenance practices. Allelopathy is defined as any direct or indirect harmful effect by one plant on another through production of chemical compounds that escape into the environment. It is hypothesized that if allelopathy is a wide-ranging phenomenon involving many plant species, it will be possible to find individual plants that can be used to establish stable communities capable of preventing the encroachment of undersirable species.

The term allelopathy has been defined by Rice (1, pp. 1-2) as any direct or indirect harmful effect by one plant, including microorganisms, on another through production of chemical compounds that escape into the environment. This definition differs slightly from that of Molisch [see Rice (2)], who first coined the term in 1937, in that Rice's definition deals only with the harmful effects, whereas Molisch used the term to describe both beneficial and harmful biochemical interactions between microorganisms and plants. Rice's use of the term may be more technically accurate in that allelopathy was derived from two Greek words meaning "mutual harm." The elimination of beneficial effects from consideration, however, has been shown to be very artificial by such researchers as Khailov [see Rice (2)] who demonstrated conclusively that the effects of any given compound may be inhibitory or stimulatory depending on the concentration of the compound in the surrounding medium. In fact, most researchers in Europe and Asia use the term as defined by Molisch. The point is that many important ecological roles of allelopathy are probably overlooked because of the concern with just the detrimental effects of added chemicals.

The effects of allelopathy depend on a chemical compound being added to the environment by an allelopathic agent. This essentially separates allelopathy from competition involving the removal or reduction of an environmental factor (e.g., water, light, or minerals) that is required by some other plant sharing the habitat. Confusion in this respect has hindered the development of research in allelopathy for years. Muller (3) suggests that, to lessen this confusion, the term "interference" be used whenever the causes of mutual inhibition are not clearly separated. Szczypanski [see Putnam and Duke (4),p. 432] recently described three possible mechanisms for plant interference: (a) allelospoly--the competition for necessary growth factors, (b) allelomediation--the possession of herbivore toxicant or repellant substances that prevent grazing, and (c) allelopathy--the addition of toxic factors to the environment. Interference is thus defined to encompass both allelopathy and competition.

In further defining allelopathy, it is important to understand that this specific phenomenon is only one of many classes of interactions termed allelochemics, which involves chemicals used by organisms of one species, which affect the growth, health, behavior, or populations biology of organisms of another species. Many interactions of attack, defense, and behavioral response involve not physical force but chemical agents. The study of these interactions and the array of chemicals involved is the subject of chemical ecology. Chemical ecology, in turn, is only one of many subjects covered under what is undoubtedly the most important scientific basis for rights-of-way (ROW) vegetation management, plant ecology.

Plant ecology is the science that treats the reciprocal relationship between plants and their environment. For example, a plant may directly affect wildlife and wildlife, in turn, may directly affect the plant. Witch hobble may furnish food for deer and hare; conversely, deer and hare may destroy witch hobble through excessive browsing.

An understanding of these ecological relationships is basic to sound ROW management. One must realize that ROW vegetation is in a dynamic state of reaction and adjustment to habitat conditions. Climate, water, soil, physiography, wildlife, man, and other plants all make for a complicated situation on ROWs.

To simplify and make something useful and understandable out of the complex ROW situation is the most difficult task in the application of ecology to management. Often, to help in this task, the theory of limiting factors is used to explain cause and effect. For example, animal destruction of weeds has been used to explain why trees do not reproduce in a scrub oak community. When this one factor was controlled, pine was established. In such a community on a ROW, a thriving small mammal population could be a limiting factor of value.

Similarly, allelopathy has been used recently to explain why black cherry does not reproduce on certain sites of the Allegheny plateau where open orchardlike stands had persisted for 50 years before they burned. For years the cause was attributed to heavy browsing by deer and hare, to frosts, and to herbaceous competition. Now it is known that an allelopathic effect, from dominant goldenrod, grass, asters, and fern, is the limiting factor.

OVERVIEW

In a review of scientific literature concerning allelopathy, several general observations can be made which, without getting into excessive detail about any one area, can yield an acceptable overview of the phenomenon and a sound basis for practical applications.

Widespread Occurrence

Allelopathic effects have been recorded for agricultural and wild species of most types of plants from forest trees to desert shrubs. Although most of the research in the field has been done within the last 20 years, reports of the phenomenon and its influence on agriculture were made as early as the fifth and third centuries B.C. by Democritus and Theophrastus. A 300-year-old document by Banzan Kumazawa, written in Japanese and found by Lee and Monsi in 1963, described the effects of rain and dew washing the foliage of red pine and inhibiting crop production under the pine. DeCandalle researched and described the effects of allelopathy in 1832.

In general, allelopathy has been related to problems with crop production on certain types of soil, with stubble-mulch farming, with certain types of crop rotation, with orchard replanting on old orchard land, with crop monoculture, and with forest site replanting. In more recent times, effects on old field succession, plankton succession, and range land and pasture management have been investigated. Investigations have been broadened in horticulture, forestry, and agronomy.

From all of the research done on such a wide array of plant types, it is quite obvious that the occurrence of allelopathy in the environment is common. Furthermore, it is reasonable to judge that the observed cases of allelopathic effects stand out from a background of more widespread, less conspicuous effects on plant growth and populations.

Significance in Plant Communities

Allelopathy, therefore, is undoubtedly of widespread significance in plant communities. In plant succession in old fields, a dominant species may, by allelopathic suppression, speed its invasion of a preceding community and delay its replacement by other species. In both successional and climax communities strongly dominated by a single species, chemical effects of that species on the soil may limit the number of other species able to occur. In communities in which a number of canopy species are mixed together, these may form a mosaic of differing chemical effects on the soil, which may contribute to the patterning and species diversity of the undergrowth.

> One observes in the forest patches of one species here and another species there, a few meters apart in environments not visibly different. Ecologists believe that light differences, root competition, wood decay remnants, differences in fungal biota, microrelief, dispersal accidents, and clonal history may all, in varied combinations, affect these intracommunity patterns. One should allow also for chemical relations among plants, broadening concern from allelopathics to leachates, exudated, and decay products in general (5, p. 51).

Autotoxicity

Allelopathic self-inhibition in many types of plants has been reported by many researchers. Although some of these plants (e.g., eucalyptus) are considered climax species, most are successional species, such as brome grass, asters, brambles, sunflower species, and ferns. In the case of successional species, self-toxicity may be no serious disadvantage because these species are generally transient populations that dominate a community for only a short period of time. Species of ferns, however, such as bracken fern, might have value in a ROW, but, because of this trait, they would have to be ruled out as a desirable species for a stable community.

In many cases, the cause of self-inhibition is the toxicity of products from their own decay. Heavy accumulations of terpenes in the soil have been attributed to self-toxicity. Self-toxicity has been described as an evolutionary paradox in that one would presume that the allelopathic substances have some adaptive advantage that outweighs the apparent selective disadvantage of autotoxicity.

Chemical Nature of Allelopathic Substances

Grummer [cited by Rice (1)] suggested in 1951 that special terms be used for the chemical agents involved in allelopathy based on the type of plant producing the agent and the type of plant affected. They are

1. Antibiotic--a chemical inhibitor produced by a microorganism and effective against a microorganism,
2. Phytoncide--an inhibitor produced by a higher plant and effective against a microorganism,
3. Marasmins--compounds produced by microorganisms and harmful to higher plants, and
4. Kolines--chemical inhibitors produced by higher plants and effective against higher plants.

Most antibiotics, marasmins, phytoncides, and kolines that have been identified fit into 14 categories as delineated by Rice. A diagram of probable major biosynthetic pathways leading to the production of these various categories is shown in Figure 1. Before Rice's system, Whittaker and Feeney (6) stated that, in general, the chemicals associated with allelopathy belong among the secondary substances and that these compounds could be classified into five major groups: phenylpropanes, acetogenins, terpenoids, steroids, and alkaloids. A diagram of the biosynthetic pathways associated with these is shown in Figure 2. In comparing the two figures it is obvious that Rice merely expanded on Feeney and Whittaker's work. Perhaps the most outstanding characteristic of these compounds shown by the figures is their diversity.

In characterizing these compounds, it is important to note that, as far as is known, they are not essential to the basic protoplasmic metabolism of the plant. As Whittaker stated, "There is, in most cases, no evident reason why the plant should produce them at all" (5, p. 53). This is true when a plant is considered free from interaction with other organisms, for, in many cases, the secondary compounds associated with allelopathy have been reported to be involved in protective or defensive functions of plants. Simple phenolic acids, for example, have been implicated in allelopathic interactions. These same compounds are associated with the lipid layer at the plant surface and may be

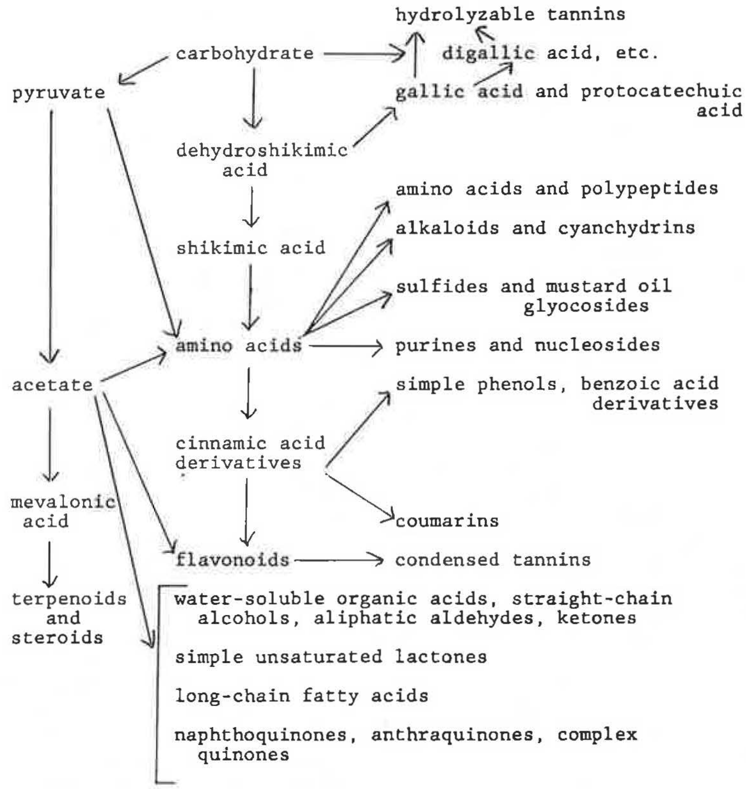

FIGURE 1 Probable major biosynthetic pathways, based on Rice *(1)*.

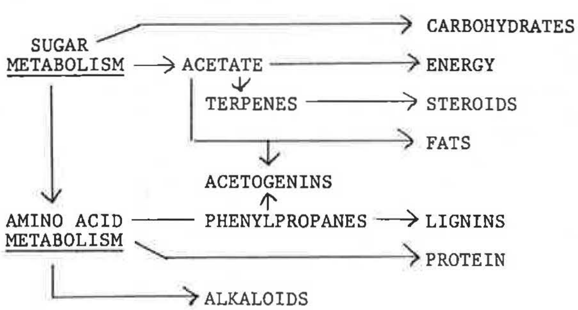

FIGURE 2 Probable major biosynthetic pathways, based on Whittaker and Feeney *(6)*.

involved in epidermal resistance to attack by plant pathogens. Chlorogenic acid, caffeic acid, and other similar common phenols are toxic to selected pathogens after building up at a more rapid rate in resistant plants than in sensitive ones in response to infections, and they are the same materials most often cited as the toxic chemicals in allelopathic reactions. There are, of course, exceptions to this; for example, the phenolic quinone, juglone, associated with black walnut, which is one of a few apparently specialized allelopathic compounds. Other quinones, however, are associated with disease resistance.

It should be understood that the roles of these compounds often depend more on their particular concentration at a given site than on their chemistry.

Routes of Release

Allelopathic materials are released from plants in a variety of ways. Discharge of secondary compounds into the environment may occur as a result of exudation of volatile chemicals (e.g., volatile terpenes such as camphor and cinede) that are released from leaves into the air and then absorbed by soil particles. This was illustrated by Muller (3) in the soft chaparral areas of southern California: Water-soluble toxins from above-ground parts are leached in response to the action of rain, fog, or dew. For example, p-hydroxybenzoic acid, vanillic acid, and furic acid were identified as kolines that were washed from the leaves of Camelina sp. and that inhibit flax. The exudation of water-soluble toxins from below-ground parts (e.g., release of juglone from roots of black walnut) inhibits many plant species. Toxins are released from nonliving plant parts through leaching from litter or sloughed root cells and microbial by-products result from little decomposition (e.g., flavonoids, such as agolycones, which are only very slightly soluble in water, are released by decomposition and are highly inhibitory).

When these secondary substances are released into the immediate environment, they must accumulate in sufficient quantity to affect other plants, persist for some period of time, or be constantly released in order to have lasting effects.

The salient point about the release of inhibitory compounds by plants is that no matter what the role of the compound in the plant may be, and regardless of its location in the plant, the substance will eventually escape into the environment through one means or another.

Treatment in the Plant

In general allelopathic compounds and other secondary substances occur in plants in ways that protect the plant against their effects. Many of these compounds occur as glycosides, in which case the substance that might be toxic is combined with a sugar and thereby rendered innocuous within the plant. Despite the innocuous nature of the substance, the glycosides are commonly in solution in vacuoles of cells and, consequently, further separated from protoplasmic functions of the plant.

Other secondary substances occur as polymers (tannins, lignins, resins, and rubbers) or as crystals (calcium oxalate raphids). Many of the substances are deposited outside living cells in the dead heartwood, in dead cells, in spaces between cells, in ducts, or in the glandular hairs found on the surface of many plants. Still other substances are discharged from the plant by leaching, exudation, or volatization as previously mentioned. Secondary substances, as this illustrates, are treated as toxic wastes to be inactivated within the plant or excreted from the plant. The evolutionary interpretation of why plants produce copious amounts of substances against which they must protect themselves was addressed by Whittaker:

> Plants have need for various specialty compounds--as pigments, regulatory substances, skeletal materials, etc. Many of these are compounds of the major secondary substance groupings. Protoplasm is the most complex and highly perfected system we know, but it cannot be quite perfect. An enormous number of transformations, rate controls, and enzymes are involved. It is impossible that protoplasmic function should provide enough of every metabolite needed and not too much of some, should exclude metabolic byways yielding some unneeded materials and recycle every product, and should do this in the face of changing environmental conditions. There is not enough selective advantage to have brought evolution of enzymes and controls for the use or recycling of ever metabolite produced (5,p.61).

In summary it can be said that allelopathy is not a peculiarity of a few plants but a widespread and normal, although not always conspicuous, phenomenon of natural plant communities and that allelopathic substances are not significant only to the functioning of plant communities, they are part of the extensive traffic in chemical influences relating organisms of all the major groups to one another.

POTENTIAL APPLICATIONS

The main thrust of research involving allelopathy has been in the field of agriculture. This, of course, is understandable because feeding the people of the world has been and still is the greatest challenge facing plant scientists. In doing this, however, scientists have approached allelopathy in terms of minimizing its effects. Only in the last 15 years have scientists looked at allelopathy as a phenomenon that might be of significant value in assisting farmers in the production of food.

This change of attitude is due in part to the expanded knowledge in the field of allelochemics and a more thorough understanding of plant interaction. A more profound influence, however, has been exerted by ecologists who have pointed out both the long- and short-term effects on the environment of continued pesticide use.

The need to develop alternatives to chemical pesticides has led researchers to investigate the possibility of exploiting naturally occurring events. In entomology, for example, pheromones are now being used to disrupt the mating cycles of insects, and the result is a decline in their population in a given area. The beauty of this kind of control is that, first, only a very small amount of pheromone need be used, which reduces the amount of chemical substances released into the environment, and second, the control is specific to the target because a pheromone is insect specific.

In addition to the previously mentioned factors affecting the accelerated interest in allelopathy, economy has played a significant role. The use of traditional techniques, commonly associated with vegetation control, is rapidly becoming too expensive. Mowing has been reduced along most highway ROWs because of the increasing costs of fuel and equipment. Labor-intensive means have been virtually eliminated because of high labor costs. The use of herbicides and growth regulators is also being restricted by increases in manufacturing and application costs. Use of the allelopathic advantage of some plants would be of great value in reducing the need for these expensive control measures. Extending a herbicide spray cycle, for example, from 3 to 10 years represents a tremendous saving to a utility. The use of herbicides, of course, could not be completely abandoned because there are situations where these tools must be used.

Despite the significance of the various factors influencing the development of allelopathy, one has to look hard and long to find a single example of its use by man. Perhaps the only agronomic advantage gained from direct use of allelopathy is the interim "smoother crops" such as *Hordeum vulgare* and *Avena sativa*. The benefits of using such practices have long been known, but not until recent times was it discovered that the benefit was due to exudations of a mixture of compounds, including scopoletin. Although plant breeders have successfully incorporated both insect and disease resistance into cultivars of many crops, not until 1974 was there a concerted effort by Putnam and Duke (4) to develop crops with competitive ability superior to that of weeds. Putnam and Duke hypothesized that predecessors of many species now grown for food and fiber, when growing in their wild habitat, may have possessed allelopathic substances that allowed them to compete effectively in their native plant community. This characteristic may have been reduced or lost as plants were bred and selected for other desirable characteristics in a weed-free environment. Screening the germplasm collection of *Cucumis sativas* and related *Cucumis* species, they found several accessions that demonstrated allelopathic activity. *Avena sativa* varieties also showed exception lines for inhibiting growth of weeds, suggesting a genetic basis for allelopathy: some varieties could reduce weed growth and others could not.

Allelopathic chemicals are usually assigned a very secondary role, as pointed out earlier, because compounds can be both repellents and phytoncides and will be allelopathic only if circumstances are favorable for their accumulation. The allelopathic properties are, therefore, labeled secondary effects of the secondary compounds. Despite the natural advantages of allelopathy, selection for this trait is not obvious in nature.

Contrary to this, however, it has been reported that secondary chemicals are rapidly synthesized and that their production may be genetically controlled.

Evidence is not available to show whether allelopathic agents are produced by chance or specifically for an effect on other plants to ensure survival of successional species. Logically one should assume genetic control of the amounts of inhibitors in plants.

Consequently, even though nature may not have selected plants that produce amounts of secondary compounds necessary for allelopathic effects, perhaps these effects can be brought about by genetic manipulation similar to that by which plants have been selected and improved for production of other secondary compounds involved in defense against disease.

A number of approaches could be taken. One might be that desirable plant species could be developed that would release kolines as natural herbicides to provide satisfactory weed control. Another approach could be to develop plants that would be used as companion plants that are selectively allelopathic but do not interfere with desirable species.

One of the main factors involved in the encroachment of undesirable species into an area is the gemination of weed seeds. Two of the major functions of allelopathic compounds, as described by Rice (1), are to prevent seed decay and to control germination. Methods of increasing weed-seed decay and methods of stimulating or inhibiting weed-seed germination would aid dramatically in stabilizing a plant community. The use of microorganisms able to destroy weed seeds and the inactivation of inhibitors that protect the seed from decay are two possible ways of accomplishing this. To a limited extent, this is already being done: ethylene is administered by soil injection to achieve suicidal germination of Striga asiatica. There are undoubtedly many other compounds that could be used in this manner.

CONCLUSION

In summary, the significance of allelopathy in the plant community is apparent and the potential for practical, environmentally sound applications is tremendous. As investigators continue to unravel the fabric of plant ecology, the role of allelopathy and its influence will continue to grow.

At present, a number of possible applications of allelopathy are available to ROW managers in the Northeast. Several indigenous shrub species are known to possess allelopathic properties. When used on proper sites these plants can effectively establish stable communities inhibiting the encroachment of undesirable species for extended periods of time. Such plants as low-bush and high-bush blueberry, barberry, maple leaf viburnum, hobble bush, witherod, narrow-leaf goldenrod, sweet fern, loosestrife, and American cranberry bush could be used to this end. Selective use of herbicides to help establish these species would hasten the effect. Development of an inventory of indigeneous species in a particular section of a ROW and attention to soil and climatic conditions in an area will also aid in establishing these plant communities. Allelopathy may well be the most potentially valuable means to sound vegetation control for the ROW manger.

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